Universitat de Lleida

# Habitat management in Mediterranean fruit orchards to foster pollinator and natural enemy communities

Neus Rodríguez Gasol

http://hdl.handle.net/10803/668668

# Habitat management in Mediterranean fruit orchards to foster pollinator and natural enemy communities

## Neus Rodríguez Gasol

2019

Universitat de Lleida

IRTA
RECERCA I TECNOLOGIA AGROALIMENTÀRIES

# Habitat management in Mediterranean fruit orchards to foster pollinator and natural enemy communities

DISSERTATION
to obtain the degree of Doctor by the University of Lleida
Doctoral Program of Agricultural and Food Science and Technology

MEMÒRIA DE TESI
per optar al grau de Doctor per la Universitat de Lleida
Programa de Doctorat en Ciència i Tecnologia Agrària i Agroalimentària

By
Per

**Neus Rodríguez Gasol**

Directors:
Dra. Georgina Alins Valls
Dr. Jesús Avilla Hernández

Lleida, September 2019

Universitat de Lleida
IRTA
RECERCA I TECNOLOGIA AGROALIMENTÀRIES

This thesis has been carried out at the Fruit Production Program of the Institut de Recerca i Tecnologia Agroalimentàries (IRTA) and supported by the Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, by means of the project RTA 2013-00039-C03-00 and by the Ministerio de Economía y Competitividad, by mean of the projects AGL2013-49164-C2-2-R and AGL2016-77373-C2-1-R. The author was funded by a predoctoral fellowship from IRTA.

*Well, we knocked the bastard off*.

Edmund Hillary

# AGRAÏMENTS

És difícil expressar en paraules tot el que m’enduc d’aquesta etapa. Dir que estic agraïda fins i tot sembla poc per mostrar el que sento vers les persones que m’han acompanyat durant aquest temps.

Als directors de tesi, Georgina i Jesús, per la seva disponibilitat, suport i confiança durant aquest temps. Georgina, gràcies pels moments de mestra sensei i l’optimisme etern, sobretot durant la recta final.

A l’IRTA, per la concessió de la beca predoctoral.

A la Judit Arnó, Rosa Gabarra, Jordi Riudavets i la resta del seu equip a l’IRTA de Cabrils pel seu temps i pels valuosos comentaris.

Al Jordi Bosch, Anselm Rodrigo, Xavi Arnan i la resta del seu equip al CREAF, pel companyerisme, el bon rotllo i tot l’assessorament. Jordi, ha estat un plaer compartir la teva passió per la investigació.

To Steve Wratten and his colleagues from the Bio-Protection Research Centre for making me feel at home and letting me collaborate in their research.

A l’equip de l’estació experimental per la bona disponibilitat a ajudar-me en totes les meves peticions estrambòtiques.

A la gent tan maca que he conegut gràcies a aquesta tesi, tant companys de l’IRTA com de fora: Lourdes, Sara, Neus, Quico, David, Núria, Anna, Guillem, Maria, Ariadna, Omar, Laura, Irene, Yahana Nathalie i altres amb els quals he tingut el plaer de topar durant aquest tortuós camí. Sou del millor que m’enduc d’aquesta etapa.

Als amics, no només perquè un cafè o una cervesa mai estan de més, sinó també per tantes estones compartides: Isa, Marta, Manyé, Òscar, Rosa, Mònica, Pep, Petit Comitè i colla de l’IRTA, merci! Laura López, moltes gràcies perquè les teves il·lustracions són brutals.

A l’Inky, per les desconnexions diàries imposades.

A la meva família, perquè sense el vostre sacrifi, valors i estima no seria qui sóc.

Al Marc, per arrelar-me a la realitat i donar-me empenta, però sobretot pel seu suport incondicional.

Tots heu estat part del procés i sense vosaltres no hauria estat possible. Gràcies!

# CONTENTS

# SUMMARY

Agricultural intensification boosted food production during the Green Revolution of the last century but it also caused loss of biodiversity. Nowadays the demand for food is expected to raise by a 15% in the next 10 years, so agriculture must face the challenge of providing more food in a sustainable way. In this context, the aim of this thesis was to give further insight in several aspects of the maintenance and promotion of ecosystem services (pollination and biological control) in Mediterranean fruit orchards. The first part of the thesis evaluates the effects of irrigation and the consequent agricultural intensification on two of the main groups of pollinators: wild bees and hoverflies. For that, we assessed these pollinator communities in the fruit-tree growing area of Lleida. Our results showed that the transformation of dryland into irrigation caused a higher flower abundance, different flower composition and reduced cover of semi-natural habitats in the irrigated areas. These environmental changes resulted in a drastic transformation of the wild bee communities: in the irrigated areas the presence of social bees increased but the presence of other solitary species was hindered, reducing overall wild bee species diversity (Chapter 1). The second part of the thesis specifically focuses on the evaluation of habitat management strategies to promote beneficials. First, we assessed the attractiveness of a specific flower margin to natural enemies of apple aphids (*Dysaphis plantaginea* and *Eriosoma lanigerum*), then we characterized the natural enemies present in the aphid colonies and finally, we evaluated the contribution of this margin to aphid biological control. Our results highlight the importance of parasitoids present in the surroundings of the orchards on the parasitism of *D. plantaginea* colonies (Chapter 2). The third part of the thesis studies the attractiveness of different flower traits to hoverflies to better understand the foraging behavior of these insects. We observed that flower shape, number and color elicit diverse behaviors in hoverflies: they showed a predilection for flat circle-shaped flowers bouquets and, that combinations with yellow and white are preferred to those that contain blue. In addition, we found behavioral differences between mated and unmated females with regard to their flower foraging (Chapter 3). The last part of the thesis addresses the potential and difficulties of using hoverflies as providers of ecosystem services in agricultural systems. For that purpose, we reviewed the existing literature related to these beneficials, with an emphasis on the key aspects of their ecology that can maximize their potential as pollinators and predators (Chapter 4).

# RESUM

La intensificació agrícola va impulsar la producció d'aliments durant la Revolució Verda del segle passat però també va causar una pèrdua de biodiversitat. Actualment, s'espera que la demanda d'aliments augmenti un 15% en els pròxims 10 anys, per tant l'agricultura enfronta el repte de produir més, i d'una manera sostenible. En aquest context, l'objectiu d'aquesta tesi és el d'aportar nous coneixements sobre diversos aspectes relacionats amb el manteniment i promoció de serveis ecosistèmics (pol·linització i control biològic) en cultius fructícoles mediterranis. La primera part de la tesi avalua els efectes del reg i la consegüent intensificació agrícola en abelles silvestres i sírfids. Per això, vam analitzar les comunitats d'aquests pol·linitzadors a l'àrea fructícola de Lleida. Els nostres resultats van demostrar que la transformació de secà a regadiu provoca més abundància de flors, diferent composició floral i reducció en la cobertura d'habitats seminaturals en les àrees regades. Aquests canvis ambientals comporten una transformació dràstica de les comunitats d'abelles silvestres: augmenta la presència d'abelles socials però disminueix la d'altres abelles solitàries, i es redueix, en conseqüència, la diversitat global d'espècies (Capítol 1). La segona part de la tesi se centra específicament en l'avaluació d'estratègies de maneig d'hàbitat per a la promoció de fauna auxiliar. Primer vam estudiar l'atracció d'un marge floral a enemics naturals de pugons de la pomera (*Dysaphis plantaginea* i *Eriosoma lanigerum*), després vam caracteritzar els enemics naturals presents a les colònies de pugó i finalment, vam avaluar la contribució d'aquest marge al control biològic de pugons. Els nostres resultats subratllen la importància dels parasitoides presents als voltants de les finques de fruiters en el parasitisme de les colònies de *D. plantaginea* (Capítol 2). La tercera part de la tesi estudia l'atracció dels sírfids a diferents característiques florals per tal d'entendre millor el seu comportament de recerca d'aliment. Vam observar que la forma, el nombre i el color de les flors provoquen diversos comportaments en els sírfids: preferien poms de flors circulars i planes, amb combinacions de groc i blanc per sobre d'aquelles que contenien blau. A més, vam observar que femelles aparellades i no aparellades es comportaven diferent (Capítol 3). L'última part de la tesi aborda el potencial i les dificultats d'utilitzar sírfids com a proveïdors de serveis ecosistèmics en els sistemes agrícoles. Per a tal efecte, vam fer una revisió de la literatura existent relacionada amb aquests insectes beneficiosos, amb especial èmfasi en els aspectes clau de la seva ecologia que poden maximitzar el seu potencial com a pol·linitzadors i depredadors (Capítol 4).

# RESUMEN

La intensificación agrícola impulsó la producción de alimentos durante la Revolución Verde del siglo pasado pero también causó la pérdida de biodiversidad. Además, se espera que la demanda de alimento aumente un 15% en los próximos 10 años, por lo que el reto actual de la agricultura es el de proveer más, y de un modo más sostenible. En este contexto, el objetivo de esta tesis es el de aportar nuevos conocimientos sobre diversos aspectos relacionados con el mantenimiento y promoción de servicios ecosistémicos (polinización y control biológico) en cultivos frutícolas mediterráneos. La primera parte de la tesis evalúa los efectos del riego y la consecuente intensificación agrícola en abejas silvestres y sírfidos. Con esta finalidad, analizamos las comunidades de polinizadores en el área frutícola de Lleida. Nuestros resultados demostraron que la transformación de secano a regadío provoca una mayor abundancia de flores, una distinta composición floral y una reducción de la cobertura de hábitats seminaturales en las áreas regadas. Estos cambios ambientales resultan en una transformación drástica de la comunidad de abejas silvestres: aumenta la presencia de abejas sociales, pero disminuye la de abejas solitarias, reduciendo, consecuentemente, la diversidad global de especies (Capítulo 1). La segunda parte de la tesis se centra específicamente en la evaluación de estrategias de manejo del hábitat para la promoción de fauna auxiliar. Primero estudiamos la atracción de un margen floral a enemigos naturales de pulgones del manzano (*Dysaphis plantaginea* y *Eriosoma lanigerum*), luego caracterizamos los enemigos naturales presentes en las colonias de pulgón y finalmente, evaluamos la contribución de este margen al control biológico de pulgones. Nuestros resultados destacan la importancia de los parasitoides presentes en los alrededores de las fincas de frutales en el parasitismo de colonias de *D. plantaginea* (Capítulo 2). La tercera parte de la tesis, estudia la atracción de distintas características florales a sírfidos con la finalidad de entender mejor su comportamiento de búsqueda de alimento. Observamos que la forma, el número y el color de las flores suscitan diversos comportamientos en los sírfidos: preferían ramos de flores circulares y planas, y combinaciones de amarillo y blanco eran preferidas ante combinaciones con azul. Además, observamos que hembras apareadas y no apareadas se comportaban de modo distinto (Capítulo 3). La última parte aborda el potencial y las dificultades de utilizar sírfidos como proveedores de servicios ecosistémicos en los sistemas agrícolas. Para tal efecto, hicimos una revisión de la literatura existente relacionada con estos insectos beneficiosos, con especial énfasis en los aspectos clave de su ecología que pueden maximizar su potencial como polinizadores y depredadores (Capítulo 4).

# General Introduction

## Introduction

Increased use of land, irrigation, plant breeding and agro-chemicals 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 agricultural production were often accompanied by major negative environmental impacts including greenhouse gas emissions, land and water degradation, pollution by agricultural chemicals and biodiversity loss (FAO 2017; Pretty et al. 2018; Tilman et al. 2011; West et al. 2014). Furthermore, nowadays human growing pressure still challenges agriculture as natural resources become increasingly stressed and the demand for food and for agricultural products is expected to raise by a 15% in the next 10 years (OECD/FAO 2019). Hence, the current priority for agriculture consists on maximizing food production while substantially shrinking its environmental footprint (Foley et al. 2011; Pretty et al. 2018). In other words, the current challenge for agriculture is to produce more but in a sustainable way.

Irrigation is a prominent component of agricultural intensification worldwide as it allows the extension of cultivated areas, as well as the maximization of crop yields (Benton et al. 2003; FAO 2011; Hanjra and Qureshi 2010). Irrigated areas produce around the 40% of the global food needs in only about 25% of the agricultural land (FAO 2011). These areas, mostly used for high-value crops such as fruits and vegetables, already achieve 80% of the maximum potential yield (The World Bank 2008). Opposed to that, production in rainfed areas is generally limited by scarce water availability (Passioura and Angus 2010). Thus, in arid and semi-arid areas like the Mediterranean basin, irrigation has been and still is a major driver of crop intensification and consequently, of agricultural landscape change (UNEP/MAP-Plan Bleu 2009).

Despite several studies have assessed the impacts of agricultural intensification on arthropods (Le Feon et al. 2010; Rusch et al. 2016; Schweiger et al. 2005), the specific effects of irrigation have been neglected. As far as we know, only two studies have focused on the impact of farmland irrigation on insect diversity. González-Estébanez et al. (2011) found that irrigated arable farms provide more favorable conditions for butterflies than dryland farms through the creation of new habitats and the increase of landscape complexity. Pérez-Fuertes et al. (2015) studied the response to irrigation in six insect groups with different ecological needs (Aphididae, Aphidiinae (Braconidae), Coccinellidae, Formicidae, Heteroptera and Syrphidae) in winter wheat fields. They found that all groups, except the Formicidae (whose richness was higher in the dryland), benefited by the conversion of dryland into irrigated land. These authors suggest that water availability might help to maintain plant growth during the summer drought, thus extending resource availability and allowing the preservation of herbivore populations. However, the apparently beneficial effects of irrigation may not be applicable to other groups of organisms. Present evidence shows that transformation of dry land into irrigated land may involve declines in diversity and abundance of populations of steppe birds (Brotons et al. 2004; De Frutos et al. 2015; Ursúa et al. 2005) and weeds (Fagúndez et al. 2016; José-María et al. 2010). This underscores the need for more information on the relative importance of different farmland irrigation types on the conservation of biodiversity and the promotion of ecosystem services in agricultural landscapes.

Furthermore, a key issue to meet both agronomic and ecological purposes 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), such as pollination and biological control, among others. Animal pollinators, like insects, birds and mammals, are essential or contribute to the sexual reproduction of about 65 % of world's wild plants and more than the 80 % of cultivated plant species (Ashman et al. 2004; Klein et al. 2007; Ollerton et al. 2011; Rader et al. 2016), the latter being estimated to be at €153 billion annually worldwide (Gallai et al. 2009). Biological control, in turn, occurs without human intervention and naturally controls most of the potential agricultural pests (Van Lenteren 2008). In fact, pest suppression from insect natural enemies has been valued at over €350 billion annually (Costanza et al. 1997).

An approach to enhance these ecosystem services is the promotion of functional biodiversity and nowadays, habitat management is an important discipline used to fulfil this purpose. The provision of favorable habitats supports beneficial populations (pollinators and natural enemies) through the supply of shelter, nectar, alternative prey/hosts and/or pollen. At the same time, it helps to counterbalance disturbances associated to cropping systems such as tillage, short-blooming period of crop plants and use of pesticides (Gurr et al. 2017; Wratten et al. 2012). Nonetheless, it is important to take into account that the diverse insect taxa might respond in different ways and at different landscape scales to the habitat manipulations (Tscharntke et al. 2007; Tscharntke et al. 2012). Moreover, success of biological control relies on promoting those predators that are more effective for each target pest. Therefore, knowledge on the presence and phenology of natural enemies in each area, as well as their prey and host preference are crucial when trying to improve biological control of pests (Symondson et al. 2002; Zehnder et al. 2007).

Globally, fruit production has been increasing continuously in recent years, with Asia and the Pacific being the world's top fruit-growing regions. Nonetheless, three countries in the Mediterranean area (Turkey, Italy and Spain) are among the world's top ten fruit-growing nations, producing about the half of the Mediterranean production (FAO 2014).

Fruit orchards remain planted for several years, thus they are less diverse systems over time if compared to arable crops. This permanency has been reported to enhance the stability of the system and as result, favor the presence of herbivores, including crop pests (Risch et al. 1983). In consequence, fruit tree protection is highly intensive and requires far more pesticide amounts than other crops (Simon et al. 2010), which emphasizes the need to explore other viable pest management options. In this regard, the pest control provided by natural enemies is also reported to be higher in perennial than in annual crops (Simon et al. 2010). However, the potential services provided by functional biodiversity, especially in supporting conservation biological control through habitat management, are less developed and utilized in fruit production than, for example in field crops and viticulture (Boller et al. 2004).

Aphids (Hemiptera: Aphididae) are major pests of several fruit trees under temperate and Mediterranean climates (Boller et al. 2004; Rousselin et al. 2017). Several aphid species can feed on the phloem of trees causing economic impacts on, for example apple (*Dysaphis plantaginea* Passerini, *Eriosoma lanigerum* Hausmann), cherry (*Myzus cerasi* Fabricius) and peach (*Myzus persicae* Sulzer). Conservation biological control seems a promising way for limiting aphid damage, as many types of natural enemies attack aphids such as ladybeetles, lacewings, hoverflies, predatory bugs and parasitoids (Boller et al. 2004; Dedryver et al. 2010; van Emden and Harrington 2017). Hence, these natural enemies could be combined to maintain aphid pest populations under the economic threshold.

In this regard, the promotion of hoverflies through the implementation of ecological infrastructures for aphid biological control has been long studied (Haenke et al. 2009; Hogg et al. 2011; Macleod 1999; Wratten et al. 2012). Their interest relies on their abundance as beneficial arthropods that can provide multiple ecosystem services in farmlands, such as pollination and biological control. About one third of the species have predatory larvae that mainly feed on aphids and other soft-bodied Hemiptera (Rojo et al. 2003). These larvae are highly voracious being able to predate between 400 and 1000 aphids during their larval development (Tenhumberg 1995). Moreover, the adults are highly mobile (Speight 2014) and able of laying eggs during all their life if they do not experience food shortages (Branquart and Hemptinne 2000). For these reasons, hoverflies have a high potential for biological control purposes (Hickman and Wratten 1996; Skirvin et al. 2011; Tenhumberg and Poehling 1995; van Rijn et al. 2006; White et al. 1995). Hence, in-depth knowledge of their ecology with their requirements and limitations is needed to maximize their potential in agricultural systems.

## References

Ashman TL et al. (2004) Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. Ecology 85:2408-2421 doi:10.1890/03-8024

Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol Evol 18:182-188 doi:10.1016/s0169-5347(03)00011-9

Boller EF, Häni F, Poehling HM (2004) Ecological infrastructures: Ideabook on functional diversity at the farm level. IOBC WPRS, Winterthur

Branquart E, Hemptinne JL (2000) Development of ovaries, allometry of reproductive traits and fecundity of *Episyrphus balteatus* (Diptera: Syrphidae). Eur J Entomol 97:165-170

Brotons L, Manosa S, Estrada J (2004) Modelling the effects of irrigation schemes on the distribution of steppe birds in Mediterranean farmland. Biodivers Conserv 13:1039-1058 doi:10.1023/b:bioc.0000014468.71368.35

Costanza R et al. (1997) The value of the world's ecosystem services and natural capital. Nature 387:253-260 doi:10.1038/387253a0

De Frutos A, Olea PP, Mateo-Tomás P (2015) Responses of medium- and large-sized bird diversity to irrigation in dry cereal agroecosystems across spatial scales. Agric Ecosyst Environ 207:141-152 doi:10.1016/j.agee.2015.04.009

Dedryver CA, Le Ralec A, Fabre F (2010) The conflicting relationships between aphids and men: A review of aphid damage and control strategies. C R Biol 333:539-553 doi:10.1016/j.crvi.2010.03.009

Fagúndez J, Olea PP, Tejedo P, Mateo-Tomás P, Gómez D (2016) Irrigation and Maize Cultivation Erode Plant Diversity Within Crops in Mediterranean Dry Cereal Agro-Ecosystems. Environ Manage 58:164-174 doi:10.1007/s00267-016-0691-5

FAO (2011) The State of the World's Land and Water Resources for Food and Agriculture (SOLAW) - Managing systems at risk. Food and Agriculture Organization of the United Nations, Rome and Earthscan, London, UK

FAO (2014) Europe and Central Asia Food and Agriculture. FAO, Budapest

FAO (2017) The future of food and agriculture – Trends and challenges. FAO, Rome

Foley JA et al. (2011) Solutions for a cultivated planet. Nature 478:337-342 doi:10.1038/nature10452

Gallai N, Salles JM, Settele J, Vaissiere BE (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol Econ 68:810-821 doi:10.1016/j.ecolecon.2008.06.014

Garibaldi LA, Gemmill-Herren B, D'Annolfo R, Graeub BE, Cunningham SA, Breeze TD (2017) Farming Approaches for Greater Biodiversity, Livelihoods, and Food Security. Trends Ecol Evol 32:68-80 doi:10.1016/j.tree.2016.10.001

González-Estébanez FJ, García-Tejero S, Mateo-Tomás P, Olea PP (2011) Effects of irrigation and landscape heterogeneity on butterfly diversity in Mediterranean farmlands. Agric Ecosyst Environ 144:262-270 doi:10.1016/j.agee.2011.09.002

Gurr GM, Wratten SD, Landis DA, You MS (2017) Habitat management to suppress pest populations: progress and prospects. Annu Rev Entomol 62:91-109 doi:10.1146/annurev-ento-031616-035050

Haenke S, Scheid B, Schaefer M, Tscharntke T, Thies C (2009) Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. J Appl Ecol 46:1106-1114 doi:10.1111/j.1365-2664.2009.01685.x

Hanjra MA, Qureshi ME (2010) Global water crisis and future food security in an era of climate change. Food Policy 35:365-377 doi:10.1016/j.foodpol.2010.05.006

Hickman JM, Wratten SD (1996) Use of *Phacelia tanacetifolia* strips to enhance biological control of aphids by hoverfly larvae in cereal fields. J Econ Entomol 89:832-840 doi:10.1093/jee/89.4.832

Hogg BN, Nelson EH, Mills NJ, Daane KM (2011) Floral resources enhance aphid suppression by a hoverfly. Entomol Exp Appl 141:138-144 doi:10.1111/j.1570-7458.2011.01174.x

José-María L, Armengot L, Blanco-Moreno JM, Bassa M, Sans FX (2010) Effects of agricultural intensification on plant diversity in Mediterranean dryland cereal fields. J Appl Ecol 47:832-840 doi:10.1111/j.1365-2664.2010.01822.x

Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proc Biol Sci 274:303-313 doi:10.1098/rspb.2006.3721

Le Feon V et al. (2010) Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. Agric Ecosyst Environ 137:143-150 doi:10.1016/j.agee.2010.01.015

Macleod A (1999) Attraction and retention of *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) at an arable field margin with rich and poor floral resources. Agric Ecosyst Environ 73:237-244 doi:10.1016/s0167-8809(99)00051-1

OECD/FAO (2019) OECD-FAO Agricultural Outlook 2019-2028.

Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? Oikos 120:321-326 doi:10.1111/j.1600-0706.2010.18644.x

Passioura JB, Angus JF (2010) Improving productivity of crops in water-limited environments. In: Sparks DL (ed) Advances in Agronomy, Vol 106, vol 106. Advances in Agronomy. pp 37-75. doi:10.1016/s0065-2113(10)06002-5

Pérez-Fuertes O, García-Tejero S, Pérez Hidalgo N, Mateo-Tomàs P, Olea PP (2015) Irrigation effects on arthropod communities in Mediterranean cereal agro-ecosystems. Ann Appl Biol 167:236-249 doi:10.1111/aab.12223

Pretty J et al. (2018) Global assessment of agricultural system redesign for sustainable intensification. Nature Sustainability 1:441-446 doi:10.1038/s41893-018-0114-0

Rader RA et al. (2016) Non-bee insects are important contributors to global crop pollination. Proc Natl Acad Sci U S A 113:146-151 doi:10.1073/pnas.1517092112

Risch SJ, Andow D, Altieri MA (1983) Agroecosystem diversity and pest control: data, tentative conclusions, and new research directions. Environ Entomol 12:625-629 doi:10.1093/ee/12.3.625

Rojo S, Gilbert F, Marcos-García MA, Nieto J, Mier MP (2003) A world review of predatory hoverflies (Diptera, Syrphidae: Syrphinae) and their prey. CIBIO Ediciones, Alicante, Spain

Rousselin A, Bevacqua D, Sauge MH, Lescourret F, Mody K, Jordan MO (2017) Harnessing the aphid life cycle to reduce insecticide reliance in apple and peach orchards. A review. Agronomy for Sustainable Development 37:13 doi:10.1007/s13593-017-0444-8

Rusch A et al. (2016) Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. Agric Ecosyst Environ 221:198-204 doi:10.1016/j.agee.2016.01.039

Schweiger O et al. (2005) Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. J Appl Ecol 42:1129-1139 doi:10.1111/j.1365-2664.2005.01085.x

Simon S, Bouvier J-C, Debras J-F, Sauphanor B (2010) Biodiversity and pest management in orchard systems. A review. Agronomy for Sustainable Development 30:139-152 doi:10.1051/agro/2009013

Skirvin DJ, Kravar-Garde L, Reynolds K, Wright C, Mead A (2011) The effect of within-crop habitat manipulations on the conservation biological control of aphids in field-grown lettuce. Bull Entomol Res 101:623-631 doi:10.1017/s0007485310000659

Speight MCD (2014) Species accounts of European Syrphidae (Diptera) vol 78. Syrph the net: The database of European Syrphidae (Diptera). Syrph the Net publications, Dublin

Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? Annu Rev Entomol 47:561-594 doi:10.1146/annurev.ento.47.091201.145240

Tenhumberg B (1995) Estimating predatory efficiency of *Episyrphus balteatus* (Diptera, Syrphidae) in cereal fields. Environ Entomol 24:687-691 doi:10.1093/ee/24.3.687

Tenhumberg B, Poehling HM (1995) Syrphids as natural enemies of cereal aphids in Germany - Aspects of their biology and efficacy in different years and regions. Agric Ecosyst Environ 52:39-43 doi:10.1016/0167-8809(94)09007-t

The World Bank (2008) Agriculture for development. The World Bank, Washington, DC

Tilman D, Balzer C, Hill J, Befort BL (2011) Global food demand and the sustainable intensification of agriculture. Proc Natl Acad Sci U S A 108:20260-20264 doi:10.1073/pnas.1116437108

Tscharntke T et al. (2007) Conservation biological control and enemy diversity on a landscape scale. Biol Control 43:294-309 doi:10.1016/j.biocontrol.2007.08.006

Tscharntke T et al. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews 87:661-685 doi:10.1111/j.1469-185X.2011.00216.x

UNEP/MAP-Plan Bleu (2009) State of the Environment and Development in the Mediterranean. UNEP/MAP-Plan Bleu Athens

Ursúa E, Serrano D, Tella JL (2005) Does land irrigation actually reduce foraging habitat for breeding lesser kestrels? The role of crop types. Biol Conserv 122:643-648 doi:10.1016/j.biocon.2004.10.002

van Emden H, Harrington R (2017) Aphids as crop pests. CAB International, UK and USA

Van Lenteren J (2008) Prólogo. In: Jacas JA, Urbaneja A (eds) Control biológico de plagas agrícolas. Phytoma-España, Valencia, Spain, pp IX-X

van Rijn PCJ, Kooijman J, Wäckers FL (2006) The impact of floral resources on syrphid performance and cabbage aphid biological control. IOBC/WPRS Bull 29:149-152

West PC et al. (2014) Leverage points for improving global food security and the environment. Science 345:325-328 doi:10.1126/science.1246067

White AJ, Wratten SD, Berry NA, Weigmann U (1995) Habitat manipulations to enhance biological control of brassica pests by hover flies (Diptera, Syrphidae). J Econ Entomol 88:1171-1176 doi:10.1093/jee/88.5.1171

Wratten SD, Gillespie M, Decourtye A, Mader E, Desneux N (2012) Pollinator habitat enhancement: Benefits to other ecosystem services. Agric Ecosyst Environ 159:112-122 doi:10.1016/j.agee.2012.06.020

Zehnder G, Gurr GM, Kuehne S, Wade MR, Wratten SD, Wyss E (2007) Arthropod pest management in organic crops. Annu Rev Entomol 52:57-80 doi:10.1146/annurev.ento.52.110405.091337

## Thesis outline

The aim of this thesis was to give further insight on different aspects of the promotion of beneficials and their ecosystem services in Mediterranean fruit orchards. The first part of the thesis evaluates the effects of the transformation of rainfed areas into irrigation on farmland biodiversity. For that, we assessed the occurrence and variation of pollinator communities in the fruit-tree growing area of Lleida (Chapter 1). The second part of the thesis specifically focuses on the evaluation of habitat management strategies to promote beneficials. First, we assessed the attractiveness of a specific flower margin to natural enemies of apple aphids (*D. plantaginea* and *E. lanigerum*) and, we evaluated the contribution of this margin to aphid biological control (Chapter 2). Finally, we studied the attractiveness of different flower traits to hoverflies to better understand the foraging behavior of these insects (Chapter 3). The last part of the thesis addresses the potential and difficulties of using hoverflies as providers of ecosystem services in agricultural systems. For that purpose, we synthesized the existing literature related to these beneficials, with an emphasis on the key aspects of their ecology that can maximize their potential to provide ecosystem services (Chapter 4).

In Chapter 1, we analyzed the effects of transformation of rainfed areas into irrigation on pollinator communities. For that, we characterized wild bee and hoverfly communities in 24 almond orchards distributed in three different zones, corresponding to different levels of agricultural intensification: dry orchards, irrigated orchards near to the dryland and irrigated orchards far from the dryland. We also described the local and landscape structure of each orchard. We then analyzed agricultural intensification effects on bee and hoverfly composition and assessed which local and landscape variables determine the pollinator structure and composition.

Thus, the objectives of this study were:

- to analyze differences between dry and irrigated orchards in local availability of floral and bee nesting resources and in landscape habitat structure,
- to assess how the structure and composition of wild bee and hoverfly communities differs between dry and irrigated orchards,
- to identify the local and landscape variables that determine the structure and composition of the wild bee and hoverfly communities.

In Chapter 2, we assessed the attractiveness of a specific flower margin and the resident vegetation of Mediterranean apple orchards to the natural enemies of apple aphids (*D. plantaginea* and *E. lanigerum*) and their contribution to aphid biological control. For that, visual and beating tray samplings were conducted to estimate the attractiveness of the margins to natural enemies and phytophagous insects. In addition, aphid colonies present in the apple orchards were sampled and the natural enemies present in them quantified and identified.

The specific objectives of this study were:

- to assess the attractiveness of a specific flower margin to auxiliary fauna,
- to characterize the natural enemies of *D. plantagin*ea and *E. lanigerum* present in Mediterranean apple orchards,
- to assess the influence of the surrounding margins in the *D. plantaginea* and *E. lanigerum* natural enemy populations present in the aphid colonies.

In Chapter 3, we studied the attractiveness of different flower traits to hoverflies to better understand the foraging behavior of these insects. We used painted artificial EVA foam flowers to perform three consecutive experiments in which the relative attractiveness of different flower traits was assessed. The behavior of three groups of adult hoverflies (virgin males, virgin females, and gravid females) was recorded. In this regard, the objectives of this study were:

- to assess the attractiveness of three flower traits (shape, number of flowers and color diversity) to hoverflies,
- to determine whether mating alters the foraging behavior of these flies.

In Chapter 4, we synthetized the existing knowledge related to the promotion of predatory hoverflies and their ecosystem services in agricultural systems. For that purpose, we divided the review into three main sections. First, we focused on those aspects of the hoverfly ecology that are relevant for their implications in biological control and habitat management. These were divided in nutrition (with a special emphasis on the nutritional requirements, feeding preferences and prey detection of the different developmental stages), overwintering and the effect of landscape. Second, we reviewed the ecosystem services that predatory hoverflies can provide. Finally, we discussed those farming practices that can affect their effectiveness as providers of ecosystem functions. The objective of this review was:

- to synthetize the existing literature and identify the current gaps of knowledge related to the promotion of predatory hoverflies and their ecosystem services in agricultural systems.

## Chapter 1

# Transformation of dry-land into irrigation-land has profound effects on pollinator communities in almond orchards

## Abstract

Irrigation is an essential component of agricultural intensification in arid and semi-arid areas that leads to a profound transformation of local and landscape environmental conditions. In spite of this, the impact of the transformation of dryland into irrigation land on biodiversity is poorly understood, and studies on the response of pollinator communities are totally lacking. In this study we analyze the effects of the implementation of irrigation on bee and hoverfly communities in almond orchards in a Mediterranean area.

We surveyed bee and hoverfly communities in 24 almond orchards across and agricultural landscape near Lleida (NE Spain). Eight orchards (henceforth dry) were non-irrigated and located in a dryland zone. The other 16 orchards were irrigated and located in an irrigated zone. Of these, 8 were close (<1Km) to the dryland zone (irrigated-near), and 8 were far (>4 km) from the dryland zone (irrigated-far). We characterized the local flower community and the landscape structure of each orchard. We then compared bee and hoverfly community structure and composition across the three orchard types.

At the local level, dry orchards were characterized by low flower abundance and high bare soil cover and hosted a flower composition radically different from that of irrigated orchards. Flower composition was almost identical in irrigated-near and irrigated-far orchards. At the landscape level, dry orchards were characterized by dry almond and natural habitat cover. By contrast, irrigated orchards were characterized by cover of irrigated mass-flowering crops including orchard (almonds, peaches, pears and apples) and arable crops (oilseed rape, sunflower and lucerne). We collected 5974 wild bees (138 species) and 632 hoverflies (23 species). Bees were less abundant but more diverse in dry orchards. Importantly, dry orchards hosted a drastically different bee community compared to irrigated orchards. Bee composition was almost identical in irrigated-near and irrigated-far orchards. Dry orchard communities were dominated by solitary species with short activity periods (*Panurgus dentipes, Osmia tricornis, Rhodanthidium sticticum, Anthophora* spp., and irrigated orchard communities by social species with long activity periods (*Lasioglossum malachurum, Halictus fulvipes*). The main environmental drivers of these differences were flower abundance and composition at the local scale and the proportion of arable crops and natural and semi-natural habitats at the landscape scale. There were differences between dry and near-irrigated orchards in hoverfly composition, but they were not nearly as pronounced as with bees.

*Synthesis and applications*. Transformation of dryland into irrigation land causes profound changes in local and landscape environmental variables that drastically transform pollinator communities. The conservation of original pollinator communities in agricultural areas depends on the preservation of natural habitats combined with traditional agricultural systems.

**Keywords:** Syrphidae, hoverfly, wild bee, Apiformes, agricultural intensification

# 1. Introduction

Animal pollinators provide a key ecosystem service by contributing to the sexual reproduction of 87% of worldwide angiosperms and 70% of the main crops (Ashman et al. 2004; Klein et al. 2007; Ollerton et al. 2011). However, numerous studies worldwide have reported substantial declines in the diversity and abundance of wild pollinators (Goulson et al. 2015; Potts et al. 2010) with serious potential impacts on crop production (Gallai et al. 2009; Garibaldi et al. 2013). This decline is currently considered to be part of a general biodiversity loss mainly driven by agricultural intensification occurred over the last decades (Goulson et al. 2015; Kremen et al. 2002; Potts et al. 2010). Among other factors, agricultural intensification is characterized by an increase in the use of external inputs, including water, fertilizers and pesticides, accompanied by a reduction of natural and semi-natural areas at the landscape level (Pretty et al. 2018; Tilman et al. 2011; Tscharntke et al. 2005; West et al. 2014).

Irrigation is a prominent component of agricultural intensification that results in increased crop yields, thus promoting the transformation of wild land into cultivated land (Benton et al. 2003; FAO 2011; Hanjra and Qureshi 2010). Irrigated crops make up around 20% of the world's agricultural land but produce 40% of the world's food (FAO 2011). In the Mediterranean basin, with low levels of rainfall, irrigation is an essential component of agricultural intensification, and has been a major driver of agricultural landscape transformation in the last decades (UNEP/MAP-Plan Bleu 2009). Mediterranean areas are characterized by severe summer droughts that hinder plant development and reproduction (Chaves et al. 2002). Thus, the implementation of irrigation in these areas leads to important changes not only to the target crop but also to the accompanying flora. First, the increase in water availability allows for a longer vegetation growth period resulting in enhanced feeding resources and shelter to phytophagous insects, including pollinators, through the summer (González-Estébanez et al. 2011). Second, irrigation usually promotes herbicide use due to the establishment of new plants, particularly weeds and exotic invasive species (Davis et al. 2000). Third, reduced competition for water between weeds and the crop entails changes in groundcover management (mowing in irrigated land *versus* tillage in dry land), which modifies the plant community present in the orchard (Hyvonen and Salonen 2002). Fourth, irrigation enables a higher stability in crop production that promotes a greater application of fertilizers and pesticides in response to higher pest pressure (Perfect 1986). Fifth, water availability allows for the cultivation of a higher diversity of crops (FAO 2011), although this diversification may be masked by the implementation of large areas of highly homogeneous systems (monocultures) (Benton et al. 2003; Tscharntke et al. 2005). At any rate, irrigation usually results in a severe reduction and fragmentation of natural habitats (Tscharntke et al. 2005).

Even though several studies have assessed the impacts of agricultural intensification on arthropod communities (Le Feon et al. 2010; Rusch et al. 2016; Schweiger et al. 2005), the specific effects of irrigation have been neglected. As far as we know, only two studies have focused on the impact of farmland irrigation on insect diversity. Irrigated arable farms were found to provide more favorable conditions for butterflies than dryland farms through the creation of new habitats and the increase of landscape complexity (González-Estébanez et al. (2011). Pérez-Fuertes et al. (2015) studied the response to irrigation in six arthropod groups with different ecological needs (Aphididae, Aphidiinae, Coccinellidae, Formicidae, Heteroptera and Syrphidae) in winter wheat fields. They found that all groups, except the Formicidae (whose richness was higher in the dryland), benefited by the conversion of dryland into irrigated land. These authors suggest that water availability may help to maintain plant growth during the summer drought, thus extending resource availability and allowing the sustainability of herbivore populations. However, these apparently beneficial effects of irrigation do not apply to other groups of organisms. Diversity of steppe birds (Brotons et al. 2004; De Frutos et al. 2015; Ursúa et al. 2005) and weeds (Fagúndez et al. 2016; José-María et al. 2010) has been found to decline with the transformation of dry land into irrigated land. Therefore, responses to irrigation appear to vary among taxa.

The aim of this study is to analyze the effects of the implementation of irrigation and associated changes in agricultural practices on pollinator communities in almond orchards in a Mediterranean area. We study wild bees and hoverflies because they are the two most important groups of pollinators (Inouye et al. 2015). Moreover, these two groups of pollinators differ in their ecological requirements, therefore it is likely that they also differ in their responses to landscape intensification. On the one hand, bees are central-place foragers and require appropriate nesting substrates (most species nest under-ground but some nest above-ground, mainly in pre-established cavities) and feeding resources in the form of pollen and nectar for both adults and larvae (Stephen et al. 1969). On the other hand, hoverflies do not build nests, and require pollen and nectar only in the adult stage, hence they are not constrained by the need to provision a nest and may move more freely in the landscape. In addition, many wild bee species are oligolectic, collecting pollen only from a few plant families (Westrich 1990), while hoverflies are usually generalists (Branquart and Hemptinne 2000). In addition, the larvae of many hoverfly species are aphidophagous (Gilbert 1993) and predate on a range of aphid species from both wild and crop plants (Rojo et al. 2003; Sadeghi and Gilbert 2000). Consequently, hoverflies, specially aphidophagous species, appear to be less sensitive to loss and fragmentation of semi-natural habitats than wild bees (Jauker et al. 2009).

Almond (*Prunus dulcis* (Mill.) D. A. Webb) orchards are an excellent model system for testing the effects of irrigation on wild bees and hoverflies. First, although almonds are traditionally grown in semi-arid lands, production is highly dependent on irrigation to achieve maximum yields (Micke 1996). In fact, production may increase 10-fold under irrigation (150 kg/ha to 1,500 kg/ha) (Miarnau et al. 2016). Second, the global demand for almonds has increased by 20% in the last ten years (International Nut and Dried Fruit Council 2018). This demand is not only prompting new plantations, but also the transformation of dry orchards into irrigated ones (MAPA 2019; USDA 2019). For example, the cultivated almond area in Spain has increased 110,000 ha (from 547,822 to 657,771 ha) from 2010 to 2018. Approximately half of this increase corresponds to irrigated orchards (from 40,855 to 94,124 ha) (MAPA 2019). Third, almond production is highly dependent on insect pollination (Free 1993; McGregor 1976). Although managed honeybees are often introduced in commercial orchards to ensure pollination (Traynor 1993), some wild bees are more effective pollinators than honeybees on a per visit basis (Bosch and Blas 1994) and provide important pollination services (Klein et al. 2012). Fourth, in addition to providing pollination, some hoverflies also provide biological control services through aphid predation (Gilbert 1993; Klein et al. 2012).

We have three objectives: (i) To analyze differences between dry and irrigated orchards in local availability of floral and bee nesting resources and in landscape habitat structure; (ii) To assess how the structure and composition of wild bee and hoverfly communities differs between dry and irrigated orchards (iii) To identify the local and landscape variables that determine the structure and composition of the wild bee and hoverfly communities. We have the following hypotheses: 1) Flower composition will vary between dry and irrigated orchards. Irrigated orchards will have increased local flower abundance and richness; 2) Irrigated orchards will have reduced cover of natural and semi-natural habitat at the landscape level; 3) These changes in floral resource availability at the local and landscape level will foster differences in pollinator composition; 4) Irrigated orchards located close to the dryland will host species typical of both habitats and therefore will have a higher pollinator richness; 5) differences across orchard types in pollinator community structure and composition will be greater for bees because they are more dependent on floral resources and show more specialized feeding habits than hoverflies.

## 2. Materials and methods

### 2.1. Study area, site selection and treatments

The study was conducted in the plain of Lleida (Catalonia, NE Spain). The area is characterized by semi-arid Mediterranean climate, with low mean annual rainfall (325-500 mm) and very dry and hot summers. In the second half of the 19th century the northern part of the plain was drastically transformed by the implementation or irrigation (Urgell canal) (Vila 1992). This area is currently dominated by intensively-farmed agricultural land, including a wide variety of orchards (mostly almond, apple, pear and peach) and herbaceous crops (mostly barley, maize and lucerne). The southern part of the plain remains non-irrigated and is dominated by extensive cereal crops, almond orchards and olive groves. Natural and semi-natural habitats are mainly occupied by scrublands. Importantly, the recent construction of a new canal (Segarra-Garrigues; Territori 2019) profoundly change agricultural practices and landscape composition of the dryland area in the close future.

Within a 54 km$^2$ area we selected 3 groups of 8 almond orchards each (Figure 1). The three groups correspond to three different orchard types (Table S1): a) non-irrigated orchards located in the dryland zone (henceforth dry (D) orchards); b) irrigated orchards located in the irrigated zone but close (<1Km) to the dryland zone (henceforth irrigated-near (IN) orchards); c) irrigated orchards located in the irrigated zone far (>4 km) from the dryland zone (henceforth irrigated-far (IF) orchards).

To ensure spatial independence among sampling sites, minimum distance between orchards was 1 km. This distance encompasses the foraging range of most wild bees (Greenleaf et al. 2007; Torné-Noguera et al. 2014) and hoverflies (Kleijn and van Langevelde 2006). Orchard size ranged from 0.5 to 15 ha. There are important differences in orchard management between dry and irrigated orchards (Table S2). In dry orchards, the groundcover is tilled, whereas in irrigated orchards the alleys are mown and herbicide is applied to the tree-rows. Pest control is conducted through conventional management in both dry and irrigated orchards, but fertilizer and pesticide load is much higher in irrigated orchards (Table S2).

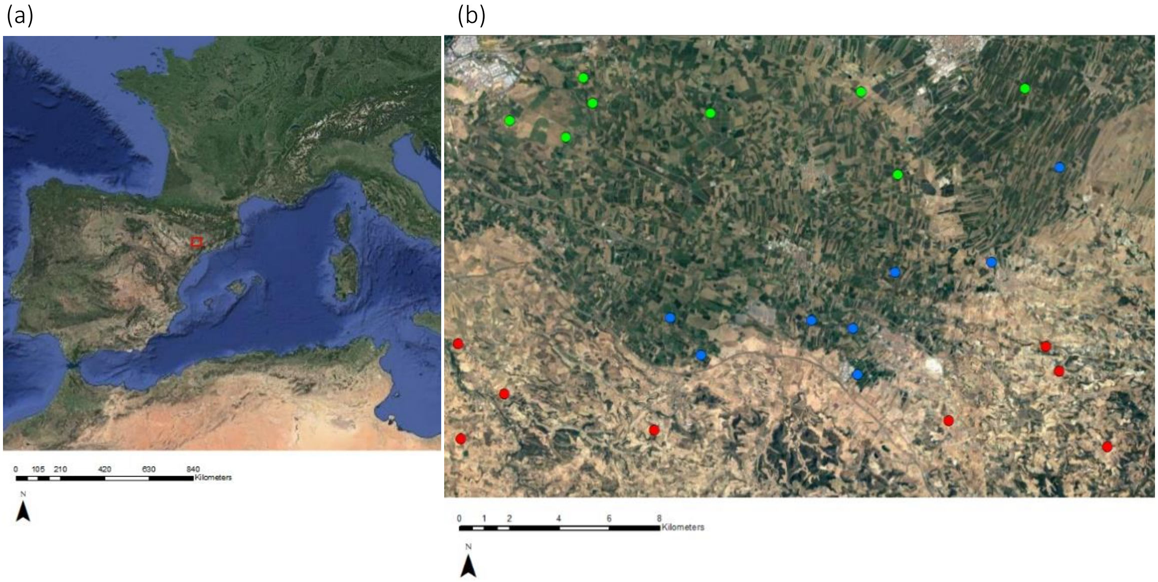


Figure 1. Location of the Lleida plain (red square) in the northwest of the Mediterranean basin (left), and location of the 24 selected orchards in the study area: dry (red dots), irrigated-near (blue dots) and irrigated far (green dots) (right).

## 2.2. Pollinator surveys

We conducted six pollinator surveys (in late-April, late-May, late-June and late-July of 2016 and early-March and late-March of 2017). All sites were surveyed simultaneously on each sampling date. In each survey we placed nine pan traps per orchard. To obtain a good representation of the various vegetation types within and around the orchard, pan traps were distributed in three levels: three traps were located in the orchard margin, three in the first almond row (orchard edge), and three 20-30 m into the orchard (middle of the orchard). Adjacent traps within each level were 12 m apart from each other (Figure 2).

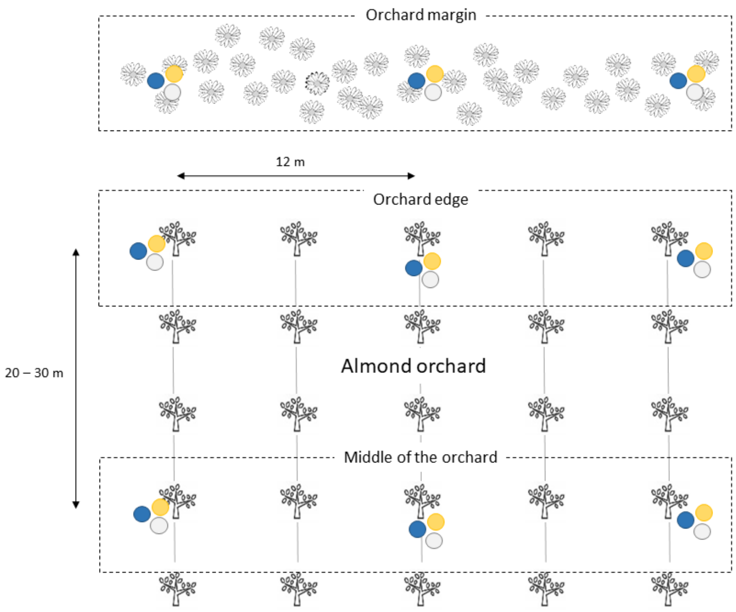


Figure 2. Location of the pan traps (colored circles) and areas in which plant surveys were conducted (orchard margin, orchard edge and middle of the orchard).

Each trap consisted of three bowls painted with UV-reflecting paint (blue, white and yellow, respectively) (Westphal et al. 2008), attached to a metal bar at the height of the herbaceous layer. Traps were operational on days under favorable weather conditions (sunny to lightly overcast days, low wind speed (0-4.2 m/s)), from sunrise to sunset. Insects caught in the traps were preserved in 70% ethanol. In subsequent months, wild bee and hoverfly specimens were sorted into morphospecies in the laboratory and when possible, determined to species level. *Apis mellifera* L. individuals were not included in the analysis due to their managed origin.

### 2.3. Local variables

On the same days on which pollinator surveys were performed, data on the availability of floral resources were collected. We counted the number of open flowers of each species in bloom in six 1 x 1 $m^2$ randomly distributed quadrats within each of the three sampling levels (orchard margin, orchard edge and middle of the orchard; Figure 2). Of the six quadrats per level located inside the orchard, two were placed on the tree row and four in the alley. The area occupied by tree rows and alley widths was also measured. For each orchard, data from the six surveys was pooled to calculate: flower abundance (density of open flowers), flower richness, flower composition (abundance of each flower species) and percentage of bare soil cover.

Most bees, nest under-ground, notably in bare soil. For this reason, we used the 18 (three sampling levels multiplied by six quadrats in each level) above-mentioned quadrats to estimate the percentage of bare soil cover within and around the orchard. In addition, for each orchard we recorded the presence of other bee nesting substrates within 100 m of the orchard edge. The following types of nesting substrates were considered: soft pith stems (mostly *Rubus* spp.), dead wood, clay embankments, bare soil, dry stone walls, old buildings (offering a variety of potential nesting cavities in adobe walls, wooden beams, thatched roofs and bricks).

## 2.4. Landscape variables

ArcGIS (Version 10.5; ESRI, Redlands, CA, 2016) was used to create 0.1 km, 0.5 km and 1 km radius buffers around the center of each orchard and determine the proportion of different habitat types. For the 0.5 km and 1 km buffers the land cover map of Catalonia (MCSC-4, 2013) and the agricultural land use map of Catalonia (DUN, 2017) were used to characterize habitat types. The MCSC-4 map was used to obtain an accurate estimate of habitat types, and the DUN map provided an updated version of the various types of crops. Habitat types for the 0.1 km buffer were verified on site. To facilitate analysis, habitat types were grouped into five categories: arable crops (mostly cereals but also some vegetable crops), irrigated orchards, non-irrigated orchards, natural and semi-natural habitats (scrublands, meadows and fallows), and urban areas (including infrastructures). The area covered by each category was measured and the Simpson's diversity index (D) was used to quantify habitat diversity.

## 2.5. Data analysis

### 2.5.1. Characterization of local floral and nesting resources

To visualize differences across orchard types in flower species composition we used non-metric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity index. We then conducted an analysis of similarities (ANOSIM) with 999 permutations to statistically test for significant differences in flower assemblages among orchard types. To establish the relationship between local variables and determine to what extent orchard types could be characterized based on these variables, we conducted a principal component analysis (PCA) with flower abundance, flower richness, flower diversity, flower composition (the scores of the first axis of the above-mentioned NMDS, which explained most of the variation in flower species composition, see results), percent of bare soil cover and nesting substrate richness. In addition, a one-way ANOVA was used to compare flower abundance, flower species richness and nesting substrate richness across orchard types.

### 2.5.2. Characterization of the landscape structure

First, we run Spearman rank correlations to assess to what extent landscape variables were correlated across spatial scales. Since results of the 0.1 and 0.5 km buffers turned out to be highly correlated to those of the 1 km buffer (Table S3), we show only the results of the 1 km buffer. Then, to establish the relationship between the various landscape variables and their association with the three orchard types we conducted a PCA with the five habitat categories and the habitat diversity index (D).

### 2.5.3. Characterization of the wild bee and hoverfly communities

All analyses were conducted separately for bees and hoverflies. We performed one-way ANOVAs followed by HSD-Tukey post-hoc tests to compare bee and hoverfly abundance, species richness and diversity across orchard types. If needed, data were log transformed to meet homoscedasticity and normality requirements.

Wild bee and hoverfly community composition were compared across orchard types with NMDS using Bray-Curtis dissimilarity. We then conducted ANOSIM with 999 permutations to statistically test for significant differences in pollinator composition among orchard types.

### 2.5.4. Effects of local and landscape variables on the structure and composition of the pollinator community

We evaluated the relationship between local and landscape variables and the structure and composition of the wild bee and hoverfly communities using general linear mixed models (GLMMs). We used a separate model for each of the eight response variables (Table 1). To characterize bee and hoverfly community composition we used the scores of the first NMDS axis of the community composition analyses. For each model, we only included explanatory variables that a priori we considered could have an effect on the response variable. To reduce the number of landscape variables we used results of the above-described PCA to identify the variables that best described the three orchard types. The explanatory variables included in each model for each response variable are shown in Table 1. Flower composition was characterized with the scores of the first NMDS axis of the flower composition analysis. Wild bee and hoverfly abundance were log transformed in order to meet normality assumptions. To account for the non-independence of the local and landscape variables within each orchard type, orchard type was included as a random effect.

Table 1. Explanatory variables included (X) in each of the eight models analyzing the effects of local and landscape factors on the structure and composition of bee and hoverfly communities.

| | Arable crop cover | Natural and semi-natural habitat cover | Habitat diversity | Flower abundance | Flower richness | Flower composition | Nesting substrate richness |
|---|---|---|---|---|---|---|---|
| Wild bee abundance | X | X | X | X | | | |
| Wild bee richness | X | X | X | X | X | | X |
| Wild bee diversity | X | X | X | X | X | | X |
| Wild bee composition | X | X | X | | | X | X |
| Hoverfly abundance | X | X | X | X | | | |
| Hoverfly richness | X | X | X | X | X | | |
| Hoverfly diversity | X | X | X | X | X | | |
| Hoverfly composition | X | X | X | | | X | |

We used Akaike's information criterion with a correction for finite sample sizes (AICc) to select the best-supported models for each response variable (Burnham and Anderson 2002). All the initial models were full models. The best supported models were selected based on their AICc weights, which reveal the relative likelihood of a given model-based on the data and the fit-scaled to one; thus, models with a delta (AICc difference) of <2 were retained. We considered variables to be relevant when they were included in the best-supported models, except when one of the best-supported models consisted only of the intercept.

NMDS and ANOSIM were performed using *metaMDS* and *anosim* functions, respectively, in the vegan package, and model selection was performed using the *dredge* function in the MuMIn package in R (R Core Team 2016). PCA analysis and Spearman correlations were performed with JMP (Version 13; SAS Institute Inc., Cary, NC, 1989-2019).

## 3. Results

### 3.1. Local environmental variables

Flower abundance significantly differed across orchard types (one-way ANOVA: $F_{2,21}$= 3.48, P= 0.049) (Figure S1). Flower species richness and nesting substrate richness did not differ between the three types of orchards (one-way ANOVAs: $F_{2,21}$= 0.86, P= 0.438 and $F_{2,21}$= 1.03, P= 0.376, respectively).

The NMDS and ANOSIM showed that flower species composition was drastically different between dry and irrigated orchards, but no differences were found between the two types of irrigated orchards (ANOSIM: global R = 0.493, P = 0.001, stress = 0.217; Figure 3). Species typical of dry orchards include *Helinanthemum apenninum* L., *Globularia alypum* L. and *Rosmarinus officinalis* L. (only present in dry orchards), as well as *Anacyclus clavatus* Desf., *Diplotaxis erucoides* L. and *Erodium cicutarium* L. (clearly more abundant in dry orchards). By contrast, irrigated orchards were dominated by *Senecio vulgaris* L., *Capsella bursa-pastoris* L., *Taraxacum officinale* Weber, *Veronica persica* Poir., *Trifolium repens* L., *Convolvulus arvensis* L. and *Plantago lanceolata* L. (Table S4).

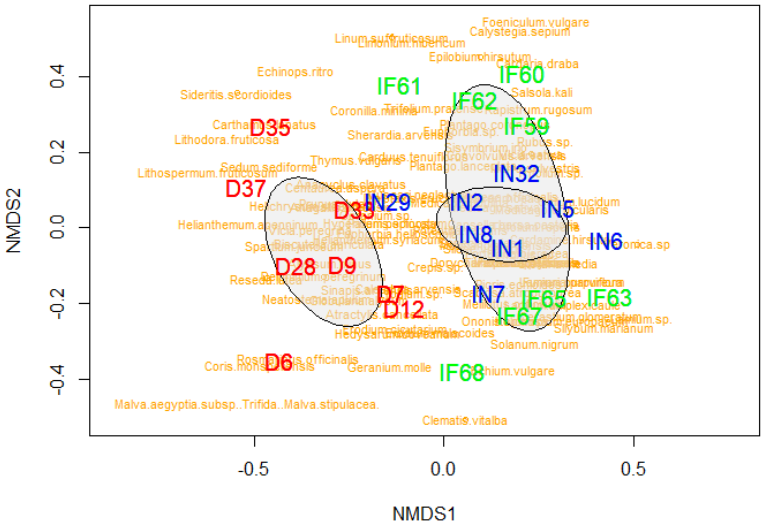


Figure 3. Graphical representation of non-metric multidimensional scaling (NMDS) analysis of flower species community composition in the orchard types: dry (red), irrigated-near (blue) and irrigated-far (green).

At the local scale, the first two PCA axes accounted for 36.0% and 26.6% of the total variation, respectively (Figure 4). Positive and high values of the first PCA axis are associated with high flower abundance and high values of the scores of the first NMDS axis for flower composition. Positive and high values of the second axis are associated with high flower and nesting substrate richness. High levels of bare soil cover are associated with negative values of both axes. Thus, in contrast to irrigated orchards, dry orchards were characterized by a high percentage of bare soil and low flower abundance. This analysis confirmed that irrigated-near and irrigated-far orchards were very similar in local variables.

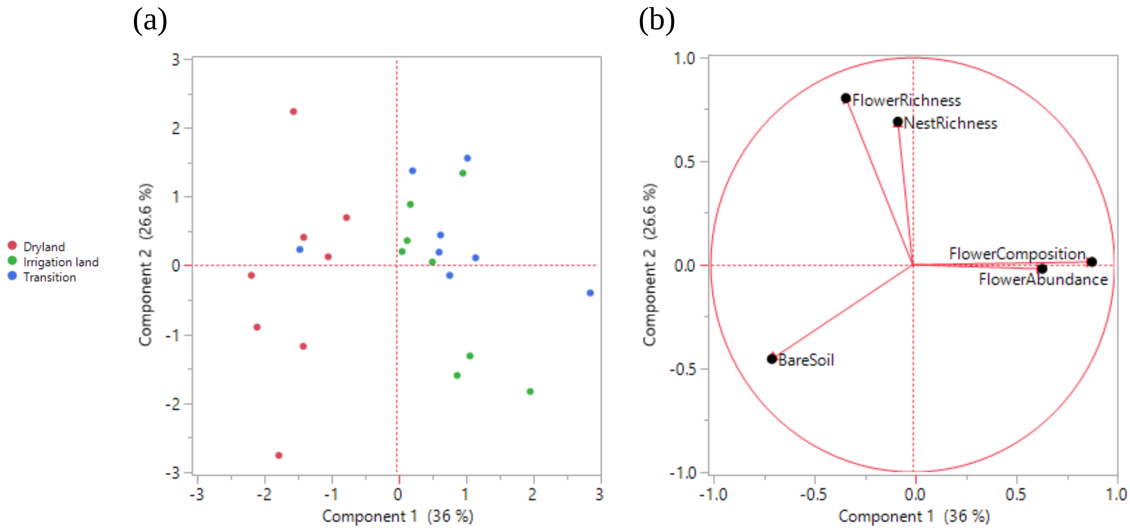


Figure 4. Score plot (a) and loading-plot (b) of PCA analysis of local variables. BareSoil = percentage of bare soil cover; FlowerRichness = flower species richness; NestRichness = nesting substrate richness; FlowerComposition = flower composition; FlowerAbundance = flower abundance.

### 3.2. Landscape environmental variables

The PCA analysis at the landscape scale (1-km buffer) showed that the three orchard types could be clearly separated based on landscape variables (Figure 5). The first two PCA axes accounted for 47.8% and 27.3% of the total variation, respectively. High positive values of the first axis were associated with high cover of irrigated orchards, arable crops and urban areas, whereas negative values were associated with cover of dry orchards and natural and semi-natural habitats. As for the second axis, high positive values were associated with high habitat diversity. Hence, the first component clearly separated dry orchards from the two types of irrigated orchards. Dry orchards were surrounded by a high proportion of non-irrigated orchards and natural and semi-natural habitats. Conversely, irrigated orchards were surrounded by irrigated orchards and arable crops. The second axis explained the differences between irrigated-near and irrigated-far orchards. Habitat diversity and urban cover were more strongly associated with irrigated-near orchards, while arable crop cover was more strongly associated with irrigated-far orchards.

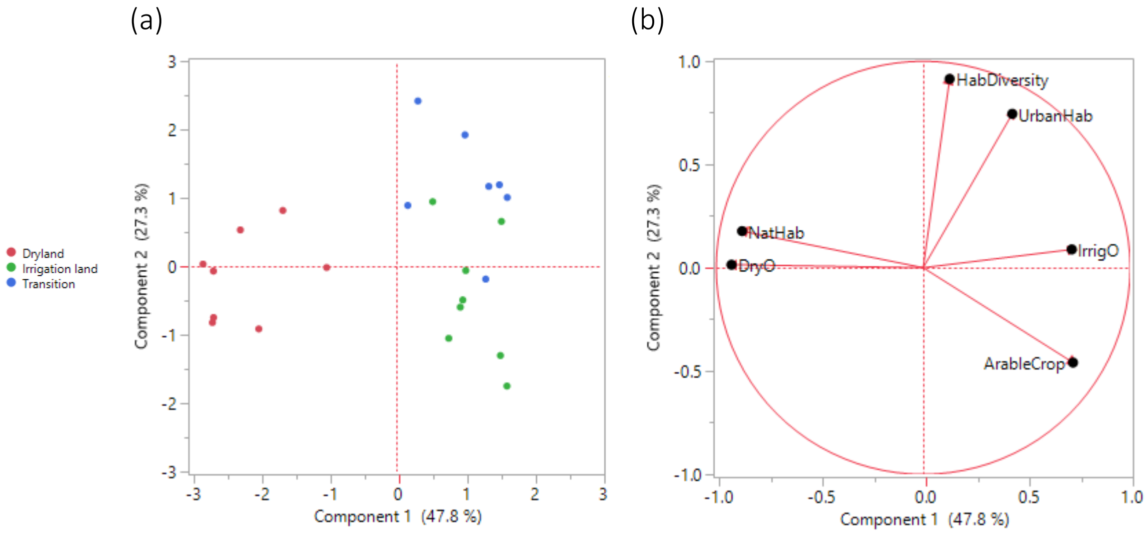


Figure 5. Score plot (a) and loading-plot (b) of PCA analysis of landscape variables (1-km buffer). DryO = non-irrigated orchard cover; NatHab = natural and semi-natural habitat cover; HabDiversity = habitat diversity; UrbanHab = urban areas cover; IrrigO = irrigated orchard cover; ArableCrop = arable crop cover.

### 3.3. Pollinator community structure and composition

Our pan traps collected 218 honey bees. There were no statistical differences between land-use types in honey bee abundance (one-way ANOVA: $F_{2,21}$=0.43, P= 0.657). In addition, our pan traps collected 5974 wild bees from 138 morphospecies (Table S5) and 632 hoverflies from 23 morphospecies (Table S6). The community structure of wild bees significantly differed between orchard types (Table 2). Wild bees were less abundant in dry than in irrigated-far orchards and irrigated-near orchards showed intermediate levels of abundance (Figure 6a). Species richness did not differ between dry and irrigated orchards but was significantly higher in irrigated-far than in irrigated-near orchards (Figure 6b). Wild bee species diversity was higher in dry orchards than in irrigated-near orchards, with irrigated-far orchards showing intermediate values (Figure 6c).

Table 2. Summary of one-way ANOVAs analyzing the effects of orchard type on abundance, species richness and diversity of wild bees and hoverflies.

| Variable | $F_{2,21}$ | P |
|---|---|---|
| Wild bee abundance | 4.52 | 0.023 |
| Wild bee species richness | 3.80 | 0.039 |
| Wild bee species diversity | 5.26 | 0.014 |
| Hoverfly abundance | 2.19 | 0.137 |
| Hoverfly species richness | 3.08 | 0.067 |
| Hoverfly species diversity | 0.26 | 0.777 |

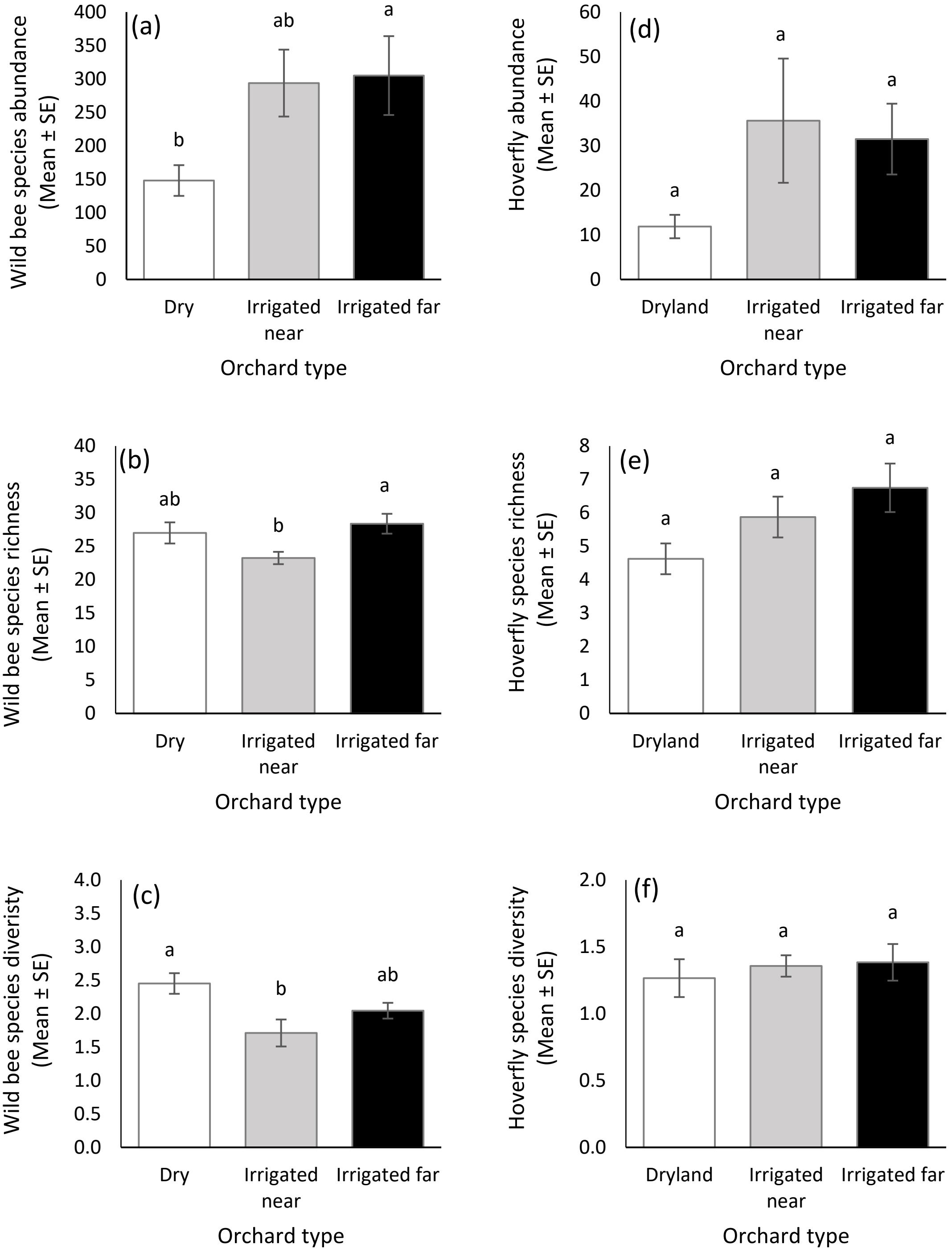


Figure 6. Abundance, species richness and species diversity of wild bees (a, b, c) and hoverflies (d, e, f) in the three orchard types: dry, irrigated-near and irrigated-far. Different letters denote significant differences among treatments (P < 0.05, HSD-Tukey test).

The NMDS and ANOSIM showed that the wild bee community composition of dry orchards was drastically different from that of irrigated orchards. However, no differences were found between the two types of irrigated orchards (ANOSIM: global R = 0.438, P = 0.001, stress = 0.200; Figure 7a). Species like *Panurgus dentipes* Latreille, *Osmia tricornis* Latreille, *Antophora* spp. and *Rodanthidium sticticum* Fabricius were abundant in the dry orchards, whereas their presence was incidental in the irrigated ones. In contrast, other species, such as *Lasioglossum* spp. (especially *Lasioglossum malachurum* Kirby) and *Halictus* spp. (especially *Halictus fulvipes* Klug), were dominant in the irrigated orchards but not in dry orchards (Table S5).

In contrast to wild bees, hoverfly abundance, richness and diversity did not differ across orchard types (Table 2, Figure 6d, e, f). We did find differences in hoverfly community composition (only between dry and irrigated-near orchards) (ANOSIM: global R = 0.132, P = 0.039, stress = 0.219; Figure 7b), but these differences were small compared to differences found for bees; Figure 7). Differences in composition were mostly attributable to *Epishyrphus balteatus* De Geer, which was most abundant in the irrigated-near orchards, and *Sphaerophoria scripta* L., which followed the opposite trend, being more abundant in the other two types of orchards (Table S6). In addition, *Platynochaetus setosus* Fabricius tended to be more abundant in the dry orchards. Contrary to what might be expected, species with saprophagous larvae (developing in water or decomposing plant matter) (*Eristalis* spp, *Eristalinus* spp.), were not particularly more abundant in irrigated orchards (Table S6). However, saprophagous species were poorly represented, as most individuals (ca. 75%) captured in the pan traps were aphidophagous.

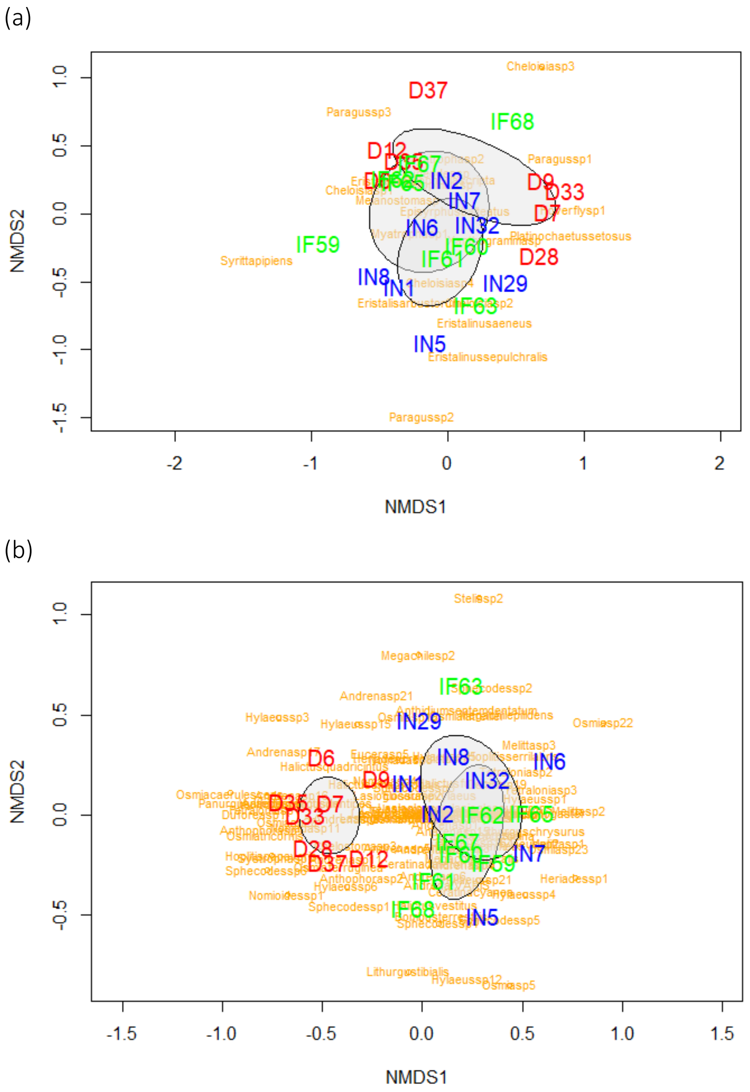


Figure 7. Graphical representation of non-metric multidimensional scaling (NMDS) analysis for wild bee (a) and hoverfly (b) species community composition in the three orchard types: dry (red), irrigated-near (blue) and irrigated-far (green).

### 3.4. Effects of local and landscape variables on the structure and composition of the pollinator community

The best-supported models for wild bee abundance included flower abundance and arable crop cover (Table 3). Higher values of flower abundance and arable crop cover were related to higher wild bee abundance. In the case of wild bee species diversity, natural and semi-natural habitat cover and flower abundance were included in the best-supported models: wild bee species diversity decreased with flower abundance, but increased with natural and semi-natural habitat cover. The best-supported models for wild bee species composition (scores of the first NMDS axis) included arable crop cover, natural and semi-natural habitat cover and flower composition. In other words, abundance of *Lasioglossum* spp. and *Halictus* spp. was positively associated with arable crop cover but negatively with natural and semi-natural habitat cover. On the other hand, species such as *O. tricornis* and *R. sticticum* showed an opposite relationship with these landscape variables. Bee species composition was also dependent on local flower species composition (scores of the first flower NMDS axis). In other words, *Lasioglossum* spp. and *Halictus* spp. were associated with flower species such as *T. officinale* and *T. repens* whereas *O. tricornis* and *R. sticticum* were associated with *D. erucoides.* None of the models explained wild bee species richness (Table 3).).

As for hoverflies, arable crop cover, habitat diversity and flower abundance were selected in the best models for hoverfly abundance. Hoverfly abundance was positively related to arable crop cover and habitat diversity, and negatively to flower abundance. None of the variables considered helped to explain hoverfly species richness, diversity or composition (Table 3).

Table 3. Best-supported models (ΔAICc<2) analyzing the effects of local (Flower abundance, Flower species richness and Flower composition) and landscape variables (Arable crop cover, habitat diversity and natural and semi-natural habitat cover) on abundance, diversity, richness and community composition of wild bees and hoverflies. Positive and negative signs between brackets denote the direction of the relationship.

| Response variable | Rank | Variables selected | Df | AICc | ΔAICc | Weight | $R^2$ |
|---|---|---|---|---|---|---|---|
| Wild bee abundance | 1 | Arable crop cover (+) + Flower abundance (+) | 5 | 37.2 | 0.00 | 0.585 | 0.52 |
| Wild bee species richness | 1 | | 3 | 142.8 | 0.00 | 0.279 | 0.06 |
| Wild bee species diversity | 1 | Natural and semi-natural habitat cover (+) + Flower abundance (-) | 5 | 34.1 | 0.00 | 0.294 | 0.49 |
| Wild bee species composition | 1 | Arable crop cover (+) + Natural and semi-natural habitat cover (-) + Flower composition (+) | 6 | -9.9 | 0 | 0.456 | 0.87 |
| Hoverfly abundance | 1 | Arable crop cover (+) | 4 | 228.0 | 0.00 | 0.246 | 0.29 |
| | 2 | Arable crop cover (+) + Habitat diversity (+) | 5 | 228.0 | 0.02 | 0.244 | 0.38 |
| | 3 | Arable crop cover (+) + Habitat diversity (+) + Flower abundance (-) | 6 | 228.1 | 0.09 | 0.235 | 0.46 |
| Hoverfly species richness | 1 | Arable crop cover (+) | 4 | 102.0 | 0.00 | 0.195 | 0.20 |
| | 2 | | 3 | 103.5 | 1.59 | 0.088 | 0.03 |
| | 3 | Habitat diversity (-) | 4 | 103.8 | 1.82 | 0.078 | 0.14 |
| | 4 | Arable crop cover (+) + Flower species richness (+) | 5 | 103.8 | 1.83 | 0.078 | 0.24 |
| Hoverfly species diversity | 1 | Flower species richness | 4 | 20.4 | 0.00 | 0.218 | 0.17 |
| | 2 | Natural and semi-natural habitat cover (-) + Flower species richness (+) | 5 | 21.5 | 1.17 | 0.122 | 0.24 |
| | 3 | | 3 | 21.9 | 1.54 | 0.101 | -1.21e-10 |
| | 4 | Flower species richness (+) + Habitat diversity (-) | 5 | 22.3 | 1.91 | 0.084 | 0.21 |
| Hoverfly species composition | 1 | | 3 | 37.7 | 0.00 | 0.148 | -1.49e-10 |
| | 2 | Natural and semi-natural habitat cover (+) + Habitat diversity (-) | 5 | 38.0 | 0.21 | 0.134 | 0.22 |
| | 3 | Arable crop cover (-) + Habitat diversity (-) | 5 | 38.1 | 0.32 | 0.126 | 0.22 |
| | 4 | Habitat diversity (-) | 4 | 38.1 | 0.34 | 0.125 | 0.10 |
| | 5 | Natural and semi-natural habitat cover (+) | 4 | 38.4 | 0.67 | 0.106 | 0.09 |
| | 6 | Flower composition (-) | 4 | 39.0 | 1.29 | 0.078 | 0.07 |
| | 7 | Arable crop cover (-) | 4 | 39.1 | 1.34 | 0.076 | 0.06 |
| | 8 | Flower composition (-) + Habitat diversity (-) | 5 | 39.7 | 1.93 | 0.057 | 0.16 |

## 4. Discussion

In agreement to our first hypothesis, the implementation of irrigation resulted in profound changes at the local scale. Irrigated orchards were characterized by a reduction of bare soil and an increase in flower abundance, especially in early spring and in summer (Figure S1). Differences in flower abundance in early spring can be explained by differences between orchard types in soil management. In contrast to irrigated orchards, dry orchards are tilled in early spring to avoid weed competition for water, drastically reducing plant cover. On the other hand, differences in flower abundance in summer are more directly attributable to irrigation. Increased water availability buffers the detrimental effects of the summer drought on plant growth and reproduction (van der Velde et al. 2010). Consequently, weeds in irrigated orchards can flower throughout the summer. Dry and irrigated orchards also differed in flower composition, hosting completely different flower assemblages. In addition to the tillage in early spring, dry almonds in the study area are usually tilled in autumn, before harvest. Autumn tillage causes buried seeds to be transported to the soil surface and receive enough light after weed removal, thus providing the adequate conditions for winter annuals, such as *D. erucoides*, to rapidly germinate and enter bloom during winter and into spring (Sans and Masalles 1995). By contrast, irrigated orchards are mown, which maintains a layer of green cover that provides a shady canopy under which *D. erucoides* seeds fail to germinate, thus losing their competitive edge (Sans and Masalles 1997). Under mowing regimes, plant species that tolerate cutting such as *T. officinale*, *T. repens* and other hemicryptophytes and creeping therophytes are favored.

In agreement with our second hypothesis, the implementation of irrigation involved an important loss in natural and semi-natural habitat cover at the landscape scale. This is in agreement with previous studies showing that farmland intensification entails a maximization of the cropping area at expense of natural and semi-natural habitats, which become progressively fragmented and eventually lost (Benton et al. 2003; Tscharntke et al. 2005). The implementation of irrigation also produced important changes in the identity of the main crops. In the irrigated zone, arable crops and irrigated orchards (including peaches, pears and apples in addition to almonds) replaced the dry almonds orchards and olive groves traditionally grown in the dryland zone. This has important consequences on floral resource availability. In the dryland zone, production of crop flowers is restricted to February-March (almond bloom). By contrast, in the irrigated zone production of crop flowers extends into April (other fruit trees), May (oilseed rape), and June-July (sunflowers, lucerne). Therefore, the above-mentioned differences between dry and irrigated orchards in local wild flower abundance and composition are exacerbated by differences in crop flower abundance at the landscape scale.

These environmental differences among orchard types at the local and landscape scales were accompanied by profound changes in pollinator community structure and composition (Hypothesis 3). Bee abundance was positively related to local flower abundance and to arable crop cover. Consequently, bees were more abundant in irrigated orchards. At the local level, flowering ground vegetation has been shown to enhance pollinator abundance in various orchard crops (Holzschuh et al. 2012; Klein et al. 2012; Rosa García and Miñarro 2014), including almonds (Saunders et al. 2013). As for the positive effect of arable crop cover, mass-flowering crops such as oilseed rape, sunflower and lucerne have been shown to enhance pollinator densities (Holzschuh et al. 2013; Rundlof et al. 2014; Westphal et al. 2003), although it is unclear whether this effect results from real increases in pollinator populations or simply from the temporary redistribution of pollinator populations temporarily attracted to highly rewarding hotspots (Beduschi et al. 2018; Holzschuh et al. 2016).

The higher bee abundance in irrigated orchards did not entail an increase in species richness. In fact, bee diversity was highest in dry orchards. High crop diversity has been found to benefit pollinators through complementarity in resource provisioning (Fahrig et al. 2015; González-Estébanez et al. 2011). However, in our study bee diversity was not related to habitat diversity and instead was positively associated with natural and semi-natural habitat cover (Kleijn et al. 2015).

Very importantly, species composition drastically differed between dry and irrigated orchards. Bee communities in irrigated orchards were characterized by a high abundance of two ground-nesting genera, *Lasioglossum* and *Halictus*. Many species in these two related genera (including the two most abundant species in our study, *L. malachurum* and *H. fulvipes*) are social (Westrich 1990), producing brood from spring to late summer. Due to their sociality and long activity period, these species require an abundant and continuous supply of floral resources throughout the season, which may explain why they were abundant in irrigated orchards but not in dry ones. By contrast, species typical of the dry orchards included four solitary taxa, *P. dentipes*, *O. tricornis*, *Anthophora* spp. and *R. sticticum.* With the possible exception of *R. sticticum* (Kasparek 2019), these species are univoltine (Vicens et al. 1994; Westrich 1990), and therefore have short nesting periods. *P. dentipes* nests underground, but *O. tricornis* and *Anthophora* spp. nest in clay embankments and in the study area are usually found in old adobe buildings, and *R. sticticum* nests in vacant snail shells and crevices in dry-stone walls. Although we did not quantify nesting resources, it is likely that a greater occurrence of old buildings and dry-stone walls in the dryland as opposed to the irrigation zone could explain the prevalence of these species in dry orchards. In addition*, O. tricornis* and *R. sticticum* have a circum-Mediterranean distribution (Kasparek 2019; Peters 1977). Bee composition was related to arable crop cover (strongly associated to irrigated orchards) and natural and semi-natural habitat cover (strongly associated to dry orchards). Bee composition was also related to flower composition, which, as mentioned, drastically differed between irrigated and dry orchards. Bee communities typically include a considerable number of oligolectic species (Cane and Sipes 2006; Torné-Noguera et al. 2014; Wcislo and Cane 1996; Westrich 1990). Consequently, flower composition is expected to have a strong influence on bee composition as found in other studies (Reverté et al. 2019; Schaffers et al. 2008; Torné-Noguera et al. 2014).

Immigration events are known to shape community composition (Fukami 2010), especially in highly mobile organisms such as bees. Therefore, we expected irrigated-near orchards to host a richer bee community with species typical of both dry and irrigated areas (Hypothesis 4). However, this expectation was not met, and bee communities of irrigated-near orchards were almost identical to those of irrigated-far orchards. Bee richness was not explained by any of the local and landscape variables measured, and bee composition was explained by a mixture of landscape variables (arable crop cover and natural and semi-natural habitat cover) and local variables (flower composition). Even if habitat diversity was (as expected) highest in irrigated-near than in irrigated-far orchards, differences between these two orchard types in arable crop cover were small and differences in natural and semi-natural cover almost non-existent. At the same time, these two types of orchard had almost identical flower composition. These results suggest that local conditions (flower composition and abundance) prevail over landscape ones concerning the determination of local bee communities, as found in a previous study on cavity-nesting bees and wasps (Osorio et al. 2015).

In contrast to wild bees, and in agreement with hypothesis 5, hoverfly community structure did not differ between the three types of orchards. Hoverfly richness, diversity and composition were not affected by the local and landscape variables that we measured. Hoverfly abundance, on the other hand, was positively related to habitat crop cover but, surprisingly and as opposed to other studies (Meyer et al. 2009), negatively associated to flower abundance. A possible explanation for this unexpected result is that other aspects of orchard management, such as a higher pesticide pressure, are outweighing the positive effects of enhanced floral resources. In fact, previous studies have observed positive effects of non-conventional agriculture on hoverfly abundance and richness (Dib et al. 2016; Klein et al. 2012; Power et al. 2016). We did find differences in hoverfly community composition, but they were not nearly as pronounced as with the bee community. Hoverflies do not build nests and are more generalized in their feeding requirements (Branquart and Hemptinne 2000) and probably for these reasons are considered to be less susceptible to landscape intensification than bees (Aguirre-Gutiérrez et al. 2015; Jauker et al. 2009). Our results confirm this view, as none of the local and landscape variables measured explained hoverfly richness, diversity or composition. In our study, most individuals captured (about 75%) were ubiquitous aphidophagous species, such as *E. balteatus*, *Eupeodes* spp. and *S. scripta.* We can only hypothesize that other non-measured factors, such as aphid availability (Perfect 1986), might have affected the distribution of hoverfly populations in our study. *P. setosus* has been associated to open areas with evergreen oaks (Speight 2014), which may explain its higher abundance in dry orchards, as these are surrounded by a greater cover of natural habitats.

To our knowledge, our study is the first to assess the effects of irrigation on pollinators. We demonstrate that conversion of dryland into irrigation land causes drastic changes in local and landscape environmental factors, which in turn result in a drastic transformation of bee communities. Irrigation has some beneficial effects on bee populations (enhanced abundance), but also some negative effects (reduced diversity). Most importantly, bee assemblages in irrigated orchards are drastically different from those in dry orchards. Probably mediated by an extended period of flower availability throughout the summer drought, irrigated orchards were dominated by social species with long activity periods. By contrast, dry orchards were dominated by solitary species with short activity periods. This outcome has very important consequences for bee conservation. Even if irrigated agricultural landscapes provide greater amounts of floral resources (both from wild and crop flowers), thus enhancing bee abundance, they favor only certain types of bee species. Ultimately, bee diversity and composition in our study were strongly dependent on natural and semi-natural habitat cover, which was negatively associated with irrigation. In addition, the expected beneficial effects of proximity to the dryland zone were not realized, and bee communities in irrigated-near orchards were virtually identical to those of irrigated-far orchards. This outcome suggests that local factors (flower composition) may be more important than landscape factors (proximity to the dryland zone) in explaining bee composition. We conclude that the conservation of original pollinator communities depends on the preservation of traditional agricultural systems along with natural habitats. This preservation is threatened in our study area, as a new irrigation system (Segarra-Garrigues canal; Territori 2019) has been recently built. Moreover, increasing surfaces of dryland are being turned into irrigation land so pressures on water resources keep escalating worldwide (FAO 2011; FAO 2017).

## 5. References

Aguirre-Gutiérrez J, Biesmeijer JC, van Loon EE, Reemer M, WallisDeVries MF, Carvalheiro LG (2015) Susceptibility of pollinators to ongoing landscape changes depends on landscape history. Divers Distrib 21:1129-1140 doi:10.1111/ddi.12350

Ashman TL et al. (2004) Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. Ecology 85:2408-2421 doi:10.1890/03-8024

Beduschi T, Kormann UG, Tscharntke T, Scherber C (2018) Spatial community turnover of pollinators is relaxed by semi-natural habitats, but not by mass-flowering crops in agricultural landscapes. Biol Conserv 221:59-66 doi:10.1016/j.biocon.2018.01.016

Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol Evol 18:182-188 doi:10.1016/s0169-5347(03)00011-9

Bosch J, Blas M (1994) Foraging behavior and pollinating efficiency of *Osmia cornuta* and *Apis mellifera* on almond (Hymenoptera, Megachilidae and Apidae). Appl Entomol Zool 29:1-9

Branquart E, Hemptinne JL (2000) Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphinae). Ecography 23:732-742 doi:10.1034/j.1600-0587.2000.230610.x

Brotons L, Manosa S, Estrada J (2004) Modelling the effects of irrigation schemes on the distribution of steppe birds in Mediterranean farmland. Biodivers Conserv 13:1039-1058 doi:10.1023/b:bioc.0000014468.71368.35

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York

Cane JH, Sipes S (2006) Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty. In: Waser NM, Ollerton J (eds) Plant-pollinator onteractions: from specialization to generalization. The University of Chicago Press, Chicago and London, Chaves MM et al. (2002) How plants cope with water stress in the field. Photosynthesis and growth. Ann Bot 89:907-916 doi:10.1093/aob/mcf105

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528-534 doi:10.1046/j.1365-2745.2000.00473.x

De Frutos A, Olea PP, Mateo-Tomás P (2015) Responses of medium- and large-sized bird diversity to irrigation in dry cereal agroecosystems across spatial scales. Agric Ecosyst Environ 207:141-152 doi:10.1016/j.agee.2015.04.009

Dib H, Sauphanor B, Capowiez Y (2016) Effect of management strategies on arthropod communities in the colonies of rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) in south-eastern France. Agric Ecosyst Environ 216:203-206 doi:10.1016/j.agee.2015.10.003

Fagúndez J, Olea PP, Tejedo P, Mateo-Tomás P, Gómez D (2016) Irrigation and Maize Cultivation Erode Plant Diversity Within Crops in Mediterranean Dry Cereal Agro-Ecosystems. Environ Manage 58:164-174 doi:10.1007/s00267-016-0691-5

Fahrig L et al. (2015) Farmlands with smaller crop fields have higher within-field biodiversity. Agric Ecosyst Environ 200:219-234 doi:10.1016/j.agee.2014.11.018

FAO (2011) The State of the World's Land and Water Resources for Food and Agriculture (SOLAW) - Managing systems at risk. Food and Agriculture Organization of the United Nations, Rome and Earthscan, London, UK

FAO (2017) The future of food and agriculture – Trends and challenges. FAO, Rome

Free JB (1993) Insect pollination of crops. 2nd edn. Academic Press, London

Fukami T (2010) Community assembly dynamics in space. In: Verhoef HA, Morin PJ (eds) Community ecology: Processes, models, and applications. Oxford Univ Press, Oxford and New York, pp 45–54

Gallai N, Salles JM, Settele J, Vaissiere BE (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol Econ 68:810-821 doi:10.1016/j.ecolecon.2008.06.014

Garibaldi LA et al. (2013) Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. Science 339:1608-1611 doi:10.1126/science.1230200

Gilbert F (1993) Hoverflies. Naturalists' Handbooks 5. 2nd edn. Richmond Publishing Co., Slough, Berkshire. doi:10.1080/00219266.1994.9655394

González-Estébanez FJ, García-Tejero S, Mateo-Tomás P, Olea PP (2011) Effects of irrigation and landscape heterogeneity on butterfly diversity in Mediterranean farmlands. Agric Ecosyst Environ 144:262-270 doi:10.1016/j.agee.2011.09.002

Goulson D, Nicholls E, Botias C, Rotheray EL (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347 doi:10.1126/science.1255957

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153:589-596 doi:10.1007/s00442-007-0752-9

Hanjra MA, Qureshi ME (2010) Global water crisis and future food security in an era of climate change. Food Policy 35:365-377 doi:10.1016/j.foodpol.2010.05.006

Holzschuh A et al. (2016) Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. Ecol Lett 19:1228-1236 doi:10.1111/ele.12657

Holzschuh A, Dormann CF, Tscharntke T, Steffan-Dewenter I (2013) Mass-flowering crops enhance wild bee abundance. Oecologia 172:477-484 doi:10.1007/s00442-012-2515-5

Holzschuh A, Dudenhoeffer J-H, Tscharntke T (2012) Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. Biol Conserv 153:101-107 doi:10.1016/j.biocon.2012.04.032

Hyvonen T, Salonen J (2002) Weed species diversity and community composition in cropping practices at two intensity levels - a six-year experiment. Plant Ecol 159:73-81 doi:10.1023/a:1015580722191

Inouye DW, Larson BMH, Ssymank A, Kevan PG (2015) Flies and flowers III: ecology of foraging and pollination. Journal of Pollination Ecology 16:115-133

International Nut and Dried Fruit Council (2018) Nuts & Dried Fruits. Statistical Yearbook 2018/2019. Statistical Yearbooks

Jauker F, Diekoetter T, Schwarzbach F, Wolters V (2009) Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecol 24:547-555 doi:10.1007/s10980-009-9331-2

José-María L, Armengot L, Blanco-Moreno JM, Bassa M, Sans FX (2010) Effects of agricultural intensification on plant diversity in Mediterranean dryland cereal fields. J Appl Ecol 47:832-840 doi:10.1111/j.1365-2664.2010.01822.x

Kasparek M (2019) Bees in the genus *Rhodanthidium*, a review and identification guide vol Supplement 24. Entomofauna,

Kleijn D, van Langevelde F (2006) Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic Appl Ecol 7:201-214 doi:10.1016/j.baae.2005.07.011

Kleijn D et al. (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nature Communications 6 doi:10.1038/ncomms8414

Klein A-M, Brittain C, Hendrix SD, Thorp R, Williams N, Kremen C (2012) Wild pollination services to California almond rely on semi-natural habitat. J Appl Ecol 49:723-732 doi:10.1111/j.1365-2664.2012.02144.x

Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proc Biol Sci 274:303-313 doi:10.1098/rspb.2006.3721

Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural intensification. Proc Natl Acad Sci U S A 99:16812-16816 doi:10.1073/pnas.262413599

Le Feon V et al. (2010) Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. Agric Ecosyst Environ 137:143-150 doi:10.1016/j.agee.2010.01.015

Superfícies y producciones anuales de cultivos (2019) Ministerio de Agricultura Pesca y Alimentación (MAPA). https://www.mapa.gob.es/es/estadistica/temas/estadisticas-agrarias/agricultura/superficies-producciones-anuales-cultivos/.

McGregor SE (1976) Insect pollination of cultivated crop plants. US Department of Agriculture, Washington, DC

Meyer B, Jauker F, Steffan-Dewenter I (2009) Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. Basic Appl Ecol 10:178-186 doi:10.1016/j.baae.2008.01.001

Miarnau X, Torguet L, Battle I, Romero A, Rovira M, Alegre S (2016) Comportamiento agronómico y productivo de las nuevas variedades de almendro. Fruticultura 49:42-59

Micke WC (1996) Almond production manual. University of California, Division of Agriculture and Natural Resources, Berkeley, USA

Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? Oikos 120:321-326 doi:10.1111/j.1600-0706.2010.18644.x

Osorio S, Arnan X, Bassols E, Vicens N, Bosch J (2015) Local and landscape effects in a host-parasitoid interaction network along a forest-cropland gradient. Ecol Appl 25:1869-1879 doi:10.1890/14-2476.1

Pérez-Fuertes O, García-Tejero S, Pérez Hidalgo N, Mateo-Tomàs P, Olea PP (2015) Irrigation effects on arthropod communities in Mediterranean cereal agro-ecosystems. Ann Appl Biol 167:236-249 doi:10.1111/aab.12223

Perfect TJ (1986) Irrigation as a factor influencing the management of agricultural pests. Philosophical Transactions of the Royal Society a-Mathematical Physical and Engineering Sciences 316:347-354 doi:10.1098/rsta.1986.0013

Peters DS (1977) Systematik und Zoogeographie der west-palaarktischen Arten von *Osmia* s. str., *Monosmia* und *Orientosmia*. Senckenb Biol 58:287-346

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345-353 doi:10.1016/j.tree.2010.01.007

Power EF, Jackson Z, Stout JC (2016) Organic farming and landscape factors affect abundance and richness of hoverflies (Diptera, Syrphidae) in grasslands. Insect Conserv Divers 9:244-253 doi:10.1111/icad.12163

Pretty J et al. (2018) Global assessment of agricultural system redesign for sustainable intensification. Nature Sustainability 1:441-446 doi:10.1038/s41893-018-0114-0

R Core Team (2016) A language and environment for statistical computing. R Foundation for Statistical Computing.

Reverté S et al. (2019) Spatial variability in a plant–pollinator community across a continuous habitat: high heterogeneity in the face of apparent uniformity. Ecography 42:1558-1568 doi:10.1111/ecog.04498

Rojo S, Gilbert F, Marcos-García MA, Nieto J, Mier MP (2003) A world review of predatory hoverflies (Diptera, Syrphidae: Syrphinae) and their prey. CIBIO Ediciones, Alicante, Spain

Rosa García R, Miñarro M (2014) Role of floral resources in the conservation of pollinator communities in cider-apple orchards. Agric Ecosyst Environ 183:118-126 doi:10.1016/j.agee.2013.10.017

Rundlof M, Persson AS, Smith HG, Bommarco R (2014) Late-season mass-flowering red clover increases bumble bee queen and male densities. Biol Conserv 172:138-145 doi:10.1016/j.biocon.2014.02.027

Rusch A et al. (2016) Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. Agric Ecosyst Environ 221:198-204 doi:10.1016/j.agee.2016.01.039

Sadeghi H, Gilbert F (2000) Aphid suitability and its relationship to oviposition preference in predatory hoverflies. J Anim Ecol 69:771-784 doi:10.1046/j.1365-2656.2000.00433.x

Sans FX, Masalles RM (1995) Phenological patterns in an arable land weed community related to disturbance. Weed Res 35:321-332 doi:10.1111/j.1365-3180.1995.tb01627.x

Sans FX, Masalles RM (1997) Demography of the arable weed *Diplotaxis erucoides* in central Catalonia, Spain. Canadian Journal of Botany-Revue Canadienne De Botanique 75:86-95 doi:10.1139/b97-011

Saunders ME, Luck GW, Mayfield MM (2013) Almond orchards with living ground cover host more wild insect pollinators. J Insect Conserv 17:1011-1025 doi:10.1007/s10841-013-9584-6

Schaffers AP, Raemakers IP, Sykora KV, Ter Braak CJF (2008) Arthropod assemblages are best predicted by plant species composition. Ecology 89:782-794 doi:10.1890/07-0361.1

Schweiger O et al. (2005) Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. J Appl Ecol 42:1129-1139 doi:10.1111/j.1365-2664.2005.01085.x

Speight MCD (2014) Species accounts of European Syrphidae (Diptera) vol 78. Syrph the net: The database of European Syrphidae (Diptera). Syrph the Net publications, Dublin

Stephen WP, Bohart GE, Torchio PF (1969) The Biology and External Morphology of Bees. Corvallis, Oregon State University

Territori (2019) Observació de projectes i debats terrtiorials de Catalunya/Canal Segarra-Garrigues. http://territori.scot.cat/cat/notices/2013/07/canal_segarra_garrigues_3218.php. Accessed 19/07/19 2019

Tilman D, Balzer C, Hill J, Befort BL (2011) Global food demand and the sustainable intensification of agriculture. Proc Natl Acad Sci U S A 108:20260-20264 doi:10.1073/pnas.1116437108

Torné-Noguera A, Rodrigo A, Arnan X, Osorio S, Barril-Graells H, da Rocha-Filho LC, Bosch J (2014) Determinants of Spatial Distribution in a Bee Community: Nesting Resources, Flower Resources, and Body Size. PLoS ONE 9 doi:10.1371/journal.pone.0097255

Traynor J (1993) Almond Pollination Handbook: For Almond Growers and for Beekeepers. Kovak Books,

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecol Lett 8:857-874 doi:10.1111/j.1461-0248.2005.00782.x

UNEP/MAP-Plan Bleu (2009) State of the Environment and Development in the Mediterranean. UNEP/MAP-Plan Bleu Athens

Ursúa E, Serrano D, Tella JL (2005) Does land irrigation actually reduce foraging habitat for breeding lesser kestrels? The role of crop types. Biol Conserv 122:643-648 doi:10.1016/j.biocon.2004.10.002

Fruit and Tree Nut Yearbook Tables/Tree Nuts/Table F-7 (2019) United States Department of Agriculture (USDA). https://www.ers.usda.gov/data-products/fruit-and-tree-nut-data/fruit-and-tree-nut-yearbook-tables/#Tree%20Nuts.

van der Velde M, Wriedt G, Bouraoui F (2010) Estimating irrigation use and effects on maize yield during the 2003 heatwave in France. Agric Ecosyst Environ 135:90-97 doi:10.1016/j.agee.2009.08.017

Vicens N, Bosch J, Blas M (1994) Biology and population structure in *Osmia tricornis* Latr. (Hymenoptera, Megachilidae). J Appl Entomol 117:300-306 doi:10.1111/j.1439-0418.1994.tb00738.x

Vila J (1992) Els Canals d'Urgell i la seva història. Diputació de Lleida, Lleida

Wcislo WT, Cane JH (1996) Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. Annu Rev Entomol 41:257-286 doi:10.1146/annurev.en.41.010196.001353

West PC et al. (2014) Leverage points for improving global food security and the environment. Science 345:325-328 doi:10.1126/science.1246067

Westphal C et al. (2008) Measuring bee diversity in different European habitats and biogeographical regions. Ecol Monogr 78:653-671 doi:10.1890/07-1292.1

Westphal C, Steffan-Dewenter I, Tscharntke T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. Ecol Lett 6:961-965 doi:10.1046/j.1461-0248.2003.00523.x

Westrich P (1990) Die Wildbienen Baden-Württembergs. Verlag Eugen Ulmer, Stuttgart, Germany

## Supplementary Materials

Table S1. Almond orchards surveyed.

| Orchard type | Orchard identification | Coordinates (UTM) Zone 31 | |
|---|---|---|---|
| Dry | D12 | X: 328858.70 | Y: 4597497.69 |
| | D28 | X: 306647.24 | Y: 4596580.13 |
| | D33 | X: 312650.91 | Y: 4595133.58 |
| | D35 | X: 304792.91 | Y: 4598590.76 |
| | D37 | X: 304905.55 | Y: 4594787.04 |
| | D6 | X: 330788.12 | Y: 4594457.43 |
| | D7 | X: 328315.53 | Y: 4598470.43 |
| | D9 | X: 324441.79 | Y: 4595496.49 |
| Irrigated-near | IN1 | X: 320776.58 | Y: 4597352.19 |
| | IN2 | X: 318926.14 | Y: 4599518.97 |
| | IN29 | X: 314515.82 | Y: 4598133.89 |
| | IN32 | X: 313277.30 | Y: 4599626.43 |
| | IN5 | X: 322273.24 | Y: 4601458.75 |
| | IN6 | X: 326131.60 | Y: 4601863.22 |
| | IN7 | X: 328868.84 | Y: 4605654.35 |
| | IN8 | X: 320591.50 | Y: 4599191.32 |
| Irrigated-far | IF59 | X: 306858.94 | Y: 4607516.12 |
| | IF60 | X: 309098.15 | Y: 4606869.46 |
| | IF61 | X: 310181.67 | Y: 4608220.10 |
| | IF62 | X: 309794.85 | Y: 4609240.20 |
| | IF63 | X: 314897.60 | Y: 4607832.81 |
| | IF65 | X: 327477.08 | Y: 4608814.38 |
| | IF67 | X: 322393.51 | Y: 4605354.39 |
| | IF68 | X: 320912.44 | Y: 4608682.23 |

Table S2. Number of pesticide and fertilizer applications and groundcover management interventions per year (mean ±SE) in the three orchard types (Dry, Irrigated-near and Irrigated far).

| Orchard type | Insecticide | Fungicide | Herbicide | Fertilizer | Tillage | Mowing |
|---|---|---|---|---|---|---|
| Dry | 1.38±0.18 | 0.88±0.17 | 1.38±0.17 | 0.50±0.33 | 2.75±0.25 | - |
| Irrigated-near | 3.69±1.02 | 5.23±1.70 | 2.62±1.39 | 1.46±0.65 | - | 3.15±0.50 |
| Irrigated-far | 10.78±2.27 | 6.89±1.11 | 5.22±0.91 | 0.78±0.24 | - | 2.22±0.56 |

Table S3. Spearman correlation coeficients and likelihood ratio (ρ) between the landscape variables at the 0.1, 0.5 and 1 km radius buffers. DryO = non-irrigated orchard cover; NatHab = natural and semi-natural habitat cover; HabDiversity = habitat diversity; UrbanHab = urban areas cover; IrrigO = irrigated orchard cover; ArableCrop = arable crop cover.

| Variable | by Variable | Spearman ρ | Prob>\|ρ\| |
|---|---|---|---|
| ArableCrop1km | HabDiversity1km | 0.0078 | 0.971 |
| IrrigO1km | HabDiversity1km | 0.2191 | 0.3036 |
| IrrigO1km | ArableCrop1km | 0.2565 | 0.2263 |
| DryO1km | HabDiversity1km | 0.0209 | 0.9228 |
| DryO1km | ArableCrop1km | -0.8686 | <.0001* |
| DryO1km | IrrigO1km | -0.5692 | 0.0037* |
| NatHab1km | HabDiversity1km | 0.0113 | 0.9582 |
| NatHab1km | ArableCrop1km | -0.6861 | 0.0002* |
| NatHab1km | IrrigO1km | -0.6522 | 0.0006* |
| NatHab1km | DryO1km | 0.7337 | <.0001* |
| UrbanHab1km | HabDiversity1km | 0.6304 | 0.0010* |
| UrbanHab1km | ArableCrop1km | 0.1339 | 0.5327 |
| UrbanHab1km | IrrigO1km | 0.1983 | 0.353 |
| UrbanHab1km | DryO1km | -0.1514 | 0.48 |
| UrbanHab1km | NatHab1km | -0.2417 | 0.2551 |
| HabDiversity0.5km | HabDiversity1km | 0.72 | <.0001* |
| HabDiversity0.5km | ArableCrop1km | 0.24 | 0.2586 |
| HabDiversity0.5km | IrrigO1km | 0.1009 | 0.6391 |
| HabDiversity0.5km | DryO1km | -0.1732 | 0.4183 |
| HabDiversity0.5km | NatHab1km | -0.0261 | 0.9037 |
| HabDiversity0.5km | UrbanHab1km | 0.4835 | 0.0167* |
| ArableCrop0.5km | HabDiversity1km | 0.1243 | 0.5626 |
| ArableCrop0.5km | ArableCrop1km | 0.9626 | <.0001* |
| ArableCrop0.5km | IrrigO1km | 0.2478 | 0.243 |
| ArableCrop0.5km | DryO1km | -0.8172 | <.0001* |
| ArableCrop0.5km | NatHab1km | -0.6887 | 0.0002* |
| ArableCrop0.5km | UrbanHab1km | 0.2878 | 0.1726 |
| ArableCrop0.5km | HabDiversity0.5km | 0.3643 | 0.0801 |
| IrrigO0.5km | HabDiversity1km | 0.2528 | 0.2333 |
| IrrigO0.5km | ArableCrop1km | 0.3321 | 0.1129 |
| IrrigO0.5km | IrrigO1km | 0.9503 | <.0001* |
| IrrigO0.5km | DryO1km | -0.5959 | 0.0021* |
| IrrigO0.5km | NatHab1km | -0.6235 | 0.0011* |
| IrrigO0.5km | UrbanHab1km | 0.1222 | 0.5693 |
| IrrigO0.5km | HabDiversity0.5km | 0.117 | 0.5862 |
| IrrigO0.5km | ArableCrop0.5km | 0.2782 | 0.1881 |
| DryO0.5km | HabDiversity1km | 0.0282 | 0.896 |
| DryO0.5km | ArableCrop1km | -0.7923 | <.0001* |
| DryO0.5km | IrrigO1km | -0.6312 | 0.0009* |
| DryO0.5km | DryO1km | 0.9357 | <.0001* |
| DryO0.5km | NatHab1km | 0.7448 | <.0001* |
| DryO0.5km | UrbanHab1km | -0.1681 | 0.4322 |
| DryO0.5km | HabDiversity0.5km | -0.0158 | 0.9414 |

| Variable | by Variable | Spearman ρ | Prob>\|ρ\| |
|---|---|---:|---:|
| DryO0.5km | ArableCrop0.5km | -0.7228 | <.0001* |
| DryO0.5km | IrrigO0.5km | -0.6711 | 0.0003* |
| NatHab0.5km | HabDiversity1km | -0.1661 | 0.438 |
| NatHab0.5km | ArableCrop1km | -0.5557 | 0.0048* |
| NatHab0.5km | IrrigO1km | -0.6061 | 0.0017* |
| NatHab0.5km | DryO1km | 0.5814 | 0.0029* |
| NatHab0.5km | NatHab1km | 0.9026 | <.0001* |
| NatHab0.5km | UrbanHab1km | -0.3165 | 0.1318 |
| NatHab0.5km | HabDiversity0.5km | -0.0113 | 0.9582 |
| NatHab0.5km | ArableCrop0.5km | -0.573 | 0.0034* |
| NatHab0.5km | IrrigO0.5km | -0.6156 | 0.0014* |
| NatHab0.5km | DryO0.5km | 0.5951 | 0.0022* |
| UrbanHab0.5km | HabDiversity1km | 0.5243 | 0.0085* |
| UrbanHab0.5km | ArableCrop1km | 0.2783 | 0.188 |
| UrbanHab0.5km | IrrigO1km | 0.2165 | 0.3095 |
| UrbanHab0.5km | DryO1km | -0.2698 | 0.2023 |
| UrbanHab0.5km | NatHab1km | -0.3209 | 0.1263 |
| UrbanHab0.5km | UrbanHab1km | 0.8791 | <.0001* |
| UrbanHab0.5km | HabDiversity0.5km | 0.4435 | 0.0300* |
| UrbanHab0.5km | ArableCrop0.5km | 0.3843 | 0.0637 |
| UrbanHab0.5km | IrrigO0.5km | 0.1779 | 0.4056 |
| UrbanHab0.5km | DryO0.5km | -0.3257 | 0.1204 |
| UrbanHab0.5km | NatHab0.5km | -0.3696 | 0.0755 |
| ArableCrop1km | HabDiversity1km | 0.0078 | 0.971 |
| IrrigO1km | HabDiversity1km | 0.2191 | 0.3036 |
| IrrigO1km | ArableCrop1km | 0.2565 | 0.2263 |
| DryO1km | HabDiversity1km | 0.0209 | 0.9228 |
| DryO1km | ArableCrop1km | -0.8686 | <.0001* |
| DryO1km | IrrigO1km | -0.5692 | 0.0037* |
| NatHab1km | HabDiversity1km | 0.0113 | 0.9582 |
| NatHab1km | ArableCrop1km | -0.6861 | 0.0002* |
| NatHab1km | IrrigO1km | -0.6522 | 0.0006* |
| NatHab1km | DryO1km | 0.7337 | <.0001* |
| UrbanHab1km | HabDiversity1km | 0.6304 | 0.0010* |
| UrbanHab1km | ArableCrop1km | 0.1339 | 0.5327 |
| UrbanHab1km | IrrigO1km | 0.1983 | 0.353 |
| UrbanHab1km | DryO1km | -0.1514 | 0.48 |
| UrbanHab1km | NatHab1km | -0.2417 | 0.2551 |
| HabDiversity0.1km | HabDiversity1km | -0.2461 | 0.2464 |
| HabDiversity0.1km | ArableCrop1km | -0.1374 | 0.522 |
| HabDiversity0.1km | IrrigO1km | -0.4678 | 0.0211* |
| HabDiversity0.1km | DryO1km | 0.2689 | 0.2038 |
| HabDiversity0.1km | NatHab1km | 0.4374 | 0.0326* |
| HabDiversity0.1km | UrbanHab1km | 0.0043 | 0.9839 |
| ArableCrop0.1km | HabDiversity1km | 0.1259 | 0.5578 |
| ArableCrop0.1km | ArableCrop1km | 0.4578 | 0.0245* |
| ArableCrop0.1km | IrrigO1km | 0.3785 | 0.0681 |
| ArableCrop0.1km | DryO1km | -0.4159 | 0.0433* |

| Variable | by Variable | Spearman ρ | Prob>\|ρ\| |
|---|---|---|---|
| ArableCrop0.1km | NatHab1km | -0.4771 | 0.0184* |
| ArableCrop0.1km | UrbanHab1km | 0.2104 | 0.3237 |
| ArableCrop0.1km | HabDiversity0.1km | -0.3099 | 0.1406 |
| IrrigO0.1km | HabDiversity1km | 0.324 | 0.1225 |
| IrrigO0.1km | ArableCrop1km | 0.5678 | 0.0038* |
| IrrigO0.1km | IrrigO1km | 0.6752 | 0.0003* |
| IrrigO0.1km | DryO1km | -0.7155 | <.0001* |
| IrrigO0.1km | NatHab1km | -0.6647 | 0.0004* |
| IrrigO0.1km | UrbanHab1km | 0.4094 | 0.0470* |
| IrrigO0.1km | HabDiversity0.1km | -0.2826 | 0.1809 |
| IrrigO0.1km | ArableCrop0.1km | 0.1364 | 0.5252 |
| DryO0.1km | HabDiversity1km | 0.0174 | 0.9357 |
| DryO0.1km | ArableCrop1km | 0.2452 | 0.2481 |
| DryO0.1km | IrrigO1km | -0.0157 | 0.9421 |
| DryO0.1km | DryO1km | -0.248 | 0.2425 |
| DryO0.1km | NatHab1km | -0.24 | 0.2586 |
| DryO0.1km | UrbanHab1km | 0.2122 | 0.3196 |
| DryO0.1km | HabDiversity0.1km | -0.0748 | 0.7284 |
| DryO0.1km | ArableCrop0.1km | 0.3028 | 0.1503 |
| DryO0.1km | IrrigO0.1km | 0.0546 | 0.8 |
| NatHab0.1km | HabDiversity1km | -0.1129 | 0.5994 |
| NatHab0.1km | ArableCrop1km | -0.7829 | <.0001* |
| NatHab0.1km | IrrigO1km | -0.6031 | 0.0018* |
| NatHab0.1km | DryO1km | 0.8789 | <.0001* |
| NatHab0.1km | NatHab1km | 0.7225 | <.0001* |
| NatHab0.1km | UrbanHab1km | -0.3062 | 0.1456 |
| NatHab0.1km | HabDiversity0.1km | 0.0929 | 0.6658 |
| NatHab0.1km | ArableCrop0.1km | -0.4271 | 0.0374* |
| NatHab0.1km | IrrigO0.1km | -0.8364 | <.0001* |
| NatHab0.1km | DryO0.1km | -0.2342 | 0.2707 |
| UrbanHab0.1km | HabDiversity1km | 0.3809 | 0.0663 |
| UrbanHab0.1km | ArableCrop1km | 0.2565 | 0.2263 |
| UrbanHab0.1km | IrrigO1km | 0.2974 | 0.1582 |
| UrbanHab0.1km | DryO1km | -0.2289 | 0.282 |
| UrbanHab0.1km | NatHab1km | -0.2948 | 0.162 |
| UrbanHab0.1km | UrbanHab1km | 0.5026 | 0.0123* |
| UrbanHab0.1km | HabDiversity0.1km | -0.1661 | 0.438 |
| UrbanHab0.1km | ArableCrop0.1km | 0.6884 | 0.0002* |
| UrbanHab0.1km | IrrigO0.1km | 0.287 | 0.1739 |
| UrbanHab0.1km | DryO0.1km | 0.3583 | 0.0856 |
| UrbanHab0.1km | NatHab0.1km | -0.3308 | 0.1143 |

Table S4. Number of open flowers of each plant species counted in the survey quadrats per orchard type. Data pooled across the six surveys.

| | | Orchard type | | | |
|---|---|---|---|---|---|
| **Plant family** | **Species** | **Dry** | **Irrigated-near** | **Irrigated-far** | **Total** |
| Amaryllidaceae | *Narcissus assoanus* | | 20 | | 20 |
| Apiaceae | *Foeniculum vulgare* | | | 15 | 15 |
| Apiaceae | *Torilis arvensis* | | 60 | | 60 |
| Apocynaceae | *Vinca* sp. | | 13 | | 13 |
| Asteraceae | *Anacyclus clavatus* | 416 | 87 | 6 | 509 |
| Asteraceae | *Atractylis cancellata* | 1 | | | 1 |
| Asteraceae | *Calendula arvensis* | 73 | 6 | | 79 |
| Asteraceae | *Carduus tenuiflorus* | 88 | 6 | 6 | 100 |
| Asteraceae | *Carthamus lanatus* | 2 | | | 2 |
| Asteraceae | *Centaurea aspera* | 8 | 21 | | 29 |
| Asteraceae | *Crepis* sp. | 245 | 935 | 70 | 1250 |
| Asteraceae | *Echinops ritro* | 1 | | 20 | 21 |
| Asteraceae | *Helichrysum stoechas* | 204 | 55 | 44 | 303 |
| Asteraceae | *Mantisalca salamantica* | 9 | | | 9 |
| Asteraceae | *Pallenis spinosa* | 32 | 17 | 7 | 56 |
| Asteraceae | *Picris echioides* | | 25 | | 25 |
| Asteraceae | *Picris hieracioides* | | | 37 | 37 |
| Asteraceae | *Picris* sp. | | | 6 | 6 |
| Asteraceae | *Senecio vulgaris* | 718 | 2247 | 1 | 2966 |
| Asteraceae | *Silybum marianum* | | | 21 | 21 |
| Asteraceae | *Sonchus* sp. | 20 | 145 | 4 | 169 |
| Asteraceae | *Taraxacum officinale* | | 434 | 63 | 497 |
| Boraginaceae | *Echium vulgare* | | | 185 | 185 |
| Boraginaceae | *Heliotropium europaeum* | | | 6 | 6 |
| Boraginaceae | *Lithodora fruticosa* | 234 | | 5 | 239 |
| Boraginaceae | *Lithospermum fruticosum* | 131 | | | 131 |
| Boraginaceae | *Neatostema apulum* | 177 | | | 177 |
| Brassicaceae | *Alyssum minus* | 95 | 10 | | 105 |
| Brassicaceae | *Biscutella auriculata* | 14 | | | 14 |
| Brassicaceae | *Capsella bursa-pastoris* | | 515 | 635 | 1150 |
| Brassicaceae | *Cardamine hirsuta* | | 54 | 19 | 73 |
| Brassicaceae | *Cardaria draba* | | 10 | 99 | 109 |
| Brassicaceae | *Diplotaxis erucoides* | 1367 | 515 | 390 | 2272 |
| Brassicaceae | *Eruca vesicaria* | 279 | | | 279 |
| Brassicaceae | *Moricandia arvensis* | 5 | 66 | | 71 |
| Brassicaceae | *Rapistrum rugosum* | | 25 | 8 | 33 |
| Brassicaceae | *Sinapis alba* | 40 | | | 40 |
| Brassicaceae | *Sinapis arvensis* | 12 | 5 | 100 | 117 |
| Brassicaceae | *Sisymbrium irio* | 6 | 45 | 304 | 355 |
| Caryophyllaceae | *Cerastium glomeratum* | | | 949 | 949 |
| Caryophyllaceae | *Silene rubella* | 12 | | | 12 |
| Caryophyllaceae | *Silene vulgaris* | | 19 | | 19 |
| Caryophyllaceae | *Stellaria media* | 223 | 52 | 2077 | 2352 |
| Chenopodiaceae | *Salsola kali* | | | 2 | 2 |
| Cistaceae | *Helianthemum apenninum* | 110 | | | 110 |

| | | Orchard type | | | |
|---|---|---|---|---|---|
| Plant family | Species | Dry | Irrigated-near | Irrigated-far | Total |
| Cistaceae | *Helianthemum syriacum* | 2 | 1 | | 3 |
| Convolvulaceae | *Calystegia sepium* | | | 13 | 13 |
| Convolvulaceae | *Convolvulus arvensis* | | 218 | 160 | 378 |
| Convolvulaceae | *Convolvulus lineatus* | 1 | | | 1 |
| Convolvulaceae | *Ipomoea* | | 1 | | 1 |
| Crassulaceae | *Sedum sediforme* | 127 | 40 | | 167 |
| Dipsacaceae | *Scabiosa atropurpurea* | | 44 | 238 | 282 |
| Euphorbiaceae | *Euphorbia helioscopia* | 111 | 77 | 36 | 224 |
| Euphorbiaceae | *Euphorbia sp.* | | 4 | 8 | 12 |
| Geraniaceae | *Erodium ciconium* | 6 | | | 6 |
| Geraniaceae | *Erodium cicutarium* | 265 | 7 | 33 | 305 |
| Geraniaceae | *Erodium malacoides* | 37 | | 45 | 82 |
| Geraniaceae | *Erodium* sp. | 135 | 5 | | 140 |
| Geraniaceae | *Geranium molle* | 3 | | 26 | 29 |
| Geraniaceae | *Geranium* sp. | 227 | 2 | | 229 |
| Globulariaceae | *Globularia alypum* | 113 | | | 113 |
| Guttiferae | *Hypericum perforatum* | 16 | 23 | | 39 |
| Labiateae | *Lamium amplexicaule* | 62 | 56 | 435 | 553 |
| Labiateae | *Lamium purpureum* | 21 | 59 | 773 | 853 |
| Labiateae | *Lamium* sp. | | | 9 | 9 |
| Labiateae | *Lavandula angustifolia* | 3 | | | 3 |
| Labiateae | *Phlomis lychnitis* | 6 | | | 6 |
| Labiateae | *Rosmarinus officinalis* | 3616 | | | 3616 |
| Labiateae | *Sideritis scordioides* | 7 | | | 7 |
| Labiateae | *Teucrium polium* | | | 28 | 28 |
| Labiateae | *Teucrium polium sbsp capitatum* | 225 | | | 225 |
| Labiateae | *Teucrium polium subsp. gnaphalodes* | 9 | | | 9 |
| Labiateae | *Thymus vulgaris* | 13 | 54 | 11 | 78 |
| Leguminoseae | *Coronilla minima* | 18 | | 31 | 49 |
| Leguminoseae | *Coronilla scorpioides* | 9 | | | 9 |
| Leguminoseae | *Dorycnium pentaphyllum* | | 52 | 8 | 60 |
| Leguminoseae | *Hedysarum boveanum* | 1 | | | 1 |
| Leguminoseae | Other | 4 | | | 4 |
| Leguminoseae | *Medicago lupulina* | 12 | 1402 | 533 | 1947 |
| Leguminoseae | *Medicago minima* | 127 | | | 127 |
| Leguminoseae | *Medicago orbicularis* | | 85 | | 85 |
| Leguminoseae | *Medicago sativa* | | 203 | 28 | 231 |
| Leguminoseae | *Melilotus indicus* | 62 | | | 62 |
| Leguminoseae | *Melilotus officinalis* | | 20 | 13 | 33 |
| Leguminoseae | *Ononis spinosa* | | 24 | 1 | 25 |
| Leguminoseae | *Spartium junceum* | 191 | | | 191 |
| Leguminoseae | *Trifolium pratense* | | 86 | 199 | 285 |
| Leguminoseae | *Trifolium repens* | | 450 | 376 | 826 |
| Leguminoseae | *Trifolium sp.* | | 58 | | 58 |
| Leguminoseae | *Vicia peregrina* | 14 | | | 14 |

| | | Orchard type | | | |
|---|---|---|---|---|---|
| Plant family | Species | Dry | Irrigated-near | Irrigated-far | Total |
| Leguminoseae | *Vicia sativa* | | 10 | | 10 |
| Liliaceae | *Iris pseudacorus* | | | 1 | 1 |
| Liliaceae | *Muscari neglectum* | 28 | 6 | | 34 |
| Linaceae | *Linum suffruticosum* | | | 15 | 15 |
| Malvaceae | *Malva aegyptia* subsp. *Trifida* *(Malva stipulacea)* | 39 | | | 39 |
| Malvaceae | *Malva sylvestris* | 3 | 335 | 109 | 447 |
| Onagraceae | *Epilobium hirsutum* | | | 11 | 11 |
| Papaveraceae | *Fumaria officinalis* | 179 | 271 | 430 | 880 |
| Papaveraceae | *Fumaria parviflora* | | 25 | 10 | 35 |
| Papaveraceae | *Hypecoum procumbens* | 27 | | | 27 |
| Papaveraceae | *Papaver rhoeas* | 8 | 24 | 24 | 56 |
| Papaveraceae | *Platycapnos spicata* | 8 | | | 8 |
| Plantaginaceae | *Plantago albicans* | 11 | | | 11 |
| Plantaginaceae | *Plantago coronopus* | | 27 | 30 | 57 |
| Plantaginaceae | *Plantago lanceolata* | | 45 | 222 | 267 |
| Plumbaginaceae | *Limonium hibericum* | | | 1314 | 1314 |
| Portulacaceace | *Portulaca oleracea* | | | 59 | 59 |
| Primulaceae | *Anagallis arvensis* | 59 | 4 | 43 | 106 |
| Primulaceae | *Coris monspeliensis* | 170 | | | 170 |
| Ranunculaceae | *Clematis vitalba* | | | 800 | 800 |
| Ranunculaceae | *Delphinium peregrinum* | 7 | | | 7 |
| Resedaceae | *Reseda lutea* | 3 | | | 3 |
| Rosaceae | *Potentilla reptans* | 2 | 305 | 2 | 309 |
| Rosaceae | *Prunus dulcis* | 39 | | | 39 |
| Rosaceae | *Rubus* sp. | | 20 | 133 | 153 |
| Rubiaceae | *Galium lucidum* | | 40 | | 40 |
| Rubiaceae | *Sherardia arvensis* | 69 | 200 | 40 | 309 |
| Scrophulariaceae | *Veronica persica* | 86 | 2101 | 1396 | 3583 |
| Scrophulariaceae | *Veronica* sp. | | 134 | | 134 |
| Solanaceae | *Solanum nigrum* | | | 81 | 81 |
| Verbenaceae | *Verbena officinalis* | | 7 | | 7 |
| Grand Total | | 10703 | 11912 | 12803 | 35418 |

Table S5. Wild bee species list, abundance and relative abundance per orchard type and nesting substrate.

| | | Orchard type | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Dry | | Irrigated-near | | Irrigated-far | | | |
| Genus | Species | Abundance | Relative abundance | Abundance | Relative abundance | Abundance | Relative abundance | Total | Nesting substrate |
| Amegilla | Amegilla sp1 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Ground |
| Andrena | Andrena sp1 | 12 | 1.01 | 15 | 0.64 | 36 | 1.48 | 63 | Ground |
| Andrena | Andrena sp10 | 44 | 3.72 | 13 | 0.55 | 33 | 1.35 | 90 | Ground |
| Andrena | Andrena sp11 | 6 | 0.51 | 0 | 0.00 | 10 | 0.41 | 16 | Ground |
| Andrena | Andrena sp12 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Ground |
| Andrena | Andrena sp13 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Ground |
| Andrena | Andrena sp14 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Ground |
| Andrena | Andrena sp15 | 7 | 0.59 | 18 | 0.77 | 26 | 1.07 | 51 | Ground |
| Andrena | Andrena sp16 | 2 | 0.17 | 0 | 0.00 | 0 | 0.00 | 2 | Ground |
| Andrena | Andrena sp17 | 2 | 0.17 | 0 | 0.00 | 0 | 0.00 | 2 | Ground |
| Andrena | Andrena sp18 | 0 | 0.00 | 0 | 0.00 | 2 | 0.08 | 2 | Ground |
| Andrena | Andrena sp19 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Ground |
| Andrena | Andrena sp2 | 1 | 0.08 | 3 | 0.13 | 7 | 0.29 | 11 | Ground |
| Andrena | Andrena sp20 | 2 | 0.17 | 0 | 0.00 | 0 | 0.00 | 2 | Ground |
| Andrena | Andrena sp21 | 1 | 0.08 | 0 | 0.00 | 1 | 0.04 | 2 | Ground |
| Andrena | Andrena sp3 | 2 | 0.17 | 7 | 0.30 | 24 | 0.98 | 33 | Ground |
| Andrena | Andrena sp4 | 1 | 0.08 | 3 | 0.13 | 17 | 0.70 | 21 | Ground |
| Andrena | Andrena sp5 | 12 | 1.01 | 2 | 0.09 | 16 | 0.66 | 30 | Ground |
| Andrena | Andrena sp6 | 3 | 0.25 | 1 | 0.04 | 9 | 0.37 | 13 | Ground |
| Andrena | Andrena sp7 | 1 | 0.08 | 2 | 0.09 | 0 | 0.00 | 3 | Ground |
| Andrena | Andrena sp8 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Ground |
| Andrena | Andrena sp9 | 5 | 0.42 | 0 | 0.00 | 2 | 0.08 | 7 | Ground |
| Andrena | Andrena? SEVERAL | 1 | 0.08 | 1 | 0.04 | 5 | 0.20 | 7 | Ground |
| Anthidium | Anthidium septemdentatum | 0 | 0.00 | 2 | 0.09 | 5 | 0.20 | 7 | Snail shells, rocks |
| Anthidium | Rodanthidium sticticum | 65 | 5.49 | 1 | 0.04 | 2 | 0.08 | 68 | Snail shells, rocks |
| Anthophora | Anthophora sp1 | 7 | 0.59 | 0 | 0.00 | 0 | 0.00 | 7 | Enbankments, adobe walls |
| Anthophora | Anthophora sp2 | 2 | 0.17 | 1 | 0.04 | 1 | 0.04 | 4 | Enbankments, adobe walls |
| Anthophora | Anthophora sp3 | 2 | 0.17 | 0 | 0.00 | 0 | 0.00 | 2 | Enbankments, adobe walls |
| Anthophora | Anthophora sp4 | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Enbankments, adobe walls |
| Anthophora | Anthophora sp5 | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Enbankments, adobe walls |
| Anthophora | Anthophora sp6 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Enbankments, adobe walls |
| Bombus | Bombus terrestris | 2 | 0.17 | 1 | 0.04 | 3 | 0.12 | 6 | Abandoned rodent nests |
| Ceratina | Ceratina cucurbitina | 2 | 0.17 | 5 | 0.21 | 10 | 0.41 | 17 | Sof pith stems |
| Ceratina | Ceratina cyanea | 1 | 0.08 | 1 | 0.04 | 5 | 0.20 | 7 | Sof pith stems |
| Ceratina | Ceratina dallatorreana | 1 | 0.08 | 4 | 0.17 | 9 | 0.37 | 14 | Sof pith stems |
| Chelostoma | Chelostoma sp1 | 14 | 1.18 | 9 | 0.38 | 8 | 0.33 | 31 | Small cavities |
| Chelostoma | Chelostoma sp2 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities |
| Chelostoma | Chelostoma sp3 | 25 | 2.11 | 1 | 0.04 | 15 | 0.61 | 41 | Small cavities |
| Duforea | Duforea sp1 | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Ground |
| Eucera | Eucera sp1 | 14 | 1.18 | 20 | 0.85 | 12 | 0.49 | 46 | Ground |

| | | Orchard type | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Dry | | Irrigated-near | | Irrigated-far | | | |
| Genus | Species | Abundance | Relative abundance | Abundance | Relative abundance | Abundance | Relative abundance | Total | Nesting substrate |
| Eucera | Eucera sp2 | 14 | 1.18 | 12 | 0.51 | 16 | 0.66 | 42 | Ground |
| Eucera | Eucera sp3 | 0 | 0.00 | 13 | 0.55 | 25 | 1.02 | 38 | Ground |
| Eucera | Eucera sp4 | 0 | 0.00 | 8 | 0.34 | 7 | 0.29 | 15 | Ground |
| Eucera | Eucera sp5 | 15 | 1.27 | 10 | 0.43 | 9 | 0.37 | 34 | Ground |
| Eucera | Eucera sp6 | 46 | 3.89 | 19 | 0.81 | 31 | 1.27 | 96 | Ground |
| Evylaeus | Lasioglossum evylaeus | 59 | 4.98 | 40 | 1.70 | 70 | 2.87 | 169 | Ground |
| Evylaeus | Lasioglossum malachurum | 54 | 4.56 | 893 | 38.00 | 947 | 38.81 | 1894 | Ground |
| Halictus | Halictus fulvipes | 12 | 1.01 | 60 | 2.55 | 92 | 3.77 | 164 | Ground |
| Halictus | Halictus pollinosus | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Ground |
| Halictus | Halictus quadricintus | 2 | 0.17 | 0 | 0.00 | 0 | 0.00 | 2 | Ground |
| Halictus | Halictus scabiosae | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Ground |
| Halictus | Halictus smaragdulus | 14 | 1.18 | 8 | 0.34 | 9 | 0.37 | 31 | Ground |
| Halictus | Halictus subauratus | 1 | 0.08 | 2 | 0.09 | 6 | 0.25 | 9 | Ground |
| Halictus | Halictus vestitus | 0 | 0.00 | 0 | 0.00 | 4 | 0.16 | 4 | Ground |
| Halictus | Halicuts gemmeus | 0 | 0.00 | 1 | 0.04 | 1 | 0.04 | 2 | Ground |
| Halictus | Halictus vestitus | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Ground |
| Heriades | Heriades crenulatus | 1 | 0.08 | 0 | 0.00 | 1 | 0.04 | 2 | Small cavities |
| Heriades | Heriades sp1 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Small cavities |
| Hoplitis | Hoplitis adunca | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities |
| Hoplitis | Hoplitis serrilabris? | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Small cavities? |
| Hoplitis | Hoplitis papaveris | 2 | 0.17 | 0 | 0.00 | 0 | 0.00 | 2 | Ground and small cavities |
| Hoplitis | Hoplitis sp1 | 0 | 0.00 | 2 | 0.09 | 0 | 0.00 | 2 | Small cavities? |
| Hylaeus | Hylaeus sp1 | 0 | 0.00 | 3 | 0.13 | 3 | 0.12 | 6 | Small cavities? |
| Hylaeus | Hylaeus sp10 | 0 | 0.00 | 0 | 0.00 | 2 | 0.08 | 2 | Small cavities? |
| Hylaeus | Hylaeus sp11 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Small cavities? |
| Hylaeus | Hylaeus sp12 | 0 | 0.00 | 1 | 0.04 | 1 | 0.04 | 2 | Small cavities? |
| Hylaeus | Hylaeus sp13 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Small cavities? |
| Hylaeus | Hylaeus sp14 | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Small cavities? |
| Hylaeus | Hylaeus sp15 | 1 | 0.08 | 1 | 0.04 | 0 | 0.00 | 2 | Small cavities? |
| Hylaeus | Hylaeus sp16 | 0 | 0.00 | 1 | 0.04 | 1 | 0.04 | 2 | Small cavities? |
| Hylaeus | Hylaeus sp17 | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Small cavities? |
| Hylaeus | Hylaeus sp18 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Small cavities? |
| Hylaeus | Hylaeus sp19 | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Small cavities? |
| Hylaeus | Hylaeus sp2 | 0 | 0.00 | 2 | 0.09 | 2 | 0.08 | 4 | Small cavities? |
| Hylaeus | Hylaeus sp20 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities? |
| Hylaeus | Hylaeus sp21 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities? |
| Hylaeus | Hylaeus sp3 | 2 | 0.17 | 0 | 0.00 | 0 | 0.00 | 2 | Small cavities? |
| Hylaeus | Hylaeus sp4 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities? |
| Hylaeus | Hylaeus sp5 | 0 | 0.00 | 1 | 0.04 | 1 | 0.04 | 2 | Small cavities? |
| Hylaeus | Hylaeus sp6 | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Small cavities? |
| Hylaeus | Hylaeus sp7 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities? |
| Hylaeus | Hylaeus sp8 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities? |
| Hylaeus | Hylaeus sp9 | 4 | 0.34 | 0 | 0.00 | 0 | 0.00 | 4 | Small cavities? |
| Lasioglossum | Lasioglossum lasioglossum BIG | 28 | 2.36 | 152 | 6.47 | 179 | 7.34 | 359 | Ground |

| | | Orchard type | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Dry | | Irrigated-near | | Irrigated-far | | | |
| Genus | Species | Abundance | Relative abundance | Abundance | Relative abundance | Abundance | Relative abundance | Total | Nesting substrate |
| Lasioglossum | Lasioglossum lasioglossum MEDIUM | 44 | 3.72 | 122 | 5.19 | 126 | 5.16 | 292 | Ground |
| Lasioglossum | Lasioglossum lasioglossum SMALL | 414 | 34.97 | 808 | 34.38 | 563 | 23.07 | 1785 | Ground |
| Lithurgus | Lithurgus chrysurus | 0 | 0.00 | 0 | 0.00 | 6 | 0.25 | 6 | Dead wood |
| Lithurgus | Lithurgus tibialis | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Dead wood |
| Megachile | Megachile apicalis | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities |
| Megachile | Megachile pilidens | 0 | 0.00 | 4 | 0.17 | 0 | 0.00 | 4 | Small cavities |
| Megachile | Megachile sp1 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities? |
| Megachile | Megachile sp2 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Small cavities? |
| Melitta | Melitta sp1 | 0 | 0.00 | 0 | 0.00 | 5 | 0.20 | 5 | Ground |
| Melitta | Melitta sp2 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Ground |
| Melitta | Melitta sp3 | 0 | 0.00 | 1 | 0.04 | 1 | 0.04 | 2 | Ground (cleptoparasite) |
| Nomada | Nomada sp1 | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Ground (cleptoparasite) |
| Nomada | Nomada sp10 | 0 | 0.00 | 1 | 0.04 | 1 | 0.04 | 2 | Ground (cleptoparasite) |
| Nomada | Nomada sp11 | 2 | 0.17 | 0 | 0.00 | 1 | 0.04 | 3 | Ground (cleptoparasite) |
| Nomada | Nomada sp2 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Ground (cleptoparasite) |
| Nomada | Nomada sp3 | 1 | 0.08 | 1 | 0.04 | 0 | 0.00 | 2 | Ground (cleptoparasite) |
| Nomada | Nomada sp4 | 2 | 0.17 | 2 | 0.09 | 0 | 0.00 | 4 | Ground (cleptoparasite) |
| Nomada | Nomada sp5 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Ground (cleptoparasite) |
| Nomada | Nomada sp6 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Ground (cleptoparasite) |
| Nomada | Nomada sp7 | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Ground (cleptoparasite) |
| Nomada | Nomada sp8 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Ground (cleptoparasite) |
| Nomada | Nomada sp9 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Ground (cleptoparasite) |
| Nomioides | Nomioides sp1 | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Ground |
| Osmia | Osmia andrenoides | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Snail shells |
| Osmia | Osmia caerulescens | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Small cavities |
| Osmia | Osmia cornuta | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities, adobe walls |
| Osmia | Osmia ferruginea | 7 | 0.59 | 0 | 0.00 | 12 | 0.49 | 19 | Snail shells |
| Osmia | Osmia latreillei | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Small cavities |
| Osmia | Osmia leaiana / melanogaster | 0 | 0.00 | 3 | 0.13 | 5 | 0.20 | 8 | Small cavities |
| Osmia | Osmia rufohirta | 1 | 0.08 | 16 | 0.68 | 1 | 0.04 | 18 | Snail shells |
| Osmia | Osmia sp18 | 0 | 0.00 | 2 | 0.09 | 0 | 0.00 | 2 | Small cavities ? |
| Osmia | Osmia sp19 | 0 | 0.00 | 2 | 0.09 | 2 | 0.08 | 4 | Small cavities ? |
| Osmia | Osmia tricornis | 85 | 7.18 | 0 | 0.00 | 1 | 0.04 | 86 | Small cavities, adobe walls |
| Osmia | Osmia sp22 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Small cavities ? |
| Osmia | Osmia sp23 | 0 | 0.00 | 2 | 0.09 | 0 | 0.00 | 2 | Small cavities ? |

| | | Orchard type | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Dry | | Irrigated-near | | Irrigated-far | | | |
| Genus | Species | Abundance | Relative abundance | Abundance | Relative abundance | Abundance | Relative abundance | Total | Nesting substrate |
| Osmia | Osmia sp5 | 0 | 0.00 | 1 | 0.04 | 0 | 0.00 | 1 | Small cavities ? |
| Osmia | Osmia sp9 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities ? |
| Osmia | Osmia tricornis | 6 | 0.51 | 0 | 0.00 | 0 | 0.00 | 6 | Small cavities, adobe walls |
| Osmia | Osmia aurulenta | 0 | 0.00 | 2 | 0.09 | 0 | 0.00 | 2 | Snail shells |
| Panurginus | Panurginus sp1 | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Ground |
| Panurgus | Panurgus arctos | 2 | 0.17 | 0 | 0.00 | 0 | 0.00 | 2 | Ground |
| Panurgus | Panurgus dentipes | 90 | 7.60 | 9 | 0.38 | 4 | 0.16 | 103 | Ground |
| Sphecodes | Sphecodes sp1 | 1 | 0.08 | 0 | 0.00 | 1 | 0.04 | 2 | Ground (cleptoparasite) |
| Sphecodes | Sphecodes sp2 | 0 | 0.00 | 0 | 0.00 | 3 | 0.12 | 3 | Ground (cleptoparasite) |
| Sphecodes | Sphecodes sp3 | 1 | 0.08 | 1 | 0.04 | 0 | 0.00 | 2 | Ground (cleptoparasite) |
| Sphecodes | Sphecodes sp4 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Ground (cleptoparasite) |
| Sphecodes | Sphecodes sp5 | 0 | 0.00 | 1 | 0.04 | 2 | 0.08 | 3 | Ground (cleptoparasite) |
| Sphecodes | Sphecodes sp6 | 1 | 0.08 | 0 | 0.00 | 0 | 0.00 | 1 | Ground (cleptoparasite) |
| Stelis | Stelis sp1 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities (cleptoparasite) |
| Stelis | Stelis sp2 | 0 | 0.00 | 0 | 0.00 | 1 | 0.04 | 1 | Small cavities (cleptoparasite) |
| Systropha | Systropha sp1 | 8 | 0.68 | 0 | 0.00 | 0 | 0.00 | 8 | Ground |
| Tetralonia | Tetralonia sp1 | 12 | 1.01 | 0 | 0.00 | 0 | 0.00 | 12 | Ground |
| Tetralonia | Tetralonia sp2 | 2 | 0.17 | 16 | 0.68 | 12 | 0.49 | 30 | Ground |
| Tetralonia | Tetralonia sp3 | 0 | 0.00 | 2 | 0.09 | 5 | 0.20 | 7 | Ground |
| Total | | 1184 | 100.00 | 2350 | 100.00 | 2440 | 100.00 | 5974 | |

Table S6. Hoverfly species list, abundance and relative abundance per orchard type and larval feeding guild.

| | | Orchard type | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Dry | | Irrigated-near | | Irrigated-far | | | |
| Genus | Species | Abundance | Relative abundance | Abundance | Relative abundance | Abundance | Relative abundance | Total | Larval feeding guild |
| Cheloisia | Cheloisia sp1 | 0 | 0.00 | 0 | 0.00 | 2 | 0.79 | 2 | Phytophagous |
| Cheloisia | Cheloisia sp2 | 0 | 0.00 | 0 | 0.00 | 2 | 0.79 | 2 | Phytophagous |
| Cheloisia | Cheloisia sp3 | 0 | 0.00 | 0 | 0.00 | 1 | 0.40 | 1 | Phytophagous |
| Cheloisia | Cheloisia sp4 | 0 | 0.00 | 0 | 0.00 | 1 | 0.40 | 1 | Phytophagous |
| Chrysotoxum | Chrysotoxum sp. | 0 | 0.00 | 0 | 0.00 | 1 | 0.40 | 1 | Aphidophagous (root aphids) |
| Episyrphus | Episyrphus balteatus | 9 | 9.47 | 98 | 34.39 | 21 | 8.33 | 128 | Aphidophagous |
| Eristalinus | Eristalinus aeneus | 3 | 3.16 | 3 | 1.05 | 2 | 0.79 | 8 | Saprophagous |
| Eristalinus | Eristalinus sepulchralis | 0 | 0.00 | 0 | 0.00 | 1 | 0.40 | 1 | Saprophagous |
| Eristalis | Eristalis arbustorum | 0 | 0.00 | 8 | 2.81 | 4 | 1.59 | 12 | Saprophagous |
| Eristalis | Eristalis tenax | 4 | 4.21 | 4 | 1.40 | 10 | 3.97 | 18 | Saprophagous |
| Eupeodes | Eupeodes sp. | 44 | 46.32 | 109 | 38.25 | 99 | 39.29 | 252 | Aphidophagous |
| Heliophilus | Heliophilus sp. | 0 | 0.00 | 6 | 2.11 | 3 | 1.19 | 9 | Saprophagous |
| Melanostoma | Melanostoma sp. | 2 | 2.11 | 8 | 2.81 | 18 | 7.14 | 28 | Aphidophagous |
| Myatropha | Myatropha sp1 | 0 | 0.00 | 1 | 0.35 | 0 | 0.00 | 1 | Saprophagous |
| Myatropha | Myatropha sp2 | 0 | 0.00 | 1 | 0.35 | 0 | 0.00 | 1 | Saprophagous |
| Paragus | Paragus sp1 | 2 | 2.11 | 1 | 0.35 | 1 | 0.40 | 4 | Aphidophagous |
| Paragus | Paragus sp2 | 0 | 0.00 | 1 | 0.35 | 0 | 0.00 | 1 | Aphidophagous |
| Paragus | Paragus sp3 | 1 | 1.05 | 0 | 0.00 | 0 | 0.00 | 1 | Aphidophagous |
| Platynochaetus | Platynochaetus setosus | 7 | 7.37 | 4 | 1.40 | 1 | 0.40 | 12 | ? |
| Sphaerophoria | Sphaerophoria scripta | 19 | 20.00 | 35 | 12.28 | 74 | 29.37 | 128 | Aphidophagous |
| Syritta | Syritta pipiens | 0 | 0.00 | 0 | 0.00 | 1 | 0.40 | 1 | Saprophagous |
| Xanthogramma | Xanthogramma sp. | 0 | 0.00 | 5 | 1.75 | 9 | 3.57 | 14 | Aphidophaogus (root aphids) |
| Unknown | Hoverfly sp1 | 4 | 4.21 | 1 | 0.35 | 1 | 0.40 | 6 | - |
| Grand Total | | 95 | 100.00 | 285 | 100.00 | 252 | 100.00 | 632 | |

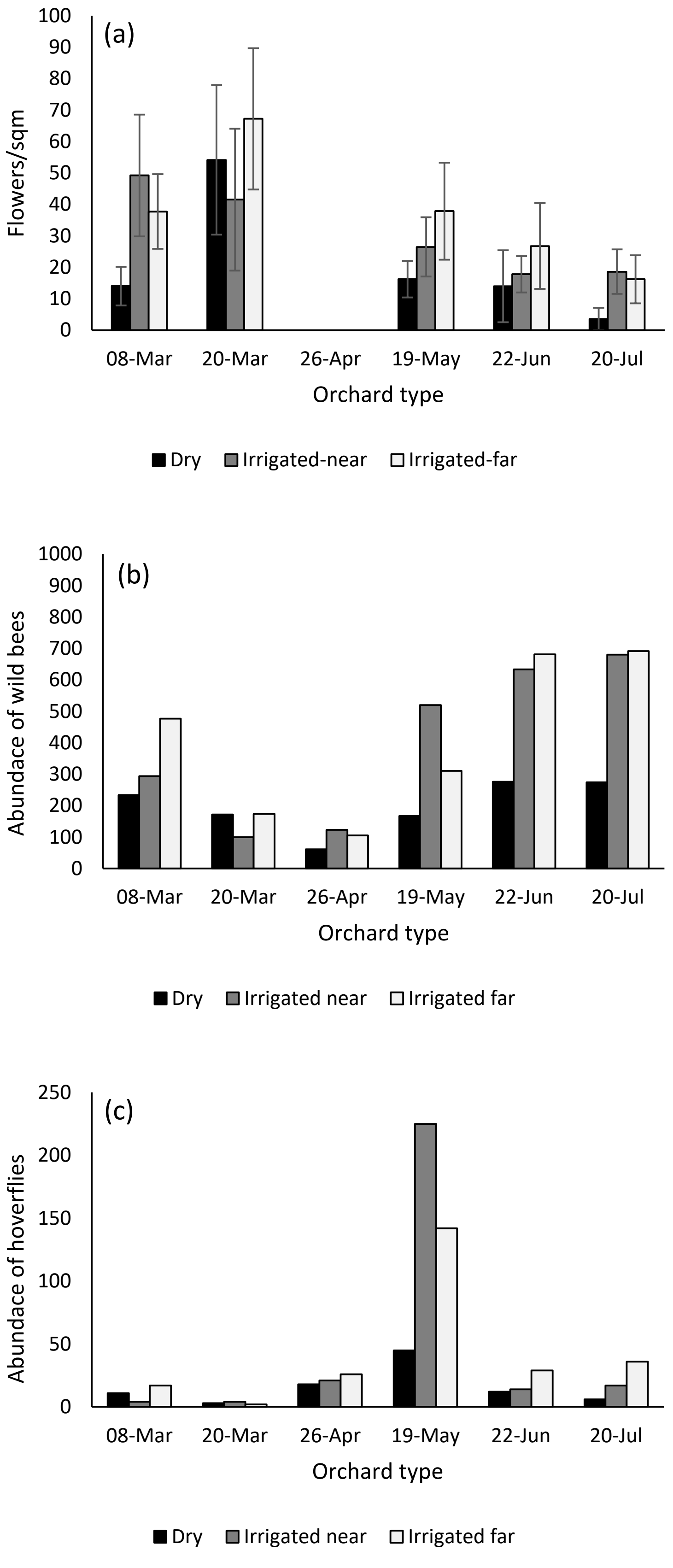
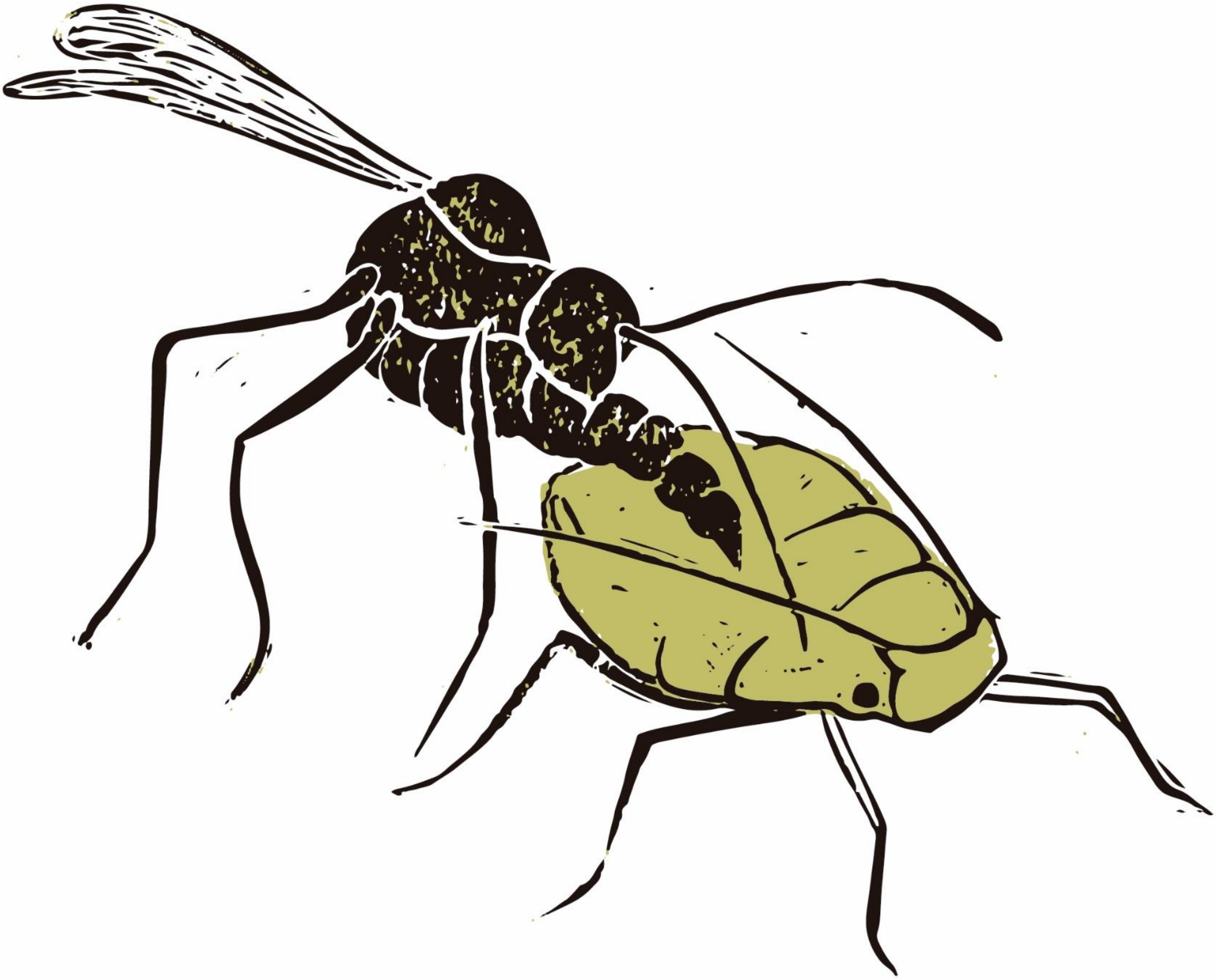


Figure S1. Abundance of flowers (a), wild bees (b) and hoverflies (c) in the three orchard types by date.

## Chapter 2

# The contribution of surrounding margins in the promotion of natural enemies in Mediterranean apple orchards

Neus Rodríguez-Gasol, Jesús Avilla, Yahana Aparicio, Judit Arnó, Rosa Gabarra,
Jordi Riudavets, Simó Alegre, Jaume Lordan and Georgina Alins



The content of this chapter has been published in
Insects (2019) 10(5):148. doi: 10.3390/insects10050148

## Abstract

(1) Habitat management can enhance beneficial arthropod populations and provide ecosystem services such as biological control. However, the implementation of ecological infrastructures inside orchards has a number of practical limitations. Therefore, planting/growing insectary plants in the margins of orchards should be considered as an alternative approach. (2) Here, we assessed the efficacy of a flower margin composed by four insectary plant species (*Achillea millefolium*, *Lobularia maritima*, *Moricandia arvensis* and *Sinapis alba*), which was placed on an edge of four Mediterranean apple orchards to attract natural enemies of two apple tree aphids (*Dysaphis plantaginea* and *Eriosoma lanigerum*). We also characterized the natural enemies present in the aphid colonies. (3) Our results show that the implementation of a flower margin at the edge of apple orchards attracts predators (Syrphidae, Thysanoptera, Araneae, Heteroptera, Coleoptera) and parasitoids. Parasitoids are the main natural enemies present in aphid colonies in our area. (4) The implementation of the flower margins successfully recruited natural enemy populations, and the presence of parasitoids in the surroundings of the orchards increased the parasitism of *D. plantaginea* colonies.

**Keywords**: agroecological infrastructures, biological control, flower strip, natural enemies, Syrphidae, parasitoids, *Eriosoma lanigerum*, *Dysaphis plantaginea*

# 1. Introduction

Agriculture faces the challenge of responding to social demands for healthier food and more environmentally friendly practices while maintaining crop yields (Foley et al. 2011; Wratten et al. 2012). Consequently, agricultural practices that reduce reliance on conventional inputs and enhance ecosystem services, such as pollination or biological control, have received much research attention in recent years (Garibaldi et al. 2017). Habitat management has the potential to meet both agronomic and ecological objectives through the regulation of insect pest populations, often by intensifying the impact of the natural enemy community and through the preservation and promotion of biodiversity (Altieri and Nicholls 2004; Gurr et al. 2017; Simon et al. 2010). In this regard, fruit orchards are ideal agricultural landscapes in which to implement habitat management practices. In contrast to arable and vegetable crops, fruit trees remain in the orchard for several seasons, so there is a higher probability of conservation biological control succeeding (Boller et al. 2004; Gurr et al. 2017; Simon et al. 2010). Additionally, orchards are usually subjected to high pesticide use due to pest control (Simon et al. 2010). Therefore, there is a need to explore other viable pest management options.

Aphids are major pests of apple (*Malus domestica* Borkh.) orchards under temperate climates, where they feed on the phloem of trees and cause an economic impact (Rousselin et al. 2017). Several aphid species can infest apple trees, of which the two most damaging are the rosy apple aphid (RAA) *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) and the woolly apple aphid (WAA) *Eriosoma lanigerum* Hausmann (Hemiptera: Aphididae) (Barbagallo et al. 2017). RAA infestations affect the aerial parts of trees, causing leaf rolling, shoot twisting, chlorosis and deformation of fruits. Severe infestations can even affect the development of flower buds the following year and reduce overall tree vigor (Bonnemaison 1959; Rousselin et al. 2017). WAA infestations can occur both on the aerial and subterranean woody tissue of the trees, also causing deformations and galling on the roots, trunk, branches and twigs (Asante et al. 1993; Brown et al. 1995).

The presence of ecological infrastructures can favor the pollinator and natural enemy community and even improve the biological control of aphids, through the provision of shelter and food (pollen, nectar or alternative prey) (Boller et al. 2004; Gurr et al. 2017; Holland et al. 2016). These infrastructures should be positioned as close as possible to the orchards in order to achieve maximum conservation biological control (Boller et al. 2004). However, the implementation of ecological infrastructures, such as flower strips, inside the orchards has major practical limitations due to the shredding of pruning waste, the mechanical control of groundcover, and water scarcity. After tree pruning, the cuttings, which are not removed and remain on the ground, are shredded in order to facilitate access to the orchards and the decomposition of the wood. In addition, the groundcover of orchards is usually mown/shredded to control the height of weeds and reduce competition for water and nutrients (Fitzgerald and Solomon 2004). Therefore, auxiliary plants that are highly competitive or that grow too high are not suitable for orchard alleys (Fitzgerald and

Solomon 2004; Gontijo et al. 2013). With regard to water scarcity, the placement of flower resources in Mediterranean orchards presents an additional challenge, as the plants must be adapted to low water regimes, therefore limiting species selection. Hence, flower margins on the edges of orchards emerge as an alternative approach to alleys because they do not need to be mowed/shredded and facilitate irrigation management systems.

The implementation of flower strips in orchard margins has been shown to have positive effects on the population of aphid natural enemies (Albert et al. 2017; Gontijo et al. 2013; Miñarro and Prida 2013; Odorizzi Santos et al. 2018). However, to the best of our knowledge, no study has found an effect of the implemented flower strips in the abundance of natural enemies on aphid colonies. For this reason, a better understanding of the relationships between the natural enemies present in surroundings and the ones present in the aphid colonies is crucial to improve aphid biological control.

Thus, the objectives of our work were to: (1) assess the attractiveness of a specific flower margin to auxiliary fauna, (2) characterize the natural enemies of RAA and WAA present in Mediterranean apple orchards and (3) assess the influence of the surrounding margins in the RAA and WAA natural enemy populations present in the aphid colonies.

## 2. Materials and Methods

### 2.1. Study Area, Orchards and Treatments

The current study was conducted in 2015 and 2016 in the fruit tree-growing area of Lleida (Catalonia, NE Spain). This area is characterized by a semi-arid Mediterranean climate, with a mean annual rainfall of 350 mm.

Five organic apple orchards were surveyed for the study: orchards E1, E3, E4 and E5 in 2015 and orchards E1, E3, E5 and E6 in 2016 (Table S1). During the period of the study, the following pesticides were applied: azadirachtin (sprayed between the end of March and April to control RAA), granulosis virus (applied from May to August to control the codling moth (*Cydia pomonella* L. (Lepidoptera: Tortricidae)), and lime sulfur (applied from March to June to control apple scab (*Venturia inaequalis* Cooke)).

In each orchard, two treatments were compared: a spontaneous margin and an implemented flower margin. The two margins were subdivided in four plots of 1 × 1 m, which were spaced 1 m from each other. Both margins were at least 16 m apart from each other and placed 5 m from the first tree of the row, perpendicularly to the rows (Figure 1).

The flower margin was formed by four insectary plant species: *Achillea millefolium* L. (Compositae), *Lobularia maritima* L. (Brassicaceae), *Moricandia arvensis* L. (Brassicaceae) and *Sinapis alba* L. (Brassicaceae) (Table S2). These plants were planted in plastic boxes of 50 cm length, 35.5 cm width and 31 cm height, and each box contained seven plants of one single species. Each plot had four boxes, one for each insectary species, which position was randomized per plot (Figure 1). The insectary plants were drip irrigated at the same frequency as the apple trees and the spontaneous weeds present in these boxes were removed fortnightly. The flower margins were established during the second half of March and were dismantled in October in both years.

The spontaneous margin was composed by native flora commonly found in the apple orchards of the area, which was mainly Gramineae (Table S3). In order to characterize the species present in both margins, fortnightly in 2015, the Braun-Blanquet cover-abundance scale (Braun-Blanquet 1932) was used, and the phenology of each species was annotated.

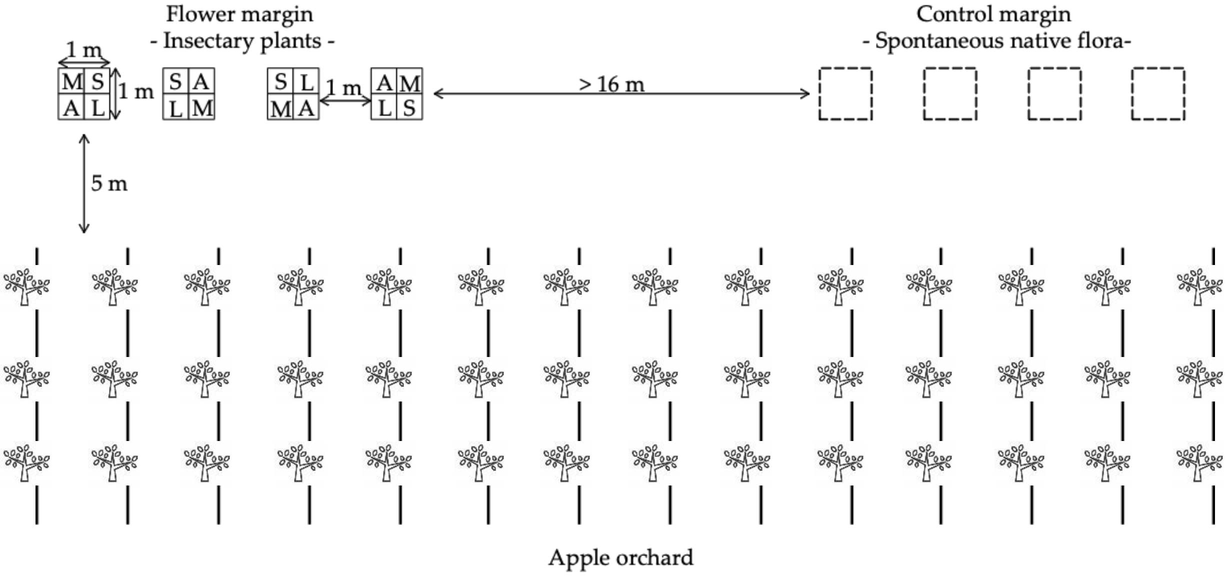


Figure 1. Setup of the experiment. A = *A. millefolium*, L = *L. maritima*, M = *M. arvensis*, S = *S. alba*.

### 2.2. Attractiveness of the Flower Margin to Natural Enemies and Phytophagous Insects

Visual samplings were performed to estimate the attractiveness of the margins to adult hoverflies. For three minutes per plot (12 minutes per margin), an observer counted the number of adult hoverflies hovering above or touching the flower of the insectary or spontaneous plant species present in a plot. The observations were conducted under favorable weather conditions: sunny to lightly overcast days, with no or low wind speed (0–4.2 m/s) and temperature above 15 °C.

Beating tray samplings (BTS) were conducted to estimate the attractiveness of the margins to natural enemies (except adult hoverflies) and phytophagous insects. BTS consisted of three consecutive beats with the hand. In each plot, four BTS were taken after visual observations had been made. In the flower margin, each BTS corresponded to an insectary plant species, while in the control margin the beatings were made on flowering species whenever possible. In the latter case, the plant species where the BTS was conducted were noted. The arthropods falling as a result of the BTS were collected on a white tray (24 × 35 cm) and classified into the following groups: predators

(Araneae, predatory Thysanoptera, predatory Coleoptera, predatory Heteroptera, Syrphidae larvae, Chrysopidae, Cecidomyiidae, Trombidiidae and Forficulidae), parasitoids (both adults and mummies), and phytophagous insects (Aphididae, phytophagous Thysanoptera and phytophagous Heteroptera). Individuals were returned to the margin after visual identification to family or order in the case of spiders (Table S4).

Both visual samplings and BTS were conducted fortnightly from April (petal fall) to September in 2015 and 2016. In both years, the samplings were performed on coincident weeks.

### 2.3. Assessment of *D. plantaginea*, *E. lanigerum* and Their Natural Enemies

To assess the presence of RAA, WAA and their natural enemies, 400 shoots per orchard (10 shoots per tree in 40 randomly selected trees, placed up to 30 m away from the margins) were revised. The shoots that were infested by any of the two mentioned aphids and were examined for natural enemies, which were removed after being quantified and identified. The number of aphids was not quantified since the assessment of biological control was not among our objectives. Then, the shoots were cut, kept in plastic glasses with fabric lids and left at the laboratory (at 20 °C temperature and 12:12 h (L:D)) for two weeks to allow unseen immature stages of the insects to develop. Then, the natural enemies were quantified and identified with the same criteria as in the other samplings (Table S4). In addition, in the case of parasitoids found in the RAA colonies, a sample of 16 individuals was randomly selected and identified to genera and species level, when possible with taxonomic keys by Barahoei et al., (Barahoei et al. 2012) and Rakhshani et al., (Rakhshani et al. 2012). These samplings were conducted fortnightly in 2016.

### 2.4. Data Analysis

In order to evaluate the attractiveness of the margins to natural enemies and phytophagous insects, two analysis were performed: a weekly and a global analysis. For the weekly analysis, the average of the four plots per treatment and orchard was calculated. For the global analysis, the average of those 13 weeks per treatment and orchard was calculated. In both analysis, data from the visual observations and the BTS were referred as the number of arthropods per area and time (number/(1 $m^2$ × 3 min)), and the number of arthropods per area (number/1 $m^2$), respectively. Response variables were modeled using linear mixed effect models where year and treatment were fixed factors and orchard was a random factor. Each orchard was considered as a replication (n = 8). Interaction between factors was considered. Residual analysis was performed to ensure that model assumptions were met and if necessary, data were log transformed.

In order to describe the natural enemies present in RAA and WAA colonies, the beneficial arthropods sampled from the aphid colonies in each week were referred to as the number of natural enemies per colony.

In order to assess the relationship between the arthropods found in the control and the implemented margin, correlations were run between these groups of arthropods: adult hoverflies recorded in the visual observations and predators, parasitoids and phytophagous insects captured in the BTS. In this case, all data from 2015 and 2016 were used (April to September). In contrast, for the correlations between the arthropods found in the margins and the ones present in the aphid colonies, only the dates when aphids were found in the orchard were used for the analysis. In the case of the RAA colonies, data from April to June of 2016 was used. Correlations were run between: the percentage of shoots infested with RAA, the number of Syrphidae predators, non-Syrphidae predators and parasitoids per infested shoot, the number of adult hoverflies assessed in the visual observations of the margins and the number of predators, parasitoids and phytophagous insects collected by the BTS of the margins. In the case of the WAA colonies, data from May to August of 2016 was used to run the correlations between the percentage of shoots infested by WAA, the number of predators and parasitoids per infested shoot, and the number of predators, parasitoids and phytophagous insects found in the flower and control margin. Data collected per week and orchard was analyzed by Spearman correlation coefficients.

A significance level of $p \leq 0.05$ was considered for all the analysis. Data were analyzed using the JMP statistical software package (Version 13; SAS Institute Inc., Cary, NC, USA).

# 3. Results

## 3.1. Attractiveness of the Margins to Natural Enemies and Phytophagous Insects

During the whole sampling period, a total of 2011 visits by hoverflies were counted in the visual observations, and 4772 predatory arthropods, 1024 parasitoid wasps and 11,778 phytophagous insects were found in the BTS.

Overall, the most abundant predators captured in the BTS were Heteroptera (46.7%), Araneae (34.2%), Thysanoptera (8.9%) and Coleoptera (6.3%). Among the predatory Heteroptera, Anthocoridae and Miridae were the most abundant and most of the predatory Coleoptera found belonged to Coccinellidae. Other groups like Trombidiidae (1.9%), Chrysopidae (1.0%), Syrphidae larvae (0.8%), Forficulidae (0.3%) and Cecidomyiidae (0.1%) were scarce and were grouped as "Other predators" for the statistical analysis. Parasitoids captured in the BTS could not be identified to lower taxonomic groups. The phytophagous insects found in the margins were mainly Aphididae (45.6%), phytophagous Tysanoptera (41.9%), and Pentatomidae (12.3%). The presence of phytophagous Colepotera was sporadic (0.2%).

Data of the average number of arthropods per week and orchard recorded from the different sampling methods were pooled for the whole sampling period to assess the attractiveness of the flower margin to the diverse arthropod groups. Overall, the mean number of adult hoverflies was significantly higher in the flower margin than in the control margin (Table 1). Neither significant interactions nor significant differences between years were found in the case of the adult hoverflies (Table 1). In the case of the BTS, significant quantitative interactions between year and treatment were only found in the case of predatory Coleoptera. Also, significant differences between years were found in the case of predatory Thysanoptera and predatory Coleoptera, which were more abundant in 2015 and 2016, respectively (data not shown). The mean number of the groups of natural enemies ("All predators", "Thysanoptera", "Araneae", "Heteroptera", "Coleoptera" and "Parasitoid wasps") was significantly higher in the flower margin in all the cases except from the group "Other predators" (Table 1). Neither significant interactions nor significant differences between years were found for the phytophagous insects captured in the margin, and these were more abundant in the flower margin than in the spontaneous one (Table 1).

Table 1. Number of natural enemies (± Standard Error) assessed during all the sampling period in the visuals observations (VO, number/1 m$^2$ × 3 min) and the beating tray samplings (BTS, number/1 m$^2$) of the margins.

| Type of Sampling | Arthropod Group | Treatment | | | | Year | | Year*Treatment | |
|---|---|---|---|---|---|---|---|---|---|
| | | Control Margin ± SE | Flower Margin ± SE | F1,12 | *p* | $F_{1,12}$ | *p* | $F_{1,12}$ | *p* |
| VO | Adult hoverflies | 0.384 ± 0.077 | 4.242 ± 0.463 | 109.052 | <0.001 | 0.968 | 0.348 | 3.182 | 0.114 |
| BTS | All predators | 0.724 ± 0.122 | 2.203 ± 0.332 | 39.991 | **<0.001** | 1.323 | 0.278 | 0.773 | 0.405 |
| | Thysanoptera | 0.035 ± 0.012 | 0.224 ± 0.039 | 42.784 | **<0.001** | 6.663 | **0.026** | 2.811 | 0.128 |
| | Araneae | 0.321 ± 0.049 | 0.679 ± 0.140 | 6.340 | **0.034** | 0.175 | 0.684 | 0.314 | 0.589 |
| | Heteroptera | 0.280 ± 0.114 | 1.085 ± 0.307 | 17.482 | **<0.001** | 4.676 | 0.057 | 0.230 | 0.644 |
| | Coleoptera | 0.045 ± 0.009 | 0.139 ± 0.048 | 6.100 | **0.038** | 7.036 | **0.023** | 5.506 | **0.046** |
| | Other predators | 0.044 ± 0.015 | 0.074 ± 0.007 | 3.810 | 0.081 | 2.003 | 0.185 | 3.446 | 0.094 |
| | Parasitoid wasps | 0.161 ± 0.015 | 0.623 ± 0.083 | 30.017 | **<0.001** | 0.282 | 0.606 | 0.799 | 0.394 |
| | Phytophagous insects | 2.828 ± 0.604 | 4.66 ± 0.598 | 7.655 | **0.025** | 1.654 | 0.229 | 0.002 | 0.968 |

* Test statistics (F-value (F)) and p (likelihood ratio) are shown. Significant *p* values (*p* <0.05) are shown in bold.

In addition, data were analyzed by week in order to discern temporality in the attractiveness of the margins to arthropods. In the case of the adult hoverflies recorded during the visual observations, these were significantly higher in the flower margin than in the control margin most of the weeks (Figure 2a). In the case of the BTS, the number of predators, parasitoids and phytophagous insects was also significantly higher in the flower margin for most of the weeks. Predators were significantly higher in the flower margin from June to September (Figure 2b). In contrast, parasitoid wasps (Figure 2c) In contrast, parasitoid wasps (Figure 2d) were more abundant in the flower margin during the middle of the sampling season. Statistically significant interactions between treatment and year, and significant differences between years were occasional (Table S5).

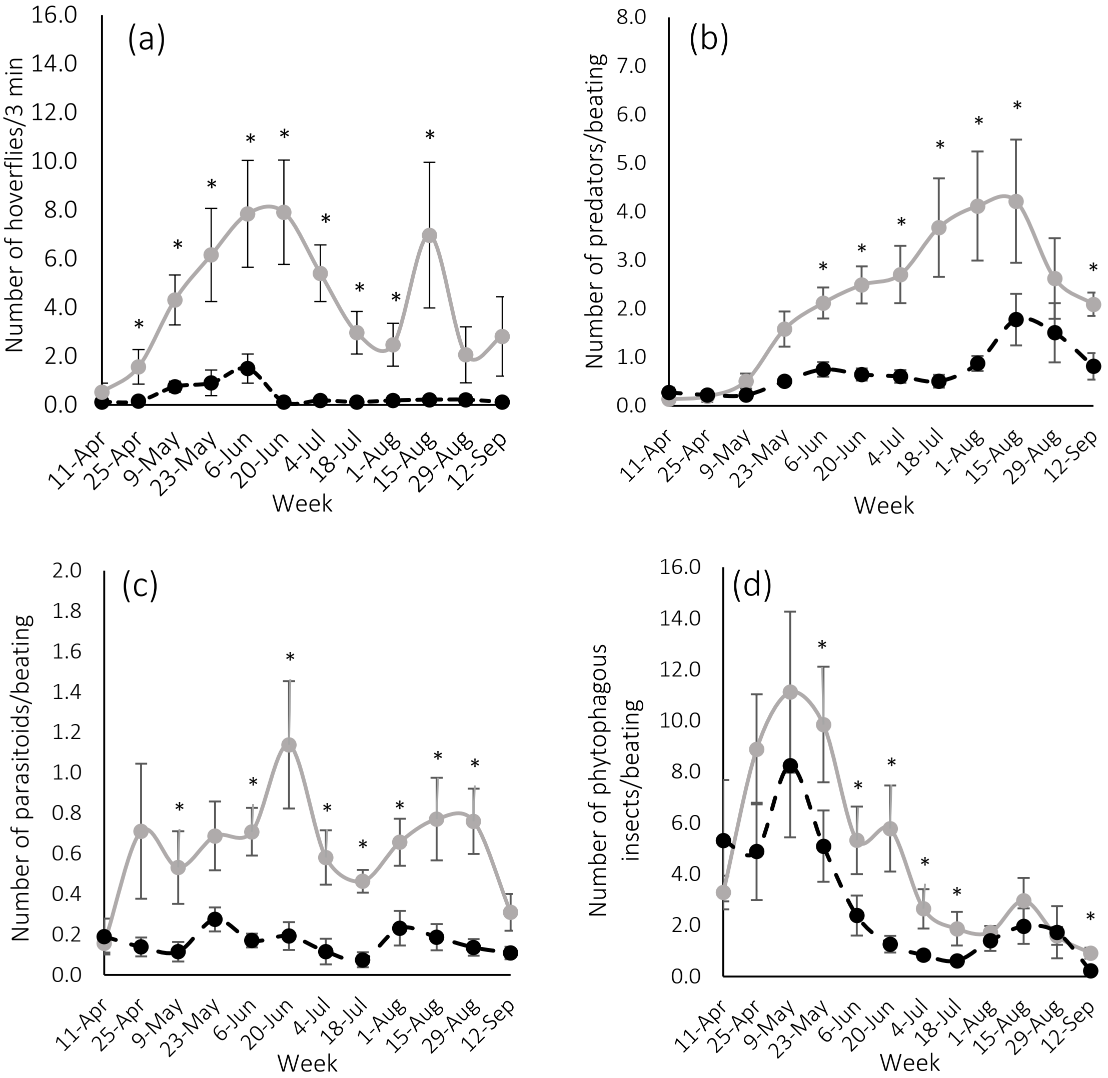


Figure 2. (a) Number of adult hoverflies per three minutes, (b) number of predators per beating, (c) number of parasitoid wasps per beating, and (d) number of phytophagous insects per beating in the flower margin (grey line) and in the spontaneous margin (black dashed line). Vertical bars show standard error. Data presented as average of 2015 and 2016 per week in 1 m$^2$. ns = $p$ >0.05, *= $p$ <0.05.

### 3.2. Assessment of *D. plantaginea*, *E. lanigerum* and Their Natural Enemies

The most abundant natural enemies present in RAA and WAA colonies were parasitoids. However, the diversity and relative abundance of the different groups of natural enemies differed between aphid species.

In the case of RAA, 173 parasitoids and 119 predators were found during the entire sampling period. Ichneumonoidea accounted for the whole diversity of the parasitoids present in RAA colonies. These were the only group of natural enemies found in April. Moreover, from early May to the end of June, Ichneumonoidea accounted for about 30–50% of the assemblage of natural enemies (Figure 3a). With regard to the species, 94% of the parasitoids were *Aphidius* spp. and the rest were *Ephedrus* *persicae* Froggatt (Hymenoptera: Braconidae). When *Aphidius* specimens could be identified to the species level, they were found to belong to *Aphidius matricariae* Haliday (Hymenoptera: Braconidae).

Hoverflies (Syrphidae) were the most abundant predators in RAA colonies (69.75%), followed by Cecidomyiidae (19.97%), Coccinellidae (6.72%) and Miridae (4.20%). Chrysopidae (1.68%), Araneae (0.84%) and Forficulidae (0.84%) abundance was minimal. Syrphidae were the first predators to reach the colonies, being the most abundant during May, while the rest of the predators appeared in late May and increased in abundance from then onwards (Figure 3a). The abundance of the natural enemies associated with the RAA colonies presented a similar pattern to that of RAA in the orchards: both increased from April to the beginning of June and decreased from then onwards (Figure 3a).

In the case of WAA, 359 parasitoids (all *Aphelinus mali* Haldeman (Hymenoptera: Aphelinidae)) and four predators (one Miridae, two Coccinellidae and one Chrysopidae) were collected from the colonies (Figure 3b). The population dynamics of WAA natural enemies was similar to that of WAA: they appeared at the end of May, were abundant during June and July, and decreased thereafter (Figure 3b).

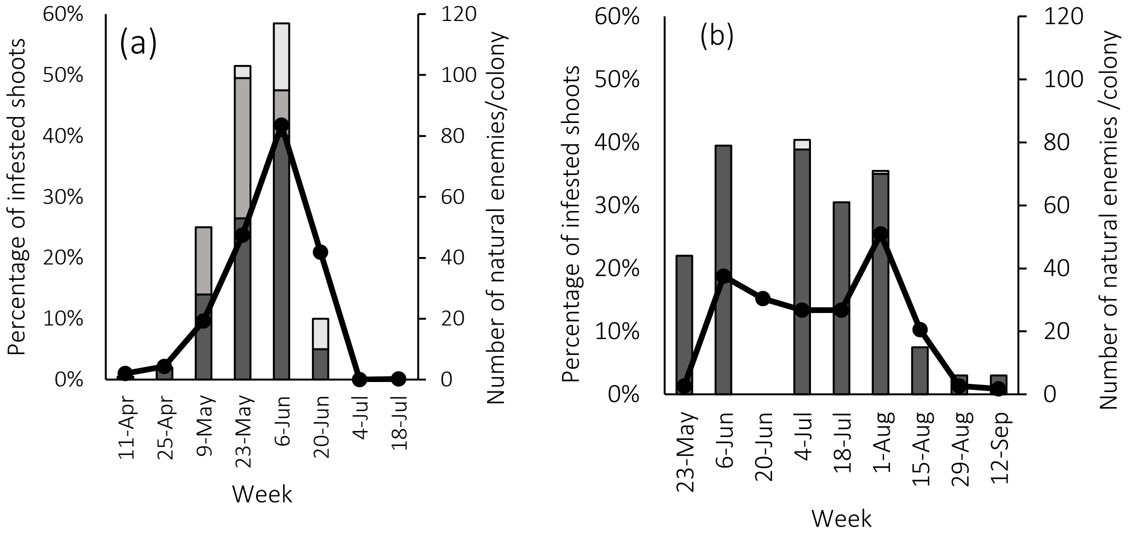


Figure 3. (a) Population dynamics of the RAA (black line) and their natural enemies per colony found in the colonies per week in 2016. Parasitoids (dark grey), Syrphidae (medium grey) and other predators (Miridae, Forficulidae, Araneae, Coccinellidae, Cecidomyiidae and Chrysopidae pooled together) (soft grey). (b) Population dynamics of the WAA (black line) and their natural enemies per colony found in the colonies per week in 2016: *A. mali* (dark grey) and other predators (Miridae and Coccinellidae pooled together) (soft grey). Primary axis shows percentage of shoots infested with RAA or WAA colonies. Secondary axis shows number of natural enemies per colony.

## 3.3. Correlations between the Natural Enemies and *D. plantaginea* and *E. lanigerum* Colonies

### 3.3.1. Arthropods Found in the Margins

Significant positive correlations were found between the number of Syrphidae (hoverfly adults from the visual observations) and the other natural enemies recorded in the flower margin. Moreover, the number of adult hoverflies found in the flower margin was positively correlated with the number of phytophagous insects found in the flower margin and in the control margin. In contrast, no significant correlations were found for the number of adult hoverflies from the control margin and the number of phytophagous (Table 2).

The number of predators and parasitoids from the flower margin was positively correlated with the number of all the natural enemy groups from the same margin, and also with their respective groups of the control margin. Moreover, significant negative correlations were found between the number of predators found in the control margin and the number of phytophagous insects from the flower margin. The number of parasitoids captured in the flower margin was also positively correlated with the number of phytophagous insects found in the same margin, and the same occurred for the parasitoids from the spontaneous vegetation (Table 2).

Table 2. Spearman correlation coefficients between: adult hoverflies (Syrphidae) from the visual observations (VO), predators, parasitoids and phytophagous insects from the beating tray samplings (BTS) found in the flower margin (FM) and in the control margin (CM).

| Type of Sampling | | Arthropod Group | Syrphidae in the FM | | Syrphidae in the CM | | Predators in the FM | | Predators in the CM | | Parasitoids in the FM | | Parasitoids in the CM | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | ρ | *p* | ρ | *p* | ρ | *p* | ρ | *p* | ρ | *p* | ρ | *p* |
| FM | VO | Syrphidae | – | – | 0.192 | 0.06 | 0.344 | **<0.001** | −0.025 | 0.806 | 0.38 | **<0.001** | 0.01 | 0.92 |
| | BTS | Predators | 0.344 | **<0.001** | 0.038 | 0.716 | – | – | 0.446 | **<0.001** | 0.514 | **<0.001** | 0.08 | 0.937 |
| | | Parasitoids | 0.38 | **<0.001** | 0.185 | 0.072 | 0.514 | **<0.001** | 0.214 | **0.036** | – | – | 0.32 | **0.002** |
| | | Phytophagous insects | 0.434 | **<0.001** | 0.183 | 0.075 | −0.124 | 0.229 | −0.383 | **<0.001** | 0.273 | **0.007** | 0.122 | 0.236 |
| CM | VO | Syrphidae | 0.192 | 0.06 | – | – | 0.038 | 0.716 | 0.027 | 0.793 | 0.184 | 0.072 | 0.126 | 0.221 |
| | BTS | Predators | −0.025 | 0.806 | 0.027 | 0.793 | 0.446 | **<0.001** | – | – | 0.214 | 0.036 | 0.176 | 0.09 |
| | | Parasitoids | 0.01 | 0.92 | 0.126 | 0.221 | 0.008 | 0.937 | 0.176 | 0.086 | 0.32 | **0.002** | – | – |
| | | Phytophagous insects | 0.302 | **0.003** | 0.158 | 0.125 | −0.125 | 0.227 | −0.193 | 0.06 | 0.129 | 0.212 | 0.234 | **0.022** |

* Test statistics (Spearman correlation coefficients (ρ) and likelihood ratio (p)) are shown. Significant *p* values ($p < 0.05$) are shown in bold.

### 3.3.2. Arthropods Found in the *D. plantaginea* Colonies

In the case of the RAA colonies, two groups of predators were considered according to their relative abundance in the aphid colonies: Syrphidae predators and non-Syrphidae predators. Correlations were run between the percentage of infested shoots and the natural enemies found in the RAA colonies (Syrphidae predators, non-Syrphidae predators and parasitoids).

During the period when RAA colonies were present in the orchard, no biologically significant correlations were found between hoverflies in the RAA colonies and the rest of arthropods from the margins (Table 3). On the other hand, significant positive correlations were found between the hoverflies of the RAA colonies and: 1) the percentage of shoots infested with RAA and 2) the parasitoids from the RAA colonies (Table 3). When correlations were run for non-Syrphidae predators from the RAA colonies, significant positive correlations were found between these and the phytophagous insects from the control margin (Table 3). In the case of the parasitoids found in the RAA colonies, significant positive correlations were found with: 1) adult hoverflies and predators from the flower margin, 2) the predators and parasitoids from the control margin and 3) the percentage of shoots infested with RAA (Table 3).

Table 3. Spearman correlation coefficients (ρ) between the percentage of infested shoots and the number of natural enemies (Syrphidae predators, non-Syrphidae predators and parasitoids) found in the RAA colonies and the number of arthropods found in visual observations (VO) and beating tray samplings (BTS) in the flower margin (FM) and control margin (CM).

| Type of Sampling | | Arthropod Group | Syrphidae Predators in the RAA Colonies | | Non-Syrphidae Predators in the RAA Colonies | | Parasiotids in the RAA Colonies | |
|---|---|---|---|---|---|---|---|---|
| | | | ρ | *p* | ρ | *p* | ρ | *p* |
| FM | VO | Syrphidae | 0.312 | 0.138 | 0.333 | 0.104 | 0.621 | **0.001** |
| | BTS | Predators | 0.309 | 0.142 | 0.146 | 0.498 | 0.488 | **0.016** |
| | | Parasitoids | 0.173 | 0.418 | 0.272 | 0.188 | 0.281 | 0.183 |
| | | Phytophagous insects | 0.312 | 0.138 | 0.025 | 0.908 | 0.226 | 0.289 |
| CM | VO | Syrphidae | 0.253 | 0.234 | −0.039 | 0.854 | 0.105 | 0.626 |
| | BTS | Predators | 0.175 | 0.414 | 0.155 | 0.471 | 0.428 | **0.037** |
| | | Parasitoids | 0.449 | **0.028** | 0.244 | 0.250 | 0.483 | **0.017** |
| | | Phytophagous insects | 0.116 | 0.589 | 0.414 | **0.040** | 0.031 | 0.887 |
| RAA | RAA colonies | % shoots infested with RAA colonies | 0.536 | **0.007** | 0.233 | 0.273 | 0.606 | **0.002** |
| | | Syrphidae predators | – | – | −0.057 | 0.793 | 0.658 | **<0.001** |
| | | Non-Syrphidae predators | −0.057 | 0.793 | – | – | 0.191 | 0.373 |
| | | Parasitoids | 0.658 | **<0.001** | 0.191 | 0.373 | – | – |

* Test statistics (Spearman correlation coefficients (ρ) and likelihood ratio (p)) are shown. Significant *p* values ($p < 0.05$) are shown in bold.

### 3.3.3. Arthropods Found in the *E. lanigerum* Colonies

During the period when the WAA colonies were present in the orchard, no significant correlations were found between the predators found in the WAA colonies and those found in the margins (Table 4). Nonetheless, significant positive correlations were found between the parasitoids from the WAA colonies and the percentage shoots infested with WAA (Table 4).

Table 4. Spearman correlation coefficients (ρ) between the number of predators and parasitoids found in the WAA colonies and the number of arthropods found in visual observations (VO) and beating tray samplings (BTS) in the flower margin (FM) and control margin (CM).

| Type of Sampling | | Arthropod Group | Predators in the WAA Colonies | | Parasitoids in the WAA Colonies | |
|---|---|---|---|---|---|---|
| | | | ρ | *p* | ρ | *p* |
| FM | VO | Syrphidae | 0.298 | 0.078 | 0.181 | 0.292 |
| | BST | Predators | 0.139 | 0.419 | 0.055 | 0.752 |
| | | Parasitoids | 0.295 | 0.081 | 0.223 | 0.190 |
| | | Phytophagous insects | 0.022 | 0.898 | 0.079 | 0.647 |
| CM | VO | Syrphidae | 0.107 | 0.536 | −0.141 | 0.413 |
| | BTS | Predators | 0.031 | 0.857 | −0.156 | 0.363 |
| | | Parasitoids | 0.093 | 0.588 | −0.101 | 0.557 |
| | | Phytophagous insects | 0.154 | 0.369 | −0.026 | 0.881 |
| WAA | WAA colonies | % shoots infested with WAA colonies | 0.227 | 0.183 | 0.597 | **<0.001** |
| | | Predators | – | – | 0.253 | 0.136 |
| | | Parasitoids | 0.253 | 0.136 | – | – |

* Test statistics (Spearman correlation coefficients (ρ) and likelihood ratio (p)) are shown. Significant *p* values (*p* <0.05) are shown in bold.

## 4. Discussion

Adult hoverflies, predators and parasitoids were highly attracted to the flower margin implemented adjacent to the apple orchards when compared to a spontaneous margin. The floral composition of the margins may explain these differences: the spontaneous margin was mainly composed by Gramineae whereas the flower margin had more abundance of floral resources. In agricultural landscapes, orchard groundcover provides few or no floral resources due to the practice of mowing (Debras et al. 2006; Horton et al. 2003). Hence, it is highly probable that the implemented flower margin represented a source of food (pollen, nectar or alternative prey) or shelter (Boller et al. 2004; Gurr et al. 2017). Thus, coinciding with previous studies (Albert et al. 2017; Campbell et al. 2017; Dib et al. 2012; Miñarro and Prida 2013; Wyss 1995; Wyss et al. 1995), the presence of the flowering insectary plants in orchard margin has boosted resource availability, which may explain the attraction of natural enemies present in the area like parasitoids, spiders, Chrysopidae, Coccinellidae and Syrphidae ultimately benefiting their populations. Even though the addition of insectary plants can provide multiple benefits, a rigorous selection of the plant species is crucial in order to avoid the ones that harbor crop pests or diseases (Gurr et al. 2017). Furthermore, the implemented flower margin reflected most of the natural enemies and phytophagous present in spontaneous vegetation of the edge of the orchard since they were positively correlated with the beneficials and phytophagous of the control margin. However, in the case of adult hoverflies this effect was not observed. In our opinion, this highlights two biological traits of these flies: high dependence on flower resources (they require pollen and nectar in order to be able to reproduce and survive)(Gilbert 1981; Schneider 1969) and high-flying ability (Wratten et al. 2003). In the case of parasitoids, our data suggest that the phytophagous present in the margins could increase the host availability for parasitoids, since positive correlations were found between these groups.

With regard to the aphid colonies, RAA populations appeared in the orchards in early April and increased their presence until the beginning of June, when they migrated to their summer host (*Plantago* spp. Plantaginaceae). The populations of natural enemies associated with these colonies showed a similar trend, although the relative importance of the distinct assemblages changed with time. Despite the natural enemy diversity that we found in the RAA colonies is consistent with the findings of other studies (Dib et al. 2016; Dib et al. 2010; Miñarro et al. 2005), their relative abundance is different and it could be affected by the type of climate. Parasitism is likely to be favored by higher temperatures (Stáry 1970). In fact, in studies carried out in Mediterranean areas (Dib et al. 2016; Dib et al. 2010; Odorizzi Santos et al. 2018) parasitoids represent an important part of the natural enemy guild, accounting for about the 30–50% of the beneficials present in the RAA colonies. While in colder climates, predators become more important relegating the importance of parasitoids (Brown and Mathews 2007; Cahenzli et al. 2017; Stewart-Jones et al. 2008). In our study, Ichneumonoidea parasitoids were the first beneficial arthropods to colonize the aphid colonies, appearing one month earlier than predators and maintaining their presence for the whole infestation season. When identification to species level was possible, parasitoids mainly belonged to *A. matricariae* and *E. persicae* species. Both species have been cited as parasitoids of RAA in Europe, although little is known about their efficiency in suppressing populations of these aphids (Bribosia et al. 2004; Cross et al. 1999; Dib et al. 2010; Michelena et al. 2004; Peusens et al. 2006). Due to our sampling method, we were not able to identify to species the parasitoids collected from the margins. Hence, we cannot confirm that the species that we collected from the RAA colonies were also present in any of our margins. However, the spontaneous vegetation seems to have a stronger influence than the implemented margin in the parasitoids present in the RAA colonies; only significant correlations were found between the spontaneous vegetation and the parasitoids present in the RAA colonies. In fact, we expected a positive correlation between the parasitoids collected in the flower margin and the ones present in RAA colonies since, in lab conditions, it was demonstrated that *L. maritima* increases the longevity of other species from the genera, such as

*Aphidius ervi* Haliday (Hymenoptera: Braconidae) (Aparicio et al. 2018). These results highlight the importance of field trials to determine the real contribution of the parasitoids present in the area on aphid control and how plant species can boost their presence.

Concerning the predators found in the RAA colonies, hoverflies were the most abundant group, accounting for more than half of the predators found in the colonies. In addition, they were the first predators present in the RAA colonies and they showed large populations during May. From mid-June onwards hoverflies stopped colonizing the RAA colonies, which can be attributed to the flies not perceiving the colonies as an adequate food source for their offspring. Adult hoverflies are known to show preferences in regard to aphid species and oviposition sites (Sadeghi and Gilbert 2000). Therefore, the lack of colonization from mid-June onwards could be explained by the presence of winged forms in the aphid colonies, which may signal an inappropriate food source for hoverfly offspring, as larvae show little mobility and may not be able to find an alternative feeding site if the colony disappears (Sadeghi and Gilbert 2000).

Despite our implemented flower margin being highly attractive to adult hoverflies, we failed to identify any correlations between the hoverflies present in the margins and the ones present in the RAA colonies. Nonetheless, the Syrphidae found in the RAA colonies, as well as the parasitoids, were positively correlated with the percentage of shoots infested with RAA. Previous studies have reported the attraction of Syrphidae and other natural enemies to herbivore-induced plant volatiles, e.g., Methyl salicylate (James 2003), and aphid alarm pheromone components, e.g., E-(β)-farnesene (Almohamad et al. 2009). Hence, it seems that the natural enemies present in the area were attracted to chemicals released by the RAA colonies. On the other hand, positive correlations were found between Syrphidae and parasitoids in the same colonies, which suggests that their populations were able to keep growing despite intraguild predation might be occurring between them (Almohamad et al. 2008; Michaud 1999).

Non-Syrphidae predators (Cecidomyiidae, Coccinellidae, Miridae, Chrysopidae, Forficulidae and Araneae) appeared about two weeks later than hoverflies and gradually increased in presence until the RAA colonies migrated. In our case, hoverflies were the main predator and the first to reach the RAA colonies, in agreement with Dib et al., (Dib et al. 2010) and Miñarro et al., (Miñarro et al. 2005). As such, they represent a key group during the key period of RAA control. In contrast, the rest of the predatory assemblage appeared later, when RAA abundance was almost peaking, so their capacity to prevent RAA outbreaks is unlikely. However, since RAA has two hosts (Bonnemaison 1959), the action of natural enemies during this period should not be underestimated, as they may contribute to reduce the abundance of summer migrants to the secondary host. As a consequence, the populations of the autumn migrants that recolonize apple trees might also be diminished.

With regard to WAA populations, these were present in the orchard from late May to September. In this case, *A. mali* was the main beneficial arthropod found in the colonies, while the presence of predators was anecdotal. Even though earwigs, which are one of the most important WAA predators (Gontijo et al. 2013; Mueller et al. 1988; Nicholas et al. 2005), are present in our study area (Lordan et al. 2015b), we failed to find them because our sampling method was not appropriated to assess this predator. Earwigs feed at night and remain concealed during the day (Sauphanor et al. 1993), so night visual samplings would be required to detect the predatory activity of this insect on WAA colonies. In the case of hoverflies, we did not find any individual predating on WAA. Although some species of hoverflies feed on this aphid, they have never been reported as present in our area (Bergh and Short 2008; Rojo et al. 2003; Short and Bergh 2004). About parasitoids, *A. mali* is known to provide effective biocontrol of WAA on the aerial parts of the host plant (Monteiro et al. 2004; Zhou et al. 2014) and moreover, its action can be consistently improved when other predators are also present (Bergh and Stallings 2016; Gontijo et al. 2015; Lordan et al. 2015a). However, in our case no correlation was found between *A.mali* and predators from the WAA colonies because, as mentioned above, our sampling method was not suitable to assess predators. On the other hand, our data suggests that neither the spontaneous vegetation nor the flower margin were used by *A. mali* because there was no correlation between the parasitoids present in the margins and the ones collected from WAA colonies. To the best of our knowledge, *A. mali* has not been previously reported to use floral resources and it is possible that adults are able to feed via host feeding (Bai and Mackauer 1990; Wu and Heimpel 2007). Basic research is needed to know the feeding requirements of *A. mali* adults.

## 5. Conclusions

In conclusion, our study highlights the capacity of the implemented flower margin to gather natural enemy populations in the edge of apple orchards due to an enhanced alimentary and shelter supply. Parasitoids and hoverflies were the most important natural enemies present in the RAA colonies. In addition, the more parasitoids were present in the spontaneous vegetation, the more parasitoids were found in the RAA colonies. In contrast, no relationships was found between the natural enemies present in the flower margins and the ones present in the aphid colonies, probably because of the size of the flower margin. These results emphasize the importance of promoting these beneficials in the surroundings of the orchards. In contrast, *A. mali*, which is a specific parasitoid of WAA colonies and the most important natural enemy we found, did not benefit by the presence of additional resources. Hence, more research is needed to figure out how to enhance the abundance of this parasitoid. Further attention should be devoted to overcoming the technical difficulties associated with the implementation of flower strips (such as placement, irrigation, seeds availability and scale costs) and to unravelling the contribution of these zones to aphid control and ecosystem services.

### Acknowledgments

We thank our team, especially Sara Muntada, for helping with data collection and arthropod identification and the farmers for allowing us to conduct research in their orchards. This research was funded by the Spanish Ministry of Economy and Competiveness (Projects AGL2013-49164-C2-1-R, AGL2013-49164-C2-2-R and AGL2016-77373-C2) and the CERCA Programme/Generalitat de Catalunya

## 6. References

Albert L, Franck P, Gilles Y, Plantegenest M (2017) Impact of agroecological infrastructures on the dynamics of *Dysaphis plantaginea* (Hemiptera: Aphididae) and its natural enemies in apple orchards in northwestern France. Environ Entomol 46:528-537 doi:10.1093/ee/nvx054

Almohamad R, Verheggen FJ, Francis F, Hance T, Haubruge E (2008) Discrimination of parasitized aphids by a hoverfly predator: effects on larval performance, foraging, and oviposition behavior. Entomol Exp Appl 128:73-80 doi:10.1111/j.1570-7458.2007.00664.x

Almohamad R, Verheggen FJ, Haubruge E (2009) Searching and oviposition behavior of aphidophagous hoverflies (Diptera: Syrphidae): a review. Biotechnol Agron Soc 13:467-481

Altieri MA, Nicholls AH (2004) Biodiversity and Pest Management in Agroecosystems. 2nd edn. Food Products Press, Haworth Press, Inc., Binghamton, NY

Aparicio Y, Gabarra R, Arno J (2018) Attraction of *Aphidius ervi* (Hymenoptera: Braconidae) and *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae) to sweet alyssum and assessment of plant resources effects on their fitness. J Econ Entomol 111:533-541 doi:10.1093/jee/tox365

Asante SK, Danthanarayana W, Cairns SC (1993) Spatial and temporal distribution patterns of *Eriosoma lanigerum* (Homoptera, Aphididae) on apple. Environ Entomol 22:1060-1065 doi:10.1093/ee/22.5.1060

Bai B, Mackauer M (1990) Oviposition and host-feeding patterns in *Aphelinus asychis* (Hymenoptera, Aphelinidae) at different aphid densities. Ecol Entomol 15:9-16 doi:10.1111/j.1365-2311.1990.tb00778.x

Barahoei H, Madjdzadeh SM, Mehrparvar M (2012) Aphid parasitoids (Hymenoptera: Braconidae: Aphidiinae) and their tritrophic relationships in Kerman province, Southeastern Iran. Iranian Journal of Animal Biosystematics 8:1-14 doi:doi.org/10.22067/ijab.v8i1.25566

Barbagallo S, Cocuzza GE, P. C, Komazaki S (2017) IPM Case Studies: Deciduous Fruit Tree In: Harrington HFvEaR (ed) Aphids as crop pests. 2 edn. CABI Publishing, Wallingford, UK, p 700

Bergh JC, Short BD (2008) Ecological and life-history notes on syrphid predators of woolly apple aphid in Virginia, with emphasis on *Heringia calcarata*. BioControl 53:773-786 doi:10.1007/s10526-007-9114-0

Bergh JC, Stallings JW (2016) Field evaluations of the contribution of predators and the parasitoid, *Aphelinus mali*, to biological control of woolly apple aphid, *Eriosoma lanigerum*, in Virginia, USA. BioControl 61:155-165 doi:10.1007/s10526-016-9714-7

Boller EF, Häni F, Poehling HM (2004) Ecological infrastructures: Ideabook on functional diversity at the farm level. IOBC WPRS, Winterthur

Bonnemaison L (1959) Le puceron cendré du pommier (*Dysaphis plantaginea* Pass.). Morphologie et biologie. Méthodes de lutte. Annales des Épiphyties 3:257-320

Braun-Blanquet J (1932) Plant sociology: The study of plant communities. MacGraw Hill, New York

Bribosia E, Bylemans D, Van Impe G, Migon M Assessing the suitability of alternative host aphids for *Ephedrus persicae* Froggatt (Hymenoptera: Braconidae), the main parasitoid attacking *Dysaphis plantaginea* (Passerini) (Homoptera: Aphididae) in Belgian apple orchards. In: Proceedings of The Sixth International Symposium on Aphids, Rennes, France, 3-7 September 2001 2004. pp 269-274

Brown MW, Mathews CR (2007) Conservation biological control of rosy apple aphid, *Dysaphis plantaginea* (Passerini), in Eastern North America. Environ Entomol 36:1131-1139 doi:10.1603/0046-225x(2007)36[1131:cbcora]2.0.co;2

Brown MW, Schmitt JJ, Ranger S, Hogmire HW (1995) Yield reduction in apple by edaphic Woolly apple aphid (Homoptera, Aphididae) populations. J Econ Entomol 88:127-133 doi:10.1093/jee/88.1.127

Cahenzli F, Pfiffner L, Daniel C (2017) Reduced crop damage by self-regulation of aphids in an ecologically enriched, insecticide-free apple orchard. Agronomy for Sustainable Development 37:8 doi:10.1007/s13593-017-0476-0

Campbell AJ, Wilby A, Sutton P, Wackers F (2017) Getting more power from your flowers: Multi-functional flower strips enhance pollinators and pest control agents in apple orchards. Insects 8:18 doi:10.3390/insects8030101

Cross JV et al. (1999) Biocontrol of pests of apples and pears in northern and central Europe: 2. Parasitoids. Biocontrol Sci Technol 9:277-314 doi:10.1080/09583159929569

Debras JF et al. (2006) Discrimination between agricultural management and the hedge effect in pear orchards (south-eastern France). Ann Appl Biol 149:347-355 doi:10.1111/j.1744-7348.2006.00102.x

Dib H, Libourel G, Warlop F (2012) Entomological and functional role of floral strips in an organic apple orchard: Hymenopteran parasitoids as a case study. J Insect Conserv 16:315-318 doi:10.1007/s10841-012-9471-6

Dib H, Sauphanor B, Capowiez Y (2016) Effect of management strategies on arthropod communities in the colonies of rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) in south-eastern France. Agric Ecosyst Environ 216:203-206 doi:10.1016/j.agee.2015.10.003

Dib H, Simon S, Sauphanor B, Capowiez Y (2010) The role of natural enemies on the population dynamics of the rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) in organic apple orchards in south-eastern France. Biol Control 55:97-109 doi:10.1016/j.biocontrol.2010.07.005

Fitzgerald JD, Solomon MG (2004) Can flowering plants enhance numbers of beneficial arthropods in UK apple and pear orchards? Biocontrol Sci Technol 14:291-300 doi:10.1080/09583150410001665178

Foley JA et al. (2011) Solutions for a cultivated planet. Nature 478:337-342 doi:10.1038/nature10452

Garibaldi LA, Gemmill-Herren B, D'Annolfo R, Graeub BE, Cunningham SA, Breeze TD (2017) Farming Approaches for Greater Biodiversity, Livelihoods, and Food Security. Trends Ecol Evol 32:68-80 doi:10.1016/j.tree.2016.10.001

Gilbert FS (1981) Foraging ecology of hoverflies - Morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. Ecol Entomol 6:245-262 doi:10.1111/j.1365-2311.1981.tb00612.x

Gontijo LM, Beers EH, Snyder WE (2013) Flowers promote aphid suppression in apple orchards. Biol Control 66:8-15 doi:10.1016/j.biocontrol.2013.03.007

Gontijo LM, Beers EH, Snyder WE (2015) Complementary suppression of aphids by predators and parasitoids. Biol Control 90:83-91 doi:10.1016/j.biocontrol.2015.06.002

Gurr GM, Wratten SD, Landis DA, You MS (2017) Habitat management to suppress pest populations: progress and prospects. Annu Rev Entomol 62:91-109 doi:10.1146/annurev-ento-031616-035050

Holland JM, Bianchi FJJA, Entling MH, Moonen A-C, Smith BM, Jeanneret P (2016) Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies. Pest Manage Sci 72:1638-1651 doi:10.1002/ps.4318

Horton DR et al. (2003) Effects of mowing frequency on densities of natural enemies in three Pacific Northwest pear orchards. Entomol Exp Appl 106:135-145 doi:10.1046/j.1570-7458.2003.00018.x

James DG (2003) Synthetic herbivore-induced plant volatiles as field attractants for beneficial insects. Environ Entomol 32:977-982 doi:10.1603/0046-225X-32.5.977

Lordan J, Alegre S, Gatius F, Sarasúa MJ, Alins G (2015a) Woolly apple aphid *Eriosoma lanigerum* Hausmann ecology and its relationship with climatic variables and natural enemies in Mediterranean areas. Bull Entomol Res 105:60-69 doi:10.1017/s0007485314000753

Lordan J, Alegre S, Moerkens R, Sarasúa MJ, Alins G (2015b) Phenology and interspecific association of *Forficula auricularia* and *Forficula pubescens* in apple orchards. SPAN J AGRIC RES 13 doi:10.5424/sjar/2015131-6814

Michaud JP (1999) Sources of mortality in colonies of brown citrus aphid, *Toxoptera citricida*. BioControl 44:347-367 doi:10.1023/a:1009955816396

Michelena JM, Gonzalez P, Soler E (2004) Parasitoides afidiinos (Hymenoptera, Braconidae, Aphidiinae) de pulgones de cultivos agrícolas en la Comunidad Valenciana. Boletín de Sanidad Vegetal y Plagas 30:317-326

Miñarro M, Hemptinne JL, Dapena E (2005) Colonization of apple orchards by predators of *Dysaphis plantaginea*: sequential arrival, response to prey abundance and consequences for biological control. BioControl 50:403-414 doi:10.1007/s10526-004-5527-1

Miñarro M, Prida E (2013) Hedgerows surrounding organic apple orchards in north-west Spain: potential to conserve beneficial insects. Agric For Entomol 15:382-390 doi:10.1111/afe.12025

Monteiro LB, Souza A, Belli EL (2004) Parasitism on *Eriosoma lanigerum* (Homoptera: Aphididae) by *Aphelinus mali* (Hymenoptera: Encyrtidae) on apple orchards, in Fraiburgo county, state of Santa Catarina, Brazil. Rev Bras Frutic 26:550-551 doi:10.1590/s0100-29452004000300043

Mueller TF, Blommers LHM, Mols PJM (1988) Earwig (*Forficula auricularia*) predation on the woolly apple aphid, *Eriosoma lanigerum*. Entomol Exp Appl 47:145-152 doi:10.1111/j.1570-7458.1988.tb01129.x

Nicholas AH, Spooner-Hart RN, Vickers RA (2005) Abundance and natural control of the woolly aphid *Eriosoma lanigerum* in an Australian apple orchard IPM program. BioControl 50:271-291 doi:10.1007/s10526-004-0334-2

Odorizzi Santos LA, Costa MB, Lavigne C, Fernandes OA, Bischoff A, Franck P (2018) Influence of the margin vegetation on the conservation of aphid biological control in apple orchards. J Insect Conserv 22:465-474 doi:10.1007/s10841-018-0074-8

Peusens G, Buntinx L, Gobin B (2006) Parasitation of the parasitic wasp *Ephedrus Persicae* (Frogatt) on the rosy apple aphid *Dysaphis Plantaginea* (Passerini). Commun Agric Appl Biol Sci 71:369-374

Rakhshani E et al. (2012) Parasitoids (Hymenoptera: Braconidae: Aphidiinae) of northeastern Iran: Aphidiine-aphid-plant associations, key and description of a new species. J Insect Sci 12 doi:10.1673/031.012.14301

Rojo S, Gilbert F, Marcos-García MA, Nieto J, Mier MP (2003) A world review of predatory hoverflies (Diptera, Syrphidae: Syrphinae) and their prey. CIBIO Ediciones, Alicante, Spain

Rousselin A, Bevacqua D, Sauge MH, Lescourret F, Mody K, Jordan MO (2017) Harnessing the aphid life cycle to reduce insecticide reliance in apple and peach orchards. A review. Agronomy for Sustainable Development 37:13 doi:10.1007/s13593-017-0444-8

Sadeghi H, Gilbert F (2000) Oviposition preferences of aphidophagous hoverflies. Ecol Entomol 25:91-100 doi:10.1046/j.1365-2311.2000.00234.x

Sauphanor B, Chabrol L, Darcier FF, Sureau F, Lenfant C (1993) Side-effects of Diflubenzuron on a pear psilla predator - *Forficula auricularia*. Entomophaga 38:163-174 doi:10.1007/bf02372550

Schneider F (1969) Bionomics and Physiology of Aphidophagous Syrphidae. Annu Rev Entomol 14:103-124 doi:10.1146/annurev.en.14.010169.000535

Short BD, Bergh JC (2004) Feeding and egg distribution studies of *Heringia calcarata* (Diptera: Syrphidae), a specialized predator of woolly apple aphid (Homoptera: Eriosomatidae) in Virginia apple orchards. J Econ Entomol 97:813-819 doi:10.1603/0022-0493(2004)097[0813:FAEDSO]2.0.CO;2

Simon S, Bouvier J-C, Debras J-F, Sauphanor B (2010) Biodiversity and pest management in orchard systems. A review. Agronomy for Sustainable Development 30:139-152 doi:10.1051/agro/2009013

Stáry P (1970) Biology of Aphid Parasites (Hymenoptera: Aphidiidae) With Respect to Integrated Control vol 6. vol Series Entomologica. Springer, Netherlands

Stewart-Jones A, Pope TW, Fitzgerald JD, Poppy GM (2008) The effect of ant attendance on the success of rosy apple aphid populations, natural enemy abundance and apple damage in orchards. Agric For Entomol 10:37-43 doi:10.1111/j.1461-9563.2007.00353.x

Wratten SD, Bowie MH, Hickman JM, Evans AM, Sedcole JR, Tylianakis JM (2003) Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. Oecologia 134:605-611 doi:10.1007/s00442-002-1128-9

Wratten SD, Gillespie M, Decourtye A, Mader E, Desneux N (2012) Pollinator habitat enhancement: Benefits to other ecosystem services. Agric Ecosyst Environ 159:112-122 doi:10.1016/j.agee.2012.06.020

Wu ZS, Heimpel GE (2007) Dynamic egg maturation strategies in an aphid parasitoid. Physiol Entomol 32:143-149 doi:10.1111/j.1365-3032.2007.00560.x

Wyss E (1995) The effects of weed strips on aphids and aphidophagous predators in an apple orchard. Entomol Exp Appl 75:43-49 doi:10.1111/j.1570-7458.1995.tb01908.x

Wyss E, Niggli U, Nentwig W (1995) The impact of spiders on aphid populations in a strip-managed apple orchard. J Appl Entomol 119:473-478 doi:10.1111/j.1439-0418.1995.tb01320.x

Zhou HX, Yu Y, Tan XM, Chen AD, Feng JG (2014) Biological control of insect pests in apple orchards in China. Biol Control 68:47-56 doi:10.1016/j.biocontrol.2013.06.009

## Supplementary Materials

The following are available online at https://www.mdpi.com/2075-4450/10/5/148/s1

Table S1. Apple orchards surveyed in 2015 and 2016: locality, coordinates (UTM), year of planting and apple cultivars.

| Orchard identification | Years of assessment | Locality | Coordinates (UTM) Zone 31 | Year of planting | Cultivars |
|---|---|---|---|---|---|
| E1 | 2015 & 2016 | Bell-lloc d'Urgell | X: 313035.23<br>Y: 4612352.66 | 2001 | Galaxy, Granny & Fuji |
| E3 | 2015 & 2016 | Mollerussa | X: 322816.55<br>Y: 4609153.69 | 1997 | Golden & Granny |
| E4 | 2015 | Lleida | X: 294761.98<br>Y: 4611459.40 | 1999 | Gala & Golden Supreme |
| E5 | 2015 & 2016 | Vilanova de Segrià | X: 301159.08<br>Y: 4620927.25 | 2000 | Fuji & Gala |
| E6 | 2016 | Vilanova de Segrià | X: 301708.90<br>Y: 4621206.98 | 2012 | Gala & Golden |

Table S2. Blooming period and percentage of plant coverage of the species present in the flower margin in 2015.

| | | | Blooming period | | | | | | | | | Coverage | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Orchard | Family | Plant species | 25-Apr | 9-May | 23-May | 6-Jun | 20-Jun | 4-Jul | 18-Jul | 7-Aug | 29-Aug | 25-Apr | 9-May | 23-May | 6-Jun | 20-Jun | 4-Jul | 18-Jul | 7-Aug | 29-Aug | Total |
| E1 | Asteraceae | *Achillea millefolium* L. | | | | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 18.00 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 79.78 |
| | Brassicaceae | *Lobularia maritima* L. | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | | | | 23.00 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 69.13 | 57.88 | 34.25 | 69.08 |
| | | *Moricandia arvensis* L. | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | | | | 18.00 | 87.50 | 87.50 | 81.38 | 87.50 | 87.50 | 87.50 | 69.00 | 48.50 | 72.71 |
| | | *Sinapis alba* L. | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | | | 33.00 | 87.50 | 81.38 | 81.38 | 69.13 | 18.00 | 5.50 | 8.63 | 1.75 | 42.92 |
| E3 | Asteraceae | *Achillea millefolium* L. | | | | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 18.00 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 79.56 |
| | Brassicaceae | *Lobularia maritima* L. | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | | | 18.00 | 87.50 | 87.50 | 81.38 | 87.50 | 75.25 | 75.13 | 50.38 | 19.88 | 64.72 |
| | | *Moricandia arvensis* L. | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | | | 18.00 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 50.50 | 75.67 |
| | | *Sinapis alba* L. | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | | | | 33.00 | 87.50 | 87.50 | 87.50 | 69.13 | 75.25 | 38.00 | 38.00 | 14.88 | 58.97 |
| E4 | Asteraceae | *Achillea millefolium* L. | | | | | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 70.13 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 85.57 |
| | Brassicaceae | *Lobularia maritima* L. | 🟩 | 🟩 | 🟩 | 🟩 | | | | | | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 69.13 | 0.00 | 26.13 | 18.00 | 61.19 |
| | | *Moricandia arvensis* L. | 🟩 | 🟩 | 🟩 | 🟩 | | | | | | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 81.38 | 34.25 | 70.13 | 78.97 |
| | | *Sinapis alba* L. | 🟩 | 🟩 | 🟩 | | 🟩 | | | | | 87.50 | 87.50 | 87.50 | 69.13 | 81.38 | 81.38 | 0.00 | 18.00 | 24.88 | 59.69 |
| E5 | Asteraceae | *Achillea millefolium* L. | | | | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 |
| | Brassicaceae | *Lobularia maritima* L. | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 87.50 | 87.50 | 87.50 | 87.50 | 81.38 | 75.25 | 69.00 | 75.13 | 75.25 | 80.67 |
| | | *Moricandia arvensis* L. | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 87.50 | 87.50 | 87.50 | 43.75 | 87.50 | 87.50 | 87.50 | 87.50 | 87.50 | 82.64 |
| | | *Sinapis alba* L. | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | | | 69.13 | 69.13 | 87.50 | 87.50 | 81.38 | 81.38 | 44.25 | 2.75 | 2.75 | 57.59 |
| Grand Total | | | | | | | | | | | | 52.70 | 86.35 | 87.11 | 82.39 | 84.05 | 78.95 | 62.18 | 56.57 | 49.89 | 71.09 |

Table S3. Blooming period and percentage of plant coverage of the species present in the control margin in 2015 (this table continues on the next page).

| | | | Blooming period | | | | | | | | | Average percentage of cover | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Orchard | Family | Plant species | 25/Apr | 9/May | 23/May | 6/Jun | 20/Jun | 4/Jul | 18/Jul | 7/Aug | 29/Aug | 25/Apr | 9/May | 23/May | 6/Jun | 20/Jun | 4/Jul | 18/Jul | 7/Aug | 29/Aug | Total |
| E1 | Apiaceae | Torilis arvensis (Huds.) Link | | | 🟩 | 🟩 | 🟩 | | | | | | | 5.50 | 5.50 | 18.00 | | | | | 9.67 |
| | Apiaceae Total | | | | | | | | | | | | | 5.50 | 5.50 | 18.00 | | | | | 9.67 |
| | Asteraceae | Carduus tenuiflorus Curtis | | 🟩 | 🟩 | 🟩 | 🟩 | | | | | 5.50 | 41.17 | 37.00 | 34.13 | 27.17 | 37.00 | 35.33 | 40.50 | 34.25 | 34.35 |
| | | Conyza sp. | | | | | | | | | 🟩 | | | | | | | | 5.50 | 11.75 | 9.67 |
| | | Dittrichia viscosa (L.) Greuter | | | | | | | 🟩 | 🟩 | | | | | | | | 21.75 | 18.00 | | 20.50 |
| | | Lactuca serriola L. | | | | | | | 🟩 | 🟩 | 🟩 | | | 5.50 | | 5.50 | 3.00 | 11.75 | 3.83 | 3.00 | 5.29 |
| | | Sonchus sp. | | | 🟩 | | | | | | | | | 5.50 | | 18.00 | | | | | 11.75 |
| | Asteraceae Total | | | | | | | | | | | 5.50 | 41.17 | 24.40 | 34.13 | 18.42 | 23.40 | 24.71 | 16.57 | 16.33 | 22.77 |
| | Brassicaceae | Diplotaxis erucoides (L.) DC. | 🟩 | | | | | | | | | 38.00 | 18.00 | | | | | | | | 28.00 |
| | Brassicaceae Total | | | | | | | | | | | 38.00 | 18.00 | | | | | | | | 28.00 |
| | Convolvulaceae | Convolvulus arvensis L. | | | | | | | | | | | | | | | | 0.50 | 0.50 | 0.50 | 0.50 |
| | Convolvulaceae Total | | | | | | | | | | | | | | | | | 0.50 | 0.50 | 0.50 | 0.50 |
| | Dipsacaceae | Scabiosa atropurpurea L. | | | | | | | | | | | | | | | 5.50 | | | | 5.50 |
| | Dipsacaceae Total | | | | | | | | | | | | | | | | 5.50 | | | | 5.50 |
| | Geraniaceae | Erodium sp. | | | | | 🟩 | | | | 🟩 | | | | | 5.50 | | | | 0.50 | 3.00 |
| | Geraniaceae Total | | | | | | | | | | | | | | | 5.50 | | | | 0.50 | 3.00 |
| | Gramineae | Gramineae | 🟩 | 🟩 | 🟩 | | | | | | | 3.00 | 8.83 | 8.63 | 21.75 | 8.63 | 0.50 | 8.00 | 9.67 | 10.50 | 7.93 |
| | Gramineae Total | | | | | | | | | | | 3.00 | 8.83 | 8.63 | 21.75 | 8.63 | 0.50 | 8.00 | 9.67 | 10.50 | 7.93 |
| | Papaveraceae | Papaver rhoeas L. | 🟩 | | | | | | | | | 0.50 | | | | | | | | | 0.50 |
| | Papaveraceae Total | | | | | | | | | | | 0.50 | | | | | | | | | 0.50 |
| | Plantaginaceae | Plantago coronopus L. | | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | | | | 38.00 | 31.33 | 34.25 | 31.33 | 20.50 | | 13.83 | 11.75 | 26.38 |
| | | Plantago lanceolata L. | | | | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | 0.50 | | | 18.00 | 5.50 | 0.50 | 5.50 | 5.50 | | 5.92 |
| | Plantaginaceae Total | | | | | | | | | | | 0.50 | 38.00 | 31.33 | 31.00 | 24.88 | 15.50 | 5.50 | 11.75 | 11.75 | 21.65 |
| E1 Total | | | | | | | | | | | | 7.64 | 22.19 | 19.69 | 28.38 | 16.75 | 15.46 | 16.92 | 12.83 | 11.00 | 16.44 |
| E3 | Amaranthaceae | Amaranthus sp. | | | | | | | | | | | | | | | | | | 0.50 | 0.50 |
| | Amaranthaceae Total | | | | | | | | | | | | | | | | | | | 0.50 | 0.50 |
| | Apiaceae | Torilis arvensis (Huds.) Link | | | | | | | | | | | | 5.50 | 5.50 | 5.50 | | | | | 5.50 |
| | Apiaceae Total | | | | | | | | | | | | | 5.50 | 5.50 | 5.50 | | | | | 5.50 |
| | Asteraceae | Sonchus sp. | | | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | | | 0.50 | 5.50 | 9.25 | 18.00 | 18.00 | 5.50 | | | 9.43 |
| | | Taraxacum officinale (L.) Weber | | | | | | | | | | | | 5.50 | | | | | | | 5.50 |
| | Asteraceae Total | | | | | | | | | | | | 0.50 | 5.50 | 9.25 | 18.00 | 18.00 | 5.50 | | | 8.94 |
| | Chenopodiaceae | Beta vulgaris L. | | | | | | | | | | | | | 18.00 | | | 0.50 | 5.50 | 5.50 | 7.38 |
| | | Chenopodium sp. | | | | | | | | | 🟩 | | | | | | | | 18.00 | 3.00 | 8.00 |
| | Chenopodiaceae Total | | | | | | | | | | | | | | 18.00 | | | 0.50 | 11.75 | 3.83 | 7.64 |
| | Convolvulaceae | Convolvulus arvensis L. | | | | | | | | 🟩 | | 5.50 | 5.50 | 11.75 | 28.00 | 18.00 | 28.00 | 28.00 | 18.83 | 24.67 | 20.50 |
| | Convolvulaceae Total | | | | | | | | | | | 5.50 | 5.50 | 11.75 | 28.00 | 18.00 | 28.00 | 28.00 | 18.83 | 24.67 | 20.50 |
| | Gramineae | Gramineae | 🟩 | 🟩 | 🟩 | | | | | | | 39.61 | 37.23 | 45.86 | 45.36 | 23.68 | 26.89 | 48.93 | 30.17 | 23.88 | 34.77 |
| | Gramineae Total | | | | | | | | | | | 39.61 | 37.23 | 45.86 | 45.36 | 23.68 | 26.89 | 48.93 | 30.17 | 23.88 | 34.77 |
| | Lamiaceae | Lamium sp. | | | | | | | | | | | | | | | | | | 0.50 | 0.50 |
| | Lamiaceae Total | | | | | | | | | | | | | | | | | | | 0.50 | 0.50 |
| | Malvaceae | Malva sylvestris L. | | | | | | | | | | | | | | | | | | 0.50 | 0.50 |
| | Malvaceae Total | | | | | | | | | | | | | | | | | | | 0.50 | 0.50 |
| | Plantaginaceae | Plantago lanceolata L. | | | | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | | | | 0.50 | 5.50 | 5.50 | 5.50 | 0.50 | 0.50 | 3.00 |
| | Plantaginaceae Total | | | | | | | | | | | | | | 0.50 | 5.50 | 5.50 | 5.50 | 0.50 | 0.50 | 3.00 |
| | Rubiaceae | Rubia tinctorum L. | 🟩 | | | | | | | | | 3.00 | | | | | | | | | 3.00 |
| | Rubiaceae Total | | | | | | | | | | | 3.00 | | | | | | | | | 3.00 |
| | Scrophulariaceae | Veronica sp. | 🟩 | | | | | | | | | 5.50 | | | | | | | | | 5.50 |
| | Scrophulariaceae Total | | | | | | | | | | | 5.50 | | | | | | | | | 5.50 |
| E3 Total | | | | | | | | | | | | 28.73 | 31.96 | 30.08 | 29.71 | 20.34 | 24.73 | 34.17 | 23.47 | 15.47 | 25.82 |

| | | | Blooming period | | | | | | | | | Average percentage of cover | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Orchard | Family | Plant species | 25/Apr | 9/May | 23/May | 6/Jun | 20/Jun | 4/Jul | 18/Jul | 7/Aug | 29/Aug | 25/Apr | 9/May | 23/May | 6/Jun | 20/Jun | 4/Jul | 18/Jul | 7/Aug | 29/Aug | Total |
| E4 | Apiaceae | Foeniculum vulgare Mill. | | | | | | | | | | 0.50 | 0.50 | 5.50 | 5.50 | | 0.50 | | | | 2.50 |
| | | Torilis arvensis (Huds.) Link | | | 🟩 | | | | | | | 3.00 | | 18.00 | | | | | | | 8.00 |
| | Apiaceae Total | | | | | | | | | | | 2.17 | 0.50 | 11.75 | 5.50 | | 0.50 | | | | 4.56 |
| | Asteraceae | Calendula arvensis (Vaill.) L. | | | | | | | | | | | | | | | 5.50 | | | | 5.50 |
| | | Carduus tenuiflorus Curtis | | | 🟩 | | | | | | | | | 5.50 | | | | | | | 5.50 |
| | | Conyza sp. | | | | | | | | | | | | | 5.50 | | 5.50 | | | | 5.50 |
| | | Lactuca serriola L. | | | | | | 🟩 | 🟩 | | | 0.50 | 0.50 | 5.50 | 5.50 | 5.50 | 3.00 | 5.50 | | | 3.83 |
| | | Picris sp. | | | | 🟩 | 🟩 | | | | | | | | 5.50 | 5.50 | 18.00 | 0.50 | | | 7.00 |
| | | Sonchus sp. | 🟩 | 🟩 | | | | | | | | 9.25 | 9.25 | 5.50 | 5.50 | | | | | | 7.64 |
| | Asteraceae Total | | | | | | | | | | | 6.33 | 4.88 | 5.50 | 5.50 | 5.50 | 7.00 | 3.00 | | | 5.59 |
| | Brassicaceae | Cardaria draba L. | | | | | | | | | | 0.50 | | | | | | | | | 0.50 |
| | Brassicaceae Total | | | | | | | | | | | 0.50 | | | | | | | | | 0.50 |
| | Chenopodiaceae | Beta vulgaris L. | 🟩 | 🟩 | | 🟩 | | | | | | 18.00 | 18.00 | | 18.00 | | | | | | 18.00 |
| | | Chenopodium sp. | | | 🟩 | | | | | | | | 0.50 | 5.50 | 5.50 | 5.50 | 0.50 | 3.00 | 5.50 | 18.00 | 5.25 |
| | Chenopodiaceae Total | | | | | | | | | | | 18.00 | 9.25 | 5.50 | 11.75 | 5.50 | 0.50 | 3.00 | 5.50 | 18.00 | 8.19 |
| | Convolvulaceae | Convolvulus arvensis L. | | | | | | | 🟩 | | | 0.50 | 5.50 | 5.50 | | 5.50 | | 0.50 | | 3.00 | 3.00 |
| | Convolvulaceae Total | | | | | | | | | | | 0.50 | 5.50 | 5.50 | | 5.50 | | 0.50 | | 3.00 | 3.00 |
| | Euphorbiaceae | Euphorbia sp. | 🟩 | 🟩 | | | | | | | | 0.50 | 0.50 | | | | | | | | 0.50 |
| | Euphorbiaceae Total | | | | | | | | | | | 0.50 | 0.50 | | | | | | | | 0.50 |
| | Fabaceae | Medicago sativa L. | | | | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 0.50 | 0.50 | 5.50 | 5.50 | 18.00 | 0.50 | 5.50 | 5.50 | 5.50 | 5.22 |
| | | Trifolium pratense L. | | | | | 🟩 | | | | 🟩 | | | | | 5.50 | | | | 0.50 | 3.00 |
| | | Trifolium repens L. | | | | 🟩 | | | | | | | | 5.50 | 5.50 | | | | | | 5.50 |
| | | Vicia sativa L. | | | | | | | | | | 5.50 | | | | | | | | | 5.50 |
| | Fabaceae Total | | | | | | | | | | | 3.00 | 0.50 | 5.50 | 5.50 | 11.75 | 0.50 | 5.50 | 5.50 | 3.00 | 4.96 |
| | Geraniaceae | Erodium sp. | | | | | | | | | | | | 5.50 | | | | | | | 5.50 |
| | Geraniaceae Total | | | | | | | | | | | | | 5.50 | | | | | | | 5.50 |
| | Gramineae | Gramineae | 🟩 | 🟩 | 🟩 | 🟩 | | | | | | 31.89 | 37.69 | 28.45 | 17.38 | 21.18 | 23.91 | 26.56 | 25.50 | 38.19 | 27.06 |
| | Gramineae Total | | | | | | | | | | | 31.89 | 37.69 | 28.45 | 17.38 | 21.18 | 23.91 | 26.56 | 25.50 | 38.19 | 27.06 |
| | Malvaceae | Malva sylvestris L. | | | | | | | | 🟩 | | | | | | | | | 5.50 | 0.50 | 3.00 |
| | Malvaceae Total | | | | | | | | | | | | | | | | | | 5.50 | 0.50 | 3.00 |
| | Primulaceae | Anagallis arvensis L. | | | 🟩 | 🟩 | | 🟩 | | | | | | 5.50 | 5.50 | | 5.50 | | | | 5.50 |
| | Primulaceae Total | | | | | | | | | | | | | 5.50 | 5.50 | | 5.50 | | | | 5.50 |
| | Rosaceae | Potentilla reptans L. | | | 🟩 | | | | | | | | | 18.00 | 5.50 | 5.50 | 5.50 | 0.50 | 11.75 | 12.17 | 10.27 |
| | | Rubus ulmifolius Schott | | | | | | | | | | 0.50 | 0.50 | 5.50 | 18.00 | 18.00 | 18.00 | 9.25 | 18.00 | 3.83 | 9.07 |
| | Rosaceae Total | | | | | | | | | | | 0.50 | 0.50 | 13.83 | 11.75 | 11.75 | 11.75 | 6.33 | 14.88 | 8.00 | 9.60 |
| | Scrophulariaceae | Veronica sp. | 🟩 | | 🟩 | | | | | | | 5.50 | | 5.50 | | | | | | | 5.50 |
| | Scrophulariaceae Total | | | | | | | | | | | 5.50 | | 5.50 | | | | | | | 5.50 |
| E4 Total | | | | | | | | | | | | 13.80 | 17.38 | 15.86 | 11.94 | 15.38 | 14.93 | 15.33 | 17.84 | 19.20 | 15.53 |
| E5 | Apiaceae | Torilis arvensis (Huds.) Link | | | | 🟩 | | | | | | | | | 5.50 | | | | | | 5.50 |
| | Apiaceae Total | | | | | | | | | | | | | | 5.50 | | | | | | 5.50 |
| | Asteraceae | Anacyclus clavatus (Desf.) Pers. | | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | | | | 5.50 | 11.75 | 9.25 | 11.75 | 18.00 | 18.00 | | 5.50 | 11.25 |
| | | Carduus tenuiflorus Curtis | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | | | | | 18.00 | 18.00 | 5.50 | 3.00 | 18.00 | 5.50 | 5.50 | | 0.50 | 8.25 |
| | | Lactuca serriola L. | | | | | | | 🟩 | 🟩 | 🟩 | | | 5.50 | 3.00 | 18.00 | 11.75 | 9.25 | 18.00 | 9.25 | 9.82 |
| | | Picris sp. | | | | | 🟩 | 🟩 | 🟩 | | | 0.50 | 5.50 | | 5.50 | 5.50 | 18.00 | 5.50 | | | 6.75 |
| | | Sonchus sp. | | | | | | | | | | | | 5.50 | | 5.50 | | | | | 5.50 |
| | Asteraceae Total | | | | | | | | | | | 9.25 | 9.67 | 7.58 | 5.14 | 11.75 | 13.00 | 9.50 | 18.00 | 6.13 | 9.09 |
| | Brassicaceae | Cardaria draba L. | 🟩 | 🟩 | | | | | | | | 11.75 | 11.75 | 5.50 | | | | | | | 10.50 |
| | Brassicaceae Total | | | | | | | | | | | 11.75 | 11.75 | 5.50 | | | | | | | 10.50 |
| | Convolvulaceae | Convolvulus arvensis L. | | | | | | 🟩 | | 🟩 | 🟩 | | | 5.50 | 2.17 | 11.75 | 18.00 | 18.00 | 9.67 | 0.50 | 7.64 |
| | Convolvulaceae Total | | | | | | | | | | | | | 5.50 | 2.17 | 11.75 | 18.00 | 18.00 | 9.67 | 0.50 | 7.64 |
| | Equisetaceae | Equisetum sp. | | | | | | | | | | | 5.50 | 5.50 | 8.63 | 23.00 | 23.00 | 14.88 | 19.88 | 18.63 | 15.50 |
| | Equisetaceae Total | | | | | | | | | | | | 5.50 | 5.50 | 8.63 | 23.00 | 23.00 | 14.88 | 19.88 | 18.63 | 15.50 |
| | Fabaceae | Trifolium repens L. | | | | | | | | | | | | 18.00 | | | | | | | 18.00 |
| | | Vicia sativa L. | 🟩 | 🟩 | | | | | | | | 5.50 | 5.50 | | | | | | | | 5.50 |
| | Fabaceae Total | | | | | | | | | | | 5.50 | 5.50 | 18.00 | | | | | | | 8.63 |
| | Gramineae | Gramineae | 🟩 | 🟩 | 🟩 | 🟩 | | | | | | 22.95 | 21.61 | 14.82 | 17.72 | 9.67 | 21.93 | 16.21 | 8.94 | 17.38 | 17.09 |
| | Gramineae Total | | | | | | | | | | | 22.95 | 21.61 | 14.82 | 17.72 | 9.67 | 21.93 | 16.21 | 8.94 | 17.38 | 17.09 |
| | Malvaceae | Malva sylvestris L. | | 🟩 | | | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 18.00 | 18.00 | | 18.00 | 9.25 | 19.25 | 38.00 | 18.00 | 18.00 | 18.50 |
| | Malvaceae Total | | | | | | | | | | | 18.00 | 18.00 | | 18.00 | 9.25 | 19.25 | 38.00 | 18.00 | 18.00 | 18.50 |
| | Primulaceae | Anagallis arvensis L. | 🟩 | | | | | | | | | 19.25 | | | | | | | | | 19.25 |
| | Primulaceae Total | | | | | | | | | | | 19.25 | | | | | | | | | 19.25 |
| | Rosaceae | Potentilla reptans L. | | 🟩 | 🟩 | 🟩 | | | | | | | 5.50 | 38.00 | 18.00 | 18.00 | 18.00 | 18.00 | 18.00 | 18.00 | 18.94 |
| | | Rubus ulmifolius Schott | | | | | | | | | | 31.75 | 40.50 | 5.50 | 9.67 | 20.50 | 20.50 | 13.83 | 14.88 | 7.38 | 16.85 |
| | Rosaceae Total | | | | | | | | | | | 31.75 | 28.83 | 16.33 | 11.75 | 19.88 | 19.88 | 14.88 | 15.50 | 9.50 | 17.34 |
| E5 Total | | | | | | | | | | | | 19.85 | 16.98 | 11.21 | 10.59 | 14.25 | 19.41 | 15.27 | 13.34 | 12.69 | 14.55 |
| Grand Total | | | | | | | | | | | | 16.98 | 20.96 | 16.98 | 16.96 | 16.36 | 18.31 | 19.14 | 16.52 | 14.70 | 17.35 |

Table S4. Level of identification, location, developmental stage of the arthropods found in the samplings and type of statistical analysis (this table continues on the next page).

| Type of sampling | Location of the identification | Order | Family (*Infraorder) | Level of identification | Developmental stage found/identified | Identification observations |
|---|---|---|---|---|---|---|
| Visual observations | Field | Diptera | Syrphidae | Family | Adults | |
| Beating tray samplings | Field | Araneae | - | Order | Immatures and adults | |
| | | Thysanoptera | Aeolothripidae | Family | Immatures and adults | |
| | | | Non-Aeolothripidae | Family | Immatures and adults | |
| | | Coleoptera | Coccinellidae | Family | Immatures and adults | |
| | | | Staphilinidae | Family | Adults | |
| | | | Carabidae | Family | Adults | |
| | | | Cantaridae | Family | Adults | |
| | | Heteroptera | Miridae | Family | Immatures and adults | |
| | | | Nabidae | Family | Immatures and adults | |
| | | | Anthocoridae | Family | Immatures and adults | |
| | | | Pentatomidae | Family | Immatures and adults | |
| | | | Lygaeidae | Family | Immatures and adults | |
| | | Neuroptera | Chrysopidae | Family | Immatures and adults | |
| | | Diptera | Cecidomyiidae | Family | Immatures and adults | |
| | | | Syrphidae | Family | Immatures | |
| | | Trombidiformes | Trombidiidae | Family | Immatures and adults | |
| | | Dermaptera | Forficulidae | Family | Immatures and adults | |
| | | Hemiptera | Aphididae | Family | Immatures and adults | |
| | | Hymenoptera | Parasitica* | Infraorder (Ichneumonoidea + Chalcidoidea) | Immatures (mummies) and adults | |
| RAA colonies | Field + Laboratory | Dermaptera | Forficulidae | Family | Immatures and adults | |
| | | Araneae | - | Order | Immatures and adults | |
| | | Coleoptera | Coccinellidae | Family | Immatures and adults | |
| | | Neuroptera | Chrysopidae | Family | Immatures and adults | |
| | | Heteroptera | Miridae | Family | Immatures and adults | |
| | | Diptera | Cecidomyiidae | Family | Immatures and adults | |
| | | | Syrphidae | Family | Immatures and adults | |
| | | Hemiptera | Aphididae | Species (*Dysaphis plantaginea* ) | Immatures and adults | |
| | | Hymenoptera | Parasitica* | Infraorder (Ichneumonoidea + Chalcidoidea)** | Immatures (mummies) and adults | Only Ichneumonoidea found |
| WAA colonies | Field + Laboratory | Coleoptera | Coccinellidae | Family | Immatures and adults | |
| | | Heteroptera | Miridae | Family | Immatures and adults | |
| | | Hemiptera | Aphididae | Species (*Dysaphis plantaginea* ) | Immatures and adults | |
| | | Hymenoptera | *Aphelinus mali* | Species | Immatures and adults | Only A mali found |

** A sample of 16 individuals was identified to the lowest taxon possible (species or genera) with taxonomic keys.

| Type of sampling | Location of the identification | Order | Family (*Infraorder) | GLM (global analysis) | | GLM (weekly analysis) | | Description of the natural enemies found in the aphid colonies | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Used for the analysis? | Grouping | Used for the analysis? | Grouping | Used for the analysis? | Grouping |
| Visual observations | Field | Diptera | Syrphidae | Yes | Syrphidae | Yes | Syrphidae | No | |
| Beating tray samplings | Field | Araneae | - | Yes | Araneae | Yes | Predators | No | |
| | | Thysanoptera | Aeolothripidae | Yes | Predatory Thysanoptera | Yes | Predators | No | |
| | | | Non-Aeolothripidae | Yes | Phytophagous insects | Yes | Phytophagous insects | No | |
| | | Coleoptera | Coccinellidae | Yes | Predatory Coleoptera | Yes | Predators | No | |
| | | | Staphilinidae | Yes | Predatory Coleoptera | Yes | Predators | No | |
| | | | Carabidae | Yes | Predatory Coleoptera | Yes | Predators | No | |
| | | | Cantaridae | Yes | Predatory Coleoptera | Yes | Predators | No | |
| | | Heteroptera | Miridae | Yes | Predatory Heteroptera | Yes | Predators | No | |
| | | | Nabidae | Yes | Predatory Heteroptera | Yes | Predators | No | |
| | | | Anthocoridae | Yes | Predatory Heteroptera | Yes | Predators | No | |
| | | | Pentatomidae | Yes | Phytophagous insects | Yes | Phytophagous insects | No | |
| | | | Lygaeidae | Yes | Phytophagous insects | Yes | Phytophagous insects | No | |
| | | Neuroptera | Chrysopidae | Yes | Other predators | Yes | Predators | No | |
| | | Diptera | Cecidomyiidae | Yes | Other predators | Yes | Predators | No | |
| | | | Syrphidae | Yes | Ohter predators | Yes | Predators | No | |
| | | Trombidiformes | Trombidiidae | Yes | Other predators | Yes | Predators | No | |
| | | Dermaptera | Forficulidae | Yes | Other predators | Yes | Predators | No | |
| | | Hemiptera | Aphididae | Yes | Phytophagous insects | Yes | Phytophagous insects | No | |
| | | Hymenoptera | Parasitica* | Yes | Parasitoids | Yes | Parasitoids | No | |
| RAA colonies | Field + Laboratory | Dermaptera | Forficulidae | No | | No | | Yes | Other predators |
| | | Araneae | - | No | | No | | Yes | Ohter predators |
| | | Coleoptera | Coccinellidae | No | | No | | Yes | Ohter predators |
| | | Neuroptera | Chrysopidae | No | | No | | Yes | Ohter predators |
| | | Heteroptera | Miridae | No | | No | | Yes | Ohter predators |
| | | Diptera | Cecidomyiidae | No | | No | | Yes | Other predators |
| | | | Syrphidae | No | | No | | Yes | Syrphidae |
| | | Hemiptera | Aphididae | No | | No | | Yes | RAA |
| | | Hymenoptera | Parasitica* | No | | No | | Yes | Parasitoids |
| WAA colonies | Field + Laboratory | Coleoptera | Coccinellidae | No | | No | | Yes | Ohter predators |
| | | Heteroptera | Miridae | No | | No | | Yes | Ohter predators |
| | | Hemiptera | Aphididae | No | | No | | Yes | WAA |
| | | Hymenoptera | *Aphelinus mali* | No | | No | | Yes | Parasitoids (*A.mali*) |

| Type of sampling | Location of the identification | Order | Family (*Infraorder) | Correlations between margins | | Correlations between RAA colonies and margins | | Correlations between WAA colonies and margins | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Used for the analysis? | Grouping | Used for the analysis? | Grouping | Used for the analysis? | Grouping |
| Visual observations | Field | Diptera | Syrphidae | Yes | Syrphidae | Yes | Syrphidae | Yes | Syrphidae |
| Beating tray samplings | Field | Araneae | - | Yes | Predators | Yes | Predators | Yes | Predators |
| | | Thysanoptera | Aeolothripidae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | | Non-Aeolothripidae | Yes | Phytophagous insects | Yes | Phytophagous insects | Yes | Phytophagous insects |
| | | Coleoptera | Coccinellidae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | | Staphilinidae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | | Carabidae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | | Cantaridae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | Heteroptera | Miridae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | | Nabidae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | | Anthocoridae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | | Pentatomidae | Yes | Phytophagous insects | Yes | Phytophagous insects | Yes | Phytophagous insects |
| | | | Lygaeidae | Yes | Phytophagous insects | Yes | Phytophagous insects | Yes | Phytophagous insects |
| | | Neuroptera | Chrysopidae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | Diptera | Cecidomyiidae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | | Syrphidae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | Trombidiformes | Trombidiidae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | Dermaptera | Forficulidae | Yes | Predators | Yes | Predators | Yes | Predators |
| | | Hemiptera | Aphididae | Yes | Phytophagous insects | Yes | Phytophagous insects | Yes | Phytophagous insects |
| | | Hymenoptera | Parasitica* | Yes | Parasitoids | Yes | Parasitoids | Yes | Parasitoids |
| RAA colonies | Field + Laboratory | Dermaptera | Forficulidae | No | | Yes | Non-Syrphidae predators | No | |
| | | Araneae | - | No | | Yes | Non-Syrphidae predators | No | |
| | | Coleoptera | Coccinellidae | No | | Yes | Non-Syrphidae predators | No | |
| | | Neuroptera | Chrysopidae | No | | Yes | Non-Syrphidae predators | No | |
| | | Heteroptera | Miridae | No | | Yes | Non-Syrphidae predators | No | |
| | | Diptera | Cecidomyiidae | No | | Yes | Non-Syrphidae predators | No | |
| | | | Syrphidae | No | | Yes | Syrphidae | No | |
| | | Hemiptera | Aphididae | No | | Yes | - | No | |
| | | Hymenoptera | Parasitica* | No | | Yes | Parasitoids | No | |
| WAA colonies | Field + Laboratory | Coleoptera | Coccinellidae | No | | No | | Yes | Predators |
| | | Heteroptera | Miridae | No | | No | | Yes | Predators |
| | | Hemiptera | Aphididae | No | | No | | Yes | - |
| | | Hymenoptera | *Aphelinus mali* | No | | No | | Yes | Parasitoids |

Table S5. Tests statistics (F-value (F)) and p (likelihood ratio) for the interaction between treatments (Year*Treatment) and Year for the number of: adult hoverflies, predators, parasitoids and phytophagous insects.

| | | VO | | BTS | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Adult hoverflies | | All predators | | Parasitoid wasps | | Phytophagous insects | |
| | | $F_{1,12}$ | p | $F_{1,12}$ | p | $F_{1,12}$ | p | $F_{1,12}$ | p |
| Year*Treatment | 11-Apr | 2.977 | 0.121 | 0.369 | 0.558 | 0.154 | 0.706 | 0.056 | 0.819 |
| | 25-Apr | 2.995 | 0.120 | 1.321 | 0.279 | 0.218 | 0.660 | 1.559 | 0.245 |
| | 9-May | 3.383 | 0.097 | 0.292 | 0.601 | 1.716 | 0.224 | 0.014 | 0.910 |
| | 23-May | 1.594 | 0.240 | 0.066 | 0.802 | 2.041 | 0.194 | 0.372 | 0.558 |
| | 6-Jun | 14.070 | **0.006** | 10.759 | **0.011** | 1.970 | 0.198 | 0.538 | 0.490 |
| | 20-Jun | 0.317 | 0.591 | 7.370 | **0.029** | 0.335 | 0.577 | 0.424 | 0.531 |
| | 4-Jul | 0.256 | 0.627 | 0.276 | 0.612 | 2.131 | 0.175 | 0.628 | 0.450 |
| | 18-Jul | 0.400 | 0.542 | 0.239 | 0.637 | 0.013 | 0.914 | 0.029 | 0.870 |
| | 1-Aug | 2.506 | 0.149 | 1.257 | 0.291 | 0.526 | 0.491 | 12.530 | **0.008** |
| | 15-Aug | 0.564 | 0.472 | 0.113 | 0.746 | 3.917 | 0.081 | 0.167 | 0.693 |
| | 29-Aug | 0.324 | 0.583 | 0.703 | 0.425 | 2.740 | 0.138 | 5.764 | **0.046** |
| | 12-Sep | 0.546 | 0.479 | 0.327 | 0.581 | 1.928 | 0.201 | 0.828 | 0.390 |
| Year | 11-Apr | 1.369 | 0.267 | 1.890 | 0.198 | 5.486 | **0.042** | 0.000 | 0.996 |
| | 25-Apr | 6.375 | **0.029** | 0.301 | 0.594 | 0.016 | 0.902 | 0.223 | 0.646 |
| | 9-May | 0.009 | 0.925 | 1.497 | 0.247 | 3.486 | 0.090 | 0.400 | 0.541 |
| | 23-May | 0.012 | 0.915 | 0.000 | 0.993 | 1.434 | 0.258 | 1.075 | 0.325 |
| | 6-Jun | 5.760 | **0.040** | 1.921 | 0.194 | 0.003 | 0.960 | 4.369 | 0.064 |
| | 20-Jun | 0.365 | 0.559 | 1.993 | 0.188 | 0.496 | 0.496 | 0.559 | 0.470 |
| | 4-Jul | 0.064 | 0.805 | 0.997 | 0.339 | 13.476 | **0.004** | 2.077 | 0.181 |
| | 18-Jul | 0.511 | 0.490 | 2.156 | 0.171 | 0.901 | 0.366 | 0.594 | 0.458 |
| | 1-Aug | 0.572 | 0.466 | 0.035 | 0.856 | 2.749 | 0.129 | 0.001 | 0.971 |
| | 15-Aug | 1.674 | 0.222 | 15.048 | **0.004** | 3.896 | 0.075 | 19.360 | **0.002** |
| | 29-Aug | 0.001 | 0.981 | 4.066 | 0.071 | 0.269 | 0.615 | 5.295 | **0.047** |
| | 12-Sep | 1.199 | 0.298 | 1.695 | 0.219 | 0.323 | 0.582 | 1.077 | 0.326 |

*Significant p values ($p<0.05$) are shown in bold.

## Chapter 3

# *Sphaerophoria rueppellii* adults change their foraging behavior after mating but maintain the same preferences to flower traits

Neus Rodríguez-Gasol, Jesús Avilla, Simó Alegre, Georgina Alins

The content of this chapter has been published in
BioControl (2019) 64(2): 149-158. doi: 10.1007/s10526-019-09928-2

## Abstract

Hoverflies can play an important role in aphid biological control. Adult hoverflies depend on pollen and nectar to survive. Therefore, the placement of flower resources in agroecosystems is a common method to enhance the populations of these insects. When foraging, hoverflies rely on visual cues to select flowers. We studied the preference of *Sphaerophoria rueppellii* (Wiedemann) (Diptera: Syrphidae) adults for several flower traits and examined whether mating influenced foraging behavior. We observed that these insects were greatly attracted to bouquets of 12 flat circle-shaped flowers (half white and half yellow). Furthermore, yellow flowers elicited landing more than other colors, regardless of the type of bouquet. With respect to the effect of mating on posterior foraging behavior, virgin individuals showed more movement than gravid ones. Our results shed light on the behavior of adult hoverflies and can be used to improve habitat management practices that seek to promote biological control.

**Keywords**: Syrphidae, Hoverfly, Biological control, Visual cues, Gravid, Sex

# 1. Introduction

Hoverflies (Diptera: Syrphidae) are an abundant group of beneficial arthropods in agroecosystems. The larvae of about one third of the species feed on soft-bodied Hemiptera, mainly aphids (Hemiptera: Aphididae) (Rojo et al. 2003) and therefore have a high potential for biological control purposes (Hickman and Wratten 1996; Skirvin et al. 2011; Tenhumberg and Poehling 1995; van Rijn et al. 2006; White et al. 1995). Adult hoverflies, in turn, feed on nectar and pollen. Nectar is rich in carbohydrates, which provide the energy required for adult survival, while pollen supplies the proteins and amino acids that allow sexual maturation in both sexes and egg production in females (Gilbert 1981; Haslett 1989a).

Flowers use a variety of cues and rewards to attract visitors, and the efficacy of these traits depends on the spatial scale and the type of pollinator. Hoverflies use floral resources selectively (Gilbert 1981), choosing flowers on the basis of one or more attractive traits (Ambrosino et al. 2006). When foraging, hoverflies rely mainly on visual cues, like the size (Conner and Rush 1996; Sutherland et al. 1999), shape (Gong and Huang 2009) and color (Day et al. 2015; Dinkel and Lunau 2001; Laubertie et al. 2006; Sutherland et al. 1999) 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; Laubertie et al. 2006; Lunau and Wacht 1994; Sutherland et al. 1999), and that this color can even elicit a proboscis extension response in some species (Dinkel and Lunau 2001; Lunau and Wacht 1994). Nonetheless, other flower traits like odors (Laubertie et al. 2006; Nordstrom et al. 2017; Primante and Dotterl 2010) and accessibility to nectar and pollen can also play an important role in hoverfly preference (Branquart and Hemptinne 2000b; Gilbert 1981; van Rijn and Wäckers 2016).

The relative attractiveness of the floral traits differs on the basis of the intrinsic attributes of the visitors, such as species (Haslett 1989b; Lunau et al. 2018), age (Almohamad et al. 2009; Sadeghi and Gilbert 2000; Sutherland et al. 1999) and sex (Sutherland et al. 1999). Sex differences are determined mainly by different nutritional requirements. Males of hoverflies only need an initial amount of pollen to allow spermatogenesis and can later feed mostly on nectar to meet their high energetic demands for sustaining their search for mates. On the other hand, females require higher amounts of pollen and for a longer period in order to achieve ovary maturation and continuous oviposition (Branquart and Hemptinne 2000a; Gilbert 1993; Gilbert 1981; Haslett 1989a). In this regard, hunger can also increase hoverfly attraction to yellow water traps, while satiated individuals are less likely to invest effort in investigating a distant food source (Hickman et al. 2001; Laubertie et al. 2006; Wratten et al. 2003).

Due to the dependence of adult hoverflies on flowers, these insects have been widely used in habitat manipulation schemes to enhance agroecosystem services in farmlands, such as biological control and pollination (Gurr et al. 2017; Haenke et al. 2009; Hogg et al. 2011; Landis et al. 2000; Macleod 1999; Wratten et al. 2012). Notwithstanding, more research is needed to identify the common visual traits that attract hoverflies to flower resources and to better understand the foraging behavior of these insects. In this regard, the objectives of this study were: 1) to assess the attractiveness of three flower traits (shape, number of flowers and color diversity) to hoverflies; and 2) to determine whether mating alters the foraging behavior of these flies.

## 2. Materials and methods

### 2.1 Insects

To study hoverfly preferences and behavior, adults of *Sphaerophoria rueppellii* (Wiedemann) (Diptera: Syrphidae) were used. Hoverfly pupae were purchased (Sphaerophoria-System, Biobest, Belgium) and left to develop in a phytoclimatic chamber (Fitoclima, ARALAB 10000 HP) under the following conditions: 25/19 ± 0.5 ºC day/night, 60 ± 2 % relative humidity, 16:8 h (L:D) photoperiod, and light intensity of 22,200 lux. The emerged individuals were separated into three categories (adult types from now onwards): virgin males, virgin females and gravid females. In order to obtain virgin individuals, adults between 1 and 24 hours old were placed in two cages: one for males and one for females. Gravid females were obtained by placing males and females in the same cage from emergence to the date of the experiment. After the experiments, virgin and gravid females were examined to check their mating status (Gilbert 1993).

Adult hoverflies were fed bee-collected commercial pollen (Apisol, Spain), water and a solution of 1.6% sucrose absorbed on filter paper, all provided ad libitum. In addition, a plastic pot (12 cm width x 12 cm length x 20 cm height) with 13 wheat plants infested with aphids was introduced into each cage in order to stimulate mating behavior and oviposition.

### 2.2 Artificial flowers

White EVA foam (FAIBO, Spain) was used to make the corolla (2 cm diameter) of the artificial flowers, and a 10 cm-long metal wire was used for the stem. The flowers were painted fluorescent yellow, blue or white (3104 Gelb, 3107 Blay, 3108 Weiss, respectively, Sparvar RAL Leuchtfarbspray (Spray-Color GmbH, Merzenich, Germany)).

To evaluate the most attractive flower traits, the following three consecutive experiments were performed (Figure 1):

- *Experiment 1*: we made yellow flowers with a diameter of 2 cm and tested the following: a sphere-shaped, a circle-shaped, and a five-petal flower ("flower-shaped").
- *Experiment 2*: the shape with the best results in the previous trial was evaluated in bouquets of 1, 3, 6, or 12 artificial flowers.
- *Experiment 3*: the bouquet with the best results obtained in Experiment 2 was used to assess five combination of colors: 1) all-yellow bouquet, 2) ½ yellow and ½ white bouquet,

3) ½ yellow and ½ blue bouquet, 4) ½ white and ½ blue bouquet, and 5) ⅓ yellow, ⅓ white and ⅓ blue bouquet.

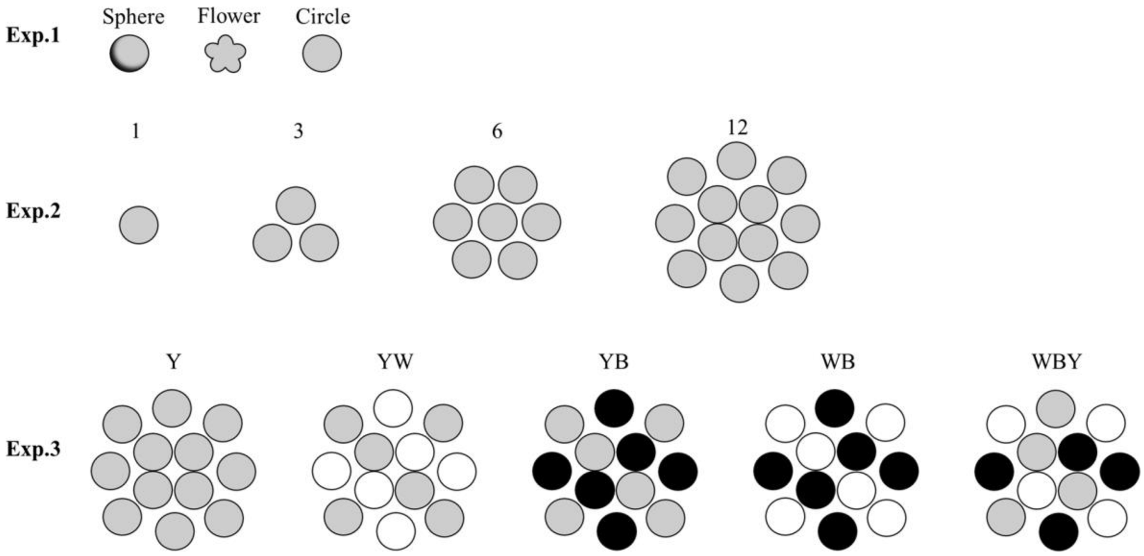


Figure 1. Schematic diagram of the three consecutive experiments performed. In Experiment **1** Grey circles represent yellow flowers, black circles represent blue flowers and white circles represent white flowers. In Experiment **2** *1* a single flower, *3* bouquet of three flowers, *6* bouquet of six flowers, *12* bouquet of 12 flowers. In Experiment **3** *Y* all-yellow bouquet, *YW* ½ yellow and ½ white bouquet, *YB* ½ yellow and ½ blue bouquet, *WB* ½ white and ½ blue bouquet, and *WBY* ⅓ yellow, ⅓white and ⅓ blue bouquet.

### 2.3 Experiments

To run the experiments, 15 individuals aged between 7 and 20 days old were exposed to the artificial flowers or bouquets for 60 min per replicate. During this period, the behavior of the hoverflies was recorded using a JVC Everio GZ-MG610 Camcorder at a distance of 50 cm from the flowers or bouquets. These flowers were placed close and along the narrowest side of the cage, spaced 15 cm from each other. The videos were watched, and visits and landings were counted in each replicate. A visit was defined as an individual hovering at less than 3 cm from a flower, and a landing as resting on a flower. A new visit or landing was considered when a hoverfly approached a flower again after previously moving more than 6 cm away from it.

In each replicate, no experienced hoverflies were used and no food or reward was offered during the experiments. Experiments were run in a climatic chamber with the same conditions as those used to maintain the insects. Recordings were performed during all day round, the groups tested were randomized in order to avoid time effects.

*Experiment 1*

Four replicates for each type of adult were done and the position of the treatments was different in every replicate. Furthermore, all the flower shapes were tested in all the possible positions, thereby avoiding positional preferences. The experimental cage measured 40 cm x 80 cm x 40 cm (width x length x height).

*Experiment 2*

Replicates and experimental conditions were as in Experiment 1.

*Experiment 3*

Five replicates for each type of adult were done. In this case, the color of the flower in each bouquet on which insects landed was noted. A larger cage was used in this experiment (50 cm width, 58 cm length and 58 cm height) because of the higher number of artificial flowers tested.

### 2.4 Data analysis

To study hoverfly preferences to the distinct artificial flowers, we calculated the percentage of visits, landings, and visits + landings and performed a two-way ANOVA (adult type and treatment). In Experiment 3, we also evaluated the color preference for landing. To this end, the percentage of landings per color, regardless of the type of bouquet was calculated. The bouquet which was only yellow (Y) was excluded from this analysis. In this case, neither non-transformed nor transformed data met the ANOVA assumptions, so a two-way analysis was not possible. Since data met the ANOVA assumptions when they were analyzed by adult type, we carried out a one-way ANOVA to test color preferences by type of adult. To analyze behavioral differences between types of adult, the total number of visits and landings was used to perform a two-way ANOVA (adult type and treatment).

When needed, data were arcsin-transformed (in the case of the percentages) or log- transformed (in the case of the sums) to meet the ANOVA assumptions. The HSD-Tukey was used as a post-hoc test after the ANOVA to compare means. Data were analyzed using the JMP statistical software package (Version 13; SAS Institute Inc., Cary, North Carolina).

## 3. Results

### 3.1. Selection of the attractive traits of flowers

In Experiment 1, there was no significant interaction between type of adult and treatment (shape of the flower) (Table 1). Flower-shaped flowers were significantly less visited and landed on by hoverflies than the circle-shaped and sphere-shaped ones. However, when considering visits and landings together, only the circle-shaped flower was significantly more attractive than the flower-shaped flower (Figure 2a). Moreover, though no statistical differences were observed between the sphere-shaped flower and the circle-shaped one, the latter was selected for the next experiments.

Table 1. Summary of the ANOVA results (F- and P-values) of the percentage of the different types of approach in Experiments 1–3.

| Experiments | Type of approach | Treatment x adult type | | Adult type | | Treatment | |
|---|---|---|---|---|---|---|---|
| | | F | P | F | P | F | P |
| 1 | % Visits | $F_{4,27}=1.571$ | 0.210 | $F_{2,27}<10^{-3}$ | 1.000 | $F_{2,27}=15.802$ | < 0.001 |
| | % Landings | $F_{4,27}=1.727$ | 0.173 | $F_{2,27}<10^{-3}$ | 1.000 | $F_{2,27}=8.435$ | 0.001 |
| | % Visits+landings | $F_{4,27}=1.537$ | 0.220 | $F_{2,27}<10^{-3}$ | 1.000 | $F_{2,27}=7.526$ | 0.003 |
| 2 | % Visits | $F_{6,24}=0.741$ | 0.622 | $F_{2,24}<10^{-3}$ | 1.000 | $F_{3,24}=11.770$ | < 0.001 |
| | % Landings | $F_{6,24}=0.855$ | 0.541 | $F_{2,24}<10^{-3}$ | 1.000 | $F_{3,24}=4.716$ | 0.010 |
| | % Visits+landings | $F_{6,24}=0.756$ | 0.611 | $F_{2,24}<10^{-3}$ | 1.000 | $F_{3,24}=15.154$ | < 0.001 |
| 3 | % Visits | $F_{8,24}=0.487$ | 0.861 | $F_{2,24}<10^{-3}$ | 1.000 | $F_{4,24}=15.824$ | < 0.001 |
| | % Landings | $F_{8,24}=0.411$ | 0.910 | $F_{2,24}<10^{-3}$ | 1.000 | $F_{4,24}=78.840$ | < 0.001 |
| | % Visits+landings | $F_{8,24}=0.274$ | 0.972 | $F_{2,24}<10^{-3}$ | 1.000 | $F_{4,24}=43.244$ | < 0.001 |

In Experiment 2 there was no significant interaction between type of adult and treatment (no. of flowers per bouquet) (Table 1). The number of visits and landings increased as the number of artificial flowers in the bouquet rose (Figure 2b). Hoverflies visited bouquets with 3 or 12 flowers significantly more than single flowers. In regard to landings, there were significantly more landings on 12-flower bouquets than on 3-flower ones or the single flower. When considering visits and landings together, bouquets of 12 flowers were more attractive than the others (Figure 2b).

In Experiment 3 there was no significant interaction between type of adult and treatment (composition of the bouquet) (Table 1). The results were similar for all types of approaches: the artificial bouquet that combined yellow and white flowers (YW) received significantly more visits and landings than the rest. The second most visited bouquet comprised only yellow flowers (Y), followed by those with white, blue and yellow flowers (WBY) and then yellow and blue flowers (YB). The least attractive bouquet combined white and blue flowers (WB) (Figure 2c).

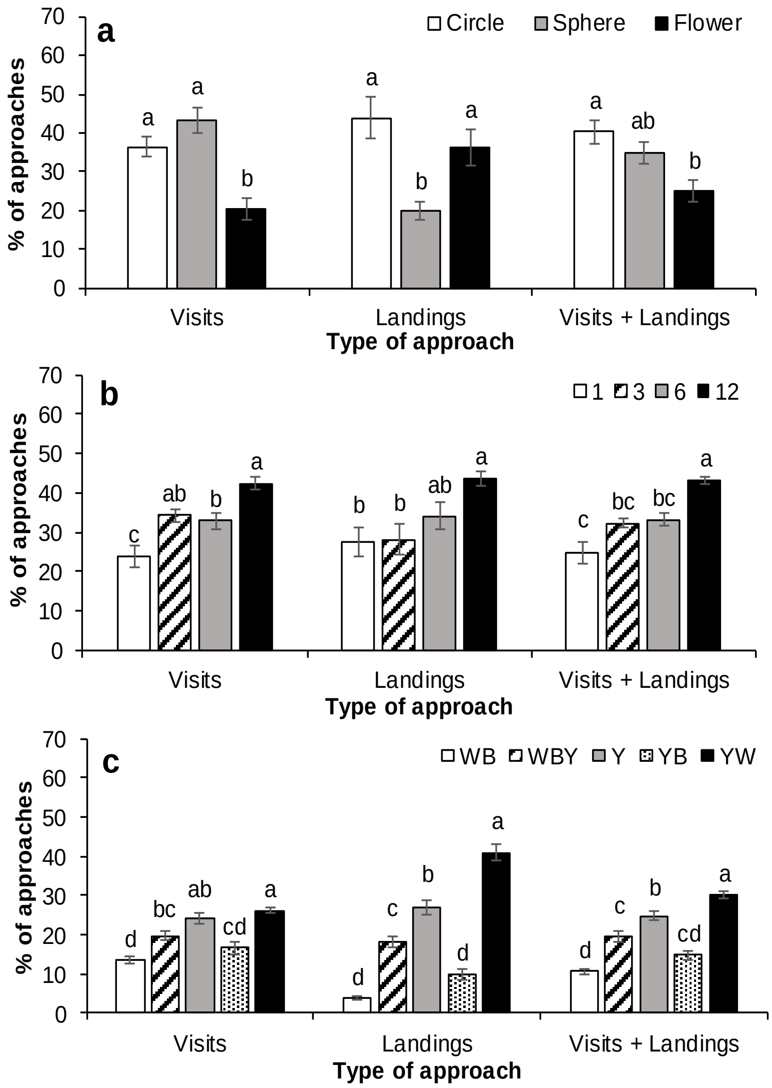


Figure 2. Percentage of hoverfly approaches (visits and landings) to the artificial flowers in **a** Experiment 1, **b** Experiment 2 and **c** Experiment 3. Vertical bars show SE. Different letters within each experiment show significant differences between treatments (P<0.05) according to the HSD-Tukey test. In Experiment 2: *1* a single flower, *3* bouquet of three flowers, *6* bouquet of six flowers, *12* bouquet of 12 flowers. In Experiment 3: *WB* 1/2 white and ½ blue bouquet, *WBY* ⅓ yellow, ⅓white and ⅓ blue bouquet, *Y* all-yellow bouquet, *YB* ½ yellow and ½ blue bouquet, and *YW* ½ yellow and ½ white bouquet.

In regard to the color that attracted most landings in Experiment 3, data were analyzed by type of adult. Significant differences were found regarding the percentage of landings on the different colors (Table 2). All adults showed a clear preference for yellow flowers and significantly discriminated between the three colors (Table 2).

Table 2. Summary of the ANOVA results (F- and P-values) of the percentage (±SE) of landings per color in Experiment 3.

| | **Virgin females** | **Gravid females** | **Virgin males** |
|---|---|---|---|
| Yellow | 66.13±3.43a | 76.49±1.04a | 68.52±5.62a |
| White | 26.62±3.00b | 19.64±0.78b | 25.93±5.01b |
| Blue | 7.25±2.13c | 3.87±0.97c | 5.55±2.25c |
| F | $F_{2,12}$=106.586 | $F_{2,12}$=1665.820 | $F_{2,12}$=50.180 |
| P | < 0.001 | < 0.001 | < 0.001 |

Different letters in the same column show significant differences between treatments (P < 0.05) according to the HSD-Tukey test.

### 3.2. Assessment of mating effects on hoverfly foraging behavior

No significant interaction between type of adult and treatment was found in any of the experiments (Table 3). Significant differences were found between the adult type in Experiments 1, 2 and 3 with regard to movement (Table 3).

Table 3. Summary of the ANOVA results (F- and P-values) of the number of visits and landings in Experiments 1–3.

| **Experiments** | **Type of approach** | **Treatment × adult type** | | **Adult type** | | **Treatment** | |
|---|---|---|---|---|---|---|---|
| | | F | P | F | P | F | P |
| 1 | Number of visits | $F_{4,27}$=0.138 | 0.967 | $F_{2,27}$=18.453 | < 0.001 | $F_{2,27}$=1.709 | 0.200 |
| | Number of landings | $F_{4,27}$=0.441 | 0.778 | $F_{2,27}$=4.167 | 0.027 | $F_{2,27}$=4.911 | 0.015 |
| 2 | Number of visits | $F_{6,24}$=0.308 | 0.927 | $F_{2,24}$=6.250 | 0.007 | $F_{3,24}$=2.022 | 0.138 |
| | Number of landings | $F_{6,24}$=0.651 | 0.689 | $F_{2,24}$=6.999 | 0.004 | $F_{3,24}$=1.904 | 0.156 |
| 3 | Number of visits | $F_{8,24}$=0.257 | 0.977 | $F_{2,24}$=30.896 | < 0.001 | $F_{4,24}$=6.025 | < 0.001 |
| | Number of landings | $F_{8,24}$=0.098 | 0.999 | $F_{2,24}$=1.340 | 0.270 | $F_{4,24}$=37.504 | < 0.001 |

In Experiments 1 and 2, virgin females made significantly more visits than virgin males and gravid females, while in Experiment 3 virgin females and virgin males moved significantly more than gravid females (Figure 3). Regarding landings, in Experiment 1 virgin females made significantly more landings than gravid females, while no significant differences were found in the case of virgin males. In Experiment 2 both virgin and gravid females, made significantly more landings than virgin males. No significant differences were found between types of adult in Experiment 3 (Figure 3).

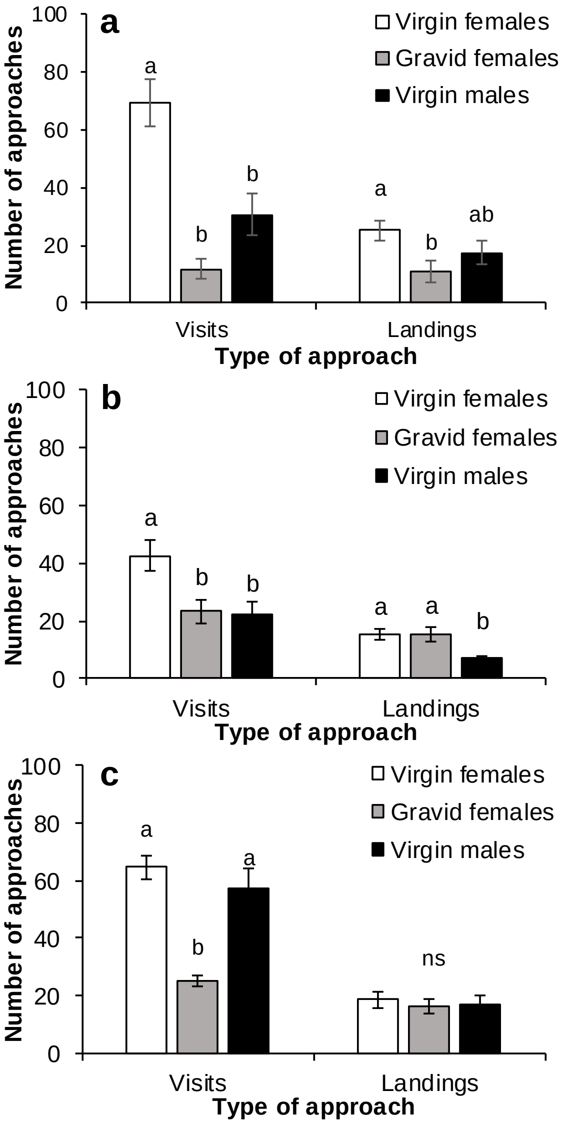


Figure 3. Number of approaches for the three types of adult in **a** Experiment 1, **b** Experiment 2 and **c** Experiment 3. Vertical bars show SE. *ns* P>0.05. Different letters within each experiment show significant differences between treatments (P<0.05) according to the HSD-Tukey test.

## 4. Discussion

To study the attractiveness of distinct flower traits to hoverflies, three consecutive laboratory experiments were run. In Experiment 1 we observed that the hoverflies preferred a circle-shaped flower to a sphere-shaped one, and landed more on the former (Figure 2a). On the basis of these observations, we conclude that the presence of petals did not have a significant effect on *S. rueppellii* attraction. Golding et al. (1999) found that the number of visits to oilseed rape (*Brassica napus* L. Brassicaceae) by *Episyrphus balteatus* De Geer (Diptera: Syrphidae) was not affected by the presence of petals, thereby suggesting that these parts of the flower are not an attractive cue to this species. On the other hand, floral guides (markings present in the corolla that act as close-range signals to direct pollinators to the floral rewards) have been demonstrated to be very effective in

*Eristalis tenax* L. (Diptera: Syrphidae) (Dinkel and Lunau 2001). Petals are often a different color to the corolla and have markings to guide pollinators to the center of the corolla. In our artificial flowers, there was no color difference between the calyx and the petals, nor were any petal markings present. It is therefore possible that hoverflies were not able to discern the different flower parts and did not detect petals as such but only a flower with an unusual contour, thus resulting in an unattractive shape. Regarding preferences between the circle- and the sphere-shaped flowers, hoverflies took longer to land on the latter (personal observation). When attempting to land on sphere-shaped flowers, they hovered above them, as if doubting how to land, and when they finally landed they continuously walked all over them. To the best of our knowledge, this is the first report of this kind of behavior. We propose that when hoverflies were on the sphere-shaped flower they were not aware of their relative position, as hoverflies always perceived the same shape. In contrast, they landed rapidly on circle-shaped flowers. We therefore assume that the presence of a flat surface helped hoverflies to land and forage. As the circle was the shape that was most approached and also the easiest to construct, it was selected for the following set of experiments.

In Experiment 2, we observed that the number of visits and landings increased with the number of flowers in the bouquet (Figure 2b). We assume that hoverflies related the higher number of flowers in the bouquet with a greater probability of finding food. In this regard, Conner and Rush (1996) stated that hoverflies prefer to visit wild radish (*Raphanus raphanistrum* L. (Brassicaceae)) inflorescences with a higher number of flowers rather than those with few flowers. In addition, several authors have reported that hoverfly populations and diversity are related to the abundance of flowers (Haenke et al. 2009; Meyer et al. 2009; Power et al. 2016; Sutherland et al. 2001). On the other hand, it could also be concluded that hoverflies are not attracted by the higher number of flowers but by the increased area as a result of it. However, Sutherland et al. (1999) demonstrated that *E. balteatus* hoverflies preferred 2 cm diameter flowers to 7 cm ones. Hence, as our results are in agreement with the aforementioned authors, we selected a 12-flower bouquet for the next step.

In Experiment 3 we observed that hoverflies showed a preference for bouquets with yellow and white flowers. In contrast, bouquets that combined white and blue were the least attractive, together with yellow and blue bouquets (Figure 2c). Previous studies have reported that flower patches with a high diversity of flowers are more attractive to hoverflies (Blaauw and Isaacs 2014; Hegland and Boeke 2006). Conversely, Warzecha et al. (2018) found that the abundance of hoverflies was enhanced by the availability of key plant species in a flower mixture rather than by the diversity of species in it. Coinciding with this author, in our case, the approaches did not increase with diversity of colors, as some colors were more attractive than others: combinations with yellow were preferred to others, and blue was less attractive than white (Figure 2c). Therefore, diversity emerges as a plus in the attraction of hoverflies: however, diversity has to be well selected in order to be functional.

With regard to the preferred landing color, all three adult types showed a preference for yellow flowers independently of the number of colors or combinations present in the bouquet (Table 2). Indeed, other studies have demonstrated that hoverflies show a strong preference for yellow (Day et al. 2015; Laubertie et al. 2006; Sutherland et al. 1999). Given that many of these insects feed preferentially on yellow pollen (Lunau 1995; Lunau and Maier 1995), this color might be interpreted as the location of a food resource. Therefore, the combination of certain colors appears to encourage the flies to approach more than a single color. However, at a closer range, yellow might elicit a change in hoverfly behavior, enhancing landings and thus foraging for pollen.

When studying hoverfly preferences to the three flowers attributes, the three types of adult behaved similarly (Table 1, Figure 2 and Table 2). However, they showed differences in movement (number of approaches). Virgin females tended to be the group that showed the most movement, followed by virgin males, gravid females being those that moved the least (Figure 3). We did not study the reasons behind this behavior. However, we can hypothesize that virgin males moved more than females with the intention of finding a mate. In several hoverfly species, male mating behavior consists of pouncing on females that are feeding on flowers, and quickly initiating copulation (Maier 1978; Maier and Waldbauer 1979). Our virgin males were observed to throw themselves over other individuals resting on the cage walls or on the artificial flowers. The males attacked in this manner responded by flying away and, as a result, the general activity in the cage was higher. Virgin females did not show such behavior. However, they also moved considerably, in most cases tending to be the group showing the most movement. We attribute the high number of visits made by virgin females to the inspection of the flowers while hovering close to them and rapidly discarding them for landing. Virgin females may have had the capacity to determine whether the artificial flower had nectar or pollen before landing and preferred to invest more energy visiting other unexplored flowers that may have provided better resources.

On the other hand, gravid females were calmer, visiting fewer flowers and landing on at least half the flowers they visited. Furthermore, when landing on an artificial flower, they spent more time on it (personal observation). This might be explained by an increased interest in finding pollen and/or nectar. Male and female hoverflies have different nutritional requirements, females usually requiring higher amounts of pollen to allow continuous oviposition (Branquart and Hemptinne 2000a). In addition, Hickman et al. (1995) and Irvin et al. (1999) found differences between mated and unmated females regarding pollen uptake. Gravid females ingested higher pollen amounts than non-gravid ones, and even the latter ingested more pollen than males. In our case, gravid females were observed to behave differently to virgin individuals.

In our study, gravid females appeared to discriminate less than virgin females and virgin males because they did not discard the flowers before landing, but landed on the few flowers they visited and explored them exhaustively, possibly driven by their increased need for pollen. The loss of discrimination in ageing hoverflies has also been reported not only when foraging (Sutherland et al.

1999) but also when searching for oviposition sites (Almohamad et al. 2009; Chandler 1968; Sadeghi and Gilbert 2000).

Our results are in agreement with Day et al. (2015), who found that under field conditions adult hoverflies laid more eggs on broad bean (*Vicia faba* L. (Fabaceae)) infested with pea aphids (*Acyrthosiphon pisum* Mordvilko (Hemiptera: Aphididae)) when yellow model flowers were present nearby, in spite of these having no reward. These authors proposed that the increased oviposition was a result of the preference of gravid females for yellow. They also concluded that color attraction had a greater effect on enhancing oviposition than food resources. Although we did not study oviposition behavior, we observed that, in addition to a strong preference for rewardless yellow flowers, gravid females were less mobile than virgin individuals and they landed more frequently on the resources that they visited.

The inherent characteristics of species imply differences in their attraction to floral cues such as petal attractiveness (Golding et al. 1999) or color preferences (Sutherland et al. 1999). However, it is important to identify the common traits between species, such as the strong attraction to yellow color, in order to select the more commonly attractive cues. This knowledge can help to improve habitat management practices through the selection of flower species that present the most common attractive cues to hoverflies. In consequence, hoverfly populations will be enhanced, and therefore an increase in biological control and pollination services is expected.

In conclusion, we have found that: 1) different flower shapes elicit diverse behaviors in hoverflies: rounded and flat shapes are the most attractive; 2) bouquets are more attractive than single flowers; 3) more doesn’t mean better in regard to flower diversity: combinations with yellow and white are preferred to those that contain blue; 4) mating modifies the behavior of females: gravid females make fewer visits than virgin females.

Our findings have given a major insight into hoverfly behavior. This information can be used to improve the design of ecological infrastructures for the promotion of biological control and pollination, and therefore can contribute to increase the environmental sustainability of crops.

## Acknowledgements

We thank Ariadna Màrmol and Quico Vila d’Abadal for their collaboration with data collection. Special thanks go to Francis Gilbert for his help differentiating between virgin and gravid females. This research was funded by Instituto Nacional de Investigación y Tecnología Agraria Alimentaria (Spain), by means of the Project RTA 2013-00039-C03-00.

## 5. References

Almohamad R, Verheggen FJ, Haubruge E (2009) Searching and oviposition behavior of aphidophagous hoverflies (Diptera: Syrphidae): a review. Biotechnol Agron Soc 13:467-481

Ambrosino MD, Luna JM, Jepson PC, Wratten SD (2006) Relative frequencies of visits to selected insectary plants by predatory hoverflies (Diptera: Syrphidae), other beneficial insects, and herbivores. Environ Entomol 35:394-400 doi:10.1603/0046-225x-35.2.394

Blaauw BR, Isaacs R (2014) Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wild flowers. Basic Appl Ecol 15:701-711 doi:10.1016/j.baae.2014.10.001

Branquart E, Hemptinne JL (2000a) Development of ovaries, allometry of reproductive traits and fecundity of *Episyrphus balteatus* (Diptera: Syrphidae). Eur J Entomol 97:165-170

Branquart E, Hemptinne JL (2000b) Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphinae). Ecography 23:732-742 doi:10.1034/j.1600-0587.2000.230610.x

Chandler AE (1968) Some factors influencing occurrence and site of oviposition by aphidophagous Syrphidae (Diptera). Ann Appl Biol 61:435-446 doi:10.1111/j.1744-7348.1968.tb04545.x

Conner JK, Rush S (1996) Effects of flower size and number on pollinator visitation to wild radish, *Raphanus raphanistrum*. Oecologia 105:509-516 doi:10.1007/bf00330014

Day RL, Hickman JM, Sprague RI, Wratten SD (2015) Predatory hoverflies increase oviposition in response to colour stimuli offering no reward: Implications for biological control. Basic Appl Ecol 16:544-552 doi:10.1016/j.baae.2015.05.004

Dinkel T, Lunau K (2001) How drone flies (*Eristalis tenax* L., Syrphidae: Diptera) use floral guides to locate food sources. J Insect Physiol 47:1111-1118 doi:10.1016/s0022-1910(01)00080-4

Gilbert F (1993) Hoverflies. Naturalists' Handbooks 5. 2nd edn. Richmond Publishing Co., Slough, Berkshire. doi:10.1080/00219266.1994.9655394

Gilbert FS (1981) Foraging ecology of hoverflies - Morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. Ecol Entomol 6:245-262 doi:10.1111/j.1365-2311.1981.tb00612.x

Golding YC, Sullivan MS, Sutherland JP (1999) Visits to manipulated flowers by *Episyrphus balteatus* (Diptera : Syrphidae): Partitioning the signals of petals and anthers. J Insect Behav 12:39-45 doi:10.1023/a:1020925030522

Gong YB, Huang SQ (2009) Floral symmetry: pollinator-mediated stabilizing selection on flower size in bilateral species. Proc R Soc Lond, Ser B Biol Sci 276:4013-4020 doi:10.1098/rspb.2009.1254

Gurr GM, Wratten SD, Landis DA, You MS (2017) Habitat management to suppress pest populations: progress and prospects. Annu Rev Entomol 62:91-109 doi:10.1146/annurev-ento-031616-035050

Haenke S, Scheid B, Schaefer M, Tscharntke T, Thies C (2009) Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. J Appl Ecol 46:1106-1114 doi:10.1111/j.1365-2664.2009.01685.x

Haslett JR (1989a) Adult feeding by Holometabolous insects - Pollen and nectar as complementary nutrient sources for *Rhingia campestris* (Diptera, Syrphidae). Oecologia 81:361-363 doi:10.1007/bf00377084

Haslett JR (1989b) Interpreting patterns of resource utilization - Randomness and selectivity in pollen feeding by adult hoverflies. Oecologia 78:433-442 doi:10.1007/bf00378732

Hegland SJ, Boeke L (2006) Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. Ecol Entomol 31:532-538 doi:10.1111/j.1365-2311.2006.00812.x

Hickman JM, Lovei GL, Wratten SD (1995) Pollen feeding by adults of the hoverfly *Melanostoma fasciatum* (Diptera: Syrphidae). N Z J Zool 22:387-392 doi:10.1080/03014223.1995.9518057

Hickman JM, Wratten SD (1996) Use of *Phacelia tanacetifolia* strips to enhance biological control of aphids by hoverfly larvae in cereal fields. J Econ Entomol 89:832-840 doi:10.1093/jee/89.4.832

Hickman JM, Wratten SD, Jepson PC, Frampton CM (2001) Effect of hunger on yellow water trap catches of hoverfly (Diptera: Syrphidae) adults. Agric For Entomol 3:35-40 doi:10.1046/j.1461-9563.2001.00085.x

Hogg BN, Nelson EH, Mills NJ, Daane KM (2011) Floral resources enhance aphid suppression by a hoverfly. Entomol Exp Appl 141:138-144 doi:10.1111/j.1570-7458.2011.01174.x

Irvin NA, Wratten SD, Frampton CM, Bowie MH, Evans AM, Moar NT (1999) The phenology and pollen feeding of three hover fly (Diptera: Syrphidae) species in Canterbury, New Zealand. N Z J Zool 26:105-115 doi:10.1080/03014223.1999.9518182

Landis DA, Wratten SD, Gurr GM (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu Rev Entomol 45:175-201 doi:10.1146/annurev.ento.45.1.175

Laubertie EA, Wratten SD, Sedcole JR (2006) The role of odour and visual cues in the pan-trap catching of hoverflies (Diptera: Syrphidae). Ann Appl Biol 148:173-178 doi:10.1111/j.1744-7348.2006.00046.x

Lunau K (1995) Notes on the colour of pollen. Plant Syst Evol 198:235-252 doi:10.1007/bf00984739

Lunau K, An L, Donda M, Hohmann M, Sermon L, Stegmanns V (2018) Limitations of learning in the proboscis reflex of the flower visiting syrphid fly *Eristalis tenax*. PLoS ONE 13(3): e0194167 doi:10.1371/journal.pone.0194167

Lunau K, Maier EJ (1995) Innate color preferences of flower visitors. J Comp Physiol, A 177:1-19 doi:10.1007/BF00243394

Lunau K, Wacht S (1994) Optical releasers of the innate proboscis extension in the hoverfly *Eristalis tenax* L. (Syrphidae: Diptera) J Comp Physiol, A 174:575-579 doi:10.1007/BF00217378

Macleod A (1999) Attraction and retention of *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) at an arable field margin with rich and poor floral resources. Agric Ecosyst Environ 73:237-244 doi:10.1016/s0167-8809(99)00051-1

Maier CT (1978) Immature stages and biology of *Mallota posticata* (Fabricius) (Diptera: Syrphidae). Proc Entomol Soc Wash 80:424-440

Maier CT, Waldbauer GP (1979) Dual mate-seeking strategies in male syrphid flies (Diptera: Syrphidae). Ann Entomol Soc Am 72:54-61 doi:10.1093/aesa/72.1.54

Meyer B, Jauker F, Steffan-Dewenter I (2009) Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. Basic Appl Ecol 10:178-186 doi:10.1016/j.baae.2008.01.001

Nordstrom K et al. (2017) In situ modeling of multimodal floral cues attracting wild pollinators across environments. Proc Natl Acad Sci U S A 114:13218-13223 doi:10.1073/pnas.1714414114

Power EF, Jackson Z, Stout JC (2016) Organic farming and landscape factors affect abundance and richness of hoverflies (Diptera, Syrphidae) in grasslands. Insect Conserv Divers 9:244-253 doi:10.1111/icad.12163

Primante C, Dotterl S (2010) A syrphid fly uses olfactory cues to find a non-yellow flower. J Chem Ecol 36:1207-1210 doi:10.1007/s10886-010-9871-6

Rojo S, Gilbert F, Marcos-García MA, Nieto J, Mier MP (2003) A world review of predatory hoverflies (Diptera, Syrphidae: Syrphinae) and their prey. CIBIO Ediciones, Alicante, Spain

Sadeghi H, Gilbert F (2000) Oviposition preferences of aphidophagous hoverflies. Ecol Entomol 25:91-100 doi:10.1046/j.1365-2311.2000.00234.x

Skirvin DJ, Kravar-Garde L, Reynolds K, Wright C, Mead A (2011) The effect of within-crop habitat manipulations on the conservation biological control of aphids in field-grown lettuce. Bull Entomol Res 101:623-631 doi:10.1017/s0007485310000659

Sutherland JP, Sullivan MS, Poppy GM (1999) The influence of floral character on the foraging behaviour of the hoverfly, *Episyrphus balteatus*. Entomol Exp Appl 93:157-164 doi:10.1046/j.1570-7458.1999.00574.x

Sutherland JP, Sullivan MS, Poppy GM (2001) Distribution and abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats. Agric For Entomol 3:57-64 doi:10.1046/j.1461-9563.2001.00090.x

Tenhumberg B, Poehling HM (1995) Syrphids as natural enemies of cereal aphids in Germany - Aspects of their biology and efficacy in different years and regions. Agric Ecosyst Environ 52:39-43 doi:10.1016/0167-8809(94)09007-t

van Rijn PCJ, Kooijman J, Wäckers FL (2006) The impact of floral resources on syrphid performance and cabbage aphid biological control. IOBC/WPRS Bull 29:149-152

van Rijn PCJ, Wäckers FL (2016) Nectar accessibility determines fitness, flower choice and abundance of hoverflies that provide natural pest control. J Appl Ecol 53:925-933 doi:10.1111/1365-2664.12605

Warzecha D, Diekoetter T, Wolters V, Jauker F (2018) Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species. Insect Conserv Divers 11:32-41 doi:10.1111/icad.12264

White AJ, Wratten SD, Berry NA, Weigmann U (1995) Habitat manipulations to enhance biological control of brassica pests by hover flies (Diptera, Syrphidae). J Econ Entomol 88:1171-1176 doi:10.1093/jee/88.5.1171

Wratten SD, Bowie MH, Hickman JM, Evans AM, Sedcole JR, Tylianakis JM (2003) Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. Oecologia 134:605-611 doi:10.1007/s00442-002-1128-9

Wratten SD, Gillespie M, Decourtye A, Mader E, Desneux N (2012) Pollinator habitat enhancement: Benefits to other ecosystem services. Agric Ecosyst Environ 159:112-122 doi:10.1016/j.agee.2012.06.020

## Electronic Supplementary Materials

The online version of this article (https://doi.org/10.1007/s10526-019-09928-2) contains supplementary material, which is available to authorized users.

Table S1. Number and percentage of visits and landings to the different treatments per adult type and experiment number (this table continues on the next page).

| Experiment number | Adult type | Repetition | Treatment | Nº Visits | Nº Landings | Nº V+L | % Visits | % Landings | % V+L |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Virgin females | A | Circle | 84 | 20 | 104 | 30.5 | 33.3 | 31.0 |
| 1 | Virgin females | A | Sphere | 99 | 11 | 110 | 36.0 | 18.3 | 32.8 |
| 1 | Virgin females | A | Flower | 92 | 29 | 121 | 33.5 | 48.3 | 36.1 |
| 1 | Virgin females | B | Circle | 91 | 31 | 122 | 35.4 | 33.0 | 34.8 |
| 1 | Virgin females | B | Sphere | 96 | 22 | 118 | 37.4 | 23.4 | 33.6 |
| 1 | Virgin females | B | Flower | 70 | 41 | 111 | 27.2 | 43.6 | 31.6 |
| 1 | Virgin females | C | Circle | 27 | 38 | 65 | 24.8 | 58.5 | 37.4 |
| 1 | Virgin females | C | Sphere | 63 | 7 | 70 | 57.8 | 10.8 | 40.2 |
| 1 | Virgin females | C | Flower | 19 | 20 | 39 | 17.4 | 30.8 | 22.4 |
| 1 | Virgin females | D | Circle | 94 | 41 | 135 | 49.0 | 48.8 | 48.9 |
| 1 | Virgin females | D | Sphere | 64 | 11 | 75 | 33.3 | 13.1 | 27.2 |
| 1 | Virgin females | D | Flower | 34 | 32 | 66 | 17.7 | 38.1 | 23.9 |
| 1 | Gravid females | A | Circle | 5 | 14 | 19 | 45.5 | 58.3 | 54.3 |
| 1 | Gravid females | A | Sphere | 5 | 7 | 12 | 45.5 | 29.2 | 34.3 |
| 1 | Gravid females | A | Flower | 1 | 3 | 4 | 9.1 | 12.5 | 11.4 |
| 1 | Gravid females | B | Circle | 5 | 6 | 11 | 27.8 | 40.0 | 33.3 |
| 1 | Gravid females | B | Sphere | 8 | 4 | 12 | 44.4 | 26.7 | 36.4 |
| 1 | Gravid females | B | Flower | 5 | 5 | 10 | 27.8 | 33.3 | 30.3 |
| 1 | Gravid females | C | Circle | 11 | 5 | 16 | 27.5 | 45.5 | 31.4 |
| 1 | Gravid females | C | Sphere | 29 | 3 | 32 | 72.5 | 27.3 | 62.7 |
| 1 | Gravid females | C | Flower | 0 | 3 | 3 | 0.0 | 27.3 | 5.9 |
| 1 | Gravid females | D | Circle | 35 | 51 | 86 | 48.6 | 63.8 | 56.6 |
| 1 | Gravid females | D | Sphere | 27 | 9 | 36 | 37.5 | 11.3 | 23.7 |
| 1 | Gravid females | D | Flower | 10 | 20 | 30 | 13.9 | 25.0 | 19.7 |
| 1 | Virgin males | A | Circle | 17 | 0 | 17 | 41.5 | 0.0 | 37.8 |
| 1 | Virgin males | A | Sphere | 13 | 1 | 14 | 31.7 | 25.0 | 31.1 |
| 1 | Virgin males | A | Flower | 11 | 3 | 14 | 26.8 | 75.0 | 31.1 |
| 1 | Virgin males | B | Circle | 12 | 23 | 35 | 31.6 | 31.1 | 31.3 |
| 1 | Virgin males | B | Sphere | 17 | 21 | 38 | 44.7 | 28.4 | 33.9 |
| 1 | Virgin males | B | Flower | 9 | 30 | 39 | 23.7 | 40.5 | 34.8 |
| 1 | Virgin males | C | Circle | 57 | 39 | 96 | 27.9 | 45.9 | 33.2 |
| 1 | Virgin males | C | Sphere | 84 | 11 | 95 | 41.2 | 12.9 | 32.9 |
| 1 | Virgin males | C | Flower | 63 | 35 | 98 | 30.9 | 41.2 | 33.9 |
| 1 | Virgin males | D | Circle | 40 | 31 | 71 | 47.1 | 67.4 | 54.2 |
| 1 | Virgin males | D | Sphere | 31 | 6 | 37 | 36.5 | 13.0 | 28.2 |

| Experiment number | Adult type | Repetition | Treatment | Nº Visits | Nº Landings | Nº V+L | % Visits | % Landings | % V+L |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Virgin males | D | Flower | 14 | 9 | 23 | 16.5 | 19.6 | 17.6 |
| 2 | Virgin females | A | 1 | 21 | 9 | 30 | 20.2 | 32.1 | 22.7 |
| 2 | Virgin females | A | 6 | 39 | 6 | 45 | 37.5 | 21.4 | 34.1 |
| 2 | Virgin females | A | 12 | 44 | 13 | 57 | 42.3 | 46.4 | 43.2 |
| 2 | Virgin females | B | 1 | 58 | 18 | 76 | 38.9 | 45.0 | 40.2 |
| 2 | Virgin females | B | 3 | 47 | 11 | 58 | 31.5 | 27.5 | 30.7 |
| 2 | Virgin females | B | 6 | 44 | 11 | 55 | 29.5 | 27.5 | 29.1 |
| 2 | Virgin females | C | 1 | 45 | 13 | 58 | 24.3 | 20.0 | 23.2 |
| 2 | Virgin females | C | 3 | 59 | 26 | 85 | 31.9 | 40.0 | 34.0 |
| 2 | Virgin females | C | 12 | 81 | 26 | 107 | 43.8 | 40.0 | 42.8 |
| 2 | Virgin females | D | 3 | 27 | 9 | 36 | 36.5 | 18.4 | 29.3 |
| 2 | Virgin females | D | 6 | 17 | 16 | 33 | 23.0 | 32.7 | 26.8 |
| 2 | Virgin females | D | 12 | 30 | 24 | 54 | 40.5 | 49.0 | 43.9 |
| 2 | Gravid females | A | 1 | 8 | 2 | 10 | 15.1 | 11.1 | 14.1 |
| 2 | Gravid females | A | 6 | 20 | 8 | 28 | 37.7 | 44.4 | 39.4 |
| 2 | Gravid females | A | 12 | 25 | 8 | 33 | 47.2 | 44.4 | 46.5 |
| 2 | Gravid females | B | 1 | 14 | 13 | 27 | 33.3 | 39.4 | 36.0 |
| 2 | Gravid females | B | 3 | 16 | 11 | 27 | 38.1 | 33.3 | 36.0 |
| 2 | Gravid females | B | 6 | 12 | 9 | 21 | 28.6 | 27.3 | 28.0 |
| 2 | Gravid females | C | 1 | 11 | 14 | 25 | 22.0 | 20.6 | 21.2 |
| 2 | Gravid females | C | 3 | 22 | 22 | 44 | 44.0 | 32.4 | 37.3 |
| 2 | Gravid females | C | 12 | 17 | 32 | 49 | 34.0 | 47.1 | 41.5 |
| 2 | Gravid females | D | 3 | 38 | 20 | 58 | 28.1 | 31.3 | 29.1 |
| 2 | Gravid females | D | 6 | 43 | 19 | 62 | 31.9 | 29.7 | 31.2 |
| 2 | Gravid females | D | 12 | 54 | 25 | 79 | 40.0 | 39.1 | 39.7 |
| 2 | Virgin males | A | 1 | 4 | 3 | 7 | 11.4 | 21.4 | 14.3 |
| 2 | Virgin males | A | 6 | 14 | 4 | 18 | 40.0 | 28.6 | 36.7 |
| 2 | Virgin males | A | 12 | 17 | 7 | 24 | 48.6 | 50.0 | 49.0 |
| 2 | Virgin males | B | 1 | 10 | 6 | 16 | 23.8 | 35.3 | 27.1 |
| 2 | Virgin males | B | 3 | 15 | 4 | 19 | 35.7 | 23.5 | 32.2 |
| 2 | Virgin males | B | 6 | 17 | 7 | 24 | 40.5 | 41.2 | 40.7 |
| 2 | Virgin males | C | 1 | 15 | 6 | 21 | 25.0 | 23.1 | 24.4 |
| 2 | Virgin males | C | 3 | 17 | 11 | 28 | 28.3 | 42.3 | 32.6 |
| 2 | Virgin males | C | 12 | 28 | 9 | 37 | 46.7 | 34.6 | 43.0 |
| 2 | Virgin males | D | 3 | 45 | 1 | 46 | 34.4 | 3.8 | 29.3 |
| 2 | Virgin males | D | 6 | 36 | 14 | 50 | 27.5 | 53.8 | 31.8 |
| 2 | Virgin males | D | 12 | 50 | 11 | 61 | 38.2 | 42.3 | 38.9 |
| 3 | Virgin females | 1 | WB | 66 | 6 | 72 | 19.9 | 5.6 | 16.4 |
| 3 | Virgin females | 1 | WBY | 54 | 19 | 73 | 16.3 | 17.8 | 16.7 |
| 3 | Virgin females | 1 | Y | 76 | 29 | 105 | 23.0 | 27.1 | 24.0 |
| 3 | Virgin females | 1 | YB | 42 | 13 | 55 | 12.7 | 12.1 | 12.6 |
| 3 | Virgin females | 1 | YW | 93 | 40 | 133 | 28.1 | 37.4 | 30.4 |
| 3 | Virgin females | 2 | WB | 51 | 2 | 53 | 15.5 | 2.2 | 12.6 |
| 3 | Virgin females | 2 | WBY | 57 | 15 | 72 | 17.3 | 16.7 | 17.1 |

| Experiment number | Adult type | Repetition | Treatment | Nº Visits | Nº Landings | Nº V+L | % Visits | % Landings | % V+L |
|---|---|---|---|---|---|---|---|---|---|
| 3 | Virgin females | 2 | Y | 91 | 25 | 116 | 27.6 | 27.8 | 27.6 |
| 3 | Virgin females | 2 | YB | 48 | 9 | 57 | 14.5 | 10.0 | 13.6 |
| 3 | Virgin females | 2 | YW | 83 | 39 | 122 | 25.2 | 43.3 | 29.0 |
| 3 | Virgin females | 3 | WB | 30 | 5 | 35 | 9.5 | 6.0 | 8.8 |
| 3 | Virgin females | 3 | WBY | 95 | 15 | 110 | 30.2 | 18.1 | 27.6 |
| 3 | Virgin females | 3 | Y | 62 | 11 | 73 | 19.7 | 13.3 | 18.3 |
| 3 | Virgin females | 3 | YB | 31 | 6 | 37 | 9.8 | 7.2 | 9.3 |
| 3 | Virgin females | 3 | YW | 97 | 46 | 143 | 30.8 | 55.4 | 35.9 |
| 3 | Virgin females | 4 | WB | 36 | 3 | 39 | 11.3 | 3.2 | 9.4 |
| 3 | Virgin females | 4 | WBY | 73 | 16 | 89 | 22.8 | 17.0 | 21.5 |
| 3 | Virgin females | 4 | Y | 84 | 30 | 114 | 26.3 | 31.9 | 27.5 |
| 3 | Virgin females | 4 | YB | 43 | 7 | 50 | 13.4 | 7.4 | 12.1 |
| 3 | Virgin females | 4 | YW | 84 | 38 | 122 | 26.3 | 40.4 | 29.5 |
| 3 | Virgin females | 5 | WB | 45 | 3 | 48 | 13.8 | 3.4 | 11.6 |
| 3 | Virgin females | 5 | WBY | 61 | 13 | 74 | 18.8 | 14.6 | 17.9 |
| 3 | Virgin females | 5 | Y | 81 | 32 | 113 | 24.9 | 36.0 | 27.3 |
| 3 | Virgin females | 5 | YB | 66 | 5 | 71 | 20.3 | 5.6 | 17.1 |
| 3 | Virgin females | 5 | YW | 72 | 36 | 108 | 22.2 | 40.4 | 26.1 |
| 3 | Gravid females | 1 | WB | 26 | 3 | 29 | 19.5 | 4.3 | 14.4 |
| 3 | Gravid females | 1 | WBY | 33 | 15 | 48 | 24.8 | 21.7 | 23.8 |
| 3 | Gravid females | 1 | Y | 26 | 19 | 45 | 19.5 | 27.5 | 22.3 |
| 3 | Gravid females | 1 | YB | 21 | 8 | 29 | 15.8 | 11.6 | 14.4 |
| 3 | Gravid females | 1 | YW | 27 | 24 | 51 | 20.3 | 34.8 | 25.2 |
| 3 | Gravid females | 2 | WB | 18 | 2 | 20 | 13.5 | 2.6 | 9.5 |
| 3 | Gravid females | 2 | WBY | 24 | 10 | 34 | 18.0 | 13.0 | 16.2 |
| 3 | Gravid females | 2 | Y | 43 | 15 | 58 | 32.3 | 19.5 | 27.6 |
| 3 | Gravid females | 2 | YB | 12 | 5 | 17 | 9.0 | 6.5 | 8.1 |
| 3 | Gravid females | 2 | YW | 36 | 45 | 81 | 27.1 | 58.4 | 38.6 |
| 3 | Gravid females | 3 | WB | 12 | 4 | 16 | 14.5 | 4.3 | 9.1 |
| 3 | Gravid females | 3 | WBY | 12 | 12 | 24 | 14.5 | 13.0 | 13.7 |
| 3 | Gravid females | 3 | Y | 11 | 23 | 34 | 13.3 | 25.0 | 19.4 |
| 3 | Gravid females | 3 | YB | 27 | 19 | 46 | 32.5 | 20.7 | 26.3 |
| 3 | Gravid females | 3 | YW | 21 | 34 | 55 | 25.3 | 37.0 | 31.4 |
| 3 | Gravid females | 4 | WB | 20 | 8 | 28 | 12.3 | 7.0 | 10.1 |
| 3 | Gravid females | 4 | WBY | 31 | 25 | 56 | 19.1 | 21.9 | 20.3 |
| 3 | Gravid females | 4 | Y | 45 | 41 | 86 | 27.8 | 36.0 | 31.2 |
| 3 | Gravid females | 4 | YB | 27 | 4 | 31 | 16.7 | 3.5 | 11.2 |
| 3 | Gravid females | 4 | YW | 39 | 36 | 75 | 24.1 | 31.6 | 27.2 |
| 3 | Gravid females | 5 | WB | 15 | 0 | 15 | 12.8 | 0.0 | 8.9 |
| 3 | Gravid females | 5 | WBY | 24 | 12 | 36 | 20.5 | 23.1 | 21.3 |
| 3 | Gravid females | 5 | Y | 24 | 11 | 35 | 20.5 | 21.2 | 20.7 |
| 3 | Gravid females | 5 | YB | 20 | 11 | 31 | 17.1 | 21.2 | 18.3 |
| 3 | Gravid females | 5 | YW | 34 | 18 | 52 | 29.1 | 34.6 | 30.8 |
| 3 | Virgin males | 1 | WB | 22 | 2 | 24 | 7.5 | 2.7 | 6.5 |

| Experiment number | Adult type | Repetition | Treatment | Nº Visits | Nº Landings | Nº V+L | % Visits | % Landings | % V+L |
|---|---|---|---|---|---|---|---|---|---|
| 3 | Virgin males | 1 | WBY | 59 | 12 | 71 | 20.1 | 16.4 | 19.3 |
| 3 | Virgin males | 1 | Y | 83 | 21 | 104 | 28.2 | 28.8 | 28.3 |
| 3 | Virgin males | 1 | YB | 47 | 6 | 53 | 16.0 | 8.2 | 14.4 |
| 3 | Virgin males | 1 | YW | 83 | 32 | 115 | 28.2 | 43.8 | 31.3 |
| 3 | Virgin males | 2 | WB | 28 | 3 | 31 | 18.7 | 4.5 | 14.4 |
| 3 | Virgin males | 2 | WBY | 44 | 23 | 67 | 29.3 | 34.8 | 31.0 |
| 3 | Virgin males | 2 | Y | 26 | 13 | 39 | 17.3 | 19.7 | 18.1 |
| 3 | Virgin males | 2 | YB | 17 | 6 | 23 | 11.3 | 9.1 | 10.6 |
| 3 | Virgin males | 2 | YW | 35 | 21 | 56 | 23.3 | 31.8 | 25.9 |
| 3 | Virgin males | 3 | WB | 53 | 1 | 54 | 11.3 | 0.7 | 8.7 |
| 3 | Virgin males | 3 | WBY | 76 | 23 | 99 | 16.2 | 15.3 | 16.0 |
| 3 | Virgin males | 3 | Y | 140 | 38 | 178 | 29.8 | 25.3 | 28.7 |
| 3 | Virgin males | 3 | YB | 82 | 19 | 101 | 17.4 | 12.7 | 16.3 |
| 3 | Virgin males | 3 | YW | 119 | 69 | 188 | 25.3 | 46.0 | 30.3 |
| 3 | Virgin males | 4 | WB | 9 | 1 | 10 | 6.4 | 4.8 | 6.2 |
| 3 | Virgin males | 4 | WBY | 18 | 3 | 21 | 12.9 | 14.3 | 13.0 |
| 3 | Virgin males | 4 | Y | 41 | 9 | 50 | 29.3 | 42.9 | 31.1 |
| 3 | Virgin males | 4 | YB | 35 | 1 | 36 | 25.0 | 4.8 | 22.4 |
| 3 | Virgin males | 4 | YW | 37 | 7 | 44 | 26.4 | 33.3 | 27.3 |
| 3 | Virgin males | 5 | WB | 61 | 6 | 67 | 16.1 | 5.7 | 13.8 |
| 3 | Virgin males | 5 | WBY | 60 | 18 | 78 | 15.8 | 17.0 | 16.1 |
| 3 | Virgin males | 5 | Y | 77 | 24 | 101 | 20.3 | 22.6 | 20.8 |
| 3 | Virgin males | 5 | YB | 66 | 10 | 76 | 17.4 | 9.4 | 15.7 |
| 3 | Virgin males | 5 | YW | 115 | 48 | 163 | 30.3 | 45.3 | 33.6 |

## Chapter 4

# The ecology of hoverflies as ecosystem service providers in agricultural systems

## 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 its ecosystem services. The Syrphinae subfamily is a widespread group of hoverflies with a high potential for biological control. Hence, the present review aims to synthetize the existing literature related to the promotion of predatory hoverflies and their ecosystem services in agricultural systems. For that purpose, the review is been divided in three main sections. First, we focus on those aspects of the ecology of hoverflies that are relevant for their implications in biological control and habitat management. These are divided in nutrition (with a special 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 that predatory hoverflies can provide: pollination, biological control, bioindication and food for other predators. Finally, we discuss those farming practices that can affect their effectiveness as providers of ecosystem functions. In this case, special attention is given to experiences related to the implementation of flower strips for the enhancement of aphid biological control by hoverflies. These review highlights the potential, as well as the limitations and current gaps of knowledge, for boosting the efficacy of these predatory hoverflies as ecosystem function providers in agricultural systems.

**Keywords:** Syrphidae, overwintering, landscape, habitat management, biological control, pollination

## 1. Introduction

Increased use of land, irrigation and agro-chemicals 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 agricultural production were often accompanied by major negative environmental impacts including greenhouse gas emissions, land and water degradation, pollution by agricultural chemicals and biodiversity loss (FAO 2017; Pretty et al. 2018; Tilman et al. 2011; West et al. 2014). Furthermore, nowadays human growing pressure still challenges agriculture as natural resources become increasingly stressed and the demand for food and for agricultural product is expected to raise by a 15% in the next 10 years (OECD/FAO 2019). Hence, the current priority for agriculture consists on maximize 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 purposes 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) 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). Hoverflies are life-history omnivores, with the immature stages presenting different food regimes than the adults: while the adults usually feed on flowers, the larvae present different feeding regimes, such as saprophagy, phytopagy, mycophagy or entomophagy (Gilbert 1993; Rotheray 1993).

The Syrphinae subfamily comprises about one third of the hoverfly species and can inhabit in a very extensive range of vegetated terrestrial habitats. The group is widespread in all the continents except Antarctica, being the Palearctic and Nearctic regions where it is best represented (Rotheray and Gilbert 2011). One of the most significant traits of this subfamily, is that the immature stages are predatory of homopteran pests and other insects such as scale insects, whiteflies, greenflies and blackflies (Gilbert 1993; Rotheray 1993). 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 the effect of habitat management practices, such as the implementation of flower strips, due to their dependency on flowers.

The present review aims to synthetize the existing literature related to the promotion of predatory hoverflies and their ecosystem services in agricultural systems. For that purpose, the review has been divided in three main sections. First, we focus on those aspects of the hoverflies' ecology that are relevant for their implications in biological control and habitat management. These are divided in nutrition (with a special 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 that predatory hoverflies can provide. Finally, we discuss those farming practices that can affect their effectiveness as providers of ecosystem functions.

## 2. The ecology of Syrphinae

### 2.1 What are the nutritional requirements of hoverflies?

**Adults.** The ecology of adult Syrphinae is closely related to flowers as they need to forage on their nectar and pollen. Nectar is the main source of carbohydrates, which provide the energy required for survival, while pollen supplies the proteins and amino acids that allow sexual maturation and gametogenesis, along with lipids and minerals (Gilbert 1981; Haslett 1989a; Schneider 1969). Most hoverfly species are synovigenic, which means that adults emerge with an immature reproductive system and undergo a prematuration period before being capable of mating. During this stage, commonly known to last 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 mating and finding females. Females, in turn, have a higher need of pollen to allow continuous production of eggs (Gilbert 1993; Haslett 1989a), which 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* Moench only during their preovipositional period, are able to produce eggs for a week thereafter and survive for another two weeks (van Rijn et al. 2013). Apart from pollen and nectar, aphids' honeydew is also a valuable resource for hoverflies: it can save the adults' foraging time and energy substituting nectar when flowers are scarce (Pinheiro et al. 2015; van Rijn et al. 2006) and even generate additional survival when flowers are available (van Rijn et al. 2013).

It is known that the diverse food sources (pollen, nectar or honeydew) affect hoverflies fitness and nutritional status in different ways depending on the flower or aphid species they belong to (Laubertie et al. 2012; Pinheiro et al. 2013a; Pinheiro et al. 2013b; Pinheiro et al. 2015; van Rijn et al. 2013; van Rijn et al. 2006; van Rijn and Wäckers 2016). For example, Laubertie et al. (2012) evaluated the effect of common insectary plants (*Calendula offcinalis* L., *Coriandrum sativum* L., *F. esculentum*, *Lobularia maritima* L., *Phacelia tanacetifolia* Bentham and *Sinapis arvensis* L.) on the fitness of *E. balteatus* and found that the same flower species enhanced different aspects of the hoverflies' fitness: *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).

**Larvae.** Syrphinae larvae are mainly aphidophagous and considered highly voracious predators (Rojo et al. 2003). For example, *E. balteatus*, one of the most abundant aphid predators in Europe (Cowgill et al. 1993a; Miñarro et al. 2005; Tenhumberg and Poehling 1995), is able to predate between 400 and 1000 aphids during its larval development, which lasts about a week under optimal conditions (Tenhumberg 1995). Nonetheless, the predatory efficiency of the larvae depends on several factors that involve, not only the hoverfly species but also the prey species and the host plant. Species of Syrphinae larvae range from generalists to specialists regarding their food requirements. Regardless of their degree of specialization, all hoverfly larvae can be peripheral predators (the larva feeds on peripheral prey but experiences declines in its fitness) or be unable to survive on certain aphid species (Sadeghi and Gilbert 2000a; Short and Bergh 2004). Moreover, tri-trophic interactions, in other words, combinations of the same aphid species with different host plants, can also have different effects on the larval performance (Vanhaelen et al. 2002).

Despite 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 present aphid preferences (Alhmedi et al. 2008; Ekukole 1996; Mizuno et al. 1997; Putra and Yasuda 2006; Sadeghi and Gilbert 2000a; Short and Bergh 2004), which in some species are related to a better performance while in others are not (Sadeghi and Gilbert 2000a). With regard to plant choice, no preferences are known to date for immature hoverflies. Vosteen et al. (2018) found that when larvae have to choose a new aphid colony, they usually select the ones with higher reproductive rates regardless the type of plant they are located. Nonetheless, it is known that some plant structures, like trichomes, can hamper the movement of the larvae and therefore their predatory efficiency (Verheggen et al. 2009).

Apart from aphids, hoverfly larvae are known to be able to feed in other soft-bodied prey such as trips, psyllids, whiteflies, mealybugs, springtails (Rojo et al. 2003) and lepidopteran larvae (Ashby and Pottinger 1974; Valentine 1967). Some species can even exhibit cannibalism on eggs and first instars of their conspecifics (Belliure and Michaud 2001). Recently, Vosteen et al. (2018) found that starving larvae are able to feed on non-prey food: individuals that feed on diluted honey and pollen lived about 10 days more than non-fed individuals despite they could not gain weight or pupate. Thus, this non-prey food could prevent the larvae from dying of hunger and give them more time to find a new aphid colony or other suitable prey.

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

As pollinators, hoverflies have to select among the attractive characters of the flowers in order to find adequate feeding resources. To do that, they rely mainly on visual cues like the size (Conner and Rush 1996; Sutherland et al. 1999), shape (Gong and Huang 2009) and color (Day et al. 2015; Dinkel and Lunau 2001; Laubertie et al. 2006; Sutherland et al. 1999) 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; Laubertie et al. 2006; Lunau 2014; Rodríguez-Gasol et al. 2019a; Sutherland et al. 1999), and that this color can even elicit proboscis extension response in some species (Dinkel and Lunau 2001; Lunau and Wacht 1994). Given that many of these insects feed preferentially on yellow pollen (Lunau 1995; Lunau and Maier 1995), this color might be interpreted as the location of a food resource. Nonetheless, other flower traits like odors (Laubertie et al. 2006; Nordstrom et al. 2017; Primante and Dotterl 2010) and amount 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 (Branquart and Hemptinne 2000b; Cowgill et al. 1993b). In fact, numerous studies have assessed adult hoverfly preferences to flower species and flower mixtures to supply suitable plant resources that can enhance hoverfly populations (and other auxiliary fauna) and promote their ecosystem services (Ambrosino et al. 2006; Barbir et al. 2015; Colley and Luna 2000; Hogg et al. 2011a; Pontin et al. 2006). However, floral preferences can be modulated by different factors such as plant phenology, presence of other flower species, competition with other pollinators and individual's previous experience (Colley and Luna 2000; Cowgill et al. 1993b; Wäckers and Van Rijn 2012), which can lead to changing levels of generalization during the season (Lucas et al. 2018). Due to the different nutritional value of the diverse food sources and the different benefits these provide to the adult's 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 do necessarily indicate suitability in terms of realized fitness benefits (Laubertie et al. 2012; van Rijn and Wäckers 2016).

The above mentioned 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). As far as we know only one study has assessed differences between the three Syrphidae subfamilies showing that Eristalinae and Pipizinae were more specialized than Syrphinae in flower preferences (Klecka et al. 2018). Syrphinae hoverflies are commonly believed to be generalist flower visitors, visiting mainly actinomorphic plants with flat corollas 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 traits characteristic of the species and the individual. Polyphagous hoverfly species, like for example the genus *Eupeodes*, *Platycheirus* and *Sphaerophoria*, are characterized by elongated mouthparts that enable them to have access to the pollen and nectar of more concealed flowers. These species are usually more ubiquitous than specialized ones because they can exploit more energy resources in diverse habitats. On the other hand, the species that present short mouthparts tend to be oligophagous feeding mainly on flowers with large inflorescences and unconcealed nectar (Branquart and Hemptinne 2000b). It should also be noted that small predatory species, such as *Melanostoma* spp. and *Platycheirus* spp., are also known to feed from wind pollinated plants like grasses and plantains (Branquart and Hemptinne 2000b; Leereveld et al. 1976).

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. About sex, as mentioned in the nutritional requirements section, females need more pollen while males are more dependable on nectar (Branquart and Hemptinne 2000a; Gilbert 1993; Gilbert 1981; Haslett 1989a). In this regard, also mating can be decisive as gravid females have been observed to ingest higher pollen amounts than non-gravid females, and even the latter more than males (Hickman et al. 1995; Irvin et al. 1999). In addition, hoverflies have been observed to become less selective as they get older (Almohamad et al. 2009; Sadeghi and Gilbert 2000b; Sutherland et al. 1999). The nutritional status of the individual can have a similar effect as age, as hungry individuals are keener to be attracted by yellow water traps while satiated individuals are less likely to invest effort in investigating a distant food source (Hickman et al. 2001).

### 2.3 How do hoverflies locate their prey?

**Adults**. Gravid hoverflies usually oviposit close to their prey in order to favor their offspring performance because neonate larvae possess a limited dispersal ability (Almohamad et al. 2009; Rojo et al. 2003; Sadeghi and Gilbert 2000a). However, different strategies are used depending on the hoverfly species, so oviposition can also occur in batches and on plants without aphids (Almohamad et al. 2009; Chandler 1968a; Chandler 1968b). Gravid individuals can discriminate among different prey types, as well as select the prey and prey-plant host combinations that provide better offspring performance. The factors that can influence the searching and oviposition behavior of aphidophagous hoverflies (from individual's intrinsic characteristics to external factors such as plant and aphid characteristic) 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 on host location, followed by olfactory cues. With regard to the latter, some herbivore-induced plant volatiles and aphid alarm pheromone components (such as E-(β)-farnesene, Glucosinolate, methyl salicylate, cis-3-hexen-1-ol and 2-phenylethanol) as well as aphid honeydew have been identified to elicit orientation towards the host plant and in some cases even stimulate egg-laying, (Almohamad et al. 2009; James 2005; Leroy et al. 2009; Leroy et al. 2014; Leroy et al. 2010; Mallinger et al. 2011; Xu et al. 2018a; Xu et al. 2018b; Zhu and Park 2005). However, little knowledge exists about the distance from which these compounds are detected. As far as we know, only Mallinger et al. (2011) found that the addition of methyl salicylate lures significantly attracted higher numbers of hoverflies and green lacewings (which significantly reduced the abundance of soybean aphids) but the effect disappeared at 1.5 m from the lure.

**Larvae.** Hoverfly larvae are commonly believed to have a limited dispersal capacity, so the oviposition choice of the adult is the main determinant of the fate of the developing larvae (Almohamad et al. 2009; Rojo et al. 2003; Sadeghi and Gilbert 2000a). However, it is highly probable 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 in 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 colony, hoverfly larvae are able to use aphid volatiles (which can consist on alive or crushed aphids, concentrated aphid extracts, 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 behaviors to the presence of honeydew depending on their instar. First instar larvae are highly responsive to honeydew as rapidly orientate themselves to zones impregnated with honeydew. Also, both first and second instar larvae increase their foraging behavior, moving more and more often in order to reach honeydew impregnated zones. Conversely, despite third instar larvae are highly mobile, they do not respond to the presence of 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 was found to be very sensitive to small amounts of aphid volatiles from aphids: the syrphid larvae responded positively to odor sources from a colony of about 500 aphids while other predators, like the coccinellid *Coccinella septempunctata* L. did not respond until the number of aphids was at least 2000 (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 in a proportion of the population staying to overwinter in the breeding grounds and the other travelling large distances in search of the milder climates (Rotheray and Gilbert 2011; Tenhumberg and Poehling 1995). 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)” (Speight 2014).

**Migration.** Compared to other migratory insects, hoverfly migration is poorly studied. The migration of hoverflies is best understood in Europe though reports of hoverfly migration also exist in other regions of the world (Menz et al. 2019; Shannon 1926; Westmacott and Williams 1954). In Europe, some common species from the Syrphinae subfamily, such as *E. balteatus* and *Eupeodes corollae* Fabr., are highly migratory (Wotton et al. 2019). These species migrate annually during autumn travelling large distances in search of the milder climates of southern Europe and Mediterranean areas (Rotheray and Gilbert 2011; Tenhumberg and Poehling 1995). Then, on spring the offspring 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 in 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 hoverflies) occur between British Isles and mainland Europe making billions of flower visits and consuming about 6 trillion aphids therefore providing extensive pollination and biological control services.

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

Genetic studies have demonstrated a lack of genetic differentiation at a continental scale and a great genetic diversity in *E. balteatus* and *S. scripta* 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; Odermatt et al. 2017; Raymond et al. 2013a), morphological (Raymond et al. 2014b) nor behavioral (Dallenbach et al. 2018) differences have been observed between migrating and overwintering phenotypes in *E. balteatus*. So it is possible that all individuals have the genetic material and therefore the capacity for both strategies, but the decision is triggered by environmental or physiological factors (Odermatt et al. 2017; Raymond et al. 2013a). Furthermore, despite 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 offspring of the migrating phenotypes are more active than those from overwintering phenotypes. This suggests the involvement of some genetic factors in the migratory tendency, which are only maintained under the appropriate environmental cues (Dallenbach et al. 2018). Further studies are needed to determine the fraction of migratory/resident individuals in a population (Raymond et al. 2013b) as well as the factors that trigger the different overwintering strategies are still unknown (Odermatt et al. 2017).

**Overwintering**. Overwintering in hoverflies can occur in the form of larva, pupa or adult 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 morphs (Hart and Bale 1997). In species with overwintering adults, almost exclusively mated females in facultative reproductive diapause are the ones that overwinter (Hondelmann and Poehling 2007). These diapausing females are believed to only use “hiding places” when conditions become harsh and remain active during winter (Hondelmann and Poehling 2007). Winter flight activity has been observed in *E. balteatus* adults at temperatures around 7ºC (Hondelmann and Poehling 2007). Males, in turn, are thought to be more susceptible to cold temperatures due to their inability of increasing their fat bodies (Hondelmann and Poehling 2007).

Hoverflies do not need special structures to overwinter as they can use different microhabitats present in the landscape such as soil litter woodlots, caves, tree hollows, cracks, joints between bricks, etc. (Hondelmann and Poehling 2007; Kula 1982; 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 habitat might favor overwintering hoverflies by providing both, undisturbed habitat (Hatt et al. 2017b; Ramsden et al. 2015) and more overwintering sites (Sarthou et al. 2014). In fact, overwintering *E. balteatus* females have been observed to be positively associated with south-facing forest edges possibly due to presence of warmer temperatures (Sarthou 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 from landscape and climatic 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, Raymond et al. (2014a) found that the abundance of aphidophagous hoverflies emerging in the spring is more related to the distances to the nearest semi-natural features than to the amount of land occupied by these features in the surrounding landscape.

Hence, agricultural practices, such as a limitation of pesticides in autumn and a reduction of mechanical weed control in winter, might preserve overwinter populations and therefore enhance biological control in the next season (Raymond et al. 2014a). Moreover, getting to know 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 large-scale 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 to maximize hoverflies and their ecosystem services they provide in agricultural landscapes (Raymond et al. 2013b).

### 2.5 Are hoverflies affected by landscape structure?

Agricultural intensification commonly implies the maximization of the cropping area at the expense natural and semi-natural habitats, which frequently become lost and fragmented (Tscharntke et al. 2005). The loss and isolation of these suitable habitats has been acknowledged to negatively affect farmland diversity (Fahrig 2003; Hendrickx et al. 2007; Schweiger et al. 2005), to the point that nowadays it is considered among the main drivers of the current global biodiversity loss (Tscharntke et al. 2005). Thus, understanding how landscape characteristics affect biodiversity patterns and ecological processes at local and landscape scale 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; Hendrickx et al. 2007; Schweiger et al. 2005). However, evidences about the effects of landscape change on hoverfly populations in agricultural systems are mixed, which emphasizes the difficulties of performing these type of studies, as well as the lack of large scale data across multiple countries (Tscharntke et al. 2012). Nonetheless, the general trend for hoverflies seems to be in accordance with the current literature: positive effects have been observed on different aspects of hoverflies community structure and composition of landscape connectivity (Öckinger et al. 2012; Sjodin et al. 2008; but see Schweiger et al. 2005) cover of natural and semi-natural habitats or proximity to these (Jauker et al. 2019; Kleijn and van Langevelde 2006; Klein et al. 2012; Kohler et al. 2008; Medeiros et al. 2018; Meyer et al. 2009; Öckinger et al. 2012; Schweiger et al. 2005; Sjodin et al. 2008; but see Ekroos et al. 2013; Hass et al. 2018; Jauker et al. 2009; Pfister et al. 2017) and diversity (Bommarco et al. 2012; Bourke et al. 2014; Burgio and Sommaggio 2007; Foeldesi et al. 2016; Meyer et al. 2009; Sommaggio 1999; but see Ekroos et al. 2013; Hass et al. 2018; Schweiger et al. 2005). Landscape effects on hoverflies can be found at relatively large spatial scales up to 4 km (Haenke et al. 2009; Power et al. 2016; Werling et al. 2011), but most hoverfly species respond to 1 km (Haenke et al. 2014; Haenke et al. 2009; Kleijn and van Langevelde 2006; Pfister et al. 2017).

One reason to explain the mentioned differences is that the extent to which landscape structure and composition affects the different hoverfly species depends on their ecological traits (Meyer et al. 2009; Moquet et al. 2018; Schweiger et al. 2007). Hoverfly species can be separated in functional guilds according to several life history traits such as larval habitat and feeding behavior, number of generations per year, adult's flight period, body size and dispersal capacity, etc. (Branquart and Hemptinne 2000b; Moquet et al. 2018; Ouin et al. 2006; Schweiger et al. 2007). Thus, species that belong to specialist guilds might require specific habitats and resources and therefore need to move between habitat patches to acquire specific resources. Consequently, specialist guilds might be more affected by local habitat diversity and quality. Conversely, generalist guilds, are more likely to find sufficient resources within a patch and to perceive a fragmented landscape as sufficiently connected. So, the scale at which these are affected increases at a landscape scale, to the point that extremely generalist guilds are nearly unaffected by landscape structure (Thomas 2000). In this regard, it should be noticed that a high species richness in a certain area does not imply a high functional richness (Schweiger et al. 2007).

The case of extremely generalist guilds is, in fact the case of highly mobile aphidophagous species such as *E. balteatus*, *E. corollae* and S*yrphus vitripennis* Meigen. Species belonging to this guild appear to be less vulnerable to landscape simplification and loss of natural and semi-natural habitats than other guilds (Raymond et al. 2014a; Schirmel et al. 2018; Schweiger et al. 2007). Aphidophagous species are known to find prey for their offspring in aphid colonies from cultivated as well as wild plants (Rojo et al. 2003; Sadeghi and Gilbert 2000a). Thus, they are usually well adapted to agricultural landscapes 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; Haenke et al. 2014; Jauker et al. 2009; Meyer et al. 2009). Moreover, studies about agricultural intensification are usually performed in landscapes in which natural and semi-natural habitats have already become lost or fragmented. These communities might already be dominated by less susceptible species with the ability to use a wide range of different resources and to reach scattered habitat patches (Tscharntke et al. 2012). This might help explain the dominance of the aphidophagous guild in syrphid communities in highly intensified land-use systems (Haenke et al. 2014; Haenke et al. 2009; Hass et al. 2018; Meyer et al. 2009) and the lack of positive relationships between Syrphinae communities and proportion of natural and semi-natural habitats at the landscape scale (Jauker et al. 2009; Pfister et al. 2017). Nonetheless, previous studies have found aphidophagous hoverflies to be positively influenced by the presence of semi-natural habitats like forest patches, hedgerows, grass margins, flower strips, grassland, heathlands, etc (Burgio and Sommaggio 2007; Jauker et al. 2009; Kohler et al. 2007; Medeiros et al. 2018; Pfister et al. 2017; Schirmel et al. 2018). Woody habitats, such as forests and hedgerows, are usually related to a high availability of larval microhabitats and undisturbed refuge, 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 landscape scale (Moquet et al. 2018).

Hoverflies require different resources at larval and adult stages thus availability of resources for both developmental stages are necessary for their presence (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 response to landscape variables within a guild. For example, Andersson et al. (2013) found opposing responses to landscape heterogeneity of two highly mobile aphidophagous species: *E. corollae* and *Syrphus torvus*. While the first primarily preys on aphid species from crops like beets which in the study mainly existed on 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 highly determined by their habitat needs (Andersson et al. 2013)

Thus, natural and semi-natural habitats might still be relevant to allow the persistence of aphidophagous hoverflies in agricultural landscapes by, for instance, providing enhanced flower 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 the diverse semi-natural habitats in providing resources can also change through the seasons (Bortolotto et al. 2016; Cole et al. 2017; Sarthou et al. 2005; Villa et al. 2016). For example, fallow land associated with close South-facing forest edges can represent an important overwintering site, whereas habitats offering abundant flower resources, such as managed weed strips, become the main habitat for hoverflies in spring (Sarthou et al. 2005). In fact, several studies have noticed more natural enemies and less pest levels in crops close to semi-natural habitats (Alignier et al. 2014; Chaplin-Kramer et al. 2013; Stutz and Entling 2011).

Despite watercourses do not seem to have an effect to 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, which included hoverflies, were observed in the shade and near bodies of water in the woodlands in summer. Thus, in case of harsh environmental conditions (wind, rain, extreme temperatures, sun irradiation, water scarcity or predators, etc.), these remnant woodlands provide more short-term refuges for hoverflies than open habitats. Similar behavior was observed 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 (personal observation). Hence, presence of refuges for high temperatures should also be taken into account during summer.

It is important to note that landscape structure can strongly interact with locals factors, such as farm management practices (Andersson et al. 2013; Dormann et al. 2007; Garratt et al. 2017; Haenke et al. 2009; Klein et al. 2012), modulating their influence on arthropod communities. For example, the attractiveness of implemented flower strips (Garratt et al. 2017) and hedgerows (Haenke et al. 2009) to hoverflies was dependent on landscape complexity, with greater numbers of hoverflies seen in areas with a lower local proportions of semi-natural habitat. Tscharntke et al. (2012) suggests that these confounding effects of the surrounding landscape probably correspond to “the intermediate landscape complexity hypothesis”. It postulates that in complex landscapes biodiversity is high and high levels of immigration from natural and semi-natural habitats occur. This can outweigh the effects of any local practices such as organic farming or habitat management practices. In the same way, landscapes without a substantial species pool do not have the capacity to respond to local management. Hence, only in simple landscapes local management will compensate the lack of structural complexity of the landscape.

## 3. Which ecosystem functions and services do Syrphinae provide?

### 3.1 Are hoverflies good pollinators?

Animal pollinators provide a key ecosystem service 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), the latter being estimated at €153 billion worldwide (Gallai et al. 2009). Adult hoverflies are prevalent visitors of flowers. However, their role as pollinators has usually been underestimated, especially in contrast with that of bees (Inouye et al. 2015), since most of the species are usually considered generalists (Branquart and Hemptinne 2000b). Nonetheless, despite hoverflies show little specialization at the species level, they are known to exhibit flower constancy. In other words, they prefer to visit one type of flower bypassing other potentially attractive species over short time scales (Fruend et al. 2010; Goulson and Wright 1998; Inouye et al. 2015). Hence, 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 hoverflies have one of the most energy-expensive forms of flight (Kevan and Baker 1983), if 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 since they do not care for their brood, so they do not need to forage within a range of a nesting site like bees 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, it has been observed that these non-bee pollinators are not as reliant as bees on the presence of natural or semi-natural habitat in the surrounding agricultural landscape, which probably makes their pollination services more robust 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 (Fontaine et al. 2006; Vance et al. 2004) and crops, such as: apple (Kendall and Solomon 1973; Solomon and Kendall 1970), 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 et al. 2012; Jauker and Wolters 2008; Rader et al. 2011; Rader et al. 2009). 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 oil-seed rape close to the efficiency of small honeybee colonies.

Therefore, despite more research is needed to further assess the role of aphidophagous hoverflies as pollinators, the present evidence shows that their presence as pollinators as well as biological control agents should be encouraged in agroecosystems.

## 3.2 How important are hoverflies as biological control agents?

Biological control is nowadays one of the bases of modern crop protection. It can be broadly defined as a reduction of pest populations (pests, pathogens or weeds) by other living organisms, such as predators and parasitoid wasps. Worldwide, pest suppression from insect natural enemies, was valued at over €350 billion annually (Costanza et al. 1997). However, current evidence shows that pest control does not just depend on increased biodiversity or natural enemy abundance per se, but on promoting the "right biodiversity at the right time" (Pfiffner and Wyss 2004).

Predatory hoverflies have long been recognized for their potential as natural enemies (Chandler 1968b; Cowgill et al. 1993a; Gilbert 1993; Tenhumberg 1995). Despite the potential for biological control is different among species because differences on predatory capacity (Hopper et al. 2011; Putra and Yasuda 2006), the larvae are considered to be highly voracious. Depending on larval stage, they are able to consume between 20 and 80 aphids per day: the first two instars feed very little, and the third instar can predate nearly the 70% of the total food consumed (Samuel and Singh 2005; Tenhumberg and Poehling 1995).

Aphidophagous larvae are usually cryptic and on many cases they hide during the day apart from the aphid, as they are mostly active during dawn and dusk (Rotheray 1993). The adults, in turn, are highly mobile (Schneider 1948; Speight 2014) and possess potentially good ovipoisitional 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), establish that a female of *E. balteatus* can lay between 2000 and 4,500 eggs during its adult life. Moreover, predatory hoverflies are among the most abundant aphid predators in several agricultural systems (Gardiner et al. 2010; Miñarro et al. 2005; Tenhumberg and Poehling 1995; White et al. 1995) and among the aphidophagous insects that can locate the aphid colonies earlier in the season (Dib et al. 2010; Miñarro et al. 2005).

The previously mentioned 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 on biological control (Hatt et al. 2017a; Hickman and Wratten 1996; Schmidt et al. 2004; White et al. 1995). Despite this, the success of biological control is going to be determined by several other factors, such as good synchronization of hoverfly and pest populations to prevent aphid outbreaks (Dib et al. 2010; Miñarro et al. 2005) and the presence of other natural enemies. In regard to the later, some authors state that a higher natural enemy diversity is going to put more pressure on pest populations instead of leading to rivalry between natural enemies. For example Wyss et al. (1999) found that hoverflies and coccinellidae combined their effects to reduce *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) populations, suggesting coexistence more than antagonism. In the same sense, 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 effects can also appear, such as intraguild predation (see section "How important are hoverflies as food/prey for other beneficials? Predatory invertebrates") or cannibalism (Branquart et al. 1997). Nevertheless, it has been observed that females usually avoid ovipositing in aphid colonies where hoverfly larvae or other predators are already present (Almohamad et al. 2009). Despite hoverflies can eat adult parasitoids (Meyhofer and Klug 2002) and parasitized aphids, they tend to avoid those aphids that are already mummified (Michaud 1999), either because they are unable to open the mummy shelter with their mouthparts or because they are unable to recognize aphid mummies as valuable prey (Meyhofer and Klug 2002). Besides, ants can strongly interfere with the natural levels of pest regulation as: reduced aphid mortality and predation have been observed in their presence of ants (Dib et al. 2010; Stewart-Jones et al. 2008).

On the other hand, hoverflies also present some constraints that can interfere in their capacity as biological control agents. As it has been previously mentioned, adult hoverflies need to feed on pollen and nectar in order to be able to oviposit, nonetheless flower resources tend to be scarce in agricultural systems. For this reason, a significant amount of research has been done to assess the effect of flower provisioning to improve biological control (discussed later in section 4.2).

### 3.3 How useful are hoverflies as bioindicators?

Bioindicators are a useful tool in evaluating the effect of agriculture on the quality of agroecosystems. The Syrphidae family is a potential good bioindicator taxa for several reasons.

First, as mentioned above, their larvae present a wide variety of feeding habits. Second, among same feeding habits, many species present different environmental requirements, such as particular macro and microhabitats 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 in Europe (Schweiger et al. 2007; Sommaggio 1999; Speight et al. 2000). 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 by several studies (Billeter et al. 2008; Burgio and Sommaggio 2007; Sommaggio 1999; Sommaggio and Burgio 2014) and particularly recognized through the development of an expert system called Syrph The Net (StN), which analyzes and evaluates hoverfly communities using the taxonomic value of each species, together with their functional traits and their relationship with the habitat (Speight et al. 2000).

### 3.4 How important are hoverflies as food/prey for other beneficials?

Adult hoverflies exhibit batesian mimicry, which consists in 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 (the ability of an organism to conceal itself by having a color, pattern, and shape that allows it to blend into the surrounding environment) as a defense against predators (Rotheray 1981). Even though, hoverflies can still be potential preys of several predators such as birds, amphibians, reptiles, spiders and predatory insects (Rotheray and Gilbert 2011).

**Predatory invertebrates.** The most studied aspect of hoverfly predation by predatory insects is intraguild predation (IGP), which occurs when the interacting organisms belong to the same guild (i.e. predators competing for the same prey). Thus, this type of predation is relevant due to the complex interactions that can affect the final biological control. Syrphinae hoverflies belong to the aphidophagous guild together with mirids, lacewings, ladybugs, earwigs and gall midges, among others. When hoverflies are present, the outcome of this interaction is determined by several factors regarding the biological characteristics of the involved predators together with the availability of prey and habitat structure. 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, since predation rates between the 20 and the 100% under laboratory conditions can occur (Frechette et al. 2007; Hindayana et al. 2001). This susceptibility decreases as the larvae gain in size, strength and mobility. So first and second instars are usually more susceptible to predation than third instar larvae (Frechette et al. 2007; Hindayana et al. 2001). 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” (Lucas et al. 1998; Polis et al. 1989). Accordingly, if hoverfly larvae are bigger than the other predator they will behave as the intraguild predator, showing attack behavior. On the other hand, if they are smaller they will behave as the intraguild prey and display defense and escaping mechanisms (Frechette et al. 2007; Hindayana et al. 2001). Nonetheless, feeding history might also influence these types of behavior, as poor-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 to behave as the intraguild predator, as occurs for example with the extreme generalist *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) (Ingels and De Clercq 2011; Ingels et al. 2015; Nedved et al. 2013). Furthermore, the abundance of extraguild prey can also modify the outcome: the incidence of IGP has been observed to decrease as the availability of extraguild prey increases (Hindayana et al. 2001; Ingels and De Clercq 2011). Finally, it is important to note that IGP is likely to be reduced under natural conditions facilitating species coexistence: a higher habitat complexity implies more refuges, reduced encounter rates and higher probability for the intraguild prey to scape (Ingels and De Clercq 2011; Janssen et al. 2007; but see Frechette et al. 2007).

**Parasitoids.** Syrphinae larvae can be parasitized by 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 that oviposits into the syrphid eggs or first-instars larvae, with the imago emerging from the syrphid puparium (Rotheray 1981). It has been particularly recognized as the most important parasitoid due to its abundance and frequency worldwide (Greco 1997; Jankowska 2004; Mayadunnage et al. 2009; Mohammadi-Khoramabadi et al. 2016; Rotheray 1981).

In order to locate their hosts, syrphid parasitoids use in first place odors released by the aphid colonies. Once in the colony, the parasitoids use their antennae to locate the hoverfly larvae, responding to the contact chemicals present in the larval intertegument (Rotheray 1981). When the host is located, females require stimulus from the host haemolymph to elicit egg release, otherwise ovipositor insertions can occur without egg deposition (Rotheray 1984). In some species, movement of the larvae is a necessary final cue to elicit oviposition (Rotheray 1981). Visual cues seem unimportant during this process (Rotheray 1981). While most of these parasitoids are monophagous, a few can be oligophagous (like for example *D. laetatorius*) (Rotheray 1984). Differences in host ranges, parasitoid phenology and target stage of the host (egg, first, second or third instar) probably enable partitioning of resources between possible competitors (Rotheray 1981; Rotheray 1984). In the case of a multiparasitized host, which parasitoid is going to emerge depend on the parasitization interval: with a 72-hour pause between multiparsitism, the older parasitoids are usually the ones that are going to survive; in contrast, if the time interval is lower the superior competitor is going to survive (Rotheray 1984). The adult parasitoid emergency time depends on the species, but it is from 10 up to 14 days (Krsteska 2014).

If parasitized, hoverfly larvae can deploy an immune response to resist parasitoid attacks. These parasitized larvae have been observed to increase their immune response with larval age, so while first instars were not able to survive, a 40% and 100% survival 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 reduced in pupal weight and adult survivorship (Hazell et al. 2005; Tinkeu and Hance 1997). Hence, parasitic pressure can decrease larval rate of predation and top-down effects provided by Syrphinae (Hazell et al. 2005; Tinkeu and Hance 1997). 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 null to more than the 50% (Gomez-Polo et al. 2014; Jankowska 2004; Krotova 1993; Likhil and Mallapur 2009; Mayadunnage et al. 2009; Mohammadi-Khoramabadi et al. 2016; Nourbakhsh et al. 2008; Smith and Chaney 2007). To our knowledge, only Sommaggio et al. (2014) has assessed the effect of agricultural management on syrphinae-parasitoid populations. In this study, higher parasitism rates of hoverfly larvae were found in habitats simplified by intensive agriculture than in more diversified ones.

**Birds.** Several bird species have been found to feed on hoverflies: *Phylloscopus collybita* Vieillot (Passeriformes: Phylloscopidae), *Sitta europea* L. (Passeriformes: Sittidae), *Parus palustris* L. (Passeriformes: Paridae), *Prunella modularis* L. (Passeriformes: Prunellidae) (Kristín 1988) and *Passer montanus* L. (Passeriformes: Passeridae) (Grass et al. 2017). However, to our knowledge only one study has specifically assessed the impact of birds on hoverfly populations: Grass et al. (2017) found that tree sparrows (*P. montanus*) usually 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 the 77% of the sparrows nestlings' diet during peak aphid density in arable land systems in Germany.

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

### 4.4 Pesticides

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

Qiaoyan et al. 2015). A good example of this outreach can be found in the work of Jepson (1989) although it did not specifically target hoverflies.

The IOBC-WPRS Working Group “Pesticides and Beneficial Organisms” jointly with the Commission “Guidelines for Integrated Production” have 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 (Table 1) and specifically three species: *E. balteatus, Eupeodes corollae* (Fabricius)*, Syrphus vitripennis* (Meigen). According to the classification by mode of action of the insecticides and acaricides (IRAC), fungicides (FRAC) and herbicides (HRAC), fungicides usually seem to be harmless to hoverflies, except for two groups (“Chemicals with multi-site activity” and “Sterol biosynthesis in membranes”) which resulted moderately harmful or harmful in initial toxicity tests and semi-field assays. Herbicides is the group that has been less tested, despite about 22% of the active ingredients have 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 (inh. of ACCase)” groups. The insecticides group has been found to be most harmful. While, 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” have found to be among the most harmful, the “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 Receptor (NACHR) Competitive Modulators” and “Ryanodine Receptor Modulators” are the most harmless. Nonetheless, it is important to take into account that the toxicity of the different active ingredients is going to be modulated depending on the dose, the formulations of the product assessed, the type of test run, and the species uses for the assays. For detailed information see the “Pesticide Side Effect Database” from IBOC (IOBC 2019).

Table 1. Distribution of the pesticide toxicity by mode of action between the toxicological categories of the IOBC (IOBC 2019).

| | Mode of action | Number of pesticides tested | IOBC Toxicity class | | | |
|---|---|---|---|---|---|---|
| | | | *% Harmless* | *% Slightly harmful* | *% Moderately harmful* | *% Harmful* |
| Fungicides | Amino Acid and Protein Synthesis | 2 | 100.0 | 0.0 | 0.0 | 0.0 |
| | Chemicals with Multi-Site Activity | 9 | 66.7 | 11.1 | 22.2 | 0.0 |
| | Nucleic Acids Metabolism | 2 | 50.0 | 50.0 | 0.0 | 0.0 |
| | Respiration | 1 | 100.0 | 0.0 | 0.0 | 0.0 |
| | Sterol Biosynthesis in Membranes | 10 | 50.0 | 30.0 | 10.0 | 10.0 |
| | Unknown Mode of Action | 3 | 66.7 | 33.3 | 0.0 | 0.0 |
| | *Not known* | 2 | 100.0 | 0.0 | 0.0 | 0.0 |
| | **Total fungicides** | **29** | **19** | **6** | **3** | **1** |
| Herbicides | Inhibition of ALS (branched chain amino acid synthesis) | 3 | 33.3 | 0.0 | 0.0 | 66.7 |
| | Inhibition of photosynthesis PS II | 5 | 60.0 | 40.0 | 0.0 | 0.0 |
| | Lipid synthesis inhibition (inh. of ACCase) | 7 | 57.1 | 0.0 | 14.3 | 28.6 |
| | Synthetic auxin | 1 | 100.0 | 0.0 | 0.0 | 0.0 |
| | *Plant growth regulator* | 2 | 100.0 | 0.0 | 0.0 | 0.0 |
| | **Total herbicides** | **18** | **11** | **2** | **1** | **4** |
| Insecticides and Acaricides | Acetylcholinesterase (ACHE) inhibitors | 34 | 2.9 | 0.0 | 8.8 | 88.2 |
| | Chordotonal Organ Modulators - Undefined target site | 3 | 0.0 | 100.0 | 0.0 | 0.0 |
| | Chordotonal Organ TRPV Channel Modulators | 1 | 100.0 | 0.0 | 0.0 | 0.0 |
| | Inhibitors of Acetyl COA Carboxylase | 1 | 100.0 | 0.0 | 0.0 | 0.0 |
| | Inhibitors of Chitin Biosynthesis, Type 0 | 1 | 0.0 | 0.0 | 0.0 | 100.0 |
| | Inhibitors of Mitochondrial ATP Synthase | 1 | 100.0 | 0.0 | 0.0 | 0.0 |
| | Mite Growth Inhibitors | 1 | 100.0 | 0.0 | 0.0 | 0.0 |
| | Mitochondrial Complex I Electron Transport Inhibitors | 3 | 66.7 | 33.3 | 0.0 | 0.0 |
| | Nicotinic Acetylcholine Receptor (NACHR) Allosteric Modulators - Site I | 1 | 0.0 | 0.0 | 0.0 | 100.0 |
| | Nicotinic Acetylcholine Receptor (NACHR) Competitive Modulators | 1 | 100.0 | 0.0 | 0.0 | 0.0 |
| | Sodium Channel Modulators | 27 | 22.2 | 18.5 | 14.8 | 44.4 |
| | Octopamine Receptor Agonists | 1 | 0.0 | 0.0 | 100.0 | 0.0 |
| | Ryanodine Receptor Modulators | 1 | 100.0 | 0.0 | 0.0 | 0.0 |
| | Compounds of unknown or uncertain MOA | 1 | 0.0 | 0.0 | 0.0 | 100.0 |
| | **Total insecticides** | **77** | **15** | **9** | **8** | **45** |
| **Total pesticides** | | **124** | **45** | **17** | **12** | **50** |

At a farm scale, several studies have confirmed the positive effects of non-conventional agriculture (organic and integrated pest management), not only on hoverfly abundance and richness (Andersson et al. 2013; Dib et al. 2016; Lu et al. 2015; Power et al. 2016; Power and Stout

2011; 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 also relies in pesticides that have potential negative impacts on insects, so further studies with more descriptive 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 generalists (Dormann et al. 2007). So, it is likely that the high mobility of hoverflies allows the rapid recolonization of pesticide-treated fields, as also hypothesized by (Gabriel et al. 2010). In fact, as discussed above, interacting effects between farming practices and the surrounding landscape are quite common (Gagic et al. 2014; Klein et al. 2012; Power et al. 2016).

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

Several studies have estimated the spillover from floral resources into the crop: the higher estimates are around 250 m for *E. balteatus* (Harwood et al. 1994) to 1 km for *S. pyrastri* (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 like dirt tracks, asphalt roads, ploughed fields (Lovei 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. 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 benefits of hedgerows and forest patches to hoverflies and other beneficials have been widely acknowledged (Haenke et al. 2014; Holland et al. 2016; Miñarro and Prida 2013; Sarthou et al. 2005), 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). Thus, the presence and location of barriers can influence different aspects of presence of hoverflies in the crop, such as recolonization after pesticide induced mortality (Wratten et al. 2003) and spillover from implemented ecological infrastructures.

### 4.3 Use of semiochemicals

As mentioned above, semiochiemicals elicit orientation towards the host plant and stimulate egg-laying. In addition, the combination of intercropping with the use of the semiochemicals E-(β)-farnesene and methyl salicylate has been proven to successfully repel aphids and simultaneously attract natural enemies in wheat-pea intercropping systems (Xu et al. 2018a; Xu et al. 2018b). These authors observed an increase in hoverfly larvae abundance and in the rate of aphid-parasitism and a decrease 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 has to be conducted on this matter, the use of semiochemicals shows promising results as a successful alternative to promote aphid biological control and reduce the use of insecticides.

### 4.4 Mowing

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

### 4.5 Implementation of ecological infrastructures

Nowadays, habitat management is an important subdiscipline of pest management that aims to promote conservation biological control through the maintenance of favorable habitats or the addition of new ones, such as flower strips and hedgerows (Boller et al. 2004). These favorable habitats promote natural enemies through the provision of shelter, nectar, alternative prey/hosts and/or pollen (Gurr et al. 2017). One approach for managing floral diversity to optimize biological control and pollination involves cultivating the single-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 tested in relation to the relative attractiveness of plant species to adult hoverflies, as well as their effects in the adult's fitness (Ambrosino et al. 2006; Colley and Luna 2000; Hogg et al. 2011a).

Despite 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. 2011a), the hoverfly species involved or the rest of resources present in the landscape. Furthermore, there is evidence that some native flowers might be as good as typically evaluated insectary plants (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; Rodríguez-Gasol et al. 2019a; Warzecha et al. 2018). Moreover, in mixed floral vegetation, the number of predator hoverflies is highly correlated with the abundance of only those flowers that have accessible nectar (van Rijn and Wäckers 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).

Nonetheless, very few studies have assessed the contribution of ecological infrastructures on pest control by hoverflies. For this purpose, we reviewed the published papers related to the enhancement of aphid biological control by hoverflies through the implementation of ecological infrastructures. To standardize the studies as much as possible, we restricted the review to those experiences evaluating the effects of sown flower strips, hence we did not include studies evaluating the effect of intercropping, mowing, native weeds, hedgerows or semi-natural habitats. Furthermore, the study should specifically search for hoverflies (any stage of their development) in the crop, so a potential effect on aphid predation could be observed.

For each study, we report the number of successes, failures or lack of assessment per type of crop and country on 1) the attraction of adult hoverflies into the flower strip, 2) the attraction of adult hoverflies into the crop, 3) the enhancement of hoverfly larvae or eggs in the crop, 4) the enhancement of aphid predation and finally, 5) the provision of an effective biological control, in other words, the reduction of pest levels under the damage threshold (Table 2).

After analyzing the papers that deal with this topic, we draw several conclusions. First, the evaluation of the attraction of an implemented flower strip to adult hoverflies is quite common among the studies. However, demonstrating that this addition of extra resources leads to an enhancement of biological control is considerably difficult. On one hand, the great mobility of hoverflies hinders the design of the experiments, as small distance between treatments could mask potential predation effects on the crop. On the other hand, long distance usually involves many external factors impacting the results. Hence, highly replicated studies would be advisable, though these are not always feasible due to limitation of resources. Second, observing a decrease in pest populations does not necessarily imply a direct relationship with an increased predation by hoverflies because other natural enemies could be interceding. In fact, this is further supported by the few studies that specifically asses the contribution of hoverflies to biological control through the provision of flower strips. Most notably, this highlights the importance of promoting a natural enemy pool. Third, although some studies have managed to demonstrate a reduction of aphid populations, the demonstration of an effective biological control (for example, by maintaining pest populations under the economic threshold or demonstrating increases in yield) has been addressed occasionally. Hence, further studies should focus on evaluating the actual contribution of ecological infrastructures to pest control. Finally, with regard to the types of crop, horticultural crops are the ones with a higher number of studies as well as a higher percentage of success in reducing pest populations. In fact, intercropping of vegetables, such as lettuce and broccoli, with insectary plants is a common practice to enhance biological control of aphids on the central coast of California (Brennan 2013; Brennan 2016; Gillespie et al. 2011; Smith and Chaney 2007). In the case of fruit orchards, apple is the most studied fruit by far, but only one third of the experiences have reported positive effects on pest control. The intrinsic characteristics of the different types of crops are an important factor to consider. For example, the implementation of flower strips in the orchard alleys is constrained by the mechanical control of the weeds present in the groundcover, but implementation on the orchard margins instead, has to address challenges like distance between the crop and the ecological infrastructure or the trees themselves hampering hoverflies dispersal.

In a nutshell, current experiences show that the provision of flower strips contribute to increase the presence of hoverflies at farm level and to reduce pest populations. However, further research is needed to discern aspects such as optimal location of these infrastructures and the extent to which an effective biological control can be achieved.

Table 2. Summary table with the analysis of cases of sown flower strips in different crops and countries. Number of cites that report successes (S), failure (F) or not assessed (NA) on 1) the attraction of adult hoverflies into the flower strip, 2) the attraction of adult hoverflies into the crop, 3) enhanced presence of hoverfly larvae or eggs in the crop, 4) enhanced predation or reduced presence of prey in the crop and 5) enhanced biological control. Abbreviations for the countries: A: Argentina, Be: Belgium, Br: Brazil, C: China, E: Egypt, F: France, G: Germany, J: Japan, NZ: New Zealand, P: Poland, S: Spain, Sw: Switzerland, UK: United Kingdom, USA: United States of America.

| Type of crop | Nº of studies | More hoverflies in the flower strip | Crop | | | |
|---|---|---|---|---|---|---|
| | | | More adult hoverflies | More hoverfly larvae or eggs | More predation | Effective biological control |
| Horticultural crops | | | | | | |
| Cabbage (*Brassica oleracea*) | 4 | S 2 Br: (Ribeiro and Gontijo 2017); J: (Morris and Li 2000). | S 2 Br: (Ribeiro and Gontijo 2017); NZ: (White et al. 1995). | S 1 Br: (Ribeiro and Gontijo 2017). | S 3 Br: (Ribeiro and Gontijo 2017); NZ: (White et al. 1995)[1], (Morris and Li 2000). | S 0 |
| | | F 1 NZ: (Morris and Li 2000). | F 2 J: (Morris and Li 2000); NZ: (Morris and Li 2000). | F 3 J: (Morris and Li 2000); NZ: (Morris and Li 2000), (White et al. 1995). | F 1 J: (Morris and Li 2000). | F 0 |
| | | NA 1 NZ: (White et al. 1995). | NA 0 | NA 0 | NA 0 | NA 4 Br: (Ribeiro and Gontijo 2017); J: (Morris and Li 2000); NZ: (Morris and Li 2000), (White et al. 1995). |
| Lettuce (*Lactuca sativa*) | 3 | S 0 | S 0 | S 1 S: (Pascual-Villalobos et al. 2006). | S 2 S: (Pascual-Villalobos et al. 2006); UK: (Skirvin et al. 2011)[2]. | S 0 |
| | | F 0 | F 1 UK: (Skirvin et al. 2011). | F 2 UK: (Skirvin et al. 2011); USA: (Hogg et al. 2011b). | F 1 USA: (Hogg et al. 2011b). | F 0 |
| | | NA 3 S: (Pascual-Villalobos et al. 2006); UK: (Skirvin et al. 2011); USA: (Hogg et al. 2011b)[3]. | NA 2 S: (Pascual-Villalobos et al. 2006); USA: (Hogg et al. 2011b). | NA 0 | NA 0 | NA 3 S: (Pascual-Villalobos et al. 2006); UK: (Skirvin et al. 2011). USA: (Hogg et al. 2011b). |
| Melon (*Cucumis melo*) | 1 | S 1 F: (Lambion and Franoux 2017). | S 0 | S 0 | S 0 | S 0 |
| | | F 0 | F 1 F: (Lambion and Franoux 2017). | F 0 | F 1 F: (Lambion and Franoux 2017). | F 0 |
| | | NA 0 | NA 0 | NA 1 F: (Lambion and Franoux 2017). | NA 0 | NA 1 F: (Lambion and Franoux 2017). |
| Potato (*Solanum tuberosum*) | 1 | S 1 Sw: (Tschumi et al. 2016). | S 0 | S 1 Sw: (Tschumi et al. 2016). | S 1 Sw: (Tschumi et al. 2016). | S 0 |
| | | F 0 | F 1 Sw: (Tschumi et al. 2016). | F 0 | F 0 | F 0 |
| | | NA 0 | NA 0 | NA 0 | NA 0 | NA 1 Sw: (Tschumi et al. 2016). |

[1] (White et al. 1995): only more predation at the last three dates

[2] (Skirvin et al. 2011): more natural enemies in plots adjacent to the wildflower strips in week 4 and 7. If considering only aerial predators only in week 7.

[3] (Hogg et al. 2011b): semi-field experiment run in cages.

| Type of crop | Nº of studies | More hoverflies in the flower strip | | | Crop | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | More adult hoverflies | | | More hoverfly larvae or eggs | | | More predation | | | Effective biological control | | |
| Strawberry (*Fragaria x ananassa*) | 1 | S | 1 | UK: (Hodgkiss et al. 2019)[4]. | S | 1 | UK: (Hodgkiss et al. 2019). | S | 0 | | S | 0 | | S | 0 | |
| | | F | 0 | | F | 0 | | F | 1 | UK: (Hodgkiss et al. 2019). | F | 1 | UK: (Hodgkiss et al. 2019). | F | 1 | UK: (Hodgkiss et al. 2019). |
| | | NA | 0 | | NA | 0 | | NA | 0 | | NA | 0 | | NA | 0 | |
| Sugar beet (*Beta vulgaris*) | 1 | S | 0 | | S | 0 | | S | 0 | | S | 1 | P: (Twardowski et al. 2005). | S | 0 | |
| | | F | 0 | | F | 0 | | F | 1 | P: (Twardowski et al. 2005). | F | 0 | | F | 0 | |
| | | NA | 1 | P: (Twardowski et al. 2005). | NA | 1 | P: (Twardowski et al. 2005). | NA | 0 | | NA | 0 | | NA | 1 | P: (Twardowski et al. 2005). |
| Sweet pepper (*Caspicum anuum*) | 1 | S | 1 | S: (Pineda and Marcos-Garcia 2008). | S | 1 | S: (Pineda and Marcos-Garcia 2008). | S | 1 | S: (Pineda and Marcos-Garcia 2008). | S | 0 | | S | 0 | |
| | | F | 0 | | F | 0 | | F | 0 | | F | 0 | | F | 0 | |
| | | NA | 0 | | NA | 0 | | NA | 0 | | NA | 1 | S: (Pineda and Marcos-Garcia 2008). | NA | 1 | S: (Pineda and Marcos-Garcia 2008). |
| Total | 12 | S | 6 | Br: (Ribeiro and Gontijo 2017); F: (Lambion and Franoux 2017); J: (Morris and Li 2000); S: (Pineda and Marcos-Garcia 2008); Sw: (Tschumi et al. 2016); UK: (Hodgkiss et al. 2019). | S | 4 | Br: (Ribeiro and Gontijo 2017); NZ: (White et al. 1995); S: (Pineda and Marcos-Garcia 2008); UK: (Hodgkiss et al. 2019). | S | 4 | Br: (Ribeiro and Gontijo 2017); S: (Pascual-Villalobos et al. 2006), (Pineda and Marcos-Garcia 2008).; Sw: (Tschumi et al. 2016). | S | 7 | Br: (Ribeiro and Gontijo 2017); NZ: (White et al. 1995), (Morris and Li 2000); P: (Twardowski et al. 2005); S: (Pascual-Villalobos et al. 2006); Sw: (Tschumi et al. 2016); UK: (Skirvin et al. 2011). | S | 0 | |
| | | F | 1 | NZ: (Morris and Li 2000). | F | 5 | F: (Lambion and Franoux 2017); J: (Morris and Li 2000); NZ: (Morris and Li 2000); Sw: (Tschumi et al. 2016); UK: (Skirvin et al. 2011). | F | 7 | J: (Morris and Li 2000); NZ: (Morris and Li 2000), (White et al. 1995). UK: (Skirvin et al. 2011); P: (Twardowski et al. 2005); UK: (Hodgkiss et al. 2019); USA: (Hogg et al. 2011b). | F | 4 | F: (Lambion and Franoux 2017); J: (Morris and Li 2000); UK: (Hodgkiss et al. 2019); USA: (Hogg et al. 2011b). | F | 1 | UK: (Hodgkiss et al. 2019). |
| | | NA | 5 | NZ: (White et al. 1995); P: (Twardowski et al. 2005); S: (Pascual-Villalobos et al. 2006); UK: (Skirvin et al. 2011); USA: (Hogg et al. 2011b). | NA | 3 | P: (Twardowski et al. 2005); S: (Pascual-Villalobos et al. 2006); USA: (Hogg et al. 2011b). | NA | 1 | F: (Lambion and Franoux 2017). | NA | 1 | S: (Pineda and Marcos-Garcia 2008). | NA | 11 | Br: (Ribeiro and Gontijo 2017); F: (Lambion and Franoux 2017); J: (Morris and Li 2000): NZ: (Morris and Li 2000), (White et al. 1995); P: (Twardowski et al. 2005); S: (Pascual-Villalobos et al. 2006), (Pineda and Marcos-Garcia 2008); Sw: (Tschumi et al. 2016); UK: (Skirvin et al. 2011); USA: (Hogg et al. 2011b). |

---

[4] (Hodgkiss et al. 2019): adult hoverflies not distinguished from the rest of the pollinator visitors. A significant effect on some fruit quality measures was found, but proportions of marketable fruit did not differ among any of the treatments

| Type of crop | Nº of studies | More hoverflies in the flower strip | | | Crop | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | More adult hoverflies | | | More hoverfly larvae or eggs | | | More predation | | | Effective biological control | | |
| Orchards | | | | | | | | | | | | | | | | |
| Apple (*Malus domestica*) | 7 | S | 5 | F: (Odorizzi Santos et al. 2018); S: (Rodríguez-Gasol et al. 2019b); Sw: (Wyss 1995); (Wyss 1996); USA: (Gontijo et al. 2013)[5]. | S | 0 | | S | 3 | F: (Albert et al. 2017); G: (Kienzle et al. 2014); Sw: (Wyss 1995)[6]. | S | 3 | F: (Albert et al. 2017); Sw: (Wyss 1995); USA: (Gontijo et al. 2013). | S | 0 | |
| | | F | 0 | | F | 1 | F: (Albert et al. 2017). | F | 3 | F: (Odorizzi Santos et al. 2018); S: (Rodríguez-Gasol et al. 2019b); USA: (Gontijo et al. 2013). | F | 2 | F: (Odorizzi Santos et al. 2018); G: (Kienzle et al. 2014). | F | 0 | |
| | | NA | 2 | F: (Albert et al. 2017); G: (Kienzle et al. 2014)[7]. | NA | 6 | F: (Odorizzi Santos et al. 2018); G: (Kienzle et al. 2014); S: (Rodríguez-Gasol et al. 2019b); Sw: (Wyss 1995), (Wyss 1996); USA: (Gontijo et al. 2013). | NA | 1 | Sw: (Wyss 1996). | NA | 2 | S: (Rodríguez-Gasol et al. 2019b); Sw: (Wyss 1996). | NA | 7 | F: (Albert et al. 2017; Odorizzi Santos et al. 2018); G: (Kienzle et al. 2014); S: (Rodríguez-Gasol et al. 2019b); Sw: (Wyss 1995; Wyss 1996); USA: (Gontijo et al. 2013). |
| Highbush blueberry (*Vaccinium corymbosum*) | 2 | S | 1 | USA: (Blaauw and Isaacs 2015)[8]. | S | 2 | USA: (Blaauw and Isaacs 2015); (Walton and Isaacs 2011). | S | 0 | | S | 1 | USA: (Blaauw and Isaacs 2015). | S | 0 | |
| | | F | 1 | USA: (Blaauw and Isaacs 2015). | F | 0 | | F | 0 | | F | 0 | | F | 0 | |
| | | NA | 1 | USA: (Walton and Isaacs 2011). | NA | 0 | | NA | 2 | USA: (Blaauw and Isaacs 2015), (Walton and Isaacs 2011). | NA | 1 | USA: (Walton and Isaacs 2011). | NA | 2 | USA: (Blaauw and Isaacs 2015), (Walton and Isaacs 2011). |
| Peach (*Prunus persicae*) | 1 | S | 0 | | S | 0 | | S | 1 | C: (Wan et al. 2019)[9]. | S | 1 | C: (Wan et al. 2019). | S | 0 | |
| | | F | 0 | | F | 0 | | F | 0 | | F | 0 | | F | 0 | |
| | | NA | 1 | C: (Wan et al. 2019). | NA | 1 | C: (Wan et al. 2019). | NA | 0 | | NA | 0 | | NA | 1 | C: (Wan et al. 2019). |

---

[5] **(Gontijo et al. 2013): presence of natural enemies and aphids assessed on potted apple trees.**

[6] (Wyss 1995): hoverflies not distinguished from the rest of the predators.

[7] (Kienzle et al. 2014): presence of natural enemies assessed on potted apple trees.

[8] (Blaauw and Isaacs 2015): More hoverflies on 2011, but not in 2010. Predation evaluated with eggs of *Helicoperva zea*: in the flower treatment, more predation found along the crop edge, similar tendency in the crop interior but no significant differences found.

[9] (Wan et al. 2019): hoverflies not distinguished from the rest of the predators.

| | Nº of | | | Crop | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Type of crop | studies | More hoverflies in the flower strip | | More adult hoverflies | | More hoverfly larvae or eggs | | More predation | | Effective biological control | |
| Total | 10 | S 5 | F: (Odorizzi Santos et al. 2018); S: (Rodríguez-Gasol et al. 2019b); Sw: (Wyss 1995); (Wyss 1996); USA: (Gontijo et al. 2013), (Blaauw and Isaacs 2015). | S 2 | USA: (Blaauw and Isaacs 2015); (Walton and Isaacs 2011). | S 4 | C: (Wan et al. 2019); F: (Albert et al. 2017); G: (Kienzle et al. 2014); Sw: (Wyss 1995). | S 5 | C: (Wan et al. 2019); F: (Albert et al. 2017); Sw: (Wyss 1995); USA: (Gontijo et al. 2013), (Blaauw and Isaacs 2015). | S 0 | |
| | | F 1 | USA: (Blaauw and Isaacs 2015). | F 1 | F: (Albert et al. 2017). | F 3 | F: (Odorizzi Santos et al. 2018); S: (Rodríguez-Gasol et al. 2019b); USA: (Gontijo et al. 2013). | F 2 | F: (Odorizzi Santos et al. 2018); G: (Kienzle et al. 2014). | F 0 | |
| | | NA 4 | C: (Wan et al. 2019); F: (Albert et al. 2017); G: (Kienzle et al. 2014); USA: (Walton and Isaacs 2011). | NA 7 | C: (Wan et al. 2019); F: (Odorizzi Santos et al. 2018); G: (Kienzle et al. 2014); S: (Rodríguez-Gasol et al. 2019b); Sw: (Wyss 1995), (Wyss 1996); USA: (Gontijo et al. 2013). | NA 3 | Sw: (Wyss 1996); USA: (Blaauw and Isaacs 2015), (Walton and Isaacs 2011). | NA 3 | S: (Rodríguez-Gasol et al. 2019b); Sw: (Wyss 1996); USA: (Walton and Isaacs 2011). | NA 10 | C: (Wan et al. 2019); F: (Albert et al. 2017; Odorizzi Santos et al. 2018); G: (Kienzle et al. 2014); S: (Rodríguez-Gasol et al. 2019b); Sw: (Wyss 1995; Wyss 1996); USA: (Gontijo et al. 2013), (Blaauw and Isaacs 2015), (Walton and Isaacs 2011). |
| Arable crops | | | | | | | | | | | |
| Wheat (*Triticum aestivum*) | 5 | S 2 | A: (Bertolaccini et al. 2008); Sw: (Frank 1999). | S 1 | Be: (Hatt et al. 2017a). | S 2 | Be: (Hatt et al. 2017a); Sw: (Hausammann 1996)[10]. | S 1 | Be: (Hatt et al. 2017a). | S 0 | |
| | | F 0 | | F 4 | A: (Bertolaccini et al. 2008); Sw: (Frank 1999), (Hausammann 1996); UK: (Hickman and Wratten 1996)[11]. | F 2 | Sw: (Hausammann 1996); UK: (Hickman and Wratten 1996). | F 3 | A: (Bertolaccini et al. 2008); Sw: (Hausammann 1996); UK: (Hickman and Wratten 1996). | F 1 | Sw: (Hausammann 1996). |
| | | NA 3 | Be: (Hatt et al. 2017a); Sw: (Hausammann 1996); UK: (Hickman and Wratten 1996). | NA 0 | | NA 2 | A: (Bertolaccini et al. 2008); Sw: (Frank 1999). | NA 1 | Sw: (Frank 1999). | NA 4 | A: (Bertolaccini et al. 2008); Be: (Hatt et al. 2017a); Sw: (Frank 1999); UK: (Hickman and Wratten 1996). |
| Faba bean (*Vicia faba*) | 1 | S 0 | | S 0 | | S 1 | E: (Rizk 2011). | S 1 | E: (Rizk 2011). | S | |
| | | F 0 | | F 0 | | F 0 | | F 0 | | F | |
| | | NA 1 | E: (Rizk 2011). | NA 1 | E: (Rizk 2011). | NA 0 | | NA 0 | | NA | E: (Rizk 2011)[12]. |

---

[10] (Hausammann 1996): two types of sampling. In the sweep netting often a larger number of aphidophagous predators (includes Coccinellidae and Syrphidae) though no significant differences found for all de dates. No differences found for hoverfly immatures found on wheat tillers.

[11] (Hickman and Wratten 1996): overall no significant differences between experimental and control fields for the number of adult hoverflies, except for the 2nd period on 1992 were significant differences were found. However, the trend was for consistently higher numbers in experimental fields. Also, overall no significant differences between experimental and control fields in aphid numbers, except in week 4, were significant differences were found.

[12] (Rizk 2011): positive correlations found between natural enemies and seed yield.

| | | | | | Crop | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Type of crop | Nº of studies | More hoverflies in the flower strip | | | More adult hoverflies | | | More hoverfly larvae or eggs | | | More predation | | | Effective biological control | | |
| Total | 6 | S | 2 | A: (Bertolaccini et al. 2008); Sw: (Frank 1999). | S | 1 | Be: (Hatt et al. 2017a). | S | 3 | Be: (Hatt et al. 2017a); E: (Rizk 2011); Sw: (Hausammann 1996). | S | 2 | Be: (Hatt et al. 2017a); E: (Rizk 2011). | S | 0 | |
| | | F | 0 | | F | 4 | A: (Bertolaccini et al. 2008); Sw: (Frank 1999), (Hausammann 1996); UK: (Hickman and Wratten 1996). | F | 2 | Sw: (Hausammann 1996); UK: (Hickman and Wratten 1996). | F | 3 | A: (Bertolaccini et al. 2008); Sw: (Hausammann 1996); UK: (Hickman and Wratten 1996). | F | 1 | Sw: (Hausammann 1996). |
| | | NA | 4 | Be: (Hatt et al. 2017a); E: (Rizk 2011); Sw: (Hausammann 1996); UK: (Hickman and Wratten 1996). | NA | 1 | E: (Rizk 2011). | NA | 2 | A: (Bertolaccini et al. 2008); Sw: (Frank 1999). | NA | 1 | Sw: (Frank 1999). | NA | 5 | A: (Bertolaccini et al. 2008); Be: (Hatt et al. 2017a); E: (Rizk 2011); Sw: (Frank 1999); UK: (Hickman and Wratten 1996). |

## 5. Conclusions and future perspectives

The present review gives detailed information about the key aspects of the ecology of hoverflies in order to promote their presence and ecosystem services in farmland agroecosystems. Predatory hoverflies have long been recognized for their particular 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 ecological intensification, interest in the other ecosystem services they can provide (pollination, bioindication and food for other natural enemies) 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 discern 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 good results, though more information is needed about the functional traits and habitat requirements of several species. Despite hoverflies usually exhibit mimicry and crypsis, they can still be potential preys to several predators. Current evidence shows that the outcome of interactions with intraguild predators depend on the larval instar, as well as the intraguild predator they are faced to. Nonetheless, this type of interactions are not common under natural conditions and coexistence is most likely to occur. Similarly to 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. With regard to 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 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 taken 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 color 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’s 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 about 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 allow prey location. Moreover, despite hoverfly larvae have been reported to be able to predate non-aphid prey, to the best of our knowledge, no studies 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, 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 1) the factors that trigger the overwintering and migration strategies, 2) what determines the ratio of migratory/resident individuals in a population, 3) the energy requirements for migrating hoverflies and overwintering individuals and 4) common overwintering places. Important implications on 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 is important to emphasize that despite 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 important to allow 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 recolonization the crops.

## 6. References

Albert L, Franck P, Gilles Y, Plantegenest M (2017) Impact of agroecological infrastructures on the dynamics of *Dysaphis plantaginea* (Hemiptera: Aphididae) and its natural enemies in apple orchards in northwestern France. Environ Entomol 46:528-537 doi:10.1093/ee/nvx054

Alhmedi A, Haubruge E, Francis F (2008) Role of prey-host plant associations on *Harmonia axyridis* and *Episyrphus balteatus* reproduction and predatory efficiency. Entomol Exp Appl 128:49-56 doi:10.1111/j.1570-7458.2008.00740.x

Alignier A et al. (2014) The effect of semi-natural habitats on aphids and their natural enemies across spatial and temporal scales. Biol Control 77:76-82 doi:10.1016/j.biocontrol.2014.06.006

Almohamad R, Verheggen FJ, Haubruge E (2009) Searching and oviposition behavior of aphidophagous hoverflies (Diptera: Syrphidae): a review. Biotechnol Agron Soc 13:467-481

Ambrosino MD, Luna JM, Jepson PC, Wratten SD (2006) Relative frequencies of visits to selected insectary plants by predatory hoverflies (Diptera: Syrphidae), other beneficial insects, and herbivores. Environ Entomol 35:394-400 doi:10.1603/0046-225x-35.2.394

Amorós-Jiménez R, Pineda A, Fereres A, Marcos-García MA (2014) Feeding preferences of the aphidophagous hoverfly *Sphaerophoria rueppellii* affect the performance of its offspring. BioControl 59:427-435 doi:10.1007/s10526-014-9577-8

Andersson GKS, Birkhofer K, Rundlof M, Smith HG (2013) Landscape heterogeneity and farming practice alter the species composition and taxonomic breadth of pollinator communities. Basic Appl Ecol 14:540-546 doi:10.1016/j.baae.2013.08.003

Arrignon F, Deconchat M, Sarthou J-P, Balent G, Monteil C (2007) Modelling the overwintering strategy of a beneficial insect in a heterogeneous landscape using a multi-agent system. Ecol Model 205:423-436 doi:10.1016/j.ecolmodel.2007.03.006

Ashby JW, Pottinger RP (1974) Natural regulation of *Pieris rapae* Linnaeus (Lepidoptera: Pieridae) in Canterbury, New Zealand. N Z J Agric Res 17:229-239 doi:10.1080/00288233.1974.10421002

Ashman TL et al. (2004) Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. Ecology 85:2408-2421 doi:10.1890/03-8024

Aubert J, Aubert JJ, Goeldlin P (1976) Twelve years of systematic collecting of syrphids (Diptera) at the Bretolet pass (Alps of Valais). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 49:115-142

Aubert J, Goeldlin de Tiefenau P (1981) Observations on the migration of hover flies (Syrphidae, Diptera) in the Alps of Western Switzerland. v. 54

Barbir J, Badenes-Perez FR, Fernandez-Quintanilla C, Dorado J (2015) The attractiveness of flowering herbaceous plants to bees (Hymenoptera: Apoidea) and hoverflies (Diptera: Syrphidae) in agro-ecosystems of Central Spain. Agric For Entomol 17:20-28 doi:10.1111/afe.12076

Bargen H, Saudhof K, Poehling HM (1998) Prey finding by larvae and adult females of *Episyrphus balteatus*. Entomol Exp Appl 87:245-254 doi:10.1046/j.1570-7458.1998.00328.x

Belliure B, Michaud JP (2001) Biology and behavior of *Pseudodorus clavatus* (Diptera: Syrphidae), an important predator of citrus aphids. Ann Entomol Soc Am 94:91-96 doi:10.1603/0013-8746(2001)094[0091:babopc]2.0.co;2

Bertolaccini I, Andrada P, Quaino O (2008) Effects of field margins strips for the attraction of predaceous wheat aphids, Coccinellidae and Syrphidae, in Central Santa Fe Province, Argentina. Agronomia Tropical (Maracay) 58:267-276

Billeter R et al. (2008) Indicators for biodiversity in agricultural landscapes: a pan-European study. J Appl Ecol 45:141-150 doi:10.1111/j.1365-2664.2007.01393.x

Blaauw BR, Isaacs R (2014) Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wild flowers. Basic Appl Ecol 15:701-711 doi:10.1016/j.baae.2014.10.001

Blaauw BR, Isaacs R (2015) Wildflower plantings enhance the abundance of natural enemies and their services in adjacent blueberry fields. Biol Control 91:94-103 doi:10.1016/j.biocontrol.2015.08.003

Boller EF, Häni F, Poehling HM (2004) Ecological infrastructures: Ideabook on functional diversity at the farm level. IOBC WPRS, Winterthur

Bommarco R, Marini L, Vaissiere BE (2012) Insect pollination enhances seed yield, quality, and market value in oilseed rape. Oecologia 169:1025-1032 doi:10.1007/s00442-012-2271-6

Bortolotto OC, Menezes Junior AdO, Hoshino AT, Campos TA (2016) Distance from the edge of forest fragments influence the abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wheat fields. Acta Scientiarum-Agronomy 38:157-164 doi:10.4025/actasciagron.v38i2.27711

Bourke D et al. (2014) Response of farmland biodiversity to the introduction of bioenergy crops: effects of local factors and surrounding landscape context. Global Change Biology Bioenergy 6:275-289 doi:10.1111/gcbb.12089

Branquart E, Hemptinne JL (2000a) Development of ovaries, allometry of reproductive traits and fecundity of *Episyrphus balteatus* (Diptera: Syrphidae). Eur J Entomol 97:165-170

Branquart E, Hemptinne JL (2000b) Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphinae). Ecography 23:732-742 doi:10.1034/j.1600-0587.2000.230610.x

Branquart E, Hemptinne JL, Bauffe C, Benfekih L (1997) Cannibalism in Episyrphus balteatus (Dipt.: Syrphidae). Entomophaga 42:145-152 doi:10.1007/bf02769892

Brennan EB (2013) Agronomic aspects of strip intercropping lettuce with alyssum for biological control of aphids. Biol Control 65:302-311 doi:10.1016/j.biocontrol.2013.03.017

Brennan EB (2016) Agronomy of strip intercropping broccoli with alyssum for biological control of aphids. Biol Control 97:109-119 doi:10.1016/j.biocontrol.2016.02.015

Burgio G, Sommaggio D (2007) Syrphids as landscape bioindicators in Italian agroecosystems. Agric Ecosyst Environ 120:416-422 doi:10.1016/j.agee.2006.10.021

Chandler AE (1968a) Some factors influencing occurrence and site of oviposition by aphidophagous Syrphidae (Diptera). Ann Appl Biol 61:435-446 doi:10.1111/j.1744-7348.1968.tb04545.x

Chandler AE (1968b) Some host-plant factors affecting oviposition by aphidophagous Syrphidae (Diptera). Ann Appl Biol 61:415-423 doi:10.1111/j.1744-7348.1968.tb04543.x

Chandler AE (1969) Locomotory behaviour of first instar larvae of aphidophagous syrphidae (Diptera) after contact with aphids. Anim Behav 17:673-678 doi:10.1016/s0003-3472(69)80011-4

Chaplin-Kramer R, de Valpine P, Mills NJ, Kremen C (2013) Detecting pest control services across spatial and temporal scales. Agric Ecosyst Environ 181:206-212 doi:10.1016/j.agee.2013.10.007

Cole LJ, Brocklehurst S, Robertson D, Harrison W, McCracken DI (2017) Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. Agric Ecosyst Environ 246:157-167 doi:10.1016/j.agee.2017.05.007

Colignon P, Haubruge E, Gaspar C, Francis F (2003) Effects of reducing recommended doses of insecticides and fungicides on the non-target insect *Episyrphus balteatus* Diptera: Syrphidae. Phytoprotection 84:141-148 doi:10.7202/008491ar

Colley MR, Luna JM (2000) Relative attractiveness of potential beneficial insectary plants to aphidophagous hoverflies (Diptera: Syrphidae). Environ Entomol 29:1054-1059 doi:10.1603/0046-225x-29.5.1054

Conner JK, Rush S (1996) Effects of flower size and number on pollinator visitation to wild radish, *Raphanus raphanistrum*. Oecologia 105:509-516 doi:10.1007/bf00330014

Costanza R et al. (1997) The value of the world's ecosystem services and natural capital. Nature 387:253-260 doi:10.1038/387253a0

Cowgill SE, Wratten SD, Sotherton NW (1993a) The effect of weeds on the numbers of hoverfly (Diptera: Syrphidae) adults and the distribution and composition of their eggs in winter wheat. Ann Appl Biol 123:499-515 doi:10.1111/j.1744-7348.1993.tb04922.x

Cowgill SE, Wratten SD, Sotherton NW (1993b) The selective use of floral resources by the hoverfly *Episyrphus balteatus* (Diptera, Syrphidae) on farmland. Ann Appl Biol 122:223-231 doi:10.1111/j.1744-7348.1993.tb04029.x

Dallenbach LJ, Glauser A, Lim KS, Chapman JW, Menz MHM (2018) Higher flight activity in the offspring of migrants compared to residents in a migratory insect. Proceedings of the Royal Society B-Biological Sciences 285 doi:10.1098/rspb.2017.2829

Day RL, Hickman JM, Sprague RI, Wratten SD (2015) Predatory hoverflies increase oviposition in response to colour stimuli offering no reward: Implications for biological control. Basic Appl Ecol 16:544-552 doi:10.1016/j.baae.2015.05.004

Dib H, Sauphanor B, Capowiez Y (2016) Effect of management strategies on arthropod communities in the colonies of rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) in south-eastern France. Agric Ecosyst Environ 216:203-206 doi:10.1016/j.agee.2015.10.003

Dib H, Simon S, Sauphanor B, Capowiez Y (2010) The role of natural enemies on the population dynamics of the rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) in organic apple orchards in south-eastern France. Biol Control 55:97-109 doi:10.1016/j.biocontrol.2010.07.005

Dinkel T, Lunau K (2001) How drone flies (*Eristalis tenax* L., Syrphidae: Diptera) use floral guides to locate food sources. J Insect Physiol 47:1111-1118 doi:10.1016/s0022-1910(01)00080-4

Dormann CF et al. (2007) Effects of landscape structure and land-use intensity on similarity of plant and animal communities. Global Ecol Biogeogr 16:774-787 doi:10.1111/j.1466-8238.2007.00344.x

Ekroos J, Rundlof M, Smith HG (2013) Trait-dependent responses of flower-visiting insects to distance to semi-natural grasslands and landscape heterogeneity. Landscape Ecol 28:1283-1292 doi:10.1007/s10980-013-9864-2

Ekukole G (1996) Prey preference in *Paragus borbonicus* Macquart (Diptera: Syrphidae) larvae and relationship with *Acantholepis capensis* (Mayr) (Hymenoptera: Formicidae), an ant attending *Aphis gossypii* Glover (Homoptera: Aphididae). Journal of African Zoology 110:195-202

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology Evolution and Systematics 34:487-515 doi:10.1146/annurev.ecolsys.34.011802.132419

FAO (2017) The future of food and agriculture – Trends and challenges. FAO, Rome

Fiedler AK, Landis DA (2007) Attractiveness of Michigan native plants to arthropod natural enemies and herbivores. Environ Entomol 36:751-765 doi:10.1603/0046-225x(2007)36[751:aomnpt]2.0.co;2

Foeldesi R et al. (2016) Relationships between wild bees, hoverflies and pollination success in apple orchards with different landscape contexts. Agric For Entomol 18:68-75 doi:10.1111/afe.12135

Foley JA et al. (2011) Solutions for a cultivated planet. Nature 478:337-342 doi:10.1038/nature10452

Fontaine C, Dajoz I, Meriguet J, Loreau M (2006) Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. PLoS Biol 4:129-135 doi:10.1371/journal.pbio.0040001

Francis FD, Martin T, Lognay G, Haubruge E (2005) Role of (E)-beta-farnesene in systematic aphid prey location by *Episyrphus balteatus* larvae (Diptera : Syrphidae). Eur J Entomol 102:431-436 doi:10.14411/eje.2005.061

Frank T (1999) Density of adult hoverflies (Dipt., Syrphidae) in sown weed strips and adjacent fields. Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie 123:351-355 doi:10.1046/j.1439-0418.1999.00383.x

Frechette B, Rojo S, Alomar O, Lucas E (2007) Intraguild predation between syrphids and mirids: who is the prey? Who is the predator? BioControl 52:175-191 doi:10.1007/s10526-006-9028-2

Fruend J, Linsenmair KE, Bluethgen N (2010) Pollinator diversity and specialization in relation to flower diversity. Oikos 119:1581-1590 doi:10.1111/j.1600-0706.2010.18450.x

Gabriel D, Sait SM, Hodgson JA, Schmutz U, Kunin WE, Benton TG (2010) Scale matters: the impact of organic farming on biodiversity at different spatial scales. Ecol Lett 13:858-869 doi:10.1111/j.1461-0248.2010.01481.x

Gagic V, Haenke S, Thies C, Tscharntke T (2014) Community variability in aphid parasitoids versus predators in response to agricultural intensification. Insect Conserv Divers 7:103-112 doi:10.1111/icad.12037

Gallai N, Salles JM, Settele J, Vaissiere BE (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol Econ 68:810-821 doi:10.1016/j.ecolecon.2008.06.014

Gardiner MA, Tuell JK, Isaacs R, Gibbs J, Ascher JS, Landis DA (2010) Implications of Three Biofuel Crops for Beneficial Arthropods in Agricultural Landscapes. Bioenergy Research 3:6-19 doi:10.1007/s12155-009-9065-7

Garibaldi LA, Gemmill-Herren B, D'Annolfo R, Graeub BE, Cunningham SA, Breeze TD (2017) Farming Approaches for Greater Biodiversity, Livelihoods, and Food Security. Trends Ecol Evol 32:68-80 doi:10.1016/j.tree.2016.10.001

Garratt MPD, Senapathi D, Coston DJ, Mortimer SR, Potts SG (2017) The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context. Agric Ecosyst Environ 247:363-370 doi:10.1016/j.agee.2017.06.048

Gervais A, Chagnon M, Fournier V (2018) Diversity and Pollen Loads of Flower Flies (Diptera: Syrphidae) in Cranberry Crops. Ann Entomol Soc Am 111:326-334 doi:10.1093/aesa/say027

Gil HK, Garg H (2014) Pesticides: environmental impacts and management strategies. doi:10.5772/57399

Gilbert F (1993) Hoverflies. Naturalists' Handbooks 5. 2nd edn. Richmond Publishing Co., Slough, Berkshire. doi:10.1080/00219266.1994.9655394

Gilbert FS (1981) Foraging ecology of hoverflies - Morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. Ecol Entomol 6:245-262 doi:10.1111/j.1365-2311.1981.tb00612.x

Gillespie M, Wratten S, Sedcole R, Colfer R (2011) Manipulating floral resources dispersion for hoverflies (Diptera: Syrphidae) in a California lettuce agro-ecosystem. Biol Control 59:215-220 doi:10.1016/j.biocontrol.2011.07.010

Gomez-Polo P, Traugott M, Alomar O, Castane C, Rojo S, Agusti N (2014) Identification of the most common predatory hoverflies of Mediterranean vegetable crops and their parasitism using multiplex PCR. J Pest Sci 87:371-378 doi:10.1007/s10340-013-0550-6

Gong YB, Huang SQ (2009) Floral symmetry: pollinator-mediated stabilizing selection on flower size in bilateral species. Proc R Soc Lond, Ser B Biol Sci 276:4013-4020 doi:10.1098/rspb.2009.1254

Gontijo LM, Beers EH, Snyder WE (2013) Flowers promote aphid suppression in apple orchards. Biol Control 66:8-15 doi:10.1016/j.biocontrol.2013.03.007

Gontijo LM, Beers EH, Snyder WE (2015) Complementary suppression of aphids by predators and parasitoids. Biol Control 90:83-91 doi:10.1016/j.biocontrol.2015.06.002

Goulson D, Wright NP (1998) Flower constancy in the hoverflies *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.) (Syrphidae). Behav Ecol 9:213-219 doi:10.1093/beheco/9.3.213

Grass I, Lehmann K, Thies C, Tscharntke T (2017) Insectivorous birds disrupt biological control of cereal aphids. Ecology 98:1583-1590 doi:10.1002/ecy.1814

Greco CF (1997) Specificity and instar preference of *Diplazon laetatorius* (Hym.: Ichneumonidae) parasitizing aphidophagous syrphids (Dipt.: Syrphidae). Entomophaga 42:315-318 doi:10.1007/bf02769823

Gurr GM, Wratten SD, Landis DA, You MS (2017) Habitat management to suppress pest populations: progress and prospects. Annu Rev Entomol 62:91-109 doi:10.1146/annurev-ento-031616-035050

Haenke S, Kovacs-Hostyanszki A, Fruend J, Batary P, Jauker B, Tscharntke T, Holzschuh A (2014) Landscape configuration of crops and hedgerows drives local syrphid fly abundance. J Appl Ecol 51:505-513 doi:10.1111/1365-2664.12221

Haenke S, Scheid B, Schaefer M, Tscharntke T, Thies C (2009) Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. J Appl Ecol 46:1106-1114 doi:10.1111/j.1365-2664.2009.01685.x

Han BY, Chen ZM (2002) Behavioral and electrophysiological responses of natural enemies to synomones from tea shoots and kairomones from tea aphids, *Toxoptera aurantii*. J Chem Ecol 28:2203-2219 doi:10.1023/a:1021045231501

Hart AJ, Bale JS (1997) Cold tolerance of the aphid predator *Episyrphus balteatus* (DeGeer) (Diptera, Syrphidae). Physiol Entomol 22:332-338 doi:10.1111/j.1365-3032.1997.tb01177.x

Harwood RWJ, Hickman JM, MacLeod A, Sherratt TN, Wratten SD (1994) Managing Field Margins for Hoverflies. In: Boatman ND (ed) Field Margins: Integrating Agriculture and Conservation, vol 58. vol BCPC Monograph. Farnharm, BCPC, pp 147-152

Haslett JR (1989a) Adult feeding by Holometabolous insects - Pollen and nectar as complementary nutrient sources for *Rhingia campestris* (Diptera, Syrphidae). Oecologia 81:361-363 doi:10.1007/bf00377084

Haslett JR (1989b) Interpreting patterns of resource utilization - Randomness and selectivity in pollen feeding by adult hoverflies. Oecologia 78:433-442 doi:10.1007/bf00378732

Hass AL et al. (2018) Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. Proceedings of the Royal Society B-Biological Sciences 285 doi:10.1098/rspb.2017.2242

Hatt S, Lopes T, Boeraeve F, Chen J, Francis F (2017a) Pest regulation and support of natural enemies in agriculture: Experimental evidence of within field wildflower strips. Ecol Eng 98:240-245 doi:10.1016/j.ecoleng.2016.10.080

Hatt S, Mouchon P, Lopes T, Francis F (2017b) Effects of Wildflower Strips and an Adjacent Forest on Aphids and Their Natural Enemies in a Pea Field. Insects 8 doi:10.3390/insects8030099

Hausammann A (1996) The effects of weed strip-management on pests and beneficial arthropods in winter wheat fields. Zeitschrift Fur Pflanzenkrankheiten Und Pflanzenschutz-Journal of Plant Diseases and Protection 103:70-81

Hazell SP, Wenlock C, Bachel S, Fellowes MDE (2005) The costs and consequences of parasitoid attack for, the predatory hoverfly, *Episyrphus balteatus*. Evol Ecol Res 7:669-679

Hendrickx F et al. (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. J Appl Ecol 44:340-351 doi:10.1111/j.1365-2664.2006.01270.x

Hickman JM, Lovei GL, Wratten SD (1995) Pollen feeding by adults of the hoverfly *Melanostoma fasciatum* (Diptera: Syrphidae). N Z J Zool 22:387-392 doi:10.1080/03014223.1995.9518057

Hickman JM, Wratten SD (1996) Use of *Phacelia tanacetifolia* strips to enhance biological control of aphids by hoverfly larvae in cereal fields. J Econ Entomol 89:832-840 doi:10.1093/jee/89.4.832

Hickman JM, Wratten SD, Jepson PC, Frampton CM (2001) Effect of hunger on yellow water trap catches of hoverfly (Diptera: Syrphidae) adults. Agric For Entomol 3:35-40 doi:10.1046/j.1461-9563.2001.00085.x

Hindayana D, Meyhofer R, Scholz D, Poehling HM (2001) Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera : Syrphidae) and other aphidophagous predators. Biol Control 20:236-246 doi:10.1006/bcon.2000.0895

Hodgkiss D, Brown MJF, Fountain MT (2019) The effect of within-crop floral resources on pollination, aphid control and fruit quality in commercial strawberry. Agric Ecosyst Environ 275:112-122 doi:10.1016/j.agee.2019.02.006

Hogg BN, Bugg RL, Daane KM (2011a) Attractiveness of common insectary and harvestable floral resources to beneficial insects. Biol Control 56:76-84 doi:10.1016/j.biocontrol.2010.09.007

Hogg BN, Nelson EH, Mills NJ, Daane KM (2011b) Floral resources enhance aphid suppression by a hoverfly. Entomol Exp Appl 141:138-144 doi:10.1111/j.1570-7458.2011.01174.x

Holland JM, Bianchi FJJA, Entling MH, Moonen A-C, Smith BM, Jeanneret P (2016) Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies. Pest Manage Sci 72:1638-1651 doi:10.1002/ps.4318

Hondelmann P, Borgemeister C, Poehling HM (2005) Restriction fragment length polymorphisms of different DNA regions as genetic markers in the hoverfly *Episyrphus balteatus* (Diptera: Syrphidae). Bull Entomol Res 95:349-359 doi:10.1079/ber2005366

Hondelmann P, Poehling H-M (2007) Diapause and overwintering of the hoverfly *Episyrphus balteatus*. Entomol Exp Appl 124:189-200 doi:10.1111/j.1570-7458.2007.00568.x

Hopper JV, Nelson EH, Daane KM, Mills NJ (2011) Growth, development and consumption by four syrphid species associated with the lettuce aphid, *Nasonovia ribisnigri*, in California. Biol Control 58:271-276 doi:10.1016/j.biocontrol.2011.03.017

Horton DR et al. (2003) Effects of mowing frequency on densities of natural enemies in three Pacific Northwest pear orchards. Entomol Exp Appl 106:135-145 doi:10.1046/j.1570-7458.2003.00018.x

Ingels B, De Clercq P (2011) Effect of size, extraguild prey and habitat complexity on intraguild interactions: a case study with the invasive ladybird *Harmonia axyridis* and the hoverfly *Episyrphus balteatus*. BioControl 56:871-882 doi:10.1007/s10526-011-9363-9

Ingels B, Van Hassel P, Van Leeuwen T, De Clercq P (2015) Feeding History Affects Intraguild Interactions between *Harmonia axyridis* (Coleoptera: Coccinellidae) and *Episyrphus balteatus* (Diptera: Syrphidae). PLoS ONE 10 doi:10.1371/journal.pone.0128518

Inouye DW, Larson BMH, Ssymank A, Kevan PG (2015) Flies and flowers III: ecology of foraging and pollination. Journal of Pollination Ecology 16:115-133

IOBC-WPRS Pesticide effect database (2019) International ORganization for Biological and Integrated Control (IOBC). https://www.iobc-wprs.org/ip_ipm/IOBC_Pesticide_Side_Effect_Database.html.

Irvin NA, Wratten SD, Frampton CM, Bowie MH, Evans AM, Moar NT (1999) The phenology and pollen feeding of three hover fly (Diptera: Syrphidae) species in Canterbury, New Zealand. N Z J Zool 26:105-115 doi:10.1080/03014223.1999.9518182

Isaacs R, Tuell J, Fiedler A, Gardiner M, Landis D (2009) Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. Front Ecol Environ 7:196-203 doi:10.1890/080035

James DG (2005) Further field evaluation of synthetic herbivore-induced plant volatiles as attractants for beneficial insects. J Chem Ecol 31:481-495 doi:10.1007/s10886-005-2020-y

Jankowska B (2004) Parasitoids of aphidophagous syrphidae occurring in cabbage aphid (Brevicoryne brassicae L.) colonies on cabbage vegetables. Journal of Plant Protection Research 44:299-305

Jansen JP (2000) A three-year field study on the short-term effects of insecticides used to control cereal aphids on plant-dwelling aphid predators in winter wheat. Pest Manage Sci 56:533-539 doi:10.1002/(SICI)1526-4998(200006)56:6<533::AID-PS165>3.0.CO;2-S

Jansen JP, Defrance T, Warnier AM (2011) Side effects of flonicamide and pymetrozine on five aphid natural enemy species. BioControl 56:759-770 doi:10.1007/s10526-011-9342-1

Jansen JP, Ug, Ug, Ug (1998) Side effects of insecticides on larvae of the aphid specific predator *Episyrphus balteatus* (Degeer) (Dipt. Syrphidae) in the laboratory. In: 50th International Symposium on Crop Protection, Pts I-Iv, vol 50. International Symposium on Crop Protection, Proceedings. pp 585-592

Janssen A, Sabelis MW, Magalhaes S, Montserrat M, Van der Hammen T (2007) Habitat structure affects intraguild predation. Ecology 88:2713-2719 doi:10.1890/06-1408.1

Jarlan A, De Oliveira D, Gingras J (1997) Pollination by *Eristalis tenax* (Diptera : syrphidae) and seed set of greenhouse sweet pepper. J Econ Entomol 90:1646-1649 doi:10.1093/jee/90.6.1646

Jauker F, Bondarenko B, Becker HC, Steffan-Dewenter I (2012) Pollination efficiency of wild bees and hoverflies provided to oilseed rape. Agric For Entomol 14:81-87 doi:10.1111/j.1461-9563.2011.00541.x

Jauker F, Diekoetter T, Schwarzbach F, Wolters V (2009) Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecol 24:547-555 doi:10.1007/s10980-009-9331-2

Jauker F, Jauker B, Grass I, Steffan-Dewenter I, Wolters V (2019) Partitioning wild bee and hoverfly contributions to plant-pollinator network structure in fragmented habitats. Ecology 100 doi:10.1002/ecy.2569

Jauker F, Wolters V (2008) Hover flies are efficient pollinators of oilseed rape. Oecologia 156:819-823 doi:10.1007/s00442-008-1034-x

Jepson PC (1989) Pesticides and non-target invertebrates. Intercept, Department of Biology, University of Southampton, UK

Kendall DA, Solomon ME (1973) Quantities of Pollen on the Bodies of Insects Visiting Apple Blossom. J Appl Ecol 10:627-634 doi:10.2307/2402306

Kendall DA, Wilson D, C.G. G, Anderson HM (1971) Testing *Eristalis* as a pollinator of covered crops. Long Ashton Research Station Reports:120-121

Kevan PG, Baker HG (1983) Insects as Flower Visitors and Pollinators. Annu Rev Entomol 28:407-453 doi:10.1146/annurev.en.28.010183.002203

Kienzle J, Foell M, Karrer E, Krismann A, Zebitz CPW (2014) Establishment of permanent weed strips with autochthonous nectar plants and their effect on the occurrence of aphid predators. Ecofruit. 16th International Conference on Organic-Fruit Growing: Proceedings, 17-19 February 2014, Hohenheim, Germany.

Klecka J, Hadrava J, Biella P, Akter A (2018) Flower visitation by hoverflies (Diptera: Syrphidae) in a temperate plant-pollinator network. Peerj 6 doi:10.7717/peerj.6025

Kleijn D, van Langevelde F (2006) Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic Appl Ecol 7:201-214 doi:10.1016/j.baae.2005.07.011

Klein A-M, Brittain C, Hendrix SD, Thorp R, Williams N, Kremen C (2012) Wild pollination services to California almond rely on semi-natural habitat. J Appl Ecol 49:723-732 doi:10.1111/j.1365-2664.2012.02144.x

Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proc Biol Sci 274:303-313 doi:10.1098/rspb.2006.3721

Kohler F, Van Klink R, Noordijk J, Kleijn D (2007) The influence of nature reserves on hoverflies and bees in agricultural areas (Diptera: Syrphidae: Hymenoptera: Apidae s.l.). Entomol Ber (Amst) 67:187-192

Kohler F, Verhulst J, van Klink R, Kleijn D (2008) At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? J Appl Ecol 45:753-762 doi:10.1111/j.1365-2664.2007.01394.x

Kristín A (1988) Coccinellidae and Syrphidae in the food of some birds. In: Niemczyk E, A.F.G D (eds) Ecology and effectiveness of aphidophaga. SPB Academic Publishing, The Hague, Netherlands, Krotova IG (1993) Parasites of aphidophagous syrphidae (Diptera) from cereals of Western Siberia. Zoologichesky Zhurnal 72:58-62

Krsteska V (2014) Biological interactions within tobacco biocenosis. Acta Entomol Serbica 19:33-43

Kula E (1982) The syrphid flies (Syrphidae, Diptera) of spruce forest. Folia Facultatis Scientiarum Naturalium Universitatis Purkynianae Brunensis, Biologia 23:61-64

Lambion J, Franoux L (2017) Agroecological infrastructures to enhance the presence of natural enemies against aphids. In: Ozetkin GB, Tuzel Y (eds) Iii International Symposium on Organic Greenhouse Horticulture, vol 1164. Acta Horticulturae. pp 419-424. doi:10.17660/ActaHortic.2017.1164.54

Laubertie EA, Wratten SD, Hemptinne J-L (2012) The contribution of potential beneficial insectary plant species to adult hoverfly (Diptera: Syrphidae) fitness. Biol Control 61:1-6 doi:10.1016/j.biocontrol.2011.12.010

Laubertie EA, Wratten SD, Sedcole JR (2006) The role of odour and visual cues in the pan-trap catching of hoverflies (Diptera: Syrphidae). Ann Appl Biol 148:173-178 doi:10.1111/j.1744-7348.2006.00046.x

Leereveld H, Meeuse ADJ, Stelleman P (1976) Anthecological relations between reputedly anemophilous flowers and Syrphid flies. 2. *Plantago media* L. Acta Bot Neerl 25:205-211 doi:10.1111/j.1438-8677.1976.tb00234.x

Leroy P, Capella Q, Haubruge E (2009) Aphid honeydew impact on the tritrophic relationships between host-plants, phytophagous insects and their natural enemies. Biotechnol Agron Soc 13:325-334

Leroy PD, Almohamad R, Attia S, Capella Q, Verheggen FJ, Haubruge E, Francis F (2014) Aphid honeydew: An arrestant and a contact kairomone for *Episyrphus balteatus* (Diptera: Syrphidae) larvae and adults. Eur J Entomol 111:237-242

Leroy PD, Verheggen FJ, Capella Q, Francis F, Haubruge E (2010) An introduction device for the aphidophagous hoverfly *Episyrphus balteatus* (De Geer) (Diptera: Syrphidae). Biol Control 54:181-188 doi:10.1016/j.biocontrol.2010.05.006

Likhil EK, Mallapur CP (2009) Studies on syrphid species complex and their natural enemies in sugarcane ecosystem in northern Karnataka. Entomon 34:53-56

Lovei GL, Macleod A, Hickman JM (1998) Dispersal and effects of barriers on the movement of the New Zealand hover fly *Melanostoma fasciatum* (Dipt., Syrphidae) on cultivated land. J Appl Entomol 122:115-120 doi:10.1111/j.1439-0418.1998.tb01471.x

Lowery DT, Isman MB (1995) Toxicity of neem to natural enemies of aphids. Phytoparasitica 23:297-306 doi:10.1007/bf02981422

Lu ZZ, Perkins LE, Li JB, Wu WY, Zalucki MP, Gao GZ, Furlong MJ (2015) Abundance of *Aphis gossypii* (Homoptera; Aphididae) and its main predators in organic and conventional cotton fields in north-west China. Ann Appl Biol 166:249-256 doi:10.1111/aab.12178

Lucas A et al. (2018) Generalisation and specialisation in hoverfly (Syrphidae) grassland pollen transport networks revealed by DNA metabarcoding. J Anim Ecol 87:1008-1021 doi:10.1111/1365-2656.12828

Lucas E, Coderre D, Brodeur J (1998) Intraguild predation among aphid predators: Characterization and influence of extraguild prey density. Ecology 79:1084-1092 doi:10.1890/0012-9658(1998)079[1084:ipaapc]2.0.co;2

Lunau K (1995) Notes on the colour of pollen. Plant Syst Evol 198:235-252 doi:10.1007/bf00984739

Lunau K (2014) Visual ecology of flies with particular reference to colour vision and colour preferences. Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology 200:497-512 doi:10.1007/s00359-014-0895-1

Lunau K, Maier EJ (1995) Innate color preferences of flower visitors. J Comp Physiol, A 177:1-19 doi:10.1007/BF00243394

Lunau K, Wacht S (1994) Optical releasers of the innate proboscis extension in the hoverfly *Eristalis tenax* L. (Syrphidae: Diptera) J Comp Physiol, A 174:575-579 doi:10.1007/BF00217378

Mallinger RE, Hogg DB, Gratton C (2011) Methyl Salicylate Attracts Natural Enemies and Reduces Populations of Soybean Aphids (Hemiptera: Aphididae) in Soybean Agroecosystems. J Econ Entomol 104:115-124 doi:10.1603/ec10253

Mayadunnage S, Wijayagunasekara HNP, Hemachandra KS, Nugaliyadde L (2009) Occurrence of aphidophagous syrphids in aphid colonies on cabbage (*Brassica oleracea*) and their parasitoids. Tropical Agricultural Research 21:99-109

Medeiros HR et al. (2018) Non-crop habitats modulate alpha and beta diversity of flower flies (Diptera, Syrphidae) in Brazilian agricultural landscapes. Biodivers Conserv 27:1309-1326 doi:10.1007/s10531-017-1495-5

Menz MHM, Brown BV, Wotton KR (2019) Quantification of migrant hoverfly movements (Diptera: Syrphidae) on the West Coast of North America. Royal Society Open Science 6 doi:10.1098/rsos.190153

Meyer B, Jauker F, Steffan-Dewenter I (2009) Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. Basic Appl Ecol 10:178-186 doi:10.1016/j.baae.2008.01.001

Meyer S, Unternahrer D, Arlettaz R, Humbert J-Y, Menz MHM (2017) Promoting diverse communities of wild bees and hoverflies requires a landscape approach to managing meadows. Agric Ecosyst Environ 239:376-384 doi:10.1016/j.agee.2017.01.037

Meyhofer R, Klug T (2002) Intraguild predation on the aphid parasitoid *Lysiphlebus fabarum* (Marshall) (Hymenoptera : Aphidiidae): mortality risks and behavioral decisions made under the threats of predation. Biol Control 25:239-248 doi:10.1016/s1049-9644(02)00104-4

Michaud JP (1999) Sources of mortality in colonies of brown citrus aphid, *Toxoptera citricida*. BioControl 44:347-367 doi:10.1023/a:1009955816396

Miñarro M, Hemptinne JL, Dapena E (2005) Colonization of apple orchards by predators of *Dysaphis plantaginea*: sequential arrival, response to prey abundance and consequences for biological control. BioControl 50:403-414 doi:10.1007/s10526-004-5527-1

Miñarro M, Prida E (2013) Hedgerows surrounding organic apple orchards in north-west Spain: potential to conserve beneficial insects. Agric For Entomol 15:382-390 doi:10.1111/afe.12025

Mitra B, Banerjee D (2007) Fly pollinators: Assessing their value in biodiversity conservation and food security in india. Rec zool Surv India 107:33-48

Mizuno M, Itioka T, Tatematsu Y, Ito Y (1997) Food utilization of aphidophagous hoverfly larvae (Diptera: Syrphidae, Chamaemyiidae) on herbaceous plants in an urban habitat. Ecol Res 12:239-248 doi:10.1007/bf02529453

Moens J, De Clercq P, Tirry L (2011) Side effects of pesticides on the larvae of the hoverfly *Episyrphus balteatus* in the laboratory. Phytoparasitica 39:1-9 doi:10.1007/s12600-010-0127-3

Mohammadi-Khoramabadi A, Lotfalizadeh H, Gharali B (2016) A study on parasitoids of the hoverflies (Dipt.: Syrphidae) and their natural effects on them in organic aphid infested lettuce farms of Yazd Province, Iran. Entomol Gen 36:107-115 doi:10.1127/entomologia/2016/0131

Moquet L, Laurent E, Bacchetta R, Jacquemart A-L (2018) Conservation of hoverflies (Diptera, Syrphidae) requires complementary resources at the landscape and local scales. Insect Conserv Divers 11:72-87 doi:10.1111/icad.12245

Morris MC, Li FY (2000) Coriander (*Coriandrum sativum*)"companion plants" can attract hoverflies, and may reduce pest infestation in cabbages. N Z J Crop Hortic Sci 28:213-217 doi:10.1080/01140671.2000.9514141

Nedved O, Fois X, Ungerova D, Kalushkov P (2013) Alien vs. Predator - the native lacewing *Chrysoperla carnea* is the superior intraguild predator in trials against the invasive ladybird *Harmonia axyridis*. Bull Insectol 66:73-78

Noordijk J, Delille K, Schaffers AP, Sykora KV (2009) Optimizing grassland management for flower-visiting insects in roadside verges. Biol Conserv 142:2097-2103 doi:10.1016/j.biocon.2009.04.009

Nordstrom K et al. (2017) In situ modeling of multimodal floral cues attracting wild pollinators across environments. Proc Natl Acad Sci U S A 114:13218-13223 doi:10.1073/pnas.1714414114

Nourbakhsh SH, Soleymannejadian E, Nemti AR (2008) Biology and population dynamics of *Scaeva albomaculata* (Diptera: Syrphidae) in almond orchards of Shahrekord, Iran. Journal of Entomological Society of Iran 27:Pe93-108

Nye WP, Anderson JL (1974) Insect pollinators frequenting strawberry blossoms and the effect of honeybees on yield and fruit quality. J Am Soc Hort Sci 99:40-44

Öckinger E, Lindborg R, Sjodin NE, Bommarco R (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. Ecography 35:259-267 doi:10.1111/j.1600-0587.2011.06870.x

Odermatt J, Frommen JG, Menz MHM (2017) Consistent behavioural differences between migratory and resident hoverflies. Anim Behav 127:187-195 doi:10.1016/j.anbehav.2017.03.015

Odorizzi Santos LA, Costa MB, Lavigne C, Fernandes OA, Bischoff A, Franck P (2018) Influence of the margin vegetation on the conservation of aphid biological control in apple orchards. J Insect Conserv 22:465-474 doi:10.1007/s10841-018-0074-8

OECD/FAO (2019) OECD-FAO Agricultural Outlook 2019-2028.

Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? Oikos 120:321-326 doi:10.1111/j.1600-0706.2010.18644.x

Ouin A, Sarthou JP, Bouyjou B, Deconchat M, Lacombe JP, Monteil C (2006) The species-area relationship in the hoverfly (Diptera, Syrphidae) communities of forest fragments in southern France. Ecography 29:183-190 doi:10.1111/j.2006.0906-7590.04135.x

Pascual-Villalobos MJ, Lacasa A, Gonzalez A, Varo P, Garcia MJ (2006) Effect of flowering plant strips on aphid and syrphid populations in lettuce. European Journal of Agronomy 24:182-185 doi:10.1016/j.eja.2005.07.003

Pfiffner L, Wyss E (2004) Use of sown wildflower strips to enhance natural enemies of agricultural pests. Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods:165-186

Pfister SC, Sutter L, Albrecht M, Marini S, Schirmel J, Entling MH (2017) Positive effects of local and landscape features on predatory flies in European agricultural landscapes. Agric Ecosyst Environ 239:283-292 doi:10.1016/j.agee.2017.01.032

Pineda A, Marcos-Garcia MA (2008) Use of selected flowering plants in greenhouses to enhance aphidophagous hoverfly populations (Diptera: Syrphidae). Annales De La Societe Entomologique De France 44:487-492 doi:10.1080/00379271.2008.10697584

Pinheiro LA, Torres L, Raimundo J, Santos SAP (2013a) Effect of floral resources on longevity and nutrient levels of *Episyrphus balteatus* (Diptera: Syrphidae). Biol Control 67:178-185 doi:10.1016/j.biocontrol.2013.07.010

Pinheiro LA, Torres L, Raimundo J, Santos SAP (2013b) Effect of seven species of the family Asteraceae on longevity and nutrient levels of *Episyrphus balteatus*. BioControl 58:797-806 doi:10.1007/s10526-013-9535-x

Pinheiro LA, Torres LM, Raimundo J, Santos SAP (2015) Effects of pollen, sugars and honeydew on lifespan and nutrient levels of *Episyrphus balteatus*. BioControl 60:47-57 doi:10.1007/s10526-014-9621-8

Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation - Potential competitors that eat each other Annu Rev Ecol Syst 20:297-330 doi:10.1146/annurev.es.20.110189.001501

Pontin DR, Wade MR, Kehrli P, Wratten SD (2006) Attractiveness of single and multiple species flower patches to beneficial insects in agroecosystems. Ann Appl Biol 148:39-47 doi:10.1111/j.1744-7348.2005.00037.x

Power EF, Jackson Z, Stout JC (2016) Organic farming and landscape factors affect abundance and richness of hoverflies (Diptera, Syrphidae) in grasslands. Insect Conserv Divers 9:244-253 doi:10.1111/icad.12163

Power EF, Stout JC (2011) Organic dairy farming: impacts on insect-flower interaction networks and pollination. J Appl Ecol 48:561-569 doi:10.1111/j.1365-2664.2010.01949.x

Pretty J et al. (2018) Global assessment of agricultural system redesign for sustainable intensification. Nature Sustainability 1:441-446 doi:10.1038/s41893-018-0114-0

Primante C, Dotterl S (2010) A syrphid fly uses olfactory cues to find a non-yellow flower. J Chem Ecol 36:1207-1210 doi:10.1007/s10886-010-9871-6

Putra NS, Yasuda H (2006) Effects of prey species and its density on larval performance of two species of hoverfly larvae, *Episyrphus balteatus* de Geer and *Eupeodes corollae* Fabricius (Diptera: Syrphidae). Appl Entomol Zool 41:389-397 doi:10.1303/aez.2006.389

Qiaoyan Y, Liu C, Zhang Y (2015) Mowing Versus Insecticide for Control of Alfalfa Aphids and their Differential Impacts on Natural Enemies. Egyptian Journal of Biological Pest Control 25:285-289

Rader R, Edwards W, Westcott DA, Cunningham SA, Howlett BG (2011) Pollen transport differs among bees and flies in a human-modified landscape. Divers Distrib 17:519-529 doi:10.1111/j.1472-4642.2011.00757.x

Rader R et al. (2009) Alternative pollinator taxa are equally efficient but not as effective as the honeybee in a mass flowering crop. J Appl Ecol 46:1080-1087 doi:10.1111/j.1365-2664.2009.01700.x

Rader RA et al. (2016) Non-bee insects are important contributors to global crop pollination. Proc Natl Acad Sci U S A 113:146-151 doi:10.1073/pnas.1517092112

Ramsden MW, Menendez R, Leather SR, Waeckers F (2015) Optimizing field margins for biocontrol services: The relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. Agric Ecosyst Environ 199:94-104 doi:10.1016/j.agee.2014.08.024

Raymond L, Plantegenest M, Gauffre B, Sarthou JP, Vialatte A (2013a) Lack of Genetic Differentiation between Contrasted Overwintering Strategies of a Major Pest Predator *Episyrphus balteatus* (Diptera: Syrphidae): Implications for Biocontrol. PLoS ONE 8 doi:10.1371/journal.pone.0072997

Raymond L, Plantegenest M, Vialatte A (2013b) Migration and dispersal may drive to high genetic variation and significant genetic mixing: the case of two agriculturally important, continental hoverflies (*Episyrphus balteatus* and *Sphaerophoria scripta*). Mol Ecol 22:5329-5339 doi:10.1111/mec.12483

Raymond L, Sarthou JP, Plantegenest M, Gauffre B, Ladet S, Vialatte A (2014a) Immature hoverflies overwinter in cultivated fields and may significantly control aphid populations in autumn. Agric Ecosyst Environ 185:99-105 doi:10.1016/j.agee.2013.12.019

Raymond L, Vialatte A, Plantegenest M (2014b) Combination of morphometric and isotopic tools for studying spring migration dynamics in *Episyrphus balteatus*. Ecosphere 5 doi:10.1890/es14-00075.1

Ribeiro AL, Gontijo LM (2017) Alyssum flowers promote biological control of collard pests. BioControl 62:185-196 doi:10.1007/s10526-016-9783-7

Ricarte A, Marcos-Garcia MA, Moreno CE (2011) Assessing the effects of vegetation type on hoverfly (Diptera: Syrphidae) diversity in a Mediterranean landscape: implications for conservation. J Insect Conserv 15:865-877 doi:10.1007/s10841-011-9384-9

Rizk AM (2011) Effect of Strip-Management on the Population of the Aphid, *Aphis craccivora* Koch and its Associated Predators by Intercropping Faba bean, *Vicia faba* L. with Coriander, *Coriandrum sativum* L. Egyptian Journal of Biological Pest Control 21:81-87

Rodríguez-Gasol N, Avilla J, Alegre S, Alins G (2019a) *Sphaerophoria rueppelli* adults change their foraging behavior after mating but maintain the same preferences to flower traits. BioControl 64:149-158 doi:10.1007/s10526-019-09928-2

Rodríguez-Gasol N et al. (2019b) The Contribution of Surrounding Margins in the Promotion of Natural Enemies in Mediterranean Apple Orchards. Insects 10 doi:10.3390/insects10050148

Rojo S, Gilbert F, Marcos-García MA, Nieto J, Mier MP (2003) A world review of predatory hoverflies (Diptera, Syrphidae: Syrphinae) and their prey. CIBIO Ediciones, Alicante, Spain

Rotheray GE (1981) Host searching and oviposition behavior of some parasitoids of aphidphagous syrphidae. Ecol Entomol 6:79-87 doi:10.1111/j.1365-2311.1981.tb00974.x

Rotheray GE (1984) Host relations, life-cycles and multiparasitism in some parasitoids of aphidophagous syrphidae (Diptera). Ecol Entomol 9:303-310 doi:10.1111/j.1365-2311.1984.tb00853.x

Rotheray GE (1993) Coulour guide to hoverfly larvae (Diptera, Syrphidae) in Britain and Europe vol 9. Dipterists Digest. Derek Whiteley, Sheffield

Rotheray GE, Gilbert F (2011) The natural history of hoverflies. Forrest Text, Ceredigion

Sadeghi H, Gilbert F (2000a) Aphid suitability and its relationship to oviposition preference in predatory hoverflies. J Anim Ecol 69:771-784 doi:10.1046/j.1365-2656.2000.00433.x

Sadeghi H, Gilbert F (2000b) Oviposition preferences of aphidophagous hoverflies. Ecol Entomol 25:91-100 doi:10.1046/j.1365-2311.2000.00234.x

Samuel RN, Singh DR (2005) Feeding potential and its effect on development of an aphid predator, *Episyrphus balteatus* (De Geer) (Diptera: Syrphidae) vis-à-vis variable prey density. Journal of Aphidology:93-100

Sarthou JP, Badoz A, Vaissiere B, Chevallier A, Rusch A (2014) Local more than landscape parameters structure natural enemy communities during their overwintering in semi-natural habitats. Agric Ecosyst Environ 194:17-28 doi:10.1016/j.agee.2014.04.018

Sarthou JP, Ouin A, Arrignon F, Barreau G, Bouyjou B (2005) Landscape parameters explain the distribution and abundance of *Episyrphus balteatus* (Diptera : Syrphidae). Eur J Entomol 102:539-545 doi:10.14411/eje.2005.077

Schirmel J, Albrecht M, Bauer P-M, Sutter L, Pfister SC, Entling MH (2018) Landscape complexity promotes hoverflies across different types of semi-natural habitats in farmland. J Appl Ecol 55:1747-1758 doi:10.1111/1365-2664.13095

Schmidt MH, Thewes U, Thies C, Tscharntke T (2004) Aphid suppression by natural enemies in mulched cereals. Entomol Exp Appl 113:87-93 doi:10.1111/j.0013-8703.2004.00205.x

Schneider F (1948) Beitrag zur Kenntnis der Generationsverhaltnisse und Diapause rauberischer Schwebfliegen (Syrphidae: Diptera). Mitteilungen der Schweizerischen Entomologischen Gesellschaft:245-285

Schneider F (1969) Bionomics and Physiology of Aphidophagous Syrphidae. Annu Rev Entomol 14:103-124 doi:10.1146/annurev.en.14.010169.000535

Schweiger O et al. (2005) Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. J Appl Ecol 42:1129-1139 doi:10.1111/j.1365-2664.2005.01085.x

Schweiger O et al. (2007) Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. Oikos 116:461-472 doi:10.1111/j.2007.0030-1299.15372.x

Shannon HJ (1926) A Preliminary Report on the Seasonal Migrations of Insects. J N Y Entomol Soc 34:199-205

Short BD, Bergh JC (2004) Feeding and egg distribution studies of *Heringia calcarata* (Diptera: Syrphidae), a specialized predator of woolly apple aphid (Homoptera: Eriosomatidae) in Virginia apple orchards. J Econ Entomol 97:813-819 doi:10.1603/0022-0493(2004)097[0813:FAEDSO]2.0.CO;2

Sjodin NE, Bengtsson J, Ekbom B (2008) The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. J Appl Ecol 45:763-772 doi:10.1111/j.1365-2664.2007.01443.x

Skirvin DJ, Kravar-Garde L, Reynolds K, Wright C, Mead A (2011) The effect of within-crop habitat manipulations on the conservation biological control of aphids in field-grown lettuce. Bull Entomol Res 101:623-631 doi:10.1017/s0007485310000659

Smith HA, Chaney WE (2007) A survey of syrphid predators of *Nasonovia ribisnigri* in organic lettuce on the Central Coast of California. J Econ Entomol 100:39-48 doi:10.1603/0022-0493(2007)100[39:asospo]2.0.co;2

Solomon MF, Kendall DA (1970) Pollination by the syrphid fly, *Eristalis tenax*. Long Ashton Research Station Reports:101-102

Sommaggio D (1999) Syrphidae: can they be used as environmental bioindicators? Agric Ecosyst Environ 74:343-356 doi:10.1016/s0167-8809(99)00042-0

Sommaggio D, Burgio G (2014) The use of Syrphidae as functional bioindicator to compare vineyards with different managements. Bull Insectol 67:147-156

Sommaggio D, Burgio G, Guerrieri E (2014) The impact of agricultural management on the parasitization of aphidophagous hoverflies (Diptera: Syrphidae). J Nat Hist 48:301-315 doi:10.1080/00222933.2013.791953

Speight MCD (2014) Species accounts of European Syrphidae (Diptera) vol 78. Syrph the net: The database of European Syrphidae (Diptera). Syrph the Net publications, Dublin

Speight MCD, Castella E, Obrdlik P (2000) Use of the syrph the net database 2000 vol 25. Syrph the net: The database of European syrphidae (Diptera). Syrph the Net publications, Dublin

Ssymank A, Kearns CA, Pape T, Thompson C (2008) Pollinating Flies (Diptera): A major contribution to plant diversity and agricultural production. Biodiversity 9 doi:10.1080/14888386.2008.9712892

Stewart-Jones A, Pope TW, Fitzgerald JD, Poppy GM (2008) The effect of ant attendance on the success of rosy apple aphid populations, natural enemy abundance and apple damage in orchards. Agric For Entomol 10:37-43 doi:10.1111/j.1461-9563.2007.00353.x

Stutz S, Entling MH (2011) Effects of the landscape context on aphid-ant-predator interactions on cherry trees. Biol Control 57:37-43 doi:10.1016/j.biocontrol.2011.01.001

Sutherland JP, Sullivan MS, Poppy GM (1999) The influence of floral character on the foraging behaviour of the hoverfly, *Episyrphus balteatus*. Entomol Exp Appl 93:157-164 doi:10.1046/j.1570-7458.1999.00574.x

Tenhumberg B (1995) Estimating predatory efficiency of *Episyrphus balteatus* (Diptera, Syrphidae) in cereal fields. Environ Entomol 24:687-691 doi:10.1093/ee/24.3.687

Tenhumberg B, Poehling HM (1995) Syrphids as natural enemies of cereal aphids in Germany - Aspects of their biology and efficacy in different years and regions. Agric Ecosyst Environ 52:39-43 doi:10.1016/0167-8809(94)09007-t

Thomas CD (2000) Dispersal and extinction in fragmented landscapes. Proceedings of the Royal Society B-Biological Sciences 267:139-145 doi:10.1098/rspb.2000.0978

Tilman D, Balzer C, Hill J, Befort BL (2011) Global food demand and the sustainable intensification of agriculture. Proc Natl Acad Sci U S A 108:20260-20264 doi:10.1073/pnas.1116437108

Tinkeu LSN, Hance T (1997) Reduction of predatory efficiency of hoverflies (Diptera, Syrphidae) in cereal fields due to parasitism. Mededelingen - Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen, Universiteit Gent 62:469-472

Tomlinson S, Menz MHM (2015) Does metabolic rate and evaporative water loss reflect differences in migratory strategy in sexually dimorphic hoverflies? Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 190:61-67 doi:10.1016/j.cbpa.2015.09.004

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecol Lett 8:857-874 doi:10.1111/j.1461-0248.2005.00782.x

Tscharntke T et al. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews 87:661-685 doi:10.1111/j.1469-185X.2011.00216.x

Tschumi M, Albrecht M, Collatz J, Dubsky V, Entling MH, Najar-Rodriguez AJ, Jacot K (2016) Tailored flower strips promote natural enemy biodiversity and pest control in potato crops. J Appl Ecol 53:1169-1176 doi:10.1111/1365-2664.12653

Twardowski JP, Hurej M, Klukowski Z (2005) The effect of the strip-management on reduction of Aphis fabae (Homoptera: Aphididae) populations by predators on sugar beet crop. Journal of Plant Protection Research 45:213-219

Valentine EW (1967) Biological control of aphids. Proceedings of the NZ Weed and Pest Control Conference 20:204-207

van Rijn PCJ, Kooijman J, Wackers FL (2013) The contribution of floral resources and honeydew to the performance of predatory hoverflies (Diptera: Syrphidae). Biol Control 67:32-38 doi:10.1016/j.biocontrol.2013.06.014

van Rijn PCJ, Kooijman J, Wäckers FL (2006) The impact of floral resources on syrphid performance and cabbage aphid biological control. IOBC/WPRS Bull 29:149-152

van Rijn PCJ, Wäckers FL (2016) Nectar accessibility determines fitness, flower choice and abundance of hoverflies that provide natural pest control. J Appl Ecol 53:925-933 doi:10.1111/1365-2664.12605

Vance NC, Bernhardt P, Edens RM (2004) Pollination and seed production in *Xerophyllum tenax* (Melanthiaceae) in the cascade range of central Oregon. Am J Bot 91:2060-2068 doi:10.3732/ajb.91.12.2060

Vanhaelen N, Gaspar C, Francis F (2002) Influence of prey host plant on a generalist aphidophagous predator: *Episyrphus balteatus* (Diptera: Syrphidae). Eur J Entomol 99:561-564

Verheggen FJ, Capella Q, Schwartzberg EG, Voigt D, Haubruge E (2009) Tomato-aphid-hoverfly: a tritrophic interaction incompatible for pest management. Arthropod-Plant Interactions 3:141-149 doi:10.1007/s11829-009-9065-8

Villa M et al. (2016) Syrphids feed on multiple patches in heterogeneous agricultural landscapes during the autumn season, a period of food scarcity. Agric Ecosyst Environ 233:262-269 doi:10.1016/j.agee.2016.09.014

Vosteen I, Gershenzon J, Kunert G (2018) Dealing with food shortage: larval dispersal behaviour and survival on non-prey food of the hoverfly *Episyrphus balteatus*. Ecol Entomol 43:578-590 doi:10.1111/een.12636

Wäckers FL, Van Rijn PCJ (2012) Pick and Mix: Selecting flowering plants to meet the requirements of target biological control insects. In: Gurr GM, Wratten S, Snyder WE, Read DMY (eds) Biodiversity and Insect Pests: Key Issues for Sustainable Management. John Wiley & Sons, Bognor Regis, UK,

Walton NJ, Isaacs R (2011) Influence of Native Flowering Plant Strips on Natural Enemies and Herbivores in Adjacent Blueberry Fields. Environ Entomol 40:697-705 doi:10.1603/en10288

Wan N-F, Ji X-Y, Deng J-Y, Kiaer LP, Cai Y-M, Jiang J-X (2019) Plant diversification promotes biocontrol services in peach orchards by shaping the ecological niches of insect herbivores and their natural enemies. Ecol Indicators 99:387-392 doi:10.1016/j.ecolind.2017.11.047

Wang K, Liu J, Zhan Y, Liu Y (2019) A new slow-release formulation of methyl salicylate optimizes the alternative control of *Sitobion avenae* (Fabricius) (Hemiptera: Aphididae) in wheat fields. Pest Manage Sci 75:676-682 doi:10.1002/ps.5164

Warzecha D, Diekoetter T, Wolters V, Jauker F (2018) Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species. Insect Conserv Divers 11:32-41 doi:10.1111/icad.12264

Werling BP, Meehan TD, Gratton C, Landis DA (2011) Influence of habitat and landscape perenniality on insect natural enemies in three candidate biofuel crops. Biol Control 59:304-312 doi:10.1016/j.biocontrol.2011.06.014

West PC et al. (2014) Leverage points for improving global food security and the environment. Science 345:325-328 doi:10.1126/science.1246067

Westmacott HM, Williams CB (1954) A migration of Lepidoptera and Diptera in Nepal. Entomologist:232-234

White AJ, Wratten SD, Berry NA, Weigmann U (1995) Habitat manipulations to enhance biological control of brassica pests by hover flies (Diptera, Syrphidae). J Econ Entomol 88:1171-1176 doi:10.1093/jee/88.5.1171

Wotton KR et al. (2019) Mass Seasonal Migrations of Hoverflies Provide Extensive Pollination and Crop Protection Services. Curr Biol 29:2167-+ doi:10.1016/j.cub.2019.05.036

Wratten SD, Bowie MH, Hickman JM, Evans AM, Sedcole JR, Tylianakis JM (2003) Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. Oecologia 134:605-611 doi:10.1007/s00442-002-1128-9

Wyss E (1995) The effects of weed strips on aphids and aphidophagous predators in an apple orchard. Entomol Exp Appl 75:43-49 doi:10.1111/j.1570-7458.1995.tb01908.x

Wyss E (1996) The effects of artificial weed strips on diversity and abundance of the arthropod fauna in a Swiss experimental apple orchard. Agric Ecosyst Environ 60:47-59 doi:10.1016/s0167-8809(96)01060-2

Wyss E, Villiger M, Muller-Scharer H (1999) The potential of three native insect predators to control the rosy apple aphid, *Dysaphis plantaginea*. BioControl 44:171-182 doi:10.1023/a:1009934214927

Xu Q, Hatt S, Han Z, Francis F, Chen J (2018a) Combining E--farnesene and methyl salicylate release with wheat-pea intercropping enhances biological control of aphids in North China. Biocontrol Sci Technol 28:883-894 doi:10.1080/09583157.2018.1504885

Xu Q, Hatt S, Lopes T, Zhang Y, Bodson B, Chen J, Francis F (2018b) A push-pull strategy to control aphids combines intercropping with semiochemical releases. J Pest Sci 91:93-103 doi:10.1007/s10340-017-0888-2

Zhu JW, Park KC (2005) Methyl salicylate, a soybean aphid-induced plant volatile attractive to the predator *Coccinella septempunctata*. J Chem Ecol 31:1733-1746 doi:10.1007/s10886-005-5923-8

# General Discussion

Advances in sustainable intensification require an accurate assessment of the positive and negative impacts of the diverse farming practices that affect farmland diversity, as well as a better understanding of the ecology of beneficial organisms in order to better promote them and the ecosystem services they provide. The work presented in this thesis provides a further insight in several aspects of the maintenance and promotion of ecosystem services, i.e. pollination and biological control, in agricultural systems.

In this thesis we show that the transformation of dryland into irrigation, as a prominent component of agricultural intensification, causes profound environmental changes at a local and landscape scale that result in a drastic transformation of the pollinator communities (Chapter 1). Increased water availability buffers the detrimental effects of the summer drought on plant growth and reproduction (van der Velde et al. 2010) and reduces competition between weeds and the crop. Consequently, irrigated orchards had a higher flower abundance as well as a different flower composition than dry ones. Moreover, at a landscape scale, the conversion into irrigation allows the cultivation of high water demanding crops (oilseed rape, sunflowers, lucerne, lettuce, tomato, apple, pear or peach) and to increase the yield of crops that are traditionally grown in dryland zones (barley, wheat, almond or olive). This higher richness in types of crops involved the extension of the blooming period from February to July, while in the dryland zone it was restricted to February-March. Conversely, it also involved an important loss in natural and semi-natural habitat cover, which is in accordance with previous studies related to farmland intensification (Benton et al. 2003; Tscharntke et al. 2005).

The mentioned environmental differences between irrigated and dry orchards were accompanied by profound differences in the pollinator assemblages. We found that wild bee communities in irrigated orchards were dominated by ground-nesting social species (such as *Lasioglossum malachurum* Kirby and *Halictus fulvipes* Klug), whereas in dry orchards communities were more diverse and characterized by the presence of solitary circum-Mediterranean species like *Osmia tricornis* Latreille and *Rodanthidium sticticum* Fabricius. Hence, increased flower abundance at a local and landscape scale benefit those species that depend on flower supply for a long period of time. However, changes in flower composition as well as the loss of natural and semi-natural habitats, might hinder other species with different floral and nesting resources. In fact, reduced cover of natural and semi-natural habitats is usually related to a constraint in the pollinator communities due to isolation and low availability of nesting (Potts et al. 2005) and food resources (Rundlof et al. 2014). Furthermore, the irrigated orchards located close to the dryland did not benefit from their proximity to the non-irrigated areas as these did not present neither a higher species richness nor a gradual change in the community composition. This highlights a strong effect of the local conditions in the shaping of the wild bee communities (Osorio et al. 2015; Schaffers et al. 2008).

Compared to bees, the hoverfly community was not as affected by the transformation into irrigation. Unlike bees, hoverflies are not constrained by the need to provision a nest and may move more freely in the landscape, thus being less susceptible to the loss of natural and semi-natural habitats that usually involves land intensification (Aguirre-Gutiérrez et al. 2015; Jauker et al. 2009). In addition, our hoverfly community was dominated by ubiquitous aphidophagous species, which are known to find prey for their offspring in aphid colonies from cultivated as well as wild plants (Rojo et al. 2003; Sadeghi and Gilbert 2000a), and therefore are well adapted to agricultural landscapes (Haenke et al. 2014; Jauker et al. 2009; Meyer et al. 2009). Because of different habitat requirements, aphidophagous hoverflies may play an important role in maintaining pollination services especially in agricultural landscapes that are unsuitable for bees (Jauker et al. 2009). This study is the first that address the effect of implementation of irrigation on pollinators. Our results are an important step in understanding the role of the addition of irrigation on insect biodiversity that will contribute to build conservation actions for a sustainable agricultural development.

Besides from preservation and restoration practices at landscape scale, another way to maintain farmland diversity is habitat manipulation at field scale. The provision of favorable habitats that supply beneficial enemies with shelter, nectar, alternative prey/hosts and/or pollen has been widely acknowledged (Gurr et al. 2017). Accordingly, and coinciding with previous studies (Albert et al. 2017; Campbell et al. 2017; Dib et al. 2012; Miñarro and Prida 2013; Wyss 1995; Wyss et al. 1995), our experience of implementing insectary plants in the margins of apple orchards (Chapter 2) boosted resource availability which may explain the higher presence of natural enemies in those plants when compared to the surrounding spontaneous vegetation.

With regard to the aphid colonies, the presence of parasitoids stood out over the rest of the natural enemy pool. In the *Dyspahis plantaginea* Passerini colonies parasitoids and hoverflies were the two most important groups and the first to colonize the aphid colonies when these were still growing, thus having a potential role on preventing aphid outbreaks. Climate seems to be an important determinant of the relative abundances of natural enemies present in the *D. plantaginea* colonies as parasitism is more frequent in Mediterranean areas (Dib et al. 2016; Dib et al. 2010; Odorizzi Santos et al. 2018), while its importance is relegated by predators in colder climates (Brown and Mathews 2007; Cahenzli et al. 2017; Stewart-Jones et al. 2008). In the *Eriosoma lanigerum* Hausmann colonies, the presence of predators was anecdotal, being *Aphelinus mali* Haldeman the main natural enemy.

Even though the addition of insectary plants can provide multiple benefits, a rigorous selection of the plant species is crucial in order to avoid those species that harbor crop pests or diseases (Gurr et al. 2017), but also to ensure that the plants selected are promoting those natural enemies that can be more effective for each target pest (Symondson et al. 2002; Zehnder et al. 2007). In fact, we could not find any relationships between the insects found in the implemented flower margin and the ones present in the aphid colonies (*D. plantaginea* and *E. lanigerum*). In contrast, positive correlations were found between the parasitoids found in the spontaneous vegetation and the ones present in the *D. plantaginea* colonies. These results highlight the importance of field trials to determine the real contribution of the parasitoids present in the area on aphid control and how plant species can boost their presence.

Moreover, natural enemies select flowers on the basis of one or more floral traits (Ambrosino et al. 2006). In this regard, several studies have evaluated the relative attractiveness of different flower species and floral traits in order to better tailor ecological infrastructures for hoverfly attraction (Colley and Luna 2000; Laubertie et al. 2006; Sutherland et al. 1999; Wäckers and Van Rijn 2012). In our study (Chapter 3) we observed that adults of *Sphaerophoria rueppellii* Weidemann (Diptera: Syrphidae) preferred bouquets of 12 flat circle-shaped flowers (half white and half yellow), to other combinations of shapes, flower number and colors. Several implications can be drawn from our results. With regard to shape, the presence of petals does not seem to be necessary for flower attraction (Golding et al. 1999), and the presence of a flat surface seems to help hoverflies to land and forage. About flower number, a higher flower number was related to an increased number of visits (Conner and Rush 1996; Haenke et al. 2009), thus it is likely that hoverflies relate a higher number of flowers with a greater probability of finding food. With reference to flower color, diversity is a plus in the attraction of hoverflies but it has to be well selected in order to be functional (Warzecha et al. 2018). Regardless of the colors present, hoverflies have a strong preference for landing on yellow flowers (Laubertie et al. 2006; Lunau and Wacht 1994), which they might interpret as where the pollen is located.

Most importantly, we observed behavioral differences between mated and virgin (un-mated) females. When compared to virgin individuals, mated females visited less flowers but landed more onto the ones they visited. It is possible that mated females are in a higher need of pollen and nectar in order to be able to maintain a continuous oviposition (Branquart and Hemptinne 2000a; Hickman et al. 1995; Irvin et al. 1999) that makes them to be less selective. Our findings have given a major insight into hoverfly behavior and can be used to improve the design and location of ecological infrastructures for the promotion of biological control and pollination, and therefore can contribute to increase the environmental sustainability of crops.

On the other hand, a better understanding of the ecology of farmland beneficials can substantially contribute to advances in ecological intensification through the selection of those strategies that maximize their promotion. Given the relevance of hoverflies in our area (Chapter 1 and Chapter 2), we decided to review the existing literature related to the promotion of predatory hoverflies and their ecosystem services in agricultural systems (Chapter 4). The adults' ecology is closely related to flowers, as they need to feed on nectar and pollen, to obtain energy and allow gametogenesis, respectively (Schneider 1969). Moreover, they are able to oviposit continuously during all their life if they do not experience food shortages (Branquart and Hemptinne 2000a). Many studies have evaluated the relative attractiveness of different flower species to adult hoverflies and it has been observed that the diverse flower species enhance different aspects of the adults' fitness (Laubertie et al. 2012). Thus, a continuous and diverse supply of flowers is highly recommended. Actinomorphic plants with flat corollas that provide easily accessible pollen and nectar (e.g. Apiaceae, Asteraceae, Ranunculaceae and Rosaceae) are the most accessible to hoverflies, though it is known that more polyphagous species have elongated mouthparts that enable them to have access to the pollen and nectar of more concealed flowers (Branquart and

Hemptinne 2000b). Furthermore, other small predatory species are also known to be able to feed on grasses and plantains (Branquart and Hemptinne 2000b). Moreover, adult selectiveness for floral traits and oviposition sites can vary depending on sex, age and the nutritional status of the individuals (Almohamad et al. 2009; Sadeghi and Gilbert 2000b; Sutherland et al. 1999).

The larvae, in turn have long been recognized for their potential as natural enemies due to their voracity (Tenhumberg 1995). Nonetheless they have a limited dispersal capacity (about 1 m) and their fate is mainly determined by the ovipositing choices of the adult females (Almohamad et al. 2009). In this regard, herbivore-induced plant volatiles and aphid alarm pheromone components, such as E-(β)-farnesene and methyl salicylate, play an important role on prey location, eliciting orientation towards the host in adults an larvae, and even stimulating egg-laying in adults (Almohamad et al. 2009). The use of these volatiles has been recently used in aphid biological control with promising results on both, hoverfly attraction and aphid reduction (Wang et al. 2019). However, more research is needed in relation to the distance from which these compounds are detected, as the only report to date states that the attractive effect disappears at 1.5 m from the volatile-impregnated lures.

About their relationship with landscape structure, aphidophagous hoverflies seem to be less affected by landscape fragmentation and natural and semi-natural habitat loss than non-aphidophagous hoverflies or bees (Jauker et al. 2009; Schweiger et al. 2007). Mainly because they usually are highly mobile and able to find prey for their offspring in both, crop and non-crop plants. Nonetheless, the presence of semi-natural habitats (such as forests, hedgerows and flower strips) is still important to ensure their presence in periods of crop disturbance, low supply of resources for the larvae and the adults, and overwintering (Moquet et al. 2018; Pfister et al. 2017; Sarthou et al. 2005). With reference to the latter, further studies are known to discern which factors trigger migration and overwintering (Odermatt et al. 2017), as well as the common overwintering sites for adults and their feeding requirements during these period. This knowledge is especially relevant due to its implications to maintain hoverfly populations and to promote early biological control in spring.

Predatory hoverflies are among the most abundant aphid predators in several agricultural systems (Gardiner et al. 2010; Miñarro et al. 2005; Tenhumberg and Poehling 1995; White et al. 1995) and among the aphidophagous insects that can locate aphid colonies earlier in the season (Dib et al. 2010; Miñarro et al. 2005), as we could also observe (Chapter 2). Despite their role as biological control agents is widely recognized, predatory hoverflies can provide other ecosystem services, such as pollination, bioindication and food for other natural enemies, which have been much less studied. Hoverflies have usually been underestimated as pollinators especially if compared to bees, since few studies have assessed their pollination efficiency to crops (Jauker et al. 2012; Jauker and Wolters 2008). However, they are known to exhibit flower constancy and to contribute to the fruit set of several crops. Moreover, they can provide additional pollination services when bees are restricted by temperature or low availability of natural and semi-natural habitats (Jauker et al. 2009; Ssymank et al. 2008)

At farm level, the maintenance and promotion of hoverflies relies on a combination of multiple strategies: i) avoid the application of pesticides that can disrupt them, ii) avoid barriers that can disrupt their dispersal and recolonization from the surrounding landscape after, for example, pesticide treatments, iii) use semiochemicals to increase their attraction to the aphid colonies and stimulate egg-laying, iv) provide enough flower resources, refuges and alternative prey in time and space either by managing mowing or by implementing ecological infrastructures like flower strips and hedgerows, and v) take into account interacting effects with the surrounding landscape in order to provide complementary resources in the different periods of the year.

Despite the addition of flower resources has been widely evaluated for the promotion of biological control, few studies have managed to demonstrate positive effects of the implementation of flower strips on aphid biological control by hoverflies. Furthermore, no evidences exist with regard to pest control under the economic threshold thanks to the promotion of hoverflies. This underlies the difficulty of evaluating the effectiveness of these type of studies, as well as the importance of promoting a natural enemy pool.

In summary the results obtained during this thesis show that: 1) transformation of dry land into irrigation causes environmental changes at a local and landscape scale that drastically transform pollinator communities, 2) the more parasitoids were present in the spontaneous vegetation, the more parasitoids were found in the *D. plantaginea* colonies, 3) bouquets of yellow and white flat flowers are the most attractive to hoverflies and 4) hoverflies can provide important ecosystem services to agricultural systems only if multiple strategies are considered for their maintenance at both, local and landscape level.

## References

Aguirre-Gutiérrez J, Biesmeijer JC, van Loon EE, Reemer M, WallisDeVries MF, Carvalheiro LG (2015) Susceptibility of pollinators to ongoing landscape changes depends on landscape history. Divers Distrib 21:1129-1140 doi:10.1111/ddi.12350

Albert L, Franck P, Gilles Y, Plantegenest M (2017) Impact of agroecological infrastructures on the dynamics of *Dysaphis plantaginea* (Hemiptera: Aphididae) and its natural enemies in apple orchards in northwestern France. Environ Entomol 46:528-537 doi:10.1093/ee/nvx054

Almohamad R, Verheggen FJ, Haubruge E (2009) Searching and oviposition behavior of aphidophagous hoverflies (Diptera: Syrphidae): a review. Biotechnol Agron Soc 13:467-481

Ambrosino MD, Luna JM, Jepson PC, Wratten SD (2006) Relative frequencies of visits to selected insectary plants by predatory hoverflies (Diptera: Syrphidae), other beneficial insects, and herbivores. Environ Entomol 35:394-400 doi:10.1603/0046-225x-35.2.394

Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol Evol 18:182-188 doi:10.1016/s0169-5347(03)00011-9

Branquart E, Hemptinne JL (2000a) Development of ovaries, allometry of reproductive traits and fecundity of *Episyrphus balteatus* (Diptera: Syrphidae). Eur J Entomol 97:165-170

Branquart E, Hemptinne JL (2000b) Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphinae). Ecography 23:732-742 doi:10.1034/j.1600-0587.2000.230610.x

Brown MW, Mathews CR (2007) Conservation biological control of rosy apple aphid, *Dysaphis plantaginea* (Passerini), in Eastern North America. Environ Entomol 36:1131-1139 doi:10.1603/0046-225x(2007)36[1131:cbcora]2.0.co;2

Cahenzli F, Pfiffner L, Daniel C (2017) Reduced crop damage by self-regulation of aphids in an ecologically enriched, insecticide-free apple orchard. Agronomy for Sustainable Development 37:8 doi:10.1007/s13593-017-0476-0

Campbell AJ, Wilby A, Sutton P, Wackers F (2017) Getting more power from your flowers: Multi-functional flower strips enhance pollinators and pest control agents in apple orchards. Insects 8:18 doi:10.3390/insects8030101

Colley MR, Luna JM (2000) Relative attractiveness of potential beneficial insectary plants to aphidophagous hoverflies (Diptera: Syrphidae). Environ Entomol 29:1054-1059 doi:10.1603/0046-225x-29.5.1054

Conner JK, Rush S (1996) Effects of flower size and number on pollinator visitation to wild radish, *Raphanus raphanistrum*. Oecologia 105:509-516 doi:10.1007/bf00330014

Dib H, Libourel G, Warlop F (2012) Entomological and functional role of floral strips in an organic apple orchard: Hymenopteran parasitoids as a case study. J Insect Conserv 16:315-318 doi:10.1007/s10841-012-9471-6

Dib H, Sauphanor B, Capowiez Y (2016) Effect of management strategies on arthropod communities in the colonies of rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) in south-eastern France. Agric Ecosyst Environ 216:203-206 doi:10.1016/j.agee.2015.10.003

Dib H, Simon S, Sauphanor B, Capowiez Y (2010) The role of natural enemies on the population dynamics of the rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) in organic apple orchards in south-eastern France. Biol Control 55:97-109 doi:10.1016/j.biocontrol.2010.07.005

Gardiner MA, Tuell JK, Isaacs R, Gibbs J, Ascher JS, Landis DA (2010) Implications of Three Biofuel Crops for Beneficial Arthropods in Agricultural Landscapes. Bioenergy Research 3:6-19 doi:10.1007/s12155-009-9065-7

Golding YC, Sullivan MS, Sutherland JP (1999) Visits to manipulated flowers by *Episyrphus balteatus* (Diptera : Syrphidae): Partitioning the signals of petals and anthers. J Insect Behav 12:39-45 doi:10.1023/a:1020925030522

Gurr GM, Wratten SD, Landis DA, You MS (2017) Habitat management to suppress pest populations: progress and prospects. Annu Rev Entomol 62:91-109 doi:10.1146/annurev-ento-031616-035050

Haenke S, Kovacs-Hostyanszki A, Fruend J, Batary P, Jauker B, Tscharntke T, Holzschuh A (2014) Landscape configuration of crops and hedgerows drives local syrphid fly abundance. J Appl Ecol 51:505-513 doi:10.1111/1365-2664.12221

Haenke S, Scheid B, Schaefer M, Tscharntke T, Thies C (2009) Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. J Appl Ecol 46:1106-1114 doi:10.1111/j.1365-2664.2009.01685.x

Hickman JM, Lovei GL, Wratten SD (1995) Pollen feeding by adults of the hoverfly *Melanostoma fasciatum* (Diptera: Syrphidae). N Z J Zool 22:387-392 doi:10.1080/03014223.1995.9518057

Irvin NA, Wratten SD, Frampton CM, Bowie MH, Evans AM, Moar NT (1999) The phenology and pollen feeding of three hover fly (Diptera: Syrphidae) species in Canterbury, New Zealand. N Z J Zool 26:105-115 doi:10.1080/03014223.1999.9518182

Jauker F, Bondarenko B, Becker HC, Steffan-Dewenter I (2012) Pollination efficiency of wild bees and hoverflies provided to oilseed rape. Agric For Entomol 14:81-87 doi:10.1111/j.1461-9563.2011.00541.x

Jauker F, Diekoetter T, Schwarzbach F, Wolters V (2009) Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecol 24:547-555 doi:10.1007/s10980-009-9331-2

Jauker F, Wolters V (2008) Hover flies are efficient pollinators of oilseed rape. Oecologia 156:819-823 doi:10.1007/s00442-008-1034-x

Laubertie EA, Wratten SD, Hemptinne J-L (2012) The contribution of potential beneficial insectary plant species to adult hoverfly (Diptera: Syrphidae) fitness. Biol Control 61:1-6 doi:10.1016/j.biocontrol.2011.12.010

Laubertie EA, Wratten SD, Sedcole JR (2006) The role of odour and visual cues in the pan-trap catching of hoverflies (Diptera: Syrphidae). Ann Appl Biol 148:173-178 doi:10.1111/j.1744-7348.2006.00046.x

Lunau K, Wacht S (1994) Optical releasers of the innate proboscis extension in the hoverfly *Eristalis tenax* L. (Syrphidae: Diptera) J Comp Physiol, A 174:575-579 doi:10.1007/BF00217378

Meyer B, Jauker F, Steffan-Dewenter I (2009) Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. Basic Appl Ecol 10:178-186 doi:10.1016/j.baae.2008.01.001

Miñarro M, Hemptinne JL, Dapena E (2005) Colonization of apple orchards by predators of *Dysaphis plantaginea*: sequential arrival, response to prey abundance and consequences for biological control. BioControl 50:403-414 doi:10.1007/s10526-004-5527-1

Miñarro M, Prida E (2013) Hedgerows surrounding organic apple orchards in north-west Spain: potential to conserve beneficial insects. Agric For Entomol 15:382-390 doi:10.1111/afe.12025

Moquet L, Laurent E, Bacchetta R, Jacquemart A-L (2018) Conservation of hoverflies (Diptera, Syrphidae) requires complementary resources at the landscape and local scales. Insect Conserv Divers 11:72-87 doi:10.1111/icad.12245

Odermatt J, Frommen JG, Menz MHM (2017) Consistent behavioural differences between migratory and resident hoverflies. Anim Behav 127:187-195 doi:10.1016/j.anbehav.2017.03.015

Odorizzi Santos LA, Costa MB, Lavigne C, Fernandes OA, Bischoff A, Franck P (2018) Influence of the margin vegetation on the conservation of aphid biological control in apple orchards. J Insect Conserv 22:465-474 doi:10.1007/s10841-018-0074-8

Osorio S, Arnan X, Bassols E, Vicens N, Bosch J (2015) Local and landscape effects in a host-parasitoid interaction network along a forest-cropland gradient. Ecol Appl 25:1869-1879 doi:10.1890/14-2476.1

Pfister SC, Sutter L, Albrecht M, Marini S, Schirmel J, Entling MH (2017) Positive effects of local and landscape features on predatory flies in European agricultural landscapes. Agric Ecosyst Environ 239:283-292 doi:10.1016/j.agee.2017.01.032

Potts SG, Vulliamy B, Roberts S, O'Toole C, Dafni A, Ne'Eman G, Willmer P (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecol Entomol 30:78-85 doi:10.1111/j.0307-6946.2005.00662.x

Rojo S, Gilbert F, Marcos-García MA, Nieto J, Mier MP (2003) A world review of predatory hoverflies (Diptera, Syrphidae: Syrphinae) and their prey. CIBIO Ediciones, Alicante, Spain

Rundlof M, Persson AS, Smith HG, Bommarco R (2014) Late-season mass-flowering red clover increases bumble bee queen and male densities. Biol Conserv 172:138-145 doi:10.1016/j.biocon.2014.02.027

Sadeghi H, Gilbert F (2000a) Aphid suitability and its relationship to oviposition preference in predatory hoverflies. J Anim Ecol 69:771-784 doi:10.1046/j.1365-2656.2000.00433.x

Sadeghi H, Gilbert F (2000b) Oviposition preferences of aphidophagous hoverflies. Ecol Entomol 25:91-100 doi:10.1046/j.1365-2311.2000.00234.x

Sarthou JP, Ouin A, Arrignon F, Barreau G, Bouyjou B (2005) Landscape parameters explain the distribution and abundance of *Episyrphus balteatus* (Diptera : Syrphidae). Eur J Entomol 102:539-545 doi:10.14411/eje.2005.077

Schaffers AP, Raemakers IP, Sykora KV, Ter Braak CJF (2008) Arthropod assemblages are best predicted by plant species composition. Ecology 89:782-794 doi:10.1890/07-0361.1

Schneider F (1969) Bionomics and Physiology of Aphidophagous Syrphidae. Annu Rev Entomol 14:103-124 doi:10.1146/annurev.en.14.010169.000535

Schweiger O et al. (2007) Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. Oikos 116:461-472 doi:10.1111/j.2007.0030-1299.15372.x

Ssymank A, Kearns CA, Pape T, Thompson C (2008) Pollinating Flies (Diptera): A major contribution to plant diversity and agricultural production. Biodiversity 9 doi:10.1080/14888386.2008.9712892

Stewart-Jones A, Pope TW, Fitzgerald JD, Poppy GM (2008) The effect of ant attendance on the success of rosy apple aphid populations, natural enemy abundance and apple damage in orchards. Agric For Entomol 10:37-43 doi:10.1111/j.1461-9563.2007.00353.x

Sutherland JP, Sullivan MS, Poppy GM (1999) The influence of floral character on the foraging behaviour of the hoverfly, *Episyrphus balteatus*. Entomol Exp Appl 93:157-164 doi:10.1046/j.1570-7458.1999.00574.x

Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? Annu Rev Entomol 47:561-594 doi:10.1146/annurev.ento.47.091201.145240

Tenhumberg B (1995) Estimating predatory efficiency of *Episyrphus balteatus* (Diptera, Syrphidae) in cereal fields. Environ Entomol 24:687-691 doi:10.1093/ee/24.3.687

Tenhumberg B, Poehling HM (1995) Syrphids as natural enemies of cereal aphids in Germany - Aspects of their biology and efficacy in different years and regions. Agric Ecosyst Environ 52:39-43 doi:10.1016/0167-8809(94)09007-t

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecol Lett 8:857-874 doi:10.1111/j.1461-0248.2005.00782.x

van der Velde M, Wriedt G, Bouraoui F (2010) Estimating irrigation use and effects on maize yield during the 2003 heatwave in France. Agric Ecosyst Environ 135:90-97 doi:10.1016/j.agee.2009.08.017

Wäckers FL, Van Rijn PCJ (2012) Pick and Mix: Selecting flowering plants to meet the requirements of target biological control insects. In: Gurr GM, Wratten S, Snyder WE, Read DMY (eds) Biodiversity and Insect Pests: Key Issues for Sustainable Management. John Wiley & Sons, Bognor Regis, UK,

Wang K, Liu J, Zhan Y, Liu Y (2019) A new slow-release formulation of methyl salicylate optimizes the alternative control of *Sitobion avenae* (Fabricius) (Hemiptera: Aphididae) in wheat fields. Pest Manage Sci 75:676-682 doi:10.1002/ps.5164

Warzecha D, Diekoetter T, Wolters V, Jauker F (2018) Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species. Insect Conserv Divers 11:32-41 doi:10.1111/icad.12264

White AJ, Wratten SD, Berry NA, Weigmann U (1995) Habitat manipulations to enhance biological control of brassica pests by hover flies (Diptera, Syrphidae). J Econ Entomol 88:1171-1176 doi:10.1093/jee/88.5.1171

Wyss E (1995) The effects of weed strips on aphids and aphidophagous predators in an apple orchard. Entomol Exp Appl 75:43-49 doi:10.1111/j.1570-7458.1995.tb01908.x

Wyss E, Niggli U, Nentwig W (1995) The impact of spiders on aphid populations in a strip-managed apple orchard. J Appl Entomol 119:473-478 doi:10.1111/j.1439-0418.1995.tb01320.x

Zehnder G, Gurr GM, Kuehne S, Wade MR, Wratten SD, Wyss E (2007) Arthropod pest management in organic crops. Annu Rev Entomol 52:57-80 doi:10.1146/annurev.ento.52.110405.091337

# Conclusions

## Chapter 1

- At local scale, the transformation of dryland into irrigation causes a reduction of bare soil, an increase in flower abundance and, a change in flower composition. At landscape scale, the addition of irrigation implies a change in the identity of the main crops and a loss in the proportion of semi-natural habitats.
- The transformation into irrigation drastically changes wild bee communities: species composition completely differs between dry and irrigated orchards, being more abundant and less diverse after the transformation. In contrast hoverflies are not as affected as wild bees.
- The main environmental drivers determining wild bee communities are flower abundance and composition at the local scale and the proportion of arable crops and natural and semi-natural habitats at the landscape scale. However, hoverfly composition is hardly influenced by local and landscape variables.

## Chapter 2

- The implementation of a flower margin (composed by four insectary plant species: *A. millefolium*, *L. maritima*, *M. arvensis*, *S. alba*) is able to gather natural enemy populations in the edge of apple orchards due to an enhanced alimentary and shelter supply.
- Parasitoids and hoverflies are the key natural enemies of *D. plantaginea* whereas the parasitoid *A. mali* is the most abundant in *E. lanigerum* colonies.
- The presence of parasitoids in the surrounding margins of the orchards increased the parasitism of *D. plantaginea* colonies.

## Chapter 3

- Different flower traits elicit diverse behaviors in hoverflies: bouquets of yellow and white flat flowers are the most attractive to hoverflies.
- Mating modifies the behavior of females: gravid females are less selective than virgin females.

## Chapter 4

- Hoverflies can provide important ecosystem services (e.g. biological control, pollination, bioindication and food for other natural enemies) to agricultural systems, only if multiple strategies are considered for their maintenance at both, local and landscape level.
- Current experiences show that the provision of flower strips contribute to increase the presence of hoverflies at farm level and to reduce pest populations. However, further research is needed to discern aspects such as optimal location of these infrastructures and the extent to which an effective biological control can be achieved.

Illustrations by Laura López Castillo