# Intensificación agrícola, biodiversidad y funcionamiento de la polinización en la región Mediterránea

## Agricultural intensification, biodiversity and pollination functioning in the Mediterranean region

Marian Mendoza Garcia

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*Barcelona, julio de 2018*

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Memoria presentada por Marian Mendoza García para optar
por el grado de Doctora de la Universidad de Barcelona

Programa de Doctorado de Biodiversidad

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# RESUMEN

# SÍNTESIS

La intensificación agrícola es una de las principales causas de la pérdida de biodiversidad, así como de los servicios ecosistémicos asociados. Por una parte, la intensificación agrícola ha causado cambios en la estructura y en la composición del paisaje, mediante la reducción y simplificación de los hábitats naturales, lo que ha promovido la agregación de los campos y la baja heterogeneidad espacial. A nivel de parcela, la intensificación se genera por la aplicación reiterada y profusa de pesticidas y fertilizantes químicos, el laboreo intensivo y la simplificación en las rotaciones, produciendo una baja diversidad en la comunidad vegetal. Estos cambios en la estructura del paisaje y en la intensidad de la gestión se correlacionan con el declive de los polinizadores y, por ende, con los servicios de polinización que estos proveen, tanto a los cultivos como a las especies que habitan en los hábitats naturales y seminaturales no cultivados. La agricultura ecológica es una práctica agrícola respetuosa con el medio ambiente, considerada para mitigar el declive de los polinizadores y, en consecuencia, mejorar el servicio de la polinización. En comparación con la agricultura convencional, se ha demostrado que la agricultura ecológica tiene efectos positivos sobre la riqueza y la abundancia de las comunidades vegetales, lo que a su vez puede incrementar las visitas de los polinizadores. Además, algunos cultivos, como las leguminosas y los cultivos de floración masiva (colza), que son incluidos frecuentemente en las rotaciones de cultivos, también se benefician con el incremento de los visitantes florales. A su vez, estos cultivos también pueden influir en la actividad de los insectos, debido a que proveen abundantes recompensas de polen y néctar que pueden incrementar su abundancia. Todas estas complejas interacciones, finalmente, afectan la reproducción de las plantas. A pesar de ello, los efectos de la intensificación agrícola, el tipo de cultivo y la disponibilidad de los recursos florales sobre la abundancia y composición de los visitantes florales, así como sobre la producción de frutos de especies diana todavía no son comprendidos en su totalidad.

En la presente tesis, se evaluaron los efectos de la intensificación agrícola sobre la abundancia de los visitantes florales y la producción de frutos de especies diana (Capítulo 1). A nivel de paisaje, la intensificación agrícola afectó negativamente la abundancia de los visitantes florales, aunque este efecto dependió del grupo considerado. Asimismo, se evaluó la abundancia de los visitantes florales (apoideos) y la producción de frutos en paisajes que variaron en la proporción de tierra arable bajo gestión ecológica

(Capítulo 2). A nivel de paisaje, la proporción de tierra arable bajo gestión ecológica no incrementó la abundancia de abejas (apoideos). A nivel de parcela, la agricultura ecológica tuvo un efecto positivo en la abundancia total de los visitantes florales, aunque las interacciones entre la gestión y el paisaje o la posición dentro del campo también dependieron del grupo de visitante floral. La abundancia de abejas tampoco incrementó en los márgenes aledaños a los cultivos de leguminosa, lo cual pudo ocurrir debido a una dilución de los visitantes florales causada por la abundante disponibilidad de recursos en el paisaje.

Nuestro estudio también analizó el efecto de la intensificación agrícola a nivel de paisaje y de parcela sobre la composición de la comunidad vegetal y de los visitantes florales, así como la relación entre la comunidad de visitantes florales y el “community-weighted mean” (CWM) de los atributos florales (Capítulo 3). La intensificación agrícola a nivel de paisaje se correlacionó con cambios en la composición florística de las comunidades vegetales de los márgenes de los campos y de algunos atributos florales de la comunidad (CWM). Por el contrario, en el centro de los campos la composición taxonómica de los ensamblajes de especies y el CWM de sus atributos florales respondieron, en gran medida, a las prácticas agrícolas a nivel de parcela. La composición de visitantes florales respondió a la intensificación agrícola a nivel de paisaje y a la composición vegetal en los márgenes de los campos. Además, nuestro estudio mostró que la respuesta de los visitantes florales a determinados atributos florales se mantuvo constante en ambos años de muestreo. Finalmente, los resultados señalaron que el color de la flor y la fenología de la comunidad vegetal afectaron la composición de los visitantes florales en el margen del campo, mientras que el tamaño de la flor influyó dicha composición en el centro del campo.

La intensificación agrícola a nivel de paisaje afectó negativamente la producción de frutos de la especie de polinización generalista. Sin embargo, el efecto del incremento de los recursos florales fue positivo sobre la producción de frutos (Capítulo 1). La proporción de tierra arable bajo gestión ecológica únicamente incrementó la proporción de frutos de la especie de polinización generalista, ya que no tuvo un efecto significativo sobre la especie de polinización especialista. La competencia por los visitantes florales pudo ocurrir entre las especies diana y las comunidades vegetales aledañas. A pesar de ello, los cultivos de leguminosa incrementaron la producción de frutos de ambas especies (Capítulo 2).

Por último, se evaluó el efecto de la estructura del paisaje y la presencia de cultivos de floración masiva (cultivos de colza) sobre la abundancia de abejas (apoideos) y otros visitantes florales (coleópteros, dípteros y otros himenópteros), así como sobre la producción de frutos de dos especies diana (Capítulo 4). La presencia de cultivos de colza incrementó la abundancia de las abejas, aunque esta disminuyó en paisajes complejos (alta densidad de márgenes). Por otro lado, la abundancia de otros visitantes florales dependió de la estructura del paisaje, particularmente de la ubicación de los campos de cereales. A pesar del incremento en la abundancia y diversidad de los visitantes florales, promovida por los cultivos de colza y los recursos florales, solo incrementó la producción de frutos de la especie de polinización generalista, ya que la competencia por los visitantes florales pudo afectar a la especie de polinización especialista.

Nuestros resultados resaltan la importancia de la implementación de medidas agroambientales que contemplen, por una parte, evitar la simplificación del paisaje, así como promover la agricultura ecológica, incluir cultivos que ofrezcan recursos florales (cultivos de leguminosas y de floración masiva) y conservar los elementos de vegetación natural o seminatural, como son los márgenes de los campos. Dichas medidas permitirán optimizar el servicio de polinización, procurado por un amplio y diverso conjunto de visitantes florales en los paisajes agrícolas mediterráneos.

# SUMMARY

Agricultural intensification is one of the main causes of biodiversity decline and disruption of associated ecosystem services. On the one hand, intensification at landscape scale has caused changes in the structure and composition of the landscape, through the substitution of most natural habitats with arable fields leading to large, uniformly-cropped areas, with low spatial heterogeneity. On the other hand, intensification at field scale occurs by use of a high amount of external inputs, intensive soil tillage and simplification of crop-rotational schemes, resulting in plant communities with low diversity within-fields and in neighbouring field margins. These changes in landscape structure and land-use intensity are generally correlated with the decline of wild pollinators and the services they provide to crops and wild plants. Organic farming practices are thought to mitigate pollinator decrease in agricultural landscapes and, in consequence, could improve pollination services. Compared with conventional farming, organically managed fields support higher levels of plant abundance and diversity, which in turn can attract more pollinator visits. Furthermore, some crops that are routinely included in crop rotations, such as legumes and some mass flowering crops as oilseed rape, also can benefit from the presence of flower visiting insects. In turn, these crops can influence the activity of the insects, as they constitute a highly rewarding resource of pollen and nectar that can enhance flower visitor abundance. These complex interactions can finally affect plant reproduction. Nevertheless, the effects of agricultural landscape at different levels, crop type and the availability of flower resources on the abundance and composition of flower visiting insects and the fruit set of insect-pollinated plants are not completely understood.

We evaluated the effects of agricultural land use intensity on the abundance of flower-visiting insects and on the fruit set of an insect pollinated target plant (Chapter 1). At landscape level, the percentage of arable land affected negatively the abundance of flower-visiting insects, although this effect was not consistent among the groups of flower visitors. Additionally, we evaluated the abundance of flower visitors (bees) and pollination delivery in landscapes varying in their proportion of organically managed arable land (Chapter 2). Bee abundance was not enhanced by the proportion of organically managed land at the landscape scale. At field level, we found that organic farming had a positive effect on the overall abundance of flower visitors, although the interactions between management and the

landscape or the position within the field also depended on the group of flower visitors. Bee abundance did not also increase in field margins next to legume crops, probably caused by abundant food resources that led to their dilution.

Our study also analysed compositional changes in plant and flower visitor communities in response to agricultural intensification at field and landscape levels, and the relation between the insect community and the community-weighted mean (CWM) of flower traits (Chapter 3). On the one hand, plant species composition and the CWM in field centre responded to field management, whereas in the margin depended on the percentage of arable land. On the other hand, flower visitor composition only responded to the percentage of arable land and to plant composition in the field margin. In addition, our results showed that flower visitor community response to specific flower traits was consistent among years. We also found that the composition of insect assemblages responded to the flower colour and flowering onset in the field margin, whereas in the field centre responded to the flower size.

The percentage of arable land had a negative effect on the fruit set of generalist insect pollinated plant species. However, the fruit set was benefited through the increase of availability of flower resources (Chapter 1). The proportion of organically managed land enhanced the fruit set of species of generalist pollination, whereas it did not have an effect on species of specialist pollination. Competition for pollinators could have occurred between the target species and species thriving in plant communities in the immediate vicinity. However, despite the negative effect of local flower cover, the fruit set benefited from nearby legume crops (Chapter 2).

Finally, we evaluated the abundance of bees and other flower visitors, and the fruit set of two insect-pollinated target plants on the margins of oilseed rape crops and cereal fields in landscapes varying in their landscape structure, as measured by the length of the field-margin network (Chapter 4). Our results showed that the abundance of bees was enhanced by oilseed rape crops, but decreased in complex landscapes (high density of field margin network). On the other hand, the abundance of non-bee flower visitors depended on the landscape structure, particularly on the location of cereal fields. Despite the numerous and diverse communities of flower visitors attracted by oilseed rape crops and wildflower resources, fruit set was enhanced only for the species of generalist pollination, because competition processes for flower visitors affect the species of specialist pollination.

Our results highlight the importance of developing agri-environmental schemes that prevent landscape simplification, deploy organic agriculture, include crops that offer flower resources and preserve field margins. These measures may increase the presence of a diverse community flower visitors, which in turn can help to maintain or increase fruit sets in agricultural landscapes.

# INTRODUCCIÓN

## Intensificación agrícola, biodiversidad y servicios ecosistémicos

La agricultura es la actividad humana que ocupa la mayor proporción de uso de la tierra, extendiéndose en casi un 38% de la superficie terrestre (Food and Agriculture Organization of the United Nations, 2015), y de la que depende en mayor medida la provisión de alimentos. Sin embargo, la agricultura es también la principal fuente de gases invernadero, de la contaminación agroquímica y de la degradación del suelo (Matson, Parton, Power, & Swift, 1997). Aunado a ello, se considera una de las principales causas de la pérdida de biodiversidad (Matson et al., 1997; Tilman et al., 2001), así como de los servicios ecosistémicos asociados (Kleijn et al., 2009). En particular, la intensificación agrícola se correlaciona con el declive de los polinizadores y, por ende, con los servicios de polinización que estos proveen, tanto a los cultivos como a las especies que habitan en los hábitats naturales y seminaturales no cultivados (Biesmeijer et al., 2006; Potts et al., 2010; Steffan-Dewenter, Potts, Packer, & Ghazoul, 2005).

La intensificación agrícola ha generado cambios tanto a nivel de campo como de paisaje en los sistemas agrícolas (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). A nivel de campo, se produce principalmente a través de la gestión de los cultivos. El modelo de gestión dominante ha sido denominado agricultura convencional, la cual está caracterizada por el laboreo intensivo, la simplificación en las rotaciones, así como la aplicación reiterada y profusa de pesticidas (fundamentalmente herbicidas e insecticidas) y fertilizantes químicos. Además, la especialización en la producción y la consecuente reducción de los tipos de cultivos ha promovido una baja diversidad cultivada (Matson et al., 1997), tanto en el tiempo como en el espacio. Por otro lado, la intensificación ha impulsado la concentración parcelaria, que genera la agregación de los campos y, por lo tanto, un incremento en su tamaño (Kleijn & Sutherland, 2003). Como consecuencia, todos los hábitats asociados a los campos, como los que constituyen los márgenes de los mismos, se reducen y simplifican. Esta reducción y fragmentación de los hábitats naturales y seminaturales, en conjunto con la escasez de variabilidad espacial y temporal en los usos del suelo, finalmente causan la homogeneización del paisaje (Tscharntke et al., 2005).

En España, se destina alrededor de un 34% de la superficie terrestre a las tierras arables, de las cuales un 41,2% (7.011.097 ha) son cultivos herbáceos extensivos de secano (Fig. 1; Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente, 2016). Estos cultivos de secano están ampliamente distribuidos en todo el territorio, por lo que su manejo, en términos de la producción del cultivo y la conservación de los recursos naturales, resulta fundamental en los sistemas agrícolas. En particular, en Cataluña los cultivos herbáceos de secano ocupan alrededor de un 38% (317.294 ha) del total destinado a las tierras arables (835.012 ha) (Fig.1; Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente, 2016). En general, la agricultura de secano se caracteriza por no recibir ningún tipo de irrigación externa, por lo que dependen del agua obtenida de forma natural. En los paisajes mediterráneos con cultivos de secano, los bajos niveles de precipitación son el principal factor que afecta su rendimiento (Armengot, José-María, Chamorro, & Sans, 2013). Sin embargo, la biodiversidad asociada a estos paisajes es afectada mayormente por las técnicas de manejo. Es decir, el uso recurrente de herbicidas y la reducción de las áreas no cultivadas, como son los márgenes de los campos, han causado un declive en la diversidad vegetal (Bassa, Chamorro, José-María, Blanco-Moreno, & Sans, 2012). A diferencia de otros paisajes agrícolas europeos, los sistemas arables mediterráneos están concentrados en llanuras no muy extensas delimitadas por una compleja red de comunidades

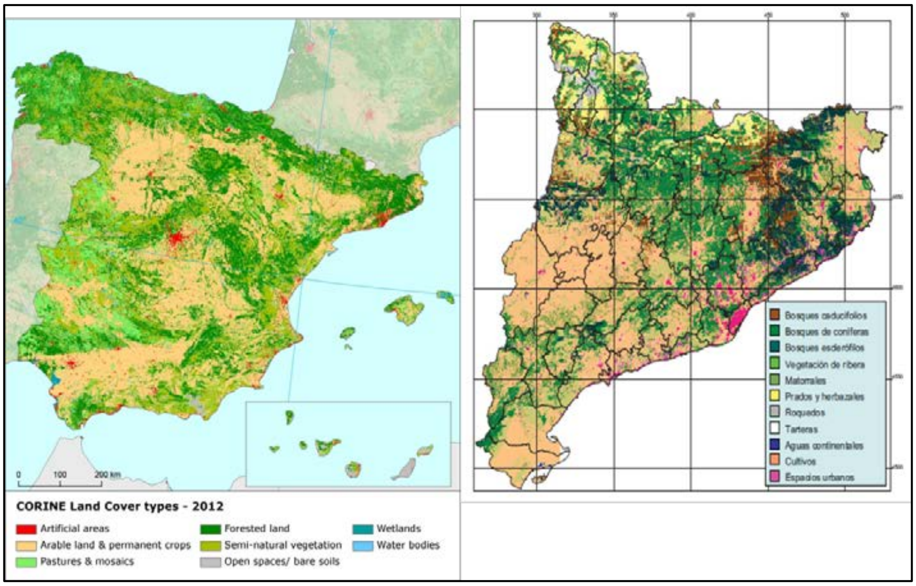

**Figura 1.** Distribución de los principales tipos de cubiertas del suelo en España (panel izquierdo; modificado de Comisión Europea, 2017) y Cataluña (panel derecho; tomado de Ibàñez i Martí & Burriel Moreno, 2010).

vegetales, tales como pastos anuales y perennes, matorrales y bosques. En este sentido, la pérdida de diversidad vegetal puede causar una disrupción de los procesos ecosistémicos, como es la polinización, afectando de esta manera la reproducción de las plantas. En consecuencia, otros componentes de los agroecosistemas también pueden verse afectados.

La proporción de cultivos herbáceos extensivos se ha utilizado frecuentemente como un indicador de la intensificación del paisaje. Esta variable se puede correlacionar con otros atributos del paisaje agrícola como, por ejemplo, la diversidad y la fragmentación de los hábitats y la densidad de márgenes. Sin embargo, en los paisajes mediterráneos estudiados, los cultivos herbáceos extensivos constituyen el uso del suelo mayoritario, por lo que la proporción de tierra arable (PAL, por sus siglas en inglés) puede ser utilizada como un indicador de la complejidad del paisaje, en tanto que es complementario al porcentaje de tierra con hábitats naturales y seminaturales. En los sistemas agrícolas mediterráneos se ha demostrado que la complejidad del paisaje afecta la riqueza y la composición de la flora, y que además es importante en los márgenes y en los bordes, pero que su importancia es mucho menor en el interior de los campos (Armengot, José-María, Blanco-Moreno, Romero-Puente, & Sans, 2011; José-María, Armengot, Blanco-Moreno, Bassa, & Sans, 2010). Sin embargo, la literatura relacionada con el efecto de la complejidad del paisaje sobre la abundancia de los visitantes florales y la provisión de la polinización en los paisajes agrícolas continúa siendo insuficiente. A partir de este conocimiento, se podrían desarrollar esquemas de gestión que permitan conservar e incentivar la biodiversidad, así como restaurar las funciones ecosistémicas, con el fin de mejorar la sostenibilidad en los sistemas agrícolas.

### Los esquemas agroambientales como instrumento para la restauración del paisaje

En Europa se han adoptado diversas políticas agrarias con el objetivo de contrarrestar y reducir los efectos negativos que causan las prácticas agrícolas modernas sobre el medio ambiente (Kleijn & Sutherland, 2003). Entre las políticas más importantes implementadas para preservar el medio ambiente y mitigar la pérdida de biodiversidad se cuentan los esquemas agroambientales. Todos los países que conforman la Unión Europea están comprometidos a desarrollar e implementar dichos esquemas, impulsándolos mediante incentivos monetarios destinados a los agricultores (Kleijn & Sutherland, 2003). La agricultura ecológica es considerada una práctica agrícola respetuosa con el medio ambiente y forma parte de los esquemas agroambientales [Reglamento (CE) Nº 834/2007]. Habitualmente se contrapone a un modelo más o menos estereotipado de la agricultura, que, aunque heterogéneo, comprende el conjunto de prácticas más extendido, por lo que se lo denomina agricultura convencional. La agricultura ecológica se diferencia de la agricultura convencional por la rotación de cultivos, la prohibición de fertilizantes químicos y de pesticidas sintéticos, así como por la incorporación de abonos verdes y abonos de origen animal a las tierras de cultivo (Reganold & Wachter, 2016). La agricultura ecológica favorece, a través de la compleja red de interacciones bióticas que se promueven mediante las estrategias de manejo, la fertilidad del suelo, el incremento del uso de recursos internos, la conservación de la biodiversidad y la producción de alimentos de calidad para el consumo humano y animal (Fig. 2; Stockdale et al., 2001).

Uno de los objetivos más relevantes planteados por la Comisión Europea, a través del "Plan de acción para el futuro de la producción ecológica de la Unión Europea", es la expansión de la agricultura ecológica. En la actualidad, se estima que la agricultura ecológica abarca alrededor del

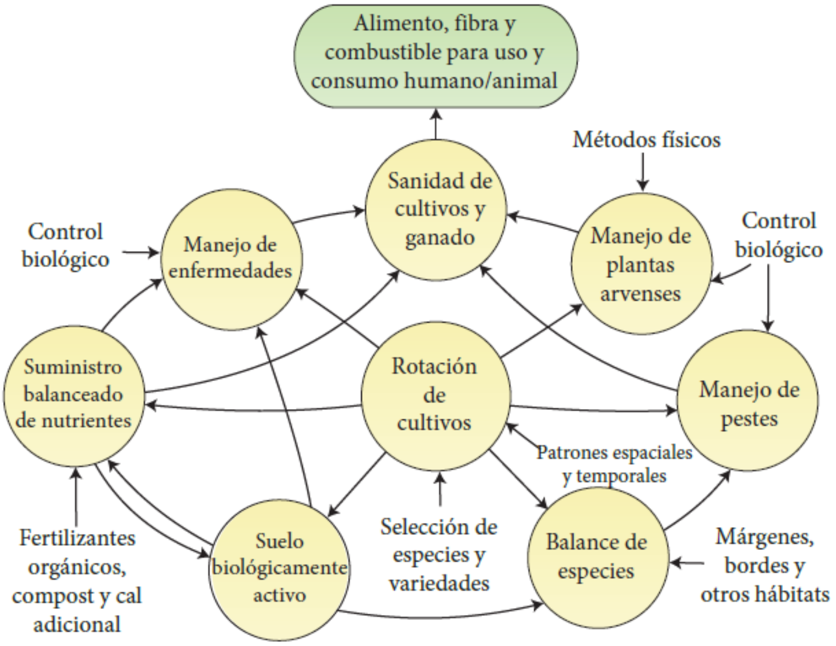

**Figura 2.** Diagrama del funcionamiento de las bases y estrategias de manejo en la agricultura ecológica (modificado de Reganold & Wachter, 2016).

1% de la superficie agrícola mundial y, en particular, en España ocupa el 7,9% (Willer & Lernoud, 2017). Cataluña es la tercera Comunidad Autónoma con el mayor porcentaje de agricultura ecológica (8,52% en el año 2016), a la que se destinan aproximadamente 171.937 ha (CCPAE, 2016). En la última década, la superficie agrícola ecológica de Cataluña se ha triplicado y, con ello, se ha incrementado la producción de cultivos ecológicos como los cereales y las leguminosas. Sin embargo, el objetivo propuesto por la Comisión Europea no es exclusivamente impulsar la producción, sino que también pueda actuar como medida para la conservación de la biodiversidad en los sistemas agrícolas.

Numerosos estudios han demostrado los efectos positivos de la agricultura ecológica sobre la riqueza y la abundancia de la flora que coloniza los campos y los hábitats adyacentes, en comparación con la agricultura convencional. La alta concentración de recursos florales en los campos ecológicos estimula la abundancia y la diversidad de polinizadores (Holzschuh, Steffan-Dewenter, & Tscharntke, 2008; Rundlöf, Nilsson, & Smith, 2008). Asimismo, se ha demostrado que los beneficios de la agricultura ecológica dependen de la heterogeneidad del paisaje (Batáry, Báldi, Kleijn, & Tscharntke, 2011; Rundlöf & Smith, 2006). Por ejemplo, Holzschuh et al. (2007) evaluaron el efecto de las prácticas ecológicas sobre la diversidad de abejas, y mostraron que el beneficio aportado por estas prácticas es más importante en paisajes homogéneos, con un alto porcentaje de tierra agrícola, que en aquellos más heterogéneos. En este sentido, determinadas medidas agroambientales pueden resultar más beneficiosas en paisajes simples, con una baja proporción de hábitats seminaturales, que en paisajes complejos, con una alta proporción de dichos hábitats (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011).

En muchos paisajes agrícolas, la producción está concentrada en cultivos que no requieren de la actividad polinizadora de los insectos, como son los cereales, lo que puede comprometer el servicio ecosistémico de la polinización en los hábitats circundantes o en aquellos cultivos minoritarios que la requieran para su desarrollo. En este contexto, la agricultura ecológica puede beneficiar a los polinizadores a través de la provisión de recursos florales, ya que la baja intensidad de la gestión permite que, incluso los cultivos de cereales, alberguen una flora más diversa y con numerosas especies entomófilas (Chamorro, Masalles, & Sans, 2016).

La agricultura ecológica también contribuye con el incremento de la diversidad espacio-temporal de los paisajes agrícolas a través de la rotación de cultivos. A pesar de que las rotaciones están orientadas principalmente hacia el rendimiento y la estabilidad de los cultivos (Seufert & Ramankutty, 2017), algunos de los cultivos que se intercalan en las rotaciones de zonas cerealistas proveen altas concentraciones de recursos florales que pueden incrementar la abundancia de los polinizadores (Klein et al., 2007). Algunos de los tipos de cultivos que se incluyen en las rotaciones son leguminosas, por su alta capacidad fijadora de nitrógeno, y cultivos de floración masiva, como puede ser la colza (*Brassica napus*). Esta última, cuyo cultivo se ha extendido recientemente por la actual demanda de aceite y biocombustible, ofrece cuantiosas recompensas de polen y néctar como atractivo para los polinizadores (Morandin & Winston, 2005). Diversos estudios han demostrado el efecto positivo que tienen los cultivos de floración masiva sobre los polinizadores, especialmente sobre las abejas (Holzschuh, Dormann, Tscharntke, & Steffan-Dewenter, 2013; Westphal, Steffan-Dewenter, & Tscharntke, 2009). Sin embargo, todos ellos también coinciden en que los beneficios que ofrecen estos cultivos dependen de la presencia de hábitats naturales y seminaturales en los paisajes agrícolas. A pesar de ello, los cultivos de floración masiva también pueden influenciar los patrones de los polinizadores en los hábitats circundantes (Montero-Castaño, Ortiz-Sánchez, & Vilà, 2016). La mayoría de estos estudios han sido realizados en paisajes centro-europeos; no obstante, existe poca información acerca del efecto que pueden tener los cultivos de floración masiva sobre la biodiversidad en paisajes cerealistas mediterráneos altamente intensificados.

Otro factor que puede afectar la magnitud de los efectos de la agricultura ecológica sobre la biodiversidad es la escala en la que se implementen estas prácticas (Bengtsson, Ahnström, & Weibull, 2005). Por ejemplo, la agregación de campos ecológicos en el paisaje puede incrementar la riqueza y abundancia de los polinizadores (Holzschuh et al., 2008). Por estas razones son fundamentales la inclusión y la evaluación de los efectos a múltiples niveles espaciales para comprender los patrones de la biodiversidad en los sistemas agrícolas, lo que permitirá implementar adecuadamente los esquemas agroambientales.

## La comunidad vegetal, sus atributos funcionales y los visitantes florales en los sistemas agrícolas

Los cambios que se producen en la estructura del paisaje por la intensificación agrícola afectan tanto la composición florística de los hábitats como la composición de los visitantes florales, modificando a su vez la interacción planta-polinizador a nivel de individuo, población y comunidad (Kremen et al., 2007). Aunque se suele considerar la interacción entre plantas y polinizadores como un proceso más o menos unívoco, el contexto en el que se desarrollan estas interacciones puede ser determinante. Por ejemplo, los cambios en la estructura del paisaje pueden causar una dilución o concentración de los visitantes florales, lo cual finalmente altera su interacción con la comunidad vegetal (Montero-Castaño et al., 2016; Tscharntke et al., 2012). Además, la comunidad vegetal circundante puede afectar las interacciones entre cualquier especie de planta y su conjunto de visitantes florales, reduciendo la tasa de visitas mediante competencia

(Pleasants, 1981) o incrementándola a través del proceso de facilitación (Moeller, 2004).

Estos cambios en la comunidad vegetal, además de generar posibles repercusiones en la abundancia de los recursos florales y posible competencia por los visitantes florales, pueden comportar cambios en el conjunto de los visitantes florales (Kremen et al., 2007). Dichos cambios, con frecuencia, están mediados por ciertas cualidades del arreglo floral. En los últimos años, se han evaluado los cambios en las comunidades vegetales, mediante el uso de los atributos funcionales, en relación con las prácticas agrícolas y las condiciones ambientales, así como los efectos de la comunidad funcional resultante sobre los servicios ecosistémicos prestados (Wood et al., 2015). Los atributos funcionales se definen como características fisiológicas, morfológicas o fenotípicas de las especies (Violle et al., 2007). Estos atributos varían entre especies, y las especies difieren en sus abundancias, por lo que el funcionamiento de la comunidad puede estar determinado por la distribución de estos atributos. Una manera de caracterizar la estructura funcional de las comunidades es promediando el valor del rasgo de las diferentes especies ("community-weighted mean" [CWM], Violle et al., 2007).

Los atributos funcionales proporcionan información sobre el papel que desempeñan las especies en la comunidad y de su respuesta ante las variaciones ambientales (Cornelissen et al., 2003), lo que permite valorar el impacto que provocan dichos cambios en la comunidad sobre los procesos ecosistémicos (Garnier et al., 2004). Para evaluar el impacto de la intensificación y las prácticas agrícolas, se ha propuesto un marco conceptual que evalúa la respuesta de las comunidades vegetales a los cambios y cómo estos afectan las funciones y los servicios ecosistémicos (Fig. 3; Esquema respuesta-efecto; Lavorel & Garnier, 2002; Suding et al., 2008). Por ejemplo, se ha demostrado que la diversidad de especies vegetales y algunos de sus

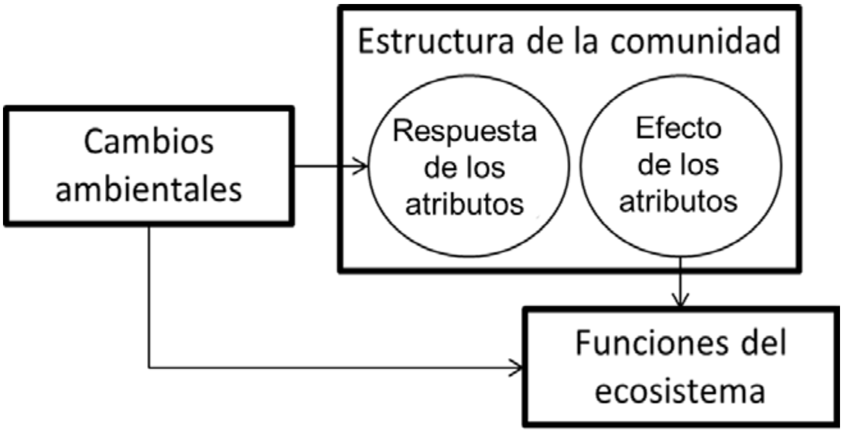

**Figura 3.** Marco conceptual que relaciona la respuesta de los atributos a los cambios ambientales y los efectos de estos cambios en el funcionamiento de los ecosistemas (modificado de Suding et al., 2008).

atributos funcionales (p. ej. formas de vida, área específica foliar) son afectadas por la intensificación agrícola en paisajes mediterráneos (Guerrero, Carmona, Morales, Oñate, & Peco, 2014; José-María, Blanco-Moreno, Armengot, & Sans, 2011; Solé-Senan, Juárez-Escario, Robleño, Conesa, & Recasens, 2017). Sin embargo, es poco conocido el efecto que tienen los cambios estructurales de las comunidades vegetales sobre la comunidad de visitantes florales y sus consecuencias sobre los servicios ecosistémicos que proveen.

En particular, los atributos visuales de las flores (p. ej. morfología, color, tamaño, recompensas florales, fenología) pueden determinar la interacción entre la comunidad vegetal y la comunidad de visitantes florales. Estos conjuntos de atributos florales, que determinan los denominados síndromes de polinización, son esenciales en el proceso de atracción, y pueden ser asociados con visitantes florales específicos (Faegri & Van Der Pijl, 1979). La mayoría de estudios que relacionan los atributos florales con la comunidad de visitantes florales se centran en las abejas (Fornoff et al., 2017), las cuales son consideradas los polinizadores más comunes y de mayor valor económico (McGregor, 1976). No obstante, otros visitantes florales también pueden contribuir con la provisión de los servicios de polinización en los paisajes agrícolas (Bosch, Retana, & Cerdà, 1997). Se ha demostrado que la tasa de visitas de otros visitantes florales, en comparación con las abejas, puede compensar su baja contribución en la deposición de polen (Rader et al., 2016). Además, los recursos florales que ofrecen los paisajes agrícolas también benefician a otros visitantes florales (Grass et al., 2016). Por lo tanto, la incorporación de otros grupos, tales como coleópteros y dípteros, en el estudio de la comunidad de visitantes florales permite ampliar nuestro conocimiento acerca de la importancia de la biodiversidad en la provisión de servicios ecosistémicos en los paisajes agrícolas.

## La polinización como servicio ecosistémico

Los cambios que se producen en la comunidad de visitantes florales, tanto en la abundancia como en la diversidad, pueden afectar la reproducción de las plantas (Potts et al., 2010). En particular, el declive en los servicios de polinización puede afectar negativamente a las plantas de polinización cruzada (Aguilar, Ashworth, Galetto, & Aizen, 2006), siendo más vulnerables las especies de polinización especializada que aquellas de polinización generalista (Biesmeijer et al., 2006).

Un amplio porcentaje de estudios han evaluado el potencial servicio de polinización a través de la abundancia y riqueza de los polinizadores, o mediante la interacción entre plantas y polinizadores. Sin embargo, la producción de frutos (*fruit set*) resulta un enfoque directo para evaluar el servicio de la polinización. Para ello, se emplean plantas diana o fitómetros, que se caracterizan por ser auto-incompatibles y polinizadas por insectos (Woodcock, Pekkola, Dawson, Gadallah, & Kevan, 2014). La auto-incompatibilidad en estas plantas requiere la interacción con insectos, por lo que la producción de frutos y semillas permite evaluar el éxito de la polinización (Ghazoul, 2006). Además, el uso de plantas diana o fitómetros permite evaluar este éxito de la polinización bajo diferentes condiciones ambientales (Woodcock et al., 2014). Esta metodología ha sido utilizada en diversos estudios para evaluar el efecto de las prácticas agrícolas, principalmente aquellas asociadas a los sistemas ecológicos, sobre la polinización (Brittain, Bommarco, Vighi, Settele, & Potts, 2010; Hardman, Norris, Nevard, Hughes, & Potts, 2016; Power & Stout, 2011). A pesar de que el uso de esta metodología se ha ampliado en los últimos años, todos los estudios se han enfocado en la evaluación de especies de polinización generalista, sin considerar las diferencias existentes en el grado de especialización en las interacciones entre las flores y los visitantes florales (Johnson & Steiner, 2000). Mediante la inclusión de diferentes síndromes de polinización, se puede evaluar la dependencia de los efectos, que son causados por los cambios en el paisaje, a la composición del conjunto de visitantes florales de cada especie de planta.

En los últimos años, se han dedicado numerosos esfuerzos para intentar comprender las causas de la pérdida de biodiversidad en los sistemas agrícolas, no solo por su valor intrínseco de conservación y las repercusiones que pudiera implicar para el funcionamiento de los hábitats naturales, sino por la dependencia de muchos cultivos con respecto a los visitantes florales (Kremen, Williams, & Thorp, 2002). Por estas razones resulta fundamental, en el contexto actual de los sistemas agrícolas, el estudio a diferentes niveles de los efectos de la intensificación agrícola sobre los visitantes florales y sobre la polinización. Asimismo, es necesario evaluar los efectos que tienen las diferentes facetas de la gestión agrícola a todos los niveles, desde el de paisaje al de campo, y sus consecuencias directas e indirectas sobre la biodiversidad en los sistemas agrícolas, particularmente en los paisajes cerealistas mediterráneos.

# OBJETIVOS

El objetivo general de esta tesis es el estudio del funcionamiento de la polinización en los paisajes agrícolas mediterráneos dominados por los cultivos herbáceos extensivos. Para la consecución de este objetivo general, se evaluó la abundancia y la composición de los principales grupos de visitantes florales y la producción de frutos de especies diana con diferentes grados de especialización en la polinización (generalista *vs*. especialista). La experimentación fue realizada en paisajes estructuralmente contrastados y bajo diferentes sistemas de gestión y tipos de cultivos.

A continuación, se detallan los objetivos específicos de cada uno de los capítulos que conforman la tesis doctoral:

**Capítulo 1:**

- Estudiar el efecto de la intensificación agrícola a nivel de paisaje (PAL), de la intensidad de gestión (ecológica *vs*. convencional), del tipo de cultivo (cereal *vs*. leguminosa) y de la distancia al margen (margen *vs*. centro), sobre la abundancia de los visitantes florales (apoideos, coleópteros y dípteros) y sobre la producción de frutos de la especie diana *Raphanus sativus*.

- Determinar el efecto de los recursos florales localizados en el margen y en el centro de campos sobre la abundancia de los visitantes florales y sobre la producción de frutos de la especie diana *Raphanus sativus*.

**Capítulo 2:**

- Estudiar el efecto de la proporción de tierra arable bajo gestión ecológica a nivel de paisaje sobre la abundancia de abejas (apoideos) y sobre la producción de frutos de las especies diana *Raphanus sativus* y *Onobrychis viciifolia* con diferente grado de especialización en su interacción con los polinizadores.

- Evaluar el efecto de la intensidad de gestión (ecológica *vs*. convencional) y del tipo de cultivo (cereal *vs*. leguminosa), así como el efecto de los recursos florales localizados en los márgenes sobre la abundancia de abejas (apoideos) y la producción de frutos de las especies diana *Raphanus sativus* y *Onobrychis viciifolia*.

**Capítulo 3:**

- Evaluar los cambios en la composición florística, sus atributos florales y la composición de familias de los visitantes florales (apoideos, coleópteros y dípteros) de los márgenes de los cultivos herbáceos extensivos de secano en relación con la intensificación agrícola (PAL) a nivel de paisaje, la intensidad de gestión (ecológico *vs*. convencional), el tipo de cultivo (cereal *vs*. leguminosa) y la distancia al margen del campo (centro *vs*. margen).

- Estudiar la relación entre la composición florística y la composición de familias de los visitantes florales (apoideos, coleópteros y dípteros), así como la relación entre la comunidad de visitantes florales y los atributos florales de la comunidad vegetal.

**Capítulo 4:**

- Analizar el efecto de la estructura del paisaje (densidad de márgenes) y de la presencia de cultivos de floración masiva (cultivo de colza) sobre la abundancia de abejas (apoideos) y otros visitantes florales (coleópteros, dípteros y otros himenópteros), así como sobre la producción de frutos de las especies diana *Raphanus sativus* y *Onobrychis viciifolia* en paisajes caracterizados por un alto porcentaje de tierra agrícola.

- Analizar el efecto de los recursos florales a nivel de parcela sobre la abundancia de abejas (apoideos) y otros visitantes florales (coleópteros, dípteros y otros himenópteros), así como sobre la producción de frutos de las especies diana *Raphanus sativus* y *Onobrychis viciifolia*.

# METODOLOGÍA

En cada uno de los capítulos se exponen todos los materiales y métodos de forma detallada y sus respectivas referencias. Sin embargo, a continuación se describe de manera abreviada la metodología general utilizada en esta tesis doctoral.

## Área de estudio

Los estudios se llevaron a cabo durante los años 2013 (Capítulos 1 y 3), 2014 (Capítulo 4) y 2015 (Capítulos 2 y 3) en Cataluña, al noreste de España (Fig. 4). La zona de estudio, concentrada principalmente en la Depresión Central Catalana, presenta un clima mediterráneo con una precipitación media anual que oscila entre los 350 y los 850 mm, y una temperatura media anual que varía entre los 11 y los 14ºC. Las localidades de muestreo se ubicaron en las comarcas de Anoia, Bages, Berguedà, Moianès, Osona, Segarra, Solsonès y Vallès Oriental.

Para el diseño experimental del capítulo 1, se seleccionaron 10 localidades que diferían en la complejidad del paisaje, obteniendo un gradiente en el uso de tierra agrícola. Para ello, se midió el porcentaje de tierra arable (PAL, por sus siglas en inglés), en áreas circulares de 1 km de radio. Los valores del PAL variaron entre el 20%, que representaron los paisajes complejos, y el 80%, que representaron los paisajes simples. En cada localidad, se seleccionaron campos que diferían en el nivel de intensidad de manejo (ecológico *vs.* convencional) y en el tipo de cultivo (cereal *vs.* leguminosa). En los campos de cereales, se evaluaron dos posiciones: centro y margen, mientras que en los campos de leguminosas únicamente se evaluó el centro (Fig. 5a). Para el diseño experimental del capítulo 2, se seleccionaron cinco localidades que diferían en la proporción de tierra arable bajo manejo ecológico (POL), estimada como la relación entre el área agrícola bajo manejo ecológico respecto al área de tierra arable.

Dicha proporción fue calculada en áreas circulares de 500 m de radio, y varió entre 0,2 y 79,6%. En cada localidad, se seleccionaron campos con diferente manejo (ecológico *vs.* convencional) y tipo de cultivo (cereal *vs.* leguminosa), en los que se muestreó el margen del campo (Fig. 5b). El diseño experimental del capítulo 3 corresponde con lo expuesto para los capítulos 1 y 2 (Fig. 5a y 5b), con la variante de que en ambos casos el PAL se calculó a una escala común de 500 m de radio. Finalmente, para el diseño experimental del capítulo 4, se seleccionaron 21 márgenes entre campos de colza (cultivo de floración masiva) y campos de cereales, y 21 márgenes entre campos de cereales, en un área con un PAL mayor del 75% (Fig. 5c). Se evaluó la estructura del paisaje mediante la densidad de hábitats no cultivados en áreas circulares de 500 m de radio; la suma total de estos elementos lineares del paisaje varió entre 6,64 y 28,52 km.

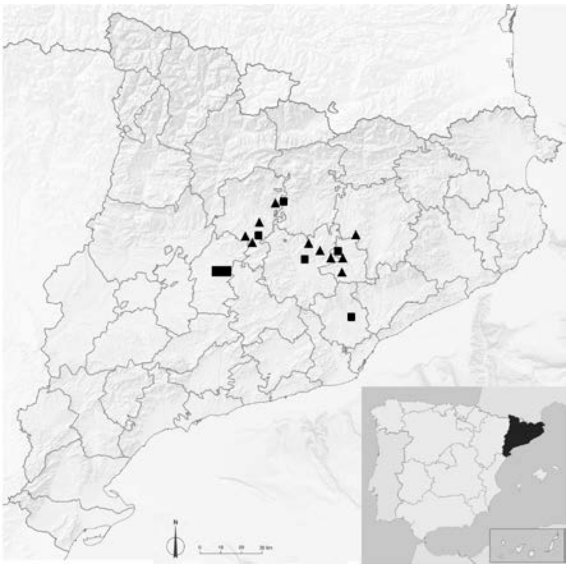

**Figura 4.** Ubicación de las localidades muestreadas en cada diseño experimental en Cataluña, España. Las localidades seleccionadas en el año 2013 están simbolizadas por triángulos, las del año 2014 por un rectángulo y las del año 2015 por cuadrados (Modificado del ICGC, 2015).

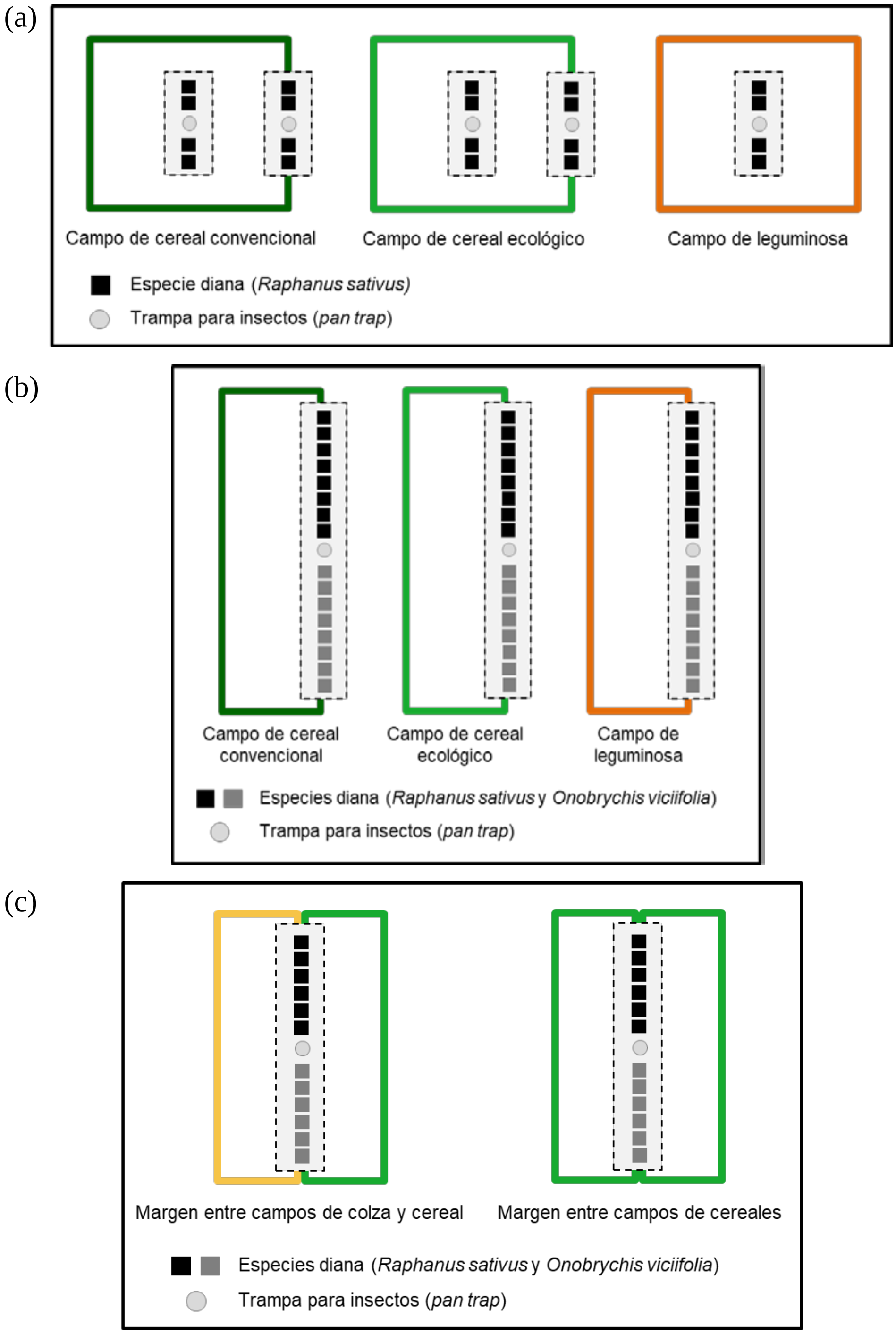

**Figura 5.** Esquema de cada diseño experimental: (a) Capítulos 1 y 3, (b) Capítulos 2 y 3, y (c) Capítulo 4.

### Recursos florales

En los campos seleccionados en cada año se evaluó la riqueza y la abundancia de las especies en flor (Fig. 6). Solo fueron consideradas aquellas especies polinizadas por insectos. Para ello, se realizaron transectos paralelos al margen en el centro (Capítulos 1 y 3), margen y borde de los campos (Capítulos 1-4). Cada muestreo se realizó una vez por semana durante cinco o seis semanas, y se contabilizó el número de flores abiertas o la cobertura de las plantas en flor en el transecto, según el diseño experimental. En el caso de la cobertura, esta fue estimada visualmente. Todas las plantas contabilizadas en los transectos fueron identificadas a nivel de especie. La nomenclatura de las especies sigue de Bolòs et al. (2005).

### Visitantes florales

Para evaluar la abundancia de los visitantes florales en cada muestreo, se utilizaron los platos-trampa (*pan traps*), localizados en el centro (Capítulos 1 y 3) y en el margen (Capítulos 1-4) de cada campo seleccionado. Estas trampas están compuestas por tres recipientes (500 mL, 160 mm diámetro) pintados de color azul, amarillo y blanco, con un esmalte sintético que refleja la luz ultravioleta (Fig. 7). Las trampas fueron colocadas 1 m por encima del suelo y separadas 1 m de cada grupo de plantas diana, y permanecieron activas durante un período de 12 o 24 horas (esta diferencia en exposición apenas afecta el volumen de capturas, ya que estas trampas son efectivas para visitantes florales diurnos). Los recipientes que componen las trampas fueron llenados con agua y una pequeña cantidad de jabón, para reducir la tensión superficial. Los muestreos se realizaron en días soleados bajo condiciones favorables de temperatura (>18 °C) y de baja velocidad del viento, coincidiendo con los muestreos de los recursos florales. Los especímenes colectados fueron almacenados en alcohol etílico al 70% y, posteriormente, identificados a nivel de familia (únicamente himenópteros, coleópteros y dípteros).

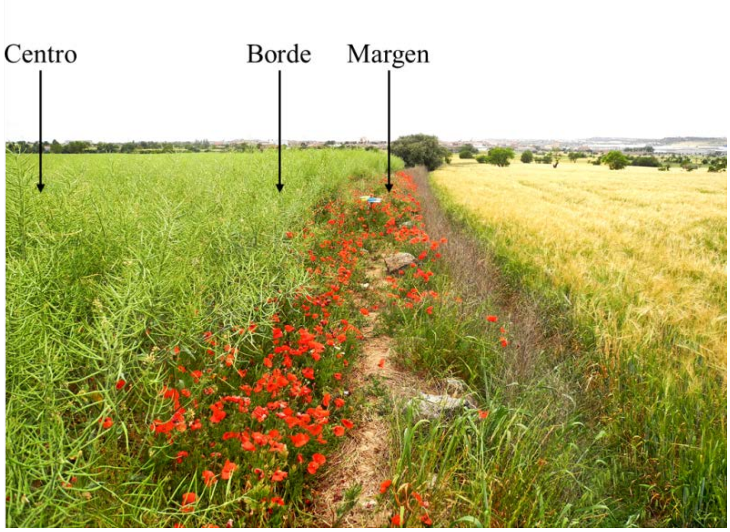

**Figura 6**. Foto de detalle de los recursos florales, en donde se señala el centro, el borde y el margen del campo.

**Figura 7.** Fotos de detalle de los platos-trampa, empleados para la captura de los visitantes florales.

### Especies diana y producción de frutos

Se seleccionaron *Raphanus sativus* L. (Brassicaceae) y *Onobrychis viciifolia* Scop. (Fabaceae) como especies diana, para evaluar la producción de frutos. *Raphanus sativus* es una planta anual que produce numerosas flores actinomorfas de color blanco o blanco-rosáceo, dispuestas en inflorescencias racemosas. Es una especie autoincompatible (Young & Stanton, 1990) y visitada por diversos tipos de polinizadores, tales como abejas, abejorros, abejas silvestres, sírfidos y mariposas (Albrecht, Duelli, Müller, Kleijn, & Schmid, 2007; Steffan-Dewenter & Tscharntke, 1999). *Onobrychis viciifolia* es una especie perenne que produce numerosas flores papilionadas de color rosado (Kells, 2001). Se caracteriza por presentar polinización entomófila obligada (Hanley et al., 2008), particularmente por abejas, abejorros y abejas silvestres (Hayot Carbonero, Mueller-Harvey, Brown, & Smith, 2011). De acuerdo con la morfología que presentan las flores, se clasificaron como especies con diferentes grados de especialización en la polinización, *R. sativus* como generalista y *O. viciifolia* como especialista (Fig. 8).

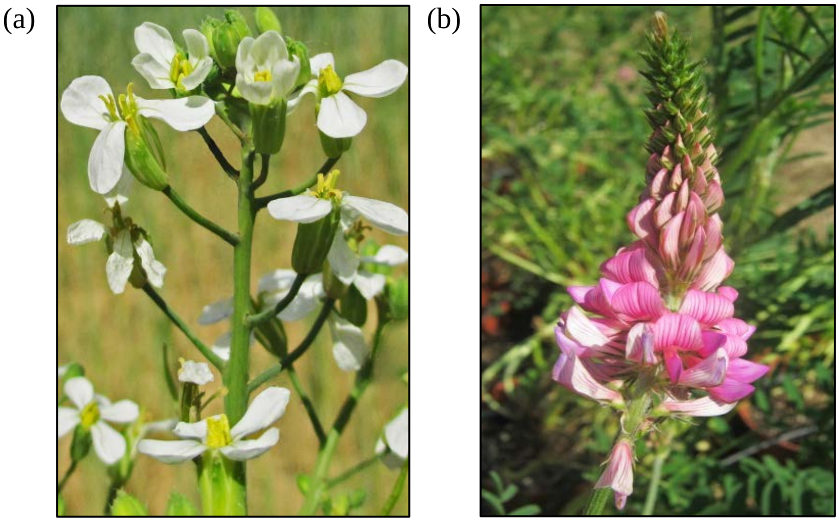

**Figura 8**. Fotos de detalle de las especies diana en floración: (a) *Raphanus sativus* y (b) *Onobrychis viciifolia*.

Para la evaluación de la producción de frutos, se sembraron semillas de cada especie en macetas de 5 L con suelo comercial (mezcla de turba, vermiculita y arcilla). Las macetas fueron colocadas en espacios abiertos en los Campos Experimentales de la Universidad de Barcelona, bajo condiciones controladas de riego. Previo al inicio de la floración, los individuos de cada especie diana fueron trasladados a los campos seleccionados, agrupados por especies y colocados a cada lado de los platos-trampa. En el diseño experimental del Capítulo 1 se utilizaron cuatro individuos de la especie diana *R. sativus* por campo y posición, para el Capítulo 2 se utilizaron ocho individuos de cada especie diana (*R. sativus* y *O. viciifolia*) por campo, y para el Capítulo 4 se utilizaron seis individuos de cada especie diana (*R. sativus* y *O. viciifolia*) por margen. Una vez concluido el período experimental (cinco o seis semanas entre los meses de abril y junio), los individuos fueron trasladados de vuelta a los invernaderos en los Campos Experimentales para evitar el contacto de las plantas con cualquier potencial polinizador. Todos los individuos se mantuvieron bajo riego periódico durante dos semanas para permitir el desarrollo de los frutos. Asimismo, durante dicho período se eliminaron los brotes florales, para evitar la sobreestimación de flores no polinizadas durante el período experimental. Finalmente, para calcular la producción de frutos se contabilizaron todos los frutos bien desarrollados y el número de flores que no fueron polinizadas.

# CAPÍTULOS

# CAPÍTULO 1

## Agricultural landscape structure and field management have contrasting effects on the community of flower visiting insects and on the fruit set of target plants

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*En fase de preparación para su envío a Journal of Applied Ecology*

## SUMMARY

1. Management intensification at different levels is one of the main causes of biodiversity decline in agricultural landscapes. Organic farming, as well as increasing availability of flower resources in the landscape, is proposed to counteract these negative effects on the community of flower visitors in agroecosystems. However, the effects of these environmental measures on the ensemble of flower visiting insects, and on the delivery of pollination services, are not fully understood.

2. We selected fields with different level of management intensity (organic *vs.* conventional) and crop type (cereal *vs*. legume) in ten localities across a gradient in agricultural land use (percentage of arable land, PAL). In each field, we placed pan traps and a set of insect pollinated target plant species of generalist pollination (*Raphanus sativus*). We analysed the effect of PAL, management, position and crop type and the effects of availability of flower resources on flower visitor abundance and on the fruit set of the target plant.

3. PAL affected negatively the abundance of flower-visiting insects, although this effect was not consistent among the groups of flower visitors (positive for Apoidea and Coleoptera). Field margins always hosted higher abundances than centres. Organic farming at field level had a positive effect on the overall abundance of flower visitors; moreover, it smoothed the effects of landscape and position within the field. The effect of legumes was not significant on the abundance of flower visitors, except for flower-visiting beetles.

4. PAL had a negative effect on the fruit set of the target plant. The fruit set was benefited through the increase of availability of flower resources in organic crops, crop margins and in legume crops.

5. *Synthesis and applications.* Flower visitor abundance and fruit set were strongly affected by PAL and flower resources, suggesting that the prevention of landscape simplification, the promotion of organic farming, the conservation of field margins and the increment of flower resources at the field level may enhance the presence of a diverse community flower visitors in agricultural landscapes, which in turn can help to the maintenance of pollination services.

**Keywords:** Agricultural intensification, agroecosystems, flower resources, flower visitors, pollination services, organic farming, field margins

# INTRODUCTION

Flower-visiting insects have undergone recent declines (Biesmeijer et al., 2006; Garibaldi, Aizen, Cunningham, & Klein, 2009; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005), which have raised academic and public concern about cascading effects on pollination delivery (Andersson, Rundlöf, & Smith, 2012; Kremen, Williams, & Thorp, 2002; Pires et al., 2014; although see Kleijn et al., 2015) with potential enormous economic consequences (Gallai, Salles, Settele, & Vaissière, 2009; Vanbergen et al., 2013). Agricultural intensification is one of the major causes for biodiversity loss in agricultural landscapes (Kleijn et al., 2009; Krebs, Wilson, Bradbury, & Siriwardena, 1999) and thus it is sensible to find management options that reconcile production with biodiversity conservation. However, agricultural intensification is compounded by several processes acting at different levels. At landscape level, it is the result of the suppression and degradation of natural and seminatural habitats, as well as reducing crop diversity and crop rotation simplification. At field level, agricultural intensity relates to the effectiveness with which agricultural practices are implemented and to the amount of external inputs, which translate into an ecological oversimplification. Both facets of intensification have been shown to have negative effects on biodiversity (Andersson, Birkhofer, Rundlöf, & Smith, 2013; José-María, Armengot, Blanco-Moreno, Bassa, & Sans, 2010) and can also affect associated ecosystem services (Andersson et al., 2012; Tilman et al., 2001).

Insect abundance is negatively affected by the management of agricultural landscapes. On the one hand, the reduction of non-crop habitats entails an oversimplification of the landscape, as field margins are often suppressed or much reduced (Tscharntke et al., 2005). In fact, in very intensively managed landscapes, field margins can be the only remnants of seminatural vegetation, and constitute the refuge for many plant and animal species (Fahrig et al., 2011; Marshall & Moonen, 2002; Meek et al., 2002; Rands & Whitney, 2011), as well as their main corridors in agricultural landscapes (Hass et al., 2018). On the other hand, homogeneous monoculture, and particularly that of cereals, narrows the habitat choices and reduces the opportunities for flower visiting insects (Nicholls & Altieri, 2013).

Organic farming is known to counteract the negative effects exerted by agricultural management on many components of agroecosystems' biodiversity, both within fields and on the neighbouring habitats (Bassa, Chamorro, José-María, Blanco-Moreno, & Sans, 2012; Bengtsson, Ahnström, & Weibull, 2005; José-María et al., 2010; Rundlöf, Bengtsson, & Smith, 2008). Organic farming differs from conventional farming in several key aspects which altogether define a lower farming intensity (Armengot et al., 2011). Fundamental differences are determined by the prohibition of most pesticides and inorganic fertilizers (Council of the European Union, 2007), needing thus alternative ways to supplement the crops' nutrient requirements, with e.g. legumes which may provide nitrogen through fixation from atmosphere (Crews & Peoples, 2004; Pe'er et al., 2017). Both aspects usually entail an increased within and among field heterogeneity and boost flower abundance and diversity compared to conventional management. The enhancement of plant communities broadens the opportunities for different organisms. These differences in relation to the common practice in conventional agriculture benefit the biodiversity of several taxonomic groups, though the effects are not always consistent (Caballero-López et al., 2011; Gabriel & Tscharntke, 2007; José-María et al., 2010; Kennedy et al., 2013; Puech, Baudry, Joannon, Poggi, & Aviron, 2014; Rundlöf & Smith, 2006; Smith, Dänhardt, Lindström, & Rundlöf, 2010).

Although many major staple crops such as cereals do not depend on pollinators, and offer very scant resources for them, these crops occupy substantial areas all over Europe. About a 40 % of the land is devoted to agriculture and about 33.2 % of it is annually tilled land devoted to cereals (Eurostat, 2013). However, these crops alternate either in time or space with insect-pollinated crops. These crops, like the legume crops that are routinely included in organic crop rotations, may benefit from the presence of flower visiting insects, but at the same time they may also influence the activity of the insects. Also, in agricultural landscapes, these crops are intermixed with the remnants of seminatural and natural habitats, where some plant species may require the interaction with insects to produce fruits and viable seed (Andersson, Ekroos, Stjernman, Rundlöf, & Smith, 2014; Bartomeus, Vilà, & Steffan-Dewenter, 2010; Biesmeijer et al., 2006). Thus, it is necessary to understand how the ensemble of flower visiting insects responds to landscape structure and crop characteristics and management, and how does their response affect the fruit set of insect-pollinated plants. Different groups of insects interact with entomophilous flowers, and although they display very different efficiencies as pollinators, it is considered that some can compensate their low efficacy through increased frequency of visits (Power, Jackson, & Stout, 2016; Rader et al., 2016).

However, it is equally important to understand the cascading effects on plant reproduction, if research aims to provide with meaningful recommendations at the whole agroecosystem level. The link between the abundance of flower visiting insects and the fruit or seed set of target plants has been investigated previously, generally supporting that the measures that favour flower visiting insects, and particularly bees, increase fruit set (Hardman, Norris, Nevard, Hughes, & Potts, 2016; Mendoza-García, Blanco-Moreno, Chamorro, José-María, & Sans, 2018; Power & Stout, 2011). Nevertheless, it is not clear whether the agricultural landscape and crop characteristics affect flower visiting insects and whether these effects make a strong difference on the fruit set of insect-pollinated plants (Bartomeus et al., 2014). A better understanding of these links will aid to enhance flower visiting insects and the delivery of pollination, thus facilitating the multiple roles that agricultural landscapes can have (Shackelford et al., 2013).

We investigated the effects of agricultural land use intensity at different levels on the abundance of flower-visiting insects and on the fruit set of an insect pollinated target plant. We aimed at answering the following questions: a) is the abundance of flower-visiting insects negatively affected by landscape level agricultural intensity? b) do crop margins affect the abundance of flower-visiting insects? c) can organic farming compensate for the negative effects of agricultural intensification at landscape level? d) what is the role of flower-resources, either offered by flower-resource rich crops such as legumes of by wildflowers in crop margins, on modulating the effects of agricultural intensification? e) how does the effect of these factors translate into the pollination service delivered by flower-visiting insects, and thus into the fruit set of a target plant?

Plant diversity follows a gradient from the high-diversity margins to the low-diversity centres owing to differences in farming intensity, and this gradient is steeper in low-intensity landscapes (low percentage of arable land) than in high intensity landscapes (José-María et al., 2010). These differences owe to the stronger landscape effects in the margins, while the in-field management plays a prominent role in the field centres. However, while this is true for plants, with passive dispersal at short distances, there are few empirical evidences that insects, and thus the services that they deliver, respond in the same way, in spite of indirect evidence (Gabriel & Tscharntke, 2007; José-María, Blanco-Moreno, Armengot, & Sans, 2011) although recent studies indicate that field margins in fact concentrate most of the movement of pollinators (Hass et al., 2018). We hypothesize that landscape level agricultural intensity should have a negative effect on the abundance of flower-visiting insects. These effects should be noticeable on the margins and on the centre of the fields. However, it is known that many bee species have relatively short-range foraging distances and respond to the local availability of foraging resources (Rands & Whitney, 2011; Torné-Noguera et al., 2014), and it is likely to be true for many different groups of insects (Hof & Bright, 2010; Millán de la Peña, Butet, Delettre, Morant, & Burel, 2003). Therefore, we hypothesize that distance to the field margins should have a negative effect on the insect abundance. However, it is not that management affects directly the insects. Flower visiting insects may be determined more by the availability of flower resources than by the management or position within the field (Haaland, Naisbit, & Bersier, 2011). In relation to the resources offered by a flower-rich crop, such as legume crops, we hypothesize that this kind of crop could concentrate flower-visiting insects (Holzschuh, Dormann, Tscharntke, & Steffan-Dewenter, 2011; Holzschuh, Steffan-Dewenter, & Tscharntke, 2008; Westphal, Steffan-Dewenter, & Tscharntke, 2003), and therefore these effects may be more noticeable in high-intensity landscapes. All these effects may translate into the fruit set of target species, although it is likely that target plants do not suffer much from pollinator limitation as dominant pollinators persist under agricultural expansion and may be easily enhanced by means of simple measures (Kleijn et al., 2015).

# MATERIALS AND METHODS

## Experimental sites

The study was conducted in 2013 in the dryland cereal region in Catalonia, NE of Spain (1.56° - 2.21°E, 41.75° - 42.05°N) (Fig. 1). To examine the dependence of flower-visiting insects on the agricultural landscape we selected ten localities, defined as non-overlapping areas of 1 km radius, that were selected to represent a gradient in agricultural land use, measured as the percentage of arable land (PAL). The set of localities covers an approximate area of 54 × 34 km. PAL was determined within a 1 km radius of each field using the land use information available in the digital Catalan Cartography of Habitats (Carreras & Diego, 2004). To test the effects of within field agricultural management on the activity-density of flower-visiting insects, we selected fields with differing level of management intensity, as displayed by organic and conventional farms (Armengot et al., 2011). The selection of the localities was limited by the availability of organic farmers who have applied organic farming for at least 10 years, as there may be some lag before the effects of agroecological transition are noticeable (Andersson et al., 2012). In each of these sites we selected a cereal field from an organic farm and a cereal field from a neighbouring conventional farm. The conventional field was selected to match the organic one in size and in the conditions of the surroundings.

To test the effects of increased flower resources offered by crops, within these cereal dominated landscapes, a legume crop was also selected in eight of the ten organic farms. It was not possible to find legumes in two of the organic farms, and the conventional farmers in the area seldom include legumes in their crop rotations, so only organic legumes were included in the experimental design. On each of these fields we carried out surveys of flower resources, insect sampling and pollination measures as described below. The measurements were taken on the edge of cereal fields and 20 m towards the centre of the field (hereinafter field centre), and in the field centre of the legume fields. Field edges of legume crops were excluded from the experimental design to avoid the confounding effects of increased flower abundance both in-crop and in the field margin.

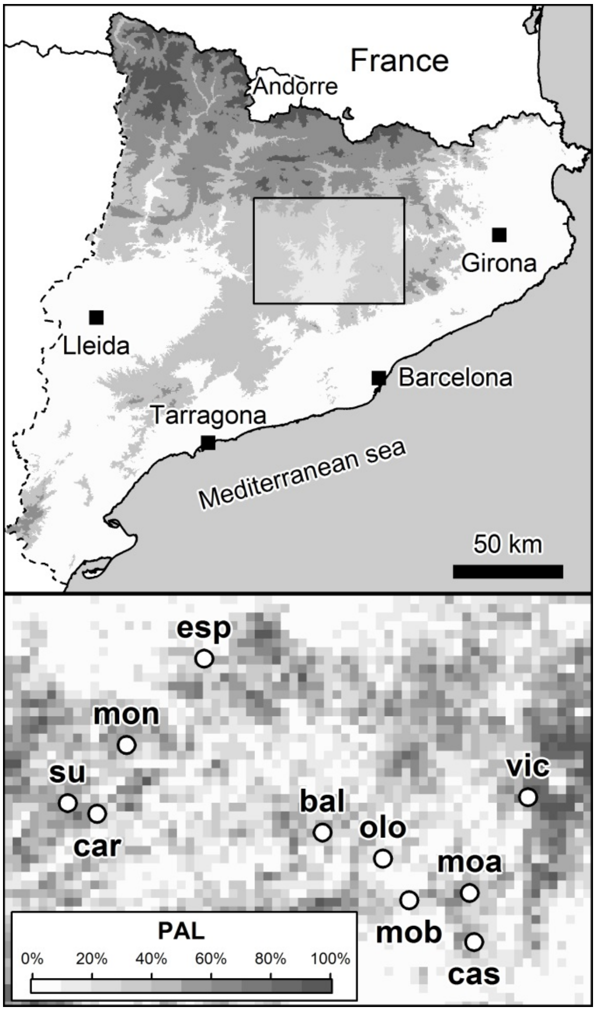

**Figure 1.** Map indicating study area within Catalonia (above) and the 10 localities selected in the study area (below). The grey shading indicates topography in 500 m intervals (above) and the percentage cover of agricultural land (PAL) within 1 × 1 km pixels (below). The names and more information on the localities can be found in Table S1.

### Flower resources

We evaluated the abundance of entomophilous plants in bloom during the sampling periods. All plants were identified to species level (Table S2), and the abundance of flowers was assessed by counting the number of open flower units per species. A flower unit was considered a single flower in most plants, but in Asteraceae and Apiaceae the smallest distinguishable inflorescence units (heads and partial umbels) were counted. However, as flower units differ greatly in their size, all flower units were weighed by their average size, so our estimates of flower abundance are a surrogate of flower size summed over the whole sample. The surveys were conducted from May 6th to June 25th in three parallel transects of 1 × 10 m in the studied fields. These transects corresponded to the field margin, the crop edge (first meter of the crop) and the centre of the field. Margin and crop edge transects were averaged, as they are in contact and may affect each other.

### Flower visitor survey

We measured insect abundance from May 6th to June 25th, covering most of the flowering period of the vegetation within crops and field margins in the area. Insect activity-density was measured by means of pan traps. We used 500 mL plastic bowls (Pro’Jet, Paris, France) painted with UV-reflecting yellow, white, and blue paint (Sparvar Leuchtfarbe, Spray-Color GmbH, Merzenich, Germany) to maximize their attractiveness to a broad array of flower-visiting insects. Each trap consisted of three plastic bowls, one of each colour, filled with water with a drop of detergent, and were located 1 m above the ground and 1 m apart from the target plants. Pan traps were set up between 7:00 and 8:00 a.m. and were collected 12 hours later, thus covering most of the daily activity period. Traps operated simultaneously on all fields, under fair weather in calm days. Pan trapping is known to underestimate flower-visiting insect richness (particularly bees) and to provide a very indirect measure of flower visitation (Popic, Davila, & Wardle, 2013; Westphal et al., 2008). However, this method allows to sample all sites simultaneously, to avoid biases inherent to collectors, and to standardize sampling effort easily (Torné-Noguera et al., 2014). Insects were identified to family in the laboratory, and only bees within Hymenoptera (Apoidea Anthophila in a restricted sense, including: Megachilidae, Apidae, Mellittidae, Andrenidae, Halictidae and Colletidae), Diptera and Coleoptera were used in the analyses. Of the latter two orders, we considered only putative flower-visiting families according to the available literature and expert criteria (Oosterbroek & Hurkmans, 2006; Willemstein, 1987).

### Fruit set measurements

*Raphanus sativus* L. (Brassicaceae) was used as a phytometer, the target species on which fruit set was measured. This plant is known to be self-incompatible and pollinated by insects (Klotz, Kühn, & Durka, 2002; Young & Stanton, 1990), and therefore it has been used frequently in pollination experiments as its reproductive success can be related to pollination by insects (Bartomeus et al., 2010; Dainese, Montecchiari, Sitzia, Sigura, & Marini, 2017; Steffan-Dewenter & Tscharntke, 1999). Furthermore, it is visited by a broad array of insects, which makes it appropriate to measure the overall effects of flower visitor assemblage on the delivery of pollination services to it (Albrecht, Duelli, Müller, Kleijn, & Schmid, 2007; Steffan-Dewenter & Tscharntke, 1999). Plants were grown in 5 L pots at the Experimental Field Services of the University of Barcelona between January and May. From May 9th to the 16th potted plants were placed in the studied fields. One cluster of four plants was placed on each of the selected positions (either on the edge or the centre of the crop, in conventional and organic cereal crops as well as in the centre in organic legume fields), at such a distance between them as to avoid accidental pollination. Plants were watered as required (once or twice per week) during the development of the experiment. On June 25th and 26th, plants were taken back to the greenhouses at the Experimental Field Services to enable the full development of recently pollinated flowers. To avoid pollination in the greenhouse, all remaining and newly developed flower buttons were cut off periodically for the following two weeks. Fruit set was assessed as the ratio of ripe fruits to flowers produced. Flowers that develop and blossom can be counted even if they do not develop into a fruit because their pedicels remain attached to the inflorescence axes, which allow them to be counted even if they do not develop into a fruit.

### Statistical analyses

We modelled insect abundance by means of generalized mixed effects models with a Poisson error distribution. We analysed separately the data for cereals, which allowed testing the effects of management and position, and the data for organic field centres, which allowed testing the effect of crop. Two models were used to model total insect abundance and the abundance of each of the groups considered (Apoidea, Diptera, Coleoptera), which were compared based on their Akaike information criterion corrected for small sample sizes (Burnham & Anderson, 2002).

In the first model (Model 1) we included management (conventional *vs.* organic), position (edge *vs.* centre) and crop (cereal *vs.* legume) as fixed effect factors, as well as the PAL as a fixed effect covariate.

In the second model (Model 2) we tested whether the differences in insect abundance could be attributed to differences in the abundance of flower resources. Given that the abundance of flowers was highly heterogeneous among localities, and that the effect of varying flower resources can only affect the local pool of insects (which we hypothesize that varies from locality to locality in relation to PAL), we log-transformed and standardised flower abundance within localities before including it in the statistical models. We did not include the abundance of flowers as a predictor in the models with crop and management factors because there is some collinearity between management and flower resources (there are more flower resources in legume crops than in cereal crops; in field margins than in field centres; and in organic fields than in conventional fields; see Fig. S1 and Table S2). Insect abundance was highly variable between localities and along the sampling period (see supplementary material Fig. S2 and Table S1). Therefore, all the models included locality as a random effect factor, plus an uncorrelated random slope for the effect of sampling period between localities.

Fruit set was modelled as a binomial process by means of generalized mixed effects models. Since fruit set was measured at the end of the experiment, a single measure of developed fruits *vs.* opened flowers per plant was obtained. For modelling fruit set, we followed a similar strategy as for insects, and analysed separately the data from cereal fields and from organic field centres. For each of these subsets of data, we set up three models. Model 1 considered the effects of landscape, management, and position for cereal fields, and landscape and crop for organic field centres. Model 2 included the effects of landscape and flower resource abundance. For fruit set, however, we set up a third model considering the abundances of the flower visiting insect groups on the fruit set of the target plants. Since management, position and crop affect flower resources, and these in turn could affect insect abundance, we decided not to include all three types of variables in the same model, but, like in the case of insects, we compared the three models in terms of their Akaike information criterion. For the inclusion of flower resource abundance and insect abundance (which were measured in the six sampling periods) in the models of fruit set (which was only measured at the end of the experiment), we obtained an overall measure for flower resources and for the different groups of flower-visiting insects. We tested the predictive values of the average, the maximum, minimum and variance of these variables; since there were no significant differences in the models (and some did not converge, results not shown), we retained the models including only the average flower resource abundance and the average insect abundance.

All models were fitted and evaluated by means of package lme4 (Bates, Maechler, Bolker, & Walker, 2015) for R (R Core Team, 2018).

# RESULTS

### Flower-visiting insects' abundance

Overall abundance of flower-visiting insects was found to be affected by the gradient in agricultural land-use (PAL), by the differences in land-use intensity and by the distance to field margin (Table 1, Fig. 2a). In general, despite the consistent positive effect of flower resources on the abundance across taxonomic groups, their abundances were better explained by Model 1 (including management and position factors), although the differences between Model 1 and Model 2 were minor.

Flower-visiting insects' abundance was lower in landscapes dominated by agricultural land-use than in landscapes with a higher proportion of non-cropped habitats, and it was also lower in conventional fields than in organic fields. However, the effect of organic farming was lower than the effect of landscape (Table 1). Flower-visiting insects concentrated significantly their activity in field margins compared to field centres, and this effect was larger than the estimated difference between organic and conventional fields. This pattern related to the response of Diptera to the tested variables. However, the positive effect of position (margin *vs.* centre) was significant for total abundance, Apoidea and Coleoptera, but not for Diptera. The interaction between position and management, as well as between position and PAL were significant, but of differing direction: whereas at high PAL the difference between margins and centres increased, under organic farming this difference was reduced. Nevertheless, PAL by itself had a positive effect on both Apoidea and Coleoptera abundances.

**Table 1**. Effect of the percentage of arable land (PAL), management (organic *vs*. conventional), position (margin *vs*. centre), corresponding to the Model 1, and the effect of PAL and the abundance of flower resources, corresponding to the Model 2, on the overall abundance of flower visiting insects and on the abundance of Apoidea, Diptera and Coleoptera. Green entries indicate statistically significant positive effects; red entries statistically significant negative effects and black entries are non-significant effects. On the last row, the Akaike Information Criterion for the best fitting model for each response variable is indicated in bold.

| | **Total abundance** | | **Apoidea** | |
|---|---|---|---|---|
| | **Model 1** | **Model 2** | **Model 1** | **Model 2** |
| **PAL** | -0.27±0.05$^{***}$ | -0.23±0.04$^{***}$ | 0.72±0.27$^{**}$ | 0.64±0.22$^{**}$ |
| **Management (M)** | 0.15±0.03$^{***}$ | | 0.37±0.18$^{*}$ | |
| **Position (P)** | 0.26±0.03$^{***}$ | | 0.61±0.17$^{***}$ | |
| **Flower resources (F)** | | 0.16±0.01$^{***}$ | | 0.33±0.07$^{***}$ |
| **PAL × M** | 0.01±0.02 | | -0.23±0.11$^{*}$ | |
| **PAL × P** | 0.04±0.02$^{**}$ | | 0.21±0.11 | |
| **M × P** | -0.22±0.04$^{***}$ | | -0.21±0.22 | |
| **PAL × F** | | 0.01±0.01 | | 0.03±0.07 |
| **AICc** | 4422.25 | **4306.88** | **763.34** | 764.53 |

| | **Diptera** | | **Coleoptera** | |
|---|---|---|---|---|
| | **Model 1** | **Model 2** | **Model 1** | **Model 2** |
| **PAL** | -0.76 ± 0.07$^{***}$ | -0.60 ± 0.06$^{***}$ | 0.67 ± 0.10$^{***}$ | 0.46 ± 0.09$^{***}$ |
| **Management (M)** | 0.15 ± 0.03$^{***}$ | | 0.09 ± 0.06 | |
| **Position (P)** | 0.02 ± 0.03 | | 0.79 ± 0.05$^{***}$ | |
| **Flower resources (F)** | | 0.07 ± 0.01$^{***}$ | | 0.34 ± 0.02$^{***}$ |
| **PAL × M** | 0.07 ± 0.02$^{***}$ | | -0.08 ± 0.03$^{**}$ | |
| **PAL × P** | 0.06 ± 0.02$^{**}$ | | -0.07 ± 0.03$^{*}$ | |
| **M × P** | -0.40 ± 0.04$^{***}$ | | 0.05 ± 0.07 | |
| **PAL × F** | | -0.05 ± 0.01$^{***}$ | | -0.02 ± 0.02 |
| **AICc** | **4354.09** | 4474.78 | **2162.65** | 2443.22 |

* $P<0.05$; ** $P<0.01$; ***$P<0.001$

For the analysis of overall insect abundance in organic field centres, Model 1 provided a better fit of the data, and supported a consistent negative effect of increasing PAL on the abundance of flower visiting insects (Table 2, Fig. 2b). The effect of legume crops on insect abundance, although positive, was not statistically significant on the overall abundance of insects.

The three groups of insects displayed a similar pattern, with differences in the goodness of fit and significance of the explanatory variables (Model 2 for Diptera should not be considered, as it did not converge to a meaningful solution, and its fit is much poorer than Model 1). Flower visiting Coleoptera were more sensitive to crop and flower resource abundance, whereas the effect of PAL, although also negative, was not statistically significant.

**Table 2.** Effect of the percentage of arable land (PAL) and crop type (cereal *vs.* legume), corresponding to the Model 1, and the effect of PAL and the abundance of flower resources, corresponding to the Model 2, on the overall abundance of flower visiting insects and on the abundance of Apoidea, Diptera and Coleoptera. Green entries indicate statistically significant positive effects; red entries statistically significant negative effects and black entries are non-significant effects. On the last row, the Akaike Information Criterion for the best fitting model for each response variable is indicated in bold.

| | **Total abundance** | | **Apoidea** | |
|---|---|---|---|---|
| | **Model 1** | **Model 2** | **Model 1** | **Model 2** |
| **PAL** | -0.41 ± 0.16$^{*}$ | -0.08 ± 0.18 | -0.05 ± 0.17 | -0.05 ± 0.15 |
| **Crop (C)** | 0.25 ± 0.21 | | 0.26 ± 0.16 | |
| **Flower resources (F)** | | 0.05 ± 0.08 | | 0.06 ± 0.15 |
| **PAL × C** | -0.08 ± 0.20 | | 0.14 ± 0.14 | |
| **PAL × F** | | -0.13 ± 0.02$^{***}$ | | 0.16 ± 0.11 |
| **AICc** | **1793.66** | 2389.25 | 395.89 | **389.11** |

| | **Diptera** | | **Coleoptera** | |
|---|---|---|---|---|
| | **Model 1** | **Model 2** | **Model 1** | **Model 2** |
| **PAL** | -0.08± 0.36 | 0.65± 0.17$^{***}$ | -0.02± 0.13 | -0.15± 0.11 |
| **Crop (C)** | 0.23± 0.27 | | 0.43± 0.10$^{***}$ | |
| **Flower resources (F)** | | 0.05± 0.03 | | 0.30± 0.05$^{***}$ |
| **PAL × C** | -0.06± 0.26 | | -0.23± 0.08$^{**}$ | |
| **PAL × F** | | -0.11± 0.02$^{***}$ | | -0.15± 0.04$^{***}$ |
| **AICc** | **1505.06** | 2324.62 | **958.59** | 967.93 |

* P<0.05; ** P<0.01; ***P<0.001

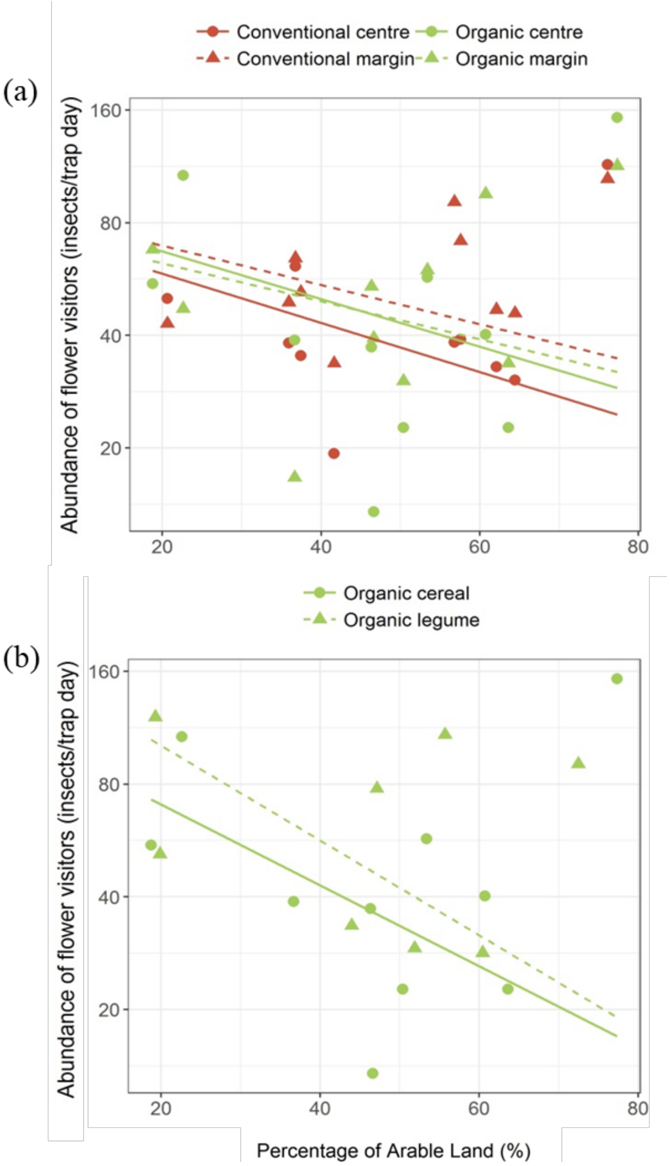

**Figure 2.** (a) Relationship between total abundance of flower visiting insects and PAL for organic and conventional field centres and margins; and (b) relationship between total abundance of flower visiting insects and PAL for organic cereal and legume field centres. The lines represent the marginal predictions of Model 1 in Table 1 (Figure 2a) and Table 2 (Figure 2b).

### Fruit set

Fruit set of *Raphanus sativus* in cereal fields was affected by PAL and management, and position (Fig. 3a). All three models yield a similar fit of the data (Table 3); the best fitting model was the one containing landscape, management and position factors, although management by itself was not statistically significant. PAL had a significantly negative effect on the fruit set of the target plants. However, it interacts significantly with management, implying that the differences between organic and conventional fields were only important for “extreme” landscapes; either with a high or a low PAL.

Management and position also interacted significantly (Table 3, M × P), whereas the fruit set of *R. sativus* was barely dissimilar between margins and centres of conventional fields, there were stronger differences in relation to position in organically managed fields. The models including flower resources or insect abundances indicate that these variables had a positive effect on fruit set. However, their interactions with PAL were of opposite sign: whereas increasing PAL and flower resources had a negative effect on fruit set, increasing PAL and insect abundances had a positive effect on fruit set.

In organic field centres the differences between models were minimal (Table 4, Fig. 3b). While most factors had the same sign as in cereal fields, the abundance of flower resources was the only statistically significant effect, favouring the fruit set of the target plants.

**Table 3.** Effect of the percentage of arable land (PAL), management (organic *vs*. conventional) and position (margin *vs*. centre), corresponding to the Model 1; the effect of PAL and the abundance of flower resources, corresponding to the Model 2; and the effect of the abundance of flower visiting insects, corresponding to the Model 3, on the fruit set of *Raphanus sativus* in conventional and organic cereal fields. Green entries indicate statistically significant positive effects, red entries statistically significant negative effects and black entries are non-significant effects. On the last row, the Akaike Information Criterion for the best fitting model for each response variable is indicated in bold.

| | Model 1 | Model 2 | Model 3 |
|---|---|---|---|
| **PAL** | -0.46 ± 0.14$^{***}$ | -0.25 ± 0.12$^{*}$ | -0.37 ± 0.11$^{**}$ |
| **Management (M)** | -0.24 ± 0.17 | | |
| **Position (P)** | -0.08 ± 0.02$^{**}$ | | |
| **Flower resources (F)** | ± | 0.15 ± 0.02$^{***}$ | |
| **Apoidea** | ± | | -0.04 ± 0.02 |
| **Coleoptera** | ± | | 0.08 ± 0.03$^{**}$ |
| **Diptera** | ± | | -0.05 ± 0.03 |
| **PAL × M** | 0.35 ± 0.17$^{*}$ | | |
| **PAL × P** | -0.00 ± 0.02 | | |
| **M × P** | 0.50 ± 0.03$^{***}$ | | |
| **PAL × F** | | -0.13 ± 0.02$^{***}$ | |
| **PAL × Apoidea** | | | 0.25 ± 0.02$^{***}$ |
| **PAL × Coleoptera** | | | 0.07 ± 0.02$^{***}$ |
| **PAL × Diptera** | | | 0.07 ± 0.02$^{***}$ |
| **AICc** | **6583.27** | 6744.36 | 6675.52 |

* P<0.05; ** P<0.01; ***P<0.001

**Table 4.** Effect of the percentage of arable land (PAL) and crop type (cereal *vs*. legume), corresponding to the Model 1; the effect of PAL and the abundance of flower resources, corresponding to the Model 2; and the effect of the abundance of flower visiting insects, corresponding to the Model 3, on the fruit set of *Raphanus sativus* in organic field centres. Green entries indicate statistically significant positive effects and black entries are non-significant effects. On the last row, the Akaike Information Criterion for the best fitting model for each response variable is indicated in bold.

| | **Model 1** | **Model 2** | **Model 3** |
|---|---|---|---|
| **PAL** | -0.21 ± 0.18 | -0.06 ± 0.13 | -0.24 ± 0.17 |
| **Crop (C)** | 0.20 ± 0.27 | | |
| **Flower resources (F)** | | 0.34 ± 0.13** | |
| **Apoidea** | | | 0.02 ± 0.17 |
| **Coleoptera** | | | -0.01 ± 0.32 |
| **Diptera** | | | -0.11 ± 0.13 |
| **PAL × C** | 0.25 ± 0.26 | | |
| **PAL × F** | | 0.15 ± 0.10 | |
| **PAL × Apoidea** | | | 0.09 ± 0.16 |
| **PAL × Coleoptera** | | | 0.12 ± 0.23 |
| **PAL × Diptera** | | | 0.07 ± 0.12 |
| **AICc** | 3351.53 | **3347.05** | 3360.92 |

* P<0.05; ** P<0.01

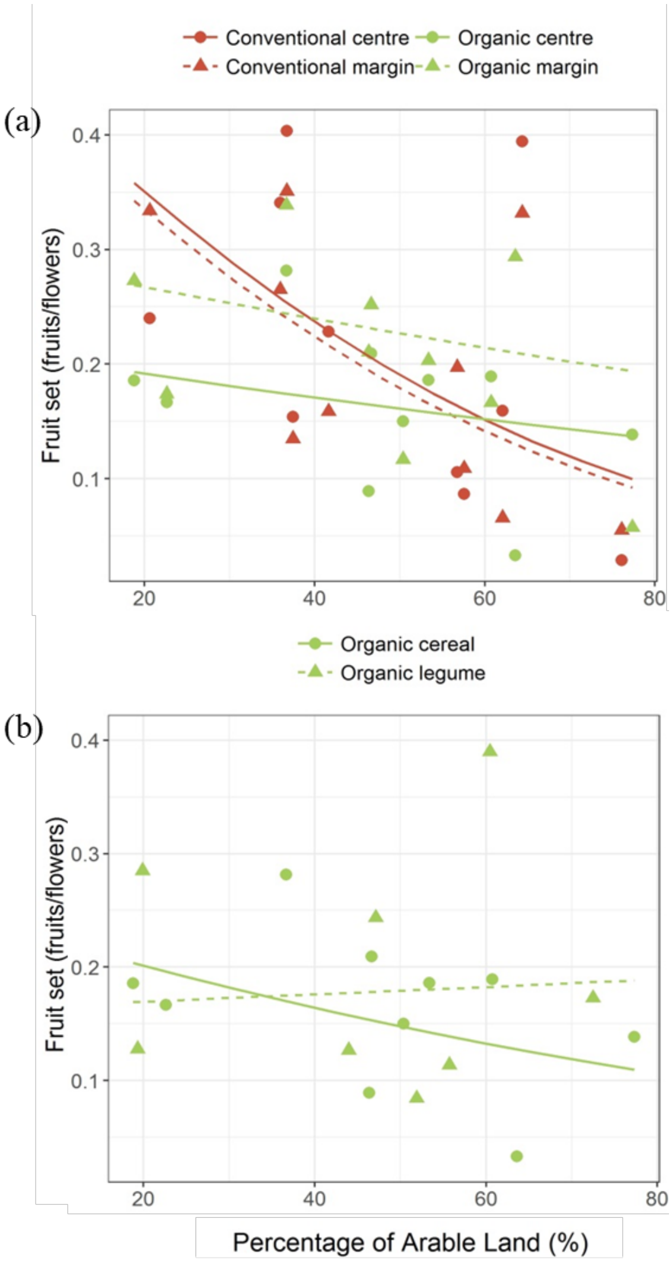

**Figure 3.** (a) Relationship between average fruit set and PAL for organic and conventional field centres and margins; and (b) relationship between average fruit set and PAL for organic cereal and legume field centres. The lines represent the marginal predictions of Model 1 in Table 3 (Figure 3a) and 4 (Figure 3b).

# DISCUSSION

## The effects of landscape and field level variables on flower visitors

### *Landscape*

Our results support that landscape level intensification affects negatively the abundance of flower-visiting insects, in agreement with previous studies that show that many flower visitor communities tend to be poorer in agricultural landscapes with a lower presence of natural and seminatural habitats (Bommarco et al., 2010; Westphal et al., 2008; Winfree, Aguilar, Vázquez, LeBuhn, & Aizen, 2009). Non-agricultural habitats support many wild flower visitors, which forage also on agricultural land (Billeter et al., 2008; Holland, Smith, Storkey, Lutman, & Aebischer, 2015; Scheper et al., 2013). However, we have found that these effects are not consistent among the groups of flower visitors, and more importantly, our results diverge from previous findings in important ways. Our results show that, in our study area, the negative response of flower-visitors to PAL is mainly driven by Diptera, whereas bees and flower-visiting Coleoptera are favoured by increasing agricultural land-use around the fields. Some authors have suggested that the amount of high-quality (non-agricultural) habitats can favour bees (Kennedy et al., 2013). However, Westphal et al. (2003) indicated that it is required a very low percentage of seminatural habitats to sustain the populations of bumblebees. The contrasting response of the different groups of insects to PAL suggests that other features of the landscape, such as crop diversity (Hass et al., 2018) or even density of field margins (Dainese et al., 2017), can have diverse effects on different groups with different requirements, and this may help to explain why some organisms respond positively to increasing agricultural land use in the landscape (Carré et al., 2009; Westphal et al., 2003; Winqvist, Ahnström, & Bengtsson, 2012).

### *Effect of field margins*

The distance to field margins, on the other hand, has a more consistent positive effect on the abundance of flower visitors. Margins have been shown to concentrate the activity as well as the diversity of many groups of invertebrates (Gabriel et al., 2010), and this pattern seems to be independent of the quality of field margin habitats, at least locally (Dainese et al., 2017). The overall abundance of flower visiting insects may be determined by surrounding landscape, but our results demonstrate that cereal fields, although visited, are not a favoured environment, and the activity density of flower visiting insects is higher in field margins (although see below for the joint effects of field margins and management). Cereal fields in general may host few species that need to be insect-pollinated and thus the resources for insects are scant (Gabriel & Tscharntke, 2007; José-María et al., 2011). However, the role of margins goes far beyond the mere provision of feeding resources, as they channel insect movement (Hass et al., 2018), which may explain why flower visiting insects are more abundant in field edges even in flower-rich crops such as oilseed rape (Stanley, Gunning, & Stout, 2013) and to some extent it may also explain why it is more important the amount than the quality of woody margins (Dainese et al., 2017).

### *Effect of crop management*

Our results indicate that the effects of in-field characteristics, as determined by management and crop, are less consistent, particularly because of its interactions with position. Brittain et al. (2010) studied the effects of management in a context where insecticides are routinely applied under conventional farming, and found that organic farming did not have a positive effect in isolated organic farms, thus pointing at the importance of surroundings when considering the effects of within-field management. In general, however, it has been shown that richness of insects is reduced by increasing management intensity (Hendrickx et al., 2007).

Our results support a positive effect of organic farming on the overall abundance of flower visitors, but there are interactions between management and the landscape or the position within the field, and these interactions depend on the group of flower visitors. In general, however, the presence of organic farming tends to smooth out the effects of both landscape and position. Some authors have also found interactions between landscape and organic management in the same direction (Batáry, Báldi, Kleijn, & Tscharntke, 2011; Holzschuh, Steffan-Dewenter, Kleijn, & Tscharntke, 2007). Cereal fields have a very low foraging quality for flower-visiting insects. Organic farming alleviates this deficiency, smoothing the effects of landscape (by concentrating the activity of insects) or position (by having more insect-appealing field centres). Nevertheless, the positive effects of organic management are restricted to the cereal field centres (no differences between margins and centres, and no differences compared to conventional margins). This fact may indicate that either the positive effects of organic farming for insects are very restricted in space, unlike plants which are favoured also in field margins by organic farming (Bassa et al., 2012; José-María et al., 2010), or that indeed the quality of field margins is irrelevant (Dainese et al., 2017). One possible explanation of this behaviour relates to concentration and dilution effects in conventional and organic fields, respectively. In our study, overall flower visitor abundance seems to be determined by the landscape structure; and most insects remain close to favoured habitats, i.e. field margins. The interaction between management and position implies that, in conventional cereal fields, flower visitors tend to concentrate much more on field margins, whereas in organic fields the better conditions of field centres cause a dilution of flower visitors, similar but weaker to that caused by mass flowering crops (Holzschuh et al., 2016, 2011).

*The effects of flower resources*

In Mediterranean cereal-devoted landscapes, where the application of insecticides is low or inexistent (Caballero-López et al., 2011), the effects attributable to PAL, management, and position within fields could be attributed to flower resources on the one hand, and availability and connectivity of nesting and alternative foraging habitats on the other hand. Some studies indicate that organic fields with an equivalent level of flower resources than conventional counterparts do not differ significantly from them (Brittain et al., 2010). Our models including flower resources indicate that they have a positive and significant effect for all groups, as well as for the whole ensemble of flower visitors, and that it is largely independent of landscape effects. However, only the model for total abundance of flower visitors that comprises flower resources is better (lower AICc) than its counterpart comprising all experimental factors. For bees, flower-visiting flies and flower-visiting beetles the models including the experimental factors are better than the ones containing flower resources. It is known that flower resources exert a positive effect on the abundance of flower visitors, but that they only determine a small fraction of insect distribution (Torné-Noguera et al., 2014). Therefore, management and position have effects beyond increased availability of flower resources, as it has been discussed (see above; Dainese et al., 2017; Hass et al., 2018). Flower resources may be of limited use for predicting flower-visitor abundance owing to their transient nature, and thus the effects of long-lasting factors or landscape structure may be more important (Torné-Noguera et al., 2014).

*Effect of legumes*

Legumes differ from cereals in many characteristics, from vegetative tissue quality to the offer of floral and extra-floral nectar (Caballero-López et al., 2011), so their effect should be comparable to that of flower resources in general. However, the role of legumes favouring flower visitors is even more tenuous than that of flower resources. Our results do not support a significant effect of legumes or their flower resources except for flower-visiting beetles. Other authors have attributed the negative effects of non-cereal crops to their management, which was considered more negative than that of cereals (Hass et al., 2018). This is not our case, as the selected organic legume fields do not receive any pesticides and their management is like that of organic cereals. Although there is a slight increase of flower visitors' abundance in these fields, this effect is significant only for flower visiting beetles and mainly in low-intensity landscapes. Beetles are the least mobile of the studied groups, and may respond positively even to a non-preferred flower resource.

## The effects on fruit set of the target species

One of the objectives of our research was to test how do the effects on the community of flower visitors translate into the pollination of target plants. *Raphanus sativus* flowers are prone to unspecialized interactions with a broad array of flower visiting insects (Mendoza-García et al., 2018; Steffan-Dewenter & Tscharntke, 1999). This feature should increase the chances of detecting a response of fruit set irrespective of the group of insects involved in the interaction with it.

One possible outcome would have been that the fruit set of target plants was dependent on insects, which may depend on flower resources, and in its turn dependent on landscape, position and management. However, only for organic field centres seems that the abundance of flower resources is the best predictor of fruit set, and, in general, the experimental factors (landscape, management, position) are a better predictor of fruit set. The increased availability of flower resources in organic crops, crop margins and in legume crops can enhance the delivery of pollination and thus fruit set of the target plant. This effect is consistent when considering both cereal fields and legumes. In legume fields, in fact, the fruit set of target plants becomes independent of the landscape conditions. Contrary to other studies, we have not found a competition for pollinators, which may explain the decrease in the fruit set of target plants owing to the abundance of surrounding flower resources under certain circumstances, particularly near the presence of mass-flowering crops (Holzschuh et al., 2011; Mendoza-García et al., 2018). Our results support the positive effect of surrounding floral abundance on the facilitation of pollination services (Hardman et al., 2016; Morandin & Winston, 2006).

Our experimental design allowed us to detect a negative effect of increasing PAL on the fruit set of the target species, which is consistent with the reduction in the overall abundance of flower visitors in response to decreasing the extent of non-agricultural habitats in the landscape. This agrees with our hypothesis and with previous studies (Albrecht et al., 2007; Steffan-Dewenter & Tscharntke, 1999) but seems to contradict the suggestions by other authors that plants may not suffer from pollinator limitation as dominant pollinators persist under agricultural expansion (Kleijn et al., 2015). Our results support that even for unspecialized pollination plants the detrimental effects of agricultural intensification at landscape level on flower visitors can impinge a decrease of pollination delivery.

The relationship to the quality of the flower visitors’ assemblage can only be hypothesized. In our case, the response of the target plants does not relate to the abundance of bees. We have found that bees (Apoidea) correlate positively with increasing PAL, which is at odds with published studies that claim a negative effect of intensification on bees and their pollination services (Kremen et al., 2002). Species-specific effects may be responsible for the disparity of results and interpretations in previous studies. Despite these patterns related to specific groups, the effect on *R. sativus* fruit set was as expected. This result reinforces the idea that it is important to consider the ensemble of flower visiting insects for the delivery of pollination services, and not a single focal group (Garibaldi et al., 2014; Rader et al., 2016). However, the nexus between the explored factors is complex, and in fact our results indicate that there is not a perfect match between insect abundance and fruit set in target plants, as the best explaining model is the one considering the experimental factors. Experimental factors summarize a more complex set of conditions than it is possible to evaluate from point measures of flower resources or flower visitor abundance, in the same way that the organic-conventional dichotomy provides meaningful information over individual practices (Puech et al., 2014), if actual visitation rates were not obtained.

Organic management counteracts the negative effect of increasing PAL, rendering fruit set of target plants largely independent of the landscape conditions, whereas plants placed in conventional fields undergo a strong (three times) reduction in fruit set from the lowest to the highest PAL. This agrees with the several studies that claim, for diverse components of agroecosystems from plant species richness to insect diversity and abundance, that organic farming compensates the negative effects of the landscape (José-María et al., 2010; Rundlöf & Smith, 2006; Tscharntke et al., 2005).

Less clear is the effect of position within fields, as the effect of position itself is low although significant, and there is a strong interaction with management. The very high variability of fruit set dictates some prudency in this issue. Fruit set of target plants does not parallel the relative total abundances of flower visitors, neither for conventional cereal, organic cereal or organic legume fields. Only in organic cereal fields we found the expected response of higher fruit set in field margins than in field centres, as it matches the findings on pollen transfer along field margins by other studies (Hass et al., 2018). These results indicate a decoupling of flower visitors and actual pollination rates. Insect abundance, even if filtered to keep only the more flower dependent groups, may conceal the actual value of insect community for pollination (Grass, Bohle, Tscharntke, & Westphal, 2018).

However, most importantly, fruit set does not parallel the abundance of bees or any other individual group. Our phytometer species, being not very selective in its interaction with flower visitors, may not suffer seriously from the decline of any particular group, but it indicates how changes in a generalist-dominated interacting community can affect overall levels of pollination (Grass et al., 2018; Potts et al., 2010).

# CONCLUSIONS

It has been proposed that ecosystem-service-based arguments are an insufficient reason to preserve the biological diversity of pollinators (Kleijn et al., 2015). But there are strong indicia that tell us that declining flower-visiting insect abundance can indeed affect pollination services (Potts et al., 2010; Vanbergen et al., 2013) and that this decline can have strong effects on the global economy (Gallai et al., 2009). It is necessary to implement efficient measures that stop the decline of flower-visiting insects, and that promote the delivery of pollination services. However, favouring flower-visitors and plant pollination may require different approaches, particularly because a “one for all” solution may be ineffective. On the one hand, the preeminent concern about bees may hinder the recognition that many insects apart from bees may be involved in pollination networks and deliver effectively the pollination service (Rader et al., 2009, 2016); on the other hand, it does not consider that there may be an enormous variation in specific insect responses (Grass et al., 2016). But more importantly, that the interplay between flower visitors and plant pollination and fruit set is a complex process, in which the result is not fully determined by each of the components, at the landscape or the field level (Grass et al., 2018). Despite these limitations, our results make us to conclude that preventing landscape simplification, deploying organic agriculture, preserving field margins and increasing flower resources at the field level may increase the presence of a diverse community flower visitors in agricultural landscapes, which in turn can help to maintain or increase fruit set levels under many circumstances.

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## SUPPLEMENTARY MATERIAL

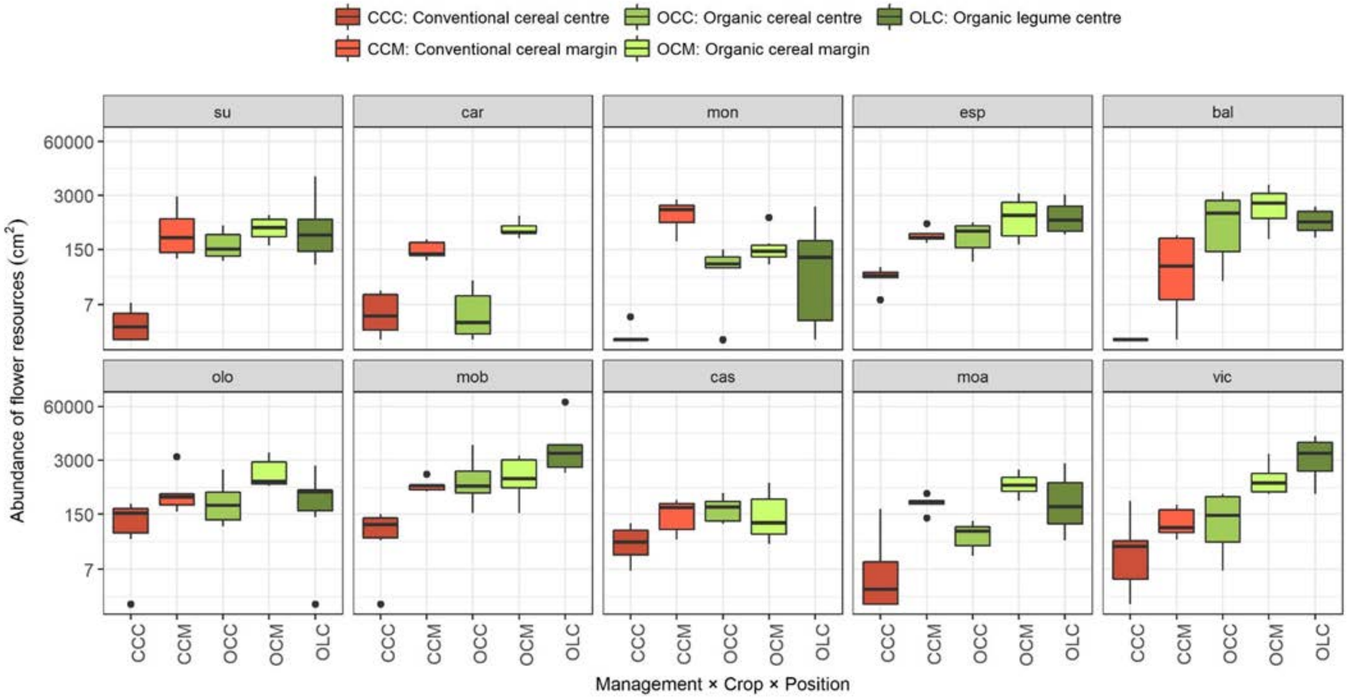

**Figure S1.** Abundance of flower resources in relation to the sampled experimental conditions. Boxplots represent the overall variability in flower resource abundance during the six sampled periods during the spring for each of the different management, crop and position combinations that were sampled. Localities are ordered approximately from west (top left) to east (lower right).

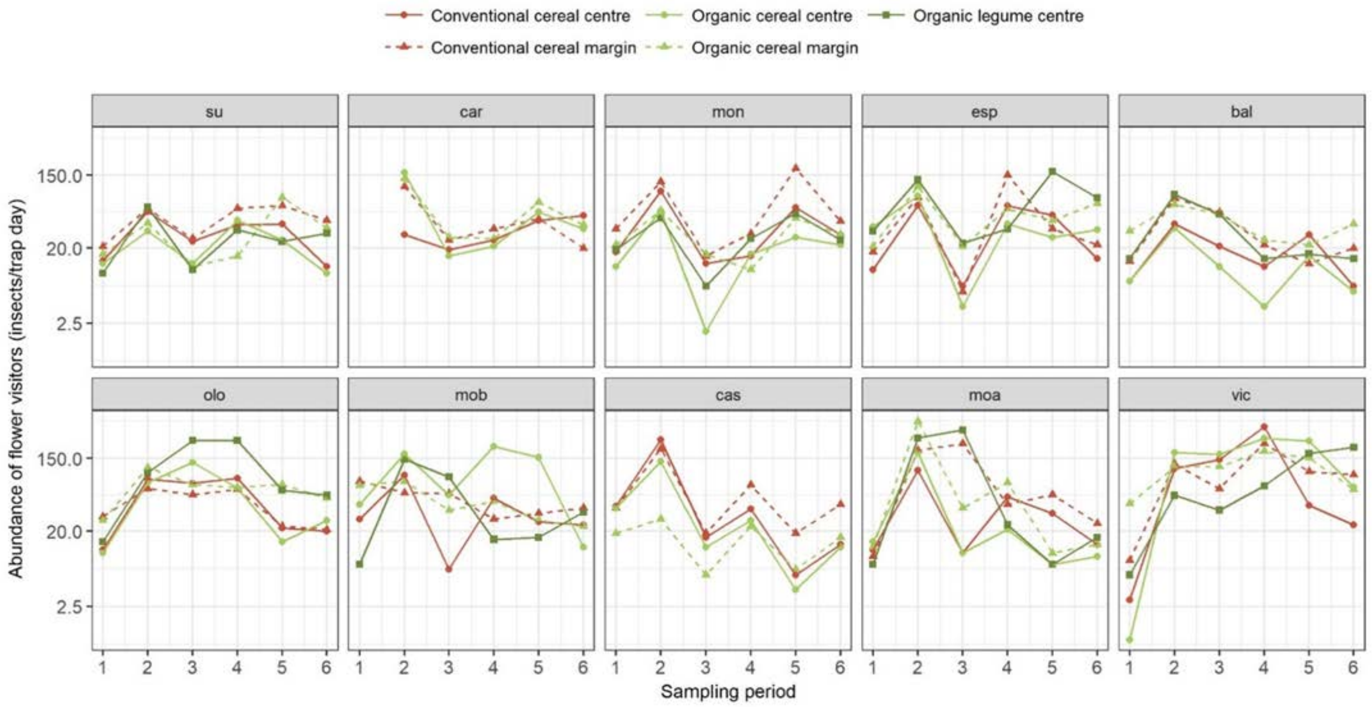

**Figure S2.** Temporal trends in total flower-visiting insect abundance/activity-density for the six sampling periods along the spring. Localities are ordered approximately from west (top left) to east (lower right). There is a strong site effect in both the overall abundance and the temporal pattern of the flower visiting insects’ abundance.

**Table S1.** Total abundance of flower-visiting insects captured over the six sampling periods in each of the fields, split by position (field centre – C – or field margin – M –). The symbol "-" denotes an experimental combination that was not sampled.

| | | | | **Apoidea** | | **Diptera** | | **Coleoptera** | |
|---|---|---|---|---|---|---|---|---|---|
| **Locality** | **code** | **Management** | **Crop** | **C** | **M** | **C** | **M** | **C** | **M** |
| **Su** | **su** | conventional | cereal | 15 | 18 | 143 | 191 | 24 | 66 |
| | | organic | cereal | 18 | 15 | 76 | 102 | 42 | 85 |
| | | organic | legume | 21 | - | 117 | - | 32 | - |
| **Cardona** | **car** | conventional | cereal | 6 | 15 | 125 | 187 | 34 | 32 |
| | | organic | cereal | 10 | 11 | 261 | 213 | 15 | 75 |
| **Montmajor** | **mon** | conventional | cereal | 12 | 19 | 131 | 168 | 91 | 242 |
| | | organic | cereal | 4 | 6 | 80 | 81 | 52 | 94 |
| | | organic | legume | 13 | - | 86 | - | 76 | - |
| **L'Espunyola** | **esp** | conventional | cereal | 3 | 9 | 173 | 249 | 36 | 55 |
| | | organic | cereal | 6 | 35 | 152 | 150 | 65 | 139 |
| | | organic | legume | 9 | - | 381 | - | 77 | - |
| **Balsareny** | **bal** | conventional | cereal | 3 | 5 | 84 | 94 | 29 | 103 |
| | | organic | cereal | 4 | 2 | 37 | 50 | 40 | 184 |
| | | organic | legume | 2 | - | 146 | - | 53 | - |
| **Santa Maria d'Oló** | **olo** | conventional | cereal | 10 | 6 | 214 | 173 | 77 | 79 |
| | | organic | cereal | 19 | 12 | 272 | 220 | 39 | 175 |
| | | organic | legume | 22 | - | 617 | - | 85 | - |
| **Moià (B)** | **mob** | conventional | cereal | 3 | 14 | 176 | 96 | 50 | 184 |
| | | organic | cereal | 6 | 7 | 589 | 96 | 47 | 180 |
| | | organic | legume | 4 | - | 173 | - | 135 | - |
| **Castellterçol** | **cas** | conventional | cereal | 1 | 2 | 301 | 311 | 65 | 73 |
| | | organic | cereal | 4 | 2 | 175 | 50 | 54 | 48 |
| **Moià (A)** | **moa** | conventional | cereal | 2 | 14 | 181 | 441 | 47 | 90 |
| | | organic | cereal | 2 | 20 | 215 | 530 | 24 | 23 |
| | | organic | legume | 2 | - | 584 | - | 64 | - |
| **Vic** | **vic** | conventional | cereal | 2 | 8 | 509 | 198 | 175 | 423 |
| | | organic | cereal | 6 | 7 | 655 | 238 | 256 | 436 |
| | | organic | legume | 13 | - | 244 | - | 286 | - |

**Table S2:** List of the species (according to de Bolòs et al. 2005) that accumulated at least the 90% of the flower resources surveyed in all transects. The figures in the table are average flower abundances for the whole sampling period and the whole set of localities. The symbol “-“ denotes the absence of a species under a given experimental condition. The * symbol after an average abundance indicates a species that constitutes the crop in at least one of the fields surveyed. On the last two rows, the global average flower resource abundance and total number of species identified in each of the experimental conditions is indicated.

| | **Conventional cereal** | | **Organic cereal** | | **Organic legume** |
|---|---|---|---|---|---|
| | **centre** | **margin** | **centre** | **margin** | **centre** |
| *Anthemis cotula* L. | - | - | 10 | 110 | 117 |
| *Arenaria serpyllifolia* L. | - | 94 | - | 20 | - |
| *Ballota nigra* L. | - | 98 | - | 2850 | 285 |
| *Campanula rapunculoides* L. | - | 70 | - | - | - |
| *Capsella bursa-pastoris* (L.) Medik. | 19 | 19 | 574 | 246 | 71 |
| *Carduus tenuiflorus* Curtis | - | 15 | - | 238 | 21 |
| *Caucalis platycarpos* L. | - | 513 | - | 7 | 19 |
| *Cirsium arvense* (L.) Scop. | 188 | 16 | - | 192 | 20 |
| *Convolvulus arvensis* L. | 113 | 28 | 9 | 28 | 8 |
| *Diplotaxis erucoides* (L.) DC. | - | 54 | 109 | 100 | 39 |
| *Echium vulgare* L. | - | 110 | - | 586 | 356 |
| *Erodium cicutarium* (L.) L'Hér. ex Aiton | - | 133 | - | 15 | - |
| *Erucastrum nasturtiifolium* (Poir.) O.E. Schulz | - | 180 | 40 | 11 | - |
| *Fumaria officinalis* L. | 105 | 109 | 67 | 259 | 353 |
| *Galium lucidum* All. | - | 1748 | - | 2600 | - |
| *Galium tricornutum* Dandy | - | 42 | 55 | 7 | 33 |
| *Genista scorpius* (L.) D.C. | - | 5508 | - | - | - |
| *Lepidium draba* (L.) Desv. | - | 146 | - | - | - |
| *Malva sylvestris* L. | - | 116 | 9 | 434 | 949 |
| *Marrubium vulgare* L. | - | - | - | 262 | 36 |
| *Matricaria maritima* subsp. *inodora* L. | - | - | 11 | 445 | - |
| *Medicago lupulina* L. | - | 68 | - | 11 | - |
| *Medicago minima* L. | - | 12 | - | 111 | - |
| *Medicago polymorpha* L. | 3 | 85 | 286 | 73 | 51 |

| | | | | | |
|---|---|---|---|---|---|
| *Medicago sativa* L. | - | 374 | 166 | 348 | 306 |
| *Odontites vernus* (Bellardi) Dumort. | - | - | - | 116 | - |
| *Onobrychis viciifolia* Scop. | - | - | - | 236 | 14156* |
| *Papaver rhoeas* L. | 16 | 105 | 181 | 115 | 405 |
| *Pisum sativum* L. | - | - | - | - | 2156* |
| *Ranunculus bulbosus* L. | - | 158 | - | 36 | - |
| *Raphanus raphanistrum* L. | - | - | 58 | 242 | - |
| *Rapistrum rugosum* (L.) All. | - | - | 297 | 226 | 1102 |
| *Reseda phyteuma* L. | - | - | 75 | - | 9 |
| *Robinia pseudoacacia* L. | - | - | - | 112 | - |
| *Rubus canescens* D.C. | - | - | - | 197 | - |
| *Scandix pecten-veneris* L. | - | 540 | 21 | 655 | 1 |
| *Sideritis hirsute* L. | - | - | - | 251 | - |
| *Sinapis alba* L. | - | - | - | - | 428* |
| *Stellaria media* (L.) Vill. | 50 | 34 | 118 | 404 | 117 |
| *Torilis arvensis* (Huds.) Link | - | 611 | - | 1729 | 1256 |
| *Trifolium campestre* Schreb. in Sturm | - | 332 | - | 39 | - |
| *Veronica arvensis* L. | 17 | 21 | - | 9 | 36 |
| *Veronica hederifolia* L. | 6 | 119 | 21 | 23 | 32 |
| *Veronica persica* Poir. in Lam. | 24 | 53 | 45 | 50 | 55 |
| *Veronica polita* Fr. | 21 | 13 | - | - | 1 |
| *Vicia cracca* L. | - | 1 | 924 | 688 | 268 |
| *Vicia ervilia* (L.) Willd. | - | - | - | - | 593* |
| *Vicia sativa* L. | 16 | 14 | 267 | 72 | 57 |
| *Vicia villosa* Roth. | - | - | - | 112 | - |
| *Viola arvensis* Murray | 25 | 41 | 8 | 8 | 157 |
| **Global average** | 40.1 | 152.0 | 97.7 | 183.8 | 453.9 |
| **Total number of species** | 16 | 82 | 36 | 83 | 54 |

# CAPÍTULO 2

## Farming practices and flower resources determine plant reproduction in Mediterranean landscapes

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*En fase de preparación para su envío a Biological Conservation*

# SUMMARY

Organic farming practices are thought to mitigate pollinator decline in intensive agricultural landscapes and, in consequence, could improve pollination services. However, there is scarce information on the effect of the proportion of organically managed arable land (POL) and local flower resources (local flower cover and local land use and management) on pollinator abundance and pollination. We evaluated pollinator abundance and pollination delivery in five landscapes varying in their proportion of organically managed arable land. We placed pan traps and two phytometer species with different pollination syndromes in field margins of both organic and conventional cereal fields and legume fields. Bee abundance was not enhanced either by POL at landscape scale or by local flower cover. Bee abundance did not also increase in field margins next to legume crops, probably caused by abundant food resources that lead to pollinator dilution. POL enhanced the fruit set of the generalist species, whereas it did not influence the specialist species. The increase in local flower cover in field margins negatively affected the fruit set, because competition for pollinators could occur between the phytometer species and species thriving in plant communities. Despite the negative effect of local flower cover, the fruit set benefited from nearby legume crops. In conclusion, policies ameliorating landscape features (*e.g.* increasing flower abundance) coupled with the promotion of organic farming at the regional level and insect-pollinated and flower-rich crops (*e.g.* legumes) are the main ways to improve pollination services in Mediterranean arable landscapes, even if they have poor effects on bees.

**Keywords**

Agri-environment schemes, bees, ecosystem services, flowering plants, organic farming, pollination syndromes, spatial scales

# INTRODUCTION

Biodiversity decline is mainly caused by the intensification of agriculture, in both natural areas and agroecosystems (Tscharntke et al., 2012). Consequently, ecosystem services, such as pollination and pest control, are negatively affected. One of the main aims of agri-environment schemes (AES) is the protection and conservation of biodiversity and ecosystem services in agricultural landscapes (Batáry et al., 2015). Environmentally friendly agricultural practices are implemented to mitigate biodiversity loss. In particular, organic farming is characterized by long crop rotations and by limiting the use of synthetic fertilizers and pesticides (Reganold and Wachter, 2016; Seufert and Ramankutty, 2017). This practice often benefits the abundance and diversity of pollinators (Holzschuh, Steffan-Dewenter, & Tscharntke, 2008; Rundlöf, Nilsson, & Smith, 2008a), which in turn can potentiate pollination services (Gabriel and Tscharntke, 2007).

Several studies have demonstrated that the benefits of AES and organic farming depend on landscape heterogeneity (Batáry et al., 2011; Rundlöf and Smith, 2006; Tuck et al., 2014). Plant and pollinator diversity can be affected by the proportion of organic farming in the landscape and the extension and quality of non-cropped habitats (Power et al., 2012). In addition, the effects of organic farming can vary among groups of organisms and spatial scales (Batáry et al., 2011; Bengtsson et al., 2005; Fuller et al., 2005; Rundlöf and Smith, 2006). Thus, the understanding of biodiversity patterns in agricultural landscapes requires the study of multiple scales (Concepción et al., 2008; Tscharntke et al., 2005).

In many agricultural landscapes, organic fields are embedded in a matrix of conventional fields, regularly combined with a low heterogeneity in the surrounding habitat (Fuller et al., 2005). For instance, Rundlöf and Smith (2006) showed that butterfly species richness and abundance were positively affected by organic farming in homogeneous intensively managed landscapes. Similarly, bee diversity was enhanced by organic farming more in homogeneous landscapes than in heterogeneous landscapes (Holzschuh et al., 2007). In a meta-analysis, Batáry et al. (2011) found that agri-environmental measures enhanced the abundance and species richness of the principal groups of pollinators, but their response was determined by landscape context. Agri-environmental schemes often benefits for example crop pollination, more in simple than in complex landscapes, which can be attributed to a spillover from surrounding habitats into the cropland (Kleijn et al., 2011).

Insect-flower interaction networks differ in magnitude and composition depending on the farming system (Power and Stout, 2011). Organically managed fields support higher levels of plant abundance, species richness, and diversity than fields with conventional farming, which in turn can attract more pollinator visits (Chamorro et al., 2016). In consequence, the increase in pollinator abundance can result in a higher visitation rate per insect-pollinated plant (Power and Stout, 2011). Plant-pollinator interactions are complex because they can be affected by a variety of factors. The surrounding plant communities can increase the frequency of pollinator visits via facilitation (Moeller, 2004; Waser and Real, 1979), or decreasing it via competition (Marja et al., 2018; Pleasants, 1981). In addition, changes in landscape composition can cause a dilution or concentration of pollinators, which can alter plant-pollinator interactions (Tscharntke et al., 2012).

Most research focuses on the study of pollination through pollinators or insect-plant interactions to evaluate the effect of organic farming. However, the direct evaluation of fruit set could be a much better approach to analysing the effect of organic farming on pollination services (Woodcock et al., 2014). For instance, in a study that evaluated different wildlife-friendly schemes, the fruit set of an open-flower plant pollinated by a broad group of pollinators was higher in organic than in non-organic farming schemes

(Hardman et al., 2016). Also, the fruit set of a self-incompatible plant pollinated by a wide range of pollinators was higher in organic than in conventional fields (Power and Stout, 2011). In contrast, a study of vineyards found that pollination, measured as the fruit set and seed weight of an open-flower plant, was negatively affected by the proportion of uncultivated land in the surrounding landscape independently of the farming system (Brittain et al., 2010). However, information about the impacts of organic farming and local flower resources on the fruit set of both generalist and specialist plants species remains scarce. By comparing a generalist with a specialist plant species, it is possible to evaluate effects of farming practices on fruit set of these two syndromes.

In this study, we evaluated the effect of the proportion of organically managed arable land (POL) and local flower resources on the abundance of bees (Hymenoptera: Apoidea) and on the fruit set of two phytometer species with different pollination syndromes (generalist vs. specialist) in organic and conventional cereal and legume fields in Mediterranean agricultural landscapes. Our mains questions are: (i) does POL and local flower resources affect the bee abundance and fruit set of generalist and specialist plant? and (ii) are there a difference in the effect on fruit set between the generalist and specialist plant species? We expected that pollinator abundance could be enhanced by the proportion of organically managed land and local flower resources, which would thus increase the fruit set of phytometers. However, we also expected a competition for pollinators between the local flower resources and the phytometer species, which would result in a decreased fruit set, that may be stronger in specialist insect visited plants (Fig. 1).

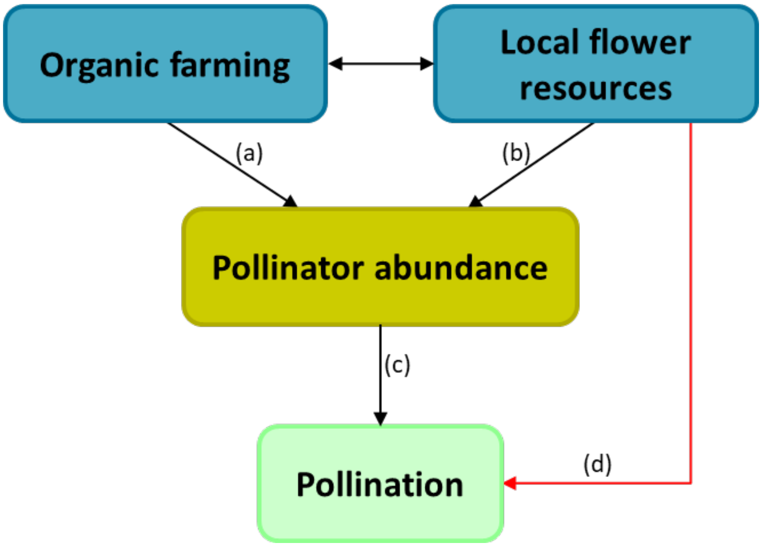

**Figure 1.** General model to predict the effect of the organic farming system on pollination. Organic farming at the landscape scale can affect the pollination of plants through an increase in pollinator abundance (a: Holzschuh, Steffan-Dewenter, & Tscharntke, 2008; c: Power & Stout, 2011). Pollination also can be affected directly by the local flower resources, through competition for pollinators (d: Mendoza-García et al., 2018), or indirectly by changes in pollinator abundance (b: Ebeling et al., 2008; Grass et al., 2016). Black and red lines represent positive and negative effects, respectively.

## MATERIALS AND METHODS

### Study design

The study was conducted in 2015 in central Catalonia, northeast Spain (41° 32′-42° 3′ N 1° 35′-2° 14′ E; see Appendix S1 in Supporting Information). The area is devoted mainly to the cropping of dryland cereals. Within the region, five landscapes were selected to encompass gradients from low to high proportion of organically managed arable land (POL). The five selected landscapes were separated by at least 20 km. Within each study landscape, we selected two organic and two conventional cereal fields and two legume fields. The selected legume fields were under conventional or organic management. The organic fields studied were managed according to the European regulations on organic farming, characterized by the prohibition of the use of any pesticides and synthetic fertilizers. In landscapes with the lowest proportion of organic farming, we could not find two legume fields.

### Proportion of organically managed arable land

We calculated the total arable land surface (excluding vegetable crops, fruit cultivation, and any other crop) under organic management within a 500 m radius for each individual field (Table S1). We used the relationship between the proportion of organically managed fields and the arable land proportion (proportion of organic agricultural land/proportion of arable land: mean ± SD = 0.32 ± 0.25; range: 0.002-0.796) as an indicator of organically managed arable land at the landscape scale. All GIS operations were conducted on ArcGIS 10.2.2 (ESRI, 2010).

### Local flower resources

We characterized the local flower resources by means of the local flower cover and the local land use and management, which represent the resources in the margin and edge, and in-crop, respectively. Both variables describe different scales of flower resources in the field. To assess the local flower cover, we surveyed the richness and abundance of flowering plants in conventional and organic cereal and legume fields between May and June 2015. The surveys were conducted once a week for a duration of five weeks, in two parallel transects of 1 × 16 m, in the studied fields. These transects corresponded to the crop edge (first metre of the crop) and the field margin. The abundance of flower resources was assessed by visual estimation of the relative cover of flowers (expressed as a percentage). The local flower cover was calculated as the mean of all species flower covers over the five surveys.

The local land use and management was described through the different levels of crop attractiveness to pollinators (see Statistical Analysis section). On one end of the spectrum, conventional cereal fields were selected by their low weed abundance and species richness (Bassa et al., 2011; José-María et al., 2010). On the other end, we sampled legume fields, which, at least temporarily, can supply a significant amount of flower resources, in addition to weed communities. Organic cereal fields were characterized by an intermediate level of flower resources, which usually host complex weed communities in terms of weed abundance and species richness. Thus, conventional cereal fields, organic cereal fields, and legume fields represented, in that order, a gradient of increasing crop attractiveness to pollinators.

### Bee surveys

We surveyed bee abundance using pan traps, which consisted of three cups (500 mL, 160 mm diameter, Pro’Jet, Paris, France) painted with blue, yellow and white UV reflecting spray colour (Sparvar Leuchtfarbe, Spray-Color GmbH, Merzenich, Germany). One pan trap was placed in the margin of each studied field. It was located 1 m above the ground and 1 m apart from each group of phytometer species. Pan traps were filled with water and a small drop of detergent to reduce surface tension, and were operating for 12 h. The surveys were performed under favourable weather conditions (no rain, low wind speeds, and diurnal temperatures above 18 °C), and were conducted once a week for a duration of five weeks (between May and June 2015). Samples were stored in 70% alcohol, and specimens of Hymenoptera were identified to family level. For this study, we only used data on bee abundance (Hymenoptera: Apoidea).

### Phytometer species and fruit set

We selected *Raphanus sativus* (Brassicaceae) and *Onobrychis viciifolia* (Leguminosae) as phytometer species to evaluate the fruit set. *R. sativus* is an annual plant that produces numerous symmetrical actinomorphic white flowers on a broad-branched inflorescence. It is self-incompatible (Young and Stanton, 1990) and commonly visited by a wide array of pollinators, such as honey bees, bumblebees, wild bees, hoverflies and butterflies (Albrecht et al., 2007; Steffan-Dewenter and Tscharntke, 1999). The perennial *O. viciifolia* produces numerous zygomorphic melliferous pink flowers on several unbranched inflorescences. It is an outbreeding insect-pollinated species, almost entirely pollinated by bumblebees, honey bees, and wild bees (Hayot Carbonero et al., 2011). *Onobrychis viciifolia* is an obligate insect-pollinated species (Hanley et al., 2008). The difference in the breadth of pollinator assemblage between both plant species allows the classification of *R. sativus* as a generalist insect-pollinated species and *O. viciifolia* as a specialist insect-pollinated species.

On January 2015, seeds of *R. sativus* and *O. viciifolia* were sown in multipots. In the seedling stage, the plants were separated into 5 L pots filled with commercial garden soil (a mixture of peat, vermiculite, and clay) and were kept outdoors at the Experimental Field Service of the University of Barcelona. Eight individuals of each phytometer species were transported to each field margin before the beginning of their flowering season. The plants were grouped by species and were separated by 2 m. Every three to five days, plants were watered, and the frequency was determined by the weather conditions. After five weeks, the phytometer species were transported back to a greenhouse at the Experimental Field Service to prevent any further interaction with pollinators. Flower buds were removed to avoid the overestimation of unpollinated flowers. We counted the number of well-developed fruits and the number of flowers that were not pollinated (no development of fruits). The fruit set was calculated as the proportion of flowers that set fruit.

### Statistical analyses

We tested the effects of the proportion of organically managed land (POL), local flower cover (%), local land use and management (conventional and organic cereal fields and legume fields), and bee abundance on the fruit set of both phytometer species using structural equation modelling (SEM). This method allows the evaluation of the indirect pathways that can influence the fruit set of generalist and specialist insect-pollinated plant species, *R. sativus* and *O. viciifolia*, respectively.

To include local land use (categorical variable) in the SEM, we encoded it as a continuous variable, which represented a level of attractiveness to bees. We considered that conventional cereal fields offered the lowest amount of flower resources, whereas organic cereal fields and especially legume fields represented an increased attractiveness, owing to their higher abundance of flowers. We tested the effects of local land use (cereal or legume) and management (organic or conventional) on the local flower cover, to support our a priori categorization. Thus, we considered local land use and management as an ordered factor variable with three levels: conventional cereal, organic cereal, and legume (the latter independent of management type). We tested the differences in local flower cover between the levels of this ordered factor through polynomial contrasts, including a linear and a quadratic term. The model was analysed with a linear mixed-effects model with normal error distribution, using the landscapes as a random effect factor. We also evaluated the effects of local land use and management on the fruit set of both phytometers.

The initial SEMs (Figs S1 and S2) contained all possible paths, including the correlations between the POL and the variables describing the local flower resources (direct survey of the local flower cover and local land use and management). To simplify the initial SEM and obtain the minimal SEM, a backward selection was conducted. We used the Akaike information criterion (AIC) to select the best model (Shipley, 2013).

SEMs included the following models: (i) the bee abundance was analysed with a linear mixed-effects model with normal error distribution, and (ii) the fruit set of the phytometer species was analysed with a generalized linear mixed-effects model with binomial error distribution. The bee abundance data were log-transformed to meet the assumptions of normality and homoscedasticity of residuals. We performed separate SEMs for the two phytometer species. In all models, we used the landscape identity (five levels) as a random effect factor to control for within-landscape correlation. The proportional contributions of direct and indirect pathways on the fruit set of both phytometer species were calculated using the standardised path coefficients (based on Grace and Bollen, 2005). The statistical analyses were conducted using the packages piecewiseSEM (Lefcheck, 2016) and lme4 (Bates et al., 2015) on R software version 3.3.2 (R Development Core Team, 2016).

# RESULTS

## Local land use and management

We found a strong linear effect of local land use and management (conventional and organic cereal fields and legume fields) on the local flower cover (Table S2; Fig. 2a). The difference in local flower cover was about the same magnitude between conventional cereals and organic cereals as than between organic cereals and legumes. Additionally, the fruit set of both phytometer species were higher in plants located next to legume fields than those next to organic and conventional cereals fields (Table S2; Figs 2b-c).

## Structural Equation Modelling

The fruit set of the generalist insect-pollinated plant species, *R. sativus,* was enhanced by bee abundance. However, local flower cover negatively affected the fruit set, even when its effect on the abundance of bees was non-significant. The effect of the POL was also non-significant on bee abundance, but it had a positive effect on the fruit set. In addition, the local land use and management enhanced the fruit set of *R. sativus* (Fig. 3a and Fig. S1). The proportional contribution of the POL to the estimated total effect on the fruit set of *R. sativus* was 16.7%. Local flower cover negatively affected the fruit set by 31.7%. Local land use and management and bee abundance contributed 20.2% and 31.5% to the fruit set, respectively (Fig. 3b).

The fruit set of the specialist plant species, *O. viciifolia,* was not enhanced by the increase in bee abundance, in contrast to the findings for *R. sativus*. Nevertheless, like the generalist plant species, the fruit set of *O. viciifolia* was decreased by local flower resources and enhanced by the local land use and management. The fruit set of *O. viciifolia* had a lower dependence on landscape identity than did the abundance of bees and the fruit set of *R. sativus*. The proportion of organically managed land, neither indirectly through the bee abundance, nor directly, affected the fruit set of the specialist phytometer species (Fig. 4a and Fig. S2). The local flower cover negatively affected the fruit set of *O. viciifolia* by 61.1%, whereas the local use and management contributed by 38.9% (Fig. 4b).

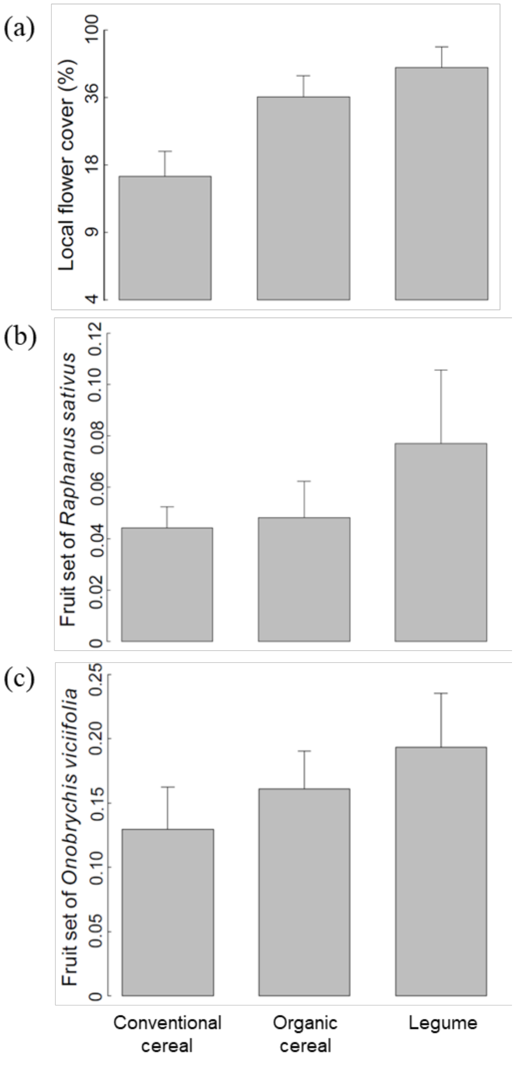

**Figure 2.** (a) Mean (± *SE*) of (a) local flower cover, (b) fruit set of *Raphanus sativus* and (c) fruit set of *Onobrychis viciifolia* in relation to the local land use and management (conventional cereal fields, organic cereal fields, and legume fields).

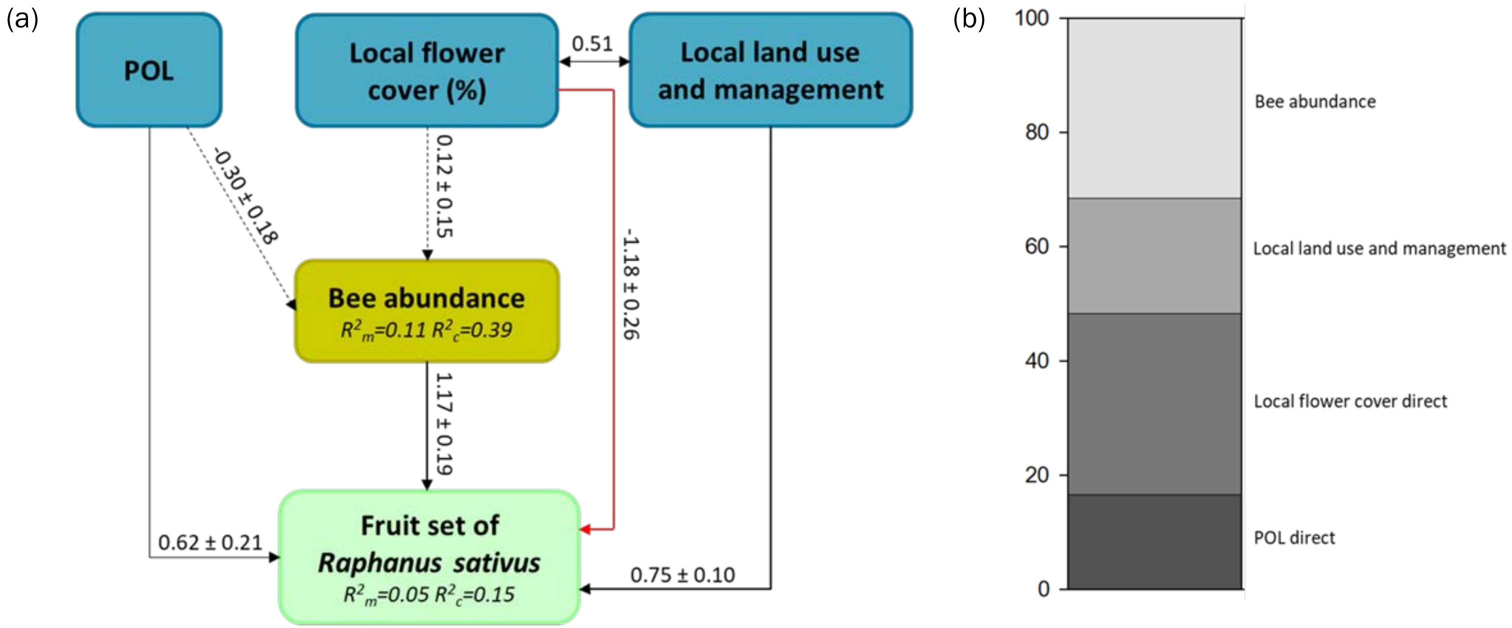

**Figure 3.** (a) Final SEM model for the fruit set of *Raphanus sativus* (Fisher's C statistic: C = 0.59, $p$ = 0.744). Unstandardised path coefficients are shown for the binomial fruit set model, standardized path coefficients for the bee abundance model, and Pearson's *r* correlation coefficients for the correlation between local variables (local flower cover and local land use and management). Marginal and conditional $R^2$ values are shown for each response variable. Dotted lines represent non-significant effects. The width of each arrow is proportional to the path coefficients. (b) The proportional contribution of significant indirect and direct pathways to the estimated total effect of the POL, local flower cover, local land use and management, and bee abundance on the fruit set of *R. sativus*, using the standardized path coefficients (following Grace & Bollen, 2005). POL = proportion of organically managed arable land.

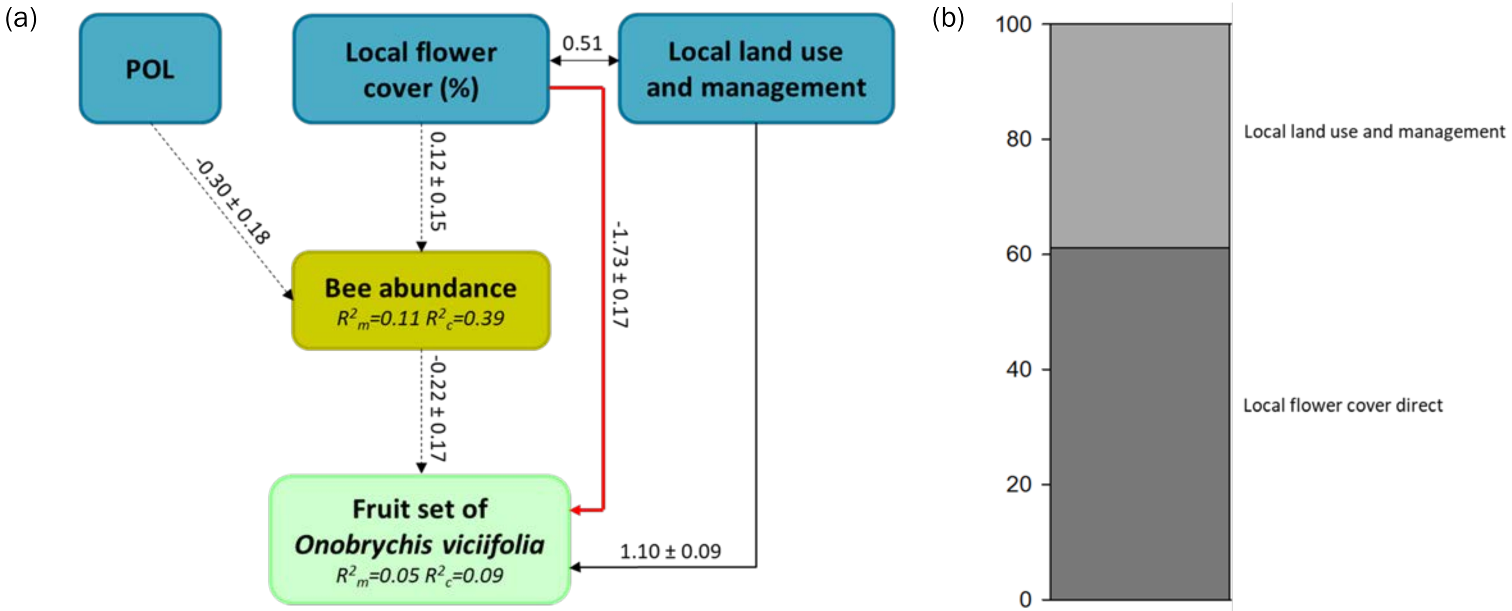

**Figure 4.** (a) Final SEM model for the fruit set of *Onobrychis viciifolia* (Fisher's C statistic: C = 2.41, $p$ = 0.66). Unstandardised path coefficients are shown for the binomial fruit set model, standardised path coefficients for the bee abundance model, and Pearson's $r$ correlation coefficients for the correlation between local variables (local flower cover and local land use and management). Marginal and conditional $R^2$ values are shown for each response variable. Dotted lines represent non-significant effects. The width of each arrow is proportional to the path coefficients. (b) The proportional contribution of significant indirect and direct pathways to the estimated total effect of the POL, local flower cover, local land use and management, and bee abundance on the fruit set of *O. viciifolia*, using the standardised path coefficients (following Grace & Bollen, 2005). POL = proportion of organically managed arable land.

# DISCUSSION

We evaluated the effect of local flower cover and POL on the abundance of bees and the fruit set of generalist and specialist plant species. We have shown that it is possible to modify the fruit set of target species by the variation in local availability of flower resources at different spatial scales, but that the effects are in opposite directions at these lower levels of action; an increased field level resource availability can enhance the delivery of pollination services, whereas increased resources at a very local level (neighbouring to target plants) may actually decrease the fruit set. In addition, our study provides the first evidence that the fruit set of plants that vary in pollination syndrome respond differently to the POL. Only the fruit set of the generalist plant species was enhanced by the POL.

## Bee abundance

The effects of organic farming on biodiversity are reported to be heterogeneous (Clough et al., 2005; Ekroos et al., 2008; Purtauf et al., 2005; Tuck et al., 2014). Our findings showed that the bee abundance was not enhanced by the POL at the landscape scale, which is in accord with other studies on bees (Brittain et al., 2010; Happe et al., 2018). Particularly, bees depend on different habitat types for their nesting and foraging requirements, which do not coincide often (Westrich, 1996). In fact, bee abundance can be supported by nearby natural habitat more than by organic farming (Winfree et al., 2008). For instance, bumblebees were not promoted by organic farming, but they benefited from landscapes dominated by small size fields, where the abundance of field margins between crops was higher (Happe et al., 2018). We therefore suggest that bee abundance could depend more on the surrounding habitat heterogeneity in the landscape than on the POL, which by itself may not provide the necessary conditions for bee enhancement.

In contrast to our results, Holzschuh et al. (2008) showed that an increase in the proportion of organic crops in the landscape enhanced species richness and density of bees. Their findings were in part attributed to differences in the flower cover, both in the field margins and in the crop, and to the absence of insecticide application in organic compared to conventional fields. In addition, when organic fields are embedded in a matrix of conventional fields, it is possible that they did not offer enough resources to enhance bee abundance (Rundlöf, Bengtsson, & Smith, 2008b). In this sense, bees could concentrate their activity density only in the patches which provide the highest amount of resources.

Contrary to our expectations, flower resources located at field margins did not enhance bee abundance, independent of the farming system of the adjacent field. In their study, Brittain et al. (2010) showed that flower resources situated between fields were cut down, both in organic and conventional fields. As a consequence, pollinators did not obtain enough benefits from field margins. Similarly, Winfree et al. (2008) did not find any effect of organic farming on flower visitation by bees. The authors suggested that the main cause of this was the low variation in flower diversity between farming systems. Thus, measures focusing on the promotion of flower strips may not suffice to enhance bee abundance.

The availability of resources in the landscape can be supported not only by field margins and edges, but also by crops providing flower resources, such as legumes. Some studies have found that pollinator visits can increase with the availability of resources offered by crops, especially during their blossoming period (Ebeling et al., 2008). We expected an increase in bee abundance in the field margins promoted by legume crops, but we did not observe any effect on their abundance. These results can be explained through the pollinator dilution caused by abundant food resources, such as those from legume crops in bloom (Veddeler et al., 2006). For instance, the expansion of mass-flowering crops caused a dilution effect on pollinators (Holzschuh et al., 2016). Therefore, our results seem to suggest that the abundance of bees can be affected differently by flower resources offered in the immediate vicinity and at the field level.

### Fruit set

Most studies have focused on species with an open floral structure, which are visited by a wide array of pollinators (Brittain et al., 2010; Hardman et al., 2016; Power and Stout, 2011). Even though these studies focused on a fairly homogeneous set of phytometer species, mixed results have been found about the effects of organic farming on their pollination. In line with our results for the generalist plant species, Power and Stout (2011) and Hardman et al. (2016) showed that organic farming had positive effects on pollination services, promoted by the high cover of flower resources and pollinator abundance. In contrast, Brittain et al. (2010) found no difference in pollination services between organic and conventional fields, which was related to low differences in the abundance of pollinators between farming systems. Likewise, we did not find differences in the abundance of bees, which are the main flower visitors of the specialist plant species.

The enhancement of fruit set of the generalist phytometer species by POL could be mediated not only through the bee abundance, but also by the activity of other flower visitors. The POL had a positive effect on the fruit set of the generalist species, which nevertheless requires the implication of flower visitors. Considering that bee abundance was not affected by the POL, plant pollination might be mediated by non-bee flower visitors. Although these non-bee flower visitors have lower pollen loads, their rate of visit can compensate for their low pollen deposition contribution when compared to bees (Rader et al., 2016). Consequently, other non-bee flower visitors could also support pollination services in agricultural landscapes. Flower resources can also benefit some non-bee flower visitors in the landscape (Grass et al., 2016). For instance, organic farming in grassland systems enhanced the abundance of hoverflies compared to conventional management (Power et al., 2016). On the other hand, the fruit set of the specialist phytometer species seems to depend more on local flower resources than on the organic management of neighbouring fields or the abundance of bees.

Despite the contrasted pattern found in the fruit set of the phytometer species in relation to POL, the effect of local flower cover was similar on both plant species. The increase in the local flower cover in the field margins and edges negatively affected the fruit set. In addition to pollinators, the surrounding plant community can also affect pollination services (Kremen et al., 2007). Competition for pollinators could occur between the phytometer species and the species thriving in plant communities in the immediate vicinity (Mendoza-García et al., 2018; Pleasants, 1981). In communities where competition occurs among numerous plants, the movement of pollen between flowers of different plant species by pollinators (interspecific pollen transfer) can reduce the effectiveness of pollination (see Morales and Traveset, 2008). Our findings showed that the local land use and management had a positive effect on the fruit set of both phytometer species, and this effect was higher in the specialist plant species. Facilitation between plant species can occur when the floral forms are similar (Ghazoul, 2006), as they may benefit from the concentration of a common set of effective pollinators. We suggest that the flower similitude between legume crops and the specialist plant species, which also belongs to the family Leguminosae, improved the fruit set of the latter, compared to that of the generalist plant species. In conclusion, the temporal availability of flower resources, for instance offered by legume fields included in the crop rotation, can affect the fruit set of the phytometer species.

# CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our results provide evidence that local flower resources and the proportion of organically managed arable land affect the fruit set of plants. Conversely, bee abundance does not depend on farming practices. Instead, other flower visitors could benefit from these landscape conditions and can deliver effective pollination services. Agri-environmental schemes should promote heterogeneous landscapes through the conservation or creation of landscape features, for instance field margins, as well as avoid the use of agro-chemicals (Pe’er et al., 2017) to promote the abundance of bees and other flower visitors. Our study also demonstrated that legume crops in dryland cereal cropping regions can improve the fruit set, particularly the one of specialist plant species. In concordance with the greening measures of the European Common Agricultural Policy, we recommend the inclusion of legume crops, which, apart from delivering other agronomic services, can also offer temporally abundant flower resources. We conclude that agri-environmental policies should incorporate landscape and local management options to support pollinator abundance and plant reproduction, which include not only a higher proportion of organic farming in the landscape, but also crops that are rich in flower resources.

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# SUPPLEMENTARY MATERIAL

**Table S1.** Proportion of organically managed arable land (POL) for each selected field.

| Locality | Local land use and management | POL |
|---|---|---|
| Cabrianes | Organic cereal | 7.53 |
| | Organic cereal | 5.96 |
| | Conventional cereal | 7.60 |
| | Conventional cereal | 0.19 |
| | Legume | 2.47 |
| Cardona | Organic cereal | 28.03 |
| | Organic cereal | 13.30 |
| | Conventional cereal | 14.21 |
| | Conventional cereal | 10.09 |
| | Legume | 22.72 |
| L’Espunyola | Organic cereal | 48.03 |
| | Organic cereal | 65.91 |
| | Conventional cereal | 30.70 |
| | Conventional cereal | 66.89 |
| | Legume | 66.19 |
| | Legume | 65.05 |
| Gallecs | Organic cereal | 20.41 |
| | Organic cereal | 40.28 |
| | Organic cereal | 72.64 |
| | Organic cereal | 15.99 |
| | Conventional cereal | 40.66 |
| | Conventional cereal | 47.39 |
| | Conventional cereal | 18.02 |
| | Conventional cereal | 20.93 |
| | Legume | 10.15 |
| | Legume | 2.63 |
| | Legume | 20.64 |
| Moià | Organic cereal | 48.51 |
| | Organic cereal | 79.26 |
| | Conventional cereal | 7.38 |
| | Conventional cereal | 26.74 |
| | Legume | 79.60 |
| | Legume | 49.28 |

**Table S2.** The effect of local land use and management (conventional cereal fields, organic cereal fields, and legume fields) as an ordered factor variable on the local flower cover (%) and the fruit sets of *Raphanus sativus* and *Onobrychis viciifolia*.

| **Local land use and management** | **Local flower cover** Est. ± Std. Error | **Fruit set of *Raphanus sativus*** Est. ± Std. Error | **Fruit set of *Onobrychis viciifolia*** Est. ± Std. Error |
|---|---|---|---|
| Linear term | 0.23±0.06*** | 0.38±0.06*** | 0.39±0.05*** |
| Quadratic term | -0.06±0.05 | 0.08±0.06 | -0.01±0.05 |

*P<0.05; **P<0.01; ***P<0.001

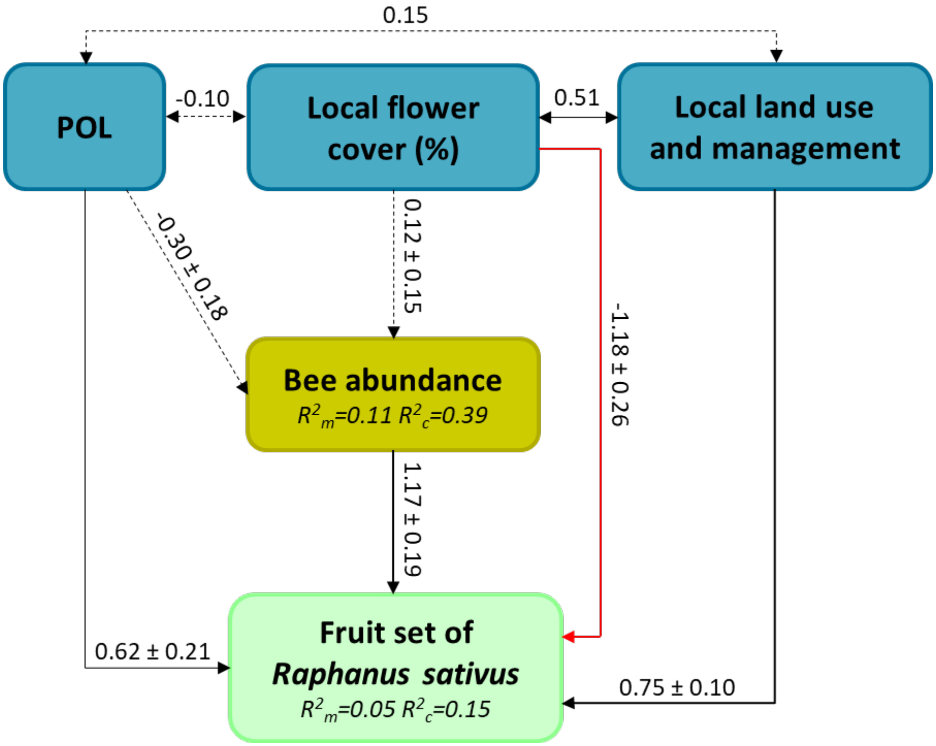

**Figure S1.** Initial complete SEM model for the fruit set of *Raphanus sativus* (Fisher's C statistic: C = 0.59, $p$ = 0.744). Unstandardised path coefficients are shown for the binomial fruit set model, standardised path coefficients for the bee abundance model, and Pearson's $r$ correlation coefficients for the correlation between the POL and local variables (local flower cover and local land use and management). Marginal and conditional $R^2$ values are shown for each response variable. Dotted lines represent non-significant effects. The width of each arrow is proportional to the path coefficients. POL = proportion of organically managed arable land.

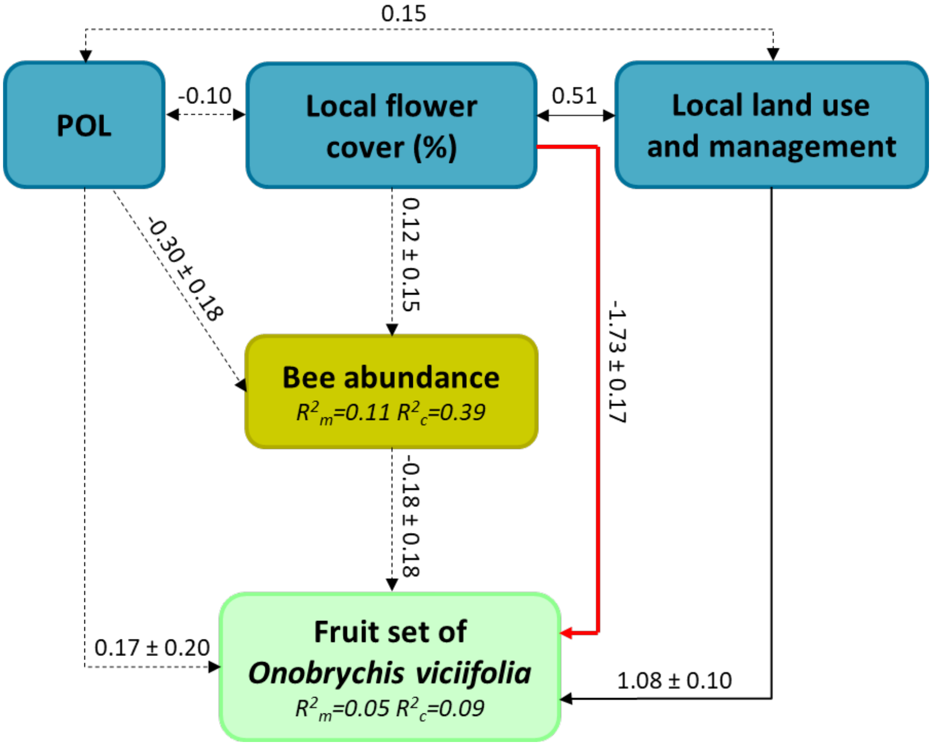

**Figure S2.** Initial complete SEM model for the fruit set of *Onobrychis viciifolia* (Fisher's C statistic: C = 0.59, *p* = 0.74). Unstandardised path coefficients are shown for the binomial fruit set model, standardised path coefficients for the bee abundance model, and Pearson's *r* correlation coefficients for correlation between the POL and local variables (local flower cover and local land use and management). Marginal and conditional $R^2$ values are shown for each response variable. Dotted lines represent non-significant effects. The width of each arrow is proportional to the path coefficients. POL = proportion of organically managed arable land.

# CAPÍTULO 3

## Agricultural intensification at field and landscape levels affects flower visitors' communities through changes in plant communities and their flower traits

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*En fase de preparación para su envío a Landscape Ecology*

# SUMMARY

*Context*

In response to the biodiversity decline caused by agricultural intensification, it is needed to understand how the changes in functional traits of plant communities may affect ecosystem functions and services, particularly those exerted by the fauna that depend on these communities.

*Objectives*

Our study analyses compositional changes in plant and flower visitor communities in response to agricultural intensification at field and landscape levels, and how does the insect community relate to the community-weighted mean (CWM) of flower traits.

*Methods*

We evaluated plant and insect assemblages and traits of plant communities, along a gradient of increasing agricultural land use at landscape level, and under managements differing in intensity and flower rewards for two years in northeast Spain.

*Results*

Plant species composition and the CWM in field centre responded to field management, whereas in the margin depended on the percentage of arable land (PAL). Flower visitor composition only responded to the PAL and to plant composition in the margin. Flower visitor community response to specific flower traits was consistent among years. Flower colour and flowering onset affected the composition of insect assemblages in the margin and flower size in the centre.

*Conclusions*

Agricultural intensification at both levels affected plant and flower visitor community trough changes in flower traits. Farming practices and landscape management can thus affect specific associations between plant and flower visitor communities which have repercussions for biodiversity maintenance and pollination services in agricultural landscapes.

**Keywords**

Agricultural intensification, flower traits, flower visitors, species composition, wildflower resources

# INTRODUCTION

Agricultural intensification at different spatial scales is a major driver of biodiversity loss in agricultural landscapes (Benton et al. 2003; Tscharntke et al. 2005; Armengot et al. 2011). Intensification at landscape scale has caused changes in the structure and composition of the landscape, through the substitution of most natural habitats with arable fields leading to large, uniformly-cropped areas, with low spatial heterogeneity. Intensification at field scale occurs by use of a high amount of external inputs (chemical fertilisers and pesticides), intensive soil tillage and simplification of crop-rotational schemes resulting in weed communities with low diversity in-fields and in neighbouring field margins (Kleijn and Sutherland 2003; Tscharntke et al. 2005). These changes in landscape structure and land-use affect insect biodiversity, which provides pollination services both in agricultural crops and wild plants (Kremen et al. 2007).

Plant-insect interaction also depends on the farming system in agricultural landscapes (Power and Stout 2011). Organic farming, as an environmentally friendly farming system, limits the use of fertilisers and pesticides, and includes crop rotations and green manures (Reganold and Wachter 2016). In contrast to conventional farming, organic farming should support high levels of species diversity, and high plant abundance as well, which in turn can benefit the abundance and diversity of pollinators (Holzschuh et al. 2008; Rundlöf et al. 2010). Likewise, organic farming includes crop diversification and the use of nitrogen-fixing crops, such as legumes (Reganold and Wachter 2016). The implementation of these crops can also support the pollinator community, through the provision of floral resources within the crop.

Recently, the approaches based on functional traits have been suggested as a way to understand the effects of farming practices and of environmental conditions on the ecosystem services provided by the plant communities and generalize results beyond specific taxa (Wood et al. 2015). This approach has the potential to link ecosystem processes across different spatial scales and different trophic levels (Lavorel et al. 2013; Carmona et al. 2016). Several studies have shown that plant community diversity and some of their response functional traits (sensu Lavorel and Garnier 2002; e.g. life form, specific leaf area, canopy height) are affected by agricultural intensification in Mediterranean arable landscapes (José-María et al. 2011; Guerrero et al. 2014; Solé-Senan et al. 2017). However, the effect of flower traits of plant communities on the assemblage of flower visitors remains still unclear. Visual flower traits allow deepening into flower visitor patterns and their interactions with plant community. Visual flower traits are relevant for the attraction of pollinators (Waser 1983), and they can be associated with specific flower visitor types (Faegri and Van Der Pijl 1979). For instance, bumblebees were related with tubular flower plants, whereas hoverflies were associated with open (Fontaine et al. 2006) and short corolla flower plants (Campbell et al. 2012). Certain flower traits, such as flower colour, are considered a good predictor of the prevalence of specific pollinator groups at high taxonomic levels (e.g. between bees, flies, beetles; McCall and Primack 1992), while others, e.g. flower rewards, can be useful to differentiate between lower taxonomic levels (Fenster et al. 2004). In this context, various frameworks have been proposed to analyse the impact of agricultural practices on functional structure of plant communities, and how these changes affect ecosystem functions and services (Lavorel and Garnier 2002).

Some flower traits related with insect pollination are affected by the landscape heterogeneity in agricultural systems (Solé-Senan et al. 2017). For instance, sown wildflower strips are incorporated in many European countries to enhance farmland biodiversity. They consist in wildflower seed mixtures, which can vary their composition and management depending of the country where they are implemented (Haaland et al. 2011). For instance, Jönsson et al. (2015) showed that bumblebees and hoverflies were benefited at field and landscape levels by the flower strips. Therefore, the selection of species based on their functional traits can enhance certain groups of insects, which in turn can improve the delivery of ecosystem services such as pollination (Wäckers and van Rijn 2012).

The effects of plant community on ecosystem functioning are mainly determined by the traits of the dominant species (see the ‘mass-ratio hypothesis’; Grime 1998). Therefore, it should be possible to portray the changes in ecosystem functions and services by means of the changes in community-weighted mean (CWM, Garnier et al. 2004; Violle et al. 2007). Recently, Fornoff et al. (2017) showed that pollinator visitation frequency and pollinator richness were affected by the CWM of floral traits, such as rewards, flower height and inflorescence area, reflectance and chemical traits. Similarly, Robleño et al. (2017) analysed the relationship between the landscape structure and field management on the CWM response of floral traits (e.g. corolla shape) to predict, in turn, the response of pollinators. However, to our knowledge, this is the first study evaluating the direct effect of CWM floral traits on the composition of the main groups of flower visitors (Apoidea, Coleoptera and Diptera) in the plant communities in agricultural landscapes.

In this study we analysed the compositional changes in plant and flower visitor communities along agricultural intensification gradients at field and landscape levels in two years. The response of three flower traits (flower size, flower colour and flowering onset) to the referred intensification gradients was also analysed. In addition, we evaluated the relationship between the plant and flower visitor community composition, and the response of the flower visitor community (Apoidea, Coleoptera and Diptera) to the CWM of the flower traits selected. We hypothesize that the percentage of arable land (intensification at landscape level) and the management (intensification at field level: organic *vs.* conventional) and crop type (cereal *vs.* legume) affect the plant composition and the CWM of flower traits and flower visitor composition. We also predicted that the CWM of flower traits drives the response of flower visitor community. However, these responses should vary among Apoidea, Coleoptera and Diptera flower visitors.

# MATERIAL AND METHODS

## Study design

We reanalysed the data obtained in two samplings to evaluate the effect of the agricultural intensification in a region dominated by dryland cereal cropping systems in northeast Spain, one conducted in 2013 (41.75°-42.05°N; 1.56°-2.21°E) and the second one in 2015 (41.53º-42.05ºN; 1.58º-2.23ºE) (Figure 1a, see Appendix S1 in Supporting Information).

### *Sampling 1*

In the first sampling year (2013), we selected ten landscapes in an area characterized by a gradient in agricultural land use. Land use intensity in each landscape was measured using the percentage of arable land (PAL) in areas of 500 m radius (mean ± SD = 57.93 ± 15.77; min = 31.13; max = 88.83). The set of landscapes covers an approximate area of 54 × 34 km. In each landscape, we selected two cereal fields differing in their level of management intensity (organic *vs.* conventional), aiming at detecting the effects of decreasing crop management intensity on flower visitors through increased plant diversity and flower resource availability. Insecticides are very rarely used in cereal crops in northeaster Spain; however, herbicides are routinely applied by farmers in conventional arable crops. Additionally, we selected legume fields to evaluate the effect that crops have on flower visitors' abundance, as such crops can provide additional flower resources. The studied legume fields were only managed under organic farming, because legumes are not commonly included in crop rotation of conventional farms. For that reason, we could not find legume fields in two of ten landscapes. We evaluated the centre and the margin of each studied field (Figure 1b).

*Sampling 2*

In the second year (2015), we selected other five landscapes differing in their proportion of organically managed arable land to test the landscape-scale effects of organic farming on the abundance of flower visiting insects. The set of landscapes covers an approximate area of 46 × 54 km. We calculated the percentage of arable land (PAL) in a radius of 500 m per field (mean ± SD = 85.11 ± 14.78; min = 50.66; max = 99.99). Within each landscape we selected two organic and two conventional cereal fields, plus two legume fields. We included legumes under conventional or organic management, but we could not find two legume fields in two of five landscapes. This design only considered the field margin (Figure 1b).

The organic fields selected in both sampling years were managed according to organic farming European' regulations (European Union 2007) by at least 10 years. We used the spatial data from the Spanish Agricultural Geographic Information System (SIGPAC). All GIS operations were conducted on ArcGIS 10.2.2 (ESRI 2010).

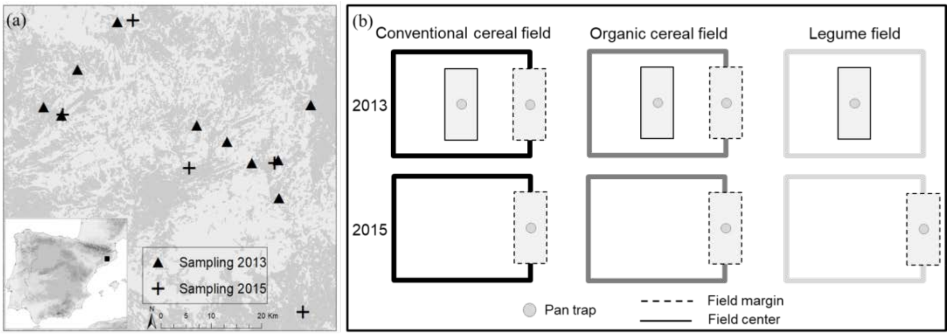

**Fig. 1.** (a) The studied localities surveyed in 2013 and 2015, represented by triangles and crosses, respectively, situated in Catalonia, Spain in cereal cropping landscapes (dark grey – arable fields, light grey – other habitats). (b) Schematic representation of 2013 and 2015 surveys. In each transect, located in the margin or in the centre of the studied fields, we placed one pan trap.

### Wildflower resource evaluation

We evaluated the species richness and abundance of flowering plants in the studied fields. During the first sampling year, the abundance was assessed six times by counting the number of open flowers per species (between May to June 2013), in three parallel transects of 1 × 10 m. Each transect was located at the field margin, at the crop edge (first meter of the crop) and 20 m inside the field. The surveys were conducted at intervals of 7 to 15 days, depending on weather conditions. In the second sampling year, we evaluated the abundance of wildflower resources by visual estimation of the relative cover of flowers (expressed as percentage over total transect area). Transects were surveyed once a week for five weeks (between May to June, 2015). The abundance was evaluated in two parallel transects of 1 × 16 m, one at the field margin and one at the crop edge.

In each year, the data collected in field margin and edge was averaged as one transect (hereinafter referred to as "margin"). The wildflower resources (number of flowers per species or species cover abundance) in both sampling years were calculated as the mean of all species flower over the surveys. All plants were identified to species level.

### Flower visitor evaluation

Simultaneously to the plant sampling, we surveyed the abundance of flower visitors using pan traps in both years. These traps were located 1 m above the ground and consisted on three plastic cups (500 mL, 160 mm diameter) painted with blue, yellow and white UV reflecting spray. We filled the traps with water and a small drop of detergent to reduce surface tension. In the sampling conducted in 2013, pan traps were placed in the margin and the centre of each studied field, whereas in 2015 only in the field margin (Figure 1b). In both samplings, the traps were exposed for 12 hours, one day per survey. Surveys were performed under favourable weather conditions (no rain, low wind speeds, and diurnal temperatures above 18 ºC). Samples were stored in 70% alcohol, and specimens of Hymenoptera, Coleoptera and Diptera were identified to family level. By means of literature (Willemstein 1987; Oosterbroek and Hurkmans 2006) and specialist support, we selected the families that interact with the plant community and can be considered flower visitors.

### Selection and evaluation of flower traits

Two representative traits related to plant strategy for flower visitor attraction and one trait related to temporal availability of resources were selected. These traits were flower size (cm), flower colour (blue, green, pink, purple, red, violet, white, yellow and various colours) and flowering onset (month). We considered the diameter of the corolla or the capitulum (species of the Asteraceae family) to represent the size of the flower. Plant traits data were extracted from BiolFlor (Klotz et al. 2002) and “Tela Botanica” (http://www.tela-botanica.org/page:eflore) databases for the 171 species recorded (see Table S1 for the most common ones). Changes in mean trait values along the agricultural land use gradients was quantified using CWMs (Ricotta and Moretti 2011). CWM indicates the average trait value weighted by the number of flowers per species (sampling 1) or species cover abundance (sampling 2). Categorical traits were included as dummy variable to compute the CWM. We can safely discard intrinsic correlations among traits; only one out of the 55 correlations had r values higher than 0.5 (Table S1).

### Statistical analysis

First, we performed redundancy analyses (RDA, van den Wollenberg 1977) to explore the response of the plant community composition, CWM of flower traits and flower visitor community composition to the percentage of arable land (PAL) and the crop type and management intensity in both years. RDA is a constrained ordination method that can be used to test the relationships between community composition and a set of explanatory variables (*i.e.* environmental variables). For the compositional data (*i.e.* flower or insect composition) the RDA was used without standardization, for the general data (*i.e.* CWM, which are measured at different scales), the response variables were centered and standardized (ter Braak and Šmilauer 2012). In the first sampling year, we compared the response variables in relation to the level of management intensity (organic *vs.* conventional), crop type (cereal *vs.* legume) and different positions (margin *vs.* centre). For the second sampling, we evaluated the level of management intensity (organic *vs.* conventional) and the crop type (cereal *vs.* legume). Also, the variance partitioning procedure was performed by means of RDA (Borcard and Legendre 1994; Legendre et al. 2005). This method was used to quantify the relative importance of the landscape (PAL) and the variables at field scale (crop type and management) on the plant species composition, CWM of flower traits and flower visitor composition.

Second, the relationship between the plant community composition and flower visitor community composition was assessed using Co-Correspondence analysis (CoCA, see Schaffers et al. 2008; ter Braak & Schaffers 2004). This method directly relates two community compositions by maximizing the weighted covariance between weighted average species scores of one community (plants) and weighted average species (families, in our study) scores of the other community (flower visitors). We conducted separated models for each year (2013 and 2015) to analyse the relationship between both plant and pollinator communities within each sampling period.

Finally, we evaluated the effect of CWM of the selected flower traits on the flower visitor community composition using RDA. We tested separately the studied positions (margin *vs.* centre) in the fields selected in 2013, and only field margin in 2015. The aim of this analysis was to evaluate the functional role of the CWM floral traits of wildflower resources on the flower visitor composition. Therefore, legume fields were removed from this analysis to evaluate the effects of wildflower resource avoiding the undue effect of the legume crops.

A log transformation was applied to plant species composition (number of flower and percentage cover), CWM of flower traits and flower visitor composition, to achieve normality. Statistical analyses were performed with CANOCO 5.0 for Windows (Microcomputer Power, Ithaca, NY, US).

# RESULTS

Plant species composition in the field centre and margin vary in relation to surrounding landscape and crop type, but the importance of those factors in the different field positions differ in relation to landscape structure (*i.e.* the percentage of arable land or the proportion of organically arable land). The plant species composition recorded in the field centre in 2013 differed along the gradient of PAL, and depending on the crop type (Table 1). In 2015, the plant species composition in the field margin differed along the gradient of PAL (Table 1). For instance, in the field margin the dominant species *Calendula arvensis* and *Sonchus oleraceus* were more abundant in areas with lower PAL (plant species composition shown in Figure 2b). We found that PAL affected significantly CWM of flower traits in field margins (2013 and 2015), whereas in field centre CWM was affected by the intensity of management (Table 1). Finally, the flower visitor composition both in field margin and centre differentiated always only along the PAL gradient (Table 1). For instance, in field margin Apidae (Apoidea) and Chloropidae (Diptera) families were more abundant in areas with higher PAL (flower visitor composition shown in Figure 2b). The results of the variation partitioning analysis showed that the overlap of variation explained by PAL and crop type was very low (which is to a large extent because we have nearly orthogonal design, *i.e.* the same representation of field types in all the landscapes). In comparison of explanatory power of PAL *vs.* crop type and management, we should keep in mind that PAL has always just 1 df, whereas management and crop type have 2 df. Despite this, PAL explained much more variability in flower visitor composition in all the types and in both the years, and similarly in CWM of flower traits in field margins. On the contrary, in the field centre, the management has higher explanatory power, both for the CWM and for the species composition (Table S2).

**Table 1.** Redundancy analysis (RDA) of the plant species composition, community weighted mean (CWM) values of flower traits and flower visitor composition collected in each year, with environmental factors (% arable land, intensity of management: organic *vs.* conventional, and crop type: cereal *vs.* legume) as explanatory variables. We conducted a RDA with a forward selection separately for each year and field position.
$^{*}$P<0.05; $^{**}$P<0.01 Only significant fractions are reported.

| **Environmental variables** | | **Plant species composition** | | **CWM flower traits** | | **Flower visitor composition** | |
|---|---|---|---|---|---|---|---|
| | | Explains (%) | pseudo-F | Explains (%) | pseudo-F | Explains (%) | pseudo-F |
| **2013** | | | | | | | |
| centre | Percentage of arable land | 6.7 | 1.9$^{*}$ | | | 11.0 | 3.2$^{**}$ |
| | Crop type | 7.2 | 2.0$^{*}$ | | | | |
| | Management | | | 9.1 | 2.5$^{**}$ | | |
| margin | Percentage of arable land | | | 11.0 | 2.2$^{*}$ | 9.5 | 1.9$^{*}$ |
| | Management | | | | | | |
| **2015** | | | | | | | |
| margin | Percentage of arable land | 5.6 | 1.8$^{*}$ | 5.7 | 1.9$^{*}$ | 24.7 | 10.2$^{**}$ |
| | Crop type | | | | | | |
| | Management | | | | | | |

Co-correspondence analysis (CoCA) showed that the plant and the flower visitor communities were not correlated which each other in the field centre in the first sampling year (2013, Table S3). In contrast, the plant and the flower visitor communities were significantly correlated in the field margin in both sampling years (Table S3, Figure 2), indicating that the communities changed in concert. Nevertheless, the amount of variation (*i.e.* total inertia; Table S3) in the communities was much larger than the variation captured by CoCA (*i.e.* total variation; Table S3).

The flower visitor community (Apoidea, Coleoptera and Diptera) was also explained through the CWM of the selected plant floral traits (Table 2). In the field centre, the CWM of flower size explained the Diptera composition. For instance, large flower size favoured Bibionidae family, but not Syrphidae family. In the field margins evaluated in 2013 and 2015, CWM of flower colour and flowering onset influenced Apoidea, Coleoptera and Diptera composition. Apoidea composition (2013) was explained by red flower colour, favouring Megachilidae family. Purple and pink flower colours explained Coleoptera composition in the first year (2013), whereas violet flower colour and flowering onset explained it in the second year (2015). For instance, purple, pink and violet flower colour correlated positively with Malachiidae, Nitidulidae and Scarabaeidae families, respectively. Diptera composition was explained by green flower colour in both years. This flower colour favoured Chloropidae family, but not Syrphidae family. In addition, Diptera composition was also explained by flowering onset in 2015. For instance, an early flowering onset favoured Syrphidae family.

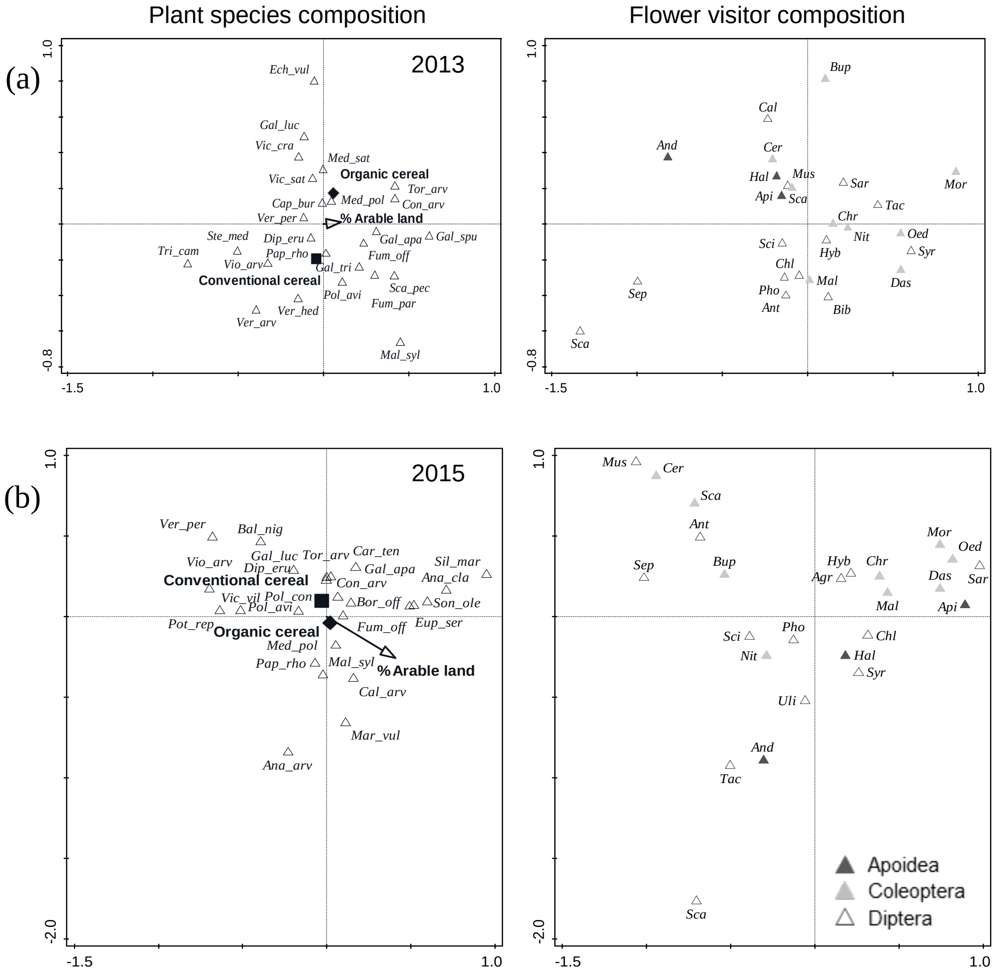

**Fig. 2.** Co-correspondence analysis (CoCA) with the first two axes and 25 plant species (left-hand subplot) in the field margin and 25 flower visitor families (right-hand subplot) with highest average abundance, corresponding to the samplings conducted in (a) 2013 and (b) 2015. The environmental descriptors are passively projected into the left-hand subplot. Plant species and flower visitor family abbreviations are given in Table 4S and 5S, respectively.

**Table 2.** Redundancy analysis (RDA) of the flower visitor composition for each order separately collected in cereal fields during both years, with community weighted mean (CWM) values of flower traits as explanatory variables. RDA with a forward selection was conducted in each year and field position.
$^{*}$P<0.05; $^{**}$P<0.01 Only significant fractions are reported.

| **Flower visitor composition within groups** | **CWM flower traits** | **2013**<br>**Centre**<br>Explains (%) | pseudo-F | <br>**Margin**<br>Explains (%) | pseudo-F | **2015**<br>**Margin**<br>Explains (%) | pseudo-F |
|---|---|---|---|---|---|---|---|
| Apoidea | Red colour | | | 24.9 | $6.0^{**}$ | | |
| Coleoptera | Pink colour | | | 12.2 | $2.9^{*}$ | | |
| | Purple colour | | | 16.1 | $3.5^{*}$ | | |
| | Violet colour | | | | | 13.3 | $4.5^{*}$ |
| | Flowering onset | | | | | 25.0 | $7.3^{*}$ |
| Diptera | Green colour | | | 12.3 | $2.5^{*}$ | 12.6 | $3.2^{*}$ |
| | Flowering onset | | | | | 11.7 | $3.3^{*}$ |
| | Flower size | 12.1 | $2.3^{*}$ | | | | |

# DISCUSSION

## Effects of agricultural intensification at different spatial scales

Several studies have shown that complete understanding of biodiversity patterns in agricultural landscapes requires their evaluation at multiples scales (Tscharntke et al. 2005; Concepción et al. 2008). Our study shows that the plant composition and the CWM flower traits in the field margin responded to the landscape variables, as measured by PAL, whereas in the field centre their response is more dependent on local characteristics, i.e. on farming practices at field level. Our results are consistent with the findings of Guerrero et al. (2014), who showed that the response of plant traits in field centre is driven by agricultural intensification at field but not at landscape scale. José-María et al. (2011) found that species plant composition can be affected more by farming practices and field position than by the surrounding landscape. Soil disturbance can affect plant species composition in the field centre, whereas the simplification of landscape complexity can influence the plant composition in field margins (José-María et al. 2011; Solé-Senan et al. 2014). Our results thus support that the farming practices have a higher effect in the field centre than in the field margin.

Despite the different effects of PAL and farming practices on the plant species composition and the CWM traits in the field centre and margin, the flower visitor composition was affected by PAL independently of the position within the field. This reflects the ability of insects to spill-over from the field margin to the field center diluting the effect of farming position. According to Batáry et al. (2011), the response of flower visitors to the management intensity is moderated by the landscape. The landscape structure can influence on the availability of food and nesting and mating habitats, which are required by flower visitors (Kremen et al. 2007). For instance, Andersson et al. (2013) found that the species composition of pollinator communities was modified by the landscape homogeneity, mainly caused by agricultural intensification. Similarly, the species composition of some beetle assemblages was modified by the agricultural land use at landscape scale (Cole et al. 2002). Our results suggest that environmental measures at landscape scale (PAL) can affect the flower visitor community, which support the maintenance of ecosystem services, such as pollination (e.g. Batáry et al. 2013).

### Relationships between plant composition and flower visitor communities

Our study indicates that plant species composition in the field margin influenced the flower visitor composition in both sampling years. Some studies have shown that the reproductive success and persistence of plants can be affected by the diversity and community composition of flower visitors (Fontaine et al. 2006; Albrecht et al. 2012), but also plants influenced the flower visitor community (Mayer et al. 2011). For instance, Schaffers et al. (2008) showed that the plant species composition thriving in a grassland is the most effective predictor of arthropod assemblage composition, which included bees, hoverflies and some beetle families. Our research also shows that the plant species composition located in the field centre did not affect the flower visitor composition. This result might be related with the lower abundance of plant and flower visitor in the field centre compared with the margin. For instance, the abundance of Apoidea and Coleoptera were 1.8 and 2.2 times lower in the field centre than in the margin, respectively (data not shown). In addition, the spatial and temporal arrangement of flowers in the plant community can influence the insect visits (Thompson 2001). We suggested that the simplification of landscape can have an indirect effect on flower visitor composition, via changes in plant composition in the field margin in agricultural landscapes.

### Effects of CWM flower traits on flower visitor composition

The wildflower resources characterized by the CWM flower traits influenced the flower visitor community located in the centre and the margin of studied fields. As we hypothesized, each group of the flower visitor community (Apoidea, Coleoptera and Diptera) had a different response to CWM flower traits. The differences in floral design (e.g. size, morphology, colour, floral rewards) and floral display (e.g. arrangement of inflorescence) determine the success of insect foraging on a specific flower type (Goulson 1999), but this choice can also be based in multiple flower traits (Hegland and Totland 2005).

Although the composition of plant and flower visitor communities varied in response to the factors considered among years, the flower visitor community response was maintained for specific flower traits. The flower colour affected the flower visitor composition in the field margin, whereas the flower size influenced the composition in field centre. According to colour preferences described in pollination syndromes, bees and coleopterans prefer blue and white flowers, respectively, and flies are more attracted by yellow and white flowers (Faegri and Van Der Pijl 1979). CWM is more influenced by traits of dominant plants; therefore, this could be the main reason because the CWM colours of flowers that correlate with the main axes of variation of flower visitor community composition do not coincide with the ones reported in the literature. However, we also found some indications that there is a linkage between flower colour and some elements of the insect community. For instance, some families of Apoidea responded to red flower colour, which in our sampled fields correspond to species that are classified as flowers pollinated by hymenopterans, according to BiolFlor database. We also observe a biological significance pattern, as families of different groups of flower visitors have similar responses to the same flower colours in both sampling years. In a study that also evaluated the CWM colour of flowers, Fornoff et al. (2017) showed that the green reflectance was negatively correlated with species richness and visitation frequency, particularly of bees, which was the pollinator group more diverse and with higher visitation rates. However, other studies indicated contrasted relationships, as e.g. Reverté et al. (2016) did not find a relationship between the pollinator composition and the flower colour in some Mediterranean communities (grasslands and scrublands), suggesting that the same corolla colour may attract different pollinators. Moreover, they also suggested that other flower traits as the floral rewards or the corolla depth can influence the preferences of pollinators. Our findings showed that flower visitor composition (Coleoptera and Diptera) did not only respond to the flower colour, but also to the flowering onset in the field margins of the second year. For instance, Guerrero et al. (2014) found that management intensification promotes an earlier flowering in the arable plant communities, probably as early flowering species may avoid the stronger negative effects of crop competition. In this sense, some flower visitors can respond to this pattern, and they may be attracted by plant species with an earlier flowering.

Our results also showed that the composition of Diptera assemblage responded to the flower size of the dominant plants in the field centre (e.g. Bibionidae correlating with larger flowers). The flower size can affect the attractiveness of a plant for pollinators, varying the rates of visitations (Stanton 1987; Elle and Carney 2003). Some studies have demonstrated a discrimination of the pollinators based on flower size, which preferred the population with the largest flowers (Elle and Carney 2003; Kennedy and Elle 2008). This pollinator preference can be caused by the positive correlation between the corolla width and the floral reward (Kennedy and Elle 2008). In addition, in the field centre, the wildflower resources are surrounded by cereal crops, therefore, a large flower size also may increase the flower visibility for flower visitors, which concentrate their activity in field margins.

## CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Agricultural intensification at field and landscape levels interacts with the plant and flower visitor community and the CWM of flower traits. On the one hand, the field management should be considered in the plant conservation measures in Mediterranean arable landscapes, promoting low-intensity agricultural practices. On the other hand, environmental measures at landscape level must be considered to promote the maintenance of ecosystem services mediated by the flower visitor community, such as pollination. Some measures may include the creation of landscape features such as field margins. However, all flower visitors did not respond uniformly to plant community traits. Therefore, a previous selection of the plant species based on their flower traits is recommended, to develop the field margins that support the conservation of specific flower visitors and, in turn, sustain the pollination services in highly intensified agricultural landscapes.

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# SUPPLEMENTARY MATERIAL

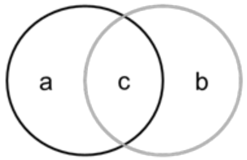
**Table S1.** Results of Pearson correlation coefficients among community-weighted flower trait values obtained in both sampling years (2013 and 2015).

| | Flower size | Flowering onset | Blue colour | Green colour | Pink colour | Purple colour | Red colour | Various colours | Violet colour | White colour |
|---|---|---|---|---|---|---|---|---|---|---|
| Flowering onset | -0.422** | | | | | | | | | |
| Blue colour | 0.027 | -0.417** | | | | | | | | |
| Green colour | -0.110 | 0.051 | -0.130 | | | | | | | |
| Pink colour | -0.175 | 0.021 | -0.163 | -0.054 | | | | | | |
| Purple colour | 0.199 | -0.104 | -0.149 | -0.058 | -0.206 | | | | | |
| Red colour | 0.757** | -0.208 | -0.154 | -0.176 | -0.202 | 0.015 | | | | |
| Various colours | 0.084 | -0.013 | 0.125 | -0.048 | 0.113 | -0.001 | 0.071 | | | |
| Violet colour | 0.013 | -0.063 | -0.018 | 0.163 | 0.034 | -0.215 | -0.061 | -0.073 | | |
| White colour | -0.444** | 0.405** | -0.150 | -0.100 | -0.200 | -0.355** | -0.270* | -0.180 | -0.156 | |
| Yellow colour | -0.119 | 0.045 | -0.223 | 0.151 | 0.095 | -0.274* | -0.129 | -0.165 | 0.155 | -0.368** |

Significance levels are as follows: * p < 0.05 and ** and p < 0.01

**Table S2.** Variation partitioning of the various unique fractions (outside of the circles' intersection, *a* and *b*) and overlap (inside the intersection, *c*) of the effect of different explanatory variables (PAL and crop type and management) on plant composition, community weighted mean (CWM) values of flower traits and flower visitor composition.

| | **Plant composition** | | | **CWM flower traits** | | | **Flower visitor composition** | | |
|---|---|---|---|---|---|---|---|---|---|
| | a | c | b | a | c | b | a | c | b |
| **2013** | | | | | | | | | |
| Field centre | 0.063 | 0.005 | 0.111 | 0.051 | 0.008 | 0.128 | 0.122 | 0.000 | 0.075 |
| Field margin | 0.059 | 0.000 | 0.047 | 0.118 | 0.000 | 0.033 | 0.099 | 0.006 | 0.040 |
| **2015** | | | | | | | | | |
| Field margin | 0.054 | 0.002 | 0.062 | 0.054 | 0.000 | 0.041 | 0.261 | 0.000 | 0.050 |



a = variation explained by PAL
b = variation explained by management and crop type
c = variation explained by both PAL and management and crop type

**Table S3.** Results of co-correspondence analyses (CoCA) testing correlations between plant and flower visitor community composition for each sampling year (2013 and 2015). Cross-corr. axes 1 and 2 represent the cross-correlation between the first and second Co-CA axes, respectively; total inertia represents the amount of variation in each community; explained variation represents the amount of variation explained by all Co-CA axes; Fist axis lambda (p-value) represents the test statistic and p-value for testing the cross-correlation between the two communities in the first axis. Bold values represent significant values, $P < 0.05$.

| **Year** | **Field position** | **Community 1** | **Community 2** | **Cross-corr. axes 1** | **Cross-corr. axes 2** | **Total inertia comm. 1** | **Total inertia Comm. 2** | **Total variation (all axes)** | **First axis lambda (p-value)** |
|---|---|---|---|---|---|---|---|---|---|
| 2013 | Centre | Plant | Flower visitor | 0.85 | 0.83 | 6.56 | 0.87 | 0.27 | 0.061 (0.512) |
| | Margin | Plant | Flower visitor | 0.95 | 0.94 | 4.64 | 0.77 | 0.20 | **0.052 (0.004)** |
| 2015 | Margin | Plant | Flower visitor | 0.92 | 0.92 | 7.46 | 0.69 | 0.27 | **0.089 (0.001)** |

**Table S4.** Plant trait data (selection of the 25 most abundant species) and species abbreviation of wildflower resources surveyed during both years (2013 and 2015). Plants were identified according to de Bolòs et al. (2005).

| **Species** | **Species abbreviation** | **Flower Size (cm)** | **Flowering Onset (month)** | **Flower colour** |
|---|---|---|---|---|
| *Anagallis arvensis* L. | Ana_arv | 0.80 | 2 | Blue |
| *Anacyclus clavatus* (Desf.) Pers. | Ana_cla | 2.50 | 5 | White |
| *Ballota nigra* L. | Bal_nig | 1.43 | 4 | Purple |
| *Borago officinalis* L. | Bor_off | 2.75 | 2 | Blue |
| *Calendula arvensis* (Vaill.) L. | Cal_arv | 2.25 | 2 | Yellow |
| *Capsella bursa-pastoris* (L.) Medik. | Cap_bur | 0.40 | 1 | White |
| *Carduus tenuiflorus* Curtis | Car_ten | 0.85 | 5 | Pink |
| *Convolvulus arvensis* L. | Con_arv | 1.75 | 4 | White |
| *Diplotaxis erucoides* (L.) DC. | Dip_eru | 1.20 | 1 | White |
| *Echium vulgare* L. | Ech_vul | 1.55 | 2 | Pink |
| *Euphorbia serrata* L. | Eup_ser | 0.20 | 2 | Green |
| *Fumaria officinalis* L. | Fum_off | 0.75 | 2 | Purple |
| *Fumaria parviflora* Lam. | Fum_par | 0.55 | 2 | White |
| *Galium aparine* L. | Gal_apa | 0.23 | 6 | White |
| *Galium lucidum* All. | Gal_luc | 0.43 | 5 | White |
| *Galium spurium* L. | Gal_spu | 0.12 | 5 | White |
| *Galium tricornutum* Dandy | Gal_tri | 0.22 | 5 | White |
| *Malva sylvestris* L. | Mal_syl | 4.50 | 3 | Purple |
| *Marrubium vulgare* L. | Mar_vul | 0.65 | 5 | White |
| *Medicago polymorpha* L. | Med_pol | 0.40 | 2 | Yellow |
| *Medicago sativa* L. | Med_sat | 0.90 | 4 | Various |
| *Papaver rhoeas* L. | Pap_rho | 5.50 | 3 | Red |
| *Polygonum aviculare* L. | Pol_avi | 0.35 | 4 | Pink |
| *Polygonum convolvulus* L. | Pol_con | 0.40 | 5 | Green |
| *Potentilla reptans* L. | Pot_rep | 1.75 | 1 | Yellow |
| *Scandix pecten-veneris* L. | Sca_pec | 0.75 | 2 | White |
| *Silybum marianum* (L.) Gaertn. | Sil_mar | 1.60 | 5 | Purple |
| *Sonchus oleraceus* L. | Son_ole | 2.00 | 2 | Yellow |
| *Stellaria media* (L.) Vill. | Ste_med | 0.70 | 1 | White |
| *Torilis arvensis* (Huds.) Link | Tor_arv | 0.35 | 5 | White |
| *Trifolium campestre* Schreb. in Sturm | Tri_cam | 0.42 | 4 | Yellow |
| *Veronica arvensis* L. | Ver_arv | 0.35 | 3 | Blue |
| *Veronica hederifolia* L. | Ver_hed | 0.70 | 3 | Blue |
| *Veronica persica* Poir. in Lam. | Ver_per | 1.05 | 1 | Blue |
| *Vicia cracca* L. | Vic_cra | 1.10 | 4 | Violet |
| *Vicia sativa* L. | Vic_sat | 2.00 | 4 | Blue |
| *Vicia villosa* Roth | Vic_vil | 1.40 | 3 | Violet |
| *Viola arvensis* Murray | Vio_arv | 1.25 | 4 | White |

**Table S5**. Family abbreviation of flower visitor composition showed in Co-correspondence analysis (CoCA) and total flower visitor abundance collected by pan traps in field centre and margin in both sampling years (2013 and 2015).

| Group | Family | Abbreviation | 2013<br>Centre | 2013<br>Margin | 2015<br>Margin |
|---|---|---|---|---|---|
| Apoidea | Andrenidae | And | 60 | 32 | 198 |
| | Apidae | Api | 98 | 98 | 444 |
| | Halictidae | Hal | 75 | 68 | 487 |
| | Megachilidae | | 6 | 11 | 23 |
| | Melittidae | | 2 | 4 | 2 |
| Coleoptera | Anthicidae | | 2 | 2 | 2 |
| | Buprestidae | Bup | 175 | 361 | 471 |
| | Cantharidae | | 40 | 29 | 70 |
| | Cerambycidae | Cer | 16 | 42 | 76 |
| | Chrysomelidae | Chr | 12 | 40 | 80 |
| | Dasytidae | Das | 211 | 273 | 889 |
| | Malachiidae | Mal | 78 | 45 | 170 |
| | Mordellidae | Mor | 57 | 294 | 163 |
| | Nitidulidae | Nit | 905 | 985 | 9976 |
| | Oedemeridae | Oed | 49 | 123 | 443 |
| | Scarabaeidae | Sca | 525 | 592 | 241 |
| Diptera | Agromyzidae | Agr | 34 | 31 | 292 |
| | Anthomyiidae | Ant | 2992 | 1554 | 3155 |
| | Bibionidae | Bib | 368 | 124 | 38 |
| | Bombyliidae | | 70 | 45 | 35 |
| | Calliphoridae | Cal | 31 | 43 | 19 |
| | Carnidae | | 7 | 12 | 39 |
| | Ceratopogonidae | | 2 | 3 | 0 |
| | Chloropidae | Chl | 897 | 302 | 2673 |
| | Conopidae | | 3 | 4 | 36 |
| | Empididae | | 29 | 32 | 60 |
| | Hybotidae | Hyb | 267 | 204 | 1060 |
| | Keroplatidae | | 0 | 1 | 6 |
| | Lonchopteridae | | 0 | 2 | 3 |
| | Milichiidae | | 48 | 10 | 27 |
| | Muscidae | Mus | 15 | 33 | 61 |
| | Mycetophilidae | | 0 | 2 | 0 |
| | Phoridae | Pho | 1044 | 707 | 4302 |
| | Sarcophagidae¡ | Sar | 69 | 87 | 76 |
| | Scatopsidae | Sca | 66 | 66 | 132 |
| | Sciaridae | Sci | 555 | 166 | 698 |
| | Sepsidae | Sep | 116 | 115 | 89 |
| | Simuliidae | | 1 | 1 | 1 |
| | Stratiomyidae | | 52 | 41 | 22 |
| | Syrphidae | Syr | 130 | 146 | 347 |
| | Tachinidae | Tac | 69 | 88 | 58 |
| | Tephritidae | | 27 | 16 | 11 |
| | Therevidae | | 0 | 1 | 1 |
| | Ulidiidae | Uli | 5 | 2 | 115 |

# CAPÍTULO 4

## Patterns of flower visitor abundance and fruit set in a highly intensified cereal cropping system in a Mediterranean landscape

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# SUMMARY

In intensive agricultural landscapes, decreased pollinator numbers have often been attributed to the loss of natural habitats. However, several studies show that certain mass flowering crops, such as oilseed rape (OSR), can alter the pattern of pollinator abundance at a field and landscape level. These studies have focused mainly on bees; information about the effect of OSR crops on other taxa is missing. We evaluated the abundance of bees and other (non-bee) flower visitors, and the fruit set of insect-pollinated target plants (*Raphanus sativus* and *Onobrychis viciifolia*) on the margins of OSR and cereal fields in landscapes with varying densities of non-cropped habitats (landscape structure). The presence of OSR crops and wildflower resources in field margins had varying effects on the abundance of bees and non-bee flower visitors. Bee abundance was enhanced by OSR crops, but decreased in complex landscapes. On the other hand, the abundance of non-bee flower visitors depended on the landscape structure, particularly on the location of cereal fields. Despite the numerous and diverse communities of pollinators attracted by OSR crops and wildflower resources, fruit set was enhanced only for generalist insect pollinated plant species, because competition processes for pollinators affect specialist plant species. We conclude that the incorporation of OSR crops and maintenance of wildflower resources in agri-environmental schemes should be considered to improve the pollination services in agricultural landscapes highly dominated by cereal fields.

**Keywords**: mass flowering crops, bees, non-bee flower visitors, pollination syndromes, landscape structure, wildflower resources

# INTRODUCTION

Agricultural intensification is one of the main causes of biodiversity decline (Matson et al., 1997; Tilman et al., 2001) and disruption of associated ecosystem services (Kleijn et al., 2009). Agricultural intensification from within field to landscape levels is generally correlated with the decline of wild pollinators and the services they provide to crops and wild plants (Steffan-Dewenter et al., 2005; Biesmeijer et al., 2006; Potts et al., 2010). Changes in land-use and landscape structure affect the composition of nearby habitats and pollinators, in turn affecting their interactions at individual, population and community levels (Kremen et al., 2007).

In agricultural landscapes that are devoted to the production of crops that do not require insect pollination, such as cereal plantations, the provision of pollination services to insect-pollinated plants can be compromised. For example, insect pollinators may depend on the presence of natural and semi-natural vegetation that provides shelter, nesting sites and food. Pollinators can be displaced from natural and semi-natural vegetation to cropland if pollinators benefit from mass flowering crops or wildflower resources thriving in the field margins (Tscharntke et al., 2012).

For diverse agronomic and economic benefits, mass flowering crops have been incorporated into crop rotations to break-up the continuous cultivation of cereals (Pimentel et al., 1997; Klein et al., 2007; Kennedy et al., 2013). Moreover, these crops can reduce the food resource limitations for pollinators, thereby supporting pollination services (Westphal et al., 2003; Diekötter et al., 2010). Oilseed rape (*Brassica napus* L., OSR) is one of the most commonly used mass flowering crops because of the demand for its oil and increasing biofuel demand (FAO, 2015). OSR crops offer a highly rewarding resource of pollen and nectar that enhance pollinator abundance (Morandin and Winston, 2005). Most studies have evaluated the effect of OSR crops on bees, particularly honeybees, which are considered the most economically valuable pollinator (McGregor, 1976). Although other pollinators could also be enhanced by OSR crops in intensive agricultural landscapes, information about this relationship and about the abundance and diversity of other taxa remains scarce.

In highly intensified arable landscapes, the presence of patches of non-cropped habitats, remnants of natural and semi-natural habitats, and the presence of wildflower resources in the field margins is extremely important for maintaining pollination services (Banaszak, 1992; Walther-Hellwig and Frankl, 2000; Garibaldi et al., 2011; Winfree et al., 2011). Several studies have demonstrated that recurrent resource pulses of mass flowering crops, such as OSR crops, can be beneficial to pollinators only when natural and semi-natural habitats are present in agroecosystems (Westphal et al., 2009; Holzschuh et al., 2013; Diekötter et al., 2014; Riedinger et al., 2015). For instance, Holzschuh et al. (2013) showed that the abundance of a wild bee species was enhanced when nesting habitats were present, particularly depending on the amount of OSR crops. Similarly, some studies proposed that the establishment of various mass flowering crops together with the maintenance of semi-natural habitats are effective conservation measures for maintaining bumblebee populations (*e.g.* Westphal et al., 2003, 2009). However, most researchers have studied landscapes where mass flowering crops are dominant. It is still unknown how discrete areas of mass flowering crops and wildflower resources at field margins, together with non-cropped habitats, can affect pollinators in cereal-dominated landscapes.

Plant communities can affect the interactions between any given plant species and its ensemble of pollinators by reducing the frequency of pollinators' visits through competition (Pleasants, 1981) or increasing this frequency via facilitation (Waser and Real, 1979; Moeller, 2004). As a consequence, changes in plant communities may strongly affect pollination processes by negatively or positively altering the pollinator's availability and effectiveness in delivering conspecific pollen.

The vulnerability of plant reproduction to land-use change depends on such factors as a species reliance on pollinators and the effect of changes in the surrounding landscape on pollination processes. Species specific plant traits, including breeding system, specialization of plant pollinator interaction, and floral traits, strongly influence the likelihood that plant-pollination interactions are disrupted (Bond, 1995; Aizen et al., 2002; Vázquez and Simberloff, 2002; Potts et al., 2010), therefore affecting their sensitivity to land-use changes. Declines in pollination services negatively affect obligate outcrossing plants, especially insect pollinated plants (Aguilar et al., 2006). Specialist insect-pollinated species are more vulnerable to changes than generalist species (Biesmeijer et al., 2006), but the magnitude of the effects can depend on landscape structure. For instance, some wild plants can compete with the crop for attention from a limited number of pollinators in the vicinity of mass flowering crops (Holzschuh et al., 2011). On the other hand, wild plants can benefit from mass flowering crops if pollinators do not limit their visits to the most attractive flowers, such as from crops, but also visit surrounding areas (Rathcke, 1983). For instance, Hanley et al. (2011) showed an increase of pollination success of wild margin plants owing to the presence of mass flowering crops. However, to our knowledge there are few studies that evaluate the impact of mass flowering crops on generalist and specialist plants species in intensive agricultural landscapes.

The purpose of this study was to evaluate the effect of the presence of a neighbouring mass flowering crop (oilseed rape), landscape structure (represented by the density of non-cropped habitats) and wildflower resources on the abundance of bees (Hymenoptera: Apoidea) and other flower visitors (non-bees) and on the fruit set of two target species with different pollination syndromes. We also compared the abundance of bees, non-bee flower visitors and target species (generalist *vs.* specialist) to landscape structure. We tested the following hypotheses: (i) availability of resources provided by OSR crops increases the abundance of both bee and non-bee flower visitors and the fruit set of target species, (ii) increasing density of non-crop habitats in the landscape enhances the abundance of bees and non-bee flower visitors and improves the fruit set of target plants in field margins near OSR crops, and (iii) the abundance of bees and non-bee flower visitors increases with wildflower resources, but this effect is negligible in field margins near OSR crops; therefore, if wildflower resources benefit the pollination process, this effect is more noticeable in field margins nearby cereal crops. However, competition and facilitation interactions for resources coupled with specific pollinator requirements can affect fruit set patterns.

# MATERIALS AND METHODS

## Study region

The experiment was conducted between April and June of 2014 in Catalonia, Spain (41° 48′–41° 40′ N; 1° 14′–1° 28′ E) (Fig. 1). The study area is primarily devoted to the production of cereals, but it also includes some mass flowering crops. The natural and semi-natural vegetation is composed of a complex mosaic of woodlands, which are mainly pines (*Pinus nigra* Arnold) but also include evergreen oaks (*Quercus rotundifolia* Lam.), deciduous oaks (*Quercus faginea* Lam.), shrublands and perennial-dominated grasslands. The remnants of this vegetation are mainly linear features intermingled between arable fields. Annual mean minimum and maximum temperatures were 8.3 and 17.4 °C, respectively, and the accumulated annual precipitation was 631.8 mm. For our study, we chose an area of 20× 15 km with over 75% of arable land (Fig. 1). Here, we selected 21 margins between oilseed rape (OSR) and cereal fields and another 21 between cereal (C) fields. Hereinafter, we call these margins OSR-C and C-C field margins, respectively. The studied field margins were located at least 400 m from each other. During the study, the landscape was dominated by cereal crops (mainly barley and wheat) due to the extremely low rainfall in autumn 2013 that forced farmers to cultivate cereals instead of oilseed rape. Fertilization was based on pig slurry and mineral fertilizers for both crop types. The OSR crop fields were treated with insecticides before the onset of the flowering period. Weed control was conducted in both cereal and oil seed rape fields by application of herbicides, also during late winter before the onset of crop flowering. Field edges were regularly managed by application of wide-spectrum herbicides. These extremely intense farming operations, as well as the recurrent herbicide deposition into the field margins due to drift, resulted in species-poor plant communities.

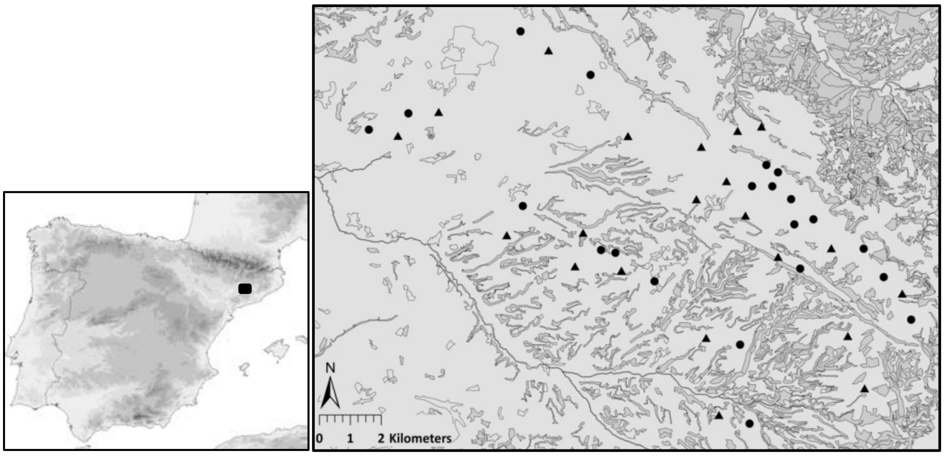

**Figure 1.** The studied oilseed rape-cereal and cereal-cereal field margins, represented by circles and triangles, respectively, were located in Catalonia, Spain in highly intensified cereal cropping landscapes (light grey – arable fields, dark grey – other habitats).

### Density of non-cropped habitats

The length of the field-margin network was used as a measure of landscape structure. Field margins were digitized on orthophotomaps (1:25,000). The field margins were defined as linear elements composed of natural and semi-natural habitats. Field margins were digitized as single lines (arcs in GIS terminology) when margins were narrower than 3 m, whereas patches of natural and semi-natural habitats wider than 3 m were delineated as surfaces (polygons in GIS terminology). The sum of all linear elements (all arcs, irrespective of whether they were single arcs or arcs enclosing polygons) within a radius of 500 m around each selected field was defined as the density of non-cropped habitats (ranging from 6.64 to 28.52 km). All GIS operations were conducted on ArcGIS 10 (ESRI, 2010).

### Wildflower resources and OSR flower resources

We evaluated the richness and abundance of plants that produce nectar and pollen in OSR-C and C-C field margins because the delivery of pollination services to a target plant depends on the surrounding plant community. The surveys were performed once a week for six weeks. During each survey, the cover of plants in full bloom in three parallel transects of 1 × 12 m in the study field margins was assessed. The central transect corresponded to the non-crop vegetation (1 m width) between fields, and the two adjacent transects corresponded to the first metre of the oilseed rape or cereal field in the OSR-C field margins or to the first metre of the cereal field in the C-C margins (Fig. 2). Abundance of wildflower resources was assessed by visual estimation of the relative cover of flowers in the transect area. All flowering plants were identified to the species level (according to de Bolòs et al., 2005). Flower resource and pollinator surveys were evaluated simultaneously during the OSR blooming period.

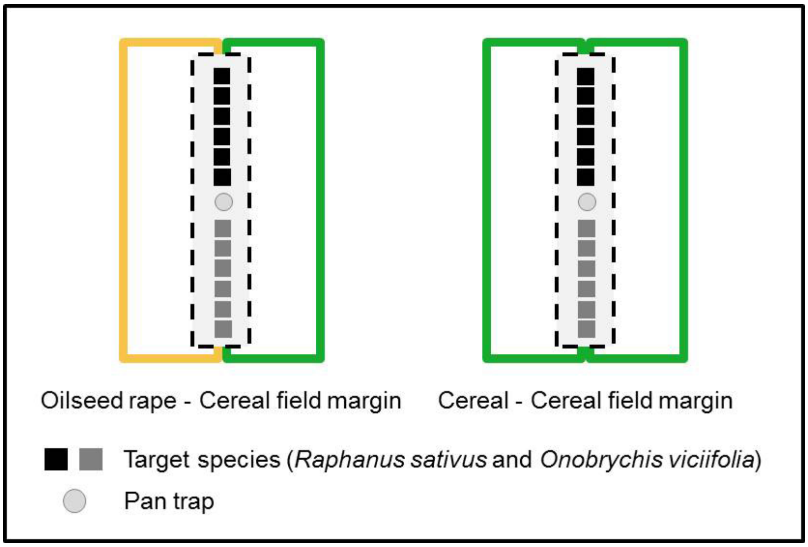

**Figure 2**. Schematic representation of oilseed rape-cereal and cereal-cereal field margins in the study system. In the centre of the central transects, we placed six individuals of each target species (*Raphanus sativus* and *Onobrychis viciifolia*) at both sides of a pan trap.

### Bee and non-bee flower visitors surveys

For each field margin, we placed one pan trap consisting of three cups (500 mL, 160 mm diameter) painted with UV reflecting blue, yellow and white spray. The use of pan traps is a common passive sampling method which evaluates the activity density of flower-visiting insects and does not cause a lasting negative effect on populations (Gezon et al., 2015). Pan traps were located 1 m above the ground and 1 m apart from each group of target species (Fig. 2). They were filled with water and a small amount of detergent to reduce surface tension and were operated for 24 h. The surveys were performed once a week for six weeks under favourable weather conditions (no rain, low wind speeds, and diurnal temperatures above 18 °C). Samples were stored in 70% alcohol, and specimens were identified to the family level. We evaluated bees (Hymenoptera: Apoidea) and non-bee flower visitors (specimens of Hymenoptera excluding Apoidea, Coleoptera and Diptera orders) separately.

### Target species

*Raphanus sativus* L. (Brassicaceae) and *Onobrychis viciifolia* Scop. (Fabaceae) were used as target species to assess the fruit set in OSR-C and C-C margins fields. *R. sativus* is an annual plant that produces numerous symmetrical actinomorphic white flowers on a broad-branched inflorescence. It is self-incompatible (Young and Stanton, 1990) and commonly visited by a wide array of pollinators, such as honey bees, bumblebees, wild bees, hoverflies and butterflies (Steffan-Dewenter and Tscharntke, 1999; Albrecht et al., 2007). The perennial *O. viciifolia* produces numerous zygomorphic melliferous pink flowers on several unbranched inflorescences (Kells, 2001). It is an outbreeding insect pollinated species, almost entirely pollinated by bumblebees, honey bees, and wild bees (Hayot Carbonero et al., 2011). *Onobrychis viciifolia* is considered to be an obligate insect-pollinated species

(Hanley et al., 2008). To achieve correct zygomorphic flower handling, pollinators can adopt only a limited number of physical orientations. In contrast, the simple morphology of actinomorphic flowers facilitates their handling and promotes visits from a wider variety of pollinators (Wolfe and Krstolic, 1999). This difference in the diversity of pollinators that can effectively interact with their flowers, allows the classification of *R. sativus* as a generalist insect-pollinated species and *O. viciifolia* as a specialist insect-pollinated species.

### Fruit set

Seeds of the target species were sown in 5 L pots filled with commercial garden soil (mixture of peat, vermiculite and clay) under outdoor conditions at the Experimental Fields Service of the University of Barcelona (January 2014). Six individuals of each target species were transported to each field margin at the beginning of the flowering season of OSR crop fields (April 2014). The plants were grouped by species and placed on either side of the pan trap along the field margin (Fig. 2). The species were 2 m apart, while plants of the same species were separated by a distance of 1 m. Plants were watered every four to seven days, depending on the weather conditions. After six weeks and once the OSR flowering season had concluded, target species were transported back to the Experimental Fields Service and placed in a greenhouse that were absent of pollinators. Plants were watered periodically for two weeks to facilitate the proper development of fruits from the pollinated flowers. Flower buds were periodically removed to avoid overestimation of unpollinated flowers. Afterwards, the number of well-developed fruits and total number of flowers that had not been pollinated were counted, and these were identified by the scars that were left on the branches. Fruit set was calculated as the proportion of flowers that set fruit.

## Statistical analyses

The effects of the type of field margin, wildflower resources and density of non-cropped habitats on the abundance of flower visitors and fruit set were tested separately for the bees, non-bee flower visitors, and each target species. The effects of field margin type (OSR-C *vs.* C-C), wildflower resources and density of non-cropped habitats on bee and non-bee flower visitors abundance were analysed with generalized least squares using the *nlme* package for R statistical software (Pinheiro et al., 2017). Because some interactions between the variables were significant, separate models were used for the different field margins (OSR-C and C-C). OSR flower resources were included in the OSR-C field margin model to evaluate its effect at field-level on bee and non-bee flower visitor abundance. The fruit set of each target species (*R. sativus* and *O. viciifolia*) was analysed separately. For each target species, a generalized linear mixed-effects model with binomial error distribution was evaluated using the lme4 package in R (Bates et al., 2015). We separated models by different field margins (OSR-C *vs.* C-C) when the interactions between a field margin and another explanatory variable were significant.

As the bee and non-bee flower visitor data did not meet the assumptions of normality and constant variance of errors, log transformation was conducted. Afterward, the abundance of bee and non-bee flower visitor data was scaled separately by survey. In addition, and to consider the potential effects caused by the spatial structure of the data, we estimated the spatial autocorrelation in the residuals of each model by means of the Moran’s I autocorrelation index, using the *spdep* package (Bivand and Piras, 2015) an implementation of Legendre’s routines (2000)[1] for R. Although some residual spatial autocorrelation was found for log transformed data, it disappeared in scaled data; therefore no correction for spatial autocorrelation was applied to the models. For the fruit set data, no adjustment or correlation was needed, since no spatial autocorrelation was detected on original data. We used the Akaike information criterion (AIC) to select the best model for each analysis (Akaike, 1973). All statistical analyses were conducted using R version 3.1.1 (R Core Team, 2016).

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[1] An R-package implementing these routines to obtain the Moran's I correlogram is available from J. M. Blanco-Moreno, on request.

# RESULTS

### Overview of flower resources and bee and non-bee flower visitors

Overall, 61 and 51 insect-pollinated species in flower were recorded in the OSR-C and C-C field margins, respectively, during the experimental period (Table A.1 in Appendix A). We recorded 4242 hymenopterans (15 families, plus Parasitica and Symphyta specimens), 3500 coleopterans (25 families) and 23,565 dipterans (40 families) in 21 OSR-C field margins. On 21 study C-C field margins, we recorded 2682 hymenopterans (15 families, plus Parasitica and Symphyta specimens), 2796 coleopterans (23 families) and 13,050 dipterans (41 families) (Table A.2 in Appendix A).

### Abundance of bee and non-bee flower visitors

Bee abundance was significantly higher in OSR-C than in C-C field margins (Table 1; $p < 0.001$). Of the remaining variables examined, only the density of non-cropped habitats had a significant effect. The density of non-cropped habitats had a negative effect on bee abundance in the studied field margins (Table 1; $p = 0.006$). Multiple significant interactions were found between the explanatory variables (field margin type, density of non-cropped habitats and wildflower resources) and the abundance patterns of the non-bee flower visitors (Table 1). Consequently, we used separate models for each field margin type (OSR-C and C-C) (Table 2). On the one hand, the abundance of non-bee flower visitors was significantly affected by the interaction between OSR flower resources and wildflower resources (Table 2; $p = 0.003$) in the OSR-C field margins. Wildflower resources had a significant effect on the abundance of non-bee flower visitors only at low OSR flower resources (Fig. 3). On the other hand, the abundance of non-bee flower visitors in the C-C field margin was increased by wildflower resources when the density of non-cropped habitats was low (Table 2; Fig. 4). In contrast, the effect of wildflower resources was negligible when the density of non-cropped habitats was high (Fig. 4).

**Table 1.** Effect of field margin type (Oilseed rape-Cereal *vs*. Cereal-Cereal), density of linear features of non-cropped habitats (radius: 500 m) and wildflower resources on the abundance of bees (Hymenoptera: Apoidea) and non-bee flower visitors (Hymenoptera excluding Apoidea, Coleoptera and Diptera). Statistical significance was obtained from type III ANOVAs with the minimum adequate model.

| | **Bee abundance** | | | | **Non-bee flower visitor abundance** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Est** | **F** | **Df** | **p-value** | **Est** | **F** | **Df** | **p-value** |
| Field margin type (FMT) | 0.90 | 50.14 | 1 | < **0.001** | 1.02 | 73.55 | 1 | < **0.001** |
| Density of non-cropped habitats (DnH) | -0.29 | 7.82 | 1 | **0.006** | -0.33 | 10.43 | 1 | **0.001** |
| Wildflower resources (WfR) | -0.03 | 0.09 | 1 | 0.764 | 0.12 | 1.79 | 1 | 0.182 |
| FMT × DnH | 0.26 | 3.63 | 1 | 0.058 | 0.34 | 6.61 | 1 | **0.011** |
| FMT × WfR | -0.14 | 1.24 | 1 | 0.267 | -0.35 | 8.23 | 1 | **0.005** |
| DnH × WfR | -0.06 | 0.26 | 1 | 0.612 | -0.38 | 10.07 | 1 | **0.002** |
| FMT × DnH × WfR | 0.26 | 2.72 | 1 | 0.101 | 0.39 | 6.81 | 1 | **0.010** |

Bold values represent significant values, $P < 0.05$.

**Table 2**. Effect of density of linear features of non-cropped habitats (radius: 500 m), wildflower resources and OSR flower resources on the abundance of non-bee flower visitors (Hymenoptera excluding Apoidea, Coleoptera and Diptera) for different field margin types (Oilseed rape-Cereal *vs*. Cereal-Cereal). Statistical significance was obtained from type III ANOVAs with the minimum adequate model.

| | **OSR-C field margin** | | | | **C-C field margin** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Est** | **F** | **Df** | **p-value** | **Est** | **F** | **Df** | **p-value** |
| Density of non-cropped habitats (DnH) | | | | | -0.33 | 8.32 | 1 | **0.005** |
| Wildflower resources (WfR) | -0.22 | 10.82 | 1 | **0.001** | 0.12 | 1.43 | 1 | 0.234 |
| OSR flower resources (OfR) | -0.02 | 0.09 | 1 | 0.771 | | | | |
| DnH × WfR | | | | | -0.38 | 8.04 | 1 | **0.005** |
| DnH × OfR | | | | | | | | |
| WfR × OfR | 0.19 | 9.21 | 1 | **0.003** | | | | |
| DnH × WfR × OfR | | | | | | | | |

Bold values represent significant values, $P < 0.05$.

### Fruit set of target species

The fruit set of *R. sativus* was higher in the OSR-C field margins than in the C-C field margins (Table 3; p = 0.011). However, the density of non-cropped habitats and wildflower resources did not significantly affect the fruit set (Table 3; p = 0.770 and p = 0.685, respectively). The fruit set of *O. viciifolia* showed a significant interaction between the field margin type and density of non-cropped habitats (Table 3; p = 0.042). Therefore, the effects on fruit set of *O. viciifolia* were evaluated separately for the OSR-C and C-C field margins. Fruit set improved according to density of non-cropped habitats and reduced according to the wildflower resources in the OSR-C field margins (Table 4; p = 0.015 and p = 0.022, respectively). In the C-C field margins, the fruit set of *O. viciifolia* was high under two different scenarios, as shown by the statistically significant interaction between wildflower resources and density of non-cropped habitats (Table 4; p = 0.038). Either a high cover of wildflower resources and a low density of non-cropped habitats or a low cover of wildflower resources and a high density of non-cropped habitats increased the fruit set of *O. viciifolia* in the C-C field margins (Fig. 5).

**Table 3.** Effect of field margin types (Oilseed rape-Cereal *vs*. Cereal-Cereal), density of linear features of non-cropped habitats (radius: 500 m) and wildflower resources on the fruit set of target species (*Raphanus sativus* and *Onobrychis viciifolia*). Statistical significance was obtained from type III ANOVAs with the minimum adequate model. Bold values represent significant values, P < 0.05.

| | ***Raphanus sativus*** | | | | ***Onobrychis viciifolia*** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Est** | **$\chi^2$** | **Df** | **p-value** | **Est** | **$\chi^2$** | **Df** | **p-value** |
| Field margin type (FMT) | 0.66 | 6.51 | 1 | **0.011** | 0.36 | 2.59 | 1 | 0.107 |
| Density of non-cropped habitats (DnH) | 0.04 | 0.09 | 1 | 0.770 | -0.14 | 0.81 | 1 | 0.367 |
| Wildflower resources (WfR) | -0.05 | 0.16 | 1 | 0.685 | -0.11 | 0.85 | 1 | 0.356 |
| FMT × DnH | | | | | 0.49 | 4.14 | 1 | **0.042** |
| FMT × WfR | | | | | | | | |
| DnH × WfR | -0.26 | 3.50 | 1 | 0.062 | -0.34 | 5.70 | 1 | **0.017** |
| FMT × DnH × WfR | | | | | | | | |

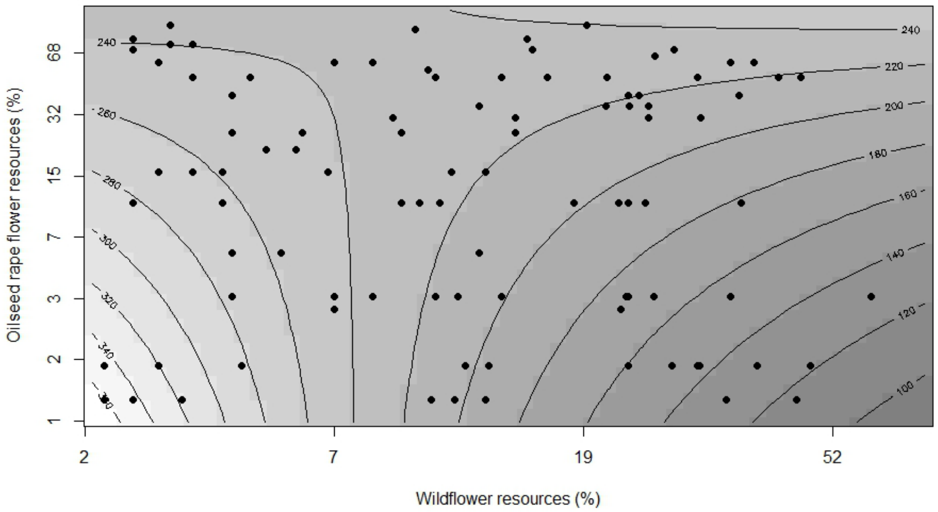

**Figure 3.** Effect of wildflower resources (%) and oilseed rape flower resources (%) on non-bee flower visitors abundance (Hymenoptera excluding Apoidea, Coleoptera and Diptera) in oilseed rape-cereal field margins. Lines are generalized least squares model predictions from the model described in Table 2. Note that the log scale is used in the axes.

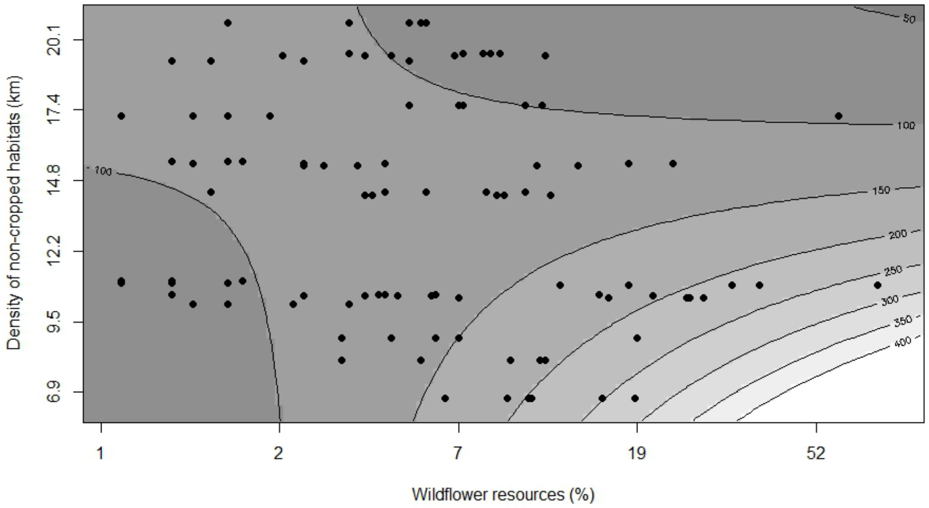

**Figure 4.** The effect of wildflower resources (%) and density of non-cropped habitats (km) on the abundance of non-bee flower visitors (Hymenoptera excluding Apoidea, Coleoptera and Diptera) in cereal-cereal field margins. Lines are generalized least squares model predictions from the model described in Table 2. Note that the log scale is used in the axes.

**Table 4**. The effect of density of linear features of non-cropped habitats (radius: 500 m) and wildflower resources on fruit set of *Onobrychis viciifolia* for different field margin types (Oilseed rape-Cereal *vs*. Cereal-Cereal). Statistical significance was obtained from type III ANOVAs with the minimum adequate model. Bold values represent significant values, P < 0.05.

| | **OSR-C field margin** | | | | **C-C field margin** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Est** | **$\chi^2$** | **Df** | **p-value** | **Est** | **$\chi^2$** | **Df** | **p-value** |
| Density of non-cropped habitats (DnH) | 0.15 | 5.94 | 1 | **0.015** | -0.22 | 1.11 | 1 | 0.291 |
| Wildflower resources (WfR) | -0.15 | 5.21 | 1 | **0.022** | -0.21 | 0.88 | 1 | 0.348 |
| DnH × WfR | | | | | -0.61 | 4.31 | 1 | **0.038** |

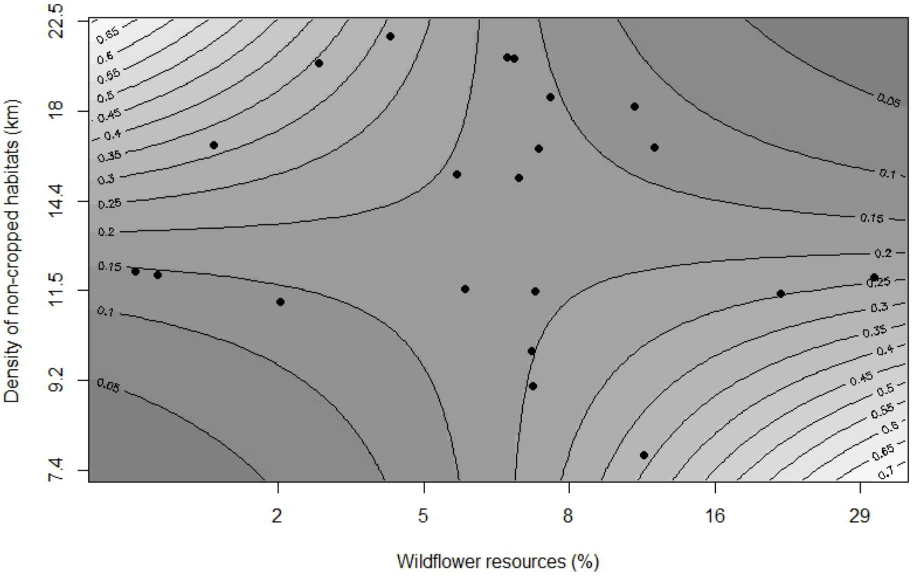

**Figure 5.** The effect of wildflower resources (%) and density of non-cropped habitats (km) on the fruit set of *Onobrychis viciifolia* in cereal-cereal field margins. Lines are generalized linear mixed-effects model predictions from the model described in Table 4. Note that the log scale is used in the axes.

# DISCUSSION

## Abundance of bee and non-bee flower visitors

Most studies have shown that the presence of mass flowering crops, such as oilseed rape, with the support of natural and semi-natural habitats enhances the abundance of bees (Westphal et al., 2009; Le Féon et al., 2010; Holzschuh et al., 2013). Our results showed that bee abundance increased in response to the scattered presence of OSR crops, although the effect of wildflower resources resulted negligible in highly intensive cereal-dominated landscapes. OSR crops are an important food resource for bees during the blooming period (Holzschuh et al., 2011; Westphal et al., 2009). Both honey bees and wild bees are more abundant nearby mass flowering crops, although the latter may depend also on the presence of non-crop habitats (Holzschuh et al., 2011).

The scattered presence of OSR crops also promoted an increased abundance of non-bee flower visitors. But, the effect of wildflower resources was only observed when it coincided with a low percentage of OSR flower resources. Holzschuh et al. (2011, 2016) found a dilution effect of pollinators related to the expansion of mass flowering crops in the landscape. However, in our study, the absence of resources provided by OSR flowers and resource-poor margins promoted the dispersal of non-bee flower visitors to adjacent areas rich in floral resources. Our results strongly support that flower visitors abundance has multiple responses depending on the local and landscape context (Steffan-Dewenter et al., 2002), and these responses can vary temporally. Nevertheless, our research suggests what may occur in the short-term, but it cannot indicate what might happen on flower visitor populations in the long-term.

Our study indicates that changes in landscape structure, as assessed as the density of non-cropped habitats, affected bee and non-bee flower visitors differently. The abundance of bees varied in complex, but not in simple landscapes. Some studies have shown that agricultural areas in complex landscapes benefit from a spillover effect from adjacent semi-natural habitats (see Tscharntke et al., 2012). Our results suggest a temporal concentration of bee populations in the resources provided by OSR fields principally. On the other hand, landscape structure had a significant effect on the abundance of non-bee flower visitors when OSR fields were absent. This landscape effect depends on the abundance of wildflower resources at a local scale, as shown by the statistically significant interaction between wildflower resources and density of non-cropped habitats. The local effect of wildflower resources was positive in a structurally simple landscape, *i.e.*, a low density of non-cropped habitats, but not in a complex landscape. According to Kleijn et al. (2011), scarce patches with resources in a poor landscape concentrate more individuals than numerous patches with resources in a rich landscape. Our data suggest that non-bee flower visitors are concentrated where resources are offered by wildflowers in a landscape with a low density of non-cropped habitats, but not in a landscape with a high density of non-cropped habitats. In a complex landscape, flower visitors can disperse throughout the mosaic of non-cropped habitat patches in the landscape. This response of non-bee flower visitors to the landscape structure should be considered in conservation management decisions. As such, the preservation or restoration of wildflower resources in a simple landscape could have a greater effect on the abundance of non-bee flower visitors than in complex landscapes (Tscharntke et al., 2012).

Despite the positive effect of mass flowering crops on flower visitor abundance, particularly on bees, it is necessary to consider their long-term effects on their populations. Westphal et al. (2009) showed that an increase of mass flowering crops did not translate into a higher reproductive success of bumblebee colonies, because resources were limited when the flowering season finished. In addition, long-term effects on insect populations can be related with the inputs of pesticides to the crops. Recent research has demonstrated the negative effects of pesticides used in mass flowering crops, for example, on honeybees (Di Prisco et al., 2013) and on bumblebees (Stanley et al., 2015), and other alternatives may have the same negative effects on insects (Klatt et al., 2016). Therefore, the benefits offered by mass flowering crops, in terms of resources, could be diminished by the continuous pesticide applications.

### Fruit set of target species

Mass flowering crops had a positive effect on the fruit set of *R. sativus*. In contrast, the fruit set of *O. viciifolia* was affected by wildflower resources at a local scale and by the density of non-cropped habitats at landscape scale, but not by OSR crops. Despite the high attractiveness of mass flowering crops for pollinators that could enhance the fruit set of *R. sativus* and *O. viciifolia* plants, their contrasting patterns of fruit set reflects strong differences in their interactions with flower resources at landscape and field scales. An increase of the fruit set of *R. sativus* is attributable to a facilitation process (Rathcke, 1983), as the pollinator visits could be enhanced due to the presence of the OSR crop. Although a facilitation process can occur between different floral forms (Ghazoul, 2006), we suggest that the same generalized open floral structure of OSR and *R. sativus* may represent an advantage over *O. viciifolia*, as its pollination appears to involve more specialized interactions. In addition to morphological differences, another advantage of the generalist species is the similitude in flower color with OSR, compared with the specialist species. Bee visits are more frequent between similar flowers than between flowers with different colors (Chittka et al., 1999). Therefore, OSR flower traits combination can increase the pollinator visits rates to similar flowers (*R. sativus*) than to dissimilar flowers (*O. viciifolia*), affecting their fruit sets. The fruit set of *O. viciifolia* was enhanced in complex landscapes (high density of non-cropped habitats) but diminished due to wildflower resources of nearby OSR crops. The decrease in fruit set can be explained by the competition for pollinators between the target species and species thriving in plant communities in the immediate vicinity (Rathcke, 1983). For instance, Holzschuh et al. (2011) indicated a decrease in the seed set of *Primula veris* L. thriving in grasslands when the percentage of OSR fields in the landscape increased, suggesting a competition for pollinators between the study species and crop.

In the vicinity of cereal fields, the fruit set of *O. viciifolia* increased with a higher percentage of wildflower resources, especially in a simple landscape. However, fruit set was enhanced in a complex landscape with a low percentage of wildflower resources. Since bees do not respond in the same way as the pollination of *O. viciifolia*, the effect of the density of non-cropped habitats in cereal-dominated landscapes suggests that this species could be pollinated by both bee and non-bee flower visitors. Specialist plant species, such as *O. viciifolia*, could be more vulnerable to changes in the landscape, such as the density of non-cropped habitats, than generalist plant species, such as *R. sativus*. In simple landscapes, wildflower resources may have attracted numerous pollinators that enhance the fruit set of *O. viciifolia*. Conversely, the competition process for pollinators occurs between the wildflower resources and target species in complex landscapes.

These results support our hypothesis that wildflower resources have different effects on the fruit set of both target species, because generalist and specialist plant species respond differently to the landscape structure. The effect of OSR crops and wildflower resources could be beneficial only for generalist plant species with flowers similar in shape or color to the OSR, because competition might affect specialist plant species. Further studies that include direct observation measures of pollinators may help to explain how the landscape and local factors can affect the flower visitation rates and define the main service provider in species with different pollination syndromes.

# IMPLICATIONS FOR MANAGEMENT

Our study suggests that the inclusion of OSR or other mass flowering crops within crop rotation schemes can promote temporally the increase of the abundance of bee and non-bee flower visitors. However, the long-term effects of mass flowering crops on pollinator abundance must be considered in conservation management decisions. In addition, the management of other factors, as wildflower resources and density of non-cropped habitats, must also be considered to improve pollination service in highly intensified Mediterranean agricultural landscapes.

Fruit set of target plants could not depend exclusively on pollinator abundance in the landscape, as it appears to also depend on the composition of the pollinator community. Our results support that plants with different pollination syndromes may react differently to changes in the environment, and this is likely to be attributed to the interaction between flower resources (both crop and wildflower) and the quality of the pollinator community. Our results highlight the importance of developing agri-environmental schemes that include OSR crops and maintain wildflower resources in field margins to improve the pollination services delivered by a diverse ensemble of pollinators in agricultural landscapes dominated by cereal fields.

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# SUPPLEMENTARY MATERIAL

## Appendix A. Supplementary material

**Table A.1.** The average abundance of wildflower resources present in the six surveys (April to June 2014) for the oilseed rape-cereal and cereal-cereal field margins in Central Catalonia.

| | **Wildflower resources surveys** | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **C-C field margins** | | | | | | **O-C field margins** | | | | | |
| | **1** | **2** | **3** | **4** | **5** | **6** | **1** | **2** | **3** | **4** | **5** | **6** |
| *Adonis flammea* Jacq. | 0.2 | 0.2 | 1.0 | | | | | | | | | |
| *Alyssum alyssoides* (L.) L. | | | | | | | | | | 1.7 | | |
| *Anacyclus clavatus* (Desf.) Pers. | 0.3 | 0.33 | 20.4 | 1.3 | 2.8 | 1.0 | 3.1 | 3.1 | 3.2 | 7.1 | 5.0 | 5.8 |
| *Anthemis arvensis* L. | | | 6.8 | 3.1 | | | | | 6.0 | 3.7 | | |
| *Astragalus stella* L. | | | | | 0.8 | | | | | | | |
| *Brassica napus* var. *oleifera* (Moench) DC. | 0.3 | 0.3 | 0.8 | 0.3 | | | 18 | 18 | 15.2 | 6.9 | 3.3 | 0.3 |
| *Bryonia dioica* Jacq. | | | | | 0.2 | 0.2 | | | | | | |
| *Calendula arvensis* L. | | | 0.2 | | 0.8 | | 8.3 | 8.3 | 1.3 | 1.7 | 0.8 | 0.2 |
| *Capsella bursa-pastoris* (L.) Medik. | 0.8 | 0.8 | 0.6 | | 0.2 | | 4.5 | 4.5 | 1.2 | 0.8 | 0.7 | 0.2 |
| *Carduus pycnocephalus* L. | | | | 1.0 | 1.0 | 1.0 | | | | 6.7 | 3.3 | |
| *Carduus tenuiflorus* Curtis | | | | | | | 0.2 | 0.2 | 1.7 | 3.3 | 1.7 | 15.8 |
| *Caucalis platycarpos* L. | 0.2 | 0.2 | | | | | 0.3 | 0.3 | 0.2 | 0.2 | | |
| *Centaurea cyanus* L. | 0.2 | 0.2 | 0.8 | 1.0 | 0.6 | 1.7 | | | | | | |
| *Cerastium glomeratum* Thuill. | | | | | | | 0.2 | 0.2 | | | | |
| *Chaenorhinum minus* (L.) Lange | | | | | | | 0.2 | 0.2 | | | | |
| *Cirsium arvense* (L.) Scop. | | | | | | 0.8 | | | | | | 0.2 |
| *Convolvulus arvensis* L. | | | | | 0.4 | 0.2 | | | | 1.0 | 0.3 | 0.3 |
| *Crepis bursifolia* L. | | | | | | | 1.67 | 1.67 | | | | |
| *Crepis capillaris* (L.) Wallr. | | | | | | | | | | | | 0.17 |
| *Crepis sancta* (L.) Bornm. | 0.2 | 0.2 | | | | | | | 0.4 | 0.2 | | |
| *Crepis vesicaria* L. | | | | | | | | | | 0.2 | 0.2 | |
| *Diplotaxis erucoides* (L.) DC. | 0.4 | 0.4 | 0.9 | 0.9 | 0.9 | 0.2 | 2.2 | 2.2 | 3.3 | 2.1 | 2.4 | 2.4 |
| *Erodium ciconium* (L.) L'Hér. in Aiton | 0.3 | 0.3 | 2.8 | 1.8 | 1.7 | 1.8 | 2.4 | 2.4 | 4.3 | 3.8 | 5.4 | 3.1 |
| *Erodium cicutarium* (L.) L'Hér. in Aiton | 0.2 | 0.2 | | 0.5 | | 0.2 | | | 0.2 | 0.2 | | |
| *Erodium malacoides* (L.) L'Hér. | | | | | 0.2 | | | | | | | |
| *Erucastrum nasturtiifolium* (Poir.) O.E. Schulz | | | 0.3 | | | | | | | | | |
| *Euphorbia characias* L. | | | | | | | | | | 2.2 | | |
| *Euphorbia falcata* L. | 0.3 | 0.3 | 0.3 | 0.3 | 0.2 | | | | | | 0.8 | |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Euphorbia serrata* L. | 0.2 | 0.2 | | 1.7 | 0.6 | | 0.3 | 0.3 | 1.3 | 0.8 | 0.8 | 1.0 |
| *Fallopia convolvulus* (L.) Á. Löve | | | | | | | | | | 1.0 | 0.3 | 1.0 |
| *Fumaria officinalis* L. | 2.8 | 3.1 | 4.0 | 2.1 | 1.7 | 1.3 | 3.0 | 2.9 | 4.4 | 2.5 | 1.0 | 0.7 |
| *Fumaria parviflora* Lam. | | | 0.2 | | | | | | | | | |
| *Galium aparine* subsp. *aparine* L. | | | | 0.2 | 0.9 | 0.5 | | | | | | 0.2 |
| *Galium aparine* subsp. *spurium* (L.) Hartm. | | | | 0.3 | 1.7 | | | | | | | |
| *Geranium rotundifolium* L. | | | | | | | 0.7 | 0.7 | 1.0 | 0.9 | 0.2 | |
| *Heliotropium europaeum* L. | | | | | 0.2 | 0.2 | | | | | | |
| *Hypecoum imberbe* Sm. in Sibth. | 0.2 | 0.2 | | | 0.8 | | 1.0 | 1.0 | 3.3 | 2.2 | 2.3 | |
| *Hypecoum pendulum* L. | | | | | | | 0.2 | 0.2 | | | | |
| *Hypecoum procubens* L. | | | 0.2 | | | | 0.2 | 0.2 | 3.8 | 2.9 | 0.2 | 0.6 |
| *Jasminum fruticans* L. | | | | | | | 0.2 | 0.2 | 6.7 | 6.7 | 7.5 | 3.3 |
| *Lamium amplexicaule* L. | | | | | | | | | 0.8 | | | |
| *Lathyrus cicera* L. | 0.2 | 0.2 | 0.8 | | | | | | 1.0 | 0.3 | | |
| *Leontodon taraxacoides* (Vill.) Mérat | | | | | | | | | 0.2 | | | |
| *Lepidium draba* L. | 11.7 | 11.7 | 5.2 | 0.9 | 0.8 | | 5.2 | 5.2 | 2.5 | 0.9 | 1.0 | 0.2 |
| *Lithospermum arvense* L. | 1.8 | 1.8 | 0.7 | 0.8 | 0.8 | 0.8 | 0.2 | 0.2 | 1.5 | 1.3 | 0.7 | 0.4 |
| *Lithospermum fruticosum* L. | | | | | | | | | | | | 0.8 |
| *Malva sylvestris* L. | | | 1.4 | 2.5 | 1.7 | 2.1 | | | 0.5 | 1.4 | 1.0 | 1.4 |
| *Medicago lupulina* L. | | | | | | | | | 0.2 | 0.2 | 0.2 | 0.2 |
| *Medicago minima* (L.) L. | | | | | | | | | | | 1.7 | |
| *Medicago orbicularis* (L.) Bartal. | | | | | | | | | | | 0.5 | |
| *Medicago polymorpha* L. | 1.0 | 1.0 | 20.0 | 0.8 | | 0.3 | 0.2 | 0.2 | 0.9 | | | |
| *Medicago rigidula* (L.) All. | | | | | | | | | | | 0.2 | |
| *Medicago sativa* L. | | | | | | | | | | | 0.2 | 0.8 |
| *Medicago truncatula* Gaertn. | | | | | 0.8 | | | | | | | |
| *Muscari comosum* (L.) Mill. | | | 0.2 | | | | | | 0.2 | | | |
| *Muscari neglectum* Guss. ex Ten. | 0.2 | 0.2 | | | | | 0.2 | 0.2 | | | | |
| *Onobrychis viciifolia* Scop. | | | 0.2 | | | | | | | | | |
| *Ononis spinosa* L. | | | | | | | | | | | | 1.7 |
| *Ornithogalum umbellatum* L. | | | | | | | 0.2 | 0.2 | | | | |
| *Papaver argemone* L. | | | | | | | 0.2 | 0.2 | | 5.0 | 0.6 | 1.7 |
| *Papaver hybridum* L. | | | 0.8 | | | | | | | | | |
| *Papaver rhoeas* L. | 1.3 | 1.3 | 5.1 | 3.6 | 2.6 | 3.6 | 0.8 | 0.8 | 5.1 | 9.6 | 6.4 | 7.0 |
| *Polygonum aviculare* L. | | | | | | | 1.8 | 1.8 | 0.3 | 1.7 | 1.7 | 2.5 |
| *Reseda phyteuma* L. | | | 0.2 | | | | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.8 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Salvia verbenaca* L. | 10.0 | 10.0 | 0.8 | 1.7 | 1.7 | 3.3 | | | | | | |
| *Scandix pecten-veneris* L. | 3.3 | 3.3 | 3.3 | 0.6 | 0.8 | | 3.0 | 3.0 | 6.0 | 0.6 | 0.8 | |
| *Senecio vulgaris* L. | 0.2 | 0.2 | | | 0.2 | 0.2 | 0.4 | 0.4 | 0.2 | 0.2 | | |
| *Silene vulgaris* (Moench) Garcke | | | | 0.5 | 0.7 | | | | | | | |
| *Silybum marianum* (L.) Gaertn. | | | | 0.3 | 1.0 | 0.2 | | | | | 0.3 | 0.2 |
| *Sisymbrium officinale* (L.) Scop. | | | | | | | 0.8 | 0.8 | | | | |
| *Solanum nigrum* L. | | | | | | 0.2 | | | | | | |
| *Sonchus oleraceus* L. | | | | | 0.8 | | 0.8 | 0.8 | | 0.2 | | |
| *Sonchus tenerrimus* L. | | | | | | | | | | 0.2 | | 0.3 |
| *Taraxacum officinale* Weber in Wiggers | | | | | | | | | 0.2 | 0.2 | | |
| *Torilis nodosa* (L.) Gaertn. | | | | | 0.2 | 0.2 | | | | | | |
| *Veronica hederifolia* L. | 0.2 | 0.2 | | | | | | | | | | |
| *Veronica pérsica* Poir. in Lam. | | | | | | | | | | | 0.8 | |
| *Vicia peregrina* L. | 0.5 | 0.5 | 1.8 | 0.9 | 0.8 | | | | 0.8 | 0.2 | 2.5 | |
| *Vicia sativa* L. | | | | | | | | | 1.3 | 3.3 | 0.2 | |

**Table A.2.** Total non-bee flower visitor (Hymenoptera excluding Apoidea, Coleoptera and Diptera) and bee (Hymenoptera: Apoidea) abundance collected by pan traps during the six surveys (April to June 2014) in the oilseed rape-cereal and cereal-cereal field margins in Central Catalonia.

| **Crop** | **Order** | **Flower visitor surveys** | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | **1** | **2** | **3** | **4** | **5** | **6** | |
| OSR | Coleoptera | 276 | 631 | 1,450 | 311 | 281 | 551 | |
| | Diptera | 2,207 | 4,194 | 9,115 | 5,031 | 1,500 | 1,518 | |
| | Hymenoptera (excluding Apoidea) | 83 | 202 | 500 | 487 | 387 | 418 | |
| | Bees | 108 | 312 | 448 | 693 | 306 | 440 | |
| Cereal | Coleoptera | 122 | 246 | 1,268 | 285 | 417 | 458 | |
| | Diptera | 1,771 | 2,661 | 4,718 | 1,980 | 842 | 1,078 | |
| | Hymenoptera (excluding Apoidea) | 55 | 115 | 393 | 316 | 362 | 228 | |
| | Bees | 28 | 169 | 433 | 241 | 165 | 247 | |
| **Total** | | 4,650 | 8,530 | 18,325 | 9,344 | 4,260 | 4,938 | 50,047 |

# DISCUSIÓN GENERAL

El estudio de los efectos de la intensificación agrícola sobre la biodiversidad ha adquirido una gran relevancia en la literatura científica en los últimos años. En este contexto, muchos estudios han evaluado las consecuencias generadas por dicha intensificación sobre los visitantes florales, en particular, sobre las abejas (apoideos). Sin embargo, el conocimiento acerca de los efectos sobre otros visitantes florales, como coleópteros y dípteros, es mucho menor. Asimismo, muchos de estos estudios han inferido, a partir de los resultados obtenidos en los visitantes florales o por su interacción con las plantas, las posibles consecuencias en la polinización. No obstante, la evaluación directa de la polinización, a través de medidas como la producción de frutos, proporciona un enfoque más preciso de los efectos de la intensificación agrícola sobre este servicio ecosistémico. En este estudio se evalúan los efectos de la intensificación agrícola, a diferentes niveles, sobre la abundancia y composición de los principales grupos de visitantes florales, que incluyen apoideos, coleópteros y dípteros. También se evalúan los efectos sobre la producción de frutos en dos especies diana con diferente grado de especialización en su interacción con los visitantes florales (generalista y especialista). A continuación, se detallan los principales resultados obtenidos, así como también las implicaciones para la gestión de dichos paisajes agrícolas.

Diversos estudios han demostrado que la reducción del área dedicada al uso agrícola favorece el incremento de los visitantes florales en el paisaje (Bommarco et al., 2010; Westphal et al., 2008; Winfree, Aguilar, Vázquez, LeBuhn, & Aizen, 2009). Esto coincide con los resultados encontrados en nuestro estudio, en donde el gradiente de intensificación agrícola a nivel de paisaje (PAL) afectó la abundancia de los visitantes florales, debido a las diferencias en la intensidad del uso de la tierra (Capítulo 1). El PAL también afectó la composición de los visitantes florales, pero independientemente de la posición en el campo (Capítulo 3). El paisaje es un importante moderador de la respuesta de los visitantes florales a la intensidad de la gestión (Batáry et al., 2011). En este sentido, la disponibilidad de los recursos requeridos por los visitantes florales, como por ejemplo las fuentes de alimentación y los hábitats para la anidación, puede ser modificada por la estructura del paisaje (Kremen et al., 2007). Además, diversos estudios han demostrado que la intensificación agrícola ha generado cambios en la composición de la comunidad de los visitantes florales (Andersson, Birkhofer, Rundlöf, & Smith, 2013; Cole et al., 2002). Nuestros resultados indican que la comunidad de visitantes florales fue afectada por los cambios acontecidos a nivel de paisaje, en relación con la intensificación agrícola.

Asimismo, la intensificación a nivel de paisaje se correlaciona con cambios en la composición florística de las comunidades vegetales de los márgenes de los campos y de algunos atributos florales de la comunidad ("community-weighted mean", CWM). Dos de los atributos que cambiaron en relación con el PAL estaban relacionados con la atracción de los visitantes florales (tamaño y color de la flor), y el tercero de los atributos está relacionado con la temporalidad de la disponibilidad de recursos (inicio de la floración). En cambio, en el centro de los campos, la composición taxonómica de los ensamblajes de especies y el CWM de sus atributos florales respondieron, en gran medida, a las prácticas agrícolas a nivel de campo (Capítulo 3). Estos resultados coinciden con otros estudios donde se muestra que la composición y algunos atributos de las especies que colonizan el centro del campo (p. ej. área específica foliar, forma de vida), varían en relación con la intensificación agrícola a nivel de campo (Guerrero et al., 2014; José-María et al., 2011). Una de las principales causas de los cambios provocados en el centro del campo se atribuye a las periódicas perturbaciones del suelo, como consecuencia de la intensidad de la gestión de las prácticas agrícolas. Por el contrario, la composición de las comunidades que habitan en el margen del campo varía principalmente en relación con la simplificación del paisaje circundante (Solé-Senan et al., 2014). Nuestros resultados sugieren que las prácticas agrícolas deben ser consideradas en el mantenimiento de las comunidades vegetales, especialmente de aquellas localizadas en el centro de los campos.

Los efectos del PAL también se evidenciaron en la producción de frutos de las especies diana (Capítulo 1). Por ejemplo, el incremento del PAL afectó negativamente la producción de frutos de la especie de polinización generalista estudiada (*Raphanus sativus*), lo cual coincidió con la reducción de los visitantes florales, relacionado con la reducción de la superficie ocupada por hábitats seminaturales y naturales en el paisaje. Otros estudios han demostrado el efecto negativo en la producción de semillas y de frutos de especies generalistas al incrementar la distancia a dichos hábitats (Albrecht et al., 2007; Steffan-Dewenter & Tscharntke, 1999). Este patrón puede estar relacionado con la abundancia de los visitantes florales en el paisaje. Aunque los resultados presentados en el Capítulo 1 demostraron que el incremento del PAL se correlacionó positivamente con la abundancia de abejas y coleópteros (ver Morrison, Izquierdo, Plaza, & González-Andújar, 2017), mientras que los dípteros no se beneficiaron del aumento del PAL. Por ende, es importante considerar el conjunto total de visitantes florales que contribuyen a los servicios de polinización en los paisajes agrícolas.

## Efectos de la agricultura ecológica a nivel de paisaje y de parcela

Además de analizar las consecuencias generadas por la intensificación agrícola (PAL) sobre los visitantes florales y sobre la polinización, también es necesario evaluar los efectos de la implementación de los diversos esquemas agroambientales, como es la agricultura ecológica. Los efectos de este esquema sobre la abundancia y diversidad de visitantes florales han sido evaluados en múltiples estudios (Holzschuh et al., 2008; Purtauf et al., 2005; Rundlöf et al., 2008). Sin embargo, pocos estudios se han enfocado en la evaluación directa de la polinización, como es la producción de frutos. En concreto, en este estudio se evaluaron los efectos de la agricultura ecológica a nivel de paisaje (Capítulo 2) y de campo (Capítulo 1, 2 y 3), tanto en la abundancia y composición de los visitantes florales, como en la producción de frutos de especies diana.

A nivel de paisaje, la proporción de tierra arable bajo gestión ecológica (POL, por sus siglas en inglés) no incrementó la abundancia de las abejas, lo cual coincidió con otros estudios (Brittain et al., 2010; Happe et al., 2018). La abundancia de abejas puede ser favorecida por el incremento del uso agrícola en el paisaje (Capítulo 1), siendo mayor este efecto que el causado por la gestión a nivel de campo. En contraste, Holzschuh et al. (2008) mostró que un incremento en la proporción de cultivos ecológicos aumentó la riqueza y densidad de abejas. Este aumento fue promovido principalmente por las diferencias en la cobertura de recursos florales entre los campos orgánicos y convencionales, tanto en el margen del campo como en el cultivo. Es decir, las abejas podrían concentrar su actividad únicamente en aquellos parches que provean la mayor cantidad de recursos florales. En este sentido, en nuestro estudio el aumento de la POL no proporcionó las condiciones necesarias para incrementar la abundancia de dichos visitantes florales, por lo que otros factores como el PAL marcaron principalmente la respuesta de los visitantes florales.

En referencia al efecto de la POL sobre la producción de frutos de las plantas diana, este fue diferente dependiendo de su grado de especialización en la polinización de la planta diana (Capítulo 2). Los resultados indicaron que la POL únicamente incrementó la producción de frutos de la especie de polinización generalista (*R. sativus*). Esto coincide con otros estudios que muestran un efecto positivo de la agricultura ecológica en los servicios de polinización, en particular, sobre la producción de frutos de especies con una estructura floral abierta (Hardman et al., 2016; Power & Stout, 2011). Considerando que la POL no tuvo un efecto sobre la abundancia de abejas, las cuales son los principales visitantes florales de la especie especialista (*Onobrychis viciifolia*), el aumento de la producción de frutos de la especie de polinización generalista pudo estar mediado por la actividad de otros tipos de visitantes florales. Esto concuerda con los resultados presentados en los Capítulos 1 y 4, donde se muestra un incremento del éxito de la producción de frutos en las plantas diana que correlaciona positivamente con la abundancia de otros visitantes florales (coleópteros, dípteros y otros himenópteros), lo que nos permite hipotetizar que estos otros grupos de visitantes florales también pueden contribuir en los servicios de polinización en los paisajes agrícolas (Rader et al., 2016).

Por otra parte, la intensidad de la gestión (ecológica *vs.* convencional), el tipo de cultivo (cereal *vs.* leguminosa) y los recursos florales a nivel de parcela, también afectaron a los visitantes florales y a la polinización. Los campos ecológicos tuvieron un efecto positivo sobre los visitantes florales, independientemente del paisaje circundante (Capítulo 1). Sin embargo, este efecto positivo estuvo limitado al centro de los campos de cereales. En este sentido, los resultados sugieren un efecto restringido de la gestión ecológica a nivel de parcela, que no se extiende sobre los márgenes ni sobre el paisaje en que se encuentran inmersos los campos con dicha gestión. Por otro lado, los cultivos de leguminosas, aunque tuvieron un efecto positivo, fue menos pronunciado, y sólo algo más acusado sobre los coleópteros florícolas. El aumento de aquellos visitantes menos especializados parece relacionarse con una mayor disponibilidad de recursos florales en el paisaje. Sin embargo, en la evaluación realizada en el Capítulo 2, los recursos florales ubicados en el margen del campo no incrementaron la abundancia de las abejas, independientemente de la intensidad de la gestión del campo colindante. De igual forma, los campos de leguminosas no tuvieron un efecto sobre la abundancia de las abejas en los márgenes colindantes. Se ha demostrado que una alta abundancia de recursos en el paisaje, como la que constituye la floración de los campos de leguminosas, puede producir la dilución de los visitantes florales (Veddeler, Klein, & Tscharntke, 2006).

En los paisajes agrícolas, además de considerar el efecto de la abundancia de los recursos florales sobre los visitantes florales, también es necesario evaluar el efecto de la composición y el CWM de sus atributos florales sobre la composición de los visitantes florales. Los resultados presentados en el Capítulo 3 mostraron que la composición de la comunidad vegetal ubicada en el margen del campo influyó en la composición de los visitantes florales. Sin embargo, la composición de la comunidad vegetal localizadas en el centro del campo no explicó la composición de los visitantes florales. Estos resultados pueden estar relacionados con la baja abundancia de plantas y visitantes florales encontradas en el centro del campo, comparada con la encontrada en el margen (Capítulo 1). Este estudio sugiere que la simplificación del paisaje puede tener un efecto indirecto en la composición de los visitantes florales, a través de los cambios que se generan en la composición de recursos florales en los márgenes de los campos.

El CWM de los atributos florales influyó en la composición de la comunidad de visitantes florales, tanto en el centro como en el margen del campo (Capítulo 3). Es importante tener en cuenta que la respuesta de los grupos de visitantes florales (apoideos, coleópteros y dípteros) al CWM de los atributos florales fue diferente entre ellos. La preferencia de los insectos a visitar un tipo específico de flor depende del diseño floral, por ejemplo del color y el tamaño de la flor, de las recompensas florales y de la disposición de las flores en la inflorescencia (Goulson, 1999). Sin embargo, dicha elección también puede depender de múltiples atributos florales (Hegland &

Totland, 2005). En este estudio (Capítulo 3), se mostró que la respuesta de los visitantes florales a determinados atributos florales se mantuvo constante, a pesar de que la composición de las comunidades vegetales y de visitantes florales varió entre ambos años de muestreo (2013 y 2015). Por ejemplo, el color de la flor afectó la composición de los visitantes florales en el margen del campo, mientras que el tamaño de la flor influyó dicha composición en el centro del campo. Las preferencias de los visitantes florales por los colores de la flores no correspondieron con los expuestos en los síndromes clásicos de polinización (Faegri & Van Der Pijl, 1979). A pesar de ello, los resultados mostraron un patrón de importancia biológica, en el que las familias de los diferentes grupos de visitantes florales respondieron de forma similar a los mismos colores en ambos años de muestreo. No obstante, en otros estudios llevado a cabo en pastizales y matorrales mediterráneos no se encontró una relación entre los colores de la flor y la composición de los visitantes florales (Bosch et al., 1997; Reverté, Retana, Gómez, & Bosch, 2016).

La comunidad de visitantes florales, en particular los coleópteros y los dípteros, no solo respondieron al color de la flor, sino también a la fenología de los ensamblajes de la comunidad vegetal en el segundo año de muestreo (Capítulo 3). Esta respuesta pudo estar asociada al incremento de intensificación en el paisaje, que según Guerrero et al. (2014), promueve una floración más temprana de las comunidades vegetales, con el fin de evitar la competencia con los cultivos. En este sentido, la comunidad de visitantes florales pudo responder a este patrón a través del incremento de aquellas especies que se ven atraídas por las especies de fenología más temprana. Los resultados de este estudio también mostraron que la composición de los dípteros respondió al tamaño de la flor de las plantas en el centro del campo. Algunos estudios han demostrado que los visitantes florales pueden discriminar entre flores, basándose en el tamaño de la flor (Elle & Carney, 2003; Kennedy & Elle, 2008). Esta preferencia de los visitantes florales puede estar causada por la correlación positiva que hay entre el ancho de la corola y las recompensas florales (Kennedy & Elle, 2008). Además, los recursos florales que se encontraban en el centro del campo estaban rodeados por el cultivo (cereal), por lo que las flores de mayor tamaño pueden incrementar su visibilidad para los visitantes florales, los cuales concentran su actividad en los márgenes de los campos (Capítulo 1).

Las repercusiones, directas e indirectas, que estas variables ambientales tienen sobre la producción de frutos son variables, pues dependen tanto de las características de la planta que es polinizada como de las características del entorno inmediato de esta. En el Capítulo 1, donde se evaluó el efecto del incremento de PAL, no se encontraron diferencias en la producción de frutos de la especie de polinización generalista en el centro o en el margen de los campos con una alta intensidad de gestión. Sin embargo, los recursos florales favorecieron la producción de frutos de la especie diana. Por ejemplo, en los campos de cultivos de leguminosas, la producción de frutos no dependió de las condiciones del paisaje. Por el contrario, los recursos locales localizados en los márgenes y los bordes de los campos afectaron negativamente la producción de frutos, tanto de la especie generalista (*R. sativus*) como especialista (*O. viciifolia*) (Capítulo 2).

La comunidad vegetal puede afectar los servicios de polinización, por ejemplo, a través de la competencia por los polinizadores (Kremen et al., 2007; Pleasants, 1981). Sin embargo, la gestión ecológica y los cultivos de leguminosas afectaron positivamente la producción de frutos de ambas especies, siendo mayor el efecto sobre la especie especialista. En algunos casos, puede ocurrir el proceso de facilitación entre especies con formas florales similares (Ghazoul, 2006), y ambas pueden beneficiarse de la concentración de los visitantes florales. Nuestros resultados sugieren que el incremento en la producción de frutos fue mayor en la especie especialista debido a la similitud con las flores de los cultivos de leguminosa, ya que también pertenece a la familia Leguminosae. Por lo tanto, la disponibilidad temporal de los recursos ofrecidos por los cultivos de leguminosa puede afectar la producción de frutos de las especies.

### Efecto de los cultivos de floración masiva

Otra de las medidas a considerar en los paisajes agrícolas son los cultivos de floración masiva. En la evaluación realizada en el Capítulo 4, se encontró que la presencia de cultivos de colza dispersos en el paisaje incrementó la abundancia de las abejas (apoideos), así como la de otros visitantes florales (otros himenópteros, coleópteros y dípteros). Diversos estudios han mostrado que la presencia de cultivos de floración masiva, en conjunción con los hábitats naturales y seminaturales, incrementan la abundancia de las abejas (Holzschuh et al., 2013; Le Féon et al., 2010; Westphal et al., 2009). No obstante, nuestro estudio indica que los recursos florales de especies no cultivadas no tuvieron un efecto significativo sobre la abundancia de las abejas, y solo incrementaron la abundancia de otros visitantes florales cuando coincidieron con un bajo porcentaje de los recursos ofrecidos por el cultivo de colza. Por otro lado, algunos estudios han encontrado que la expansión de los cultivos de floración masiva pueden causar la dispersión de los polinizadores en el paisaje (Holzschuh, Dormann, Tscharntke, & Steffan-Dewenter, 2011; Holzschuh et al., 2016). Sin embargo, en los paisajes agrícolas mediterráneos con márgenes muy pobres en recursos florales, cuando los cultivos de colza ya no están en flor, se genera la dispersión de los visitantes florales. Estos resultados sugieren que la respuesta de la abundancia de los visitantes florales depende del contexto a nivel local y de paisaje.

Aunado al efecto de los cultivos de floración masiva, la estructura del paisaje (densidad de márgenes) también afectó la abundancia de las abejas y la de otros visitantes florales. La abundancia de abejas incrementó en los paisajes complejos, pero no en los simples. Se ha demostrado que las áreas agrícolas localizadas en paisajes complejos se benefician, a través del efecto de “spillover”, de las áreas naturales y seminaturales adyacentes (Tscharntke et al., 2012). En este sentido, nuestros resultados sugieren que la concentración temporal de la población de abejas se debe principalmente a los recursos ofrecidos por los cultivos de colza (Capítulo 4). Por otro lado, la estructura del paisaje afectó la abundancia de otros visitantes florales cuando el período de floración de los cultivos de colza había finalizado y, por tanto, cesó la disponibilidad de los recursos ofrecidos por el cultivo. En consecuencia, el efecto del paisaje dependió de la abundancia de los recursos florales a nivel local. Además, el efecto de estos recursos fue positivo en los paisajes simples (con una baja densidad de márgenes), pero no en los paisajes complejos (con una alta densidad de márgenes). Por lo tanto, es posible que estos otros visitantes florales se concentraran en las áreas con recursos florales ofrecidos por las plantas arvenses en paisajes con una baja densidad de márgenes, pero no en paisajes con una alta densidad. En estos paisajes complejos, en cambio, es factible que los visitantes florales se dispersaran en los hábitats que no estaban cultivados. Por estas razones, la estructura del paisaje debe ser considerada en la toma de decisiones de conservación y manejo, especialmente, para otros visitantes florales.

En relación con el efecto de los cultivos de floración masiva sobre la producción de frutos, se encontró un efecto positivo sobre la especie de polinización generalista (*R. sativus*). Por el contrario, la especie de polinización especialista (*O. viciifolia*) fue afectada por los recursos florales a nivel local y por la estructura del paisaje, sin embargo no por los cultivos de colza. Estos resultados reflejan importantes diferencias en la interacción de las especies diana con los recursos florales a nivel de parcela y de paisaje. Por una parte, el incremento en la producción de frutos de la especie de polinización generalista puede ser atribuido al proceso de facilitación (Rathcke, 1983), donde el incremento de las visitas de polinizadores (y en consecuencia de producción de frutos) se debe a la presencia de los cultivos de colza. Además de ello, la flor de la especie de polinización generalista presenta características similares a la del cultivo de colza (estructura floral abierta y colores similares), lo que pudo representar una ventaja sobre la especie de polinización especialista. Por lo tanto, la combinación de determinados atributos en las flores de colza pudo incrementar las visitas de los polinizadores en flores similares, como la de *R. sativus*. Por otra parte, la producción de frutos de la especie de polinización especialista incrementó en paisajes complejos, pero disminuyó debido a los recursos florales cerca de los cultivos de colza. Esta disminución puede atribuirse a la competencia por los polinizadores entre la especie de polinización especialista y la comunidad vegetal adyacente (Rathcke, 1983). En general, la especies especialistas son más vulnerables a los cambios en el paisaje que las especies generalistas (Biesmeijer et al., 2006). La producción de frutos de la especie de polinización especialista incrementó cuando aumentó la abundancia de los recursos florales cerca de los cultivos de cereal, especialmente en los paisajes simples. En los paisajes complejos, la producción de frutos incrementó cuando coincidió con un bajo porcentaje de recursos florales. Debido a que las abejas no respondieron de forma similar a la especie de polinización especialista, el efecto causado por la densidad de márgenes sugiere, a pesar de la especialización asumida, que esta especie pudo ser polinizada por otros visitantes florales, además de las abejas.. En los paisajes más simplificados, los recursos florales pudieron atraer numerosos visitantes florales que incrementaron la producción de frutos de la especie de polinización especialista. En contraste, en los paisajes complejos los recursos florales y la especie diana pudieron competir por los visitantes florales. En este sentido, las medidas orientadas a preservar los servicios ecosistémicos de polinización deben considerar tanto el nivel de parcela como el de paisaje para garantizar el éxito reproductivo de especies con diferentes grados de especialización en su polinización en los paisajes agrícolas.

# CONCLUSIONES

La tesis doctoral estudia el efecto de la intensificación agrícola a nivel de paisaje y de parcela sobre el funcionamiento de la polinización en los paisajes agrícolas mediterráneos dominados por los cultivos herbáceos extensivos, mediante el análisis de la abundancia y composición de los principales grupos de visitantes florales y la producción de frutos de especies diana con diferentes síndromes de polinización (generalista *vs*. especialista). A continuación, se enumeran las principales conclusiones:

1. La intensificación agrícola a nivel de paisaje afecta negativamente la abundancia de los visitantes florales, sin embargo, en la región de estudio este patrón se debe fundamentalmente a la respuesta de los dípteros, mientras que apoideos y coleópteros responden positivamente la a intensificación a nivel de paisaje.

2. La gestión ecológica a escala de parcela tiene un efecto positivo sobre la abundancia total de los visitantes florales. Estos efectos solo son importantes en el centro de los campos, y su relevancia es menor en los paisajes complejos y en los márgenes de los campos. Sin embargo, para los apoideos, que son consideradas los polinizadores más efectivos, los efectos de la gestión ecológica no se manifiestan a nivel de paisaje, ya que la proporción de tierra arable bajo gestión ecológica no incrementa su abundancia.

3. Cuando se considera la variación de los recursos florales a diferentes niveles, su incremento tiene un efecto positivo sobre la abundancia de todos los grupos de visitantes florales. Sin embargo, el incremento de dichos recursos en el centro de los campos, debido a los cultivos de leguminosas, solo promueve la abundancia de los visitantes florales pertenecientes al grupo de los coleópteros.

4. En paisajes con una alta proporción de tierra arable bajo gestión ecológica, los recursos florales localizados en los márgenes de los campos no generan un incremento de la abundancia de los apoideos. Por el contrario, los recursos ofrecidos por los cultivos de leguminosas causan una reducción de su abundancia en los márgenes.

5. Los cultivos de floración masiva y los recursos florales a nivel de parcela tienen diferentes efectos sobre la abundancia de apoideos y sobre la abundancia de otros visitantes florales. Los cultivos de colza incrementan la abundancia de apoideos, aunque esta disminuye en los paisajes complejos con más densidad de márgenes. La abundancia de otros visitantes florales depende de la estructura del paisaje; ya que se concentran en los recursos florales disponibles en los paisajes simples, pero no en los paisajes complejos.

6. Las respuestas de los visitantes florales a las características del paisaje, a la gestión y a la disponibilidad de recursos florales no se manifiestan de forma directa en cambios en la producción de frutos de plantas diana (fitómetros); por esta razón, es importante considerar simultáneamente los efectos sobre los visitantes florales y sobre los servicios que proveen, preferentemente sobre especies con grados de especialización en la polinización diferenciados.

7. La intensificación agrícola a nivel de paisaje afecta negativamente la producción de frutos de la planta de polinización generalista, pero esta es beneficiada mediante el incremento de los recursos florales a nivel de parcela.

8. La proporción de tierra arable bajo gestión ecológica a nivel de paisaje incrementa la producción de frutos de la especie de polinización generalista, pero no tiene un efecto sobre la especie de polinización

especialista. La producción de frutos de ambas especies puede incrementar debido a la disponibilidad de recursos florales a nivel de campo que concentra los visitantes florales en determinadas zonas del paisaje agrícola, pero también puede disminuir debido a la competencia con la oferta floral localizada en las inmediaciones.

9. Los cultivos de floración masiva tienen un efecto positivo sobre la producción de frutos de la especie de polinización generalista; por el contrario, los recursos florales a nivel de parcela y la estructura del paisaje afectan la producción de frutos de la especie de polinización especialista.
10. La intensificación agrícola, la intensidad de gestión, el tipo de cultivo y la distancia al margen del campo afectan la composición de la comunidad vegetal y sus atributos florales, mientras que la composición de familias de visitantes florales responde a la intensificación agrícola a nivel de paisaje.
11. Los atributos florales de la comunidad vegetal influencian la composición de familias de los visitantes florales; el color y el inicio de la floración afectan la composición en el margen del campo, mientras que el tamaño de la flor influencia la composición en el centro del campo.

## Implicaciones para la gestión y el desarrollo de medidas agroambientales

Los resultados obtenidos en los diferentes estudios constituyen una base para la implementación de medidas agroambientales a diferentes niveles, tanto de paisaje como de parcela, con el objetivo de armonizar la producción de los cultivos con el mantenimiento de los servicios ecosistémicos, como la polinización, en los paisajes cerealistas mediterráneos.

La mejora del servicio de la polinización en los paisajes agrícolas, mediado por la comunidad de visitantes florales, requiere la aplicación de medidas que consideren tanto la abundancia como la composición de esta comunidad. A pesar de que el incremento de la proporción de tierra arable bajo gestión ecológica parece no incrementar la abundancia de las abejas en los paisajes agrícolas estudiados, otros visitantes florales pueden beneficiarse de dichas condiciones. Además, las medidas agroambientales para promover la abundancia de los visitantes florales deberían evitar la simplificación del paisaje, mediante la conservación elementos de vegetación natural o seminatural, como son los márgenes de los campos, así como la implementación de la agricultura ecológica. Estos cambios tienen relación de manera directa, por una parte, con la estructura del paisaje agrícola, pero por otra parte con los efectos causados por su relación con la comunidad vegetal presente en estos sistemas agrícolas. Estas medidas, no solo pueden incrementar la abundancia de visitantes florales, sino que también pueden afectar a la composición de la comunidad, ya que las respuestas de los diferentes grupos de visitantes florales a los atributos florales de las comunidades vegetales no son uniformes. Por lo tanto, se recomienda la selección previa de las especies vegetales, basada en sus atributos florales, para establecer en los márgenes de los campos, con la finalidad de facilitar la presencia de visitantes florales específicos, lo cual a su vez sustentará el servicio de la polinización. En este contexto, este estudio también sugiere que puede ser beneficiosa la inclusión de cultivos que ofrezcan recursos florales, como las leguminosas, e incluso de floración masiva, como por ejemplo de colza, dentro de los esquemas de rotación de cultivos. Esta medida puede promover el incremento temporal de la abundancia tanto de abejas como de otros visitantes florales.

Debido a que la intensificación agrícola también comporta cambios en la composición de las comunidades vegetales que habitan en los márgenes de los cultivos, se deben aplicar diversas medidas agroambientales, aunque a un nivel diferente del considerado para los visitantes florales. Este estudio sugiere que la gestión a nivel de parcela y, en particular, la implementación de prácticas agrícolas de baja intensidad como la agricultura ecológica, puede ser una medida adecuada, ya que sus efectos sobre la comunidad vegetal son los de mayor intensidad.

A pesar de que la simplificación del paisaje, bajo los condicionantes sociales y económicos actuales, es difícilmente reversible, su efecto negativo sobre la producción de frutos se puede aminorar mediante el incremento de la disponibilidad de recursos florales en los márgenes. Los beneficios derivados de este incremento, de acuerdo con nuestros estudios, parecen tener un carácter amplio y favorecerían especialmente las especies de polinización generalista. De igual forma, el incremento de la proporción de tierra arable bajo gestión ecológica a nivel de paisaje también beneficiaría especies de polinización generalista. Sin embargo, este estudio señala que la inclusión de cultivos de leguminosa, además de procurar servicios agronómicos como la fijación de nitrógeno, también pueden ofrecer temporalmente abundantes recursos florales que benefician la producción de frutos de las plantas entomófilas, independientemente del síndrome de polinización de la planta. En este sentido, incluir cultivos de floración masiva así como mantener los recursos florales de los márgenes de los campos, puede optimizar el servicio de polinización, procurado por un amplio y diverso conjunto de visitantes florales en los hábitats agrícolas de los paisajes mediterráneos.

# CONCLUSIONS

The doctoral thesis studies the effects of agricultural intensification at the landscape and at the field level on the pollination in Mediterranean agricultural landscapes dominated by extensive arable crops, through the analysis of the abundance and composition of the main groups of flower visitor insects and the fruit set of target species with different degree of pollination specialization (generalist *vs.* specialist). Below are presented the main conclusions:

1. Agricultural intensification at landscape level affects negatively the abundance of flower-visiting insects; however, in the studied region this pattern is mainly related to the response of Diptera, whereas Apoidea and Coleoptera respond positively to landscape level intensification.

2. Organic farming management applied at field level has a positive effect on the overall abundance of flower visitors, but its effects are only important in field centres, and of lesser importance in complex landscapes and in field margins. However, for bees, which are the most effective pollinators, the effects of organic farming do not scale up at landscape level, because the proportion of organically managed arable land does not enhance their abundance.

3. When the variation of flower resources over the landscape is considered, increasing flower resources have a positive effect on the abundance of all flower visitor groups. Nonetheless, the increase of flower resources in field centres by sown legumes is only relevant for the abundance of Coleoptera flower visitors.

4. Nevertheless, in landscapes with a high proportion of organically managed arable land, the abundance of bees is not enhanced by the

wildflower resources in the field margins, and the flower resources offered by legume crops promote a dilution of bees in the field margins.

5. Bee and non-bee flower visitors are affected by different factors in intensively managed landscapes where mass flowering crops are present. Bee abundance is enhanced by oilseed rape crops, but their abundance decreases in complex landscapes with higher density of field margins. The abundance of non-bee flower visitors depends on the landscape structure; they are concentrated where resources are offered by wildflowers in simple landscapes, but not in complex landscapes.

6. The responses of flower visitors to the landscape, management and availability of flower resources do not translate directly into differences in the fruit set of phytometer plants; therefore, it is important to consider simultaneously the effects of on the flower visitors and on the service they deliver, preferably on plants with differing level of pollination specialization.

7. The increase of agricultural intensification at landscape level has a negative effect on the fruit set of plant species of generalist pollination, but it is benefited through the increase of availability of flower resources at field level.

8. The proportion of organically managed land enhances the fruit set of species of generalist pollination, whereas it does not have an effect on species of specialist pollination. At field level, increasing local availability of flower resources can enhance the delivery of pollination services, whereas in the immediate vicinity to target plants it can actually decrease the fruit set.

9. Mass flowering crops have a positive effect on the fruit set of species of generalist pollination in the immediate vicinity, whereas the fruit set of

plant species of specialist pollination is affected by wildflower resources at a local scale and landscape structure.

10. Plant species composition and the community-weighted mean of flower traits in the field margin and field centre varied in relation to intensification at landscape level, and intensity of farming, crop type and position within fields at field level. However, flower visitor composition both in field margins and centres only responds to intensification at landscape level.

11. The community-weighted means of wildflower resources' traits influence the community of flower visitors. The flower colour and flowering onset affect the flower visitor composition in the field margins, whereas the flower size is the main driver of composition in field centres.

## Management implications and development of agri-environmental measures

The results of our different studies provide the grounds for the implementation of agro-environmental measures at different levels, regarding both landscape and field, with the aim of harmonizing the fruit set with the maintenance of ecosystem services, such as pollination, in Mediterranean landscapes.

The improvement of pollination services in agricultural landscapes, which is mediated by the flower visitor community, requires the application of strategies that consider both the abundance and the composition of this community. Although an increment in the proportion of organically managed arable land did not enhance the abundance of bees in the agricultural landscapes under study, other flower visitors could also benefit from these conditions. Moreover, agri-environmental measures to promote the abundance of flower visitors should avoid simplifying the landscape, through the preservation of natural or semi-natural vegetation elements, like field margins, and should implement organic farming. The changes are directly related to the structure of the agricultural landscape, as well as with the effects caused by the relationship with the existing plant community. These measures can increase the abundance of flower visitors and they can also affect the community composition, because the responses of different groups of flower visitors to the flower traits of the plant community are not uniform. We recommend that plant species to be sown in the field margins must be previously selected based on their flower traits, to promote the presence of specific flower visitors, which will ultimately sustain pollination services. In this context, our study suggests that including crops with floral resources, like legumes or mass flowing crops, like oilseed rape, within crop rotation schemes, will be beneficial and promote a temporary increment on the abundance of bees and other flower visitors.

Because agricultural intensification is also related to changes in the composition of the plant communities located in the field margins, agri-environmental measures must also be applied to mitigate it. However, a different spatial level to the one of flower visitors needs to be considered. In this study, we suggest that field management must be taken into account, by incorporating low-intensity agricultural practices like organic farming, since its effects on the plant community are the most intense.

Although landscape simplification under the current social and economic conditions is difficult to reverse, its negative effect on fruit set can be reduced by increasing flower resources availability at the margins. According to our studies, the benefits yielded by this increment seem to have far-reaching implications, as the effects on species of generalist pollination are especially profound. Similarly, an increment in the proportion of organically managed arable land at the landscape level only benefited generalist plant species. Our study highlights how the incorporation of legume crops provides abundant temporary floral resources that benefit fruit set of entomophilous plants, in addition to agronomic services like nitrogen fixation. It is important to emphasize that the observed increment in fruit production is independent of plant pollination syndromes. Finally, by incorporating mass flowering crops and maintaining floral resources at field margins, it is possible to optimize pollination services through a broad diverse groups of flower visitors in agricultural habitats in Mediterranean landscapes.

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