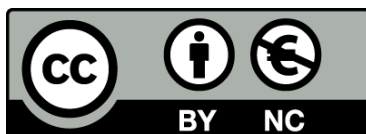




UNIVERSITAT<sub>DE</sub>  
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# Efectos de la heterogeneidad del paisaje agrícola mediterráneo sobre los polinizadores y la eficacia de la polinización

Pablo Neira Vidal



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EFECTOS DE LA  
HETEROGENEIDAD DEL  
PAISAJE AGRÍCOLA  
MEDITERRÁNEO SOBRE LOS  
POLINIZADORES Y LA  
EFICACIA DE LA  
POLINIZACIÓN

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UNIVERSITAT DE  
BARCELONA

Facultad de Biología

Departamento de Biología Evolutiva, Ecología y Ciencias ambientales

Programa de Doctorado en Biodiversidad

## **Efectos de la heterogeneidad del paisaje agrícola mediterráneo sobre los polinizadores y la eficacia de la polinización**

Memoria presentada por

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Para optar al grado de

**Doctor por la Universitat de Barcelona**

Doctorando/a



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Efectos de la diversidad agrícola cultivada en la biodiversidad y polinización de la región mediterránea.

Tesis doctoral. Septiembre, 2024

Supervisores: F. Xavier Sans Serra & José M. Blanco Moreno

Esta tesis ha sido financiada por el Programa de Becas de Doctorado en el Extranjero BECAS CHILE de la Agencia Nacional de Desarrollo e Investigación (ANID), Chile Folio 72210385 y por los proyectos RTI2018-095597-B-I00 y PID2021-127575OB-I00 financiadas por MCIN/AEI/ 10.13039/501100011033 del Ministerio de Ciencia e Innovación y por “ERDF A way of making Europe”, de la Unión Europea

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*“La amabilidad en palabras crea confianza. La amabilidad en el pensamiento  
crea profundidad. La bondad de dar crea amor”*

*-LaoTse*

*-To my little honeys*

## AGRADECIMIENTOS

Quiero comenzar agradeciendo a Xavier por animarse a recibirme después de un par de llamadas y por la energía que puso desde el principio, ayudándome a ser aceptado en el doctorado cuando los plazos estaban a punto de terminar. Quién diría que fue una epifanía, y que durante estos cuatro años vivimos al filo del mañana. Gracias a él, el ánimo nunca faltó. Me quedo, o más bien quisiera quedarme, con esa energía de seguir haciendo siempre, porque, aunque no quiere recibir más doctorados, siguen llegando.

Al José por abrirme los ojos y enseñarme que no se nada. No de mala manera. Sino que encuadrando mi camino y pensamientos que a veces tenían más que ver con astrología y física cuántica que con la ecología del paisaje. Se que en buenos momentos más que al Xavier te hice Respirar profundo. Por ponerme los pies en la tierra. Y por compartir tus scripts, los atesoraré. También como ya viste aprendí a ocupar la R (o bueno al menos más de que cuando llegué).

Es increíble la capacidad que ambos tienen de parecer ponerse de acuerdo para fijar la mirada en partes completamente distintas del manuscrito o de la tesis, y terminar con un documento totalmente en rojo. Sin duda, son dos personas muy distintas, pero saben lo que hacen y espero haber aprendido lo suficiente de ustedes.

A los predocs, tanto los que siguen como los que ya se fueron: Alice, Idoia y al Alex (Dr. Honoris Causa), a todos muchas gracias. Especialmente en estos dos últimos años, donde la confianza permitió que soltáramos la voz y las emociones, con gritos al cielo y victorias silenciosas. Paso a paso para los que vienen, y mucha suerte, Dra. Alba, tus consejos siempre fueron oportunos. Mención especial a Dani, por compartir sobre literatura y las enseñanzas de Don Juan. Y también a Guadalupe, por los tremendos mates desde el día uno. Con agua caliente cuando hacía frío y tererés en verano. Sé que les irá bien, aunque a veces sientan que están perdidos en el tiempo y el espacio. Toda semilla necesita oscuridad para crecer, así que ánimo.

A Berta, Lourdes, Estefanía y Ester, en diferentes ámbitos y momentos, hicieron que este paso por el doctorado fuera más fácil, desde el día a día hasta poner bolsas en las plantas de colza y validar mis ideas. A Laura, por tener conversaciones diferentes, por la agroforestería, por esa visión de madre y padre con la que vemos la vida. Por esa "templanza" que da el cansancio, sino que también nos permite seguir adelante.

Finalmente, pero no menos importante, a Trull, mi fiel ayudante de campo, que disfrutó tanto como yo recorriendo la Cataluña Central, haciendo más agradables los días de trabajo en campo, incluso cuando íbamos solos bajo el sol. Sus obligadas caminatas diarias me ayudaron a desconectar y respirar. Mil gracias.

A toda mi gente en Chile, que, a la distancia, me ha hecho sentir que hay cosas que ni se olvidan ni se rompen: mis amigos y mi familia. A mis papás, por querer estar presentes en la vida de mis chicas y por ayudarme en todo lo que pueden.

Mención especial a Óscar y Cristian de Rebrotá, no por algo ocurrido durante el doctorado, sino antes de venir. Gracias a ellos y al mundo en el que habitan, y del cual pude ser parte, aprendí muchas herramientas para conocerme, gestionarme y continuar con mis procesos. Gracias por eso, porque creo que fue fundamental para atravesar esta montaña rusa de pensamientos intrusivos que aparecen durante el doctorado.

A mis chiquitas, mis princesas, mis torbellinos de emociones: nada de esto habría sido igual sin ustedes, y tampoco me lo imagino de otra manera. Son mis ganas de levantarme (y de acostarme). Sin duda, me han enseñado a superar los obstáculos y, sobre todo, a seguir y seguir adelante. Son una verdadera motivación para vivir y, especialmente, para sonreír. No hay nada como un abrazo suyo para recuperar energías. Inarita, Aina y Mel, las amo y las amaré por todo el mundo. Me detengo aquí porque no hay palabras que puedan expresar todo lo que siento por ustedes.

Quiero expresar mi más profundo agradecimiento a todas las personas que han sido parte de este camino, brindándome su apoyo. Cada paso que he dado ha sido impulsado por el amor, la guía y el aliento que me han dado. A ustedes, que han estado presentes en cada uno de esos pasos, les agradezco de todo corazón por caminar a mi lado y ayudarme a llegar hasta aquí.

## SINOPSIS

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Agricultural intensification, which alters land use and crop sequences in search of maximizing productivity and revenue, affects pollinator abundance and diversity, which are crucial for pollination. This thesis investigates how agricultural landscape characteristics affect pollinator abundance in the northwestern Mediterranean region, with a focus on hoverflies and bees. Over a two-year period, the study monitored pollinator density and pollination effectiveness in twenty-two oilseed rape fields located in landscapes that differed in terms of crop diversity, the extent of semi-natural habitats, and field size. These differences provided a basis for analyzing how specific landscape features influence pollinator abundance and effectiveness. While many studies have focused on the non-cultivated fraction of agricultural landscapes, few have examined the temporal effects of agricultural land management, specifically how crop diversity and the prevalence of certain crops providing floral resources influence pollinators. This thesis adopts a more comprehensive approach by considering both the role of semi-natural habitats and the temporal effects of agricultural practices within the cultivated matrix on pollinator activity. This dual focus underscores the importance of understanding the interplay between cultivated and non-cultivated areas in shaping pollinator abundance and pollination services, by examining the effects in a facultative allogamous crop species.

This thesis is organized into two primary sections, each addressing distinct aspects of the agricultural matrix. The first section addresses crop diversity, while the second focuses on the cover of mass flowering crops, both analyzed with a temporal perspective.

Four landscape characteristics were examined: equivalent crop diversity in the sampling year (ERG), equivalent crop diversity from the previous year (ERGp), the percentage of semi-natural habitats (SNH), and mean field size (MFS). The study, conducted in twenty-two oilseed rape fields in landscapes with varying characteristics, found that different landscape variables influenced pollinator groups in distinct ways. SNH positively influenced bumblebee abundance, while ERGp and MFS were important for other wild bees and for hoverflies. These findings provide actionable insights to prioritize strategies for benefiting specific pollinator groups, improve agricultural landscape planning, and promote wild pollinator conservation through crop diversity.

The study also explored how certain landscape features — ERGp, SNH and MFS— as well as pollinator densities (wild bees [WB] and honeybees [HB]) influenced pollination outcomes and seed quantity and quality in oilseed rape crops. The research in a subset of twenty oilseed rape fields revealed a positive relationship between ERGp and pollinator density. A pollinator

exclusion experiment in these fields showed that insect pollination significantly improved rapeseed quality and quantity. ERGp emerged as a relevant landscape feature, positively impacting WB density and pollination effectiveness, thereby improving oilseed rape production. Additionally, the study examined the effects of mass flowering crop cover (MFC) from the previous year (MFC1) and accumulated over three years (MFC3). It also considered semi-natural habitats and mean field size effects on pollinators and oilseed rape yield. Structural equation modeling indicated that MFC1 and MFC3 positively influenced wild bee (WB) densities. Smaller field sizes promoted higher densities of large bees (LB). The number of seeds per pod was positively related to WB in general and LB in particular. It was also positively related to MFC1 and MFS. Seed oil content was positively associated with LB densities and negatively with MFS. SNH correlated with an increase in thousand seed weight. Overall, the study highlights the importance of off-crop habitats and of on-crop floral resources and their temporality to promote pollination services in cereal-dominated Mediterranean agricultural landscapes. Therefore, landscape management should focus on these factors to promote sustainability and maximize agricultural and ecological benefits.



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# INTRODUCCIÓN GENERAL

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## **4.1 Biodiversidad y paisaje agrícola**

La biodiversidad es un componente clave en la sostenibilidad de los sistemas agrícolas, ya que provee múltiples servicios ecosistémicos esenciales como el reciclaje de nutrientes, el control biológico de plagas y la polinización (Anthony et al., 2023; Dainese et al., 2019a; Li et al., 2024). Esta biodiversidad, sin embargo, depende estrechamente de la diversidad del paisaje agrícola, que se refiere a la variedad de ecosistemas que ofrecen hábitat a una amplia gama de organismos, incluidos plantas, animales y microorganismos, los cuales interactúan en y alrededor de los cultivos (Altieri & Nicholls, 2007). Cuanto más diverso es el paisaje, mayor es su capacidad para sostener una biodiversidad rica y funcional, lo que, a su vez, fortalece la productividad y la resiliencia de los sistemas agrícolas (Wang & Brose, 2018; Wu, 2013).

La diversidad dentro del paisaje agrícola también ofrece una serie de beneficios específicos. Por ejemplo, la presencia de enemigos naturales de plagas, como depredadores y parásitos, ayuda a mantener bajo control las poblaciones de insectos dañinos, reduciendo así la necesidad de pesticidas químicos (Christmann et al., 2021). Además, la variabilidad espacial y temporal de los cultivos en el paisaje contribuye a prevenir la propagación de plagas y enfermedades (Ratnadass et al., 2021). Por otro lado, los fragmentos de vegetación natural, así como los márgenes con vegetación arbórea y arbustiva, actúan como corredores ecológicos que facilitan el movimiento y la dispersión de especies benéficas, lo que refuerza la resiliencia del ecosistema agrícola (Benton et al., 2003). Así mismo, la biodiversidad floral en los márgenes de los campos agrícolas es vital para la salud de polinizadores como las abejas y los sírfidos, de los que dependen muchos cultivos (Hautier et al., 2018; Sutter et al., 2017; Tilman et al., 1997). En definitiva, la integración de la biodiversidad en la gestión agrícola no solo mejora la producción de los cultivos, sino que puede asegurar la sostenibilidad del sistema al permitir una mejor adaptación a condiciones cambiantes (Balvanera et al., 2006).

## **4.2 Polinizadores y servicios de polinización**

Los polinizadores son esenciales para el equilibrio de los ecosistemas y la producción de alimentos (Benadi et al., 2012; Sargent & Ackerly, 2008; Turo et al., 2024). Se estima que entre el 65% y el 85% de las angiospermas dependen de la polinización por insectos para su reproducción (Ollerton et al., 2011). Pero los polinizadores no solo facilitan la reproducción de plantas silvestres, fundamentales para el funcionamiento de los ecosistemas, sino que también contribuyen a la sostenibilidad de los paisajes agrícolas (Biesmeijer et al., 2006; Ollerton et al., 2011). En términos agrícolas, aproximadamente el 35% de los cultivos a nivel global dependen

de la polinización animal para optimizar su rendimiento y calidad. De una muestra de 107 cultivos principales que se benefician de la polinización en el mundo, un 10% requiere estrictamente de la polinización entomófila (alogamia) para reproducirse, y un 75% se beneficia de esta polinización, mejorando notablemente su producción (Klein et al., 2007).

Los servicios ecosistémicos proporcionados por los polinizadores representan aproximadamente el 10% del valor global de la producción agrícola, generando beneficios económicos cuya estimación se sitúa entre 153 y 577 mil millones de dólares anuales según diversas investigaciones (Gallai et al., 2009; Potts, 2016). El declive de las poblaciones de polinizadores podría tener consecuencias graves para la estabilidad de los sistemas agrícolas (Dainese et al., 2019a; Lee et al., 2024). Sin su intervención, la producción de muchos alimentos sería significativamente más escasa y costosa (Fijen et al., 2018).

Asimismo, la polinización mediante insectos es fundamental para mejorar la calidad de los cultivos (Aizen et al., 2008; Bommarco et al., 2012, 2012). Este proceso no solo incrementa el contenido de nutrientes esenciales en los alimentos, sino que también eleva la calidad de las cosechas en cultivos que dependen de polinizadores, como los almendros, los manzanos y la colza (Chaplin-Kramer et al., 2014; Ellis et al., 2015; Gazzea et al., 2023; Ramírez-Mejía et al., 2024; Smith et al., 2015). La eficiencia de la polinización, es decir, la capacidad de los polinizadores para transferir polen de manera efectiva entre flores y facilitar la fecundación, y su eficacia, que se refiere al impacto final en la producción de semillas y frutos, evaluado por la cantidad y calidad de estos (Rader et al., 2009), dependen de varios factores, como la diversidad de polinizadores y sus rasgos funcionales. Por ello, entender las variaciones en la eficiencia y la eficacia de la polinización es fundamental para optimizar los beneficios que esta aporta a los cultivos.

Las abejas, tanto las silvestres como las domésticas, son los polinizadores más conocidos y eficientes (Bartomeus et al., 2018; Jauker et al., 2012). Sin embargo, otros insectos, como los sírfidos o las mariposas, también juegan roles importantes en la polinización agrícola. Aunque la abeja melífera (*Apis mellifera* L. 1758) es el polinizador gestionado más extendido en todo el mundo (Potts, 2016), los polinizadores silvestres también contribuyen a la polinización de los cultivos y suelen ser más eficaces que las abejas melíferas (Garibaldi et al., 2013; Rollin et al., 2013a). Un aspecto fundamental de la diversidad de los polinizadores es la divergencia en sus rasgos funcionales, como el tamaño corporal, que influye directamente en la distancia de forrajeo y en la eficacia de la polinización (Cortés-Gómez et al., 2023; Greenleaf et al., 2007; Ne'eman et al., 2010; Pfister et al., 2017). Además, características como los hábitos de forrajeo

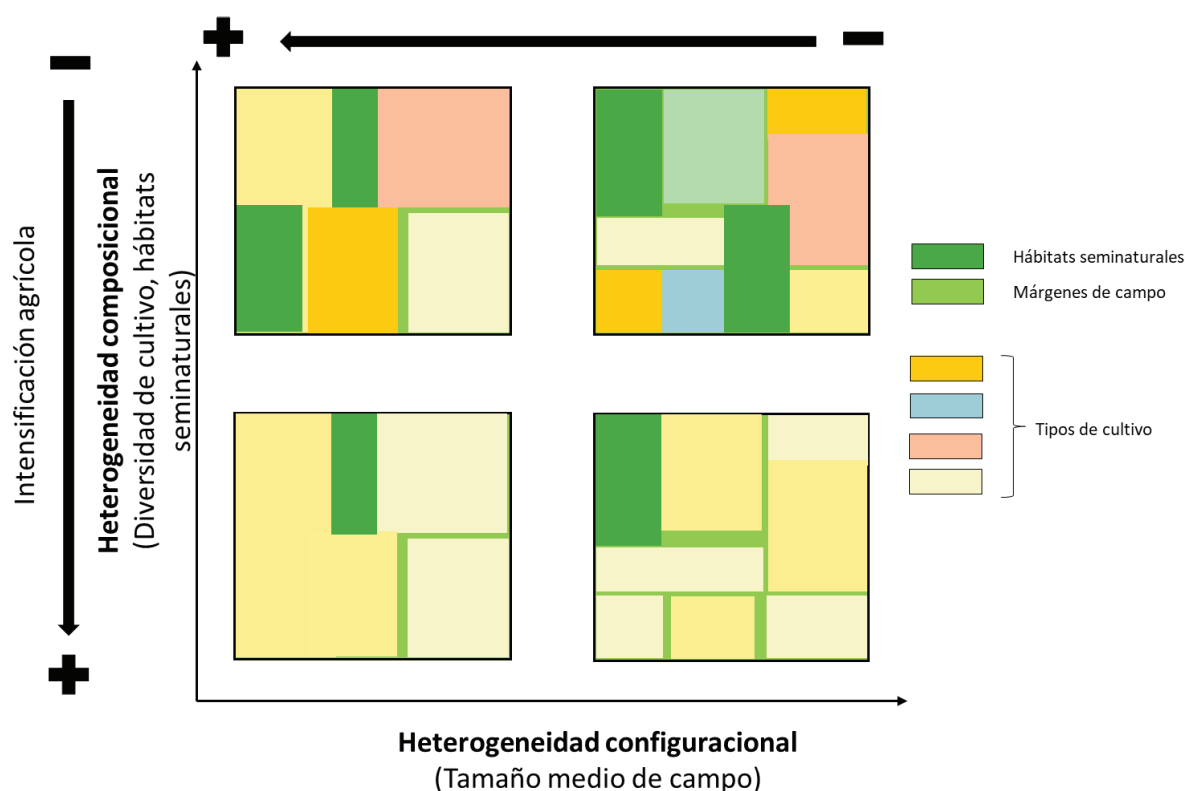
permiten a los polinizadores ocupar roles específicos y complementarios en los ecosistemas agrícolas y naturales (Blüthgen & Klein, 2011; Fenster et al., 2004).

La diversidad de especies de polinizadores no solo permite la polinización de una mayor variedad de cultivos, sino que también garantiza la resiliencia del sistema frente a los cambios en las condiciones ambientales. La presencia de especies con rasgos funcionales únicos asegura la estabilidad de los servicios de polinización y contribuye a un rendimiento agrícola más consistente a lo largo del tiempo (Albrecht et al., 2012; Brittain et al., 2014; Garibaldi et al., 2014; Hoehn et al., 2008). La coexistencia de múltiples especies no solo optimiza la polinización, sino que también incrementa la resiliencia de los ecosistemas ante cambios ambientales, asegurando que siempre haya polinizadores adecuados para cada circunstancia (Winfrey et al., 2011). Por lo tanto, la diversidad funcional es clave para el mantenimiento de los servicios ecosistémicos de polinización (Fontaine et al., 2006; Hoehn et al., 2008).

### **4.3 Crisis de los polinizadores e intensificación agrícola**

Actualmente, los polinizadores se encuentran en una profunda crisis, con una disminución de su abundancia que oscila entre un 20% y un 50% en regiones como Europa y América del Norte desde la década de 1990 (Hallmann et al., 2017; Potts et al., 2010; Zattara & Aizen, 2021). En los Estados Unidos, se ha registrado una disminución del 23% en la diversidad de especies de polinizadores en áreas agrícolas intensivas, mientras que el Reino Unido muestra una reducción del 33% (Kremen et al., 2007; Powney et al., 2019). Esta crisis se origina por una serie de factores interrelacionados, entre los cuales destacan la urbanización, el cambio climático y la intensificación agrícola (Aizen et al., 2022; Seibold et al., 2019; Thomas et al., 2004).

La intensificación agrícola se identifica como una de las principales causas de esta pérdida de biodiversidad y de la degradación de los ecosistemas. Estas alteraciones del medio afectan gravemente servicios clave como la polinización (Biesmeijer et al., 2006; Chapin III et al., 2000). La intensificación se manifiesta a distintos niveles, y en cada uno de ellos conlleva transformaciones significativas. A nivel de paisaje, implica una homogeneización de la estructura y de la composición del entorno agrícola, principalmente debido al incremento de las áreas cultivadas y la disminución de las áreas seminaturales (Figura 1). Estos cambios perjudican indirectamente la diversidad taxonómica y funcional de los polinizadores, y afectan negativamente a los servicios ecosistémicos disponibles (De Palma et al., 2015; Gámez-Virúes et al., 2015; Grab et al., 2019; Wood et al., 2015).



**Figura 1.** Esquema de los efectos de la intensificación agrícola (flechas negras) sobre la heterogeneidad de la composición y configuración del paisaje agrícola. Modificado de Priyadarshana et al. (2024).

A nivel de campo, la intensificación agrícola se refleja en una simplificación de las prácticas agrícolas, que se manifiesta mediante el uso de prácticas como la labranza intensiva y la repetida aplicación de biocidas y fertilizantes. Estas prácticas, lejos de beneficiar la productividad a largo plazo, incrementan la presión sobre los polinizadores (Foley et al., 2011; Garibaldi et al., 2019; Robinson & Sutherland, 2002).

La agricultura debe adoptar prácticas de adaptación y mitigación para frenar la pérdida de polinizadores, especialmente en un planeta con recursos finitos. El sector agrícola enfrenta el reto de equilibrar la producción de alimentos con la conservación de la biodiversidad y los servicios ecosistémicos. En las próximas décadas el cambio climático afectará gravemente la producción agrícola y a los polinizadores. Por lo tanto, es crucial implementar medidas de adaptación para hacer frente a nuevas condiciones ambientales (Kammerer et al., 2021; Outhwaite et al., 2022). Al mismo tiempo, la agricultura ejerce presión sobre la biodiversidad



y los polinizadores, lo que requiere acciones de mitigación para reducir su impacto negativo (Su et al., 2021).

Ante estos desafíos, la Comunidad Europea ha impulsado acciones para reorientar la producción de alimentos a través de distintas políticas y programas. La reforma de la Política Agrícola Común (PAC) introduce estrategias como el Pacto Verde Europeo y el Plan de Acción para la Agricultura Ecológica (European Commission, 2022). Estas iniciativas buscan apoyar a agricultores, científicos y responsables políticos en la adopción de medidas que beneficien a los polinizadores, como el aumento de los márgenes de los campos y la preservación de las áreas seminaturales. Aunque estas políticas se han implementado en diversas regiones de Europa, sus efectos varían entre países y regiones. Esto se debe a que las interacciones entre los servicios ecosistémicos, la biodiversidad y las funciones del ecosistema dependen del contexto geográfico, cultural y ambiental (Wu, 2013). Esta variabilidad resalta la necesidad de investigar cómo la biodiversidad responde regionalmente a las modificaciones en el paisaje agrícola.

#### **4.4 Estrategias de conservación de los polinizadores en los agroecosistemas**

La gestión de los sistemas agrícolas es fundamental para la salud humana y ambiental a nivel global. Es necesaria una producción sostenible desde las perspectivas, ecológica, ambiental, económica y social, que satisfaga las crecientes necesidades de la población (Blaser et al., 2018). Sin embargo, el dramático impacto de la pérdida de biodiversidad sobre el funcionamiento de los sistemas agrícolas pone de manifiesto que únicamente una gestión agrícola que preserve la biodiversidad, incluyendo los polinizadores, a diferentes escalas temporales y espaciales permitirían la adaptación a los nuevos escenarios agrícolas (Bibi y Rahman, 2023; Rashwan et al., 2023).

Aunque los requisitos para el futuro de la agricultura son claros, las soluciones integrales y aplicables son escasas (Pathak, 2022). En este sentido, es fundamental entender cómo la estructura, la composición y la gestión de los paisajes agrícolas pueden promover la sostenibilidad ambiental y la conservación de la biodiversidad. La intensificación agrícola ha llevado a una reducción significativa de la heterogeneidad del paisaje, afectando negativamente la biodiversidad y los servicios ecosistémicos como la polinización (Gámez-Virúes et al., 2015). Algunas estrategias clave para revertir estos efectos negativos incluyen la expansión de las áreas seminaturales, la reducción del tamaño de los campos y la diversificación de cultivos (Burian et al., 2024; Eisenstein, 2020).

Los cambios en la configuración del paisaje como la reducción del tamaño de los campos agrícolas tienen un efecto positivo sobre los polinizadores, especialmente sobre las abejas. Estos paisajes más fragmentados rompen la homogeneidad impuesta por la matriz agrícola y crean un mosaico de hábitats diversos que favorece la supervivencia y la movilidad de los insectos polinizadores (Happe et al., 2018). En particular, los márgenes de estos pequeños campos ofrecen refugio, alimento y áreas de anidación, aumentan la conectividad de los hábitats para los insectos, facilitando su movimiento y mejorando la polinización en las áreas adyacentes, como los bordes de los campos (Clough et al., 2020; Dainese et al., 2019a).

La expansión de las áreas seminaturales también es una opción que beneficia a los polinizadores (Proesmans et al., 2019; Rollin et al., 2013a). Sin embargo, esta expansión puede entrar en conflicto con los intereses económicos de los agricultores, ya que destinar tierras para la vida silvestre sería a costa del área destinada a la producción, reduciendo el rendimiento agrícola (Rey Benayas y Bullock, 2012). A pesar de que algunos estudios muestran que crear hábitats para la vida silvestre en las áreas agrícolas puede ser rentable a largo plazo al mejorar los servicios ecosistémicos (Blaauw & Isaacs, 2014; Pywell et al., 2015), los costos iniciales pueden superar beneficios inmediatos para los agricultores (Campbell et al., 2012; Olschewski et al., 2006; Sutter et al., 2017). No obstante, el establecimiento de áreas de compensación ecológica con la finalidad de promover la biodiversidad forma parte de la de los ecorregímenes de la PAC.

Si bien modificar la configuración del paisaje o aumentar la proporción de áreas seminaturales puede ser complicado, incrementar la diversidad de cultivos representa una alternativa más factible. Un paisaje agrícola con mayor diversidad de cultivos a escala de paisaje puede ofrecer mayor variedad de recursos alimenticios y de hábitats para los polinizadores, proporcionando una fuente más continua de néctar y polen a lo largo del año, lo que ayuda a mantener las poblaciones de insectos polinizadores (Aguilera et al., 2020; Dempewolf et al., 2010). Este enfoque es clave para avanzar hacia paisajes agrícolas más sostenibles y para revertir los efectos negativos de la intensificación agrícola (Fahrig et al., 2011; Priyadarshana et al., 2024).

La selección de cultivos favorables para los polinizadores, en particular los cultivos de floración masiva (MFC), puede aumentar la disponibilidad de polen y néctar en el paisaje, promoviendo un entorno agrícola más favorable para estos organismos (Holzschuh et al., 2011; Requier et al., 2015; Westphal et al., 2003). La integración de distintos cultivos, como los de floración masiva (por ejemplo, los almendros, el girasol, la mostaza o la colza), diversifican el paisaje con recursos florales abundantes en diferentes épocas que atraen polinizadores (Beyer et al., 2021).

La colza (*Brassica napus* L.), en particular, se ha utilizado como cultivo diana de varios estudios debido a su capacidad para atraer polinizadores (Holzschuh et al., 2011). Su amplia distribución en la agricultura global permite estudiar los efectos de la polinización en diferentes paisajes (Fijen et al., 2022). Además, el hecho que sea especie alógama facultativa la convierte en un fitómetro ideal para evaluar la eficacia de los polinizadores (Bartomeus et al., 2018; Bommarco et al., 2012; Fijen et al., 2018).

La integración de prácticas que favorezcan la diversidad de cultivos y la disponibilidad de recursos florales en el tiempo puede transformar el entorno agrícola en un espacio más propicio para los polinizadores, y de esta manera mejorar la eficacia de la polinización y contribuir a una agricultura más sostenible y resiliente. No obstante, aún falta información específica sobre cómo afecta la diversidad de cultivos a la disponibilidad en el tiempo de recursos florales agrícolas y al servicio ecosistémico de la polinización en paisajes mediterráneos con diferentes tamaños de campo y proporción de áreas seminaturales. Desde la perspectiva aplicada a los agroecosistemas, la comprensión del papel de la diversidad cultivada sobre los polinizadores y el servicio de la polinización podría ser capital para el diseño de políticas encaminadas a la protección de la biodiversidad, la polinización y la productividad agrícola (Godfray et al., 2010; Sirami et al., 2019).

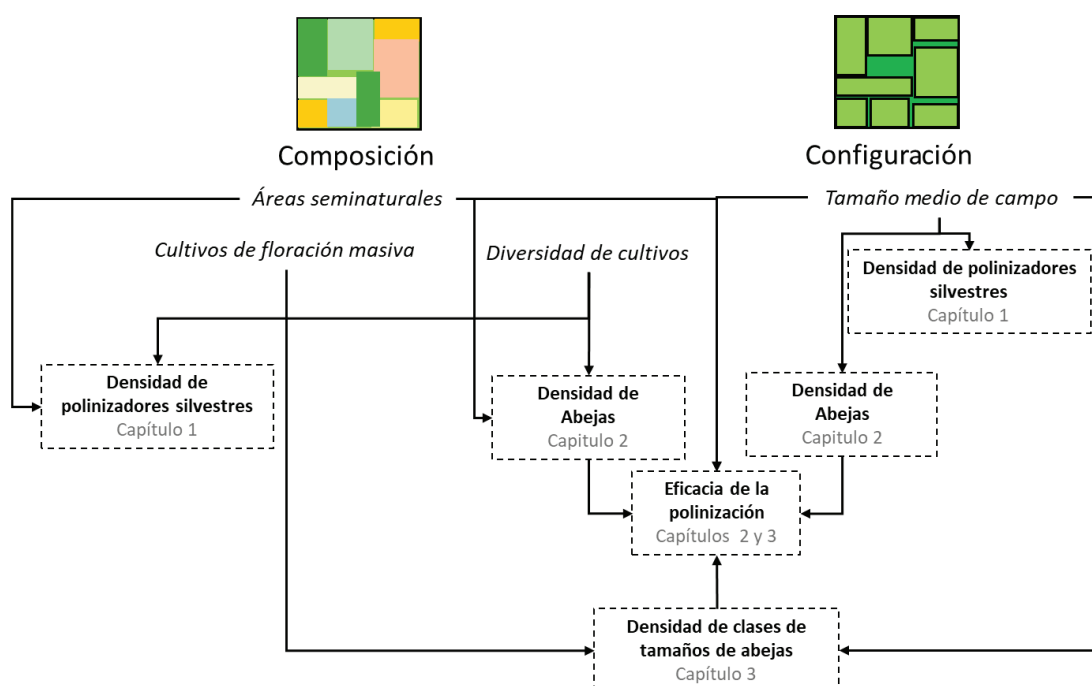




Esta tesis doctoral investiga el efecto de la heterogeneidad del paisaje sobre la densidad de polinizadores y sobre la eficacia de polinización en los cultivos de colza, un cultivo alógamo facultativo. La selección de la colza como planta diana permite evaluar la densidad de polinizadores en el paisaje (al atraer los polinizadores del entorno más o menos inmediato) y permite evaluar cómo la densidad de estos varía con la diversidad cultivos, el tamaño medio de los campos y la proporción de áreas seminaturales (*Capítulos 1 y 2*) (Figura 2). Se ha analizado también cómo la acumulación temporal de recursos florales en la matriz agrícola, estimada a través de la suma del área de cultivos de floración masiva en los años previos al muestreo, afecta la densidad total de abejas silvestres y la densidad de abejas de diversas clases de tamaño (*Capítulo 3*). Finalmente, se investiga la relación entre las métricas de composición —diversidad de grupos de cultivos y proporción de áreas seminaturales— y las métricas de configuración —tamaño medio de los campos— con la densidad de polinizadores y la eficacia de la polinización, evaluada mediante la producción de semillas de colza y medidas de su calidad (*Capítulo 2*). También se analizan los efectos directos de métricas de composición, métricas de configuración y acumulación temporal de cultivos de floración masiva sobre la polinización, y los efectos indirectos a través de la densidad de las abejas (*Capítulo 3*). La tesis plantea la hipótesis general que la heterogeneidad del paisaje agrícola y en particular la diversidad de grupos de cultivos y la acumulación temporal de la cobertura de cultivos de floración masiva aumenta la densidad de polinizadores y en consecuencia la eficacia de la polinización. De las que se desprenden las siguientes hipótesis específicas:

- Hipótesis 1: El incremento de la diversidad de grupos de cultivos en el paisaje agrícola, tanto en el año de muestreo como en años anteriores, aumentará la densidad de polinizadores silvestres (abejas y sírfidos), al proporcionar una mayor disponibilidad de recursos florales y hábitats a lo largo del tiempo.
- Hipótesis 2: La cobertura de los cultivos de floración masiva en años previos incrementará la densidad de abejas silvestres, y sus efectos serán distintos en función de sus atributos funcionales (tamaño) debido a la diferente capacidad de explotar estos recursos cuya posición espacial cambia en el paisaje entre años.
- Hipótesis 3: Los efectos que tienen la diversidad de grupos de cultivos y la cobertura de los cultivos de floración masiva sobre los polinizadores mejorarán la eficacia de la polinización de la colza, incrementando tanto la cantidad como la calidad de las semillas producidas.

- Hipótesis 4: La mayor proporción de áreas seminaturales y el tamaño más reducido de los campos agrícolas aumentarán la densidad de abejas y otros polinizadores, al mejorar la disponibilidad de refugios y recursos florales y la conectividad de los hábitats en el paisaje agrícola.
- Hipótesis 5: La eficacia de la polinización estará más influenciada por la diversidad funcional de los polinizadores que por la densidad total. Además, el diferente comportamiento de las abejas grandes y las pequeñas, sí como de las abejas silvestres y domésticas tendrá consecuencia sobre los parámetros de cantidad y calidad de las semillas de colza.



**Figura 2 .** Mapa conceptual del estudio realizado en esta tesis. Las *variables explicativas* del paisaje (en cursiva) incluyen características de composición y de configuración del paisaje agrícola, mientras que las **variables respuesta** (en negrita) dentro de los rectángulos con línea discontinua incluyen las densidades de los diferentes grupos de polinizadores silvestres (sírfidos y abejas) evaluados y la eficacia de la polinización. Las flechas indican las relaciones entre variables investigadas, derivadas de las hipótesis planteadas en esta tesis. En gris se señalan los capítulos donde se estudió cada componente.

## OBJETIVOS

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El objetivo principal de esta tesis es avanzar en el conocimiento del efecto que la diversidad de grupos de cultivos y la acumulación temporal de recursos florales ofrecidos por los cultivos de floración masiva tienen sobre la densidad y eficacia de los polinizadores en los paisajes agrícolas de la Cataluña Central, caracterizados por la dominancia de cultivos herbáceos extensivos de secano. Este estudio pretende establecer una base para predecir cómo las variaciones en la diversidad de grupos de cultivos y la cobertura de los cultivos de floración masiva influyen en las poblaciones de polinizadores y, en consecuencia, en los servicios de polinización. A largo plazo, se espera que estos hallazgos contribuyan al diseño de propuestas de manejo sostenible de los agroecosistemas.

Los objetivos específicos son:

**OE1.** Analizar el efecto de la estructura del paisaje agrícola, evaluada mediante la diversidad de grupos de cultivos, el tamaño medio de los campos y la proporción de áreas seminaturales, sobre la densidad de polinizadores silvestres.

**OE2.** Evaluar el impacto de la diversidad temporal de los cultivos de floración masiva a nivel de paisaje sobre la densidad de abejas que visitan los campos de colza, así como su efecto sobre la producción y calidad de las semillas de colza.

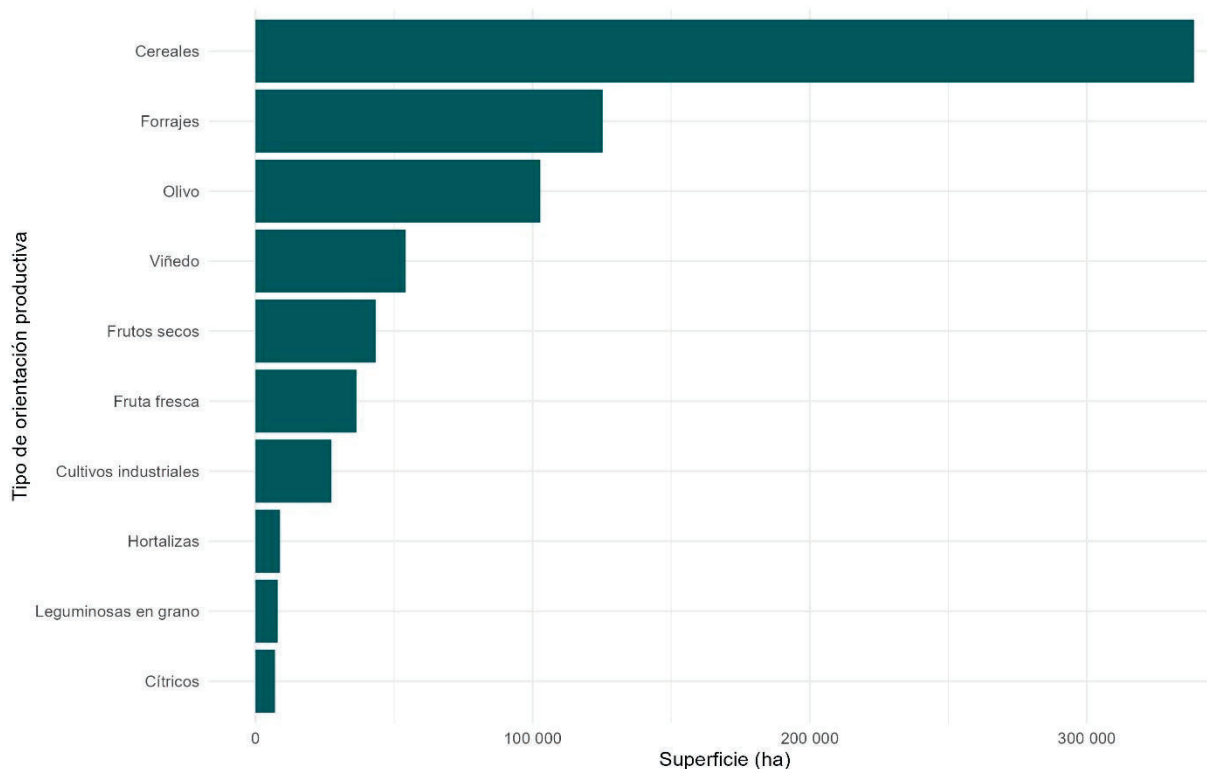
**OE3.** Estudiar el efecto de la acumulación temporal de la cobertura de los cultivos de floración masiva a nivel de paisaje sobre la densidad y el tamaño de las abejas que visitan los campos de colza, y su influencia en la producción de semillas de colza.



## SELECCIÓN DE PAISAJES Y RECOGIDA DE DATOS

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El estudio se realizó durante las primaveras de 2021 y de 2022 en Cataluña, en el noreste de España. El paisaje agrícola de esta zona está dominado por cultivos herbáceos de secano, principalmente cereales de invierno como el trigo y la cebada intercalados con cultivos leñosos comunes en la región mediterránea (Figura 3), como los olivares, los almendrales y los viñedos. También forman parte del paisaje cultivos herbáceos como la alfalfa, los garbanzos, las lentejas y la colza. El tipo de paisaje estudiado ocupa la mayor parte de la Cataluña central, donde la tierra arable ocupa el 54% de los suelos agrícolas (Institut d'Estadística de Catalunya, 2023). Las áreas no cultivadas están ocupadas principalmente por diversos tipos de hábitats forestales (pinares, encinares y robledales), arbustivos, que ocupan antiguas áreas forestales degradadas a causa de los incendios y el pastoreo, y pastizales xerófilos y mesoxerófilos que ocupan antiguos cultivos y otras áreas marginales (Departament d'Acció Climàtica, Alimentació i Agenda Rural, 2023).



**Figura 3.** Importancia relativa (ha) de los diez tipos de orientaciones productivas más abundantes en Cataluña durante el 2022. Fuente: Departamento de Acción Climática, Alimentación y Agenda Rural.

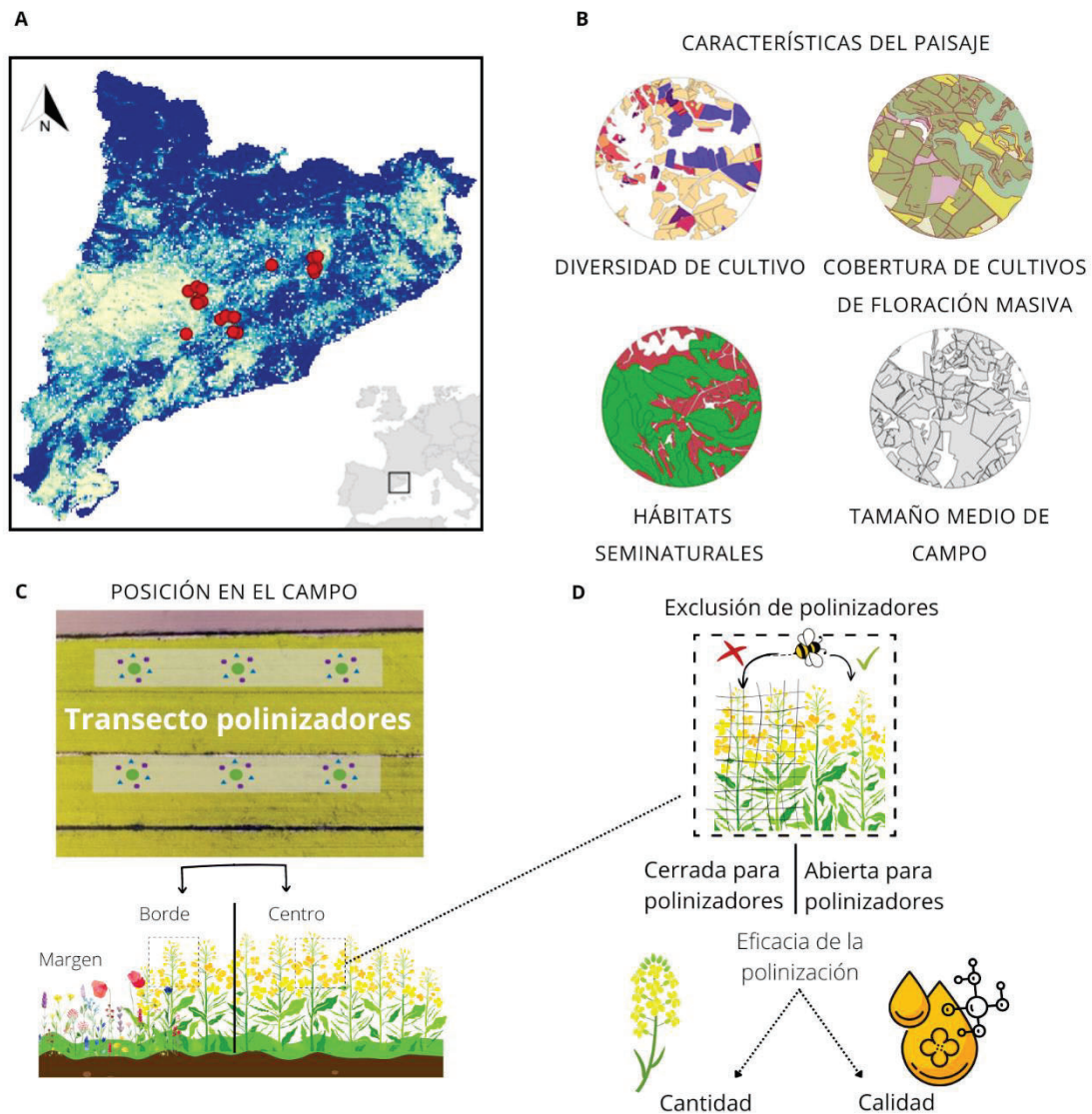
Para este estudio, se seleccionaron 22 localidades (Figura 4A), en un gradiente de diversidad de cultivos. En cada una de ellas se seleccionó un campo de colza gestionado de forma

convencional y sembrado con variedades híbridas de colza de invierno. Para caracterizar el paisaje, se delimitó un área circular de 1 km de radio alrededor de cada campo. Además, se escogió estas localidades asegurando que el área sembrada con colza fuera inferior al 10%, con el fin de generar un efecto de concentración de polinizadores (Beyer et al., 2021; Magrach et al., 2018) (Figura 4B). Todas las localidades estaban separadas por al menos 2 km para evitar que dos campos colza fueran visitados por el mismo grupo de polinizadores (Holzschuh et al., 2016; Westphal et al., 2003).

En cada localidad se calculó la diversidad de cultivos del año de muestreo (ERG, por las siglas en inglés de *Equivalent Richness of Groups*, ver a continuación), y del año anterior al muestreo (ERGp), el porcentaje de áreas seminaturales (SNH, por sus siglas en inglés), el tamaño medio de campo (MFS, por sus siglas en inglés). Cabe destacar que la diversidad de cultivos no se calculó sobre tipos de cultivos individuales, sino sobre grupos funcionales de cultivos, definidos según su contribución a las poblaciones de los polinizadores. Por ejemplo, el trigo, la cebada, la avena y la espelta se agruparon en el grupo funcional de los cereales. El ERG se calculó mediante el índice de Shannon, ponderando la abundancia de los grupos funcionales de cultivos en relación con la proporción del área del paisaje ocupada y convirtiéndolo en diversidad real, es decir el número equivalente de grupos funcionales de cultivos (Jost, 2006).

En el capítulo 3 también se calculó la cobertura de los cultivos de floración masiva del año anterior al muestreo (MFC1, por sus siglas en inglés) y la cobertura acumulada de los cultivos de floración masiva durante los tres años anteriores al muestreo (MFC3).

El muestreo de los polinizadores se realizó en cada campo de colza durante abril y mayo (2021 o 2022 dependiendo del campo). Solo se evaluó la abundancia de insectos que han sido clasificados como polinizadores silvestres eficientes (Jauker et al., 2009). Se registró los contactos con las flores de colza de tres grupos de polinizadores silvestres: abejorros, otras abejas silvestres y sírfidos. También se registró la abundancia de la abeja melífera, ya que puede afectar el comportamiento del resto de los polinizadores silvestres (Hudewenz & Klein, 2013).



**Figura 4.** A) Distribución geográfica de los 22 campos de colza en la Cataluña central. B) Representación esquemática de las características del paisaje de una localidad (diversidad de grupos de cultivos, cobertura de cultivos de floración masiva, hábitats seminaturales y tamaño medio de campo de una localidad (área de influencia de 1 km de radio). C) Esquema de la distribución de los transectos (75 m × 2 m) utilizados para evaluar el forrajeo de polinizadores, junto con los puntos de instalación del experimento de exclusión de polinizadores dentro de un campo. D) Diagrama del análisis de la eficacia de la polinización en cultivos de colza, basado en el experimento de exclusión de polinizadores.

Un observador registró los insectos que visitaban flores de la colza en dos días diferentes durante el pico de floración del cultivo en dos transectos de 150 m<sup>2</sup> cada uno (75 m × 2 m) paralelos al margen del campo, uno situado en el borde del cultivo y el otro en el centro del

campo (a 25 m de cualquier margen del campo) (Figura 4C). Se tomaron muestras en dos posiciones dentro del cultivo para estimar el efecto de la distancia a los márgenes sobre los visitantes florales. La densidad de cada grupo de polinizadores se calculó sumando las observaciones de los dos días de muestreo para el centro del campo y el borde por separado. El esfuerzo total de muestreo fue de  $15 \text{ minutos/transecto/día} \times 2 \text{ transectos/campo} \times 2 \text{ días} = 60 \text{ minutos/campo}$ .

Antes de la floración, se implementó un experimento de exclusión de polinizadores en veinte campos de colza. En cada campo, se seleccionaron 20 plantas de colza, la mitad de ellas ubicadas en el centro y la otra mitad en el borde, que se sometieron a un tratamiento de polinización con dos niveles experimentales (polinizadores excluidos vs. no excluidos). En cada posición del campo, se seleccionaron cinco plantas, marcando una rama en cada una de ellas para el tratamiento de polinización abierta (OP). Esto permitió que las inflorescencias fueran polinizadas por todos los vectores posibles, como el viento y los insectos. Para la exclusión de los polinizadores (EP), en cada posición del campo, se eligieron sendas ramas en cada una de las plantas restantes, que fueron protegidas mediante una bolsa de malla fina para limitar el contacto con insectos polinizadores ( $10 \text{ inflorescencias} \times \text{dos posiciones dentro del campo} \times 20 \text{ campos} = 400 \text{ inflorescencias}$ ) (Figura 4D).

La eficacia de la polinización se evaluó mediante seis parámetros, tres relacionados con la producción y tres con la calidad de las semillas para cada una de las inflorescencias de colza seleccionadas. La producción se estimó mediante (1) la relación de vainas por flor, (2) el número de semillas por vaina y (3) el peso de mil semillas; mientras que la calidad se evaluó a partir (4) del porcentaje de contenido de aceite en las semillas, (5) la composición y cuantificación de tocoferoles, y (6) la cuantificación de clorofila total y carotenoides. (Figura 4D).





## INFORME DE LOS DIRECTORES DE TESIS DEL FACTOR DE IMPACTO DE LOS ARTÍCULOS PUBLICADOS

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El Dr. F. Xavier Sans i Serra y el Dr. José M. Blanco Moreno, directores de la tesis doctoral de Pablo Neira Vidal, presentan el siguiente informe sobre la contribución del doctorando en cada una de las publicaciones presentadas en esta memoria.

## **Capítulo 1**

Effects of agricultural landscape heterogeneity on pollinator visitation rates in Mediterranean oilseed rape. P. Neira, J.M. Blanco-Moreno, M. Olave, B. Caballero-López, F. X. Sans.

***Contribución del doctorando:*** participó en el diseño experimental del estudio, el análisis formal y trabajo de campo, análisis de datos, validación, análisis y visualización de los datos, y redacción del borrador original, así como en la posterior revisión y edición del manuscrito.

***Contribución de los otros autores:*** Xavier Sans estuvo a cargo de la conceptualización, obtención de fondos, metodología, análisis de datos, administración del proyecto, supervisión, y también contribuyó en la revisión y edición del manuscrito. Magdalena Olave realizó trabajo de campo, análisis de datos y participó en la revisión del manuscrito. Berta Caballero-López contribuyó en la conceptualización, investigación formal, metodología, supervisión y revisión y edición del manuscrito. José Manuel Blanco-Moreno se encargó del análisis de datos, metodología, supervisión, validación, visualización, redacción y edición del manuscrito, así como de la conceptualización, obtención de fondos y trabajo de campo.

## **Capítulo 2**

Landscape crop diversity contributes to higher pollination effectiveness and positively affects rapeseed quality in Mediterranean agricultural landscapes. P. Neira, M. Morales, S. Munné-Bosch, J.M. Blanco-Moreno, F.X. Sans

***Contribución del doctorando:*** participó en el diseño experimental del estudio, el análisis formal y trabajo de campo, análisis de datos, validación, análisis y visualización de los datos, y redacción del borrador original, así como en la posterior revisión y edición del manuscrito.

***Contribución de los otros autores:*** Melanie Morales contribuyó en la conceptualización, el análisis de laboratorio, análisis de datos, la metodología, la supervisión, y la revisión y edición del manuscrito. Sergi Munné-Bosch se encargó de la metodología de laboratorio, la supervisión, y la revisión y edición del manuscrito. José Manuel Blanco-Moreno estuvo a cargo de la conceptualización, análisis de datos, la obtención de fondos, la investigación, la metodología, la supervisión, la validación, la visualización, así como de la revisión y edición del manuscrito. Xavier Sans participó en la conceptualización, la obtención de fondos, análisis de datos, la metodología, la supervisión, la administración del proyecto y la revisión y edición del manuscrito.

### **Capítulo 3**

Past mass flowering crop cover enhances pollinator density and oilseed rape yield in Mediterranean agroecosystems. P. Neira; J. Nabau; M. Morales; Chamorro-Lorenzo, L; J.M. Blanco-Moreno; F.X. Sans

***Contribución del doctorando:*** participó en el diseño experimental del estudio, el análisis formal y trabajo de campo, análisis de datos, validación, análisis y visualización de los datos, y redacción del borrador original, así como en la posterior revisión y edición del manuscrito

***Contribución de los otros autores:*** Joana Nabau participó en la recogida y el análisis de datos y la redacción del manuscrito. M. Morales se encargó de la metodología, la supervisión de las actividades de laboratorio y la revisión y edición del manuscrito. Lourdes Chamorro-Lorenzo: contribuyó a la metodología, a la revisión y edición del manuscrito. José Manuel Blanco-Moreno participó en el análisis de datos, la metodología, la supervisión, la validación, la conceptualización y la obtención de fondos, además de la revisión y edición del manuscrito. Xavier Sans se ocupó de la conceptualización, la obtención de fondos, análisis de datos, la metodología, la administración del proyecto, la supervisión y la revisión y edición del manuscrito.

Finalmente certifican que ninguno de los coautores de los artículos ha utilizado estos datos obtenidos de manera implícita o explícita para la elaboración de otras tesis doctorales.

Estos tres artículos que forman parte de la memoria de la tesis doctoral de Pablo Neira Vidal han sido sometidos para su publicación a revistas científicas de ámbito internacional y que constan en el Science Citation Index. El artículo del capítulo 1 está publicado en *Agriculture, Ecosystems & Environment*, revista con un factor de impacto de 6.0 que se sitúa en el primer cuartil del área *Agronomy and Crop Science*. En cuanto al capítulo 2 se ha publicado en la revista *Science of the Total Environment*, con un factor de impacto de 8.2 y que se sitúa en el primer cuartil de *Environmental Science*. Por último, el capítulo 3 está en revisión en *Agricultural Systems*, esta revista tiene un factor de impacto de 6.1 y se ubica en el primer cuartil de *Agronomy and Crop Science*

Barcelona, septiembre de 2024.



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# CAPÍTULO 1

Efectos de la heterogeneidad del paisaje agrícola sobre las tasas de visita de polinizadores en la colza mediterránea





**Effects of agricultural landscape heterogeneity on  
pollinator visitation rates in Mediterranean oilseed  
rape**

Agriculture, Ecosystems & Environment

Volume 363, 1 April 2024, 108869

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## Effects of agricultural landscape heterogeneity on pollinator visitation rates in Mediterranean oilseed rape

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## ARTICLE INFO

## Keywords:

Wild pollinators

Oilseed rape

Landscape heterogeneity

Land uses

Ecosystem services

## ABSTRACT

Agricultural intensification, by changing land use and modifying the yearly configuration and composition through crop sequences, affects the abundance and diversity of pollinators and, consequently, pollination. This study aims to assess the impact of the characteristics of agricultural landscapes on pollinator abundance in the Mediterranean region. We studied the response of three major wild pollinator groups (hoverflies, bumblebees, and wild bees) to four landscape characteristics: three related to composition, namely, equivalent crop diversity in the sampling year (eRg), previous year equivalent crop diversity (eRgP) and percentage of seminatural habitats (SNH), and one related to landscape configuration, namely, mean field size (MFS). For this evaluation, we selected twenty-two oilseed rape fields (OSRs) differing in surrounding landscape characteristics within a 1-km radius. Multimodel inference indicates that landscape variables affect pollinator groups differently. The percentage of SNH was the most important variable having a positive influence on the abundance of bumblebees, while eRgP and MFS were found to be important for the abundance of wild bees and hoverflies. These data allow us to prioritize actions aimed at specific groups of pollinators, improve agricultural landscape schemes, promote the conservation of wild pollinators, promote crop diversity at the landscape scale and increase the extent of seminatural areas.

## 1. Introduction

Pollinators provide essential services for the sexual reproduction of many wild plant species and increase the yields of many globally traded food and biofuel crops (Bommarco et al., 2012; Klein et al., 2007; Raderschall et al., 2021). It is estimated that one-third of food depends, directly or indirectly, on entomophilous pollination, an amount that represents approximately 153 billion € per year worldwide (Gallai et al., 2009). Therefore, maintaining sufficient levels of pollinators in the landscape is key to preserving plant diversity and ensuring food production (Balzan et al., 2014; Dainese et al., 2019).

In the last 50 years, a marked decrease in the abundance of bees has been observed (Biesmeijer et al., 2006; Zattara and Aizen, 2021), so pollination is considered a declining ecosystem service (Kearns et al., 1998; Klein et al., 2007). The decline in pollinators has been attributed to diverse anthropogenic causes, such as land use changes caused by the intensification of agricultural land management (Hass et al., 2018;

Kennedy et al., 2013; Kovács-Hostyánszki et al. 2017; Raven and Wagner, 2021). Agricultural intensification has modified the configuration and composition of agricultural landscapes through the reduction and fragmentation of seminatural habitats (SNH), the enlargement of fields and the reduction of crop diversity, which has homogenized agricultural land (Gámez-Virués et al., 2015; Tilman et al., 2001). All these factors have altered the functioning of agroecosystems, generating loss of feeding and nesting opportunities and resulting in a decrease in pollinator populations such as wild bees (Wersebeckmann et al., 2023).

The maintenance of pollinators and pollination services requires the availability of sufficient resources in both noncultivated areas and crops of these agricultural landscapes (Rickerts et al., 2008). These resources include suitable nesting habitats as well as sufficient nectar- and pollen-rich floral resources within their flight ranges (Le Feon et al., 2010; Liczner and Colla, 2019). While floral resources can be obtained both in noncrop and crop areas, many pollinators cannot complete their life cycle in crops but visit them only to forage, and their nesting habitats

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Received 17 May 2023; Received in revised form 12 December 2023; Accepted 20 December 2023

Available online 11 January 2024

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are usually found in noncrop areas (Cavigliasso et al., 2022; Williams and Kremen, 2007).

To supply the resources and habitats needed by pollinators, agricultural landscapes need to display a certain degree of heterogeneity, which relates to two different components, configuration and composition. Mean field size is a characteristic related to landscape configuration, as it determines field boundary density and the availability of small linear noncropped fragments, increasing connectivity with natural and seminatural areas (Hass et al., 2018). On the other hand, both noncrop areas and cropped areas contribute to the compositional heterogeneity of agricultural landscapes. Several authors have shown that the extent of seminatural habitats (SNH) has a positive relationship with the abundance and diversity of wild bee communities (Bukovinsky et al., 2017; Loyola and Martins, 2008; Nayak et al., 2015; Rollin et al., 2013). Moreover, landscapes with larger extents of seminatural habitats and higher connectivity have also been shown to increase yields in different crops through pollinators and their pollination services (Castle et al., 2019; Martin et al., 2019; Petersen and Nault, 2014; Rollin et al., 2013). However, the proportion of SNH present in agricultural landscapes may not provide sufficient pollen and nectar resources to maintain viable pollinator populations. Therefore, the relationship between SNH and pollinators can be strongly affected by the floral resources offered by crops in agricultural landscapes (Bartual et al., 2019; Holzschuh et al., 2011; Winfree et al., 2007). Agricultural landscape composition can also vary in relation to the crop diversity in a landscape. Crop diversity has been reported to have a positive relationship with the abundance of pollinators by providing a more diverse matrix of food resources and habitats for nesting and dispersal (Fahrig et al., 2011; Raderschall et al., 2021; Sirami et al., 2019). Especially in cereal-dominated arable land, the diversity of crops, some of which have abundant floral resources, allows pollinators to complement their diet (Fahrig et al., 2011).

Mass-flowering crops offer abundant floral resources and are very attractive to a wide diversity of pollinators (Holzschuh et al., 2011). At a low proportion, these crops have a concentration effect in agricultural landscapes, they can be used as phytometers to obtain estimates of the abundance of pollinators in the landscape during flowering (Magrach et al., 2018; Martínez-Núñez et al., 2022). Oilseed rape (*Brassica napus* L.) (OSR) is a mass-flowering crop that is widely cultivated worldwide and can concentrate the abundance of pollinators in the agricultural landscape (Beyer et al., 2021; Mendoza-García et al., 2018). Wild pollinators that visit oilseed rape flowers include honeybees, wild bees, bumblebees, hoverflies and flower-visiting beetles (Rader et al., 2009; Stanley et al., 2013).

However, the composition of the agricultural landscape varies from year to year, especially in arable landscapes, where the crops grown are mainly annuals. Thus, a deeper knowledge about pollinators and their interactions with landscape elements, as well as with crop diversity and its temporal changes, could help in promoting the pollinator community and its pollination services.

In recent years, some progress has been made in understanding the effect of changing heterogeneity at the agricultural landscape level on the abundance and diversity of pollinators. However, the abundance of pollinators increases with increasing availability of resources, the role of the spatiotemporal compositional heterogeneity of the landscape on the different pollinator groups is still unknown, especially in Mediterranean agricultural landscapes.

We studied the response of three major wild pollinator groups (hoverflies, bumblebees, and other wild bees) to four landscape characteristics related to the configurational and compositional heterogeneity of agricultural landscapes. We selected 22 OSR fields in Mediterranean agricultural landscapes of Spain, and we tested the following hypotheses: (1) landscape metrics related to cropland (i.e., crop diversity and mean field size) and seminatural habitats in agricultural landscapes have a differential effect on the abundance of different group of pollinators, and (2) Temporal changes in crop

diversity influence the abundance of pollinators that visit OSR fields.

## 2. Materials and methods

The study was conducted in the spring of 2021 and 2022 in central Catalonia in northeastern Spain (Fig. 1). The landscape is dominated by rainfed arable crops, mainly winter cereals such as wheat, barley or spelt interspersed with woody crops common to the Mediterranean region, such as olive groves and vineyards but many others such as alfalfa, fruit trees, chickpeas, lentils, almond, onion, pumpkin, corn or oilseed rape (Institut d'Estadística de Catalunya 2023). The noncropped areas are mainly occupied by various types of forest habitats (pine forests, holm oak forests, oak groves), shrubs derived from their degradation (usually by fire) or bushes and mesoxerophilic grasslands that occupy former crops and other marginal areas (Departament de Territori i Sostenibilitat, 2018).

### 2.1. Landscape metrics

We selected conventionally managed OSR fields, all sown to hybrid winter OSR varieties, with varieties differing between farmers. For the characterization of the landscape, we selected a circular area of 1 km radius around each OSR field. The radius was chosen because previous studies have shown that most foraging flights for wild bees are within this distance and corresponds to the range of the average landscape response for hoverflies (Holzschuh et al., 2011; Madureira et al., 2023; Steffan-Dewenter and Kuhn, 2003). We selected 22 localities in which the area sown with OSR around the selected fields was less than 10% to ensure the concentrating effect on bees (Beyer et al., 2021; Magrach et al., 2018). All localities were at least 2 km apart to prevent any two OSR fields from being visited by the same pool of pollinators (Holzschuh et al., 2016; Westphal et al., 2003).

The characterization of the composition and configuration of the landscape around each of the OSR fields was carried out based on the spatial information of the DUN-SIGPAC Crop Map (Departament d'Acció Climàtica, Alimentació i Agenda Rural 2023) and the Cartografia dels Hàbitats de Catalunya, v.2 (Departament de Territori i Sostenibilitat, 2018) using R software with package sf (Edzer Pebesma, 2018). Four landscape metrics were calculated for each circular area. Three of them are related to composition: the equivalent crop group diversity (eRg) for the current year, the equivalent crop group diversity for the previous year (eRgP) and percentage of area occupied by seminatural habitats. To compute the latter, crop groups were defined according to their functional contribution to pollinators, e.g., wheat, barley, oats, and spelt are included in cereal functional groups (see all groups in Table A.1). With these functional groups, the eRg metric was obtained by calculating the Shannon index (Eq. 1), weighting the groups according to their proportion of the landscape area ( $p_i$ ), and converting it into true diversity (Eq. 2) (Jost, 2006).

$$H_g = \left( - \sum_{i=1}^s p_i \ln p_i \right) \quad (1)$$

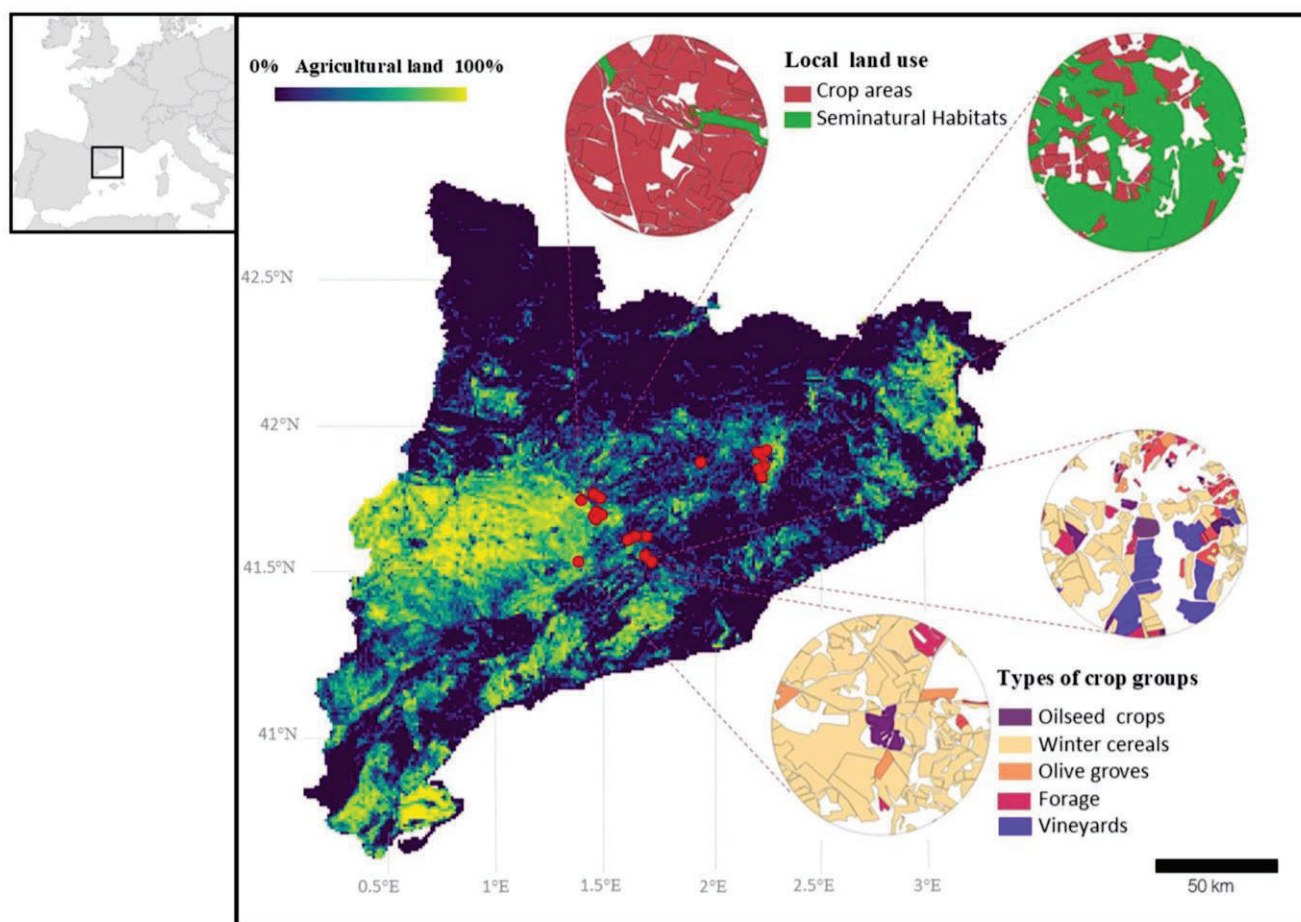
$$eRg = \exp(H_g) \quad (2)$$

The equivalent crop group diversity corresponds to the effective number of crop functional groups if all crop groups were equally represented. We also computed the equivalent crop group diversity of the previous year with the same method but using crop data for the preceding year. The fourth metric is related to configuration, and we used the mean field size (MFS). A detailed listing of the characteristics of the studied agricultural landscapes is provided in Table A.3.

### 2.2. Pollinator evaluation

Sampling was carried out in each OSR field during April and May





**Fig. 1.** Map of Catalonia (NE of Spain) and the distribution of the 22 localities. The blue—yellow gradient represents the percentage of agricultural land. Information available in the Cartografia dels Hàbitats de Catalunya, v.2 (Departament de Territori i Sostenibilitat, 2018). The circles represent the agricultural landscape around the localities, and this buffer zone has a radius of 1 km. The upper circles represent examples of landscapes with contrasting local land use. The lower circles represent examples of landscapes with contrasting diversity of crop groups. Only five of the thirteen types of crops present in the 22 agricultural landscapes are shown, complete list in Table A.1.

(2020 or 2021 depending on the field). We only evaluated the abundance of insects that have been classified as efficient wild pollinators (Jauker et al., 2009). We recorded three groups: wild bees, bumblebees, and hoverflies. The abundance of the honeybee (*Apis mellifera* L. 1758) was also recorded since it could affect the behaviour of the rest of the wild pollinators (Hudewenz and Klein, 2013), although it was not analysed since it depends more on farmers' preferences than on landscape properties.

One observer recorded insects visiting OSR flowers on two different days during peak flowering in two transects of 150 m<sup>2</sup> each (75 × 2 m) parallel to the field margin, one at the crop edge and the other in the field centre (25 m away from any field margin). We sampled on these positions within the crop to estimate the effect of the distance to margins in the floral visitors. The abundance of each group of pollinators was calculated by adding the observations of the two sampling days together for the field centre and the edge separately. The total sampling effort was 15 minutes/transect/day × 2 transects/field × 2 days = 60 minutes/field.

### 2.3. Data analysis

The analysis of the relationship of the abundance of the pollinator groups and total abundance of pollinators with landscape variables was carried out using generalized linear mixed models using the 'glmmTMB' package (Brooks et al., 2017). We used the variance inflation factor

(VIF) to test for potential collinearity between explanatory variables (Zuur et al., 2010), but the VIF was below 4 in all cases (Table A.2). The relationship between landscape variables and the abundance of pollinators was tested. As fixed effects variables, we included eRg, eRgP, MFS and SNH as continuous variables (scaled to minimum = 0 and maximum = 1) and within-field position (edge and centre) and year as categorical variables. Locality was included as a random effect factor since the abundance of pollinators between localities was variable.

We ran all possible model combinations using the 'dredge' function in the 'MuMIn' package (Barton and Barton, 2023) to test several hypotheses simultaneously across the models. For each pollinator group, we explored the set of 64 models that included all possible combinations of the four landscape variables plus within-field position and year, and a null model. For each model, we computed its Akaike information criterion corrected for small sample sizes (AICc). We averaged the whole set of models (Burnham, 2002). For each average model, the 90% and 95% confidence intervals of coefficients and their weights ( $w_i$ ) were obtained. We report all predictor variables ( $\sum w_i$ ). All analyses were performed in the R environment v3.4.4 (R Core Team, 2020).

### 3. Results

During the study, 1462 pollinating organisms were recorded contacting the OSR flowers, of which 16.3% corresponded to the group of hoverflies, 18.9% to bumblebees and 65.5% to wild solitary bees.



Within-field position and crop diversity from the previous year (eRgP) at the agricultural landscape have a positive and significant impact on the abundance of total pollinators visiting OSR fields. The average model indicates strong support for each of these variables, according to their accumulated weights ( $\Sigma w_i$ , 0.79 and 0.69, respectively) and their CI (Table 1) (Fig. 2). The other metrics studied (SNH, MFS, and eRg) had less clear effects with lower weights and their CI including zero.

### 3.1. Response of bumblebees to landscape metrics

The seminatural habitats and mean field size in the landscape have an impact on bumblebee abundance visiting OSR fields. The average model has substantial support, both in terms of relative importance and CIs (Table 1). The landscape variables SNH ( $\Sigma w_i = 0.95$ ) and MFS ( $\Sigma w_i = 0.71$ ) both had a positive effect on bumblebees (Fig. 3), and the variable eRgP ( $\Sigma w_i = 0.37$ ) also had a positive effect; however, the confidence interval of the latter contained zero. On the other hand, eRg ( $\Sigma w_i = 0.27$ ) and within-field position ( $\Sigma w_i = 0.24$ ) (Fig. 2) were not significant.

### 3.2. Response of wild bees to landscape metrics

The abundance of wild bees that visit OSR responds to three of the agricultural landscape variables that were examined: eRgP, MFS in crop areas and the amount of SNH that is present in the noncropped areas. The average model has eRgP ( $\Sigma w_i = 0.65$ ) as the most important variable, which has a positive effect on this group of pollinators (Fig. 3). Additionally, SNH ( $\Sigma w_i = 0.62$ ) and MFS ( $\Sigma w_i = 0.47$ ) have a high relative weight, both of which have a negative effect, although the interval of MFS includes 0 at 90% CI (Table 1). Thus, there is strong support for the influence of these three factors on wild bees. Different patterns occur with eRg ( $\Sigma w_i = 0.34$ ) and within-field position ( $\Sigma w_i = 0.30$ ) (Fig. 2), which have lower weights.

### 3.3. Response of hoverflies to landscape metrics

The effect of within-field position (edge) ( $\Sigma w_i = 0.93$ ) was significant for the hoverflies, supported by their CI (Table 1) (Fig. 2). Two of the remaining agricultural landscape variables, MFS ( $\Sigma w_i = 0.56$ ) and SNH ( $\Sigma w_i = 0.56$ ), both had a clear negative effect (Fig. 2), although the confidence intervals of these variables included zero. The remaining models included the other agricultural landscape variables, eRgP and eRg, but with lower weights  $\Sigma w_i = 0.30$  and  $\Sigma w_i = 0.28$ , respectively (Table 1).

## 4. Discussion

Our study reveals that pollinator abundance responds to within-field position and past year crop diversity, moreover, the responses to seminatural habitat cover, mean field size and past and current crop diversity differed between the pollinator groups assessed.

These findings support our first hypothesis: Each group of pollinators reacts differently to landscape features. The proportion of seminatural areas and mean field size have a strong positive effect on the abundance of bumblebees and a negative effect on other wild bees. Wild bees respond positively to past crop diversity. Hoverflies, on the other hand, respond to field environment rather than to landscape features.

Our second hypothesis has been partially supported. Past crop diversity has a consistently positive effect across all three pollinator groups, although its strength is variable. This effect is particularly strong (statistically significant) for wild bees, which are the most abundant group of pollinators in our study.

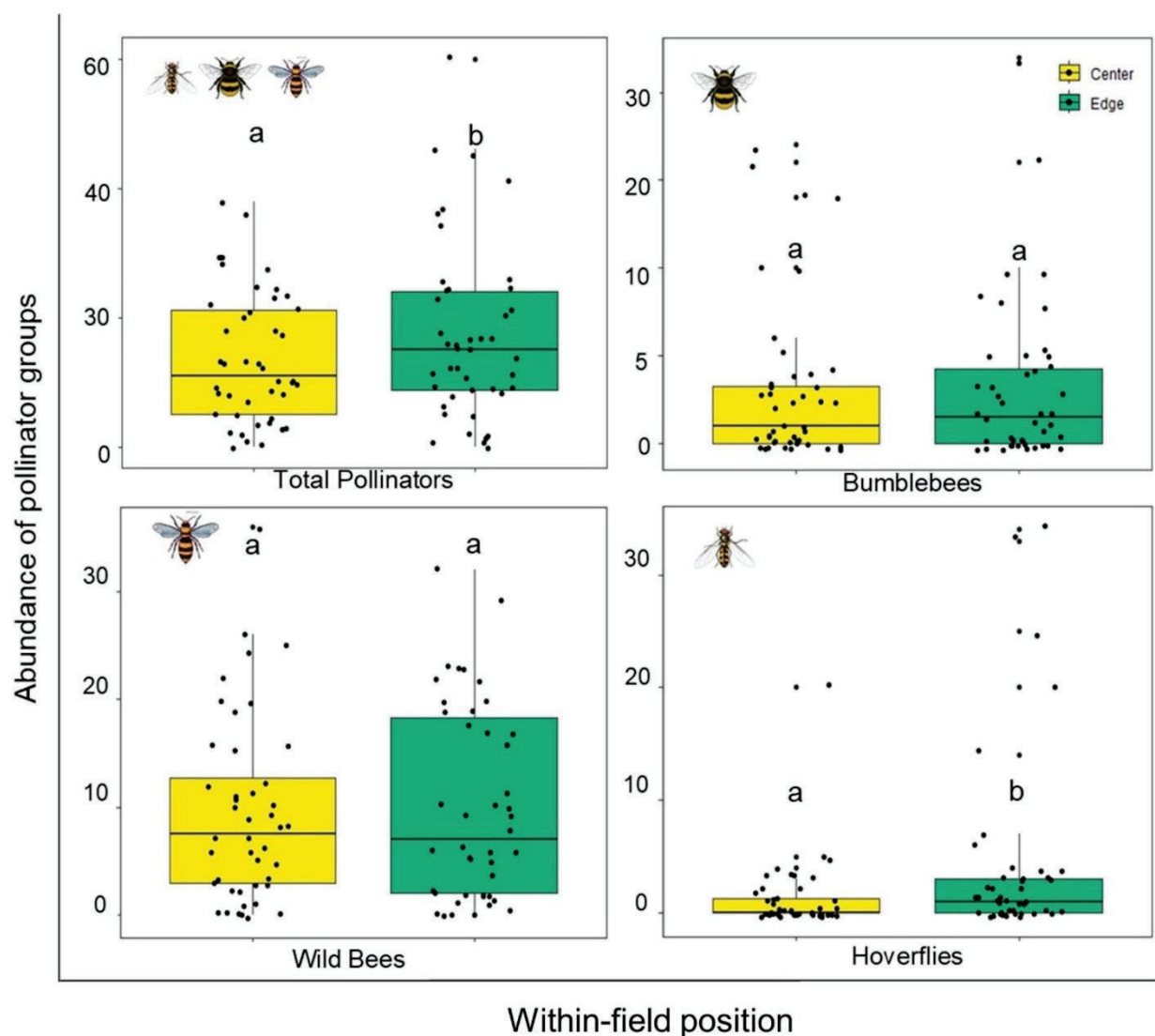
### 4.1. Past and present effects of crop diversity

Crop diversity in the current year had no significant effect on the abundance of any pollinator group. Although increasing last year's crop diversity correlated positively with the abundance of all three pollinator

**Table 1**

Estimates and standard error (SE) for each predictor in the average models obtained through multimodel inference. For each fixed effect factor, its confidence intervals (CI at 90% and 95%) and sum of weights ( $\Sigma w_i$ ) are indicated. Bold numbers indicate cases where the confidence intervals do not include 0. eRg: Crop Diversity, eRgP: Previous Year Crop Diversity, MFS: Mean Field Size, SNH: Seminatural Habitats percentage.

|                      |             | Estimate | SE    | $\Sigma w_i$ | CI           |               |               |               |
|----------------------|-------------|----------|-------|--------------|--------------|---------------|---------------|---------------|
|                      |             |          |       |              | -2.50%       | -5%           | -95%          | -97.50%       |
| a) Total Pollinators | Year (2022) | 8.955    | 3.299 | 0.9          | <b>2.489</b> | <b>3.547</b>  | <b>14.364</b> | <b>15.422</b> |
|                      | Edge        | 3.659    | 1.633 | 0.79         | <b>0.457</b> | <b>0.981</b>  | <b>6.336</b>  | <b>6.86</b>   |
|                      | eRgP        | 4.473    | 2.136 | 0.69         | <b>0.286</b> | <b>0.971</b>  | <b>7.976</b>  | <b>8.661</b>  |
|                      | SNH         | -1.672   | 1.995 | 0.32         | -5.583       | -4.944        | 1.6           | 2.238         |
|                      | MFS         | -2.825   | 2.827 | 0.38         | -8.366       | -7.464        | 1.814         | 2.715         |
|                      | eRg         | 1.174    | 2.648 | 0.29         | -4.016       | -3.17         | 5.519         | 6.364         |
|                      |             |          |       |              |              |               |               |               |
| b) Bumblebees        | SNH         | 2.689    | 0.909 | 0.95         | <b>0.907</b> | <b>1.197</b>  | <b>4.181</b>  | <b>4.472</b>  |
|                      | MFS         | 2.22     | 1.204 | 0.71         | -0.139       | <b>0.244</b>  | <b>4.196</b>  | 4.58          |
|                      | eRgP        | 0.999    | 1.298 | 0.37         | -1.546       | -1.132        | 3.13          | 3.544         |
|                      | Year (2022) | -1.438   | 1.503 | 0.34         | -4.385       | -3.903        | 1.026         | 1.508         |
|                      | eRg         | 0.169    | 1.07  | 0.27         | -1.928       | -1.586        | 1.924         | 2.266         |
|                      | Edge        | 0.09     | 0.553 | 0.24         | -0.994       | -0.816        | 0.998         | 1.175         |
|                      |             |          |       |              |              |               |               |               |
| c) Wild Bees         | Year (2022) | 7.725    | 2.442 | 0.96         | <b>2.938</b> | <b>3.721</b>  | <b>11.729</b> | <b>12.511</b> |
|                      | eRgP        | 3.299    | 1.662 | 0.65         | <b>0.04</b>  | <b>0.572</b>  | <b>6.026</b>  | <b>6.558</b>  |
|                      | SNH         | -2.529   | 1.428 | 0.62         | -5.328       | <b>-4.871</b> | <b>-0.186</b> | 0.269         |
|                      | MFS         | -2.867   | 2.213 | 0.47         | -7.206       | -6.501        | 0.766         | 0.195         |
|                      | eRg         | 1.645    | 1.83  | 0.34         | -1.943       | -1.358        | 4.648         | 5.233         |
|                      | Edge        | 0.727    | 0.913 | 0.3          | -1.062       | -0.769        | 2.223         | 2.517         |
|                      |             |          |       |              |              |               |               |               |
| d) Hoverflies        | Edge        | 2.84     | 1.013 | 0.93         | <b>0.854</b> | <b>1.179</b>  | <b>4.502</b>  | <b>4.827</b>  |
|                      | MFS         | -2.227   | 1.422 | 0.56         | -5.06        | -4.561        | 0.106         | 0.56          |
|                      | SNH         | -1.894   | 1.161 | 0.56         | -4.17        | -3.799        | 0.009         | 0.381         |
|                      | Year (2022) | 3.028    | 1.91  | 0.52         | -0.716       | -0.104        | 6.161         | 6.774         |
|                      | eRg         | -0.472   | 1.38  | 0.28         | -3.178       | -2.737        | 1.792         | 2.234         |
|                      | eRgP        | 0.654    | 1.504 | 0.3          | -2.293       | -1.813        | 3.123         | 3.603         |
|                      |             |          |       |              |              |               |               |               |



**Fig. 2.** Effects of within-field position on the abundances per field of total pollinators and the three pollinator (hoverflies, bumblebee and other wild bee) groups studied. Model predictions with 95% confidence intervals were obtained from the average model of the multimodel analysis (Table 1). Different letters above boxes indicate significant differences between within-field position, centre (yellow) and edge (green).

groups, statistical significance was observed solely in the case of wild bees and when considering the collective abundance of all three pollinator groups. The abundance of wild bees is more related to preceding features of the agricultural landscape, with the crop diversity of the prior year of sampling being more important than the crop diversity around the area where they are thriving. This pattern is in line with earlier studies that have demonstrated how an increase in crop diversification benefits the agricultural landscape biodiversity of wild bees (Martin et al., 2019; Sirami et al., 2019) and that interannual changes in crop composition are also well known to affect ecological processes such as pollination and biological control (Holzschuh et al., 2011; Schellhorn et al., 2015; Tschamtko et al., 2021). Crop diversity did not affect bumblebee abundance, in clear contrast with earlier studies, which indicated that high crop diversity was related to higher bumblebee prevalence in the agricultural landscape (Hemberger et al., 2021). For hoverflies, our findings are consistent with those of Hass et al. (2018) in that they also show that the abundance of these insects is independent of crop diversity.

According to recent studies, crop diversification in highly intensified landscapes creates spatial and temporal heterogeneity of habitats and

resources that enable bee populations to be sustained at higher levels (Beyer et al., 2021; Cavigliasso et al., 2022). This may hold a relationship with our findings, where past year crop diversity had a stronger effect on the abundance of pollinators than crop diversity in the current year. Similar effects have been observed in relation to the presence of mass flowering crops, as they can contribute to pollinator population growth, and spillage is generated to plants in noncultivated areas as well as to other crops (Blaauw and Isaacs, 2014). Therefore, planning agricultural schemes that increase crop diversity and consider crops producing flower resources could be relevant in relation to the maintenance of pollinators or the provision of pollination services in the following year.

#### 4.2. Relationship between seminatural areas and pollinators

Our findings suggest that the proportion of seminatural areas in the landscape is important for the abundance of the three pollinator groups, even though they exhibited the contrasting pattern. While solitary bees and hoverflies benefit from lower percentages of seminatural habitats, bumblebees were more abundant when the landscape had a higher



are enhanced by cultivated areas, especially for generalist species, which are generally found in agricultural landscapes (Haenke et al., 2014; Jauker et al., 2009; Speight, 2017).

On the other hand, for bumblebees, the proportion of seminatural areas had a positive effect and was the most important variable explaining their abundance. This positive relationship between bumblebees and the proportion of seminatural areas agrees with previous research (Hopfenmüller et al., 2014; Raderschall et al., 2021). Bumblebees prefer environments that have constant resources, such as those offered by natural and seminatural habitats. Furthermore, bumblebee habitat is enhanced by heterogeneous landscapes comprising a variety of seminatural habitats (Proesmans et al., 2019), and certain species of the genus *Bombus* use uncropped areas to form colonies (Goulson et al., 2008; Kells and Goulson, 2003).

#### 4.3. Agricultural landscape configuration and its relationship with pollinators

The mean field size has a positive correlation with the abundance of bumblebees visiting OSR. Bumblebees are more abundant in environments with larger fields and thus fewer crop margins. Bumblebees have larger body sizes, which allows them to have larger foraging ranges and makes them less reliant on herbaceous habitats in intensive agricultural landscapes (Gathmann and Tschamtkke, 2002; Westphal et al., 2006). Bumblebees feed instead on available natural resources present in seminatural woody areas but can exploit mass-flowering crops when present in the landscape (Rollin et al., 2013). This is the case with *Bombus terrestris* L. 1758, a species that can adapt readily due to its generalist behaviour (Dafni et al., 2010).

Conversely, field size has been proposed as a reliable and widely available indicator that can help identify potential areas of high natural value since reducing field size can bring substantial benefits to biodiversity (Clough et al., 2020). Previous research has reported a 70% higher abundance of pollinators on small fields (Martin et al., 2019). Smaller fields with more margins facilitate pollinator movement by boosting landscape connectivity (Hass et al., 2018; Magrach et al., 2023; Sutherland et al., 2001). Benefits of field size could be enhanced by the negative correlation that exists with crop diversity ( $p < 0.05$ ). According to other studies, wild pollinators such as solitary bees nest mainly outside of arable fields (Clough et al., 2020). Therefore, field margins not only increase connectivity but also contribute to the stabilization of pollinator populations (Gardner et al., 2021; Mendoza-García et al., 2018). The relationship of field size with hoverflies is not straightforward. Some studies have shown that the presence of margins in cultivated fields benefits hoverflies because it provides habitat and floral supplies (Schirmel et al., 2018; Sutherland et al., 2001). In our case, we found a field-level response to the proximity of the field margin, related to the greater abundance of hoverflies on the edge compared to the centre of the crop, but no landscape-scale effects of field size. Similar to data from Hass et al. (2018), who also found where hoverflies do not respond to the average field size or crop diversity.

#### 4.4. Conclusions

The results of our study may have a few significant implications for pollinator conservation in Mediterranean climate agricultural landscapes to report how different groups of pollinators respond differently to landscape properties. This feature indicates that it is important to define a target group of pollinators for the trade-offs that are considered in agricultural landscape planning.

Despite the difficulty of changing the configuration of an agricultural landscape, composition is a more controllable landscape quality. The crop diversity would be the easiest target landscape feature for benefiting pollination services. Adjusting crop diversity can have a faster influence on pollination due to the inherent dynamic nature of crops in arable landscapes and its positive effect on wild bees, which are the most

abundant group of pollinators.

On the other hand, promoting the maintenance of seminatural habitats, although less amenable to management, can have an impact on bumblebee conservation. A balance between the persistence of natural habitats, mean field size, and increasing crop diversity can benefit the populations of different guilds of pollinators and thus their pollination service in agroecosystems.

Landscape-scale management of crop planning both spatially (crop diversity and field size) and temporally were all important and can be considered complementary to seminatural habitats. The information presented in this study reinforces its value in the design of agricultural landscape schemes for pollination service preservation.

#### Funding

We would like to thank the farmers for their cooperation and for providing access to their fields. This research was partially supported by the projects RTI2018-095597-B-I00 and PID2021-127575OB-I00 of the Spanish Ministry of Science and Innovation. P.N. was supported by Scholarship Program Doctorado en el Extranjero BECAS CHILE of the Agencia Nacional de Desarrollo e Investigación (ANID), Chile Folio 7221038.

#### CRediT authorship contribution statement

**Sans F. Xavier:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review & editing. **Olave Magdalena:** Formal analysis, Investigation, Visualization, Writing – review & editing. **Caballero-López Berta:** Conceptualization, Investigation, Methodology, Supervision, Writing – review & editing. **Neira Pablo:** Data curation, Formal analysis, Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing. **Blanco-Moreno José Manuel:** Data curation, Methodology, Supervision, Validation, Visualization, Writing – review & editing, Conceptualization, Funding acquisition.

#### Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Pablo Neira Vidal reports financial support was provided by Chilean National Agency for Research and Development. F. Xavier Sans and José M. Blanco-Moreno report financial support was provided by Spanish Ministry of Science and Innovation.

#### Data Availability

Data will be made available on request.

#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108869.

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**Table A.1** List of types of crops that have been considered for the characterization of the equivalent diversity of crops (eRg).

| <b>Crop functional group</b> | <b>Crops</b>                                                      |
|------------------------------|-------------------------------------------------------------------|
| Winter cereals               | Khorasan wheat, common wheat, barley, oats, spelt, triticale      |
| Summer cereal                | corn, sorghum                                                     |
| Forage                       | Alfalfa, peas, barley, sainfoin, wheat, oats                      |
| Sweet fruits                 | Cherry trees, pear trees, apples, other fruit trees               |
| Stone fruits                 | Almond, walnut, pistachio trees                                   |
| Horticultural                | Pumpkin, artichoke, onion, leeks, garlic, lettuce, potato, tomato |
| Legumes                      | Chickpeas, beans, lentils                                         |
| Oilseeds                     | Oil seedrape, sunflowers                                          |
| Olive groves                 | Olives                                                            |
| Other products               | Herbaceous aromatics, Saffron                                     |
| Proteinaceous                | Peas                                                              |
| Vineyards                    | vineyards                                                         |

**Table A.2** VIF values for landscape metrics

| <b>Metrics</b> | <b>VIF</b> |
|----------------|------------|
| eRg            | 2.454451   |
| eRgP           | 3.335684   |
| SNH            | 1.518418   |
| MFS            | 3.617351   |

**Table A.3** Landscape metrics characterization of the 22 studied localities

| Locality | Crop Diversity<br>(eRg) | Past Crop Diversity<br>(eRgP) | % Semi Natural<br>Habitat (SNH) | Mean field size (m <sup>2</sup> )<br>(MFS) |
|----------|-------------------------|-------------------------------|---------------------------------|--------------------------------------------|
| Cap21    | 4.14                    | 3.04                          | 0.68                            | 12393.07                                   |
| Cas21    | 1.65                    | 2.08                          | 0.03                            | 34858.39                                   |
| Cla21    | 3.62                    | 3.62                          | 0.55                            | 9763.09                                    |
| Est21    | 2.12                    | 1.70                          | 0.18                            | 30391.48                                   |
| Eula21   | 3.03                    | 2.44                          | 0.30                            | 10123.70                                   |
| Gav21    | 2.94                    | 2.26                          | 0.36                            | 17404.58                                   |
| Pil21    | 1.53                    | 1.34                          | 0.16                            | 41075.66                                   |
| Od21     | 3.68                    | 4.01                          | 0.25                            | 11755.18                                   |
| Sai21    | 3.57                    | 2.60                          | 0.46                            | 10312.63                                   |
| Sal21    | 2.02                    | 1.98                          | 0.70                            | 15291.26                                   |
| Vic21    | 2.72                    | 3.14                          | 0.20                            | 14355.86                                   |
| Al22     | 2.16                    | 2.19                          | 0.30                            | 25680.86                                   |
| Cas22    | 2.82                    | 2.06                          | 0.12                            | 34047.72                                   |
| Mor22    | 2.73                    | 3.18                          | 0.27                            | 11111.39                                   |
| Mel22    | 2.36                    | 2.15                          | 0.18                            | 23148.39                                   |
| Od22     | 3.44                    | 3.29                          | 0.24                            | 16402.19                                   |
| Spe22    | 3.51                    | 3.06                          | 0.20                            | 11340.33                                   |
| Teu22    | 3.13                    | 3.08                          | 0.06                            | 11254.31                                   |
| Ton122   | 2.33                    | 3.22                          | 0.43                            | 11802.40                                   |
| Ton222   | 2.65                    | 2.87                          | 0.48                            | 10797.62                                   |
| Ton322   | 2.98                    | 2.87                          | 0.36                            | 12882.41                                   |



**Table A.4** Set of 64 mixed generalized linear models used in the Multi-Model Inference analysis for each group of pollinators.

| <b>Model - Total Pollinators</b>                                      | <b>AICc</b> | <b>R<sup>2</sup> conditional</b> | <b>R<sup>2</sup> marginal</b> |
|-----------------------------------------------------------------------|-------------|----------------------------------|-------------------------------|
| year+ Within-field position + eRgP + (1   Locality)                   | 645.95      | 0.60                             | 0.36                          |
| year+ Within-field position + eRgP + SNH + (1   Locality)             | 647.94      | 0.60                             | 0.37                          |
| year+ Within-field position + eRgP + MFS + (1   Locality)             | 648.19      | 0.60                             | 0.36                          |
| year+ Within-field position + MFS + (1   Locality)                    | 648.27      | 0.60                             | 0.32                          |
| year+ Within-field position + eRgP + eRg + (1   Locality)             | 648.31      | 0.60                             | 0.36                          |
| year+ eRgP + (1   Locality)                                           | 648.62      | 0.57                             | 0.34                          |
| year+ Within-field position + MFS + SNH + (1   Locality)              | 649.05      | 0.60                             | 0.35                          |
| year+ Within-field position + eRg + (1   Locality)                    | 649.18      | 0.60                             | 0.31                          |
| year+ Within-field position + eRgP + MFS + SNH + (1   Locality)       | 649.68      | 0.60                             | 0.38                          |
| year+ Within-field position + eRg + MFS + (1   Locality)              | 650.16      | 0.60                             | 0.33                          |
| year+ Within-field position + eRgP + eRg + SNH + (1   Locality)       | 650.31      | 0.60                             | 0.37                          |
| Within-field position + eRgP + (1   Locality)                         | 650.45      | 0.60                             | 0.23                          |
| year+ eRgP + SNH + (1   Locality)                                     | 650.55      | 0.57                             | 0.34                          |
| year+ Within-field position + eRgP + eRg + MFS + (1   Locality)       | 650.61      | 0.60                             | 0.36                          |
| year+ eRgP + MFS + (1   Locality)                                     | 650.80      | 0.57                             | 0.34                          |
| year+ Within-field position + (1   Locality)                          | 650.86      | 0.60                             | 0.23                          |
| year+ eRgP + eRg + (1   Locality)                                     | 650.92      | 0.57                             | 0.34                          |
| year+ MFS + (1   Locality)                                            | 650.94      | 0.57                             | 0.30                          |
| year+ Within-field position + eRg + MFS + SNH + (1   Locality)        | 651.06      | 0.60                             | 0.35                          |
| year+ Within-field position + eRg + SNH + (1   Locality)              | 651.29      | 0.60                             | 0.31                          |
| Within-field position + eRgP + SNH + (1   Locality)                   | 651.42      | 0.60                             | 0.26                          |
| year+ MFS + SNH + (1   Locality)                                      | 651.67      | 0.57                             | 0.32                          |
| year+ eRg + (1   Locality)                                            | 651.85      | 0.57                             | 0.28                          |
| year+ Within-field position + eRgP + eRg + MFS + SNH + (1   Locality) | 652.17      | 0.60                             | 0.38                          |
| year+ eRgP + MFS + SNH + (1   Locality)                               | 652.24      | 0.57                             | 0.35                          |
| Within-field position + eRgP + eRg + (1   Locality)                   | 652.58      | 0.60                             | 0.24                          |
| Within-field position + MFS + SNH + (1   Locality)                    | 652.66      | 0.60                             | 0.24                          |
| Within-field position + eRgP + MFS + (1   Locality)                   | 652.74      | 0.60                             | 0.23                          |
| year+ eRg + MFS + (1   Locality)                                      | 652.77      | 0.57                             | 0.31                          |
| year+ eRgP + eRg + SNH + (1   Locality)                               | 652.86      | 0.57                             | 0.34                          |
| Within-field position + eRgP + MFS + SNH + (1   Locality)             | 652.94      | 0.60                             | 0.28                          |
| year+ Within-field position + SNH + (1   Locality)                    | 653.09      | 0.60                             | 0.23                          |
| year+ eRgP + eRg + MFS + (1   Locality)                               | 653.17      | 0.57                             | 0.34                          |
| eRgP + (1   Locality)                                                 | 653.18      | 0.57                             | 0.21                          |
| year+ (1   Locality)                                                  | 653.58      | 0.57                             | 0.20                          |
| year+ eRg + MFS + SNH + (1   Locality)                                | 653.61      | 0.57                             | 0.33                          |
| Within-field position + MFS + (1   Locality)                          | 653.73      | 0.60                             | 0.16                          |
| Within-field position + eRgP + eRg + SNH + (1   Locality)             | 653.77      | 0.60                             | 0.26                          |
| year+ eRg + SNH + (1   Locality)                                      | 653.91      | 0.57                             | 0.29                          |
| eRgP + SNH + (1   Locality)                                           | 654.09      | 0.57                             | 0.24                          |
| year+ eRgP + eRg + MFS + SNH + (1   Locality)                         | 654.66      | 0.57                             | 0.35                          |

|                                                                 |        |      |      |
|-----------------------------------------------------------------|--------|------|------|
| Within-field position + eRgP + eRg + MFS + (1   Locality)       | 654.87 | 0.60 | 0.24 |
| Within-field position + eRg + MFS + SNH + (1   Locality)        | 654.91 | 0.60 | 0.24 |
| Within-field position + eRgP + eRg + MFS + SNH + (1   Locality) | 655.24 | 0.60 | 0.28 |
| eRgP + eRg + (1   Locality)                                     | 655.26 | 0.57 | 0.21 |
| MFS + SNH + (1   Locality)                                      | 655.33 | 0.57 | 0.21 |
| eRgP + MFS + (1   Locality)                                     | 655.41 | 0.57 | 0.21 |
| Within-field position + eRg + (1   Locality)                    | 655.48 | 0.60 | 0.11 |
| eRgP + MFS + SNH + (1   Locality)                               | 655.55 | 0.57 | 0.26 |
| year+ SNH + (1   Locality)                                      | 655.76 | 0.57 | 0.20 |
| Within-field position + eRg + MFS + (1   Locality)              | 655.91 | 0.60 | 0.16 |
| Within-field position + (1   Locality)                          | 656.28 | 0.60 | 0.02 |
| eRgP + eRg + SNH + (1   Locality)                               | 656.38 | 0.57 | 0.24 |
| MFS + (1   Locality)                                            | 656.46 | 0.57 | 0.13 |
| Within-field position + eRg + SNH + (1   Locality)              | 656.82 | 0.60 | 0.14 |
| eRgP + eRg + MFS + (1   Locality)                               | 657.48 | 0.57 | 0.22 |
| eRg + MFS + SNH + (1   Locality)                                | 657.53 | 0.57 | 0.21 |
| eRgP + eRg + MFS + SNH + (1   Locality)                         | 657.80 | 0.57 | 0.26 |
| eRg + (1   Locality)                                            | 658.21 | 0.57 | 0.09 |
| Within-field position + SNH + (1   Locality)                    | 658.46 | 0.60 | 0.03 |
| eRg + MFS + (1   Locality)                                      | 658.58 | 0.57 | 0.14 |
| (1   Locality)                                                  | 659.06 | 0.57 | 0    |
| eRg + SNH + (1   Locality)                                      | 659.50 | 0.57 | 0.11 |
| SNH + (1   Locality)                                            | 661.19 | 0.57 | 0.00 |

| <b>Model - Bumblebees</b>                                          | <b>AICc</b> | <b>R<sup>2</sup> conditional</b> | <b>R<sup>2</sup> marginal</b> |
|--------------------------------------------------------------------|-------------|----------------------------------|-------------------------------|
| MFS + scSNH + (1   Locality)                                       | 465.07      | 0.68                             | 0.29                          |
| eRgP + MFS + scSNH + (1   Locality)                                | 465.76      | 0.68                             | 0.33                          |
| year + MFS + scSNH + (1   Locality)                                | 466.79      | 0.68                             | 0.30                          |
| eRg + MFS + scSNH + (1   Locality)                                 | 466.89      | 0.68                             | 0.30                          |
| scSNH + (1   Locality)                                             | 467.18      | 0.68                             | 0.19                          |
| year + eRgP + MFS + scSNH + (1   Locality)                         | 467.19      | 0.68                             | 0.34                          |
| Within-field position + MFS + scSNH + (1   Locality)               | 467.35      | 0.68                             | 0.29                          |
| year + scSNH + (1   Locality)                                      | 467.90      | 0.68                             | 0.23                          |
| Within-field position + eRgP + MFS + scSNH + (1   Locality)        | 468.09      | 0.68                             | 0.33                          |
| eRgP + eRg + MFS + scSNH + (1   Locality)                          | 468.10      | 0.68                             | 0.33                          |
| eRgP + scSNH + (1   Locality)                                      | 468.74      | 0.68                             | 0.21                          |
| year + eRg + MFS + scSNH + (1   Locality)                          | 468.74      | 0.68                             | 0.31                          |
| eRg + scSNH + (1   Locality)                                       | 468.76      | 0.68                             | 0.20                          |
| year + Within-field position + MFS + scSNH + (1   Locality)        | 469.12      | 0.68                             | 0.30                          |
| Within-field position + eRg + MFS + scSNH + (1   Locality)         | 469.22      | 0.68                             | 0.30                          |
| Within-field position + scSNH + (1   Locality)                     | 469.40      | 0.68                             | 0.19                          |
| year + Within-field position + eRgP + MFS + scSNH + (1   Locality) | 469.58      | 0.68                             | 0.34                          |
| year + eRgP + eRg + MFS + scSNH + (1   Locality)                   | 469.61      | 0.68                             | 0.34                          |
| year + eRg + scSNH + (1   Locality)                                | 469.70      | 0.68                             | 0.24                          |



|                                                                          |        |      |      |
|--------------------------------------------------------------------------|--------|------|------|
| year + eRgP + scSNH + (1   Locality)                                     | 469.94 | 0.68 | 0.23 |
| year + Within-field position + scSNH + (1   Locality)                    | 470.18 | 0.68 | 0.23 |
| Within-field position + eRgP + eRg + MFS + scSNH + (1   Locality)        | 470.49 | 0.68 | 0.33 |
| eRgP + eRg + scSNH + (1   Locality)                                      | 470.94 | 0.68 | 0.21 |
| Within-field position + eRgP + scSNH + (1   Locality)                    | 471.02 | 0.68 | 0.21 |
| year + (1   Locality)                                                    | 471.03 | 0.68 | 0.08 |
| Within-field position + eRg + scSNH + (1   Locality)                     | 471.04 | 0.68 | 0.20 |
| (1   Locality)                                                           | 471.12 | 0.68 | 0    |
| year + Within-field position + eRg + MFS + scSNH + (1   Locality)        | 471.14 | 0.68 | 0.31 |
| year + Within-field position + eRg + scSNH + (1   Locality)              | 472.04 | 0.68 | 0.24 |
| year + eRgP + eRg + scSNH + (1   Locality)                               | 472.07 | 0.68 | 0.24 |
| year + Within-field position + eRgP + eRg + MFS + scSNH + (1   Locality) | 472.07 | 0.68 | 0.34 |
| year + Within-field position + eRgP + scSNH + (1   Locality)             | 472.28 | 0.68 | 0.23 |
| year + eRgP + (1   Locality)                                             | 473.22 | 0.68 | 0.08 |
| year + eRg + (1   Locality)                                              | 473.23 | 0.68 | 0.08 |
| year + Within-field position + (1   Locality)                            | 473.25 | 0.68 | 0.08 |
| MFS + (1   Locality)                                                     | 473.26 | 0.68 | 0.00 |
| year + MFS + (1   Locality)                                              | 473.27 | 0.68 | 0.08 |
| Within-field position + eRgP + eRg + scSNH + (1   Locality)              | 473.28 | 0.68 | 0.21 |
| Within-field position + (1   Locality)                                   | 473.29 | 0.68 | 0.00 |
| eRg + (1   Locality)                                                     | 473.30 | 0.68 | 0.00 |
| eRgP + (1   Locality)                                                    | 473.31 | 0.68 | 0.00 |
| year + Within-field position + eRgP + eRg + scSNH + (1   Locality)       | 474.46 | 0.68 | 0.24 |
| eRg + MFS + (1   Locality)                                               | 475.29 | 0.68 | 0.01 |
| year + eRgP + MFS + (1   Locality)                                       | 475.37 | 0.68 | 0.08 |
| eRgP + eRg + (1   Locality)                                              | 475.44 | 0.68 | 0.00 |
| year + eRg + MFS + (1   Locality)                                        | 475.45 | 0.68 | 0.08 |
| Within-field position + MFS + (1   Locality)                             | 475.48 | 0.68 | 0.00 |
| eRgP + MFS + (1   Locality)                                              | 475.49 | 0.68 | 0.00 |
| year + Within-field position + eRgP + (1   Locality)                     | 475.50 | 0.68 | 0.08 |
| year + Within-field position + eRg + (1   Locality)                      | 475.51 | 0.68 | 0.08 |
| Within-field position + eRg + (1   Locality)                             | 475.52 | 0.68 | 0.00 |
| year + eRgP + eRg + (1   Locality)                                       | 475.52 | 0.68 | 0.08 |
| Within-field position + eRgP + (1   Locality)                            | 475.53 | 0.68 | 0.00 |
| year + Within-field position + MFS + (1   Locality)                      | 475.55 | 0.68 | 0.08 |
| Within-field position + eRg + MFS + (1   Locality)                       | 477.57 | 0.68 | 0.01 |
| eRgP + eRg + MFS + (1   Locality)                                        | 477.59 | 0.68 | 0.01 |
| year + eRgP + eRg + MFS + (1   Locality)                                 | 477.70 | 0.68 | 0.08 |
| year + Within-field position + eRgP + MFS + (1   Locality)               | 477.71 | 0.68 | 0.08 |
| Within-field position + eRgP + eRg + (1   Locality)                      | 477.72 | 0.68 | 0.00 |
| Within-field position + eRgP + MFS + (1   Locality)                      | 477.76 | 0.68 | 0.00 |
| year + Within-field position + eRg + MFS + (1   Locality)                | 477.78 | 0.68 | 0.08 |
| year + Within-field position + eRgP + eRg + (1   Locality)               | 477.86 | 0.68 | 0.08 |
| Within-field position + eRgP + eRg + MFS + (1   Locality)                | 479.92 | 0.68 | 0.01 |
| year + Within-field position + eRgP + eRg + MFS + (1   Locality)         | 480.10 | 0.68 | 0.08 |

| <b>Model - Wild bees</b>                                              | <b>AICc</b> | <b>R<sup>2</sup> conditional</b> | <b>R<sup>2</sup> marginal</b> |
|-----------------------------------------------------------------------|-------------|----------------------------------|-------------------------------|
| year+ eRgP + SNH + (1   Locality)                                     | 554.62      | 0.76                             | 0.50                          |
| year+ eRgP + (1   Locality)                                           | 554.71      | 0.76                             | 0.46                          |
| year+ MFS + SNH + (1   Locality)                                      | 555.02      | 0.76                             | 0.49                          |
| year+ eRgP + MFS + SNH + (1   Locality)                               | 555.43      | 0.76                             | 0.52                          |
| year+ eRg + MFS + SNH + (1   Locality)                                | 556.19      | 0.76                             | 0.51                          |
| year+ Within-field position + eRgP + SNH + (1   Locality)             | 556.33      | 0.77                             | 0.50                          |
| year+ Within-field position + eRgP + (1   Locality)                   | 556.36      | 0.77                             | 0.46                          |
| year+ eRgP + eRg + SNH + (1   Locality)                               | 556.39      | 0.76                             | 0.50                          |
| year+ Within-field position + MFS + SNH + (1   Locality)              | 556.73      | 0.77                             | 0.49                          |
| year+ eRgP + eRg + (1   Locality)                                     | 556.86      | 0.76                             | 0.46                          |
| year+ eRgP + MFS + (1   Locality)                                     | 556.99      | 0.76                             | 0.46                          |
| year+ Within-field position + eRgP + MFS + SNH + (1   Locality)       | 557.20      | 0.77                             | 0.52                          |
| year+ eRg + (1   Locality)                                            | 557.27      | 0.76                             | 0.41                          |
| year+ eRg + SNH + (1   Locality)                                      | 557.41      | 0.76                             | 0.45                          |
| year+ eRgP + eRg + MFS + SNH + (1   Locality)                         | 557.58      | 0.76                             | 0.52                          |
| year+ MFS + (1   Locality)                                            | 557.72      | 0.76                             | 0.40                          |
| year+ Within-field position + eRg + MFS + SNH + (1   Locality)        | 557.96      | 0.77                             | 0.51                          |
| year+ Within-field position + eRgP + eRg + SNH + (1   Locality)       | 558.16      | 0.77                             | 0.51                          |
| year+ Within-field position + eRgP + eRg + (1   Locality)             | 558.57      | 0.77                             | 0.46                          |
| year+ Within-field position + eRgP + MFS + (1   Locality)             | 558.70      | 0.77                             | 0.46                          |
| year+ eRg + MFS + (1   Locality)                                      | 558.83      | 0.76                             | 0.43                          |
| year+ Within-field position + eRg + (1   Locality)                    | 558.93      | 0.77                             | 0.41                          |
| year+ Within-field position + eRg + SNH + (1   Locality)              | 559.12      | 0.77                             | 0.45                          |
| year+ eRgP + eRg + MFS + (1   Locality)                               | 559.22      | 0.76                             | 0.46                          |
| year+ Within-field position + MFS + (1   Locality)                    | 559.38      | 0.77                             | 0.41                          |
| year+ Within-field position + eRgP + eRg + MFS + SNH + (1   Locality) | 559.41      | 0.77                             | 0.52                          |
| year+ (1   Locality)                                                  | 560.06      | 0.76                             | 0.31                          |
| eRgP + SNH + (1   Locality)                                           | 560.46      | 0.76                             | 0.35                          |
| year+ Within-field position + eRg + MFS + (1   Locality)              | 560.54      | 0.77                             | 0.43                          |
| year+ Within-field position + eRgP + eRg + MFS + (1   Locality)       | 560.99      | 0.77                             | 0.46                          |
| MFS + SNH + (1   Locality)                                            | 561.03      | 0.76                             | 0.34                          |
| eRgP + MFS + SNH + (1   Locality)                                     | 561.16      | 0.76                             | 0.38                          |
| year+ Within-field position + (1   Locality)                          | 561.66      | 0.77                             | 0.31                          |
| Within-field position + eRgP + SNH + (1   Locality)                   | 562.12      | 0.77                             | 0.35                          |
| year+ SNH + (1   Locality)                                            | 562.13      | 0.76                             | 0.31                          |
| eRgP + (1   Locality)                                                 | 562.14      | 0.76                             | 0.25                          |
| Within-field position + MFS + SNH + (1   Locality)                    | 562.68      | 0.77                             | 0.34                          |
| eRgP + eRg + SNH + (1   Locality)                                     | 562.70      | 0.76                             | 0.35                          |
| Within-field position + eRgP + MFS + SNH + (1   Locality)             | 562.87      | 0.77                             | 0.38                          |
| eRg + MFS + SNH + (1   Locality)                                      | 562.93      | 0.76                             | 0.34                          |
| eRgP + eRg + MFS + SNH + (1   Locality)                               | 563.52      | 0.76                             | 0.38                          |
| Within-field position + eRgP + (1   Locality)                         | 563.74      | 0.77                             | 0.26                          |
| year+ Within-field position + SNH + (1   Locality)                    | 563.79      | 0.77                             | 0.31                          |
| eRgP + eRg + (1   Locality)                                           | 564.33      | 0.76                             | 0.26                          |

|                                                                 |        |      |      |
|-----------------------------------------------------------------|--------|------|------|
| eRgP + MFS + (1   Locality)                                     | 564.39 | 0.76 | 0.25 |
| Within-field position + eRgP + eRg + SNH + (1   Locality)       | 564.42 | 0.77 | 0.35 |
| Within-field position + eRg + MFS + SNH + (1   Locality)        | 564.64 | 0.77 | 0.35 |
| Within-field position + eRgP + eRg + MFS + SNH + (1   Locality) | 565.29 | 0.77 | 0.38 |
| eRg + SNH + (1   Locality)                                      | 565.88 | 0.76 | 0.21 |
| MFS + (1   Locality)                                            | 565.93 | 0.76 | 0.15 |
| Within-field position + eRgP + eRg + (1   Locality)             | 565.98 | 0.77 | 0.26 |
| Within-field position + eRgP + MFS + (1   Locality)             | 566.04 | 0.77 | 0.26 |
| eRgP + eRg + MFS + (1   Locality)                               | 566.63 | 0.76 | 0.26 |
| eRg + (1   Locality)                                            | 566.82 | 0.76 | 0.12 |
| Within-field position + MFS + (1   Locality)                    | 567.53 | 0.76 | 0.15 |
| Within-field position + eRg + SNH + (1   Locality)              | 567.53 | 0.77 | 0.22 |
| eRg + MFS + (1   Locality)                                      | 567.81 | 0.76 | 0.16 |
| (1   Locality)                                                  | 568.03 | 0.76 | 0    |
| Within-field position + eRgP + eRg + MFS + (1   Locality)       | 568.35 | 0.77 | 0.26 |
| Within-field position + eRg + (1   Locality)                    | 568.41 | 0.76 | 0.12 |
| SNH + (1   Locality)                                            | 569.46 | 0.76 | 0.03 |
| Within-field position + eRg + MFS + (1   Locality)              | 569.47 | 0.76 | 0.16 |
| Within-field position + (1   Locality)                          | 569.57 | 0.76 | 0.00 |
| Within-field position + SNH + (1   Locality)                    | 571.06 | 0.76 | 0.03 |

| <b>Model - Hoverflies</b>                                          | <b>AICc</b> | <b>R<sup>2</sup> conditional</b> | <b>R<sup>2</sup> marginal</b> |
|--------------------------------------------------------------------|-------------|----------------------------------|-------------------------------|
| Within-field position + MFS + scSNH + (1   Locality)               | 558.20      | 0.46                             | 0.19                          |
| year + Within-field position + MFS + scSNH + (1   Locality)        | 558.85      | 0.46                             | 0.22                          |
| year + Within-field position + (1   Locality)                      | 558.89      | 0.45                             | 0.13                          |
| year + Within-field position + MFS + (1   Locality)                | 559.86      | 0.46                             | 0.16                          |
| Within-field position + eRg + MFS + scSNH + (1   Locality)         | 559.90      | 0.46                             | 0.20                          |
| Within-field position + (1   Locality)                             | 560.24      | 0.45                             | 0.05                          |
| year + Within-field position + eRgP + (1   Locality)               | 560.40      | 0.46                             | 0.15                          |
| Within-field position + eRgP + MFS + scSNH + (1   Locality)        | 560.49      | 0.46                             | 0.19                          |
| year + Within-field position + scSNH + (1   Locality)              | 560.58      | 0.46                             | 0.15                          |
| year + Within-field position + eRg + MFS + scSNH + (1   Locality)  | 560.75      | 0.46                             | 0.23                          |
| Within-field position + MFS + (1   Locality)                       | 560.80      | 0.45                             | 0.09                          |
| Within-field position + eRgP + (1   Locality)                      | 561.00      | 0.45                             | 0.09                          |
| year + Within-field position + eRg + (1   Locality)                | 561.02      | 0.45                             | 0.14                          |
| year + Within-field position + eRgP + MFS + scSNH + (1   Locality) | 561.08      | 0.46                             | 0.23                          |
| Within-field position + eRgP + scSNH + (1   Locality)              | 561.11      | 0.45                             | 0.13                          |
| Within-field position + scSNH + (1   Locality)                     | 561.37      | 0.45                             | 0.08                          |
| year + Within-field position + eRgP + scSNH + (1   Locality)       | 561.46      | 0.46                             | 0.18                          |
| year + Within-field position + eRg + MFS + (1   Locality)          | 561.91      | 0.46                             | 0.17                          |
| year + Within-field position + eRgP + MFS + (1   Locality)         | 562.23      | 0.46                             | 0.16                          |
| Within-field position + eRg + (1   Locality)                       | 562.30      | 0.45                             | 0.06                          |
| Within-field position + eRgP + eRg + MFS + scSNH + (1   Locality)  | 562.31      | 0.46                             | 0.20                          |
| year + Within-field position + eRg + scSNH + (1   Locality)        | 562.37      | 0.46                             | 0.16                          |

|                                                                          |        |      |      |
|--------------------------------------------------------------------------|--------|------|------|
| year + Within-field position + eRgP + eRg + (1   Locality)               | 562.61 | 0.46 | 0.15 |
| Within-field position + eRg + MFS + (1   Locality)                       | 562.66 | 0.45 | 0.10 |
| Within-field position + eRgP + eRg + (1   Locality)                      | 562.82 | 0.45 | 0.10 |
| Within-field position + eRg + scSNH + (1   Locality)                     | 562.88 | 0.45 | 0.10 |
| Within-field position + eRgP + MFS + (1   Locality)                      | 562.98 | 0.45 | 0.09 |
| year + Within-field position + eRgP + eRg + MFS + scSNH + (1   Locality) | 563.22 | 0.46 | 0.23 |
| Within-field position + eRgP + eRg + scSNH + (1   Locality)              | 563.35 | 0.45 | 0.14 |
| MFS + scSNH + (1   Locality)                                             | 563.53 | 0.39 | 0.14 |
| year + Within-field position + eRgP + eRg + scSNH + (1   Locality)       | 563.86 | 0.46 | 0.18 |
| year + MFS + scSNH + (1   Locality)                                      | 564.12 | 0.39 | 0.17 |
| year + Within-field position + eRgP + eRg + MFS + (1   Locality)         | 564.23 | 0.46 | 0.17 |
| year + (1   Locality)                                                    | 564.27 | 0.39 | 0.08 |
| Within-field position + eRgP + eRg + MFS + (1   Locality)                | 564.49 | 0.45 | 0.11 |
| eRg + MFS + scSNH + (1   Locality)                                       | 565.17 | 0.39 | 0.15 |
| year + MFS + (1   Locality)                                              | 565.20 | 0.39 | 0.11 |
| (1   Locality)                                                           | 565.68 | 0.39 | 0    |
| year + eRgP + (1   Locality)                                             | 565.73 | 0.39 | 0.10 |
| eRgP + MFS + scSNH + (1   Locality)                                      | 565.77 | 0.39 | 0.14 |
| year + scSNH + (1   Locality)                                            | 565.91 | 0.39 | 0.10 |
| year + eRg + MFS + scSNH + (1   Locality)                                | 565.96 | 0.39 | 0.18 |
| MFS + (1   Locality)                                                     | 566.19 | 0.39 | 0.04 |
| year + eRgP + MFS + scSNH + (1   Locality)                               | 566.29 | 0.39 | 0.17 |
| year + eRg + (1   Locality)                                              | 566.35 | 0.39 | 0.09 |
| eRgP + (1   Locality)                                                    | 566.38 | 0.39 | 0.04 |
| eRgP + scSNH + (1   Locality)                                            | 566.44 | 0.39 | 0.08 |
| year + eRgP + scSNH + (1   Locality)                                     | 566.74 | 0.39 | 0.12 |
| scSNH + (1   Locality)                                                   | 566.75 | 0.39 | 0.03 |
| year + eRg + MFS + (1   Locality)                                        | 567.18 | 0.39 | 0.12 |
| year + eRgP + MFS + (1   Locality)                                       | 567.50 | 0.39 | 0.11 |
| eRgP + eRg + MFS + scSNH + (1   Locality)                                | 567.52 | 0.39 | 0.15 |
| year + eRg + scSNH + (1   Locality)                                      | 567.65 | 0.39 | 0.11 |
| eRg + (1   Locality)                                                     | 567.68 | 0.39 | 0.00 |
| year + eRgP + eRg + (1   Locality)                                       | 567.88 | 0.39 | 0.10 |
| eRg + MFS + (1   Locality)                                               | 567.99 | 0.39 | 0.05 |
| eRgP + eRg + (1   Locality)                                              | 568.15 | 0.39 | 0.05 |
| eRg + scSNH + (1   Locality)                                             | 568.22 | 0.39 | 0.05 |
| eRgP + MFS + (1   Locality)                                              | 568.31 | 0.39 | 0.04 |
| year + eRgP + eRg + MFS + scSNH + (1   Locality)                         | 568.37 | 0.39 | 0.18 |
| eRgP + eRg + scSNH + (1   Locality)                                      | 568.62 | 0.39 | 0.09 |
| year + eRgP + eRg + scSNH + (1   Locality)                               | 569.07 | 0.39 | 0.12 |
| year + eRgP + eRg + MFS + (1   Locality)                                 | 569.44 | 0.39 | 0.12 |
| eRgP + eRg + MFS + (1   Locality)                                        | 569.76 | 0.39 | 0.06 |



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## CAPÍTULO 2

La diversidad de cultivos en el paisaje contribuye a una mayor eficacia de la polinización y afecta positivamente a la calidad de la colza en los paisajes agrícolas mediterráneos





# **Landscape crop diversity contributes to higher pollination effectiveness and positively affects rapeseed quality in Mediterranean agricultural landscapes**

Science of the Total Environment

Volume 950, 10 November 2024, 175062

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Science of the Total Environment

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# Landscape crop diversity contributes to higher pollination effectiveness and positively affects rapeseed quality in Mediterranean agricultural landscapes

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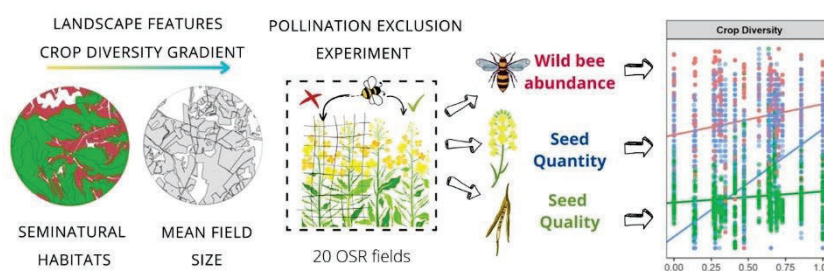
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## HIGHLIGHTS

- Few studies relate the crop diversity and the quantity and quality of seed OSRs.
- A total of 20 OSR fields were evaluated across a gradient of crop diversity.
- OSR seed parameters were evaluated with and without insect pollination.
- Crop diversity plays a key role in developing OSR seed quantity and quality.
- The results highlight the importance of considering heterogeneous agricultural systems.

## GRAPHICAL ABSTRACT



## ARTICLE INFO

Editor: Elena Paoletti

**Keywords:**  
Landscape  
Pollination  
Bees  
Seed quality  
Oil content  
Tocopherols

## ABSTRACT

Pollination is crucial for biodiversity and food security. Heterogeneous agricultural landscapes have a positive effect on pollinator abundance and enhance crop production and quality. In this study, we explored the effects of three landscape features (past crop diversity measured as the Equivalent Richness of crop functional Groups in the previous year [ERGp], semi-natural habitat percentage [SNH], and mean field size [MFS]) and pollinator densities (wild bees [WB] and honey bees [HB]) on pollination and seed quantity and quality in rapeseed crops. Surveying the pollinator density in 20 rapeseed fields revealed a positive relationship with ERGp in the landscape. A pollinator exclusion experiment compared bagged and open-pollinated self-compatible rapeseed plants and revealed insect pollination effectiveness (fruits per flower and number of seeds per pod) and seed quality (oil content). Seed parameters were evaluated in relation to pollinator density (WB-HB) and landscape characteristics. The ERGp emerged as a crucial landscape feature that positively impacted WB density. When insect pollinators were excluded, plants exhibited reduced pollination effectiveness and seed quality. Analysis of open-pollinated plants highlighted ERGp as the most influential variable, positively affecting both sets of parameters. The MFS and SNH showed different but important relationships. Total tocopherol and  $\alpha$ -tocopherol were positively correlated with pollinator density in HB, whereas WB showed a positive correlation with  $\gamma$ -tocopherol levels. Increased ERGp positively affected pollinator density and pollination effectiveness, thereby improving oilseed rape production quantity and quality. This study provides new insights into agroecosystem management and pollinator-friendly practices.

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<https://doi.org/10.1016/j.scitotenv.2024.175062>

Received 29 February 2024; Received in revised form 22 July 2024; Accepted 24 July 2024

Available online 3 August 2024

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## 1. Introduction

Insect pollination is crucial for agricultural productivity and research has shown that this ecosystem service boosts crop yields across a wide range of crops (Bommarco et al., 2012; Dainese et al., 2019; Klein et al., 2007; Potts et al., 2010). The benefits of insect pollination services to agricultural productivity are estimated to range from US \$153–577 billion annually (Gallai et al., 2009). Pollinators may also have beneficial effects on food security by increasing the availability of essential macronutrients and micronutrients in the diet (Chaplin-Kramer et al., 2014; Eilers et al., 2011). Pollinator-dependent crops provide 74 % of lipids, 98 % of vitamin C, 70 % of vitamin A, and 34–65 % of vitamin E worldwide (Ellis et al., 2015). Furthermore, the insect pollination of insect-dependent crops produces high-quality yields. For instance, pollinated crops of strawberry, apple and tangerine show higher sugar to acidity ratios, higher calcium content and higher sugar content respectively. Seeds from pollinated rapeseed crop have higher oil content, and pollinated almond trees have lower vitamin E content (Bommarco et al., 2012; Brittain et al., 2014; Garratt et al., 2014; Klatt et al., 2014; Wietzke et al., 2018). Therefore, pollination not only increases production but also improves the crop quality (Gazzea et al., 2023; Prado et al., 2018).

Worldwide, 75 % of the over 100 crop species cultivated rely on or benefit from pollination (Klein et al., 2007). Moreover, the cultivation area for crops that do not depend on pollinators only grew by 17.3 %, whereas the area for pollinator-dependent crops expanded by 136.9 %, which also increased the demand for pollinators and pollination. Despite significant increases in their reliance on pollinators, European countries have not exhibited increased crop diversity yet (Aizen et al., 2019).

The ecosystem service of pollination is declining owing to agricultural intensification at the farm level. This is exacerbated by the reduction of semi-natural areas and crop diversification at the landscape level (Mandelik et al., 2012). If the global trend of increasingly intensive agriculture relying on pollinators continues, there will be a major mismatch in pollination demand, which could worsen the current food security scenario in terms of crop quantity and quality (Chaplin-Kramer et al., 2014; Smith et al., 2015). Therefore, to guarantee stable crop yields, functional pollinator communities must be preserved urgently (Wietzke et al., 2018).

Landscape characteristics, such as the extent of semi-natural habitats, agricultural and urban areas, and crop diversity, have been shown to influence crop yield and biochemical processes (Cunha et al., 2023; Halinski et al., 2020; Magrach et al., 2023; Pioltelli et al., 2024a). In agricultural landscapes, for example, areas with higher crop diversity help maintain more diverse sets of pollinators and, as a result, more efficient and stable pollination services (Aguilera et al., 2020; Hass et al., 2018a, 2018b). Numerous studies have been conducted to assess potential pollination services by analysing the abundance and diversity of pollinator species and agricultural production, or through the interaction of plants and pollinators (Bartomeus et al., 2014; Bommarco et al., 2012; Cunha et al., 2023; Holzschuh et al., 2016; Perrot et al., 2018). Furthermore, the functional role of crop diversity and past crop diversity at the landscape level has been documented, owing to their potential capacity to provide a greater abundance and density of pollinators (Aguilera et al., 2020; Neira et al., 2024). However, knowledge of the relationships between crop diversity, pollinator abundance, pollination effectiveness, and the quality of agricultural production at the landscape scale remains limited.

Oilseed rape (OSR) (*Brassica napus* L.) is a valuable, economically important, and rapidly expanding crop. This crop is recognized as a mass flowering crop that attracts a high density of pollinators from semi-natural zones when it occupies a low proportion of the landscape (Holzschuh et al., 2016, 2011). During its flowering stage, and when it covers <10 % of the landscape, it can concentrate up to 55 % of pollinator species from grasslands (Magrach et al., 2018). OSR crops are mostly self-pollinated, but benefit from wind and insect pollination

(Bartomeus et al., 2014; Beyer et al., 2021; Bommarco et al., 2012). Seed quality is measured by parameters such as oil content (%), chlorophyll content and moisture, which are routinely used by agricultural product traders to assess the quality of OSR seeds and indicate the quality of the resulting oil (Australian Oilseeds Federation, 2011). Oil extracted from OSR seeds has been used in the food industry for human and animal consumption and is considered a rich source of antioxidants and health-promoting bioactive compounds, such as tocopherols and carotenoids, owing to their nutritional value as vitamin E and provitamin A, respectively. Conversely, high chlorophyll content reduces the price of oil because it decreases durability and negatively alters the colour of the extracted oil (Bommarco et al., 2012; Schneider, 2005). However, studies regarding the association between landscape crop diversity and quantity (e.g., seeds per pod) and quality (e.g., antioxidants or plant pigments) of seeds from insect-pollinated OSR have not yet been conducted in Mediterranean climates.

We conducted a pollinator exclusion experiment and assessed wild pollinator and honeybee (HB) densities in 20 rapeseed fields in central Catalonia across a gradient of crop diversification, abundance of semi-natural areas, and mean field sizes. We evaluated the influence of the agricultural landscape on the density of pollinators and the effectiveness of pollinators visiting rapeseed flowers on the quantity and quality parameters of OSR seeds. This approach allows for an interdisciplinary understanding of the effects of the agricultural landscape on pollinators, and consequently, on the qualitative and quantitative characteristics of rapeseeds. We hypothesised that: i) OSR fields in landscapes with higher past crop diversity receive more visits from wild bees (WB), and ii) the amount and quality of OSR fruits pollinated by insects are higher than those produced by self-pollination; consequently, iii) past crop diversity in an agricultural area affects both the quantity and quality of OSR seeds, with wild bees playing an important role.

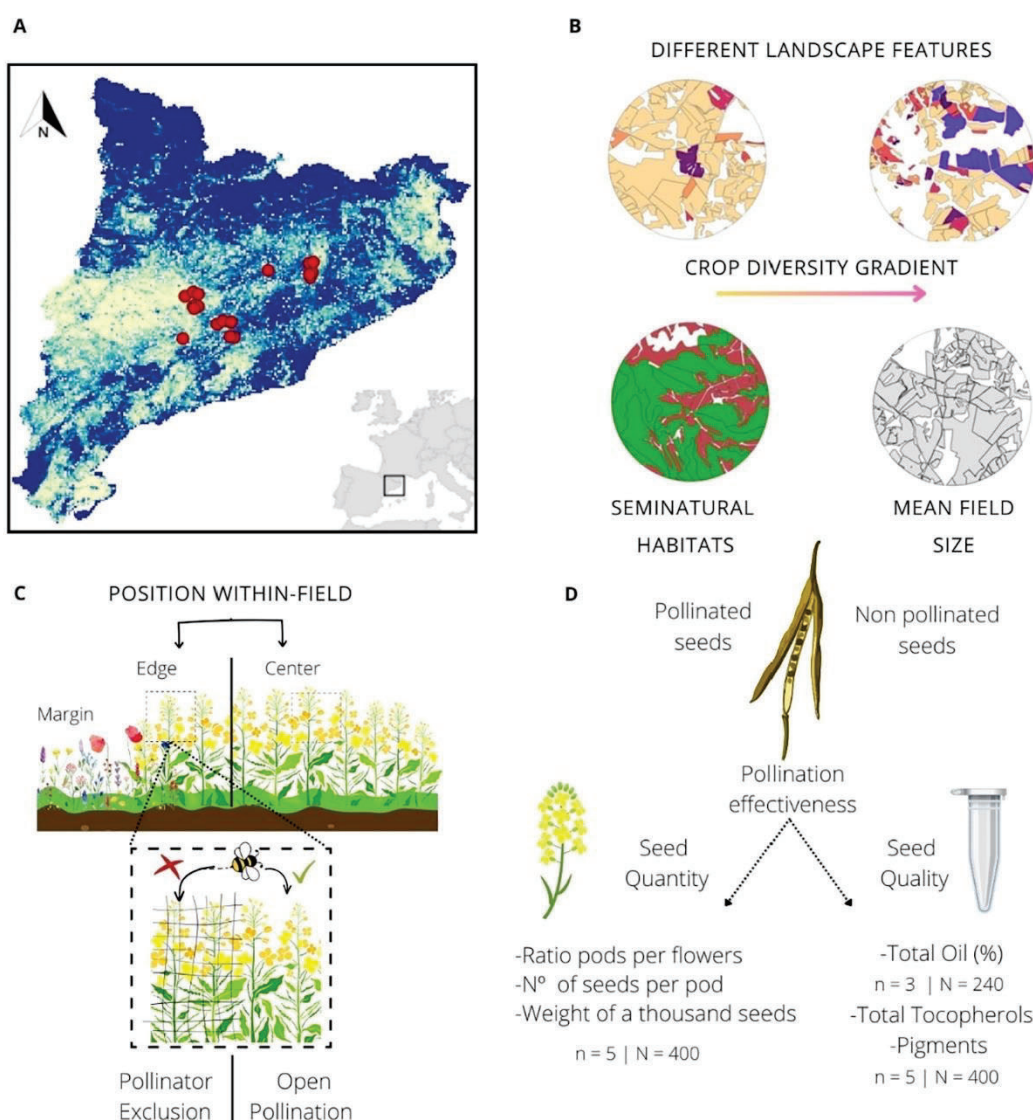
## 2. Materials and methods

### 2.1. Study fields and landscape metrics

During the years 2021 and 2022, we chose 20 conventional arable fields seeded with different varieties of OSR (*Brassica napus* L.), in total (10 per year), each field in a dryland cereal region situated in Central Catalonia, in the NE Spain (41°24'–42°05'N; 1°05'–2°05'E) (Fig. 1A). All localities were at least 2 km apart to prevent any two OSR fields from being visited by the same pollinator pool (Holzschuh et al., 2016; Westphal et al., 2003). The agricultural environment is characterised by the dominance of dryland arable crops and woody crops, whereas uncultivated areas are dominated by forests, shrublands, and grasslands (Departament d'Acció Climàtica, Alimentació i Agenda Rural, 2023).

A circular area with a radius of 1000 m was chosen around each rapeseed field to characterise the landscape of each locality, as it has been shown that the majority of pollinator feeding flights occur within this distance (Holzschuh et al., 2011; Steffan-Dewenter and Kuhn, 2003). Landscape heterogeneity was characterised by three components, two of which were associated with its composition: (1) the equivalent crop richness of the past year (ERGp), which corresponds to the effective number of crop functional groups of crops computed as the exponential of the Shannon diversity of functional groups of crops (e.g. legumes, oilseeds, sweet fruits, cereals) (Neira et al., 2024); (2) the percentage of land covered by seminatural habitats (SNH); and (3) one component associated with its configuration, the mean field size (MFS). The localities were chosen according to an ERGp gradient, with a maximum of 10 % agricultural area cultivated with rapeseed crops, to guarantee the effect of bee concentration (Fig. 1B) (Holzschuh et al., 2011; Magrach et al., 2023). The composition and structure of the landscape in each locality were characterised using spatial data from the DUN-SIGPAC Crop Map (Departament d'Acció Climàtica, Alimentació i Agenda Rural, 2023) and the Cartografia dels Hàbitats de Catalunya, v.2 (Departament de Territori i Sostenibilitat, 2018) using R software with





**Fig. 1.** Study fields and experimental design. A) Map of Catalonia (NE of Spain) and the distribution of the 20 localities. The blue-yellow gradient represents the percentage of agricultural land. Information is available in the Cartografia dels Hàbitats de Catalunya, v.2 (Departament de Territori i Sostenibilitat, 2018). B) Representation of the 1-km radius buffer zone of the selected localities in a gradient of crop diversity; representation of the other characteristics of the agricultural landscape evaluated; seminatural habitats; and mean field size. C) Scheme of the pollinator exclusion experiment design within each rapeseed field. D) Methodological diagram of the use of samples and their respective parameters. n: Number of samples per field, N: Total number of samples.

package ‘sf’ (Pebesma, 2018).

## 2.2. Pollination assessment

A pollinator exclusion experiment was set up prior to flowering in the twenty rapeseed fields. Within each field, crop plants in two within-field positions (centre and edge) were subjected to two different pollination treatments: open pollination (OP), which included plants whose inflorescences could be pollinated through all vectors (wind and insects), and pollinator-excluded plants (EP), whose contact with insects was limited (Fig. 1) (Bommarco et al., 2012; Perrot et al., 2018). In each within-field position, five plants  $\times$  two pollination treatments from ten size-equivalent plants, split into five pairs 18 m apart, were chosen at random in an area of 75 m  $\times$  2 m (10 inflorescences  $\times$  two within-field positions  $\times$  20 fields = 400 inflorescences). To prevent pollinating insects from visiting EP plants, a fine mesh nylon bag (0.8 mm  $\times$  0.8 mm) was installed around each inflorescence from randomly selected plants within each pair. Although inflorescences from OP plants were available

for both self-pollination and wind and insect pollination, insect pollination was completely excluded from inflorescences from EP plants (Fig. 1D). A previous evaluation inside and outside the mesh nylon bag did not reveal any significant differences in photon flux ( $p > 0.05$ ) (Table S1) that could have an impact on the physiological responses of OSR plants. In both cases, the levels of photon flux are higher than what is considered to be shadow stress (Wang et al., 2023). This experimental approach, which allows for both self-pollination and wind pollination, was developed in previous field studies (Bartomeus et al., 2014; Beyer et al., 2021; Bommarco et al., 2012; Islam et al., 2022). Plants from both treatments were collected one day before the crop was harvested in July to ensure pod ripening in the field (Beyer et al., 2021; Bommarco et al., 2012). Plant material collected were stored in paper bags at room temperature (22–26 °C) until they were processed, and then preserved in cold conditions for future analysis.



### 2.3. Pollinator evaluation

A pollinator survey was conducted in each rapeseed field between April and May (2021 and 2022). Two parallel transects of 150 m<sup>2</sup> (75 m × 2 m) were established in each field, one at the centre and the other at the edge of the field. To determine the densities of WBs and HBs, the number of contacts with rapeseed flowers was recorded for 15 min per transect (Holzschuh et al., 2016). The surveys were conducted on two different days during the peak flowering period under fair weather no rain, temperature above 15 °C, low wind speed. The total sampling effort was 15 min/transect × two transects/field/day × two days = 60 min/field.

### 2.4. Pollination effectiveness

To quantify the pollination effectiveness, three parameters were estimated for each of the 400 OSR inflorescences: (1) pods per flower ratio (PPF), (2) number of seeds per pod (NSP), and (3) thousand seed weight (TSW). The total number of pods was divided by the number of flowers in each inflorescence to calculate PPF as an indicator of pollination effectiveness. NSP was obtained from a mean of five pods per infructescence (a total of 2000 pods). The TSW was calculated using the following formula:  $1000 \times (\text{weight of all seeds from the infructescence}) / (\text{average number of seeds per pod} \times \text{total pods})$ .

### 2.5. Phytochemical analyses and quality of seeds

Three analyses were performed to assess the quality of OSR seed production: (1) percentage of oil content in the seeds, (2) tocopherol composition and quantification, and (3) quantification of total chlorophyll and carotenoids. Oil content was determined using a modified gravimetric protocol (Bligh and Dyer, 1959). Seeds from three infructescence were randomly chosen for each pollination treatment condition and within-field position (centre/edge) per field ( $N = 240$ ). Seeds from each infructescence were crushed and 100 mg of each sample was weighed. One millilitre of the extraction solvent (chloroform:methanol, 2:1 v/v) was added to each sample and an ultrasonication bath was applied for 15 min before centrifugation at 5000 rpm for 10 min. The supernatant was extracted and transferred to glass vials that had previously been weighed. The solvent extraction procedure was repeated three times until a white pellet was obtained. The glass vials containing the supernatant were exposed to nitrogen until the solvent evaporated and the weight was stabilised. The oil content corresponded to the percentage of the final weight minus the initial weight of the vial over the weight of the initial OSR sample.

Tocopherols were analysed following the procedure described by Amaral et al. (2005). Seeds from five infructescences were randomly chosen for each pollination treatment condition and each within-field position (centre/edge) per field ( $N = 400$ ). Cold extraction was performed as follows: samples were kept cold using ice, and extraction products were extracted with 100 % methanol containing 0.01 % butylhydroxytoluene on 30 mg of seeds from each sample, which had previously been crushed and placed in Eppendorf tubes (2 mL). Methanol (400 µL) was then added to each sample, and ultrasonication bath was applied for 30 min, with the samples passing through a vortex before and after this step, and finally the samples were centrifuged at 10,000 rpm for 10 min. The extraction procedure was repeated two more times until a completely white pellet was obtained, and the final supernatant was separated into two aliquots: one for tocopherols analysis and the other one for total pigment determination. Extracts were filtered using single-use 0.45-µm polytetrafluoroethylene hydrophobic filters and a portion was transferred to glass vials for analysis using high-performance liquid chromatography. A Waters 600 controller pump, Waters 717 plus autosampler, and Jasco FP-1520 fluorescence detector (Jasco, Tokyo, Japan) were used. Tocopherol compounds were separated on a normal-phase column (Inertsil SIL-100 A, 5 µm, 3.0 × 250

mm, GL Sciences, Tokyo, Japan) with an isocratic mobile phase of n-hexane and 1,4-dioxane (95.5/4.5; v/v). The flow rate was 0.7 mL·min<sup>-1</sup> and the injection volume was 10 µL. The excitation wavelength was 295 nm, and the emission wavelength was 330 nm for fluorescence detection. A calibration curve with authentic standards using a concentration range from 0.1 to 5 µg/mL (Sigma-Aldrich, Steinheim, Germany) was used to quantify the compounds.

The second aliquot was used for dual-beam ultraviolet/visible spectrophotometric analyses of chlorophylls a and b, and total carotenoids using a CE Aquarius UCE7400 (Cecil Instruments Ltd., Cambridge, United Kingdom). To quantify chlorophylls a and b, as well as total carotenoids, we measured absorbance at 750 nm, 665.2 nm, 652.4 nm, and 470 nm and applied the equations with absorption coefficients as described by Lichtenthaler and Buschmann (2001).

### 2.6. Statistical analysis

To analyze the obtained data, we used Generalized Mixed Linear Models (GLMMs) with the 'glmmTMB' package (Brooks et al., 2017). First, to check for significant correlations, a Spearman rank's correlation analysis was conducted between the landscape characteristics and the densities of WBs, HBs, and total bees (Fig. S1). A strong correlation was identified between the MSF and ERGp. Therefore, a sequential regression approach (Graham, 2003) was used to create a new purged explanatory variable by reciprocally subtracting the common variation from the MFS to the ERGp. This approach allowed the inclusion of both variables in the model. We then used the variance inflation factor (VIF) to test for potential collinearity between these explanatory variables (Zuur et al., 2010); however, the VIF indicated low multicollinearity in all cases (Table S2). To analyze WB density and its relationship with the agricultural landscape, the landscape metrics ERGp, MFS, and SNH were treated as continuous explanatory variables (scaled to minimum = 0 and maximum = 1), whereas within-field position (edge and centre) and year were used as categorical explanatory variables.

In the pollinator exclusion experiment, the total pollinator density (the sum of WB and HB) was treated as a continuous variable. Pollination treatment (OP or EP), within-field position (edge or centre), and year were the categorical variables. We also considered the interactions between the total density of bees and pollination treatment, and the interaction between the total density of bees and the within-field position. The interaction term is needed when analysing the effect of total density of bees on both EP and OP plants in the same model, as it is expected a lack of effect in EP but a significant effect in OP. The interaction term allows us to attribute any effect to the total density of bees and not to wind pollination or any other uncontrolled effect. Crop variety was included as a random effects factor. Finally, to test the influence of the agricultural landscape and pollinators on the pollination effectiveness and the quality of OSR seeds of OP OSR plants, the agricultural landscape variables (ERGp, MFS, and SNH) were scaled and treated as continuous variables as in the first analysis. Bee densities (WB and HB) were log transformed before analysis, to reduce variability at the higher end of the variable and improve the homogeneity of distribution of this explanatory variable. We used the OSR variety as a random effect variable.

In these three analyses, we used the 'dredge' function in the 'MuMIn' package (Bartoń, 2023) to test multiple hypotheses simultaneously across the models. We investigated all possible combinations for each dataset. For each model (i), we computed the Akaike information criterion corrected for small sample sizes (AICc), and we ranked and calculated relative Akaike weights ( $w_i$ ) (Akaike, 1998; Burnham and Anderson, 2002). Then, a relative weight of evidence for each model ( $w_i$ ) can be interpreted as the probability of model a being the best approximating model from the entire set of candidate models. The sum of the weights ( $w_i$ ) of all possible models is scaled to 1. We calculated the confidence sets for each response variable, which are the smallest subsets of candidate models for which the sum of  $w_i$  equals 0.95, and we



averaged the entire set. For each variable included in the set of candidate models, its relative importance is calculated based on its contribution to explaining the variability in the response variable. We report all predictor variables, considering as relevant all variables that have a relative importance ( $\Sigma w_i$ )  $> 0.5$ , and 95 % confidence intervals (CI) as critical tools for assessing variable effects. We inspected residual plots to validate model assumptions and calculated the marginal ( $R_m^2$ ) and conditional ( $R_c^2$ )  $R^2$  values (Nakagawa et al., 2017). Furthermore, in the case only one model had a weight of  $> 0.95$ , we calculated the estimates and  $p$ -values. Statistical analyses were performed using R software version 4.1.2.

### 3. Results

#### 3.1. Agricultural landscape effects on pollinators

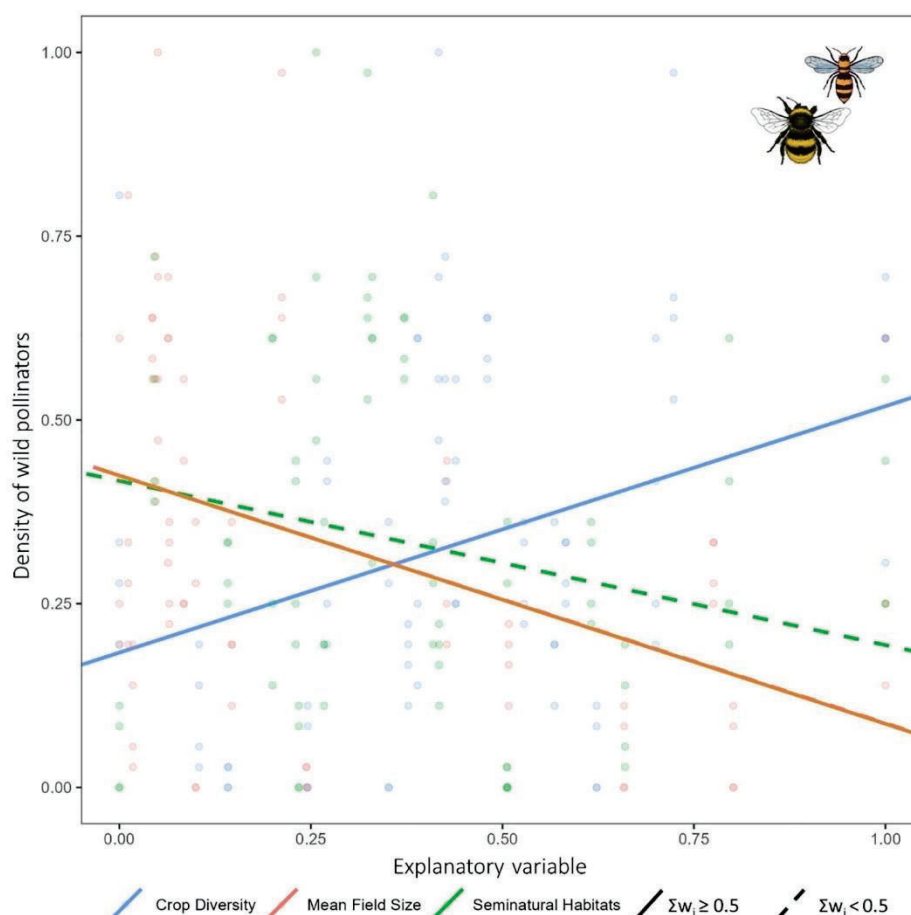
In the 20 OSR fields, 2592 HBs and 992 WBs were recorded. The total number of WBs belonging to the genus *Bombus* was 231, whereas 761 belonged to other WB genera. The average model for WBs indicated that ERGp influenced them positively, with a relative importance ( $\Sigma w_i$ ) of 0.73, the unique feature of the landscape was supported by the CI. The second most important landscape feature was MFS ( $\Sigma w_i = 0.68$ ) with a negative effect. Both features showed a clear effect. Within-field position displayed higher pollinators density in the edge than in field centres, but this effect had a relative importance ( $\Sigma w_i$ ) of 0.43, whereas SNH ( $\Sigma w_i = 0.28$ ) had a negative effect. Both features showed an unclear effect and

without support from their CIs (Fig. 2).

#### 3.2. Pollinator exclusion effects on seed quantity

The parameters associated with seed quantity were responsive to both pollination treatment and pollinator density (Table 1). The observed PPF in rapeseed fields was explained by a single model ( $w_i > 0.95$ ) encompassing all variables studied. Within-field position and pollinator density exhibited negative effects ( $P < 0.001$ ), thereby decreasing the PPF. The interaction between total pollinator density and within-field position a positive influence ( $P < 0.001$ ), decreasing less PPF ratio in edge plants than in centre plants with higher pollinator density. In contrast, plants subjected to the pollination treatment in the interaction with pollinator densities demonstrated a statistically significant positive effect ( $P < 0.001$ ) in OP plants. Inflorescences from OP plants produced 39 % more pods per flower than that produced by EP plants ( $P < 0.001$ ) (Fig. 3A).

The NSP, as indicated by the average model (Table 1), decreased in response to pollinator density. This negative response was more pronounced at the edge of the field than at the centre. Both variables had a relative importance of  $\Sigma w_i = 1.00$ . However, when both variables interacted (TD:P in Table 1), we observed a positive effect ( $\Sigma w_i = 0.62$ ), indicating that the NSP of plants at the edge decreased less than centre plants in response to increasing pollinator density. The pollination treatment revealed that OP inflorescences had a higher NSP than EP ( $\Sigma w_i = 1.00$ ). The pollination treatment also revealed that OP



**Fig. 2.** Relationship between agricultural landscape variables and density of wild pollinators. Lines represent the model effects for each landscape metric of the agricultural landscape individually and were obtained from the average model of the multimodel analysis. Relative importances greater than or equal to 0.5 are represented with solid lines. Relative importances  $< 0.5$  are represented with dashed lines.

**Table 1**

Estimates and relative importance ( $\Sigma w_i$ ) for each predictor in the average models obtained through multimodel inference or estimate and p-values when it corresponds to a single model from the pollinator exclusion experiment. For each fixed effect factor, confidence intervals (CI at 95 %) are provided. Bold numbers indicate relevant variables. Total pollinator density (TD), pollination treatment (PT), within-field position (P), (TD:PT): interaction between total pollinator density and pollination treatment, (TD:P): interaction between total pollinator density and within-field position.

| Quantity parameters                    |                                            | Estimate      | $\Sigma w_i$ /<br>p-value | CI            |               |
|----------------------------------------|--------------------------------------------|---------------|---------------------------|---------------|---------------|
|                                        |                                            |               |                           | Lower         | Upper         |
| Pods per flower (PPF) (only one model) | Total pollinator density                   | <b>−0.000</b> | <b>P &lt; 0.001</b>       | <b>−0.001</b> | <b>−0.000</b> |
|                                        | Pollination treatment (Open vs. Exclusion) | <b>0.250</b>  | <b>P &lt; 0.001</b>       | <b>0.235</b>  | <b>0.265</b>  |
|                                        | Within-field position (edge vs centre)     | <b>−0.063</b> | <b>P &lt; 0.001</b>       | <b>−0.076</b> | <b>−0.049</b> |
|                                        | TD:PT                                      | <b>0.001</b>  | <b>P &lt; 0.001</b>       | <b>0.000</b>  | <b>0.001</b>  |
|                                        | TD:P                                       | <b>0.000</b>  | <b>P &lt; 0.001</b>       | <b>0.000</b>  | <b>0.000</b>  |
| N° seeds per pod (NSP)                 | Total pollinator density                   | <b>−0.047</b> | <b>1.00</b>               | <b>−0.063</b> | <b>−0.031</b> |
|                                        | Pollination treatment (open vs. exclusion) | <b>3.236</b>  | <b>1.00</b>               | <b>2.354</b>  | <b>4.118</b>  |
|                                        | Within-field position (edge vs centre)     | <b>−3.976</b> | <b>1.00</b>               | <b>−4.883</b> | <b>−3.070</b> |
|                                        | TD: PT                                     | <b>0.045</b>  | <b>1.00</b>               | <b>0.030</b>  | <b>0.060</b>  |
|                                        | TD:P                                       | <b>0.013</b>  | <b>0.62</b>               | <b>−0.002</b> | <b>0.027</b>  |
| Thousand seed weight                   | Total pollinator density                   | <b>0.002</b>  | <b>0.67</b>               | <b>−0.001</b> | <b>0.004</b>  |
|                                        | Pollination treatment (open vs. exclusion) | <b>0.650</b>  | <b>1.00</b>               | <b>0.506</b>  | <b>0.795</b>  |
|                                        | Within-field position (edge vs centre)     | <b>−0.076</b> | <b>0.82</b>               | <b>−0.158</b> | <b>0.006</b>  |
|                                        | TD: PT                                     | <b>−0.002</b> | <b>0.51</b>               | <b>−0.004</b> | <b>0.001</b>  |
|                                        | TD:P                                       | <b>0.000</b>  | <b>0.13</b>               | <b>−0.002</b> | <b>0.002</b>  |
| Oil content (%)                        | Total pollinator density                   | <b>−0.012</b> | <b>1.00</b>               | <b>−0.035</b> | <b>0.011</b>  |
|                                        | Pollination treatment (open vs. exclusion) | <b>2.328</b>  | <b>1.00</b>               | <b>0.959</b>  | <b>3.698</b>  |
|                                        | Within-field position (edge vs centre)     | <b>−0.750</b> | <b>1.00</b>               | <b>−2.153</b> | <b>0.654</b>  |
|                                        | TD:PT                                      | <b>0.044</b>  | <b>1.00</b>               | <b>0.021</b>  | <b>0.066</b>  |
|                                        | TD:P                                       | <b>−0.024</b> | <b>1.00</b>               | <b>−0.047</b> | <b>−0.001</b> |
| Total tocopherols                      | Total pollinator density                   | <b>0.167</b>  | <b>0.63</b>               | <b>−0.07</b>  | <b>0.404</b>  |
|                                        | Pollination treatment (open vs. exclusion) | <b>3.308</b>  | <b>0.29</b>               | <b>−7.283</b> | <b>13.899</b> |
|                                        | Within-field position (edge vs centre)     | <b>15.947</b> | <b>0.92</b>               | <b>−1.415</b> | <b>33.309</b> |
|                                        | TD:PT                                      | <b>−0.025</b> | <b>0.29</b>               | <b>−0.278</b> | <b>0.229</b>  |
|                                        | TD:P                                       | <b>−0.255</b> | <b>0.43</b>               | <b>−0.517</b> | <b>0.008</b>  |
| $\alpha$ -Tocopherol                   | Total pollinator density                   | <b>9.812</b>  | <b>0.80</b>               | <b>−0.596</b> | <b>20.220</b> |

**Table 1 (continued)**

| Quantity parameters  |                                            | Estimate       | $\Sigma w_i$ /<br>p-value | CI             |                |
|----------------------|--------------------------------------------|----------------|---------------------------|----------------|----------------|
|                      |                                            |                |                           | Lower          | Upper          |
| $\gamma$ -Tocopherol | Pollination treatment (open vs. exclusion) | <b>−9.947</b>  | <b>0.67</b>               | <b>−21.046</b> | <b>1.152</b>   |
|                      | Within-field position (edge vs centre)     | <b>19.808</b>  | <b>1.00</b>               | <b>8.676</b>   | <b>30.985</b>  |
|                      | TD:PT                                      | <b>−0.214</b>  | <b>0.08</b>               | <b>−11.267</b> | <b>10.839</b>  |
|                      | TD:P                                       | <b>−11.987</b> | <b>0.61</b>               | <b>−23.360</b> | <b>−0.382</b>  |
|                      | Total pollinator density                   | <b>2.350</b>   | <b>1.00</b>               | <b>−1.451</b>  | <b>6.151</b>   |
| Chlorophylls         | Pollination treatment (open vs. exclusion) | <b>17.254</b>  | <b>1.00</b>               | <b>13.109</b>  | <b>21.398</b>  |
|                      | Within-field position (edge vs centre)     | <b>−15.463</b> | <b>1.00</b>               | <b>−19.612</b> | <b>−11.313</b> |
|                      | TD:PT                                      | <b>−7.981</b>  | <b>0.18</b>               | <b>−4.005</b>  | <b>4.290</b>   |
|                      | TD:P                                       | <b>−0.142</b>  | <b>1.00</b>               | <b>−12.279</b> | <b>−3.683</b>  |
|                      | Total pollinator density                   | <b>−0.002</b>  | <b>0.61</b>               | <b>−0.007</b>  | <b>0.003</b>   |
| Carotenoids          | Pollination treatment (open vs. exclusion) | <b>−0.019</b>  | <b>1.00</b>               | <b>−0.025</b>  | <b>−0.013</b>  |
|                      | Within-field position (edge vs centre)     | <b>−0.005</b>  | <b>0.56</b>               | <b>−0.011</b>  | <b>0.001</b>   |
|                      | TD:PT                                      | <b>−0.004</b>  | <b>0.27</b>               | <b>−0.010</b>  | <b>0.002</b>   |
|                      | TD:P                                       | <b>−</b>       | <b>—</b>                  | <b>—</b>       | <b>—</b>       |
|                      | Total pollinator density                   | <b>−0.002</b>  | <b>0.42</b>               | <b>−0.005</b>  | <b>0.001</b>   |
|                      | Pollination treatment (open vs. exclusion) | <b>−0.014</b>  | <b>1.00</b>               | <b>−0.017</b>  | <b>−0.01</b>   |
|                      | Within-field position (edge vs centre)     | <b>0.001</b>   | <b>0.30</b>               | <b>−0.002</b>  | <b>0.005</b>   |
|                      | TD:PT                                      | <b>0.002</b>   | <b>0.08</b>               | <b>0.002</b>   | <b>−0.002</b>  |
|                      | TD:P                                       | <b>0.002</b>   | <b>0.04</b>               | <b>−0.002</b>  | <b>0.005</b>   |

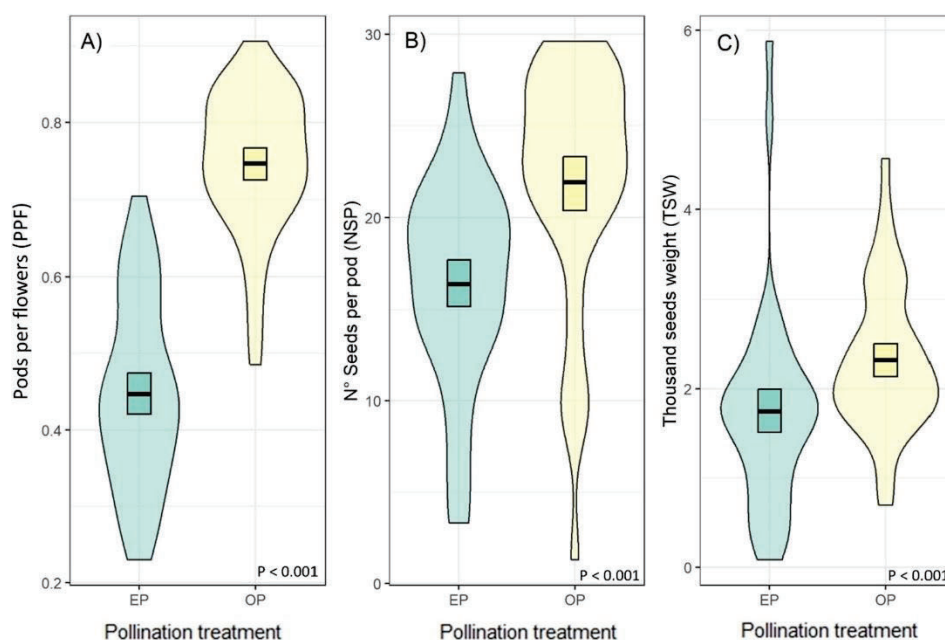
inflorescences also showed a lower decrease of NSP in response to increasing total pollinator density than EP inflorescences ( $\Sigma w_i = 1.00$ ) (TD:PT in Table 1). EP plant inflorescences exhibited a 15 % lower of NSP than those from OP plants ( $P < 0.001$ ) (Fig. 3B).

The average model for the TSW (Table 1) shows an increased trend for both the total pollinator density ( $\Sigma w_i = 0.67$ ) and the pollination treatment, where OP plant seeds were heavier ( $\Sigma w_i = 1.00$ ). Both variables exhibited clear effects. Conversely, the within-field position ( $\Sigma w_i = 0.82$ ) had negative effects, indicating that the edge plants show lower TSW compared with those at the centre of the field. Regarding the interactions, only the interaction between total pollinator density and pollination treatment showed a negative and clear effect ( $\Sigma w_i = 0.51$ ) (TD:PT in Table 1), indicating that OP plants exhibited a decrease in TSW relative to EP plants in the presence to increasing total pollinator density. Notably, seeds from the EP plant inflorescences weighed 40 % less than those from OP plants open to insect visits ( $P < 0.001$ ) (Fig. 3C).

### 3.3. Pollinator exclusion effects on seed quality

The quality parameters of the rapeseed seeds primarily showed responsiveness to pollination treatment and location within the field (Table 1). The analysis of oil content (%) in rapeseed seeds reveals a positive response for OP plants of the pollination treatment ( $\Sigma w_i =$



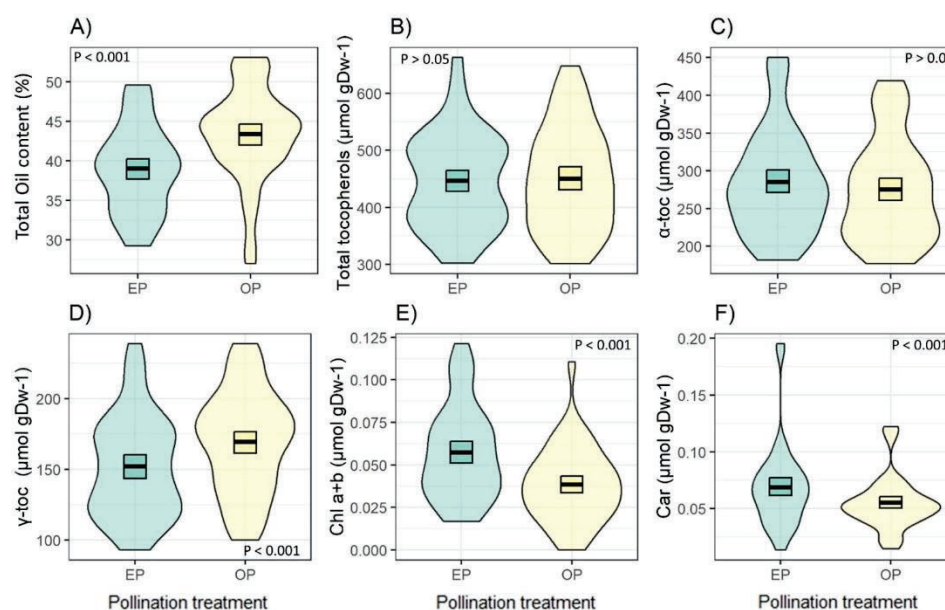


**Fig. 3.** Effects of the pollination treatment on (A) pods/flowers, (B) the number of seeds per pod and (C) the thousand seed weight. The 95 % confidence intervals for treatments are shown in boxes inside of each violin graph. Results of statistical comparison among inflorescences from pollinator-excluded plants (EP) and open-pollinated plants (OP) are indicated below each graph.

1.00), showing more oil content than that in EP plants, and this finding is supported by its confidence interval. The total density of pollinators and the position in the field had a negative effect ( $\Sigma w_i = 1.00$ ). Whereas the interaction between the pollinator density and within-field position (TD: P in Table 1) exhibits a negative effect ( $\Sigma w_i = 1.00$ ) indicating that the seeds of plants on the field edge have even less oil content in the presence of a higher density of pollinators than plants in the field centre. A positive effect is observed in the interaction between total pollinator density and pollination treatment (TD:PT in Table 1) ( $\Sigma w_i = 1.00$ ), showing that OP plant seed oil content increases as pollinator density

increases, and both interactions are supported by their confidence interval. Notably, seeds from the inflorescences of EP plants contained 10 % less oil than those from OP plants ( $P < 0.001$ ) (Fig. 4A).

The average model for total tocopherols in OSR seeds indicates an increase in relation to within-field position showing more content at the edge ( $\Sigma w_i = 0.92$ ). The tocopherol content also increased as the pollinator density increased ( $\Sigma w_i = 0.63$ ), and although its confidence intervals encompass zero, it exhibits clear positive effects (Table 1). Overall, pollination treatment doesn't show a clear effect ( $\Sigma w_i = 0.29$ ). Seeds from the inflorescences of EP and OP plants did not show any



**Fig. 4.** Effects of the pollination treatment on (A) seed oil content (%), (B) total tocopherols ( $\alpha$ -toc +  $\gamma$ -toc), (C)  $\alpha$ -toc, (D)  $\gamma$ -toc, (E) chlorophyll (a + b) and (F) carotenoids. The 95 % confidence intervals for treatments are shown in boxes inside each violin graph. P-values of statistical comparison among inflorescences from EP and OP plants are indicated in each graph.



significant differences in total tocopherol content ( $P > 0.05$ ) (Fig. 4B).

Tocopherol composition shows two predominant tocopherols,  $\alpha$ - and  $\gamma$ -tocopherol. The  $\alpha$ -tocopherol content was higher in plants from field edge than in plants from field centre ( $\Sigma w_i = 1.00$ , Table 1). However, we detected an important interaction with total pollinator density ( $\Sigma w_i = 0.61$ , TD:P in Table 1), causing a steeper positive response of  $\alpha$ -tocopherol to total pollinator density in the field centre than in field edge (i.e. total pollinator density effect on  $\alpha$ -tocopherol content is higher in the field centres than in field edges). Each variable was supported by its respective confidence intervals. The  $\alpha$ -tocopherol content increased in response to increased pollinator density ( $\Sigma w_i = 0.80$ ) and pollination treatment ( $\Sigma w_i = 0.67$ ). There was no difference between OP and EP plants in the  $\alpha$ -tocopherol content ( $P > 0.05$ ) (Fig. 3C). For  $\gamma$ -tocopherol, the variables carrying the greatest relative importance, as outlined by the average model (Table 1), encompassed the total pollinator density, within-field position, their interaction, and the pollination treatment, all boasting a relative importance of  $\Sigma w_i = 1.00$ , with clear effects. The  $\gamma$ -tocopherol content increased as pollinator density increased ( $\Sigma w_i = 1.00$ ) and showed higher levels in plants from the centre. Their interactions exhibited negative trends, indicating that the increase was smaller in the edge plants than in the centre (TD:P in Table 1). In seeds from OP plants,  $\gamma$ -tocopherol content was also higher, but the interaction with pollinator density had no clear effect (TD:PT in Table 1). The  $\gamma$ -tocopherol content of seeds from OP plants was 10 % higher than that from EP plants ( $P < 0.001$ ) (Fig. 4D).

The total chlorophylls, as indicated by the average model, only showed a relationship with the pollination treatment ( $\Sigma w_i = 1.00$ ) which is supported by the confidence interval. Seeds from OP plants have a lower chlorophyll content than those from EP plants. In contrast, the remaining variables had an unclear effect. Seeds from the inflorescences of EP plants contained 60 % more total chlorophyll than those from the inflorescences of OP plants ( $P < 0.001$ ) (Fig. 4E). Total carotenoids were primarily influenced by the pollination treatment ( $\Sigma w_i = 1.00$ ), as per the average model (Table 1). This effect was supported by its confidence interval, which indicated that seeds from OP plants had a lower carotenoids content than those from EP plants. The remaining variables exhibited lower relative importance, and their confidence interval contained zero, with a tendency towards symmetry; therefore, we could not consider their effects. Seeds from EP plants had 20 % higher total carotenoids content than those from OP plants ( $P < 0.001$ ) (Fig. 4F).

### 3.4. Agricultural landscape and pollinator density affected pollination effectiveness and rapeseed seeds quality

The average model indicated that the pollination effectiveness parameters of the OP treatment seeds responded to agricultural landscape and pollinator density variables (Table 2 and Fig. 5). The average model for PPF revealed that ERGP ( $\Sigma w_i = 0.71$ ) and SNH ( $\Sigma w_i = 0.95$ ) were the variables with the highest relative importance, both corroborated by their confidence intervals (Table 2). PPF increased in plants from landscapes with higher crop diversity and decreased with increasing SNH proportion in the agricultural landscape. In contrast, MFS, WB and HB densities did not have a clear effect. Crop diversity (ERGP) was the most important ( $\Sigma w_i = 1.00$ ) variable influencing NSP, with greater crop diversity resulting in increased NSP. MSF ( $\Sigma w_i = 0.60$ ) and SNH ( $\Sigma w_i = 0.67$ ) presented lower relative importance, and although their confidence intervals included zero, they also showed clear effects, thereby increasing NSP in landscapes with small field sizes or with a higher proportion of SNH. The WB ( $\Sigma w_i = 0.25$ ) and HB ( $\Sigma w_i = 0.41$ ) densities did not have a clear effect. For the TSW, the average model revealed that only SNH ( $\Sigma w_i = 1.00$ ) had effects on TWS, which was the variable with the highest relative importance, with a positive effect supported by their respective confidence intervals. This indicated that the greater the proportion of SNH in the agricultural landscape, the higher the TSW.

The percentage of oil content in the seeds was explained by an

**Table 2**

Estimates and relative importance ( $\Sigma w_i$ ) for each predictor in the average models obtained through multimodel inference or estimate and  $p$ -value when it corresponds to a single model from the analysis of landscape effects on open pollination treatments plants. For each fixed effect factor, confidence intervals (CI) (95 %) are provided. Bold numbers indicate relevant variables.

| Quantity parameters                    |                                        | Estimate       | $\Sigma w_i$ | CI            |               |              |
|----------------------------------------|----------------------------------------|----------------|--------------|---------------|---------------|--------------|
|                                        |                                        |                |              | Lower         | Upper         |              |
| Pods per flower (PPF)                  | Wild bees (WB)                         | 0.008          | 0.32         | -0.010        | 0.026         |              |
|                                        | Honeybees (HB)                         | 0.005          | 0.24         | -0.013        | 0.022         |              |
|                                        | Crop diversity (ERGP)                  | <b>0.017</b>   | <b>0.71</b>  | <b>0.000</b>  | <b>0.034</b>  |              |
|                                        | Mean field size (MFS)                  | -0.016         | 0.49         | -0.037        | 0.005         |              |
|                                        | Seminatural habitats (SNH)             | <b>-0.031</b>  | <b>0.95</b>  | <b>-0.053</b> | <b>-0.009</b> |              |
|                                        | Within-field position (edge vs centre) | 0.000          | 0.19         | -0.025        | 0.021         |              |
|                                        | N° seeds per pod (NSP)                 | Wild bees (WB) | -0.516       | 0.25          | -1.842        | 0.810        |
|                                        |                                        | Honeybees (HB) | -0.748       | 0.41          | -1.965        | 0.469        |
| Crop diversity (ERGP)                  |                                        | <b>2.789</b>   | <b>1.00</b>  | <b>1.522</b>  | <b>4.056</b>  |              |
| Mean field size (MFS)                  |                                        | <b>-1.603</b>  | <b>0.60</b>  | <b>-3.587</b> | <b>0.381</b>  |              |
| Seminatural habitats (SNH)             |                                        | <b>1.492</b>   | <b>0.67</b>  | <b>-0.085</b> | <b>3.070</b>  |              |
| Within-field position (edge vs centre) |                                        | -0.004         | 0.18         | -1.536        | 1.528         |              |
| Thousand seed weight                   |                                        | Wild bees (WB) | -0.026       | 0.22          | -0.168        | 0.115        |
|                                        |                                        | Honeybees (HB) | -0.063       | 0.29          | -0.204        | 0.079        |
|                                        | Crop diversity (ERGP)                  | 0.016          | 0.23         | -0.136        | 0.168         |              |
|                                        | Mean field size (MFS)                  | 0.109          | 0.36         | -0.100        | 0.318         |              |
|                                        | Seminatural Habitats (SNH)             | <b>0.440</b>   | <b>1.00</b>  | <b>0.270</b>  | <b>0.610</b>  |              |
|                                        | Within-field position (edge vs centre) | 0.001          | 0.20         | -0.180        | 0.181         |              |
|                                        | Total oil (%)                          | Wild bees (WB) | -0.048       | 0.29          | -0.180        | 0.084        |
|                                        |                                        | Honeybees (HB) | -            | -             | -             | -            |
| Crop diversity (ERGP)                  |                                        | <b>1.132</b>   | <b>1.00</b>  | <b>0.974</b>  | <b>1.291</b>  |              |
| Mean field size (MFS)                  |                                        | <b>-0.384</b>  | <b>1.00</b>  | <b>-0.500</b> | <b>-0.267</b> |              |
| Seminatural habitats (SNH)             |                                        | <b>1.079</b>   | <b>1.00</b>  | <b>0.882</b>  | <b>1.277</b>  |              |
| Within-field position (edge vs centre) |                                        | <b>-0.070</b>  | <b>1.00</b>  | <b>-0.105</b> | <b>-0.035</b> |              |
| Total tocopherols                      |                                        | Wild bees (WB) | 0.021        | 0.24          | -0.067        | 0.109        |
|                                        |                                        | Honeybees (HB) | <b>0.110</b> | <b>1.00</b>   | <b>0.043</b>  | <b>0.177</b> |
|                                        | Crop diversity (ERGP)                  | 0.049          | 0.30         | -0.049        | 0.148         |              |
|                                        | Mean field size (MFS)                  | <b>-0.803</b>  | <b>1.00</b>  | <b>-0.879</b> | <b>-0.727</b> |              |
|                                        | Seminatural habitats (SNH)             | <b>-0.244</b>  | <b>1.00</b>  | <b>-0.355</b> | <b>-0.133</b> |              |
|                                        | Within-field position (edge vs centre) | <b>0.025</b>   | <b>0.88</b>  | <b>0.002</b>  | <b>0.047</b>  |              |
|                                        | $\alpha$ -Tocopherol                   | Wild bees (WB) | -0.017       | 0.24          | -0.133        | 0.099        |
|                                        |                                        | Honeybees (HB) | <b>0.121</b> | <b>1.00</b>   | <b>0.031</b>  | <b>0.211</b> |
| Crop diversity (ERGP)                  |                                        | 0.002          | 0.24         | -0.112        | 0.115         |              |
| Mean field size (MFS)                  |                                        | <b>-0.617</b>  | <b>1.00</b>  | <b>-0.719</b> | <b>-0.515</b> |              |
| Seminatural habitats (SNH)             |                                        | -0.040         | 0.26         | -0.180        | 0.100         |              |
| Within-field position (edge vs centre) |                                        | <b>0.101</b>   | <b>1.00</b>  | <b>0.070</b>  | <b>0.132</b>  |              |
| $\gamma$ -Tocopherol                   |                                        | Wild bees (WB) | <b>0.104</b> | <b>0.56</b>   | <b>-0.008</b> | <b>0.215</b> |
|                                        |                                        | Honeybees (HB) | 0.037        | 0.14          | -0.047        | 0.121        |

(continued on next page)



Table 2 (continued)

| Quantity parameters |                                        | Estimate | $\Sigma w_i$ | CI      |        |
|---------------------|----------------------------------------|----------|--------------|---------|--------|
|                     |                                        |          |              | Lower   | Upper  |
| Chlorophylls        | Crop diversity (ERGp)                  | 0.142    | 0.77         | 0.010   | 0.274  |
|                     | Mean field size (MFS)                  | -0.799   | 1.00         | -0.910  | -0.689 |
|                     | Seminatural habitats (SNH)             | -0.427   | 1.00         | -0.589  | -0.265 |
|                     | Within-field position (edge vs centre) | -0.118   | 1.00         | -0.146  | -0.089 |
|                     | Wild bees (WB)                         | -0.010   | 0.21         | -0.144  | 0.124  |
|                     | Honeybees (HB)                         | -0.161   | 1.00         | -0.264  | -0.058 |
|                     | Crop diversity (ERGp)                  | -0.322   | 1.00         | -0.453  | -0.191 |
|                     | Mean field size (MFS)                  | -0.189   | 1.00         | -0.296  | -0.081 |
|                     | Seminatural habitats (SNH)             | 0.086    | 0.30         | -0.089  | 0.260  |
|                     | Within-field position (edge vs centre) | -0.014   | 0.27         | -0.050  | 0.021  |
| Carotenoids         | Wild bees (WB)                         | 0.061    | 0.33         | -0.062  | 0.185  |
|                     | Honeybees (HB)                         | 0.067    | 0.47         | -0.027  | 0.162  |
|                     | Crop diversity (ERGp)                  | -0.468   | 1.00         | -0.605  | -0.331 |
|                     | Mean field size (MFS)                  | -0.109   | 0.80         | -0.211  | -0.006 |
|                     | Seminatural habitats (SNH)             | -0.482   | 1.00         | -0.644  | -0.320 |
|                     | Within-field position (edge vs centre) | 0.016    | 0.30         | -0.0151 | 0.047  |

average model that did not contain the variable HB. Both ERGp ( $\Sigma w_i = 1.00$ ) and SNH ( $\Sigma w_i = 1.00$ ) had a positive effect on oil content, whereas MFS ( $\Sigma w_i = 1.00$ ) had a negative effect. Consequently, the oil content in OSR seeds was higher in landscapes with more ERGp and SNH and in agricultural landscapes with smaller field sizes. Conversely, the oil content was lower in edge plants ( $\Sigma w_i = 1.00$ ).

The average model for the total tocopherols obtained from seeds of the OP treatment (Table 2) indicated a positive response to the HB densities ( $\Sigma w_i = 1.00$ ) and within-field position, being higher in edge ( $\Sigma w_i = 0.88$ ). In contrast, total tocopherols decreased in landscapes with a higher proportion of SNH ( $\Sigma w_i = 1.00$ ) and with larger field sizes ( $\Sigma w_i = 1.00$ ). The remaining variables had a relatively minor impact on the overall outcome; however, their effects were not entirely clear.

The average model for  $\alpha$ -tocopherol indicated that the HB density, in addition to MFS and within-field position, were the variables with the greatest relative importance ( $\Sigma w_i = 1.00$ ). Only MFS had a negative effect. All three variables were supported by the confidence intervals. The model indicated that seeds grown on the field's edge and in landscapes with smaller field sizes exhibited a higher  $\alpha$ -tocopherol content, as well as in the presence of a higher HB density (Table 2). The average model for  $\gamma$ -tocopherol explained that all landscape variables had a high relative importance and were supported by their confidence intervals. The WB density ( $\Sigma w_i = 0.56$ ) demonstrated a positive and clear effect despite containing zero in its confidence interval. The MFS, SNH, and within-field position had negative effects. This model indicated that  $\gamma$ -tocopherol decreased in landscapes with a higher proportion of SNH and in plants from the edge of the field. However, it increased in landscapes with smaller fields and a higher WB density (Table 2).

The pigments present in the seeds varied with all the studied variables. According to the average model, the HB density, ERGp, and MFS variables showed the highest relative importance ( $\Sigma w_i = 1.00$ ) and were supported by their respective confidence intervals. Moreover, they all had a negative effect on total chlorophylls content. The remaining variables had a lower relative importance and less clear effects. The model indicated that the chlorophylls content was diluted in landscapes with higher HB density, lower crop diversity, and larger fields.

Finally, the average model indicated that agricultural landscape variables (ERGp, MFS, and SNH) had the highest relative importance (Table 2) and influenced the reduction in the total carotenoids content in OP treatment seeds. This trend was supported by the respective confidence intervals. HB ( $\Sigma w_i = 0.47$ ) densities positively impacted carotenoids with a clear effect even though its confidence interval contained zero. Consequently, the model indicated that the carotenoids content in

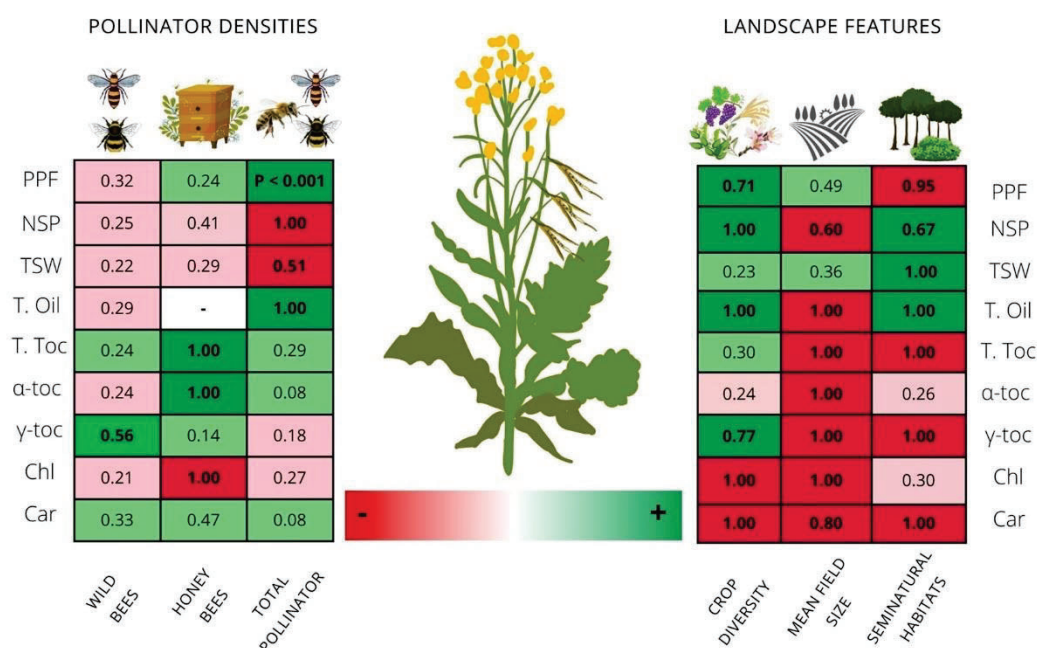


Fig. 5. Summary of the influence of different pollinator densities and agricultural landscape features on seed quantity parameters, pod per flower (PPF), number of seeds per pod (NSP), thousand seed weight (TSW) and seed quality parameters, oil content (T.Oil), total tocopherols (T.toc),  $\alpha$ -tocopherol ( $\alpha$ -toc),  $\gamma$ -tocopherol ( $\gamma$ -toc), chlorophyll (Chl) a + b, and carotenoids (Car). Bold numbers indicate relevant variables.



OSR seeds was higher in landscapes with smaller field sizes and higher HB density, whereas it decreased in landscapes with greater crop diversity and a higher SNH proportion.

#### 4. Discussion

The key finding of this study is the identification of relationships and influences among different characteristics of the agricultural landscape, with a specific emphasis on crop diversity and pollinator densities and their impact on agronomic parameters (quantity/quality) in OSR. This study highlights the fact that WB density increases in agricultural landscapes with greater crop diversity. Moreover, landscapes characterised by higher crop diversity are associated with improved quantity and improvements in OSR seed quality. These findings confirm our first two hypotheses, and in part the third, because WB does not play an important role individually in the quantity and quality of OSR seeds.

##### 4.1. Landscape characteristics influence WB density

Our findings revealed a positive correlation between WB density in rapeseed fields and landscape crop diversity, and a negative correlation with the mean field size. These trends align with those of previous research, indicating that higher crop diversity benefits WB abundance (Aguilera et al., 2020; Sirami et al., 2019). In productive landscapes, diverse crops create temporal variations in habitats and resources, supporting larger bee populations (Cavigliasso et al., 2022; Neira et al., 2024; Raderschall et al., 2021).

In contrast, an inverse correlation has been documented between wild pollinator density and mean field size. Martin et al. (2019) reported that there were 70 % more pollinators in small fields. Small fields with more margins improve landscape connectivity, making it easier for pollinators to move around (Hass et al., 2018a, 2018b; Sutherland et al., 2001). In addition, WBs typically require natural areas for nest or colony establishment and adapt by utilising disturbed or less dense areas compared to forest such as field margins (Hellwig et al., 2022; Rollin et al., 2013). Therefore, the outer part of the crop edge borders with diverse neighbouring microhabitats provide resources for many insects that are favourable for the establishment, growth, and diversification of WB populations in agroecosystems (Bartholomée et al., 2020; Coutinho et al., 2021; Morrison et al., 2017). This could explain the higher abundance of bees observed on the field edges than in the centre.

##### 4.2. Influence of pollinator density and pollinator exclusion on seed quantity and quality

Our study highlights that insect visitation plays a crucial role in OSR yields. The deposition of pollen, facilitated by insect visits, had a positive influence on the flower ratio, and the interaction between open OSR plants and total pollinator density produced a joint effect, increasing PPF while decreasing NSP and TSW. Individually the different groups density of pollinators (WB-HB) did not explain the pollination effectiveness parameters like reported in other studies (Beyer et al., 2021). Pollinators only improve effectiveness in a total way, not individually (Bartomeus et al., 2014; Jauker et al., 2012). Nevertheless, our results underscore the indispensable role of pollinators in maximising yield in OSR crops, consistent with the findings of other authors (Bommarco et al., 2012; Klein et al., 2007) and with more recent studies indicating that HBs and wild insects contribute similar amounts to crop yields (Reilly et al., 2024).

Most quality components of OSR seeds were affected by both the exclusion of pollinators and pollinator density, albeit at different intensities. Plants that interact with pollinators exhibit higher oil content, underscoring the importance of insect pollination in the development of OSR seed oil content (Bartomeus et al., 2014; Perrot et al., 2024). The relationship between oil content and pollinators remains under-researched, yet its importance to market value is significant

(Bommarco et al., 2012; Marini et al., 2015). It is likely that this is due to an increase in hybrid vigour, as only a small amount of exogenous pollen is needed to increase the productive parameters of OSR (Lankinen et al., 2018). The total tocopherol content in the rapeseed crop was within the usual range, as reported by Flakelar et al. (2015). However, total tocopherols were not affected by pollination treatment or the density of total pollinators on open inflorescences, but increased with the closeness of the edge and with increasing HB density. The  $\alpha$ - and  $\gamma$ -tocopherol concentrations exhibited distinct responses to the pollination treatment. Specifically,  $\gamma$ -tocopherol increased in seeds from inflorescences accessible to pollinators. The observed pattern may be attributed to chlorophyll degradation, which triggers the recycling of phytol into an alternative metabolic pathway for vitamin E biosynthesis (Muñoz et al., 2024). The accumulation of  $\gamma$ -tocopherol suggests that seeds from inflorescences accessible to pollinators have initiated the maturation process and are in a more advanced stage of development. This increased chlorophyll degradation leads to higher production of  $\gamma$ -tocopherol, the form of vitamin E that tends to accumulate in seeds (Munné-Bosch and Falk, 2004).

Higher HB densities were associated with an increase in  $\alpha$ -tocopherol, whereas WB density correlated with an increase in  $\gamma$ -tocopherol. The higher concentration of  $\gamma$ -tocopherol in seeds from insect-pollinated inflorescences may be linked to an enhanced maturation process, resulting in the production of more mature seeds in inflorescences accessible to pollinators. This relationship may also be associated with the fact that a higher WB density increases  $\gamma$ -tocopherol, contributing to seeds with greater maturation, as WBs are considered more effective pollinators than HBs owing to a higher likelihood of contact with the flower stigma (Woodcock et al., 2013).

HB density significantly reduced chlorophyll content in insect-pollinated plants. This indicates that a higher density of these pollinators has a direct impact on pigment content. Analysis of the pollinator exclusion experiment demonstrated that insect pollination plays a crucial role in enhancing both the quantitative and qualitative parameters of rapeseed production. Pigments found in OSR seeds were more abundant in plants without pollinators than in OP plants, suggesting that insect pollination influenced pigment concentrations. All pollinator densities, specifically HB densities, were associated with lower chlorophyll levels. Insect pollination expedites fruit and seed ripening, which causes greater decomposition of chlorophylls (Smolikova and Medvedev, 2016). The pattern of chlorophylls in seeds is opposite to that of  $\alpha$ -tocopherol, possibly because both compounds have a common precursor (Mène-Saffrané, 2018). This response could be explained because HB are the most abundant group of pollinators in the fields studied. HB collect pollen with high flower constancy, which can be linked to improved pollination efficiency (Montgomery, 2009). Lower concentrations of chlorophyll and higher concentrations of carotenoid are indicators of higher oil quality (Flakelar et al., 2015; Hannoufa et al., 2014). Therefore, based on our findings, insect pollination to enhances oil quality.

##### 4.3. The quantity and quality of OSR seeds are affected by the agricultural features of landscape

The characteristics of the agricultural landscape influence the quantity and quality of rapeseed seeds. Crop diversity was positively correlated with PPF and increased the number of seeds per pod. In contrast, semi-natural areas are particularly important for augmenting the TSW, but they are associated with fewer pods per flower. Rapeseed seed quality was also responsive to diverse landscape features, with specific effects varying depending on the parameters considered.

Crop diversity is a pivotal characteristic of agricultural landscapes that positively affects pollination effectiveness and seed quality. Furthermore, it plays a role in increasing the oil content and  $\gamma$ -tocopherol, while concurrently reducing the presence of pigments in seeds. These patterns are consistent with the findings of previous studies. The



positive effect of crop diversity is attributed to its ability to enhance pollinator diversity, leading to increased pollination services for crops (Dainese et al., 2019). Notably, both WBs and HBs have been associated with higher fruit set, elevated oil content, and reduced chlorophyll levels (Bartomeus et al., 2014; Bommarco et al., 2012; Garibaldi et al., 2013). In this study, we could not find a relationship between the crop diversity of the landscape and the improvement in OSR parameters mediated by WBs, but this is not the first report of landscape characteristics affecting both production and phytochemical processes (Magrach et al., 2023; Pioltelli et al., 2024a, 2024b), which is an interesting and novel aspect that requires further investigation.

The observed positive response may be attributed to the correlation between crop diversity in the landscape and WBs. WB density, in conjunction with the contribution of HBs, influences some quantity and quality parameters. HBs showed no relationship with landscape characteristics in the localities (Fig. S1); instead, WBs made the difference in the total pollinator density, a group that is directly related to crop diversity, as indicated above. Our study is the first to show connections between landscapes with diverse crops, pollinator density, and an increase in  $\gamma$ -tocopherol and total tocopherols in seeds. Having various crops in an area appears to create a better environment for OSR production.

Our data indicate that agricultural landscapes with smaller field sizes correlate with an improved number of seeds per pod and generally with better seed quality. Smaller fields may be associated with higher OSR crop yield and plant reproduction (Hass et al., 2018a, 2018b; Magrach et al., 2023). Semi-natural areas positively affect the number of seeds per pod and the weight of a thousand seeds. This is consistent with other studies indicating that oil content in seeds increases with the number of seeds per pod (Vera et al., 2007). Mazzei et al. (2021) underscored the pivotal role of forest fragments in close proximity to OSR fields and their substantial influence on seed production parameters. This highlights the significance of semi natural habitats and their proximity, as emphasised by Halinski et al. (2020, 2018).

## 5. Conclusions

This novel study provides nuanced exploration, unveiling new insights into the agricultural landscape and the quantity and quality of rapeseed crop yield. Our findings underscore the pivotal role of crop diversity through its positive influence on WBs and the enhancement of both seed quantity and quality in OSR crops. In addition, there were positive effects of a greater proportion of semi-natural areas for quantity parameters and smaller fields for quality parameters.

Our investigation of pollination effectiveness revealed a complementary relationship between WBs and HBs. Both groups of bees have a joint effect by increasing the percentage of oil in seeds. Besides, Notably, WBs are linked to seeds that exhibit increased maturity profiles compared with those associated with HBs. This study emphasises the implications of the presence of WBs for seed maturity.

Although this study contributes novel perspectives, our research also underscores the necessity for further enquiries into the intricate dynamics between landscapes, bees, and cultivation practices.

In a broader context, our findings advocate for prioritising the preservation and augmentation of agricultural landscape heterogeneity in the design of agricultural eco-schemes. This underscores the role of agricultural landscape management in supporting WBs and high-quality crop production, presenting a win-win scenario for both biodiversity and agricultural communities.

## Funding

This research was partially supported by projects obtained from FXS & JMBM: Grants RTI2018-095597-B-I00 and PID2021-127575OB-I00 funded by MCIN/AEI/ 10.13039/501100011033 and by "ERDF A way of making Europe", by the European Union. PN was supported by

Scholarship Program Doctorado en el Extranjero BECAS CHILE of the Agencia Nacional de Desarrollo e Investigación (ANID), Chile Folio 72210385. MM is grateful for a Beatrui de Pinós MSCA-COFUND post-doctoral grant (2018 BP-00106) received from the Government of Catalonia.

## CRedit authorship contribution statement

**P. Neira:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **M. Morales:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **S. Munné-Bosch:** Writing – review & editing, Supervision, Methodology. **J.M. Blanco-Moreno:** Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **F.X. Sans:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

## Declaration of Generative AI and AI-assisted technologies in the writing process

The authors used *ChatGPT* to improve readability and language usage during the writing of this paper. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

## Declaration of competing interest

The authors declare no competing financial interests or personal relationships that may have influenced the work reported in this study.

## Data availability

Data will be made available upon reasonable request.

## Acknowledgements

We thank the farmers for their cooperation and for access to their fields. We also thank the Biomolecular Analysis Unit from Scientific and Technological Centers (CCiTUB, Centres Científics i Tecnològics de la UB), Universitat de Barcelona, as well as Esther Miralles and Alberto Adeva for their support, advice, and technical help with high-performance liquid chromatography.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.175062>.

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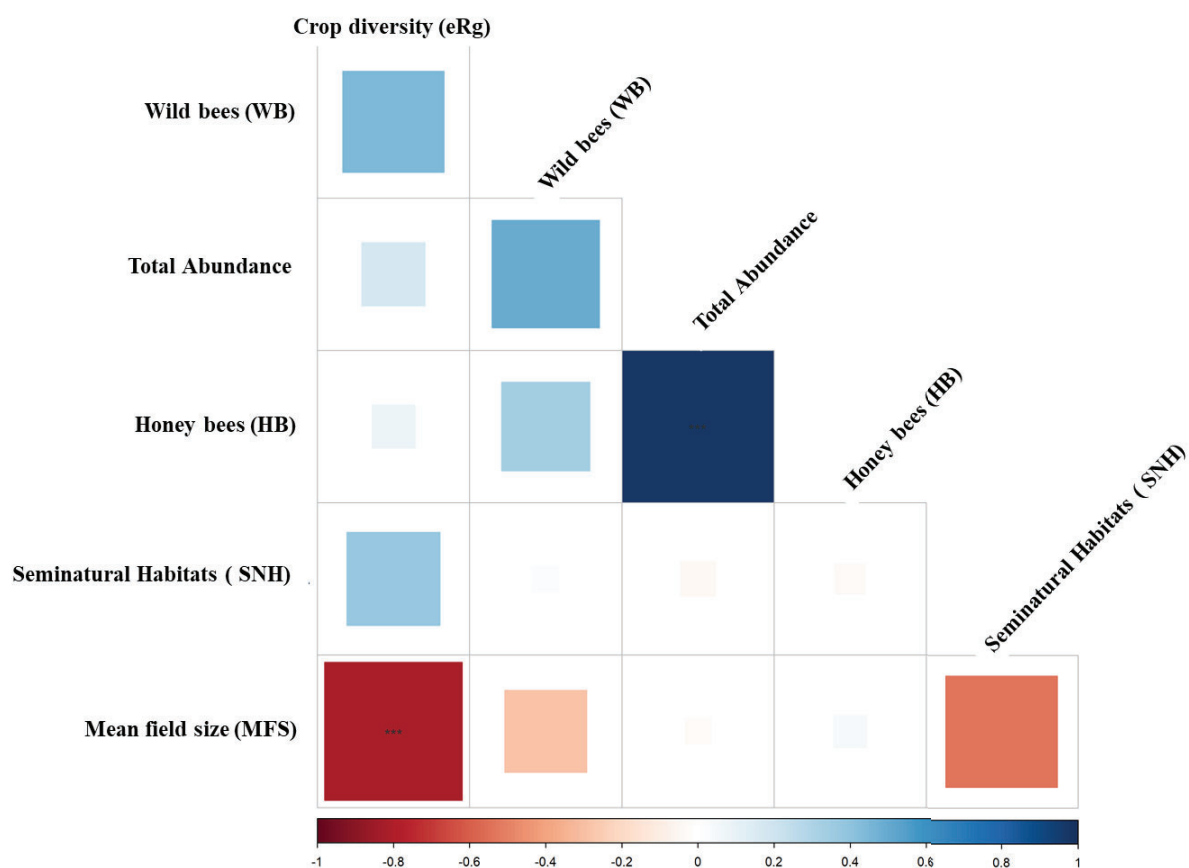


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**Fig S1.** Spearman rank correlation matrix showing significance between the characteristics of the landscape and the visit ratio of wild, honey and total bees



**Table S1** Photon flux evaluation inside and outside the mesh nylon

| Out mesh | Inside mesh |
|----------|-------------|
| 1741     | 1740        |
| 1830     | 1795        |
| 1855     | 1781        |
| 1824     | 1763        |
| 1820     | 1791        |
| 1765     | 1762        |
| 1825     | 1738        |
| 1737     | 1778        |
| 1832     | 1823        |
| 1821     | 1769        |
| 1810     | 1786        |
| 1742     | 1759        |

---

t test results
**P value and statistical significance:****P value = 0.0702****By conventional criteria, this difference is considered to be not quite statistically significant.****Confidence interval:**

The mean of Group One minus Group Two equals 26.42

95% confidence interval of this difference: From -2.37 to 55.21

Intermediate values used in calculations:

t = 1.9030

df = 22

standard error of difference = 13.882

Review your data:

| Group | Out mesh | Inside mesh |
|-------|----------|-------------|
| Mean  | 1800.17  | 1773.75     |
| SD    | 41.7     | 23.94       |
| SEM   | 12.04    | 6.91        |
| N     | 12       | 12          |

Table S2. VIF values for landscape metrics and bee densities

| Term                   | VIF                |                        |
|------------------------|--------------------|------------------------|
| Crop diversity         | <b>1.020186726</b> | <b>Low Correlation</b> |
| SNH                    | <b>1.602689765</b> |                        |
| MFS                    | <b>1.510651554</b> |                        |
| Year                   | <b>1.141169955</b> |                        |
| Whithin-field position | <b>1</b>           |                        |

| Term                                    | VIF                |                        |
|-----------------------------------------|--------------------|------------------------|
| Total Density                           | <b>2.41456003</b>  | <b>Low Correlation</b> |
| Exclusion Treatmeant                    | <b>2.469835245</b> |                        |
| Whithin-field position                  | <b>2.651186558</b> |                        |
| Year                                    | <b>1.003862401</b> |                        |
| Total Abundance :Exclusion Treatmeant   | <b>3.578025102</b> |                        |
| Total Abundance :Whithin-field position | <b>2.96426317</b>  |                        |

| Term                   | VIF                |                        |
|------------------------|--------------------|------------------------|
| Whithin-field position | <b>1.022698689</b> | <b>Low Correlation</b> |
| Honey bees (HB)        | <b>1.195828293</b> |                        |
| Crop diversity         | <b>1.21925348</b>  |                        |
| MFS                    | <b>1.493726991</b> |                        |
| SNH                    | <b>1.710202485</b> |                        |
| Wild bees (WB)         | <b>1.520857063</b> |                        |
| Year                   | <b>1.346143997</b> |                        |





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## CAPÍTULO 3

La cobertura de cultivos de floración masiva en el pasado mejora la densidad de polinizadores y el rendimiento de la colza en los agroecosistemas mediterráneos.





# **Past mass flowering crop cover enhances pollinator density and oilseed rape yield in Mediterranean agroecosystems**

En revisión en Agricultural Systems

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## **Past cover of mass flowering crops affects bee density, increases pollination effectiveness and improves the oilseed rape yield in Mediterranean agricultural landscapes.**

### **Abstract**

*Context:* The heterogeneity of agricultural landscapes, including both in-crop and off-crop areas, is crucial for maintaining agroecosystem functions. Mass-flowering crops provide essential resources for pollinators, enhancing pollination services over time.

*Objective:* This study aimed to examine how four landscape features—mass-flowering crop cover from the previous year (MFC1), cumulative cover over three years (MFC3), semi-natural habitats (SNH), and mean field size (MFS)—influence bee densities and pollination effectiveness on oilseed rape (OSR) yield. We also explored how small and large bees contribute differently to pollination.

*Methods:* Over two years, we analyzed 18 OSR fields in the Central Catalan Depression, using structural equation modeling to evaluate the impact of landscape features on wild bee densities and pollination effectiveness. Wild bee density and bee size-class criteria, categorized into small bees (SB) (<1.5 cm) and large bees (LB) (>1.5 cm), were assessed separately, each in its own structural equation model, to understand their distinct effects.

*Results and conclusions:* MFC1 increased wild bee densities, while MFC3 promoted LB. Also, smaller MFS was associated with higher densities of LB. OSR productivity was more strongly linked to bee size class than WB density. Seeds per pod correlated positively with WB, LB, MFC1, SNH and MFS. Oil content was positively related to LB but negatively to MFS, while SNH boosted thousand-seed weight.

*Significance:* LB are vital for OSR productivity, but SB can complement pollination services. These findings highlight the need for agricultural strategies that account for landscape diversity and bee size to optimize pollination and crop yield.

**Keywords:** Agricultural landscape, Mass Flowering Crops, wild bees, temporal landscape metrics, semi-natural habitats.



## 1. Introduction

Landscape has been man-shaped for a long time, particularly in the Mediterranean, and consequently natural and agricultural ecosystems are intermingled, favouring the interrelation among different land uses. This complexity has an impact on ecological processes, especially those involving interactions among plants and animals (Farina, 2015; Potts et al., 2006). The functioning of the agricultural landscape is contingent upon its composition and configuration, which in turn influence the ecosystem services provided, such as pollination and pest control (Tittone et al., 2020; Tscharntke et al., 2012). From an agroecological perspective, achieving sustainability in agricultural landscapes requires the maximisation of ecological processes at different scales (Jeanneret et al., 2021; McGranahan, 2014; Wezel et al., 2020).

Their relationship with human activities is dual. On the one hand, agricultural intensification at both landscape and field levels has dramatically reduced wild pollinator communities, negatively impacting pollination service provision (Klein et al., 2007). On the other hand, agricultural landscapes that support ecosystem services are the result of years of human land use, with landscape history playing a key role in determining ecosystem service provision (Bürgi et al., 2015; Foster et al., 2003). Therefore, the availability of suitable habitats and sufficient resources for pollinator communities largely depends on the configuration and composition of agricultural landscapes over time (Bottero et al., 2023; Estrada-Carmona et al., 2022). Therefore, the availability of suitable habitats and sufficient resources for pollinator communities largely depends on the configuration and composition of agricultural landscapes over time (Cavigliasso et al., 2022; Neira, Blanco-Moreno, et al., 2024).

Landscape characteristics at different spatial scales affect both the abundance and taxonomic richness of pollinators and their functional traits (Elzay & Baum, 2021). One of the key functional traits impacting pollination services is the body size of flower visitors (Cortés-Gómez et al., 2023). This trait is positively correlated with their foraging distance, pollen carrying, and deposition capacity, all of which are closely linked to pollination effectiveness and the fruit set of insect-pollinated crops (Greenleaf et al., 2007; Ne'eman et al., 2010; Pfister et al., 2017). Agricultural landscape simplification has been linked to a reduction in bee size, with smaller body size serving as an early indicator of environmental stress (Grab et al., 2019). The reduction in body size is associated with a decrease in floral resources and a decline in the quality of pollen and nectar available to larvae (Borchardt et al., 2023; Burkle & Irwin, 2009; Roulston & Cane, 2002). This reduction results in diminished total offspring production, ultimately leading to a decrease in pollinator abundance (Brasil et al., 2023; Lawson et al.,

2021; Nooten & Rehan, 2019). Consequently, landscape-induced declines in body size have significant implications for the persistence of bee communities and the effectiveness of pollination services.

In this context, the agricultural landscape plays a crucial role. Essential resources for pollinator survival are found in various habitats. Semi-natural areas like forests, thickets, and flower-rich grasslands provide these resources, as do field margins between crops as well as crops with floral rewards as such mass flowering crops (MFCs) (Ammann et al., 2024; Bassa et al., 2012; Rollin et al., 2013b). MFCs are characterized by an intense bloom over a short period, attracting pollinators with concentrated pollen and nectar (Mendoza-García et al., 2018). Oilseed rape (*Brassica napus* L., hereinafter OSR) is an oleaginous crop widely cultivated across Europe. In Mediterranean landscapes, it blooms massively between April and May. Although OSR is not entirely reliant on pollinators, available evidence suggests that effective insect pollination can enhance its yield and other productivity parameters (Da Cunha & Aizen, 2023; Fairhurst et al., 2022; Fijen et al., 2022; Halinski, Garibaldi, dos Santos, et al., 2020; Neira, Morales, et al., 2024). Previous research has explored the impact of MFCs on pollinators over time, revealing positive relationships between MFC cover from the previous year (Blasi et al., 2021; Kallioniemi et al., 2017; Riedinger et al., 2014) and up to three years prior to sampling (Beyer et al., 2021). Notably, MFCs have a positive effect on bee abundance, acting as drivers of bee populations.

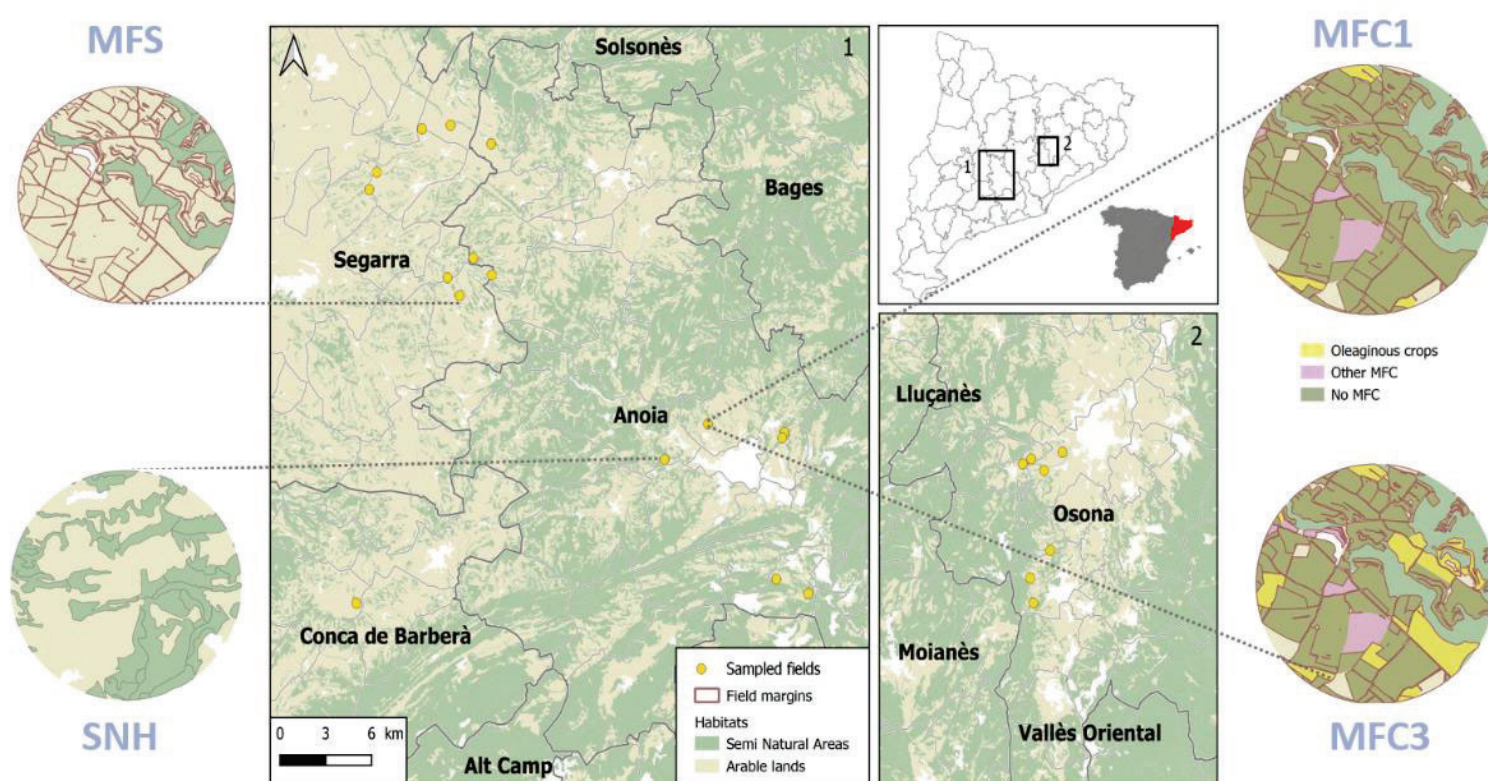
Despite some research (Beyer et al., 2021; Blasi et al., 2021), there remains a scarcity of studies investigating the long-term effects of MFC and the body size of bees that visit crops, especially in Mediterranean regions. Considering this gap, our study proposes an approach to explore the temporal relationship between different MFC cover in Mediterranean agricultural landscapes and densities of wild bees and their size as well as their potential impact on oilseed rape (OSR) crops. We hypothesize that OSR fields situated in agricultural landscapes with greater MFC area accumulation over the past three years will have higher wild pollinator density and support communities of larger pollinators. Furthermore, the impact of the accumulated MFC over three years will be higher than the MFC cover from the previous year. Our hypotheses posit that OSR fields within agricultural landscapes exhibiting greater MFC area accumulation over the past three years will demonstrate higher wild pollinator density and foster communities of larger pollinators compared to the MFC cover from the previous year. Given that pollinator density and body size significantly influence pollination effectiveness in OSR, we anticipate that fields

experiencing more visits from larger bees will exhibit enhanced pollination effectiveness in OSR crops.

## 2. Material and methods

### 2.1 Landscape metrics

In 2021 and 2022, 20 OSR fields were selected in the Central Catalan Depression, the NE Iberian Peninsula ( $41^{\circ}24'-42^{\circ}05'N$ ;  $1^{\circ}05'-2^{\circ}05'E$ ) (Figure 1). All the selected fields were managed conventionally and sown with winter OSR varieties. The studied landscapes are dominated (average 66%) by arable cropland intermingled with non-cropped areas. The main crops in the area are winter cereals; other common crops are almond trees, olive groves, vineyards, forage and oilseed crops. Forest habitats, thickets and grasslands occupy the non-cropped areas (Departament d'Acció Climàtica, Alimentació i Agenda Rural, 2023).



**Figure 1.** Location of study areas in the Central Catalan Depression, in the context of Catalonia (right above), and distribution of the 18 localities (yellow points). The circles represent the agricultural landscape around the localities, with a buffer zone of 1 km. The zoomed-out buffers represent examples of the four landscapes features used as explanatory variables. MFS = mean

field size, SNH= semi-natural habitats, MFC1 and MFC3 = mass flowering crop in the previous and in the cumulative three past years. Names indicate Catalan shires (“comarques”).

A buffer area of 1 km radius from the centre of each OSR field was used to describe the landscape around the sampled fields. The buffer radius was established following previous studies that have found that most feeding flights of the surveyed pollinators are within this distance (Steffan-Dewenter & Kuhn, 2003). We selected localities where less than 10% of the buffer area was covered by OSR crop during the sampling year to promote a concentration effect on pollinators (Beyer et al., 2021; Holzschuh et al., 2011; Magrach et al., 2018). Fields sampled in any given year were at least 2 km away from each other to prevent overlapping and to ensure that different OSR fields were not visited by the same pollinator pools.

For each locality, we calculated four landscape features, including the cover of mass-flowering crops that overlapped their bloom with OSR flowering in the year previous to sampling (MFC1), cumulative mass flowering crop cover in the three years previous sampling (MFC3), mean field size (MFS) and percentage of the buffer area occupied by seminatural habitats (SNH). Spatial information for the calculation of these features was obtained from the DUN-SIGPAC Crop Map and the Cartography of Habitats of Catalunya (Departament d’Acció Climàtica, Alimentació i Agenda Rural, 2023; Departament de Territori i Sostenibilitat, 2018). MFS is used as an indicator of agricultural landscape configuration, while the rest of indicators refer to landscape composition. MFC1 cover for the first year prior to sampling considers all identified MFC. MFC3 cover is calculated as the sum of MFC cover for the three years prior to sampling.

The set of crops considered as MFC has been established from the list of crops present in the study localities and the information on flowering periods (crops potentially blooming during the sampling period) (de Bolos et al., 2005 ). The MFCs present in the landscapes include oilseed crops such as rapeseed and mustard, as well as sweet fruit trees like pears, cherries, peaches, and apples.

## 2.2 Pollinator sampling

Sampling was conducted during April and May. The survey was performed by a single observer who counted individual pollinators visiting OSR flowers during two standardized transect walks per field at different within-field positions. One walk was carried out in the crop centre and the other in the crop edge, both parallel to the field margin. The transects covered an area of 150 m<sup>2</sup> (75 × 2 m), and each walk lasted 15 minutes. Each transect was sampled twice during



the OSR bloom period. Transects were surveyed on days when the air temperature was above 15°C, the wind speed was low, and there was no rain following similar studies.

To assess the densities of pollinator groups, we recorded during transect walks wild bees (WB), which are classified as efficient wild pollinators for OSR crops (Jauker et al., 2012; Stanley et al., 2013), and honeybees (HB). Although the abundance of honeybees (*Apis mellifera* L.) is not directly related to the resources provided by the ecosystem but rather to the location of hives, it was still recorded because honeybees contribute to OSR pollination (Bommarco et al., 2012; Hudewenz & Klein, 2013). Wild bees were grouped according to size class criteria into *small bees* (SB) (<1.5 cm) and *large bees* (LB) (>1.5 cm) since bee of similar size have similar effects on pollination. Wild bees and honeybees were both considered for the evaluation of pollination effects on OSR.

### 2.3 Evaluating pollination effectiveness in OSR

Two sampling zones were established in each study field, one in the centre and one at the crop edge, coinciding with pollinator transects. In each sampling area, 5 OSR plants were selected, and one inflorescence of similar size was chosen from each plant (N=200). Inflorescences were manually collected once the plants had completed its development, when OSR crop was ready to harvest, at the beginning of July.

To quantify pollination effectiveness, three parameters were estimated for the selected OSR inflorescences: (1) The number of seeds per pod (NSP) was characterized by examining five pods per inflorescence (50 pods per field). (2) The thousand-seed weight (TSW) was estimated by calculating the total weight of all seeds in each inflorescence and dividing it by the product of the average number of seeds per pod and the total number of pods, using the formula  $1000 \times (\text{weight of all seeds} / (\text{average number of seeds per pod} \times \text{total pods}))$ . (3) Percentage of oil content in seeds (TO) was determined using a modified gravimetry protocol (Bligh & Dyer, 1959) of three inflorescences randomly chosen for each within-field position (centre/edge) per field (N = 120).

### 2.4 Statistical analyses

We tested the effects of the landscape metrics on bee density and on OSR pollination effectiveness by means of structural equation modelling (SEM). This method allows the evaluation of the direct and indirect pathways that can influence the OSR pollination effectiveness. We used piecewise SEMs, which allow for a wide range of response distributions in a hierarchical (mixed effects) framework (Lefcheck 2016). We used the package

“piecewiseSEM” to assess the goodness-of-fit based on Shipley’s test of directed separation that combines the P-values of all independence claims in Fisher’s C statistic (Shipley, 2009). We constructed two different hypothetical models comprising either total wild bee density (WB) and honeybees (HB), or density split by size-class criteria (SB and LB). The first model included effects of landscapes features (MFC1, MFC3, SNH, MFS) as continuous explanatory variables affecting total wild bee density (WB). Also, we aggregated HB densities and WB densities for the pollination effectiveness models (number seeds per pod, weight of thousand seeds and oil content in seeds). As we expected correlations between honeybee densities and wild bee densities, we added correlated errors between those variables (Figure S1a). The second model includes only wild bee densities split according to size classes (SB and LB) instead of total wild bee density (WB) (Figure S1b). Locality was included as a random effect factor for models that relate landscape and wild bee density, while OSR variety was used as a random effect factor in pollination effectiveness models.

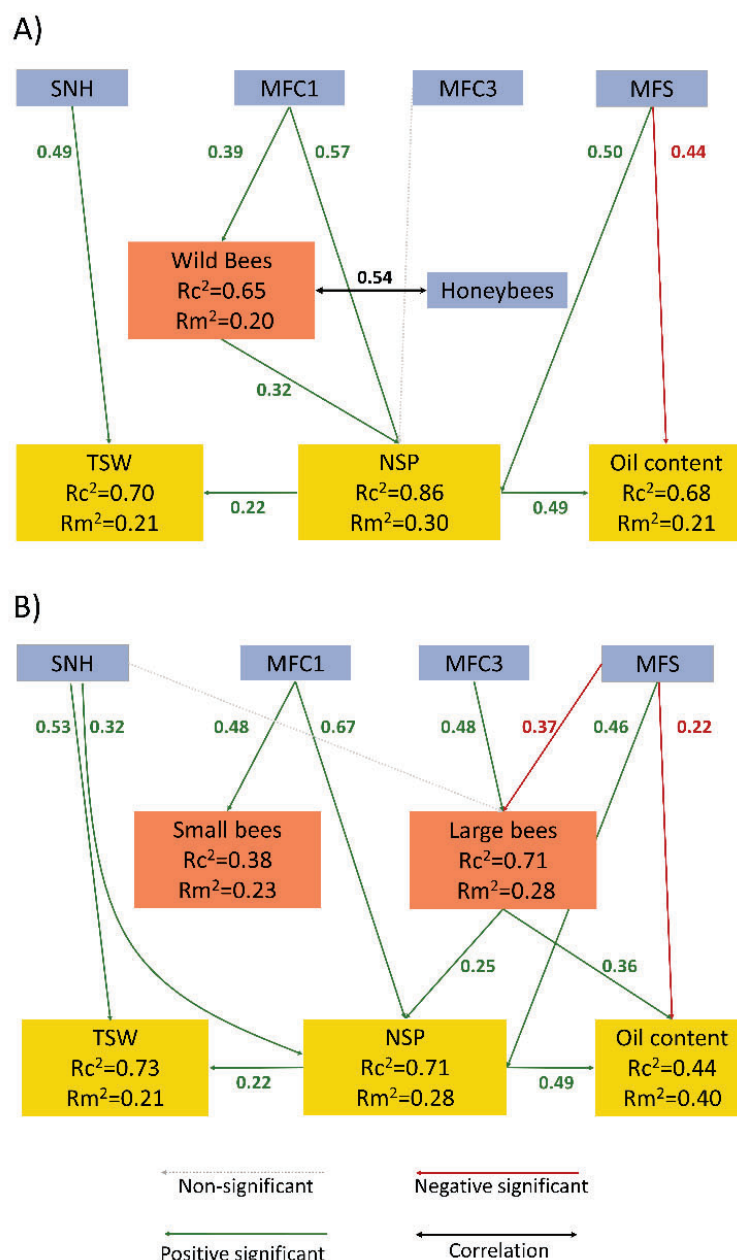
Each pathway in the SEM represents a single model for which we used generalized linear mixed models fit through the 'glmmTMB' package (Brooks et al., 2017). A strong correlation was identified between the MFC1 and MFC3, and between MFS and SNH ( $R^2 > 0.8$ ). Therefore, a sequential regression approach (Graham, 2003) was used to create new purged explanatory variables by reciprocally subtracting the common variation from the MFC1 in relation to MFC3, and from SNH in relation to MFS. These procedures allowed us to obtain new independent surrogate variables for MFC1 and SNH from their residue’s vs MFC3 and MFS, respectively. This approach allowed the inclusion of both adjusted variables in the model. We tested for potential collinearity between explanatory variables using the variance inflation factor (VIF) through the 'check\_collinearity' function from the 'performance' package (Lüdtke et al., 2021). The set of variables showed low collinearity, all VIFs were  $< 2$  (Zuur et al., 2010). All SEMs were manually simplified by removing stepwise pathways with the highest P-value until the best model was found based on the AIC. All statistical analyses were conducted using R version 4.2.1 (R Core Team, 2022) under RStudio version 4.1.2.2 (RStudio Team, 2022).

### 3. Results

A total of 2592 individuals of honeybees and 992 of wild bees were recorded in both sampled years. The average density of honeybees and of wild bees recorded was 32 and 12 individuals per transect, respectively. We collected 1000 pods from oilseed rape plants, with an average of 23 seeds per pod. The average weight of a thousand seeds varied between 1.2 g and 5.6 g across locations, while the oil content averaged 43% of the seed weight, ranging from 28% to 53%.

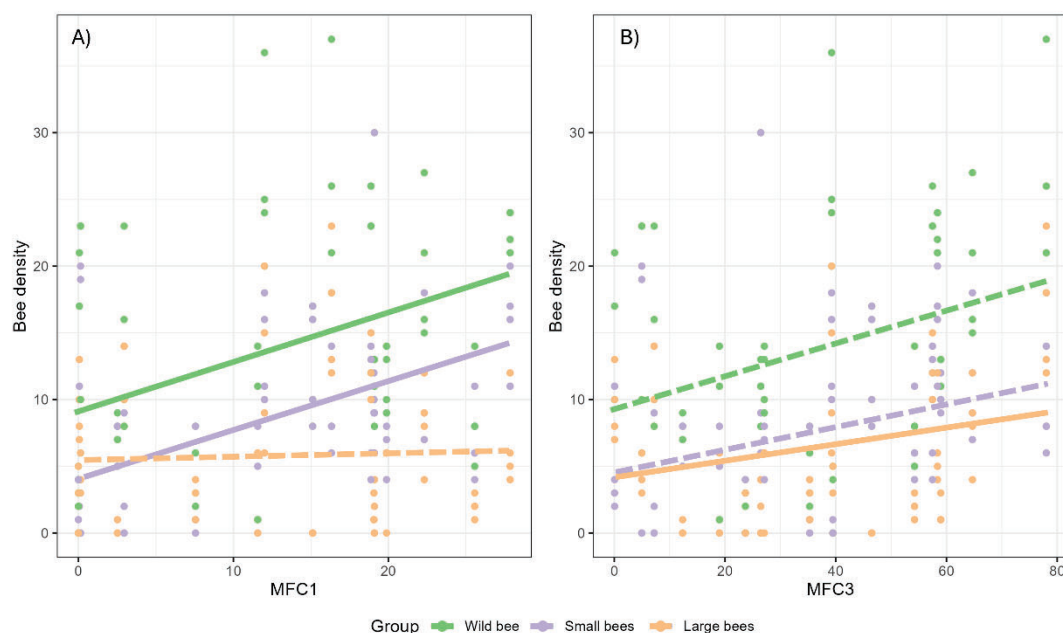
The first SEM model, which included total wild bee density, fit the data well (best simplified model Fisher's  $C = 33.89$ ,  $P\text{-value} = 0.287$ , Fig. 2A). None of the independence claims remained significant, indicating no important links were missing from the model. The best model for wild bee density revealed that an increase in the previous year mass flowering crop cover (MFC1) had a strong effect on the density of wild bees visiting the oilseed rape fields (Fig. 2A and 3A). This was the only landscape variable affecting wild bee density. In turn, WB significantly increases the number of seeds per pod (Fig 4a). Honeybee density positively correlated with wild bees but did not impact pollination efficacy.

MFS positively affected the number of seeds per pod and negatively affected the oil content in seeds (Fig. 3b). An increase in the percentage of semi-natural habitats in the landscape had a strong positive effect on the thousand-seed weight (Fig. 2b). Additionally, the number of seeds per pod was positively related to the thousand-seed weight and the oil content in seeds.



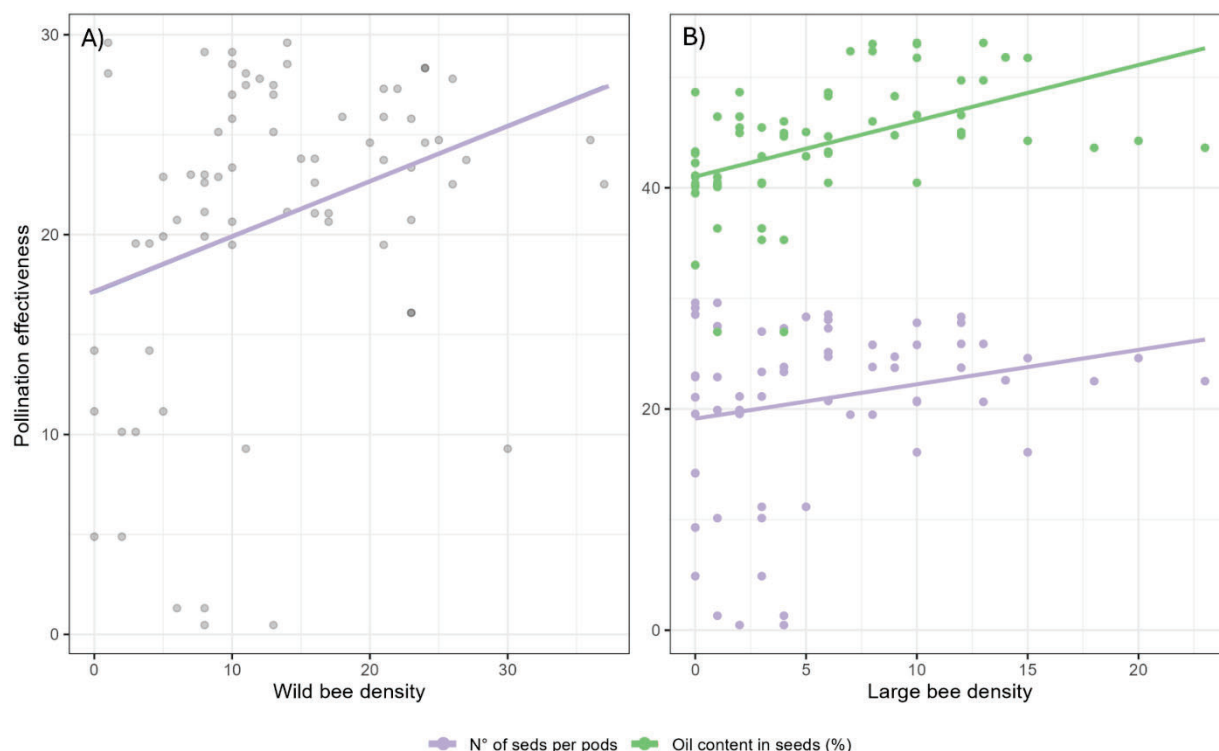
**Figure 2.** Results of the best piecewise SEMs based on AIC values, analyzing the relationships between the previous year mass flowering crop cover (MFC1), cumulative mass flowering crops cover (MFC3), mean field size (MFS), and the proportion of seminatural habitats (SNH) in the landscape. The analysis includes (A) wild bee and honeybee densities and (B) size-class criteria (small and large bee density), and their effects on pollination effectiveness (TSW = thousand-seed weight, NSP = number of seeds per pod). Numbers next to arrows indicate standardized regression coefficients. Conditional ( $R_c^2$ , including random effects) and marginal ( $R_m^2$ , excluding random effects)  $R^2$  values are presented for the response variables.





**Figure 3** Effect of previous year mass flowering crop cover (ha) (MFC1) on wild bees (WB) density and on bee density split by size-class (small and large bees (SB-LB)) (A) and effect of cumulative mass flowering crop cover (MFC3) on wild bee (WB) densities and on bee density split by size-class (SB-LB) (B). Lines show predictions from mixed models included in the SEMs. Solid lines indicate significant relationships ( $P$ -value  $< 0.001$ ) and dashed lines indicate non-significant relationships ( $P$ -value  $> 0.05$ ) from best fitting SEM.

By replacing the honeybee and wild bee density with wild bee size class (small and large) in the SEM (best simplified model  $C = 24.699$  with  $P$ -value = 0.644, Fig. 2b), it was found that MFC1 had strong effects on small wild bees and the number of seeds per pod (Fig. 2b, 3a). MFC3 showed a strong effect on the density of large bees. The MFS had a negative effect on the oil content in seeds and on the density of large wild bees (Fig. 3b). The percentage of semi-natural habitats maintained its positive effect on the weight of a thousand seeds and number of seeds per pod. A higher density of large wild bees had a positive effect on the number of seeds per pod and a stronger effect on the oil content in seeds (Fig. 2b, 4b). The density of small wild bees had a negative effect on the oil content in seeds.



**Figure 4.** Effect of wild bee density (WB) (A) and large bee density (B) on pollination effectiveness parameters. Lines show predictions from mixed models that were examined in the SEMs. Solid lines indicate significant relationships from best fitting SEM.

## 4. Discussion

Overall, our results indicate that wild bee densities increased with the previous year mass flowering crop cover in the landscape, though the effect of agricultural landscape features is different depending on their body size. The density of small bees was related to previous year mass flowering crop cover, while the density of large bees was related to the cumulative mass flowering crops cover and mean field size, partially confirming our first hypothesis.

The analysis of oilseed rape quality indicators shows that large bees play an important function on two of the evaluated parameters, thereby confirming our second hypothesis.

### 4.1 Mass-flowering crops and small field size increase wild bee densities

The positive effect of mass-flowering crops cover over previous years, on the visitation rate of wild bee in the Mediterranean landscapes of the Central Depression of Catalonia is consistent with Previous studies (Beyer et al., 2021; Bürgi et al., 2015; Foster et al., 2003). This confirms the importance of landscape history in shaping pollination services.

The presence of mass-flowering crops (MFCs) in cereal-dominated landscapes enhances and supports pollination services in agroecosystems (Estrada-Carmona et al., 2022; Fijen et al., 2022; Hass, Kormann, Tscharncke, Clough, Baillod, Sirami, Fahrig, Martin, Baudry, Bertrand, Bosch, Brotons, Burel, et al., 2018). The cumulative mass flowering crops cover in the agricultural landscapes increases wild bee abundance by consistently providing large amounts of pollen and nectar for bees. In line with Beyer et al (2021), our results highlight the importance of MFC cover accumulated in the past. On the other hand, the presence of honeybees did not negatively affect the density of wild bee. It is likely that competitive relationships are alleviated due to the large resource supply during MFCs blooming period (Wignall et al., 2020; Zanini et al., 2024).

The previous year mass flowering crop cover also influenced wild bee density, depending on their body size in OSR fields. The coverage from the previous year increased the density of small-sized bees, likely because their limited foraging range makes them more dependent on consistent resource availability. In contrast, the cumulative mass MFC cover had a positive effect on the density of large bees, but the previous year mass flowering crop cover did not have any effect on these. These positive effects of mass flowering crop coverages from the previous year have been previously reported for bees with smaller sizes and therefore a smaller range of feeding areas (Greenleaf et al., 2007; Kennedy et al., 2013; Van Reeth et al., 2018). Conversely, larger bees, with their extensive foraging areas, may benefit differently (Happe et al., 2018; Westphal et al., 2006). Small bees rely heavily on the conditions of the previous year due to their limited foraging range, whereas larger bees, with their greater mobility, can more effectively capitalize on landscape resources, even when these resources shift due to crop rotation. In the studied landscapes, OSR is included in crop rotational schemes, mainly with cereals. This rotation in the location of crops could disadvantage small bees due to their limited spatial resource exploitation range. Conversely, it may not significantly impact on larger bees, which can utilize these crops even if they change location annually, benefiting from accumulated MFC cover in the landscape.

In our agricultural landscapes, we found that the smaller the fields, the greater the density of large bees. This pattern may be attributed to the dominance of the genus *Bombus* among the large bees in our observations. Species from this genus rely heavily on high-quality feeding habitats and flower-rich field margins, which are more prevalent in small-scale agricultural settings (Happe et al., 2018). The increased number of crop edges and field margins in landscapes with smaller fields enhances connectivity, which benefits large bees by facilitating

their movement and access to diverse resources (Clough et al., 2020). Additionally, landscapes with smaller fields allow large bees to better complement the temporal availability of agricultural resources (Bishop et al., 2024; Carvell et al., 2004). This could explain why smaller average field sizes in agricultural landscapes are particularly advantageous for large bees, enabling them to effectively forage and thrive.

## **4.2 The influence of agricultural landscape and large bees on pollination effectiveness**

The features of the agricultural landscape significantly influenced pollination effectiveness parameters. Among the landscape parameters evaluated, only MFC3 did not have a direct effect on OSR yield parameters, underscoring the importance of the surrounding landscape in crop development (Bommarco et al., 2012; Burchfield et al., 2019). Specifically, the percentage of semi-natural areas positively affected the weight of a thousand seeds in rapeseed crops, a finding consistent with previous studies by Halinski et al. (2020) and Mazzei et al. (2021). Additionally, agricultural landscapes with smaller average field sizes were associated with higher oil content in seeds. Such landscapes have been reported to enhance crops that benefit from pollination by increasing the density of pollinator visits and improving landscape connectivity (Dainese et al., 2019b; Hass, Kormann, Tschardtke, Clough, Baillod, Sirami, Fahrig, Martin, Baudry, Bertrand, Bosch, Brotons, Burel, et al., 2018). Furthermore, MFC1 had a direct effect on the number of seeds per pod, highlighting the significance of the landscape's previous conditions in influencing current crop outcomes (Beyer et al., 2021).

Furthermore, the density of wild bees has a positive impact on OSR production, affecting the number of seeds per pod. These findings are consistent with previous research (Bartomeus et al., 2014; Bommarco et al., 2012; Jauker et al., 2012). Our findings add complexity to the results, by showing that bee body size significantly impacts pollination effectiveness. Crop harvest quantity and quality (number of seeds per pod and oil content) are influenced by the densities of different-sized bees. In contrast, the density of wild bees only relates to the number of seeds per pod. SEM results show that both models explain the number of seeds per pod, similarly, as indicated by the comparable percentage of explained variability (Fig 2). However, for oil content in seeds, the SEM model that includes size class explains the response better than the model that considers honeybee and wild bee density. This highlights the importance of pollinator size over the visit density in pollination efficacy of OSR crops.



Bee body size may influence pollination, since it affects the quantity of pollen load (Földesi et al., 2021; Goulson et al., 2002; Greenleaf et al., 2007). The amount and type of pollen bees deposit on flowers' stigma significantly impacts OSR crops yield. Excessive pollen load can reduce seed production per pod due to stigma obstruction (Thomson, 1989) while pollen from different individuals can increase the outcrossing of oilseed rape by pollinating with pollen from different plants enhancing ovules' fertilization rates (Artz & Nault, 2011; Sun et al., 2021).

Our data indicate that large bees do not deposit an excess pollen on flowers, given that they are positively related to the number of seeds per pod and the percentage of oil in seeds. These effects are likely due to enhanced cross-pollination caused by the foraging behaviour of the large bees (Brittain et al., 2014; Chang et al., 2023; Hudewenz et al., 2014; Perrot et al., 2024). Large bees are more effective pollinators due to their longer flight ranges, enabling them to visit various fields and flower types, thus transporting a greater diversity and quantity of pollen (Bartomeus et al., 2018). Their stronger buzz also allows them to deposit more pollen per visit, enhancing the chances of cross-pollination (De Luca et al., 2019; Greenleaf et al., 2007).

Our results also indicate that small bees do not significantly affect production parameters. They are specialized pollen and nectar collectors with shorter flight ranges, tending to visit flowers within the same inflorescence (Chang et al., 2023; Tschamntke et al., 2005). Small bees often gather and carry less pollen from just a few flowers and do not transfer much pollen between plants, suggesting they might be ineffective pollinators (Koski et al., 2018). This behaviour reduces cross-pollination as they consistently transfer pollen of the same plant while minimizing pollen transfer of different individuals. This is supported by other research that larger bee species have higher rates of stigma contact and deposit more pollen grains than smaller bees, which benefits OSR yields (Chang et al., 2023; Willmer & Finlayson, 2014). Their superior thermoregulation allows them to forage earlier in the day, often leaving little pollen available for smaller bees (Christopher et al., 2021). Consequently, small bees may have minimal impact on plant reproduction in areas where large bee are abundant. However, in areas with few large bees, these smaller bees might still provide valuable pollination services (Mitchell et al., 2024).

These findings highlight the importance of considering both bee density and size-class in crop pollination and promotion landscape heterogeneity. Our research agrees with recent data indicating that landscape heterogeneity even improves pollen transport of agricultural species by bees, one of the possible explanations for these improvements in OSR yield parameters (Marrero et al., 2024).

## 5. Conclusions

In conclusion, our research provides a complementary perspective on the relationship between landscape features and pollination services, emphasizing their importance in enhancing the productivity of oilseed rape fields. The mass flowering crops cover (MFC) from the previous year, along with its accumulation over the last three years, is important for sustaining wild bee populations and ensuring a higher proportion of large bees. Notably, high previous year MFC cover in the past, especially in landscapes with more semi-natural areas and smaller fields, has been shown to benefit the density of large bees, which in turn improves OSR crop quality by raising the oil content in seeds.

While large bees are vital for rapeseed production, in areas where they are less abundant, small bees can complement the pollination service. Although the effects of small bees on seed quality are not yet fully understood, further studies are necessary to clarify their role in the absence of large bees.

A balanced presence of both small and large bees can optimize seed production and promote genetic diversity through cross-pollination, ultimately contributing to more resilient and productive agricultural landscapes. Therefore, there is a need for agricultural strategies that consider the variability in bee size to optimize pollination in agroecosystems.

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## 7. Funding

This research was partially supported by projects obtained from FXS & JMBM: RTI2018-095597-B-I00 and PID2021-127575OB-I00 from the Spanish Ministry of Science and Innovation. PN was supported by Scholarship Program Doctorado en el Extranjero BECAS CHILE of the Agencia Nacional de Desarrollo e Investigación (ANID), Chile Folio 72210385. MM is grateful for a Beatriu de Pinós MSCA-COFUND postdoctoral grant (2018 BP-00106) received from the Government of Catalonia.

## 8. CRediT authorship contribution statement

P.Neira: Data curation, Formal analysis, Investigation, Validation, Visualization, Writing – original draft, and Writing – review & editing. J.Nabau: Formal analysis, Investigation, Methodology, and Writing. M.Morales: Methodology, new reagents/analytical tools, Supervision, and Writing – review & editing. L.Chamorro-lorenzo: Formal analysis and Writing – review and editing JM.Blanco-Moreno: Data curation, Methodology, Supervision, Validation, Visualisation, Writing – review and editing, Conceptualisation, and Funding acquisition. FXS: Conceptualisation, Funding acquisition, Investigation, Methodology, Project administration, Supervision, and Writing – review and editing.

## 9. Declaration of Competing Interest

The authors declare no competing financial interests or personal relationships that may have influenced the work reported in this study.

## 10. Declaration of generative AI in scientific writing

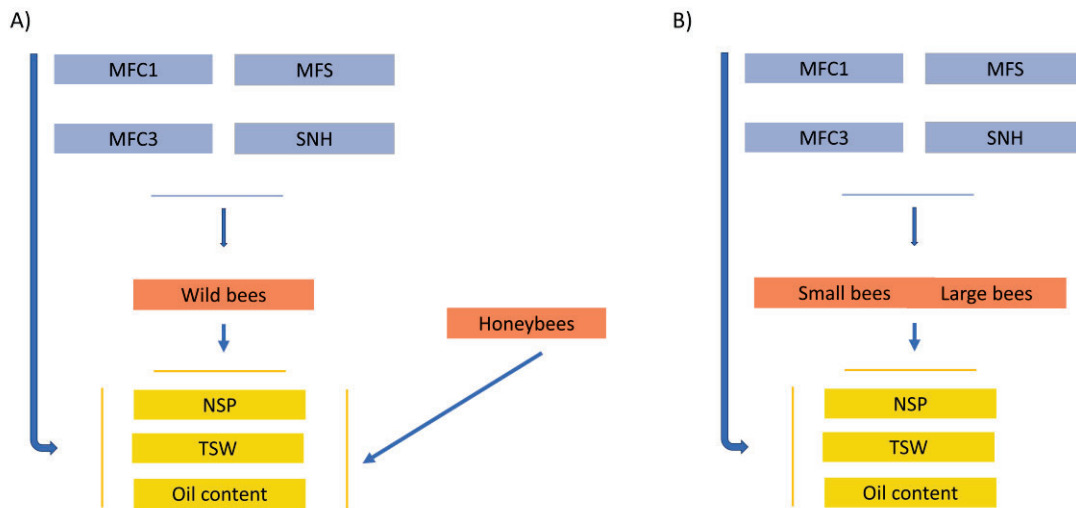
The authors used *ChatGPT* to improve readability and language usage during the writing of this paper. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

## 11. Data Availability

Data will be made available upon reasonable request.

## **12. Acknowledgements**

We thank the farmers for their cooperation and for access to their fields. We also thank the Biomolecular Analysis Unit from Scientific and Technological Centers (CCiTUB, Centres Científics i Tecnològics de la UB), Universitat de Barcelona.



**Figure S1.** General model to predict the effect of the agricultural landscape on A) Wild bees and Honeybee densities and B) size-class criteria and on OSR pollination effectiveness.

**Table S1.** Best fitting SEMs considering A) Wild bee and honeybee densities and B) separate size-classes, small and large bees (SB/LB).

| A) | Response    | Predictor | Estimate | Std.Error | DF | Crit.Value | P.Value | Std.Estimate |     |
|----|-------------|-----------|----------|-----------|----|------------|---------|--------------|-----|
|    | WB          | HB        | 0.1068   | 0.0235    | 72 | 4.5528     | 0.0000  | 0.4274       | *** |
|    | WB          | MFC1      | 4.2479   | 1.2711    | 72 | 3.3418     | 0.0008  | 0.4766       | *** |
|    | NSP         | WB        | 0.2805   | 0.0788    | 72 | 3.5575     | 0.0004  | 0.3192       | *** |
|    | NSP         | MFC1      | 4.4377   | 0.9857    | 72 | 4.5019     | 0.0000  | 0.5667       | *** |
|    | NSP         | MFC3      | -4.0876  | 1.4295    | 72 | -2.8595    | 0.0562  | -0.5620      |     |
|    | NSP         | MFS       | 3.8462   | 0.9738    | 72 | 3.9496     | 0.0001  | 0.5018       | *** |
|    | TSW         | NSP       | 0.0232   | 0.0105    | 72 | 2.2034     | 0.0276  | 0.2227       | *   |
|    | TSW         | SNH       | 0.3919   | 0.0853    | 72 | 4.5951     | 0.0000  | 0.4914       | *** |
|    | Oil Content | MFC1      | -1.4536  | 1.1064    | 72 | -1.3137    | 0.1889  | -0.2525      |     |
|    | Oil Content | NSP       | 0.1955   | 0.0982    | 72 | 1.9897     | 0.0466  | 0.2659       | *   |
|    | Oil Content | MFS       | -2.4937  | 1.0562    | 72 | -2.3611    | 0.0182  | -0.4427      | *   |
|    |             |           |          |           |    |            |         |              |     |
| B) | Response    | Predictor | Estimate | Std.Error | DF | Crit.Value | P.Value | Std.Estimate |     |
|    | SB          | MFC1      | 3.0906   | 0.8395    | 72 | 3.6815     | 0.0002  | 0.4797       | *** |
|    | LB          | MFC3      | 2.6855   | 1.1908    | 72 | 2.2553     | 0.0241  | 0.4786       | *   |
|    | LB          | MFS       | -2.5913  | 0.9566    | 72 | -2.7087    | 0.0068  | -0.4719      | **  |
|    | LB          | SNH       | 1.4812   | 1.1609    | 72 | 1.2758     | 0.2020  | 0.2640       |     |
|    | NSP         | SNH       | 2.4932   | 0.9169    | 72 | 2.7193     | 0.0065  | 0.3184       | **  |
|    | NSP         | MFS       | 3.4978   | 0.9906    | 72 | 3.5311     | 0.0004  | 0.4564       | *** |
|    | NSP         | MFC1      | 5.2255   | 1.1354    | 72 | 4.6024     | 0.0000  | 0.6673       | *** |
|    | NSP         | LB        | 0.3548   | 0.1412    | 72 | 2.5134     | 0.0120  | 0.2542       | *   |
|    | NSP         | SB        | 0.1832   | 0.1141    | 72 | 1.6051     | 0.1085  | 0.1507       |     |
|    | TSW         | NSP       | 0.0211   | 0.0104    | 72 | 2.0385     | 0.0415  | 0.2030       | *   |
|    | TSW         | SNH       | 0.4309   | 0.0935    | 72 | 4.6102     | 0.0000  | 0.5288       | *** |
|    | Oil Content | NSP       | 0.2594   | 0.0691    | 72 | 3.7541     | 0.0002  | 0.3530       | *** |
|    | Oil Content | MFS       | -1.2544  | 0.5449    | 72 | -2.3023    | 0.0213  | -0.2227      | *   |
|    | Oil Content | SB        | -0.2562  | 0.0820    | 72 | -3.1245    | 0.0018  | -0.2867      | **  |
|    | Oil Content | LB        | 0.3726   | 0.1016    | 72 | 3.6677     | 0.0002  | 0.3633       | *** |

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05



## DISCUSIÓN GENERAL

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Los estudios sobre la heterogeneidad espacial y temporal de los componentes del paisaje agrícola se han centrado en comprender los efectos sobre la densidad y la eficacia de la polinización como una herramienta fundamental para aumentar la biodiversidad y la funcionalidad de los agroecosistemas (Fahrig et al., 2011; Priyadarshana et al., 2024). No obstante, la magnitud del efecto del ensamblaje espacial y temporal de los elementos que conforman el paisaje agrícola varía en función del contexto biogeográfico (Wu, 2013). Debido a esta importancia del contexto resulta esencial examinar la manera en que la composición de la matriz agrícola y sus cambios temporales, junto con la configuración y composición de las áreas no cultivadas, afectan a los polinizadores y a la eficacia de la polinización. Para ello, en esta tesis se ha empleado la colza, un cultivo alógamo facultativo como un fitómetro en paisajes agrícolas dominados por cultivos herbáceos extensivos de Cataluña.

Un aspecto relevante de esta tesis doctoral es el análisis de la relación entre la diversidad de grupos funcionales de cultivos y la densidad de diferentes grupos de polinizadores. Los resultados muestran que la mayor diversidad de grupos de cultivos en el paisaje, tanto del año de muestreo como del año anterior, están asociadas con el aumento de la densidad de polinizadores. La diversidad de grupos de cultivos del año actual correlaciona positivamente con el número total de polinizadores, y con las densidades de abejorros y otras abejas silvestres, mientras que la diversidad de grupos de cultivos del año anterior tiene un efecto positivo y significativo sobre la abundancia de polinizadores totales y sobre las abejas silvestres. Además, los diferentes grupos de polinizadores respondieron de manera diferente a las otras características del paisaje como son el porcentaje de áreas seminaturales y el tamaño medio de campo. Las densidades de los diferentes grupos de abejas que visitan los campos de colza tienen un efecto sobre la eficacia de la polinización, estimada mediante parámetros relacionados con la producción y la calidad de las semillas de colza. El estudio refleja que la densidad total de abejas tiene un impacto significativo y positivo sobre la proporción de flores que se convierten en frutos y sobre la concentración de aceite en las semillas de colza. Además, se observó la labor complementaria entre las abejas silvestres y las abejas de la miel en el proceso de polinización, pero con diferentes grados eficacia sobre los distintos parámetros analizados en las semillas de colza.

Finalmente, la tesis también analiza la relación entre la cobertura de los cultivos de floración masiva y la densidad de abejas silvestres, diferenciando entre dos clases de tamaño, abejas pequeñas y las grandes. La cobertura de cultivos de floración masiva del año anterior está

positivamente asociada con una mayor densidad de abejas pequeñas, mientras que la cobertura acumulada de cultivos de floración masiva en los últimos tres años favorece a las abejas grandes. Además, el estudio pone de manifiesto que la cobertura de cultivos de floración masiva afecta la eficacia de la polinización de manera diferente según el tamaño de las abejas. La densidad de abejas grandes está asociada con un mayor peso de las semillas y una mayor concentración de aceite en las semillas, mientras que la densidad de abejas pequeñas está relacionada principalmente con el número de semillas por vaina.

En conjunto, esta tesis proporciona una visión integral de cómo la presencia de cultivos de floración masiva y la diversidad de grupos de cultivos del paisaje agrícola puede aumentar la eficacia de la polinización y, en consecuencia, mejorar la producción y calidad de las semillas de especies alógamas facultativas como es la colza. Este trabajo de investigación destaca la importancia de promover la diversidad temporal de cultivos, así como la presencia de cultivos de floración masiva, además de conservar las áreas seminaturales y promover los campos más pequeños para el mantenimiento de las poblaciones de polinizadores y mejorar la eficacia de la polinización. A continuación, exploraremos cómo estas características composicionales de la matriz agrícola, junto con las áreas seminaturales y la configuración medida a través del tamaño medio de los campos influyen en la eficacia de la polinización.

## **12.0 Importancia de la diversidad de grupos de cultivos y los cultivos de floración masiva para los polinizadores**

La diversidad de grupos de cultivos en el paisaje agrícola y su variación temporal tienen un impacto complejo en la densidad de polinizadores. En particular, la diversidad de grupos de cultivos del año anterior muestra una correlación positiva y significativa con las densidades de abejas silvestres. Nuestros resultados indican que esta diversidad pasada tiene un mayor impacto que la diversidad de grupos de cultivos actual (*Capítulos 1 y 2*). Este hallazgo subraya la importancia de la diversidad histórica de cultivos para las poblaciones de polinizadores.

Según estudios previos, la diversidad de cultivos contribuye a una mayor biodiversidad de polinizadores en el paisaje agrícola al favorecer la disponibilidad espacial y temporal de hábitat y recursos florales necesarios para el mantenimiento de las poblaciones de polinizadores (Holzschuh et al., 2011; Martin et al., 2019; Sirami et al., 2019). Nuestros resultados sugieren que las estrategias agrícolas que promuevan una mayor diversidad de grupos de cultivos, tanto en términos espaciales como temporales, beneficiarían a los polinizadores presentes, pero es importante enfatizar la importancia de la diversidad pasada en lugar de la actual. Esta

perspectiva sugiere que los efectos de las prácticas agrícolas no solo se manifiestan en el presente, sino que también tienen repercusiones sobre la densidad de polinizadores en el futuro. Además, las investigaciones en otras regiones geográficas respaldan que una mayor diversidad de cultivos incrementa la abundancia de abejas silvestres al proveerles de hábitats y recursos que favorecen la persistencia temporal de sus poblaciones (Aguilera et al., 2020; Cavigliasso et al., 2022).

En este contexto, la planificación agrícola debe considerar tanto la diversidad de grupos de cultivos coetánea como la continuidad temporal de esta para optimizar la densidad de polinizadores. Una forma efectiva de diversificar los paisajes cerealistas es mediante la integración de cultivos de floración masiva, que a su vez tienen efectos temporales positivos sobre la densidad de abejas (Beyer et al., 2021). Nuestros resultados destacan que la cobertura de los cultivos de floración masiva también juega un rol importante para entender el aumento de la densidad de abejas silvestres que visitan la colza. Este efecto, de la misma manera que el observado para la diversidad de grupos de cultivos, es temporal y resalta la importancia de la historia del paisaje agrícola sobre los polinizadores (*Capítulo 3*).

El análisis de los patrones de densidad de las abejas en función de su tamaño en relación con la cobertura de los cultivos de floración masiva refleja diferencias entre las abejas grandes y las pequeñas. Tanto la cobertura en el pasado inmediato como la pasada acumulada tuvieron efectos significativos, aunque sobre distintos grupos de abejas, lo que demuestra la importancia de la temporalidad de los cultivos de floración masiva en la provisión de recursos para los polinizadores en el paisaje agrícola. La cobertura acumulada de cultivos de floración masiva durante los tres años consecutivos anteriores correlaciona más fuertemente con las abejas grandes, mientras que cobertura de los cultivos de floración masiva del año anterior lo hace fundamentalmente con las abejas pequeñas. Las abejas pequeñas dependen en gran medida de las condiciones del año anterior debido a que tienden a forrajear en áreas más limitadas (Van Reeth et al., 2018), mientras que las abejas más grandes, con su mayor movilidad, son más independientes de la cercanía del recurso y pueden aprovechar de manera más efectiva los recursos del paisaje, incluso cuando estos recursos cambian de lugar de un año a otro debido a la rotación de cultivos (Greenleaf et al., 2007). En los paisajes estudiados, la colza está incluida en los esquemas de rotación de cultivos, principalmente con cereales. Esta rotación en la ubicación de los cultivos podría afectar a las poblaciones de las abejas pequeñas debido a su rango limitado de explotación de recursos espaciales. Las poblaciones locales se benefician cuando los cultivos están cerca. Por el contrario, para las abejas más grandes, que podrían



utilizar estos cultivos incluso si cambian de ubicación anualmente, es más importante la cobertura de los cultivos de floración masiva acumulada durante los últimos tres años en el paisaje.

Estos resultados invitan a reflexionar sobre las estrategias más efectivas para el beneficio de los polinizadores y proporcionan un punto de partida valioso para futuras investigaciones. Desde el punto de vista de la planificación de los servicios ecosistémicos en paisajes agrícolas, la información obtenida durante el desarrollo de la tesis sugiere que la diversificación espacial y temporal de los cultivos y la promoción de los cultivos de floración masiva son estrategias necesarias para mejorar la polinización en paisajes agrícolas mediterráneos de secano.

### **12.1 Efectos de las áreas seminaturales y del tamaño de los campos sobre los polinizadores**

Las áreas seminaturales, como pastizales, tierras abandonadas, márgenes de caminos y bosques, y el tamaño medio del campo juegan un papel fundamental en la conservación de los polinizadores (Clough et al., 2020; Raderschall et al., 2021). Estas zonas, que han sido moderadamente perturbadas por la actividad humana, ofrecen hábitats esenciales para diversas especies de abejas, permitiéndoles prosperar y desempeñar su rol como polinizadores (Michener, 2007). Las áreas seminaturales y la densidad de márgenes proporcionan una variedad de recursos florales y refugios necesarios para la supervivencia de los polinizadores. Este apartado de la tesis explora cómo estas características del paisaje influyen en la densidad de los diferentes grupos de polinizadores, destacando su importancia para la polinización de los sistemas agrícolas.

Los hallazgos de esta tesis revelan que tanto la proporción de áreas seminaturales como el tamaño medio de los campos agrícolas influyen de manera diferente en la abundancia de los polinizadores, dependiendo del grupo al que pertenezcan. En general, la abundancia total de polinizadores fue mayor en los bordes de los campos, lo que resalta la importancia de los márgenes y de las áreas seminaturales adyacentes como hábitats para la nidificación, para el establecimiento de colonias, o como corredores (Bartholomée et al., 2020; Coutinho et al., 2021; Hass, Kormann, Tschardtke, Clough, Baillod, Sirami, Fahrig, Martin, Baudry, Bertrand, Bosch, Brotons, Bure, et al., 2018).

Sin embargo, al analizar cada grupo de polinizadores por separado, surgen patrones específicos. Los sírfidos, por ejemplo, parecen depender principalmente de características locales, como

indicaría las diferencias en densidad en función de la ubicación dentro del campo. Su densidad es mayor en los bordes del cultivo y no parece estar influenciada por la proporción de áreas seminaturales ni por el tamaño medio de los campos en el paisaje (*Capítulo 1*). Esta relación con los márgenes de los campos puede explicarse por la disponibilidad de recursos florales y hábitats de esas zonas adyacentes a los campos que se adecuan al limitado rango de forrajeo de los sírfidos (Schirmel et al., 2018; Sutherland et al., 2001).

En contraste, los abejorros sí se beneficiaron de una mayor proporción de áreas seminaturales en el paisaje (*Capítulo 1*). Este grupo, que tiene un rango de vuelo más amplio y depende de la disponibilidad prolongada de recursos, muestra una fuerte relación positiva con estos hábitats, que, según algunos autores, les proporcionan recursos alimenticios continuos y espacios adecuados para formar colonias (Hopfenmüller et al., 2014; Proesmans et al., 2019). Esta preferencia por ambientes diversos y ricos en recursos también ha sido observada en otros estudios (Goulson et al., 2008; Kells & Goulson, 2003).

Por otro lado, otras abejas silvestres mostraron patrones distintos. En paisajes con mayor proporción de áreas seminaturales, su densidad fue menor (*Capítulo 1*). Además, la densidad total de abejas silvestres y la abundancia de abejas grandes no mostraron una relación significativa con estos hábitats (*Capítulos 2 y 3*). Morrison et al. (2017) encontraron patrones similares en paisajes agrícolas mediterráneos dominados por cereales. Otros estudios llevados a cabo en otras regiones que sugieren que las áreas seminaturales no son tan favorables para algunas abejas como lo son los márgenes de los campos o los hábitats herbáceos cercanos (Martin et al., 2019; Rollin et al., 2013a), lo que podría explicar este patrón.

La configuración del paisaje agrícola, especialmente el tamaño de los campos tiene un impacto significativo en la visita de los polinizadores en los campos de colza. Los paisajes con campos más pequeños están asociados con una mayor densidad de abejas silvestres y abejas silvestres totales (*Capítulos 1 y 2*). También evaluamos cómo estas características del paisaje agrícola afectaron la densidad de las abejas según su tamaño y encontramos que, en paisajes agrícolas con tamaños de campo más pequeños, la proporción de abejas grandes también era mayor (*Capítulo 3*).

Aunque no hemos evaluado la disponibilidad de recursos en los márgenes, otros estudios sugieren que los márgenes, a pesar de su extensión, proporcionan recursos necesarios para la anidación y alimentación (Hass, Kormann, Tschardtke, Clough, Baillod, Sirami, Fahrig, Martin, Baudry, Bertrand, Bosch, Brotons, Bure, et al., 2018; Martin et al., 2019). Además, los

campos pequeños con más márgenes facilitan la conectividad del paisaje, lo que podría promover el movimiento de los polinizadores y contribuir a la estabilidad y diversidad de las abejas (Gardner et al., 2021; Happe et al., 2018). En la misma línea, Mendoza-García et al. (2018) sugieren que los márgenes ricos en recursos pueden favorecer la presencia y densidad de actividad de las abejas en paisajes mediterráneos. Según Clough et al. (2020), los paisajes agrícolas con campos más pequeños ofrecen una mayor densidad de márgenes, lo que junto con una mayor disponibilidad de recursos beneficiaría directamente a las abejas silvestres. En conjunto, los resultados de esta tesis destacan la compleja relación entre las áreas seminaturales, la configuración del paisaje agrícola y los polinizadores.

## 12.2 Eficacia de la polinización por abejas.

El estudio realizado en esta tesis ha revelado el papel fundamental de la eficacia de la polinización por abejas silvestres (*Capítulo 2*) y las densidades según las clases de tamaños (*Capítulo 3*) en los cultivos alógamos facultativos como la colza, a través de un experimento de exclusión de polinizadores, como también los efectos de las abejas de la miel (*Capítulo 2*). Estos resultados demuestran que, a pesar de que la colza es un cultivo que no depende estrictamente de la interacción con insectos para su polinización, la ausencia de polinizadores tiene un fuerte impacto negativo sobre los parámetros productivos.

La exclusión de los polinizadores resultó en una reducción significativa del número de frutos por flor, del número de semillas por vaina, del peso de mil semillas y del contenido de aceite en las semillas. Estos resultados subrayan la importancia de la eficacia de polinización, ya que no solo aumenta la proporción de flores que producen frutos en la colza, sino que también mejora parámetros clave de rendimiento. En particular, la contribución de los polinizadores al contenido de aceite en las semillas fue notable: un 10% más que en las inflorescencias embolsadas, superando el aumento del 2,4% observado en otros estudios realizados en otras regiones (Bartomeus et al., 2014; Bommarco et al., 2012; Jauker et al., 2012; Perrot et al., 2018, 2024). Esto resalta la función esencial de los polinizadores en la producción de colza y cómo su ausencia impacta negativamente en la polinización y el rendimiento del cultivo.

Buena parte de estos efectos cabe atribuirlos a las abejas silvestres. Nuestros resultados revelan que las abejas silvestres tienen efectos positivos sobre la eficacia de la polinización de la colza. La densidad total de abejas se correlaciona con el aumento en la proporción de flores que producen fruto y con el contenido de aceite en las semillas. Sin embargo, nuestros resultados

sugieren que el grado de eficacia de los polinizadores no es uniforme entre los diferentes grupos (*Capítulos 2 y 3*).

Los análisis de la relación entre la densidad de las abejas y la calidad de las semillas de colza reflejan efectos distintos para cada grupo de abejas (*Capítulo 2*). Las abejas silvestres se asocian al aumento de  $\gamma$ -tocoferol en semillas, mientras que la abundancia de abejas de la miel se asocia con una disminución significativa del contenido de clorofila de las semillas. Una mayor concentración de  $\gamma$ -tocoferol en las semillas de las flores polinizadas por las abejas silvestres está relacionada con una etapa de maduración más adelantada de las semillas (Munnè-Bosch & Falk, 2004). Las abejas silvestres son más efectivas que las abejas de la miel, ya que tienen mayor contacto con el estigma de la flor (Chang et al., 2023), lo que adelantaría los procesos de maduración. Sin embargo, las densidades de las abejas de la miel se relaciona significativamente con un menor contenido de clorofila lo que aumenta el valor de mercado del aceite resultante (Bommarco et al., 2012). Aunque las abejas melíferas no son tan eficientes en la polinización, su abundancia puede compensar los déficits de polinizadores silvestres, ayudando a mantener la producción. (Woodcock et al., 2013).

Estas relaciones entre las abejas y su efecto en la calidad de las semillas de colza resultan un beneficio para los agricultores, quienes obtendrían cosechas más maduras y con un mayor valor comercial. Por lo que este resultado destaca la importancia de no solo contar con una alta densidad de polinizadores, sino también con una combinación adecuada de tipos de polinizadores para maximizar los beneficios para el cultivo (Bartomeus et al., 2018).

En esta tesis se explora cómo el tamaño corporal de las abejas silvestres influye en la eficacia de la polinización. Nuestros resultados muestran que el tamaño de las abejas tiene un impacto significativo en los parámetros de la eficacia de la polinización (*Capítulo 3*). En particular, las abejas de mayor tamaño transportan una mayor cantidad de polen por visita (Chang et al., 2023) y, gracias a su mayor rango de vuelo, favorecería la polinización cruzada y la mejora de aspectos productivos de la colza, como el número de semillas por vaina y el contenido de aceite (Hudewenz et al., 2014). En contraste, las abejas pequeñas, que tienden a visitar flores dentro de la misma inflorescencia y por tanto tenderían a transportar menos polen entre plantas (Koski et al., 2018), tienen, en general, un menor impacto en la producción y en la calidad de las semillas (Tscharntke et al., 2005).

Estos resultados sugieren que el tamaño de las abejas es un factor crucial que afecta la eficacia de la polinización y, por ende, la cantidad y calidad de la producción de colza. Las abejas

grandes no solo son más eficaces en la transferencia de polen, sino que su mayor movilidad y capacidad de zumbido contribuyen a una mayor diversidad y cantidad de polen depositado (De Luca et al., 2019; Greenleaf et al., 2007), y en consecuencia mejoran la eficacia de polinización de este cultivo alógamo facultativo.

En resumen, los resultados de los Capítulos 2 y 3 destacan la importancia de los polinizadores en la mejora de la eficacia de la polinización en cultivos alógamos facultativos como la colza. La densidad de abejas junto con su tipo y tamaño influye de manera significativa en la producción y calidad de las semillas. Las abejas silvestres grandes, en particular, contribuyen de manera más efectiva a la polinización cruzada, lo que aumenta la cantidad de semillas y su contenido de aceite.

### **12.3 La eficacia de la polinización se ve afectada por las características del paisaje agrícola**

Una de las áreas más novedosas que se exploran en esta tesis es la relación que existe entre las características del paisaje y la eficacia de la polinización evaluada mediante distintos parámetros productivos de la colza. Recientemente, algunas publicaciones han señalado que las características del paisaje agrícola, como la diversidad de cultivos, las áreas seminaturales y el tamaño de los campos, tienen un efecto significativo en los procesos bioquímicos de las plantas, en la polinización y en la producción agrícola (Pioltelli et al., 2024; Raderschall et al., 2021).

#### **12.3.1 Efectos de la matriz agrícola sobre la eficacia de la polinización**

Nuestro estudio confirma que las características del paisaje agrícola afectan la eficacia de la polinización de los cultivos de colza. Los resultados revelan que la diversidad de grupos de cultivos del año anterior tiene una correlación positiva con la eficacia de la polinización y mejora la calidad de las semillas, como lo indican el aumento en el número de semillas por vaina y el contenido de aceite de las semillas (*Capítulo 2*). La diversidad de grupos de cultivos también está asociada con un aumento en el contenido de  $\gamma$ -tocoferol y una reducción en los pigmentos de las semillas, mejorando su calidad.

El efecto positivo de paisajes con mayor diversidad de grupos de cultivos sobre la producción ha sido señalado recientemente para diversos cultivos. Así, Magrach et al. (2023) realizaron un estudio, que incluyó todas las provincias de España, donde indican que la diversidad de cultivos incrementa la producción de cultivos que se benefician de los polinizadores. Aunque el estudio



no encuentra relación entre la diversidad de cultivos y la mejora de los parámetros productivos mediado por la actividad de las abejas, sí confirmó que la diversidad de cultivos crea un entorno más favorable para la producción. Estos efectos de la diversidad de cultivos a escala paisaje sobre el rendimiento o sobre procesos bioquímicos de plantas han despertado un gran interés durante los últimos años (Raderschall et al., 2021; Redlich et al., 2021; Zymarioieva et al., 2021).

La presencia de los cultivos de floración masiva en años anteriores en la matriz agrícola mostró efectos positivos sobre la eficacia de la polinización en la colza. Específicamente, la cobertura de los cultivos de floración masiva del año anterior influyó de manera positiva en el número de semillas por vaina. Aunque la cobertura acumulada en los últimos tres años no tuvo un efecto directo en los parámetros de producción y de calidad de las semillas evaluados, fue necesario incluirla en el modelo para obtener un mejor ajuste, y refleja la importancia de los años anteriores en la historia del paisaje agrícola (*Capítulo 3*). En un estudio reciente, Beyer et al. (2021) también encontraron una relación positiva entre las coberturas de los cultivos de floración masiva y el peso de mil semillas, así como un aumento en la densidad de las abejas. Aunque este efecto no se pudo explicar completamente, estas características del paisaje parecen ser un buen indicador de los servicios de polinización. Por lo tanto, mantener una disponibilidad constante y abundante de recursos florales mediante de la inclusión de los cultivos de floración masiva podría contribuir a la salud de las comunidades de polinizadores. Si bien es conocido el papel que tiene la incorporación medidas a escala local como las bandas florales y los setos para favorecer la fauna útil como son los polinizadores Blaauw y Isaacs (2014) nuestros resultados evidencian que los cultivos de floración masiva también pueden beneficiar a los polinizadores a escala de paisaje.

### **12.3.2 Efectos de las áreas seminaturales y el tamaño medio de campo sobre la eficacia de la polinización**

El análisis de los efectos de la composición del paisaje agrícola sobre la polinización refleja que las áreas seminaturales benefician la producción de semillas de colza al mejorar parámetros como el peso de las semillas y el número de semillas por vaina (*Capítulos 2 y 3*). Sin embargo, también se observó una disminución en la proporción de flores que forman vainas.

Los efectos positivos de la proximidad de las áreas seminaturales sobre la producción agrícola han sido reportados por diversos autores (Mazzei et al., 2021a; Raderschall et al., 2021). El estudio de Raderschall et al. (2021), centrado en un cultivo de floración masiva diferente, reportó

un efecto positivo de estas características del paisaje sobre los parámetros productivos. Sin embargo, estos autores tampoco encontraron que la relación entre el aumento de la productividad y las áreas seminaturales fuera debida a un aumento de las poblaciones abejas (*Capítulo 3*). Este patrón plantea la reflexión acerca si aspectos como el aumento de las interacciones bióticas como el control biológico y la polinización, la calidad de los suelos e incluso la regulación microclimática, que no han sido considerados en nuestro estudio, podrían tener un impacto directo en la producción (Holland et al., 2016; Papanikolaou et al., 2017).

Nuestros resultados indican que la proporción de zonas seminaturales en el paisaje también tienen un efecto significativo en la calidad de las semillas de colza, que se manifiesta por la reducción del contenido de tocoferoles totales y carotenoides, compuestos importantes que juegan un papel clave en la protección de las células vegetales contra el daño oxidativo especialmente bajo condiciones de estrés ambiental como las altas temperaturas (*Capítulo 2*) (Huang et al., 2019; Muñoz & Munnè-Bosch, 2019). La alta proporción de hábitats seminaturales en el paisaje agrícola podría estar correlacionado con una mayor capacidad de amortiguar la temperatura ambiental, y en consecuencia favorecer un ambiente más propicio para el desarrollo de los cultivos de colza y disminuir a su vez la síntesis de compuestos protectores. Aunque estos hallazgos indican una posible relación entre la presencia de áreas seminaturales y el rendimiento agrícola, es fundamental llevar a cabo investigaciones adicionales para determinar su efecto real y si su integración en los cultivos puede conducir a mejoras consistentes en los rendimientos. Además, estos resultados sugieren que los agricultores podrían incrementar su productividad al incorporar un mayor número de áreas seminaturales en sus prácticas agrícolas.

La configuración de los paisajes agrícolas con tamaños de campo más pequeños se correlaciona con una mejor calidad de las semillas y un mayor número de semillas por vaina, lo que está relacionado con una mayor eficacia en la polinización (*Capítulos 2 y 3*). Halinski et al (2020) resaltan que los campos de colza situados a más de 300 m de algún fragmento de área seminatural estaban mal polinizados, por lo que campos pequeños pueden verse más beneficiados de los servicios de polinización provenientes de las áreas seminaturales adyacentes. Sin embargo, el tamaño del campo agrícola influye directamente en el modelo de producción agrícola. Las grandes explotaciones tienden promover campos grandes con la finalidad de facilitar su mecanización y a aumentar la eficiencia en términos de costos, mientras que las pequeñas pueden ser más sostenibles. Diversos estudios destacan la importancia de esta variable de configuración del paisaje agrícola. (Fahrig et al., 2015; Hass, Kormann, Tschardtke,

Clough, Baillod, Sirami, Fahrig, Martin, Baudry, Bertrand, Bosch, Brotons, Bure, et al., 2018; Magrach et al., 2023; McDougall et al., 2019). Esta variable del paisaje puede tener mayor importancia que la diversidad de cultivo: Hass et al. (2018) señalan que la eficacia de la polinización está más relacionada con el tamaño de los campos que con otras características del paisaje agrícola como la diversidad de cultivos. No obstante, la dificultad de modificar el tamaño de los campos, debido a las dimensiones económicas y sociales que implica como son, entre otras, la gestión y coordinación colectiva, hace más compleja la actuación a través de ella (Pelosi et al., 2010).



## CONCLUSIONES

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La presente tesis doctoral ha tenido como objetivo evaluar la eficacia del servicio de polinización, tomando como planta diana la colza, una planta alógama facultativa común en los paisajes dominados por cultivos herbáceos extensivos de secano en la región mediterránea. Metodológicamente, este estudio se ha centrado en analizar cómo la composición y configuración del paisaje agrícola de 22 localidades de Cataluña central influyen en la densidad de polinizadores silvestres y en la eficacia de la polinización, a través, de la diversidad de grupos de cultivos, la cobertura de cultivos de floración masiva, la presencia de áreas seminaturales y el tamaño de campo. Esta influencia, directa o indirecta, en la polinización se refleja en la producción del cultivo de colza desde una perspectiva tanto cuantitativa como de calidad.

Las principales conclusiones de esta tesis son las siguientes:

- La diversidad de grupos de cultivos del año anterior en paisajes agrícolas incrementa la densidad de polinizadores silvestres y mejora tanto la cantidad como la calidad de la producción, indicando una mayor eficacia de la polinización. Por tanto, el incremento de la diversidad de grupos cultivos en el paisaje agrícola podría ser una estrategia viable para beneficiar las poblaciones de polinizadores y los servicios ecosistémicos que ofrecen los paisajes agrícolas.
- Los cultivos de floración masiva son esenciales para sostener tanto las poblaciones de abejas grandes como de abejas pequeñas. Mientras que las abejas grandes, con su mayor capacidad de movimiento, mejoran de forma notable la eficacia de la polinización, las abejas pequeñas también contribuyen al proceso, aunque en menor medida. Es crucial tener en cuenta esta variabilidad en el tamaño de las abejas al diseñar estrategias agrícolas que busquen maximizar los beneficios del servicio de polinización.
- Los campos de menor tamaño, al estar asociados con una mayor cantidad de márgenes y una mejor conectividad del paisaje, resultan en un aumento de la eficacia de la polinización, a través de mayores densidades de abejas silvestres y abejas grandes.
- La presencia de hábitats seminaturales mejora los parámetros de producción del cultivo de colza. Por tanto, su conservación debe ser un componente clave en la gestión de los paisajes agrícolas.

- Las abejas silvestres, y especialmente las grandes, son esenciales para la mejora de la eficacia de la polinización en cultivos alóamos facultativos. Las estrategias de manejo agrícola deben priorizar la conservación de estos grupos funcionales de abejas, dada su importancia en los paisajes agrícolas dominados por los cultivos herbáceos extensivos de secano de la Cataluña Central.
- La integración de medidas como el manejo adecuado de la diversidad de grupos de cultivos, la incorporación de cultivos de floración masiva, la optimización del tamaño de los campos y la conservación de áreas seminaturales favorecerá tanto la biodiversidad como la producción agrícola. Desde una perspectiva aplicada, aumentar la diversidad de grupos de cultivos e incluir los cultivos de floración masiva en las rotaciones resultan opciones más manejables y con impactos a corto plazo en la eficacia de la polinización, en comparación con cambios en el tamaño de los campos y en la abundancia de las áreas seminaturales. La integración de estas medidas en la planificación territorial contribuirá a mejorar tanto la sostenibilidad de los sistemas agrícolas mediterráneos como la rentabilidad y resiliencia de los cultivos, equilibrando la productividad y la conservación de los polinizadores.

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