Contribution des pollinisateurs dans la production de colza et de tournesol en zone atelier “ Plaine et Val de Sèvre ”

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Titre : Contribution des pollinisateurs dans la production de colza et de tournesol en zone atelier « Plaine et Val de Sèvre »titre (en français)

Mots clés : Pollinisation, abeilles sauvages, abeilles domestiques, syrphe, agroécologie, intensification écologiques

Résumé : La pollinisation entomophile est essentielle pour la production de 70% des cultures à travers le monde. Cependant la contribution des pollinisateurs dans la production agricole reste peu renseignée ainsi que les insectes impliqués. De plus, lorsque la contribution des pollinisateurs est quantifiée, le bénéfice est calculé à des échelles biologiques ou dans des conditions simplifiées qui peuvent être non représentatives des bénéfices à l'échelle de la parcelle. Par ailleurs, les possibles interactions entre les pollinisateurs et les pratiques agricoles ne sont généralement pas prises en compte. L'objectif général de cette thèse est donc de quantifier la contribution des pollinisateurs directement dans les parcelles agricoles dans deux cultures fréquemment retrouvées en Europe, le colza et le tournesol. Ces estimations sont réalisées à l'échelle de la parcelle ainsi qu'à l'échelle de la plante pour comprendre les mécanismes qui permettent l'augmentation de la production agricole. Ces études nous ont permis aussi d'identifier les principaux pollinisateurs de ces deux cultures.

Dans un premier temps, nous avons quantifié le bénéfice des pollinisateurs dans les rendements de tournesol et de colza. Nous montrons que le colza et le tournesol partagent une même guilde de pollinisateurs, les abeilles domestiques. Les abeilles sauvages sont aussi d'importants pollinisateurs pour le colza. Les pollinisateurs augmentent les rendements de colza de plus de 35% et ceux du tournesol de 40%, à l'échelle de la parcelle. A l'échelle de la plante, que ce soit pour le colza ou le tournesol, les pollinisateurs augmentent le succès de pollinisation et donc le nombre de graines par plante. Dans un deuxième temps, nous avons comparé le bénéfice des pollinisateurs par rapport à ceux des pratiques agricoles en termes de rendement et de gain monétaires dans les parcelles de colza, tout en regardant plus précisément leurs possibles interactions. Nous montrons que le bénéfice des pollinisateurs dans les rendements s'additionne à celui des pratiques agricoles excepté avec les insecticides qui réduisent la contribution des pollinisateurs. De plus, nous montrons que les pollinisateurs sont d'importants contributeurs du rendement et des revenus agricoles en augmentant le bénéfice des agriculteurs de 250 € par hectare alors qu'au contraire plusieurs pratiques peuvent être très coûteuses pour ces mêmes agriculteurs. Finalement, nous étudions l'effet des pollinisateurs sur la qualité lipidique des graines de colza qui est une autre facette de la production agricole. Nous montrons que les abeilles domestiques améliorent la qualité des graines en augmentant le pourcentage d'acides gras insaturés tout en réduisant les acides gras trans- et saturés. Pour certaines années, les abeilles domestiques augmentent aussi le pourcentage de lipide par graine.

En conclusion, nous montrons que les pollinisateurs sont essentiels à la production agricole à la fois sur le rendement, les revenus agricoles et sur la qualité. Plusieurs mesures doivent être mises en place pour promouvoir les pollinisateurs dans les milieux agricoles dans le but de les préserver et d'assurer une production agricole durable pour ces deux cultures.

Title : Contribution of pollinators to oilseed rape and sunflower production in the zone atelier « Plaine et Val de Sèvre »

Keywords : pollination, wild bee, honeybee, hoverfly, agrocecology, ecological intensification

Abstract: Insect pollination is essential for over 70% of crops around the world. However, the contribution of pollinators to crop production and the insects involved in crop pollination have rarely been studied. Moreover, assessments of pollinator contributions have mostly been conducted on a small scale or under simplified conditions, which do not represent the real contributions at the field scale and do not take into account possible interactions between pollinators and farming practices. The aim of this study is to quantify directly under field conditions, the contribution of pollinators in two crops frequently cultivated in Europe: oilseed rape and sunflower. Estimations are realized both at the plant and at the field scale to understand mechanisms that increase crop production. Our studies identify also these crops' pollinators.

In a first step, we quantified the contributions of pollinators to oilseed rape and sunflower yield. Oilseed rape and sunflower share a pollinator guild - the honeybee. Wild bees also increase oilseed rape yield. Pollinators increase the yield of oilseed rape by up to 35% and of sunflower by up to 40%. At the plant scale, pollinators increase pollination success and consequently the number of seeds per plant.

In a second step, we compared for oilseed rape the yield and the monetary contributions of pollinators and farming practices by taking their potential interactions more accurately into account. We show that the benefits of pollinators and farming practices on yield were additive except for insecticide use, which decreased the contribution of pollinators. In addition, we show that pollinators were important contributors to the farmers' incomes by increasing gain by 250 € per hectare while some practices were very expensive for farmers.

Finally, the effect of pollinators was studied on oilseed rape seed quality - another component of crop production. We show that honeybees improve seed quality by increasing the percentage of unsaturated fatty acids in seeds and decreasing trans-saturated and saturated fatty acids. In some years, honeybees increased also the percentage of lipids per seed.

We conclude, pollinators are essential for crop production by increasing both yield, monetary gain and quality. Several measures must be taken to promote pollinators in agricultural land in order to conserve them and ensure sustainable crop production for these two crops.

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Introduction

A. L'importance des services écosystémiques pour la production agricole :

1. L'évolution de l'agriculture moderne et son impact sur l'environnement :

Les écosystèmes agricoles ou agroécosystèmes fournissent de nombreuses ressources nécessaires au maintien et au développement des populations humaines, comme par exemple une partie de la nourriture consommée, du carburant, des fibres pour l'industrie du textile, … (Zhang et al., 2007). Les populations humaines ont pu se développer grâce à l'agriculture et la domestication de nombreuses espèces végétales et animales créant une ressource stable de nourriture dans le temps (Thrall et al., 2010). Ce développement va être très important après la seconde guerre mondiale à une période où la population humaine passe de 2.5 milliards à 7 milliards d'habitants (octobre 2011, Gerland et al., 2014). Cette explosion de la population humaine a pu se produire grâce à la modernisation des pratiques agricoles. La mécanisation du matériel agricole, l'utilisation massive de produits chimiques tels que les fertilisants ou les pesticides (Pretty, 2008; Tilman et al., 2001) ainsi que l'amélioration variétale ont permis d'augmenter la production agricole, soit en augmentant la productivité des cultures pour une même surface (c.-à-d. le rendement, Brisson et al., 2010; Grassini et al., 2013; Ray et al., 2012), soit en augmentant la proportion de surfaces terrestres utilisées pour l'agriculture (cultures ou prairies utilisées pour l'élevage). Cette augmentation des surfaces agricoles a eu lieu principalement dans les pays en voie de développement (Pretty, 2008).

Ce mode d'agriculture arrive à une limite depuis les années 2000, avec une stagnation des rendements voire une diminution pour de nombreuses cultures dans différentes régions du monde (Fig. 1. Brisson *et al.* 2010; Ray *et al.* 2012; Grassini, Eskridge & Cassman 2013). De plus, cette modernisation de l'agriculture a d'importantes externalités négatives sur l'environnement terrestre et marin. L'utilisation abondante de fertilisants et l'augmentation du nombre d'animaux d'élevage ont considérablement augmenté la production de gaz à effet de serre (Clark and Tilman, 2017; Matson et al., 1997; Stoate et al., 2001). Cette utilisation importante de produits chimiques a contaminé les surfaces d'eau potable (Carpenter and et al, 1998) et même les populations humaines via l'utilisation de pesticides (Nicolopoulou-Stamati et al., 2016). L'utilisation du labour (travail du sol profond avec retournement de la terre) a aussi fortement réduit la fertilité des terres (Matson et al., 1997; Stoate et al., 2001). L'intensification de l'agriculture a également considérablement impacté la biodiversité animale et végétale (Geiger et al., 2010) et est considérée comme la deuxième cause de déclin de la biodiversité dans le monde (Maxwell et al., 2016). L'augmentation des surfaces

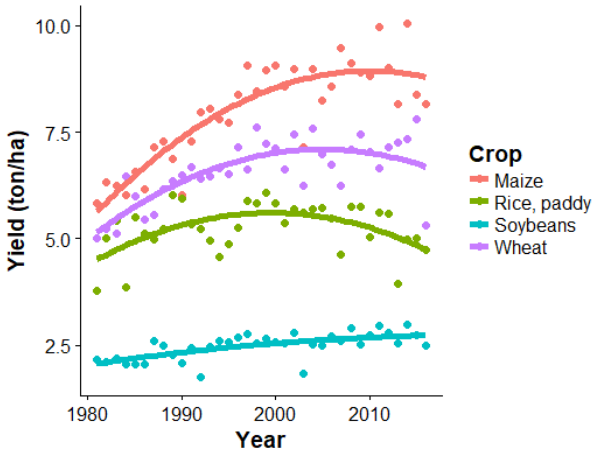

Fig 1. Evolution des rendements pour 4 cultures importantes (Mais, Soja, Blé, Riz) en France depuis 1980 (les données proviennent de FAOSTAT 2014)

agricoles s'est faite au détriment des espaces naturels, espaces de ressources et de niches pour la majorité des espèces animales ou végétales (Meyer and Ii, 1992; Robinson and Sutherland, 2002). L'effet nocif des pesticides a été démontré sur plusieurs taxons d'invertébrés (Beketov et al., 2013) et de vertébrés (Gibbons et al., 2015). Le déclin de la biodiversité a de nombreuses répercussions négatives sur le fonctionnement des écosystèmes, qu'ils soient naturels ou anthropisés comme les agrosystèmes, et, par conséquence sur les ressources que peuvent en retirer les humains. En effet, la biodiversité animale ou végétale est à la base de nombreuses fonctions écologiques telles que la fertilité des sols ou la régulation du climat (Altieri, 1999; Balvanera et al., 2006; Cardinale et al., 2012; Chapin et al., 2000; Foley et al., 2005; Oliver et al., 2015; Soliveres et al., 2016).

De par ces répercussions négatives sur l'environnement pouvant amener à la réduction de la productivité des agroécosystèmes (Foley et al., 2005) et sa dépendance à des ressources limitées comme le phosphore (Cordell et al., 2009), ce mode d'agriculture intensive est remis en cause quant à sa capacité à nourrir durablement la population humaine (Foley et al., 2005; Godfray et al., 2010; Tilman et al., 2002) dont les prévisions de croissance l'amène à 9 milliards d'habitants d'ici 2050 (Gerland et al., 2014). Il paraît donc nécessaire de développer de nouveaux modes d'agricultures, plus durables (Godfray *et al.* 2010) ; c.à.d. une agriculture capable de produire des biens sur le long terme (nourriture, bois, fibre) tout en réduisant l'utilisation d'eau, de fertilisants, de pesticides, de terres, et de machineries (Pretty, 2008). Plusieurs auteurs ont proposé un mode d'agriculture appelé « intensification écologique » dont le but est d'augmenter ou maintenir les rendements tout en réduisant les externalités négatives de l'agriculture en se servant des services écosystémiques fournis par différents organismes dont les fonctions pourraient être comparables aux fertilisants ou aux pesticides (Doré et al., 2011; Wezel et al., 2015).

2. Les services écosystémiques et l' « intensification écologique » dans les milieux agricoles

Les services écosystémiques se définissent comme les bénéfices (monétaires, culturels, …) que les humains obtiennent des écosystèmes (terrestres ou aquatiques) et qui soutiennent directement ou indirectement leur survie et leur qualité de vie (Harrington et al., 2010). Ce terme est apparu dans les années 1980 mais c'est avec le Millenium Ecosystem Assessment 2005, la première large étude commandée par l'Organisation des Nations Unies sur l'impact de l'homme sur les écosystèmes et leurs services, que le terme va se populariser. A partir de ce moment, les recherches sur les services écosystémiques vont s'accélérer (Vihervaara et al., 2010) et de nombreuses expertises sur l'état de la biodiversité et des services rendus aux sociétés sont en cours, par exemple l'IPBES (Science-Policiy Platform on Biodiversity and Ecosystem Service) ou l'EFESE (l'Evaluation Française des Ecosystèmes et Services Ecosystémiques).

Les services écosystémiques sont classés en 4 catégories (Millenium Ecosystem Assessment 2005; Harrington *et al.* 2010) :

- Les services d'approvisionnement sont les produits obtenus des écosystèmes. Ce sont les ressources en eau, les hydrocarbures, le bois, l'ensemble des productions agricoles pour les agroécosystèmes, etc.

- Les services de régulation sont les bénéfices obtenus par la régulation des processus écosystémiques comme la régulation du climat, des maladies, l'érosion, etc.
- Les services culturels sont l'ensemble des bénéfices non matériels obtenus des écosystèmes. Ces bénéfices peuvent être un enrichissement spirituel, la réflexion, la création, etc.
- Les services de support sont l'ensemble des services qui permettent la production des autres services comme le cycle des nutriments, la formation des sols, etc.

La provision des services écosystémiques est fortement étudiée dans les agroécosystèmes (Boerema et al., 2017). Les agroécosystèmes sont principalement utilisés par l'homme en vue du service d'approvisionnement, c'est-à-dire la production de nourritures, de fibres, et d' agrocarburants. Différents services, principalement classifiés comme étant des services de régulations ou de supports pourraient être gérés pour augmenter la production de ces ressources (Zhang et al., 2007). Ces principaux services sont (voir Zhang *et al.* 2007; Power 2010 pour une liste non exhaustive des services écosystémiques dans les milieux agricoles):

- *La structure et la fertilité du sol* ont un rôle important sur la quantité et la qualité de la production et sont régulées par de nombreux organismes (micro-organismes ou vers de terre).
- *La disponibilité en eau*, essentielle au développement des plantes utilisées dans les cultures, régulée par la communauté végétale et la communauté biotique du sol en modifiant la structure de celui-ci.
- *Le contrôle biologique des pestes de cultures* est là aussi assuré par une multitude d'organismes (araignées, oiseaux, chauves-souris). Il vise à réguler tous les organismes qui peuvent avoir un impact négatif sur la production agricole (pucerons, pyrales, les méligèthes,…).
- *La pollinisation,* dont dépend un certain nombre de cultures pour la production de graines, de fruits etc., est assurée par divers animaux (mouches, abeilles, chauve-souris, papillons de nuit,…).

L' « intensification écologique » propose d'augmenter ces différents services en augmentant la présence et l'abondance des espèces à la base de ces processus (lire Kremen (2005) pour une liste d'organismes et leur fonctions associés) et de réduire en partie ou totalement l'utilisation d'intrants chimiques et l'utilisation des matériels agricoles consommateurs de carburants (Bommarco et al., 2013). L'abondance de ces espèces pourrait être favorisée par différentes mesures, comme l'augmentation des éléments semi-naturels pour le contrôle biologique (Holland et al., 2017), la réduction du labour pour les organismes du sol (Zuber and Villamil, 2016) ou l'implémentation de bandes fleuries pour les pollinisateurs (Blaauw and Isaacs, 2014). L' « intensification écologique » pourrait amener à un système « gagnant-gagnant » (« win-win » en anglais) entre biodiversité et production agricole (Power, 2010) mais le rôle de la plupart de ces espèces dans ces services reste peu connu (Hortal et al., 2015; Noriega et al., 2017) de même que les facteurs paysagers ou les pratiques influençant la présence de ces espèces (Holland et al., 2017). De plus, lorsque le rôle d'une espèce est identifié, la quantification fine de sa fonction (contrôle biologique, fertilité du sol…) est rarement réalisée (Fig 2, Boerema *et al.* 2017; Noriega *et al.* 2017). C'est le cas pour le

service de « pollinisation » qui reste dans beaucoup d'études cantonné à la description des pollinisateurs dans les parcelles (Liss *et al.* 2013; Noriega *et al.* 2017). Ces processus écologiques ne dépendent pas simplement de la diversité des organismes mais aussi de leurs interactions entre eux et avec leur environnement, ce qui peut rendre leur service difficile à quantifier (Gaba et al., 2014; Tylianakis et al., 2008). Cependant, l'implémentation de l' « intensification écologique » dans les milieux agricoles dépend de la quantification fine de ces services ainsi que des processus écologiques à la base de ceux-ci (Garbach et al., 2017; Guerry et al., 2015; Posner et al., 2016).

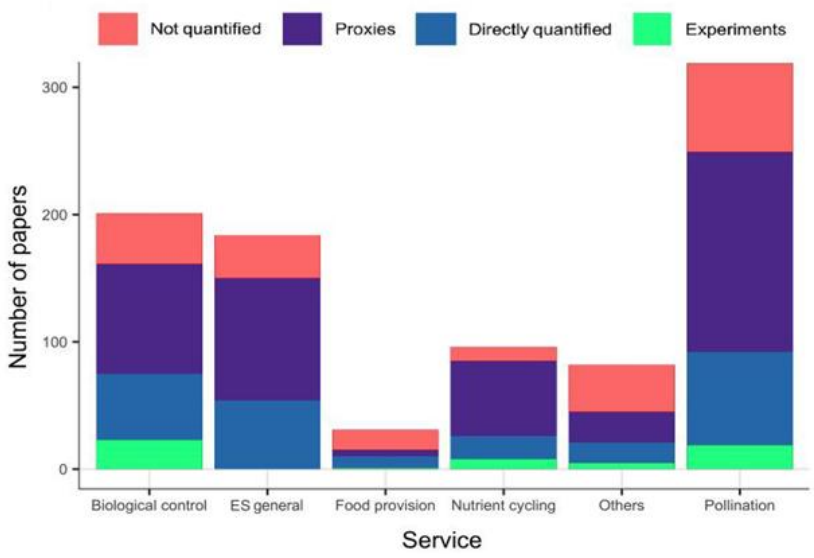

Fig 2. Nombre d'articles sur le bénéfice des insectes classés pour différents services écosystémiques et sur la méthodologie utilisée pour la quantification du service (pas quantifié, proxies (description des communautés de pollinisateurs dans les parcelles), directement quantifiés ou quantifiés expérimentalement, issu de Noriega *et al.* 2017).

B. Le service de pollinisation dans les milieux agricoles

1. Pollinisation et diversité des systèmes de reproduction :

La pollinisation est le passage du pollen issu de la structure mâle de la fleur (les anthères) à la partie femelle (les stigmates). Il s'ensuit le développement d'un tube pollinique qui va permettre aux gamètes mâles (cellules spermatiques) d'atteindre le gamète femelle (l'oosphère). Le passage du pollen peut se faire par allopollinisation, c'est-à-dire le passage du pollen des anthères d'une plante et aux stigmates d'une autre plante, ou par autopollinisation, le passage du pollen de la partie mâle et femelle d'une même plante qui amène à l'autofécondation. Ce taux d'autofécondation et d'allofécondation va dépendre de l'identité de la plante. 14% des espèces ont une autofécondation stricte (Goodwillie et al., 2005) avec le plus souvent des fleurs mâles et femelles séparées (Barrett, 2010). 44% des plantes ont une allofécondation stricte (Goodwillie et al., 2005) et pour les 42% des plantes restantes, elles ont un régime de fécondation mixte où le taux d'autofécondation ou d'allofécondation varient en fonction des espèces (Goodwillie et al., 2005). Ces plantes ont le plus souvent des fleurs hermaphrodites c.-à-d. avec la présence d'anthères et de pistil dans la même fleur (Barrett, 2010).

2. Les pollinisateurs des milieux agricoles

a. *Une diversité restreinte de pollinisateurs dans les cultures*

La plupart des plantes sont dépendantes de vecteur de pollen pour leur pollinisation. Le vent (pollinisation anémophile) est le principal vecteur abiotique mais ce processus de pollinisation est présent chez seulement 10% des plantes (Barrett, 2010). Les principaux vecteurs de pollen sont en fait les animaux, notamment les insectes (pollinisation entomophile). Ce type de pollinisation concerne plus de 80% des plantes (Kearns et al., 1998; Ollerton et al., 2011).

Plus de 300 000 espèces de pollinisateurs ont été identifiées dans le monde (Nabhan, Gary; Buchmann, 1997) représentant des taxons aussi divers que des oiseaux, des reptiles, des mammifères en passant par de nombreux invertébrés comme les coléoptères, les lépidoptères ou les diptères. Parmi les pollinisateurs, les abeilles (ordre des hyménoptères) sont les plus fréquentes visiteuses des fleurs (Winfree et al., 2011). Les abeilles représentent entre 17 500 et 30 000 espèces dans le monde (Michener, 2000; Winfree et al., 2011) et 960 espèces en France (Kuhlmann et al., 2015). Les diptères sont les deuxièmes plus importants visiteurs. Ils représentent plus de 150 000 espèces dans le monde dont les principaux représentants seraient les syrphes (Winfree et al., 2011). En France, les syrphes représentent 500 espèces (Castella-Martin et al., 2008).

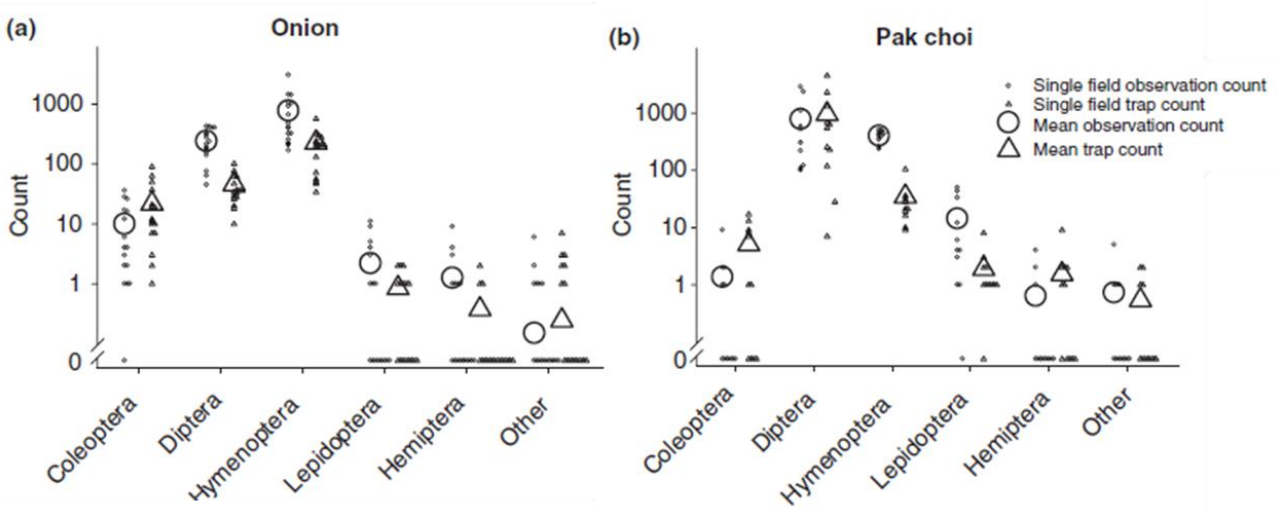

Fig 3. Nombre d'observations ou de captures des différents groupes de pollinisateurs pour deux cultures : (a) les oignons et (b) le chou chinois estimé par deux méthodes différentes: un comptage visuel et des captures avec des pièges à couleurs. Les principaux genres hyménoptères capturés ou observés sont 3 genres d'abeilles : *Apidae, Colletidae* et *Halictidae* (issue de Howlett *et al.* 2009**).**

Ces deux groupes sont les principaux pollinisateurs retrouvés dans les cultures (Howlett *et al.* 2009; Rader *et al.* 2015, Fig 3). Dans une étude portant sur 18 cultures différentes, Rader *et al.* (2015) montre que la hiérarchie du nombre de visites aux cultures est conservée entre les abeilles et les diptères avec 62% des visites (dont 39% pour l'abeille domestique) pour les abeilles. Le nombre d'espèces de pollinisateurs visitant les cultures est faible comparé à l'ensemble du nombre d'espèces existantes. Kleijn *et al.* (2015) a montré que sur 1400 études décrivant les pollinisateurs des cultures du monde entier, seulement 785 espèces d'abeilles et de bourdons ont été retrouvées, soit 12.6% des espèces d'abeilles existantes, et seulement 2%

de ces espèces représentent plus des 95% des visites. D'après Pisanty & Mandelik (2015), ces espèces sont majoritairement des espèces nichant au sol, avec un régime oligolectique (c.-à-d. se nourrissant du nectar et du pollen venant de différentes espèces de plantes), et vivant en colonie (primitivement sociale, Michener 2000).

b. *L'efficacité pollinisatrice des insectes*

L'interaction plantes-pollinisateurs est une relation mutualiste où les plantes fournissent pollen et nectar aux pollinisateurs alors que les pollinisateurs transportent et dispersent le pollen dans l'espace, permettant d'assurer la reproduction des plantes (Faegri and Van Der Pijl, 1979). La reproduction d'une plante est souvent associée à une communauté de pollinisateurs, la spécialisation d'une espèce d'abeille à une seule espèce de plante étant rare dans les réseaux plantes-pollinisateurs (Bosch et al., 2009; Fontaine et al., 2009). L'efficacité pollinisatrice des communautés de pollinisateurs diffère selon les espèces qui les composent (Gómez et al., 2010; Rader et al., 2012). L'efficacité pollinisatrice d'une communauté peut être décomposée en trois parties : (i) l'efficacité individuelle de pollinisation, (ii) l'efficacité de pollinisation d'une espèce, et (iii) l'efficacité pollinisatrice de la communauté (Ne'Eman et al., 2010; Willcox et al., 2017).

- L'efficacité individuelle de pollinisation est déterminée par la quantité de pollen déposée en une seule visite (Ne'Eman et al., 2010; Willcox et al., 2017). Cette quantité de pollen déposée est fortement corrélée à la pilosité des pollinisateurs (Stavert et al., 2016) et de la concordance entre la morphologie florale et celle des pollinisateurs (Solís-Montero and Vallejo-Marín, 2017). L'exemple classique est la fleur à long tube qui ne peut être pollinisée que par les pollinisateurs à longue langue (Fig 4). Pour une même espèce de pollinisateurs, il a été montré que leur taille détermine la quantité de pollen transportée et ainsi l'efficacité pollinisatrice (Jauker et al., 2016), mais cette relation n'existe pas entre espèces (Larsen et al., 2005). En général, les abeilles sont beaucoup plus efficaces que les syrphes pour transporter du pollen (Rader et al., 2015; Sahli and Conner, 2007).

Fig 4. Un skipper à grande queue (Urbanus proteus) pollinisant le buissson aux colibris (Hamelia Patens, issue de http://aggie-horticulture.tamu.edu/galveston).

- L'efficacité pollinisatrice d'une espèce dépend de son efficacité individuelle multipliée par le nombre de visites par plante de cette espèce (Ne'Eman et al., 2010; Willcox et al., 2017). Parmi les pollinisateurs, ce sont, en général, les abeilles domestiques qui effectuent le plus de visites dans les parcelles (Brittain et al., 2013a; Garantonakis et al., 2016; Garratt et al., 2014b; Pisanty et al., 2016; Rader et al., 2009; Woodcock et al., 2013). Ceci est potentiellement dû au grand nombre d'abeilles domestiques vivant dans une seule ruche, mais cela peut dépendre de la culture (Garratt et al., 2014b; Rader et al., 2015).
- L'efficacité pollinisatrice de la communauté est la capacité d'un ensemble de pollinisateurs de différentes espèces à polliniser une plante à un temps et un endroit donné (Ne'Eman et al., 2010; Willcox et al., 2017). Cela comprend la somme de leurs effets ainsi que de leurs interactions. De nombreuses cultures montrent une meilleure

production lorsqu'une riche communauté de pollinisateurs est présente (Mallinger and Gratton, 2015; Rogers et al., 2014). Plusieurs mécanismes de complémentarité ont été mis en évidence entre les pollinisateurs. Cette complémentarité peut être temporelle, les pollinisateurs ne butinant pas aux mêmes horaires (Albrecht et al., 2012; Frund et al., 2013; Hoehn et al., 2008), ou spatiale, les différentes espèces ne butinant pas aux mêmes emplacements de la plante, (Brittain et al., 2013a; Hoehn et al., 2008) ou de la parcelle (Pisanty et al., 2016). Cette complémentarité peut aussi s'exprimer à travers les températures auxquelles butinent les pollinisateurs (Frund et al., 2013; Rader et al., 2013) ou la vitesse du vent (Brittain et al., 2013a) à laquelle certains pollinisateurs sont plus sensibles que d'autres. Des mécanismes d'interactions entre pollinisateurs ont été aussi mis en évidence dans les cultures de tournesols (Carvalheiro et al., 2011; Greenleaf and Kremen, 2006) et d'amandiers (Brittain et al., 2013b). Sur ces cultures, les abeilles sauvages augmentent le nombre de visites des abeilles domestiques par plante et ainsi leur efficacité pollinisatrice en obligeant les abeilles domestiques à aller visiter une autre fleur lors de leur rencontre sur une même fleur.

c. *L'importance des éléments semi-naturels et des ressources florales pour le service de pollinisation*

La présence des pollinisateurs dans les parcelles va dépendre de la présence de leur habitat et des ressources florales nécessaires à leur reproduction (Winfree et al., 2011). Que ce soient les abeilles ou les syrphes, ils sont souvent associés aux milieux ouverts (Winfree et al., 2011).

L'habitat des abeilles domestiques est principalement une ruche dont la présence est déterminée par l'homme. En effet, les populations sauvages d'abeilles domestiques dites « férales » sont très peu présentes dans les milieux agricoles (Oleksa, Gawroński & Tofilski 2013) suite à l'apparition du parasite *Varroa destructor* en Europe et aux Etats-Unis qui a décimé les populations (Potts *et al.* 2010). La distance des ruches aux parcelles déterminent leur abondance dans les parcelles agricoles (Cunningham et al., 2016). Pour les pollinisateurs sauvages, il n'y pas de consensus entre les études sur les paysages qui influencent la présence de ces insectes dans les parcelles. Dans une synthèse de 29 études, Garibaldi *et al.* (2011) a montré que le nombre de visites des pollinisateurs ainsi que le succès de pollinisation diminuaient avec la distance aux éléments semi-naturels (haies, forêt, prairie). Cette diminution du nombre de visites est corroborée par une autre étude sur 23 cultures, mais cette diminution n'affecte pas le succès de pollinisation des plantes (Ricketts et al., 2008). Alors que Kleijn *et al.* (2015, Fig 5) ont

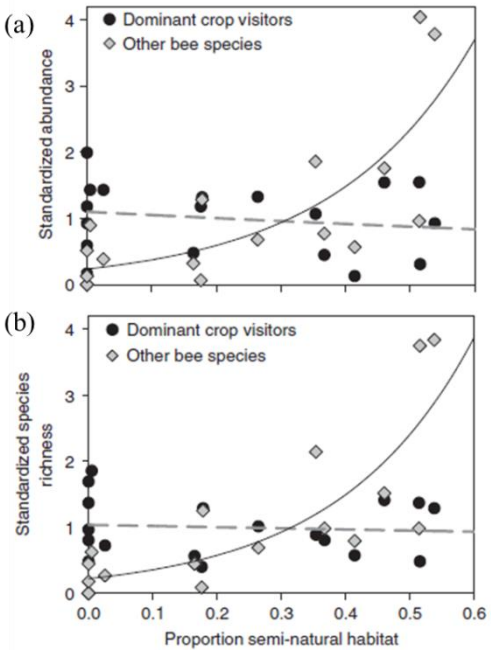

Fig 5. Relation entre la surface d'éléments semi-naturels et (a) l'abondance ou (b) la richesse standardisé des espèces d'abeilles pour les principaux pollinisateurs visitant les cultures et donc responsable du service pollinisations (supérieur à 5% des visites ,point noir) et les espèces plus rarement retrouvées dans les cultures (inférieur à 5% des visites, losange gris, issue de Kleijn *et al.* 2015)

montré que les visites des principaux pollinisateurs dans les cultures ne sont pas influencées par les éléments semi-naturels. La diminution des visites avec la distance aux éléments semi-naturels pourrait dépendre de la zone géographique de l'étude. En effet, cette diminution est beaucoup plus importante dans les zones tropicales que dans les zones tempérées (Garibaldi et al., 2011; Ricketts et al., 2008). En zones tempérées, les abeilles nichent plutôt dans le sol et seraient moins dépendantes des éléments semi-naturels type bois ou haie que les espèces tropicales (Potts et al., 2005). Finalement, l'effet du paysage pourrait varier en fonction de l'identité des pollinisateurs (Cariveau et al., 2013), mais les traits déterminant cette réponse (taille du corps, niveau de sociabilité) restent pour le moment peu identifiés (Bartomeus et al., 2017).

Les études sont par contre en accord sur le rôle des ressources florales sur le maintien des pollinisateurs dans les paysages agricoles et sur leur rôle dans le service de pollinisation. Plusieurs études ont montré que les paysages agricoles qui ont des ressources florales plus importantes (présentes naturellement ou implantées par l'homme, par exemple des bandes fleuries) ont une diversité et une abondance en pollinisateurs plus importante ce qui se traduit par une augmentation des visites de pollinisateurs dans les cultures dépendantes des pollinisateurs (Blaauw and Isaacs, 2014; Feltham et al., 2015; Motzke et al., 2016; Norfolk et al., 2016). En effet, il a été montré que ces ressources supplémentaires augmentent la reproduction des pollinisateurs (Bukovinszky et al., 2017). De plus ces ressources florales supplémentaires peuvent augmenter l'attractivité de la parcelle pour les pollinisateurs (Motzke et al., 2016; Norfolk et al., 2016). Les cultures à fleurs fournissent elles aussi une grande quantité de ressources pour les pollinisateurs (Requier et al., 2015; Rollin et al., 2013; Todd et al., 2016) ce qui augmente la reproduction des pollinisateurs (Holzschuh et al., 2013). En augmentant la taille des populations de pollinisateurs, la présence d'une culture peut faciliter la pollinisation de la prochaine culture en fleurs (Grab et al., 2017; Häussler et al., 2017; Riedinger et al., 2014). Toutefois si une trop grande quantité de cultures fleurissent en même temps, cela peut se traduire par une dilution des pollinisateurs dans l'espace (Grab et al., 2017; Holzschuh et al., 2016).

3. Importance de la pollinisation entomophile dans la production agricole

a. Effet bénéfique à l'échelle de la plante

Les pollinisateurs peuvent augmenter le nombre de fruits par plante comme c'est le cas pour les pastèques, les fraises ou les melons (Garibaldi et al., 2013; Rader et al., 2015) ainsi que le nombre de graines par fruit comme chez la moutarde (Atmowidi et al., 2007) ou la féverole (Garratt et al., 2014b). La pollinisation entomophile peut également se traduire par une augmentation du poids moyen d'un fruit (ex. les pommes, Garratt *et al.* 2014a, ou la myrtille Bos *et al.* 2007) ou une modification de la qualité de la production (Chautá-Mellizo et al., 2012; Stein et al., 2017). Les traits associés à la qualité varient en fonction de l'identité de la plante. Par exemple, la pollinisation entomophile améliore l'aspect esthétique des fraises (Klatt et al., 2014) ou diminue la quantité de graines vides dans le sarrasin (Bartomeus et al., 2014). Cependant, il n'existe pas de consensus sur les effets de la pollinisation entomophile. En effet, plusieurs études ont montré des effets négatifs des pollinisateurs sur le poids, la qualité des graines ou des fruits (Brittain et al., 2014; Garratt et al., 2014a; Zou et al., 2017b).

Les mécanismes qui entraînent la modification (l'augmentation ou la diminution) de la quantité, du poids, ou de la qualité des graines ou des fruits suite à la pollinisation des fleurs par les pollinisateurs restent peu étudiés. Plusieurs études ont avancé un mécanisme d'investissement préférentiel dans les graines issues d'une pollinisation entomophile (Chautá-Mellizo et al., 2012; Stein et al., 2017) car cette graine serait issue d'une allopollinisation plutôt que d'une autopollinisation. En effet les pollinisateurs peuvent augmenter le taux d'allopollinisation (Matsuki et al., 2008; Wang et al., 1998) mais ils peuvent aussi augmenter le taux d'autopollinisation (Devaux et al., 2014; Karron et al., 2009). De plus, l'importance de l'origine du pollen pour la pollinisation dépend fortement de l'espèce de plante (Chamer et al., 2015; Dogterom et al., 2000; Niesenbaum, 1999). Il est aussi possible que certains compromis (voir Encadré 1) au sein de la plante amènent à un effet négatif des pollinisateurs comme entre le nombre de graines et le poids des graines de colza (Zou et al., 2017b).

Encadré 1.

Un compromis d'allocation (ou « trade-off » en anglais) est, en évolution et en écologie, une contrainte entre deux (ou plusieurs) traits dont les valeurs ne peuvent être maximisées en même temps, c.-à-d. lorsque la valeur du trait « A » augmente, la valeur du trait « B » diminue (Roff and Fairbairn, 2007; Stearns, 1989). Le choix de l'investissement dans le trait « A » plutôt que dans le trait « B » va varier selon les espèces, populations ou individus, ce qui va amener à des stratégies d'allocations différentes. Chez les plantes, plusieurs compromis ont été étudiés comme ceux entre le nombre de graines et le poids des graines (Jakobsson and Eriksson, 2000) ou la croissance de la plante et la défense contre l'herbivorie (Züst and Agrawal, 2017). Cependant ces stratégies ne sont pas forcément fixées au sein d'une espèce. Des variations pour une stratégie d'allocation peuvent exister entre individus d'une même espèce, on parle de « plasticité phénotypique », c.à.d. la capacité d'exprimer plusieurs phénotypes (ici stratégie d'allocation) pour une même espèce. Ces variations entre individus peuvent être dues à une adaptation locale à l'environnement (biotique ou abiotique) (Roff and Fairbairn, 2007; Stearns, 1989) comme la présence ou non des pollinisateurs (Wesselingh, 2006).

b. *Contribution du service de pollinisation des cultures à l'échelle mondiale : rendement et économie*

La proportion de cultures dépendantes des pollinisateurs est de 70 % à l'échelle du monde (Klein et al., 2007) et 84% à l'échelle de l'Europe (Williams, 1994). La dépendance aux pollinisateurs varie avec l'espèce cultivée notamment avec leur tolérance à l'auto-fécondation (Fig. 6., Klein *et al.* 2007). Les cultures les plus dépendantes aux pollinisateurs

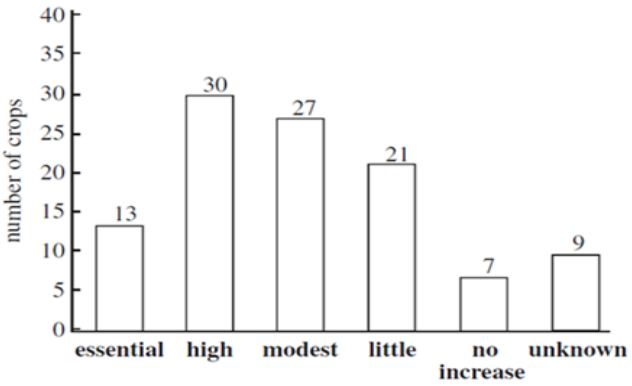

Fig 6. Niveau de dépendance des 70 cultures à la zoogamie (issue de Klein *et al.* 2007)

sont les cultures à fruits secs (amandes), à fruits charnus (cerises, pommes,…) et les cultures à huiles (tournesol, moutarde ; Gallai *et al.* 2009). Ces cultures ne représentent que 35% de la production agricole mondiale (Klein et al., 2007). La majorité de la production vient de cultures totalement autofécondes comme le blé ou le riz, qui sont produites sur de plus larges surfaces. Néanmoins, cette étude ne prend pas en compte la qualité nutritionnelle des productions. Certaines vitamines ou antioxydants nécessaires à la santé humaine sont issus des fruits ou des graines venant de plantes cultivées dont la pollinisation dépend seulement des insectes (Eilers et al., 2011). Plusieurs études ont cherché à évaluer monétairement le service de pollinisation. En estimant la contribution des pollinisateurs pour la production totale de chaque culture et en multipliant par le prix de ventes des fruits et des graines par continents, les études ont estimé le service de pollinisation entre 127 et 152 milliards d'euros par an soit 10 % de la production agricole mondiale (Bauer and Sue Wing, 2016; Gallai et al., 2009). En prenant en compte la différence de prix de vente plus finement entre pays, le service de pollinisation a été estimé entre 167 milliards d'euros et 253 milliards d'euros par an (Lautenbach et al., 2012). La contribution des pollinisateurs à la production agricole ne cessent de croître depuis les années 1990 (Lautenbach et al., 2012) suite à l'augmentation des surfaces agricoles dépendantes des pollinisateurs (Aizen et al., 2008). Cette valeur varie spatialement en fonction de la quantité de cultures dépendantes des insectes. Ainsi la Chine fait partie des pays les plus dépendants aux pollinisateurs (Fig. 7.a, Lautenbach *et al.* 2012; Potts *et al.* 2016). A l'échelle française, le service de pollinisation est estimé à 2.3 à 5.3 milliards d'euros (MEEM Ministère de l'Environnement de l'Energie et de la Mer, 2016) ce qui représente entre 5.2 à 12% de la production pour la France. Le pourtour méditerranéen est la partie de la France dont les surfaces agricoles sont les plus dépendantes aux pollinisateurs (Fig. 7.b, MEEM Ministère de l'Environnement de l'Energie et de la Mer 2016).

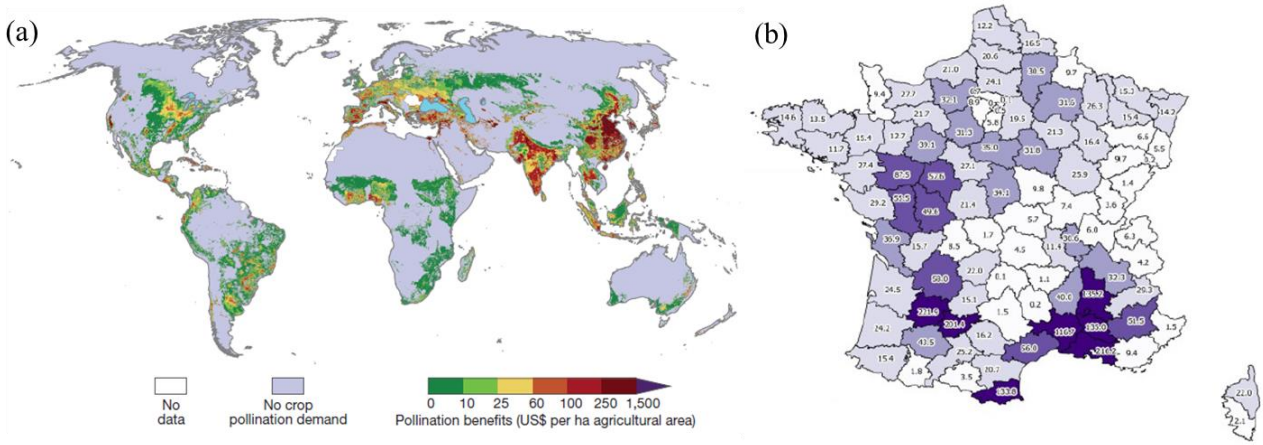

Fig 7.(a) Contribution du service de pollinisation à la vente des production agricoles en US$ par hectare pour l'année 2000 (issue de Potts *et al.* 2016) . (b) Valeur du service de pollinisation en € pour les différents départements français pour l'année 2014 (issue et modfié de MEEM Ministère de l'Environnement de l'Energie et de la Mer 2016).

Cependant, les contributions des pollinisateurs varient fortement pour une même culture, pouvant aller de 10% à 100% par exemple pour le production d'amandes (référence dans Gallai *et al.* 2009), alors que les estimations précédentes sont issues d'une moyenne globale entre plusieurs études portant sur une même culture. Outre la différence de pollinisateurs entre

les parcelles qui modifie la contribution des insectes (Gómez et al., 2010; Rader et al., 2012), ces variations peuvent venir en partie des méthodes utilisées pour estimer la contribution des insectes.

C. Limites des études sur le service de pollinisation

Malgré l'importance des pollinisateurs dans la production agricole, leur utilité est mal reconnue par les agriculteurs (Chen et al., 2017; Misganaw et al., 2017; Munyuli, 2011) et est donc rarement prise en compte dans la conception des systèmes agricoles (Austin et al., 2015; Breeze et al., 2014). Cela pourrait venir des méthodes utilisées pour estimer le bénéfice des pollinisateurs qui peuvent être erronées et ne sont pas réalisées à une échelle et dans des conditions pertinentes pour les agriculteurs. En effet, plusieurs critiques ont été émises sur la façon de calculer la contribution des pollinisateurs aux productions agricoles (Breeze et al., 2016; Holland et al., 2017; Noriega et al., 2017).

1. Les méthodes

Une large diversité de méthodes a été utilisée dans les études qui ont cherché à estimer le service de pollinisation (Liss et al., 2013; Noriega et al., 2017). Ces méthodes peuvent être classées en 3 catégories (Noriega et al., 2017) :

- Reposant sur des proxys : Ces études relatent les observations d'abondances, de richesses, ou du nombre de visites des pollinisateurs dans les parcelles agricoles (Liss et al., 2013; Noriega et al., 2017). Ces métriques servent de proxy pour évaluer le service de pollinisation et sont souvent utilisées pour décrire l'effet du paysage sur les visites des pollinisateurs dans les cultures (Holland et al., 2017).
- Les méthodes expérimentales : Dans cette catégorie, les contributions des pollinisateurs sont évaluées par deux méthodes; la première est l'utilisation de cages dans laquelle les plantes d'une culture sont cultivées sur une surface généralement supérieure à 1 m² (Clement et al., 2007; Jauker et al., 2012; Oz et al., 2009). Dans une des cages, des pollinisateurs sont introduits et dans une autre, aucun pollinisateur n'est mis. Dans la seconde méthode, un filet est utilisé pour empêcher l'accès aux pollinisateurs soit à l'échelle de la fleur (Bos et al., 2007), d'une branche (Garratt et al., 2014a), de la plante entière(Stein et al., 2017), voire de plusieurs m² (Bishop et al., 2016). Une autre partie de la plante (ou la plante, le m² selon l'échelle utilisée) est laissée sans exclusion des pollinisateurs et ces derniers, naturellement présents dans l'environnement, peuvent donc venir visiter les fleurs. Quelle que soit la méthode utilisée, la contribution des pollinisateurs à la production de la plante est obtenue par la différence entre la production de la plante (ou une partie de la plante, toujours selon l'échelle) avec accès aux pollinisateurs et celle sans accès à ces pollinisateurs. Cette comparaison permet d'obtenir, pour une culture, un ratio de dépendance de la culture aux pollinisateurs (Breeze et al., 2016). Un ou plusieurs traits peuvent être utilisés pour calculer cette contribution (ex. le succès de pollinisation, le poids total de graines au m²,…).
- Les estimations directes : Ces études regardent l'augmentation (ou la diminution), d'un ou plusieurs traits de la plante liés à sa production le long d'un gradient de pollinisateurs. Ce gradient peut être naturel ou créé par l'ajout de ruches par exemple

(Lindström *et al.* 2016). La contribution des pollinisateurs est estimée en comparant la différence de production entre les parcelles avec peu ou pas de pollinisateurs et celles avec beaucoup de pollinisateurs (Fig 8, Vaissière, Freitas & Gemmill-Herren 2010).

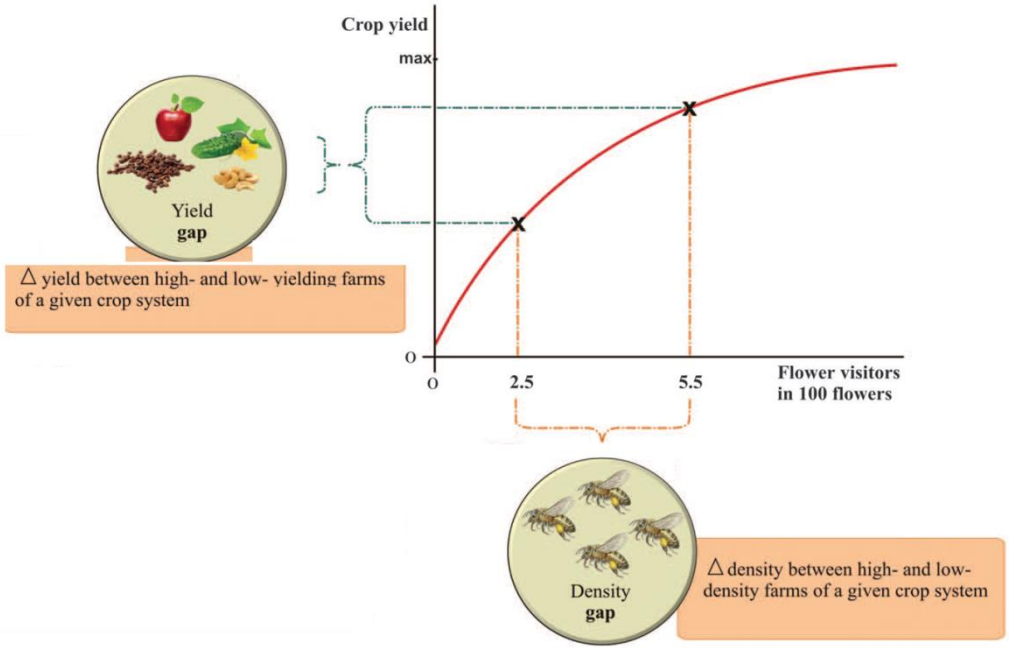

Fig 8. Relation entre l'abondance des pollinisateurs et le rendement. La contribution des pollinisateurs est calculée par la différence de rendement entre les parcelles avec peu de pollinisateurs et celles avec beaucoup de pollinisateurs (Figure issue et modifié de Garibaldi et al. 2016).

2. Avantages et biais respectifs:

Ces méthodes présentent différents avantages mais sont soumises à différents biais qui pourraient modifier la contribution des pollinisateurs et leur importance dans la production agricole. Ces biais et ces avantages varient selon la méthode utilisée:

- L'utilisation de proxys comme le nombre de visites des pollinisateurs par parcelle est une méthode peu coûteuse en termes de matériel et de temps. Cependant, l'utilisation de proxys n'explique pas le lien entre les pollinisateurs, la fonction de la pollinisation, et le bénéfice qu'en retire l'agriculteur (rendement) étant donné que le nombre de visites ou l'abondance des pollinisateurs ne déterminent pas nécessairement le succès de pollinisation de la fleur (King et al., 2013). De plus l'efficacité pollinisatrice de chaque pollinisateur varie entre espèces et entre cultures (lire *« L'efficacité pollinisatrice des insectes »*). Par exemple, le succès de fructification de nombreuses cultures ne dépend pas des abeilles domestiques malgré leur visite dans les parcelles (Garibaldi et al., 2013).
- L'utilisation de cages, avec absence ou présence de pollinisateurs, est une méthode plus coûteuse en temps (mise en place de la cage et des pollinisateurs) et en matériel (achat des cages et des pollinisateurs). Cette méthode permet de quantifier et de comparer la contribution de différentes espèces de pollinisateurs (Clement et al., 2007; Jauker et al., 2012) ou de différents assemblages de ces espèces (Albrecht et al., 2012) pour la production d'une même culture. Toutefois, cette méthode peut forcer

l'interaction plantes-pollinisateurs qui *in natura* est très rarement observée (Banda and Paxton, 1991). Une modification du comportement des pollinisateurs sous cage a été aussi observée (Kunjwal et al., 2014). Par exemple, l'abeille domestique visite en moyenne 7.7 fleurs de moutarde brune (*Brassica juncea*) par minute sous cage alors que le nombre de visites en moyenne est de 10.7 fleurs *in natura*, donc l'utilisation de pollinisateurs sous cage peut diminuer l'efficacité des pollinisateurs (Kunjwal et al., 2014). Finalement, l'abondance des pollinisateurs ne reflète pas celle présente dans les parcelles agricoles. L'utilisation de filet peut être une méthode moins coûteuse en temps et en argent; la présence des pollinisateurs n'étant pas manipulée. L'utilisation de différentes mailles de filet permet de décomposer la contribution des insectes à la production en fonction de leur taille (Sakamoto et al., 2012), voire de différencier la contribution du vent et de l'autopollinisation (Wragg and Johnson, 2011). Les filets sont connus pour restreindre une partie du pollen reçu par la plante via le vent (Jacobs et al., 2009; Wragg and Johnson, 2011), ou entraîner des changements de conditions microclimatiques (Martin et al., 2013) et impacter négativement la production de la plante sous filet. Par exemple, 30% du pollen de *Cyperus tenax* amené par le vent est retenu par le filet (Wragg and Johnson, 2011).

- L'estimation directe de la contribution des pollinisateurs nécessite l'existence de paysages variés (par exemple, en termes d'éléments semi-naturels) sur un même site d'étude pour obtenir un gradient de pollinisateurs suffisamment contrasté pour établir la relation entre pollinisateurs et productions d'une culture ou l'achat d'un nombre important de ruches pour créer ce gradient.
- Ces études sont réalisées soit en conditions expérimentales c.-à-d. que les cultures sont mises en place par les équipes scientifiques, où les ressources (fertilisants, eau) et pesticides sont contrôlés entre les différents réplicas de l'expérience, ou soit en condition naturelle c.-à-d. directement dans les parcelles des agriculteurs, où les ressources varient en fonction des pratiques agricoles. Par conséquent, les études en conditions expérimentales pourraient ne pas prendre en compte la complexité des systèmes agricoles dans la contribution des pollinisateurs. De plus, plusieurs études ont montré que les pratiques agricoles pouvaient déterminer la présence des pollinisateurs (Boreux et al., 2013) ou modifier directement leur contribution, par exemple en faisant varier les ressources du sol (Tamburini et al., 2016).
- Que ce soit pour les méthodes utilisant les cages, les filets ou des estimations directes dans les parcelles agricoles ou expérimentales, l'échelle (fleur, branche, plante, m²…) à laquelle est estimée la contribution des pollinisateurs peut surestimer ou sous-estimer la contribution des pollinisateurs. Le trait le plus souvent utilisé pour estimer cette contribution est le succès de pollinisation ou de fructification (Garibaldi et al., 2013; Ricketts et al., 2008). Ce trait n'intègre pas les compromis entre les différents traits d'une plante et peut donc amener à une surestimation de la contribution des pollinisateurs (Encadré 1). L'échelle de la plante intègre ces différents compromis mais la variation de taille entre les plantes doit être contrôlée puisque le bénéfice net (production totale de graines à l'échelle du pied) d'un pollinisateur va varier entre une plante produisant 10 fleurs et une plante en produisant 100. L'évaluation à l'échelle de la plante n'intègre pas la densité de plantes qui diffère entre parcelles ou dans la

parcelle (Kayad et al., 2016). Cette densité peut être d'ailleurs négativement corrélée à production de graines par plante due à une compétition pour les ressources entre plantes (Deng et al., 2012). L'échelle de la parcelle permet d'intégrer l'ensemble de ces compromis et de ces variations de densité de plantes mais la contribution des pollinisateurs ne peut être évaluée que grâce à un gradient de pollinisateurs ; les filets ou les cages ne pouvant pas être utilisés à cette échelle. De plus, évaluer la production à cette échelle peut être coûteux car elle nécessite le ramassage des plantes sur de grandes surfaces (par exemple, l'achat d'une mini moissonneuse batteuse, Lindström *et al.* 2016). Cette tâche peut être réalisée par les agriculteurs et les métriques de la production (généralement le rendement par hectare) sont ensuite récupérées par des enquêtes auprès de ces mêmes agriculteurs (Gaines-Day and Gratton, 2016) et donc limiter les coûts.

Relier la production agricole à l'échelle de la parcelle à un gradient d'abondance ou de richesse des pollinisateurs directement dans les champs des agriculteurs semble être la méthode la plus précise pour calculer la contribution des pollinisateurs dans les productions agricoles. C'est à cette échelle que les agriculteurs estiment leur rendement ce qui en ferait l'échelle la plus pertinente. Les études qui ont estimé le bénéfice des insectes à cette échelle restent rares (pour la féverole (Cunningham and Le Feuvre, 2013), la canneberge (Gaines-Day and Gratton, 2016), et le café (Veddeler et al., 2008)). D'autres études ont été réalisées à grande échelle (supérieur à 10 m², Garibaldi *et al.* 2016; Lindström *et al.* 2016), mais n'englobent pas la totalité de la parcelle. Finalement, la majorité des publications ont étudié l'effet des pollinisateurs sur les traits qui déterminent le rendement : le nombre de fruits, le poids des fruits, … , mais elles sont beaucoup plus rares sur la qualité de la production (Bartomeus et al., 2014; Brittain et al., 2014; Klatt et al., 2014; Stein et al., 2017). L'absence de la prise en compte de cette variable peut amener à une sous-estimation du service de pollinisation puisque la qualité de la production peut modifier la valeur de la récolte (Bommarco et al., 2012).

Dans cette thèse, nous allons nous appliquer à quantifier la contribution des pollinisateurs à la production, à la fois en termes de quantité et qualité de rendement, pour deux cultures dépendantes des pollinisateurs, le colza et le tournesol, directement dans les parcelles des agriculteurs. Cette contribution sera calculée à différentes échelles (branche, plante et parcelle) en utilisant plusieurs méthodes (gradients de pollinisateurs et expérimentation d'exclusion à l'aide de filets).

D. Le cas du colza et du tournesol

1. Importance de la production de colza et de tournesol dans l'agriculture

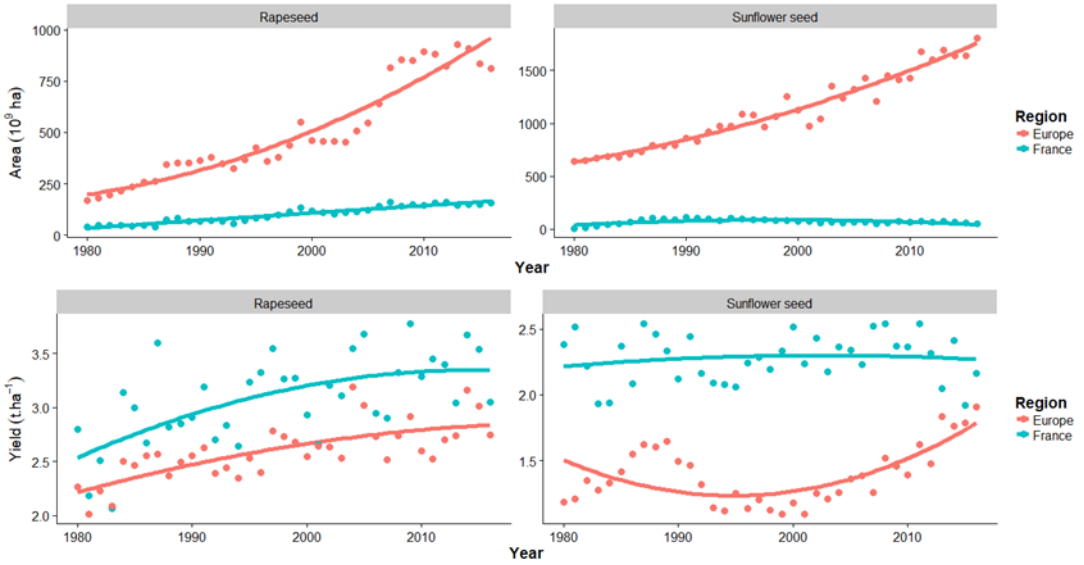

Fig 9. Evolution des surfaces et des rendements de colza et de tournesol pour l'Europe (rouge) et la France (Bleu) depuis 1980 (données issues de FAOSTAT 2016).

Le colza (*Brassica napus L.*) et le tournesol (*Helianthus annuus L.*) sont deux cultures à fleurs annuelles importantes dans les systèmes agricoles. Elles représentent respectivement, en terme de surface, respectivement la 7ème (37 millions d'hectares) et 13ème (25 millions) culture dans le monde, la 5ème (8 millions) et 3ème (18 millions) en Europe, et la 3ème (1.5 millions) et la 7ème en France (0.5 millions, FAOSTAT 2016). Depuis 1980, les surfaces et le rendement de colza ne cessent d'augmenter en Europe et en France, même si une stabilisation du rendement a été observée en France depuis une dizaine d'années (Fig 9.). Après une diminution de rendement entre 1980 et 2000 à l'échelle Européenne, le rendement en tournesol augmente dès lors. Les surfaces cultivées en tournesol sont quant à elles restées stables depuis les années 1980 (Fig 9.).

2. Les déterminants du rendement de colza et sa qualité de production

a. *Les composants du rendement*

La structure végétale diffère entre le colza et le tournesol (Fig 10). Cela va induire une élaboration du rendement différente entre ces deux cultures. A l'échelle du pied, le poids total de graines du colza est déterminé par le poids moyen d'une graine multiplié par le nombre de graines, ce dernier étant dépendant du nombre de siliques (fruit du colza) et du nombre de graines par silique. Le nombre de siliques dépend, en plus de la tige principale, du nombre de branches secondaires et tertiaires (Fig 10.a) alors que le nombre de graines par siliques dépend du nombre d'ovules fécondés par fleur au moment de la pollinisation (Pechan, 1988). Le poids total des graines à l'échelle du pied est par ailleurs positivement corrélé à la biomasse du pied qui détermine en partie le nombre de fleurs par pied (Kuai et al., 2015). Le rendement à l'échelle de la parcelle est obtenu en multipliant le poids total des graines par pied par la densité de plantes de la parcelle (ou approximé au m²).

L'élaboration du rendement du tournesol est plus simple car il possède une tige unique avec une seule tête où se développent des milliers de fleurs (Fig 10.b). A l'échelle du pied, le rendement dépend du poids moyen d'une graine et du nombre de graines par pied de tournesol. Ils sont tous les deux positivement corrélés au diamètre de la tête de tournesol (Marinkovic, 1992). Le diamètre de la tête de tournesol est positivement corrélé au nombre de fleurs à polliniser (Marinkovic, 1992). Comme pour le colza, le rendement à l'échelle de la parcelle est obtenu en multipliant le poids total des graines par pied par la densité de plante de la parcelle (ou approximé au m²).

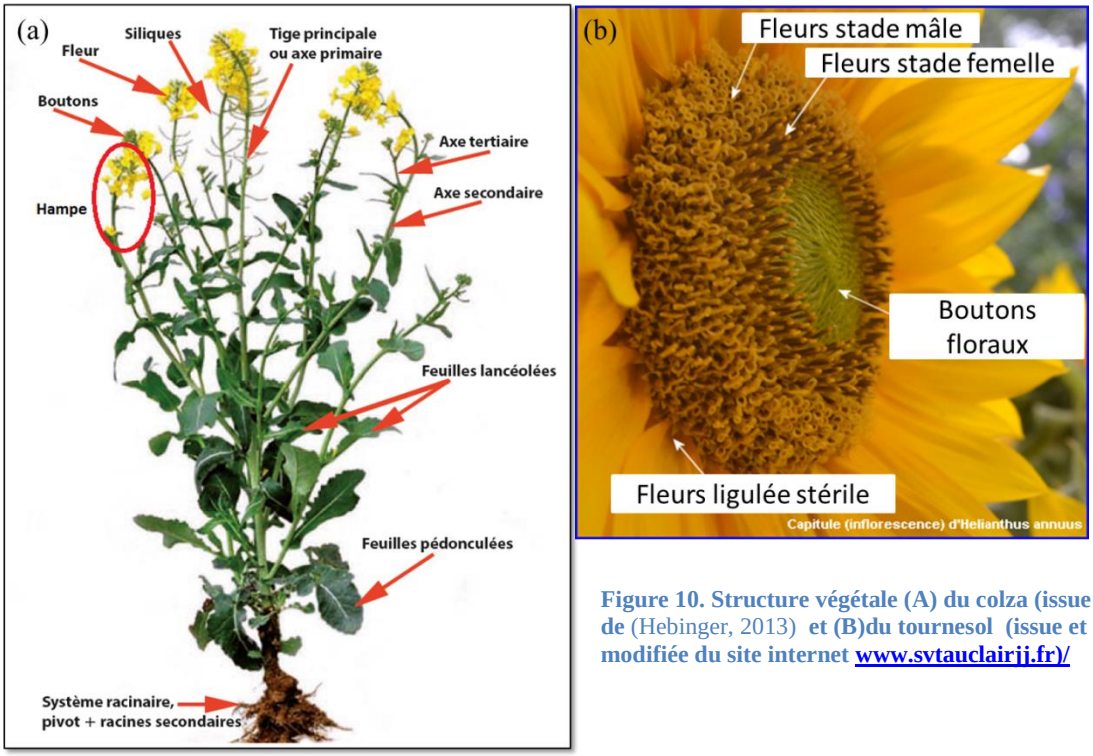

Figure 10. Structure végétale (A) du colza (issue de (Hebinger, 2013) **et (B)du tournesol (issue et modifiée du site internet www.svtauclairjj.fr)/**

b. ***Les composants de la qualité de production***

Le tournesol et le colza sont cultivés pour leurs graines riches en lipides utilisées pour la consommation humaine ou les agrocarburants (Abiodun OA, 2017). La qualité de la production est déterminée par le pourcentage de lipides des graines. Ce pourcentage détermine la quantité d'huile obtenue une fois les graines pressées (Abiodun OA, 2017). Les lipides représentent près de 45% de la graine pour le colza (Rathke et al., 2005) et 50% pour le tournesol (Botella Miralles et al., 1997).

La qualité nutritionnelle de ces huiles, second paramètre de la qualité de la production de colza ou tournesol, est déterminée par leur composition en acides gras. En effet, ces acides gras sont associés à différents effets bénéfiques ou nocifs pour l'homme (Tableau 1). Les compositions diffèrent entre ces deux cultures (Jahreis and Schäfer, 2011). Le colza est principalement composé d'acide gras mono-insaturés (principalement acide oléique, 60%) suivi par les acides gras polysaturés dont les principaux sont l'acide linoléique (22%) et l'acide alpha-linolénique (10%) et complété par les acides gras saturés (6%) et trans-saturés (1%) (Adamska *et al.* 2004; Jahreis & Schäfer 2011; Orsavova *et al.* 2015). Pour le tournesol, le profil d'acides gras se distingue selon le type de variétés : les variétés classiques et les variétés oléiques. Les variétés classiques sont riches en acides linoléiques (72%) suivis par

des acides alpha-linoléniques (27%) et saturés (12%, Zimmerman, Fick & Dakota 1973; Jahreis & Schäfer 2011) alors que les variétés oléiques sont principalement composées d'acides oléiques (80%) suivies par des acides linoléiques (10%) et des acides gras saturés (<10%, Flagella *et al.* 2002; Angeloni *et al.* 2017). Les acides alpha-linolénique et trans sont quasiment inexistants (<1%) dans l'huile de tournesol et cela indépendamment de la variété (Zimmerman, Fick & Dakota 1973; Flagella *et al.* 2002; Jahreis & Schäfer 2011; Angeloni *et al.* 2017). Le ratio « oméga 6 sur oméga 3 » est aussi important dans la qualité nutritionnelle de l'huile que la composition en acide gras. En effet, des huiles trop riches en oméga 6 (principalement représenté par l'acide linoléique pour le colza et le tournesol) comparé aux omégas 3 (acide alpha-linolénique) peuvent amener à un épaississement du sang et à diverses maladies cardiovasculaires, cancers, … (Simopoulos, 2002). Un ratio inférieur à 5 est conseillé pour un effet bénéfique sur la santé humaine (Simopoulos, 2002). Ce ratio est de 2 pour l'huile de colza et est très élevé pour le tournesol (> 100) car les omégas 3 sont quasi inexistants dans sa composition en huile (Jahreis and Schäfer, 2011). D'autres paramètres comme les micronutriments peuvent rentrer en compte dans la qualité nutritionnelle des huiles, comme la vitamine E, importante pour lutter contre certaines maladies (Weber, Bendich & Machlin 1997) et présente en plus grande quantité dans les graines de tournesol que dans les graines du colza (respectivement 55 *versus* 30 mg pour 100g).

Tableau 1. Liste des principaux acides gras du colza et du tournesol classés par grand groupes d'acides gras associés à leurs effets sur la santé humaine

Classe acide gras	Principaux Acide gras (*Carbone : Insaturation - position première insaturation)*	Effet bénéfique	Effet nocifs	Reference
Saturés	Palmitique (*16:0*), stéarique (*18:0*)		Augmentation des maladies coronariennes, des maladies cardio-vasculaires	(Astrup and Dyerberg, 2011; de Souza et al., 2015)
Mono-insaturé	Oléique (*18:1-9*), Eicosénoïque (20:1-9)	Diminution des maladies inflammatoires		(Carrillo et al., 2012)
Polyinsaturé	Linoléique (18:2-6), Alpha-linolénique (18:2-3)	Réduction des maladies inflammatoires, des maladies cardiovasculaires, augmentation des agents anticancéreux		(Van Hoorn, Kapoor & Kamphuis 2008,Calder and Yaqoob, 2009; Jandacek, 2017; Ruxton et al., 2004)
Acide gras trans	Elaïdique (*t C18:1-9*)		Augmentation du surpoids chez les enfants et leurs mères, des maladies coronariennes, des maladies vasculaires	(Anderson et al., 2010; de Souza et al., 2015)

3. Rôle des pratiques agricoles et de la pollinisation entomophile sur le rendement de colza et de tournesol

a. *Importance de la pollinisation entomophile dans la production de colza et de tournesol*

Les fleurs de colza et tournesol sont hermaphrodites (Abrol 2007; Çetinbaş & Ünal 2014), c'est-à-dire capables d'autopollinisation. Ce taux d'autopollinisation est beaucoup plus important chez le colza, entre 53 et 83% (Becker et al., 1992), que chez le tournesol, entre 35

et 53.5% (Javed and Medhi, 1992; Roumet et al., 2012). Cette différence peut s'expliquer en partie par un système de protandrie semi-synchrone des parties mâles et femelles décrit chez le tournesol (Çetinbaş & Ünal 2014), c'est-à-dire que la maturité de la partie mâle et femelle est partiellement asynchrone, ce qui limite l'autopollinisation. Le colza est aussi pollinisé par le vent (Renard & Mesquida 1982; Hudewenz *et al.* 2014), cà hauteur de 3 à 12 % des rendements. Ce processus de pollinisation n'est pas décrit dans la littérature pour le tournesol.
La contribution de la pollinisation entomophile aux rendements varie fortement entre études et cultures. Pour le colza, elle varie d'un effet nul (0%) jusqu'à une augmentation de 176% (Tableau 2). Pour le tournesol, la contribution minimale des pollinisateurs est de base plus importante que pour le colza, elle va de 20 à 226%. Que ce soit pour le tournesol ou le colza, la méthode la plus utilisée pour estimer cette contribution est l'utilisation de filet (« PF », Tableau 2). Les méthodes qui utilisent un gradient de pollinisateurs ou l'ajout de ruches pour calculer la contribution des pollinisateurs fournissent des estimations plus faible (< 20%, excepté pour Sabbahi, de Oliveira & Marceau (2005) que les études qui utilisent des filets. Cette différence de contribution entre les deux méthodes pourraient venir de biais inhérents à ces méthodes (lire la partie « Limite des études sur le service de pollinisation »). Cependant ces biais sont rarement estimés (Bartomeus et al., 2014; Bommarco et al., 2012). Pour le tournesol, la variation des estimations de la contribution des pollinisateurs entre études ne semblent pas être déterminée par la méthode utilisée.
Les traits les plus communément utilisés pour calculer la contribution des pollinisateurs sont le poids de graines à l'échelle de la plante ou du m² pour le colza (Tableau 2). Pour le tournesol, il s'agit du poids des graines à l'échelle de la plante ou, à plus petite échelle, du succès de pollinisation (Tableau 2). Les études qui ont estimé la contribution des pollinisateurs sur le succès de pollinisation dans le tournesol ont des contributions plus importantes (Tableau 2) possiblement car ce trait ne prend pas en compte le compromis qui existe entre nombre de graines et poids moyen d'une graine chez le tournesol (Tamburini et al., 2017). Globalement, les échelles pour estimer la contribution des pollinisateurs n'intègrent pas les variations de densité de plantes entre parcelles (Tableau 2, excepté pour Lindström et al., 2016) mais cette échelle (quadrat de 50m²) ne prend pas en compte les variations de densité de plantes intra-parcellaires (Kayad et al., 2016).
Les études sur le colza et le tournesol sont en majorité cantonnées à des études expérimentales et sont donc rarement réalisées directement dans les parcelles des agriculteurs (7 études sur 18 pour le colza et 3 études sur 14 pour le tournesol, Tableau 2). D'autre part ; la contribution des pollinisateurs n'a jamais été évaluée à l'échelle de la parcelle (Tableau 2). Par conséquent, la part des pollinisateurs dans les rendements de colza et de tournesol reste incertaine.
Finalement, l'estimation de la contribution de la pollinisation entomophile sur la qualité de production de colza ou de tournesol est restreinte à quelques études. Pour le colza, 4 études ont montré que la pollinisation entomophile augmente le pourcentage d'huile par graine (Bartomeus et al., 2014; Bommarco et al., 2012; Marini et al., 2015; Oz et al., 2008) et 2 études pour le tournesol (Aslan et al., 2010; Nderitu et al., 2008) montrent des résultats similaires. Aucune étude n'a été réalisée sur la qualité nutritionnelle (par exemple, la composition en acides gras), et donc une partie de la contribution des pollinisateurs à la production du colza et du tournesol reste inconnue.

Tableau 2 Résumé des études sur la contribution des pollinisateurs sur les rendements de colza et de tournesol. Les cases en gris signalent une absence de données. Les variétés utilisées pour le colza sont toutes auto-compatibles et sont classées entre variété conventionnelle (Conv) et hybride (Hyb). Pour le tournesol, les variétés sont classées comme self-compatible (SC) ou self-incompatible (SI). Le trait utilisé pour calculer la contribution est identifié ainsi que l'échelle de l'expérimentation. La méthodologie identifie la méthode utilisée pour déterminer la contribution (lire « Limite des études sur la pollinisation »), la colonne expérimentation détermine si l'expérience a été réalisée dans les parcelles des agriculteurs (« plein champs ») ou dans des parcelles plantées pour cette occasion « expérimental ». PTD signifie Poids Total des Graines, GrP : gradient de pollinisateurs, Fi : pose de filet, Ca : cage avec pollinisateur et Ru : ruches ajoutées

Culture	Variété	Auteur	Experimen-tation	Méthodologie	Echelle	Traits (contribution)	Contribution insectes (%)	Augmenation rendement (t/ha)
Colza		Woodcock & al. 2016	Plein champs	GrP+Fi	Quadrat (1m²)	PTD par pied		**0.4**
		Samnegard & al. 2016	Expérimental	GrP+Fi	Plante	PTD par pied	**0**	
	Conv +	Lindström & al. 2016	Plein champs	Ru	Quadrat (50 m²)	PTD par m²	**0-10.6**	**0.45**
	Conv + Hyb	Marini & al. 2015	Expérimental	Fi	Quadrat (4m²)	PTD par m²	**0-19**	
		Mesquida & al. 1988	Expérimental	Ca+Fi	Quadrat (18m²)	PTD par m²	**0-30**	
		Koltowski & al. 2002	Expérimental	Fi	Quadrat (8m²)	PTD par m²	**10**	**0.6**
	Conv	Zou & al. 2017	Plein champs	GrP+Fi	Quadrat (0.4m²)	PTD par pied	**12**	
	Hyb	Sutter & Albrecht. 2016	Expérimental	Fi	Quadrat (4m²)	PTD par m²	**7-23**	
	Conv + Hyb	Hudewenz & al. 2014	Expérimental	Fi	Plante	PTD par pied	**13.7-50.9**	
		Maning & Boland 2000	Expérimental	Ru	Quadrat (1m²)	Siliques au m²	**16**	**0.32**
		Bommarco & al. 2012	Plein champs	GrP+Fi	Plante	PTD par pied	**18**	
		Bartomeus & al. 2014	Plein champs	GrP+Fi	Plante	PTD par pied	**20**	
		Desouza & al. 2011	Expérimental	Fi	Plante	PTD par pied	**22**	
	Conv	Stanley & al. 2013	Plein champs	Fi	Silique	PTD par silique	**30**	
		Sabbahi & al. 2005		Ru		PTD par pied	**46**	
	Hyb	Duran & al. 2010	Plein champs	Fi	Quadrat (2m²)	PTD par m²	**50**	**2.6**
		Abdel-Rahman & al. 2014	Expérimental	Fi	Plante	PTD par pied	**61**	
		Oz & al. 2008	Expérimental	Ca+Fi	Quadrat (20m²)	PTD par m²	**76**	**1.4**
		Adegas & Couto 1992	Expérimental	Ca+Fi	Quadrat (12m²)	Siliques au m²	**159**	
		van Gils & al. 2016	Expérimental	Fi	Plante	PTD par pied	**176**	
Tournesol	SC	Tamburini & al. 2016	Expérimental	Fi	Quadrat (2m²)	PTD par tête	**19.8**	
	SC	DeGrandhi-Hoffamn & Chambers 2006	Expérimental	Fi	Plante	Succès de pollinisation	**15-25**	
	SC	Tamburini & al. 2017	Expérimental	Fi	Quadrat (1m²)	PTD par tête	**25**	
	SC	Aslan & al. 2010	Expérimental	Fi+Ca	Quadrat (3m²)	PTD par tête	**37**	
	SC	Chambo & al. 2011	Expérimental	Fi	Plante	PTD par tête	**43**	
		Krishna & al. 2014	Expérimental	Fi	Plante	PTD par tête	**48.2**	
	SC	Nderitu & al. 2008	Expérimental	Fi	Plante	PTD par tête	**53**	
	SC	Carvalheiro & al. 2011	Plein champs	GrP+Fi	Plante	Succès de pollinisation + Poids moyen de 100 graines	**47-62**	
	SC	Dag & al. 2001	Expérimental	Fi	Plante	Succès de pollinisation	**49-86**	
	SI	Parker & al. 1982	Expérimental	Fi	Plante	Succès de pollinisation	**59**	
		Pisanty & al. 2013	Plein champs	GrP	Plante	Succès de pollinisation	**62**	
	SI	Greenleaf & al. 2006	Plein champs	GrP	Plante	Succès de pollinisation	**100**	
	SC	Altayeb & al. 2015	Expérimental	Ca+Fi	Quadrat (9m²)	PTD par m²	**162.3**	**1.04**
	SI + SC	Oz & al. 2009	Expérimental	Ca	Quadrat (22m²)	PTD par tête	**206-226**	

b. *Les pollinisateurs impliqués*

Que ce soit le colza ou le tournesol, ces deux plantes fournissent des ressources nectarifères et polliniques en importantes quantités pour les insectes sauvages (Rollin et al., 2015; Todd et al., 2016) ou domestiques (Requier et al., 2015; Rollin et al., 2015). Une large diversité d'insectes (papillons, coléoptères, mouches et abeilles) visitent les fleurs de colza ou de tournesol (Bommarco et al., 2012; Carvalheiro et al., 2011; Rader et al., 2015). Toutefois, la majorité des études ne fournit qu'une description de la communauté d'insectes visitant les

cultures mais n'identifie pas ceux qui sont responsables de la pollinisation des cultures. En effet, tous les insectes qui visitent les fleurs de colza ou de tournesol ne sont pas forcément des pollinisateurs. Une étude a montré que parmi les insectes qui visitaient les fleurs de colza, 60% d'entre eux ne portaient pas de pollen (Chifflet et al., 2011).

Deux méthodes permettent d'établir le lien entre production et pollinisateurs : l'utilisation de cage avec pollinisateurs (mais soumis à des biais, lire « Limite des études sur le service de pollinisation ») et les gradients de pollinisateurs. Plusieurs espèces ou guildes d'insectes ont été identifiées comme des pollinisateurs du colza (Tableau 3), mais il n'existe pas de consensus entre les études (Tableau 3). Les abeilles domestiques augmentent les rendements de colza sous cage ou lorsque des ruches sont ajoutées près des parcelles, mais cette augmentation n'est pas observée le long d'un gradient d'abondance de ce pollinisateur (Tableau 3). Pour les abeilles sauvages, seules des études en cage ont permis de mettre en évidence leur effet bénéfique sur les rendement de colza mais uniquement pour le genre *Osmia*, qui semble être peu présent *in natura* dans les parcelles de colza (Bommarco et al., 2012; Samnegard et al., 2016; Zou et al., 2017b). Seules deux études réalisées en cage ont étudié l'effet des bourdons sur les rendements de colzas et montrent des résultats contradictoires (Tableau 3). Les syrphes ont montré un effet positif sur les rendements de colza que ce soit grâce à l'utilisation des cages ou sur un gradient de visites (Tableau 3). Cela est étonnant puisque plusieurs études ont comparé leur efficacité pollinisatrice du colza à d'autres pollinisateurs et ont montré que cette efficacité était plus faible que pour les abeilles domestiques, les abeilles sauvages et les bourdons (Garratt et al., 2014b; Jauker et al., 2012). D'autres études ont montré que l'ensemble des pollinisateurs ou des pollinisateurs sauvages augmentent les rendements de colza (Tableau 3) mais n'identifient pas parmi ces insectes lesquels étaient les principaux contributeurs. Finalement, une seule étude a montré l'effet bénéfique de la diversité des pollinisateurs sauvages sur le colza (Tableau 3).

Les études qui ont cherché à identifier les pollinisateurs du tournesol sont beaucoup moins nombreuses que pour le colza. La majorité des études a montré un effet positif des abeilles domestiques sur les rendements du tournesol, excepté une étude (Tableau 3). L'effet des abeilles sauvages sur les rendements de tournesol est plus contrasté (Tableau 3). Les abeilles sauvages auraient une efficacité moindre pour polliniser le tournesol et leur bénéfice viendrait en partie d'un effet synergique avec les abeilles domestiques (Greenleaf and Kremen, 2006). En effet, la présence d'autres pollinisateurs augmente le nombre de visites des abeilles domestiques sur les têtes de tournesol et ainsi, leur efficacité (Carvalheiro et al., 2011; Greenleaf and Kremen, 2006). L'effet positif de la diversité des pollinisateurs sur la production du tournesol (Tableau 3) pourrait venir en partie de cette synergie entre abeilles domestiques et sauvages. Seule une étude en cage a montré que les bourdons augmentaient les rendements et pouvaient avoir un effet plus important que les abeilles domestiques (Aslan et al., 2010), mais cet effet n'a jamais été vérifié *in natura*.

Tableau 3. Résumé de l'effet des pollinisateurs sur la production de colza ou de tournesol selon la guilde de pollinisateurs. La métrique utilisée pour les pollinisateurs peut être une abondance (A), une richesse (R), ou un nombre de visite (V). Les taxons présents dans la communauté de pollinisateurs sont précisés si la communauté de pollinisateurs est décrite dans l'étude. Uniquement les études qui ont établi ou chercher à établir la relation entre la métrique des pollinisateurs et un trait de production (succès de pollinisation, graines au m²) sont présentées dans ce tableau. L'augmentation entre la métrique des pollinisateurs et le trait de production peut être nulle (0, case remplie en rouge) ou positive (+, case en bleu). L'effet des pollinisateurs est étudier au sein d'une cage où se trouve la culture et une communauté de pollinisateurs ajoutée (Ca), un ajout de ruches dans le paysage (Ru), ou l'analyse le long d'un gradient d'abondance ou de diversité de pollinisateurs (GP).

Culture	Etude	Guilde	Taxon (Famille ou genre)	Methode	Augmentation
Colza	van Gils & al. 2016	Abeille (A)		GrP	0
	Samnegard & al. 2016	Abeille (A)	*Apis, Patellapis, Lasioglossum, Lipotriches, Seladonia*	GrP	0
	Samnegard & al. 2016	Abeille (R)	*Apis, Patellapis, Lasioglossum, Lipotriches, Seladonia*	GrP	0
	Garratt & al. 2014	Abeille domestique (A)	*Apis*	Ca	+
	Oz & al 2008	Abeille domestique (A)	*Apis*	Ca	+
	Adegas & Couto 1992	Abeille domestique (A)	*Apis*	Ca	+
	Mesquida & al 1988	Abeille domestique (A)	*Apis*	Ca	0
	Zou & al. 2017	Abeille domestique (A)	*Apis*	GrP	0
	Bommarco & al. 2012	Abeille domestique (A)	*Apis*	GrP	0
	Samnegard & al. 2016	Abeille domestique (A)	*Apis*	GrP	0
	Lindstrom & al. 2016	Abeille domestique (A)	*Apis*	Ru	+
	Maning & Boland 2000	Abeille domestique (A)	*Apis*	Ru	+
	Sabbahi & al. 2000	Abeille domestique (A)	*Apis*	Ru	+
	Jauker & al. 2012	Abeille sauvage (A)	*Osmia*	Ca	+
	Garratt & al. 2014	Abeille sauvage (A)	*Osmia*	Ca	+
	Garratt & al. 2014	Bourdon (A)	*Bombus*	Ca	+
	Sutter & Albrecht 2016	Bourdon (A)	*Bombus*	Ca	+
	Mesquida & al 1988	Bourdon (A)	*Bombus*	Ca	0
	Mesquida & al 1988	Mouche (A)	*Calliphora*	Ca	0
	Bommarco & al. 2012	Pollinisateurs sauvages (A)	*Syrphidae, Bombus, Empis*	GrP	0
	Zou & al. 2017	Pollinisateurs sauvages (A)	*Pieris, Eucera, Lasioglossum*	GrP	+
	Zou & al. 2017	Pollinisateurs sauvages (R)	*Pieris, Eucera, Lasioglossum*	GrP	+
	Jauker & al. 2012	Syrphe (A)	*Episyrphus, Eristalis*	Ca	+
	Garratt & al. 2014	Syrphe (A)	*Episyrphus*	Ca	+
	van Gils & al. 2016	Syrphe (V)		GrP	+
	Bommarco & al. 2012	Tous pollinisateurs (R)	*Syrphidae, Bombus, Empis*	GrP	0
	Woodcock & al. 2016	Tous pollinisateurs (V)	*Apis, Bombus, Andrenidae, Halictidae, Syrphidae, Anthomyiidae, Muscidae*	GrP	+
	Bartomeus & al. 2014	Tous pollinisateurs (V)	*Apis, Bombus, Syrphidae*	GrP	+
Tournesol	Aslan & al. 2010	Abeille domestique (A)	*Apis*	Ca	+
	Altayeb & al. 2015	Abeille domestique (A)	*Apis*	Ca	+
	Oz & al 2009	Abeille domestique (A)	*Apis*	Ca	+
	Pisanty & al. 2013	Abeille domestique (A)	*Apis*	GrP	+
	Greenleaf & al. 2006	Abeille domestique (A)	*Apis*	GrP	+
	Hevia & al. 2006	Abeille domestique (A)	*Apis*	GrP	0
	Pisanty & al. 2013	Abeille sauvage (A)	*Lasioglossum*	GrP	0
	Greenleaf & al. 2006	Abeille sauvage (A)	*Svastra, Antphora, Melissodes*	GrP	+
	Hevia & al. 2006	Abeille sauvage (A)	*Lasioglossum*	GrP	+
	Aslan & al. 2010	Bourdon (A)	*Bombus*	Ca	+
	Carvalheiro & al. 2011	Tous pollinisateurs (R)		GrP	+

c. *Interaction entre pratiques agricoles et pollinisation entomophile*

La production de tournesol ou de colza n'est pas seulement dépendante des pollinisateurs. Les rendements de colza et de tournesol augmentent avec l'application de plusieurs fertilisants: l'azote (Abbadi et al., 2008; Rathke et al., 2005), le phosphore (Lickfett et al., 1999; Zubillaga et al., 2002) et le potassium (Amanullah and Khan, 2010; Cong et al., 2015). Les mécanismes qui permettent cette augmentation (augmentation du nombre de graines, du poids d'une graine) sont peu décrits dans la littérature, mais un compromis entre nombre de graines et qualité des graines est observé lorsque les fertilisants sont utilisés en grande quantité. En effet, le pourcentage de lipides par graine est diminué pour le colza avec l'augmentation de l'azote que ce soit pour le colza ou le tournesol (Abbadi et al., 2008; Rathke et al., 2005).

Les rendements de tournesol et de colza augmentent avec la densité de plantes, en augmentant le nombre de graines par m² (Barros et al., 2004; Kuai et al., 2015; Zhang et al., 2012) malgré une corrélation négative entre nombre de graines par pied et densité de plantes. L'augmentation de la densité par parcelle pourrait avoir un effet négatif sur la qualité des graines, possiblement dû à la compétition entre plantes (Zhang et al., 2012).

D'autres pratiques comme l'utilisation d'herbicides ou d'insecticides pour réduire les populations d'adventices ou d'insectes ravageurs retrouvés dans les parcelles de colza et de tournesol (Bijanzadeh et al., 2010; Michaud et al., 2007; Simić et al., 2011; Zhang et al., 2017) peuvent influencer la présence des pollinisateurs. Les insecticides ne sont pas spécifiques aux insectes ravageurs. Plusieurs insecticides peuvent réduire la survie des abeilles domestiques (Henry et al., 2012; Woodcock et al., 2017) ainsi que celle des bourdons et des abeilles sauvages (Goulson et al., 2015; Ben A. Woodcock et al., 2016; Woodcock et al., 2017). Ces insecticides peuvent par exemple réduire la reproduction des reines chez les bourdons (Woodcock et al., 2017), et réduire le nombre de bourdons qui vont visiter les parcelles (Stanley et al., 2015) ou diminuer le taux de retour des abeilles domestiques la ruche (Henry et al., 2012). Toutefois, il a été montré que les parcelles traitées par des insecticides pouvaient être plus attractives pour les pollinisateurs car en réduisant les insectes ravageurs qui s'attaquent aux bourgeons floraux, le nombre de fleurs disponibles pour les pollinisateurs est plus important ainsi que la quantité de nectar dans ces fleurs (Lindstrom et al., 2017). De façon similaire, d'autres pratiques, comme la densité de semis, pourraient augmenter la présence des pollinisateurs dans les parcelles en proposant des ressources florales plus importantes. La réduction d'herbicide peut indirectement réduire la présence des pollinisateurs dans les parcelles : en réduisant la présence d'adventices dans la parcelle celle-ci pourrait être moins attractive pour les pollinisateurs (Norfolk et al., 2016). Outre l'étude de Stanley *et al.* (2015), peu d'études ont montré une modification du service de pollinisation par ces pratiques.

Finalement, certaines pratiques pourraient modifier directement la contribution des pollinisateurs, plutôt que leur présence, comme le choix des variétés. Pour le tournesol, deux types de variétés sont utilisés : les variétés auto-incompatibles (seulement allofécondation) et les variétés autofertiles (fécondation croisée et autofécondation). Les variétés auto-incompatibles, par définition, sont plus sensibles aux pollinisateurs que les variétés autofertiles qui peuvent compenser l'absence de pollinisateurs par de l'autopollinisation. Pour le colza, deux types de variétés sont utilisées par les agriculteurs : les variétés dites

« conventionnelles » issues de croisement entre colzas d'une même lignée et les colzas « hybrides restaurés » issues du croisement de deux lignées. Plusieurs études ont montré que les colzas « conventionnels » étaient plus dépendants des pollinisateurs que les colzas hybrides (Lindström et al., 2016; Marini et al., 2015) car ceux-ci sont capables de compenser l'absence de pollinisateurs (Marini et al., 2015). Une autre étude a montré que cet effet était plutôt dû à une différence entre variétés et ne dépendait pas du type de variété (Hudewenz et al., 2014).

E. Objectifs et plan de thèse

1. Problématique

Le service de pollinisation délivré par les insectes est capital pour la production agricole (Gallai et al., 2009; Klein et al., 2007). Cependant dans la plupart des études qui ont cherché à quantifier le bénéfice issu de la pollinisation entomophile, les méthodes utilisées sont soumises à différents biais, ou les expérimentations sont réalisées à des échelles trop petites qui ne sont pas forcément représentatives de la production de graines à l'échelle de la parcelle. De plus, la majorité des études sont réalisées en conditions expérimentales, c.-à-d. dans des conditions simplifiées par rapport aux parcelles agricoles et ne prennent pas en compte les possibles interactions entre pratiques agricoles et pollinisateurs. Le peu d'études réalisées directement dans les parcelles agricoles pourraient d'ailleurs être la principale origine de l'absence de prise en compte des pollinisateurs par les agriculteurs dans leur système de production (Austin et al., 2015; Chen et al., 2017; Misganaw et al., 2017).

L'objectif premier de cette thèse sera donc de quantifier l'importance de la pollinisation entomophile dans la production de colza et de tournesol dans des conditions les plus réalistes possible, c.-à-d. directement dans les parcelles des agriculteurs. Les parcelles utilisées dans nos expérimentations seront choisies le long de gradients de différents éléments du paysage connus pour déterminer la présence des pollinisateurs. Ceci nous a permis d'obtenir des gradients de pollinisateurs sur lesquels les parcelles ont été choisies. Ce gradient de pollinisateurs nous permettra de quantifier le bénéfice total des pollinisateurs sur le rendement de colza et de tournesol à une échelle pertinente : la parcelle. Le rendement, ainsi que les différentes pratiques agricoles réalisées dans les parcelles ont été obtenues grâce à des enquêtes auprès des agriculteurs. Ces enquêtes permettront d'identifier les pratiques agricoles qui peuvent modifier la contribution des pollinisateurs.

Dans ces mêmes parcelles, la contribution des pollinisateurs sera calculée à l'échelle de la plante. Ces expérimentations à l'échelle de la plante viseront aussi à identifier les traits des plantes qui sont modifiés par les pollinisateurs (succès de pollinisation, nombre de graines, poids moyen des graines,…), ainsi que d'autres traits indépendants de la pollinisation comme les densités de plantes, mais néanmoins nécessaires à l'élaboration du rendement dans le but de relier la mesure du bénéfice des pollinisateurs calculé à l'échelle de la plante à celle de la parcelle.

Toujours dans ces mêmes parcelles, des filets seront utilisés pour exclure différents processus de pollinisation. Cette approche aura pour but de quantifier l'importance de la pollinisation entomophile par rapport aux autres processus de pollinisation (vent et autofécondation) et permettra d'identifier les biais inhérents à cette méthode. La contribution des insectes calculée

par cette méthode sera comparée à celle obtenue à l'échelle de la parcelle, dans le but de déterminer si l'utilisation de filets peut être un moyen fiable d'évaluer la contribution totale des pollinisateurs à l'échelle de la parcelle. Cette comparaison n'a jamais été réalisée malgré l'utilisation prépondérante des filets dans les études qui quantifient la contribution entomophile dans la production agricole.
L'effet des pollinisateurs sera aussi évalué sur la qualité des graines, à la fois sur le pourcentage de lipides par graine et sur leur composition en acide gras, qui restent pour le moment peu étudiés. Les filets ainsi que le gradient de pollinisateurs seront utilisés pour quantifier l'effet des pollinisateurs et de la pollinisation entomophile sur la qualité des graines.
Finalement, tout au long de ces études, en utilisant deux méthodes différentes de captures des insectes, nous chercherons à déterminer quels sont les pollinisateurs importants du colza et du tournesol qui pour le moment restent en débat. Leurs contributions relatives seront évaluées en excluant les pollinisateurs selon leur taille grâce à l'utilisation de filet avec différentes tailles de mailles.

2. Plan de thèse :

La thèse sera organisée en 4 chapitres, rédigés sous forme d'articles.

Chapitre 1 : Les abeilles augmentent les rendements de colza en conditions réelles de culture
Auteurs : Thomas Perrot, Sabrina Gaba, Maryline Roncoroni, Jean-Luc Gautier & Vincent Bretagnolle

Cette étude quantifie le bénéfice des pollinisateurs en termes de rendement dans la production de colza à l'échelle de la parcelle et à l'échelle de la plante. Elle identifie aussi les principaux pollinisateurs, ainsi que les mécanismes à l'échelle de la plante, qui permettent l'augmentation du rendement à l'échelle de la parcelle.

- ⇨ Ce chapitre est publié dans la revue *Agriculture, Ecosystem and the Environment*

Chapitre 2: Quantification expérimentale de l'effet de la pollinisation par les insectes sur les rendements de tournesol: réconcilier les estimations à l'échelle de la plante à celles de la parcelle
Auteurs : Thomas Perrot, Sabrina Gaba, Maryline Roncoroni, Jean-Luc Gautier, Alexis Saintilan & Vincent Bretagnolle

Cette étude quantifie le bénéfice des pollinisateurs en termes de rendement dans la production de tournesol à l'échelle de la parcelle et à l'échelle de la plante. Elle identifie aussi les principaux pollinisateurs ainsi que les mécanismes à l'échelle de la plante qui permettent l'augmentation du rendement à l'échelle de la parcelle.

- ⇨ Ce chapitre fait l'objet d'un article en révision majeure dans la revue *Basic and Applied Ecology*

Chapitre 3: Une solution basée sur la nature en pratique : une modélisation écologique et économique montre que les pollinisateurs sont plus efficaces que les produits agrochimiques dans la production de colza

Auteurs : Rui Catarino, Thomas Perrot, Vincent Bretagnolle & Sabrina Gaba

Ce chapitre quantifie la contribution relative des pollinisateurs et des pratiques agricoles dans la production de colza, et réalise une évaluation économique du service de pollinisation. Ce chapitre identifie aussi les principales pratiques agricoles qui peuvent modifier la contribution des pollinisateurs.

- ⇨ Ce chapitre fait l'objet d'un article qui sera soumis à *Ecology letters.*

Chapitre 4: Les abeilles domestiques améliorent la qualité de la production de colza

Auteurs : Thomas Perrot, Vincent Bretagnolle, Valérie Febvret, Annick Matejicek, Stéphane Grégoire & Sabrina Gaba

Cette étude détermine l'effet des pollinisateurs sur la qualité du colza en analysant les variations de pourcentages de lipides et de composition en acide gras. Les effets des pollinisateurs sont quantifiés le long d'un gradient de pollinisateurs et à l'aide d'une expérimentation d'exclusion des différents processus de pollinisation, en tenant compte de l'effet des principales pratiques agricoles.

- ⇨ Ce chapitre fait l'objet d'un article qui sera soumis à la revue *Proceeding of the Royal Society London B*

Matériel et méthode

A. Site d'étude

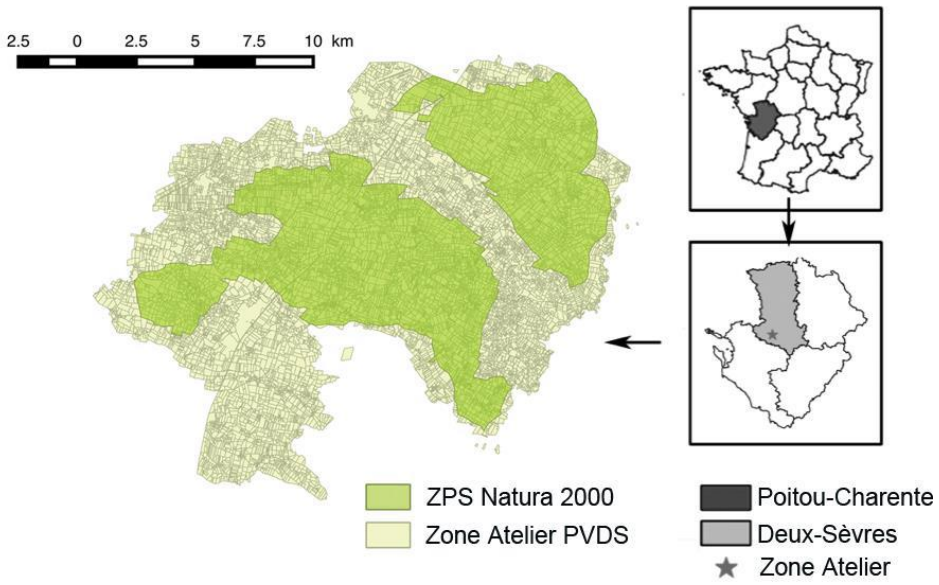

Fig. 11. Localisation de la Zone atelier « Plaine et Val de Sevre »

Toutes les expérimentations ont été réalisées dans la Zone Atelier « Plaine & Val De Sèvre » (ZA PVS, Fig 11, Bretagnolle *et al.* 2018) de 2013 à 2017. C'est une zone de 430 km², comptant 13 000 parcelles partagées entre 450 exploitants. Les surfaces agricoles représentent 87% de la zone. C'est une agriculture principalement céréalière et intensive. Les colzas et les tournesols représentent respectivement en moyenne 8% et 10% des cultures de la ZA PVS (Bretagnolle et al., 2018). Cependant des paysages variés se côtoient, allant de grandes zones céréalières, avec des parcelles de très grandes surfaces et peu d'éléments semi-naturels (ESN, haie, bois, Fig 12.a) à des zones agricoles plus extensives avec des parcelles de petites tailles et une large proportion d'éléments semi-naturels et de haies (Fig 12.b). De plus, une large partie de la ZA PVS est classée Natura 2000 (Fig 11) qui offre des aides aux agricultures pour promouvoir une agriculture plus extensive, comme le passage en agriculture biologique. L'occupation du sol (l'espèce de plante cultivée dans chaque parcelle agricole, les éléments semi-naturels (ESN), les habitations) est répertoriée chaque année depuis 1994.

Fig. 12. Exemple de paysage de la ZA PVS

B. Choix des parcelles

Le choix des parcelles a été réalisé en tenant compte de trois gradients paysagers :

- La quantité d'ESN (bois et haie) ;
- La quantité de prairies ;
- La quantité de parcelles en agriculture biologique.

Ces éléments ont tous montrés une influence sur la présence des pollinisateurs dans différentes études (pour les ESN (Le Féon et al., 2010), pour les prairies (Bennett and Isaacs, 2014), pour les cultures en agriculture biologique (Holzschuh et al., 2008)).

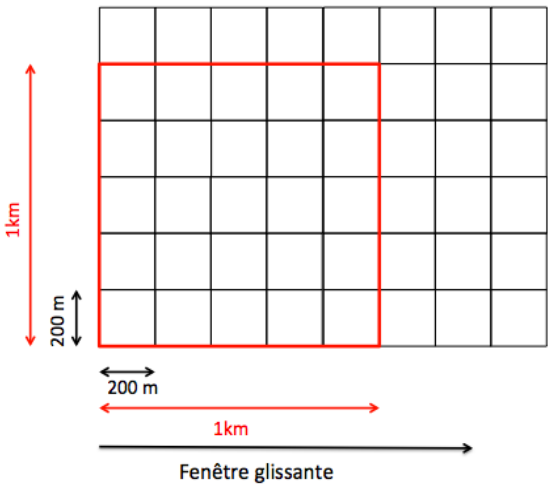

Fig. 13. Fenêtre glissant utilisé pour la sélection de paysages avec des pas de 200m

Les métriques du paysage sont calculées dans des carrés de 1 km² (Bretagnolle et al., 2018) en utilisant une fenêtre glissante (Fahrig et al., 2011; Pasher et al., 2013) avec des pas de 200 m (Fig 13). Une fois ces métriques calculées pour chacun des carrés, un tirage aléatoire est réalisé. Entre 40 et 60 paysages (carrés de 1km²) sont choisis par année. Ces paysages sont choisis pour maximiser le contraste au sein d'un gradient et minimiser la corrélation des métriques entre elles. Les paysages avec une autoroute, ou avec une proportion trop importante d'habitations ou de forêt sont exclus du tirage. Une distance d'au moins 200 m entre chaque paysage sélectionné est respectée. Le tirage est réitéré chaque année. Les paysages sélectionnés l'année suivante sont choisis en évitant le recouvrement avec ceux de l'année précédente (Fig 14). Dans chaque carré, entre 3 et 4 parcelles sont sélectionnées, chacune appartenant à un type de culture différent (colza, tournesol, céréale, maïs et prairie) et les agriculteurs propriétaires de ces parcelles sont appelés pour obtenir leur accord en vue de mettre en place les expérimentations.

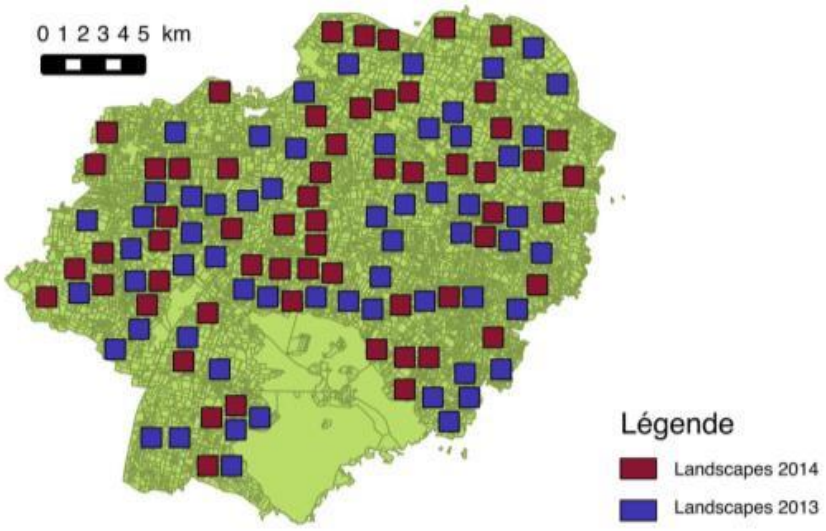

Fig. 14. Les paysages sélectionnés de 2013 et 2014

C. Les expérimentations :

1. Les captures de pollinisateurs

Deux méthodes complémentaires ont été utilisées pour estimer l'abondance et la richesse des pollinisateurs visitant les cultures de colzas et de tournesols. La première méthode consiste en la mise en place de pièges de couleurs (*pan trap* en anglais, Westphal *et al.* 2008). Ce sont des bols en plastique, remplis d'eau savonneuse peints de différentes couleurs, (bleu, jaune, ou blanc) pour prendre en compte les préférences de couleurs chez les pollinisateurs (Westphal et al., 2008). Ils sont placés sur des piquets en bois à la hauteur de la végétation (Westphal et al., 2008). De 2013 à 2015, les pan-traps sont placés au bord et au centre de la parcelle (50m) et à partir de 2016, seuls les pan-traps au centre de la parcelle sont installés. Chaque bol de couleur est doublé par position (Fig 15). Les pan-traps sont laissés 4 jours dans la parcelle. Les pan-traps sont placés dans les parcelles de colza ou de tournesol au moment de la floraison mais aussi dans les parcelles adjacentes pour éviter la dilution ou un effet attractif des captures de pollinisateurs au milieu des colzas ou des tournesols (Holzschuh et al., 2016). Ces parcelles seront utilisées pour estimer l'abondance des pollinisateurs qui visitent les parcelles de colzas et de tournesol (voir Chapitre I et II). Les pan-traps sont connus pour sous-

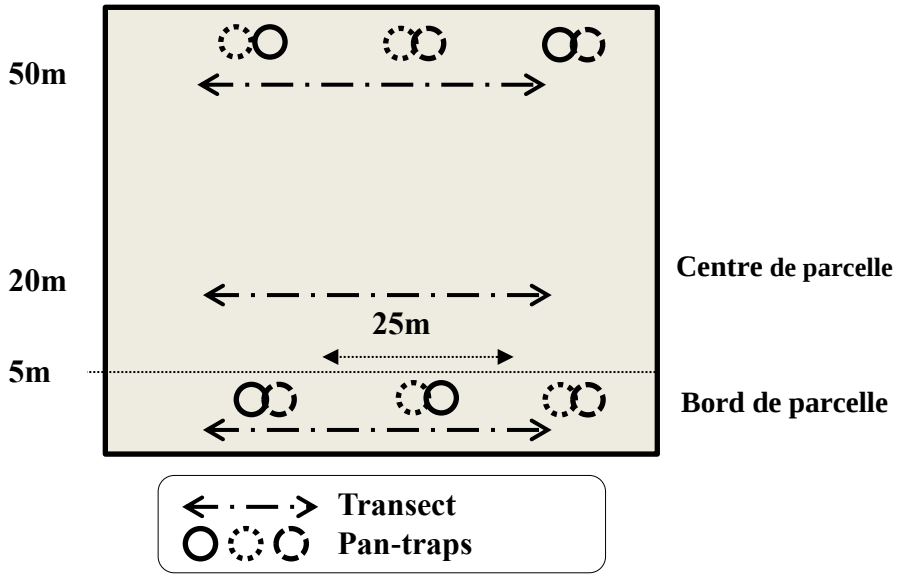

Fig. 15. Position des pièges à couleur (pan traps) et des transects filet fauchoir dans les parcelles

estimer fortement l'abondance des abeilles domestiques (Westphal et al., 2008). Pour compléter les captures de pollinisateurs par les pan-traps, une seconde méthode est utilisée. Les pollinisateurs sont capturés par des filets fauchoirs (*sweep net*) le long de transects de 50m (Westphal et al., 2008). Ces transects sont réalisés au bord et au centre de la parcelle (Fig 15) et à partir de 2016, un transect supplémentaire est réalisé à 20m (Fig 15). En 2013-2014, les pollinisateurs sont capturés sur 50 tentatives représentant 50 « coup de filets » fauchoirs. A partir de 2015, les pollinisateurs sont capturés sur 10 minutes par transect sans prendre en compte le nombre de tentatives de captures. Tous les pollinisateurs sont capturés par filet fauchoirs excepté les abeilles domestiques qui sont comptées visuellement. Chaque transect est chronométré pour s'assurer d'un effort de capture similaire entre parcelles. Chaque fois qu'un insecte est capturé, le chronomètre est arrêté, le temps de sortir l'insecte du filet et de le

placer dans un tube pour une identification future. Ces transects sont réalisés pour obtenir des conditions optimales de capture des pollinisateurs, c.-à-d. par temps ensoleillé avec une température supérieure à 15°C et des vitesses de vent faible (Westphal et al., 2008).
Une fois les pollinisateurs capturés, ils sont ramenés au laboratoire et identifiés par des entomologistes professionnels. Quatre guildes de pollinisateurs sont particulièrement ciblées ; les abeilles domestiques, les bourdons, les abeilles sauvages et les syrphes. Les individus sont déterminés à l'espèce sauf les abeilles sauvages de 2013 et 2014 qui sont déterminées au genre mais encore en cours de détermination à l'espèce.

2. La contribution des pollinisateurs

a. *Les métriques de production du colza et du tournesol*

La contribution des pollinisateurs va être calculée à différentes échelles. Le rendement à l'échelle de la parcelle est obtenu par enquête auprès des agriculteurs à l'issue de la saison d'expérimentions entre septembre et mars. Les enquêtes permettent également d'acquérir des informations sur les pratiques agricoles réalisées dans les parcelles (fertilisants, pesticides, variétés semées,…). Ces enquêtes sont disponibles de 2013 à 2016.
Les expérimentations à l'échelle de la plante se sont déroulées de 2013 à 2016 pour le colza et de 2015 à 2017 pour le tournesol. Pour le colza, 6 plantes ont été choisies à deux différentes positions, au bord de la parcelle et à 20m dans la parcelle (3 par position). Pour les tournesols, 4 plantes sur une même ligne ont été sélectionnées à 3 ou 5 positions différentes selon l'année ; 5 positions en 2015 (bord de la parcelle, 5, 15, 35 et 75 m) et 3 en 2016 et 2017 (bord de la parcelle, 15 et 75 m. Les expérimentations d'exclusion sont réalisées (voir partie suivante) et 5 jours avant la récolte de la parcelle par les agriculteurs, les branches sous expérimentations et la plante complète à partir de 2015 sont récoltées pour le colza. Pour le tournesol, la plante complète est ramassée et ramenée au laboratoire. Différentes métriques sont alors mesurées et calculées ; le succès de fructification, le nombre de graines par silique, le poids moyen des graines, la biomasse de la plante et le poids total des graines par pied, ainsi que le pourcentage de lipides et la composition en acides gras des graines pour le colza ; le diamètre des têtes de tournesol, le poids moyen des graines, le nombre de graines et leurs poids par plante pour le tournesol.
Ces différentes métriques de la production sont utilisées pour calculer la contribution des pollinisateurs.

b. *Les filets d'exclusions*

Des filets avec différentes tailles de mailles ont été posés sur les branches de colza et sur les têtes de tournesol afin d'estimer la contribution des processus de pollinisation par les gros pollinisateurs (« GP »), les petits pollinisateurs (« PP »), le vent (« V ») et l'autopollinisation (« AP »). L'échelle à laquelle le filet est posé diffère selon la culture. Pour le colza, les filets vont être posés sur la même plante mais sur des branches secondaires différentes (Fig 16). Pour le tournesol, un seul type de filet sera posé par plante (Fig 16) mais les différents types de filets seront posés sur des tournesols d'une même ligne (Fig 16). Une branche de colza ou une plante de tournesol servira de témoin et reflètera les effets de l'ensemble des processus de pollinisation (« GP +PP +V +AP », Fig. 16). Un filet à grandes mailles (taille = 3 mm, Fig. 16) est utilisé pour empêcher la pollinisation des gros pollinisateurs (« PP +V +AP », Fig. 16). Un filet à petites mailles (taille = 0.6mm, Fig 16) empêche la pollinisation de tous les

pollinisateurs (« V +AP », Fig 16). Finalement, un tissu « Osmolux » (Prantek France, Fig 16) est utilisé. Ce tissu permet uniquement les échanges gazeux et empêche tous les processus de pollinisation sauf l'autopollinisation («AP», Fig 16). Le nombre de traitements peut varier en fonction de l'année (voir chapitre I, II & IV).

Par un jeu de différences entre ces traitements, la contribution des différents processus de pollinisation est estimée. La différence entre le contrôle et le traitement grande maille donne la contribution des gros pollinisateurs, celle entre le traitement grande maille et petite maille donne la contribution des petits pollinisateurs. La différence entre la petite maille et l'osmolux donne la contribution du vent. La contribution de l'autopollinisation est obtenue par la production sous « osmolux ». Cette production peut être calculée à partir de différents traits du colza ou tournesol ; le succès de pollinisation, le poids des graines… . Les différences obtenues sont divisées par le contrôle pour obtenir un pourcentage qui pourra être comparé à celui obtenu à plus grande échelle comme le rendement grâce aux gradients de pollinisateurs.

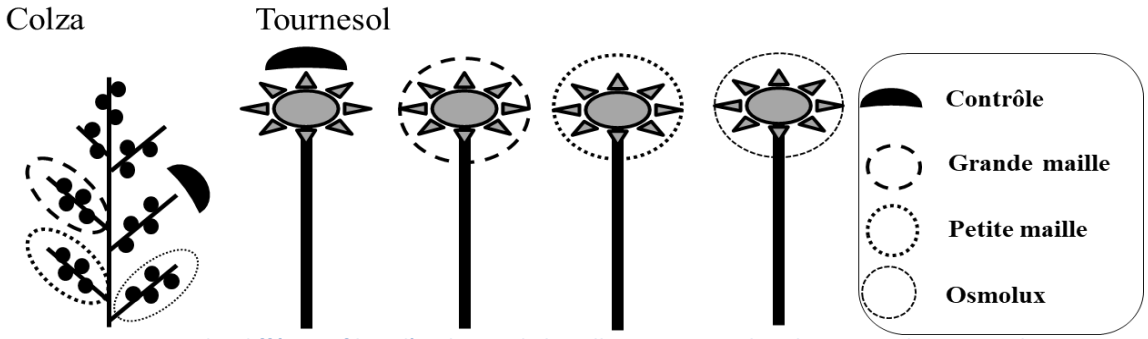

Fig. 16. Disposition des différents filets d'exclusion de la pollinisation pour le colza et pour le tournesol

c. *Le gradient de pollinisateurs*

Cette méthode est similaire à celle proposée par Vaissière, Freitas & Gemmill-Herren (2010). Elle met en relation une métrique de production de la culture (colza ou tournesol) à une métrique représentant les pollinisateurs. Différentes métriques peuvent être calculées pour les pollinisateurs, leur abondance totale, par guilde, par genre ou la diversité spécifique,… . La métrique de production peut être le rendement à l'échelle de la parcelle, le succès de pollinisation à l'échelle de la plante, la quantité de lipides par graines ou même la contribution des pollinisateurs calculée dans la partie précédente (voir Chapitre I, II, IV, Fig 17). Le bénéfice des pollinisateurs est calculé grâce au modèle statistique entre la métrique de production et la métrique des pollinisateurs. Le bénéfice est déterminé en soustrayant la valeur du trait de production pour la valeur maximale des pollinisateurs (B dans Fig 17) à la valeur du trait pour la valeur minimale des pollinisateurs (A dans Fig 17). La contribution, en termes de pourcentage, est obtenue en

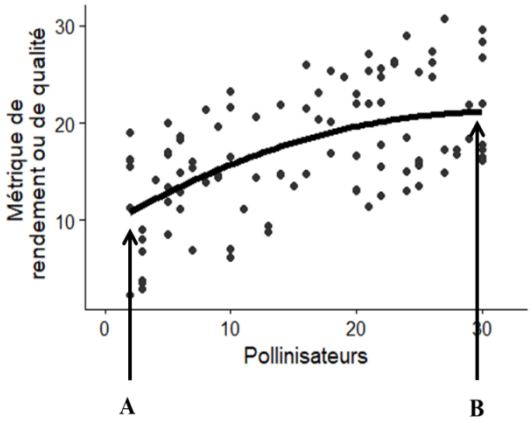

Figure 17. Relation entre la métrique des pollinisateurs (abondance, richesse,…) et une métrique de production (rendement, qualité,…). La ligne noire représente la relation prédite par un modèle statistique et la bande grise l'intervalle de confiance de cette relation.

divisant le bénéfice précédemment calculé par la valeur du trait de production pour la valeur minimale (A dans Fig 17). Un intervalle de confiance du bénéfice ou de la contribution peut être obtenu grâce à l'intervalle de confiance de la courbe calculé par le modèle.

Chapitre I :

Les abeilles augmentent les rendements de colza en conditions réelles de culture

Avant-propos et résumé du chapitre 1 :

Plus de 70% des plantes utilisées pour la production agricole sont dépendantes des pollinisateurs pour leur production de graines. De nombreuses études ont cherché à évaluer la contribution des pollinisateurs dans les rendements de ces cultures en utilisant différentes méthodes. Néanmoins, ces expérimentations sont pour la plupart réalisées en utilisant des méthodes pouvant comporter différents biais ou sur de petites échelles n'incluant pas les potentiels compromis entre les différents traits des plantes ou les variations de densité de plante. La plupart des études sont réalisées en condition simplifiée ne prenant pas en compte les potentielles interactions entre pollinisateurs et pratiques agricoles et donc pouvant amener à une estimation biaisée de l'importance des pollinisateurs dans ces cultures. Dans cette première étude, nous nous sommes intéressés au bénéfice des pollinisateurs dans les rendements de colza. Cette culture est très présente dans les agrosystèmes français et européens et sa surface ne cesse de croître. La contribution des pollinisateurs aux rendements de colza a été évaluée par de nombreuses études mais les bénéfices des pollinisateurs varient très fortement entre études : les pollinisateurs pouvant n'avoir aucun effet sur la production de graines ou allant jusqu'à la doubler. De plus, le bénéfice des pollinisateurs n'a jamais été évalué à l'échelle de la parcelle en condition réelle, laissant l'importance des pollinisateurs dans les rendements du colza peu renseignée. Similairement, les pollinisateurs impliqués dans la pollinisation du colza varient entre études.

Dans cette étude, la contribution des pollinisateurs au rendement de colza est à la fois estimée à l'échelle de la plante ainsi qu'à l'échelle de la parcelle. Grâce à des gradients de pollinisateurs, nous estimons que ces derniers peuvent augmenter les rendements de colza à l'échelle de la parcelle de plus de 35% entre les deux cas extrêmes du gradient de pollinisateurs. A l'échelle de la plante, les pollinisateurs augmentent le succès de pollinisation et ainsi le nombre de graines par plante malgré un compromis entre le succès de pollinisation et le nombre de graines par silique. En utilisant des filets à cette même échelle, la contribution des pollinisateurs est similaire à celle obtenue à l'échelle de la parcelle, mais ce résultat n'est obtenu qu'après avoir pris en compte différents biais dus à l'utilisation de cette méthode. Cette expérimentation nous permet aussi de déterminer que le principal processus de pollinisation dans le colza est l'autofécondation suivi par la pollinisation entomophile et complété par la pollinisation par le vent.

Les principaux pollinisateurs du colza dans notre site d'étude sont les abeilles domestiques et les abeilles sauvages (principalement le genre *Lasioglossum).* Nous n'avons trouvé aucun effet des syrphes confirmant que leur efficacité à polliniser le colza est plus faible que celle des abeilles. La contribution relative des gros pollinisateurs (associés aux abeilles domestiques) calculée grâce à l'utilisation des filets est similaire à celle des petits pollinisateurs (associés à la diversité des genres d'abeilles). Cela démontre que les abeilles sauvages (comme la majorité des genres sont des genres d'abeille sauvages) contribuent à part égale avec les abeilles domestiques dans la pollinisation du colza.

Cette étude confirme l'importance capitale des abeilles dans la production de colza et la nécessité de les intégrer dans les systèmes agricoles.

Bees increase oilseed rape yield under real field conditions

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Authors' contributions

M. Roncoroni, J-L Gautier and T. Perrot collected the field data; V. Bretagnolle and S. Gaba designed the study. V. Bretagnolle, S. Gaba and T. Perrot designed the methodology, analysed the data and wrote the manuscript.

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Abstract
Oilseed rape (OSR, *Brassica napus* L.) is a common crop found in many European agricultural landscapes. It is pollinated by a wide variety of insects, but the reported contribution of pollinators to yield varies widely between studies (from 0 to 50%). Moreover, such a contribution has seldom been estimated at the field scale in real farming conditions. We analysed OSR yields in response to insect pollination; over four years, at two different scales: farm fields and individual plants. We used both empirical and experimental approaches along a gradient of pollinator diversity and abundance. The empirical approach was based on farm surveys (151 fields) while the experimental approach used various pollination exclusion methods (570 plants in 101 fields) to estimate the relative contributions of insect, wind, and self-pollination. The OSR yields were positively correlated to total bee abundance and bee genera diversity, through improved fruiting success and plant seed mass (after adjusting for plant biomass). Hoverfly diversity and abundance, and bumblebee abundance did not have any effect. The main OSR pollinators in our study were honeybees (*Apis mellifera*) and wild bees (*Lasioglossum* spp.). Yields were increased, on average, by up to 37.5% (27.7% to 47.5%) at field scale when bee genera diversity increased from a single genus to more than 10 genera (pan-trap data). Insect pollination contributed about 30% of plant yield. Self-pollination and wind pollination accounted for the remaining 70%, with self-pollination being the major contributor. Our study demonstrates that pollinator diversity and abundance, at least at very high levels, have a major effect on OSR yields. This suggests that establishing a monetary value for pollination services in OSR farming systems could be used to balance the cost of managing semi-natural habitats or meadows to maintain bees and other pollinators.

Highlights

- Pollination by insects increased oilseed rape yield at field scale by up to 35%.
- Insects improved pollination success at plant scale.
- Bee diversity (at genus), and honeybee and wild bees abundances contributed most.
- Monetarised pollination services can be used to balance the cost of conservation of pollinator habitats.

Keywords
Agroecology, Bumblebee, Hoverfly, Ecosystem services, Honeybee, Lasioglossum, Pollination

1. Introduction

In most angiosperms, pollen transfer depends on animals (Ollerton et al., 2011), and this holds true for both wild and domesticated plant species, of which 70% are pollinator dependent (Klein et al., 2007). The economic value of pollination service has been estimated at 10% (€149 billion) of yearly global world agricultural production (Gallai et al., 2009), being particularly important for the yield of many small farms (Garibaldi et al., 2016). The dependence of crop yields on insect pollination, however, varies widely between crops, from independent to obligate (Klein et al., 2007). Pollinators not only increase yields by increasing seed set, but they may also enhance crop quality (Bartomeus et al., 2014), and stabilise food production either in time (Garibaldi et al., 2011) or space (Deguines et al., 2014). However, despite the global importance of pollinators for food production, pollination is rarely taken into account in the development of farming systems or practices (Breeze et al., 2014), partly because it is difficult to disentangle pollination by insects from other factors that affect yield (Marini et al., 2015). Additionally, there may be an order of magnitude variation in the effect of insect pollination on yields within a particular crop (Gallai *et al.*, 2009). This variability is explained by the spatial variation of pollinator communities, leading to a spatial variation of pollination potential and pollen limitation (Gómez et al., 2010), reducing agricultural production (Wilcock and Neiland, 2002).

Oilseed rape (OSR, *Brassica napus* L.) is the fourth largest oil crop in terms of production in the world and the most common in the European Union (FAOSTAT, 2014). OSR is not only pollinated by insects but also by wind and self-pollination (Becker et al., 1992; Mesquida and Renard, 1982). Wind pollination is the transfer of pollen from one plant to another by passive wind transport, while self-pollination is the direct passage of pollen between the male and female parts of the same flower or between two flowers on the same plant. There is huge uncertainty in estimates of the relative importance of insect pollination for OSR yields, with reported values ranging from negligible (Samnegard et al., 2016) to 50% (Araneda Durán et al., 2010) with a range of values in between (Bartomeus et al., 2014; Bommarco et al., 2012; Lindström et al., 2016; Stanley et al., 2013; Zou et al., 2017a). There is no accepted explanation for such a high variability, which may result from farming practices (Marini et al., 2015), plant varieties (Hudewenz et al., 2014), or variation in pollinator communities (Rader et al., 2015). The major pollinators also depend strongly on the study being honeybees (*Apis mellifera*), bumblebees, wild bees or hoverflies (Garratt et al., 2014; Lindström et al., 2016; Zou et al., 2017b). Factors affecting OSR yields include pollinator visitor rate (Bartomeus et al., 2014; Woodcock et al., 2013), nearby honeybee hives (Lindström et al., 2016), and bee diversity (Zou et al., 2017b). In addition, the measurements used to estimate the effects on OSR yields varied between studies, from being a small part of the OSR plant (Stanley et al., 2013), total seed production per plant (Hudewenz et al., 2014; Zou et al., 2017b), or a set of OSR plants from either small (< 2 m², Araneda Durán et al. 2010, Bommarco et al. 2012, Bartomeus et al. 2014) or large (> 50m², Lindström et al. 2016) field section (in this latter study, only the contribution by honeybees was investigated). So far, to our knowledge, no study has ever quantified the effect of pollinators on yield at field scale for oilseed rape.

Here, we use, for the first time, a systemic approach by quantifying the effect of insect pollination on OSR yields, at both field scale and individual plant scale, combining field scale

yields and field scale assessments of pollination. We used both empirical data obtained for 151 fields and experimental manipulation of pollination in 101 fields. The yield estimates from both methods were compared with pollinator abundance and diversity, obtained by trapping in the fields. The OSR focus fields were distributed along gradients of landscapes with varying concentration of meadows, semi-natural habitats and organically farmed fields, which are all known to affect pollinator abundance and diversity (Holzschuh et al., 2008; Kennedy et al., 2013; Steffan-Dewenter et al., 2002; Woodcock et al., 2013). By using landscape gradients, we aimed to maximise the variation in the pollinator community to be able to quantify its effects on yield and identify the main pollinators involved. By measuring various fecundity traits of the OSR plants, such as the fruiting success, seeds per pods, seed unit weight and seed mass, we also identified the traits that were most affected by pollinators. Finally, we quantified the relative contributions of insects (large *versus* small), wind and self-pollination at plant level. Our experimental design, changing pollinator abundances using landscape variations as well as using pollinator exclusion, allowed us to i) quantify the effect of pollinator rich landscapes on pollination rate, and ii) quantify the contribution of pollination by insects at plant (grain biomass per plant) and field (yield) scales.

2. Material and methods

2.1. Study site, experimental fields and landscape context

Pollinator exclusion experiments and farming surveys were conducted between 2013 and 2016 in the LTSER "Zone Atelier Plaine & Val de Sèvre", a 450 km² study site located in the south of *Deux-Sèvres* district (Fig 1.a), central western France (Fig S.A, http://www.za.plainevalsevre.cnrs.fr/, Bretagnolle et al. 2018). Only winter OSR is grown in the LTSER, representing about 8% of the agricultural area (Fig 1.a). Experiments were conducted directly in commercial farm fields. Since we were interested in quantifying insect pollination in OSR fields under normal conditions, we did not request any modification of the farming practices. We used a moving window to randomly select 1 km² squares (Fahrig et al., 2011) that represented density gradients of three environmental features: semi-natural habitats (hedges and forest fragments), meadows, and organically farmed fields (obtained from the French parcel register 2014). All these landscape features are known to strongly influence the abundance of pollinators (Kennedy et al., 2013) and were mapped in the GIS LTSER (Bretagnolle et al., 2018). Within the selected squares, an OSR focus field was then chosen, if present (usually, there was only one OSR field). On average, OSR fields were at 365 m (48 to 1152m) from the nearest OSR neighbour. Field size ranged from 0.65 ha to 28.5 ha (mean 6.3 ha). The selected fields had similar soil types according to the IGCS soil map (available at https://www.geoportail.gouv.fr/). In 93% of the fields the soil was calcareous and in the rest the soil was red (with some clay).

A first set of 151 OSR fields (27 in 2013, 45 in 2014, 48 in 2015, and 31 in 2016) was used for an empirical assessment of the effects of pollinator abundance and diversity on crop yield at the field scale. No field was used twice in the four years. We interviewed the farmers, owners of the fields, to collect information on practices (fertilizer, pesticides, and OSR variety) and yield at the end of each cropping season (during winter). A second set of 101 fields (15 in 2013, 29 in 2014, 27 in 2015, and 30 in 2016) was used for pollinator exclusion experiments, of which 66 were also in the first set. The two sets differed because some

farmers refused the survey or refused permission for the exclusion experiment. There were 28 varieties of OSR, mainly restored hybrid (88.7%) and conventional (11.1%). All OSR varieties in this study could be self-pollinated or cross-pollinated.

2.2. Experimental treatments

Six individual OSR plants were selected in each field at two positions: one at the field edge and one at 20m from the edge in the field core. These two positions were selected to assess whether the distance from semi-natural habitats affected the pollination by insects (Woodcock et al., 2016). For each individual OSR plant, three (2013), two (2014) and four (2015-16) secondary branches were selected for pollinator exclusion treatments (Fig 1.c). There were different numbers of branches in each year because we tested different exclusion treatments. The branches were selected so as to be at the same flowering stage and adjacent or opposite to each other. The various exclusion treatments allowed self-pollination (SF), wind-pollination (W), small-bodied (SP) and large-bodied (LP) insect pollinators. One of the branches was used as a control (570 branches in total) where all flowers could be pollinated in any way (insects, wind and self-pollination, "LP+SP+W+SF"). A second branch was enclosed in a small mesh bag (0.6 mm mesh size, 517 branches), for which the flowers could only be self-pollinated or wind pollinated ("W+SF"). In 2013, 2015 and 2016, a third branch was enclosed in large mesh bag (3 mm mesh size, 403 branches), allowing self-pollination and pollination by wind and small insects ("SP+W+SF"). Finally, in 2015 and 2016, a fourth branch was enclosed in a gas-permeable Osmolux bag (Pantek, France) (272 branches), excluding all except self-pollination ("SF"). In 2013 only, each treatment was replicated for each plant (i.e. two controls, two large and two small mesh treatments per plant). The branches were bagged before onset of flowering and plants were visited weekly to adjust the bags, lifting them upwards to cover new or future flowers while releasing those flowers that had faded. The bags were completely removed after the last flower had faded. The operations were carried out gently to avoid as far as possible any effect on pod development (Wragg and Johnson, 2011). Branches were collected five days before the harvest. In 2015 and 2016, the rest of plant was also collected to estimate the total plant biomass and total seed biomass. In 2016, six further OSR plants were collected, three from the edge and three at 20m from the edge, from each of the 44 fields monitored that year, to estimate the effect of pollinators on the total plant production (see Appendix A for sample sizes and treatments for each year).

2.3. Oilseed rape fecundity trait measurements

In the laboratory, each selected branch (control or exclusion treatment) was stored in individual paper bags. All bags were left 48 hours in a climate chamber at 60°C. Three traits were recorded for each branch: the fruiting rate (the ratio of pods per branch to the number of flowers per branch: even if the flower is unsuccessful, the caudal peduncle is still present and visible), the individual seed weight, and the number of seeds per pod. We assumed that four to six pods per branch were enough to assess the number of seeds per pod and the number varied between years (average 4.84 pods per branch for 2013, 4.38 for 2014, 4.16 for 2015 and 3.51 for 2016). This was due to the variability in branch length (hence number of pods) as we selected one pod every three pods on the branch for counting the seeds. Individual seed weight was obtained using three randomly selected seeds per branch (and per treatment),

individually weighed to the nearest .01 mg. For the whole plant measurements in 2015 and 2016, we used the experimental plants by combining their control and experimental branches, plus the rest of the plant. In 2016, we also used the six OSR plants collected from each of the 44 fields monitored that year . We extracted all the seeds, counted and weighed them, and weighed the rest of the plant (without seeds).

2.4. Pollinator sampling

Pollinators were sampled by two complementary methods: pan-traps and sweep nets. Pan-traps can be a good predictor of pollinator abundance especially the abundance of Halictidae family bees (Toler et al., 2005), as well as an efficient trapping method for investigating the benefits of pollinators for chili pepper crops (Landaverde-González et al., 2017), strawberry crops (Connelly et al., 2015) and oilseed rape crops (Zou et al., 2017b). Pan traps are, however not effective for catching honeybees and their abundance is better estimated using sweep nets (Rogers et al., 2014; Westphal et al., 2008). We used coloured pan traps (Westphal *et al.*, 2008), 12cm diameter, 10cm deep plastic bowls sprayed fluorescent yellow (RAL 1026, Euro industry Supply, Stuttgart, Germany), sprayed fluorescent blue (Sparvar 3107, Euro industry Supply, Stuttgart, Germany) or left white. Different colours capture different pollinators by their colour preferences (Westphal et al., 2008). The traps were mounted on wooden stakes, with the height of the bowls being adjusted that they were at the vegetation canopy (Westphal et al., 2008). The bowls were filled with about 600 ml of water with drops of soap to catch insects. For a given field, pan traps were set only once, left for 4 days and removed afterwards. The pan traps were installed throughout spring (from April to June), covering the OSR flowering period. Given that bees, in particular honeybees, but also bumblebees and at least some wild bees, forage over large distances, we also sampled fields near the OSR focal field to estimate the local pollinator community. Sampling bees on neighbouring fields provides more robust estimates of bee abundance and the pollinator community at the landscape scale (maximum of 2 km^2), since sampling only the focal fields may be biased by dilution, spillover or attraction to OSR (Holzschuh et al., 2016). Two arable fields (mainly OSR and wheat) and meadows were surveyed. The number of fields surveyed at a given buffer distance was variable, between 1 and 8 fields at 1250m from each OSR focal field (on average, 30 pan traps sampled in 3.4 fields; see Appendix B for robustness analyses). In 2013 to 2015, we put 12 pan traps in each field (four of each of the three colours), six at the edge and six 50 m from the edge in the core. For each position, the pan traps were grouped in pairs of two randomly selected different colours, with the pairs spaced 25 m apart (Fig 1.b). As the pollinator abundance and richness did not differ between pan traps at the edge and in the core for 2013-2015 (see appendix C), in 2016, the sampling effort was reduced to the field core only and three pan traps were used, twice during the season.

In addition, 71 OSR fields were swept in 2015 and 2016. Two transects, one at the edge and one 50 m from the edge of the field were swept (Fig 1.b) in 2015, and three in 2016 with an additional transect 20 m from the edge (see appendix A for the protocol used each year). All transects were 50 m in length and the lasted 10 minutes, measured with a chronometer to ensure equal sampling effort. Transects were swept between 8.30 am and 5.30 pm when the air temperature was > 15°C and the weather was sunny.

All insects caught were identified in the laboratory by professional entomologists, at genera level for wild bees and species level for hoverflies. Bee species were identified in 2015 and 2016. As large numbers were caught in 2013 and 2014 (about 70% of the whole sample) and identifying the species is very time consuming given that there are almost 300 species in the LTSER (Rollin et al. 2013) the species were not identified these years. Four guilds of pollinators were targeted: honeybees (*Apis mellifera*), bumblebees (genus *Bombus*), wild bees (Hymenoptera: Apoidea) and hoverflies (Diptera: Syrphidea). Abundance for each genus was obtained by a nested averaging procedure, starting with mean count per bowl colour and position in the field (core *vs*. edge), then averaging per position in field, and finally per field (in 2016, pan traps were set twice in each field, and were thus further averaged). For each focal field, this final average per genus was averaged with all other fields within a radius of 1250 m and within a time window spanning from day 90 (30/31 March) to day 170 (18/19 June), thus covering the full OSR flowering period every year (see Appendix B for a sensitivity analysis of window size and time period). The total pollinator abundance was the sum of all individuals caught. The total number of genera caught was used as a proxy for the diversity. A similar procedure was used for the sweep net samples.

2.5. Statistical analyses

We used a linear model to analyse the effect of farming practices on the crop yield of 151 OSR fields, including the main fertilizers (nitrogen, phosphorus, potassium and sulphur), pesticides (frequency of insecticide, herbicide, and fungicide treatments) and OSR type (restored hybrid *versus* conventional). Only main effects were included (no interactions), and stepwise selection (backward and forward) was used to select only those variables with significant or marginally significant effects on yield ($P < 0.1$). We then used linear models to test the effects of total pollinator diversity, bee diversity, hoverfly diversity as well as total pollinator abundance, bee abundance and hoverfly abundance on yields, accounting for the farming practice variables selected at the previous step. Significant farming practice variables were added as covariates as well as their two-way interactions with pollinator metrics. The year and its interactions with pollinator metrics were also included. The models were fitted independently for pan trap and sweep net abundance data. In addition, stepwise multiple regression was used to find those pollinator genera that most affected the yield among the nine most common genera caught with pan traps or the eight most common genera caught with sweep nets, corresponding to genera with abundances greater than 1% of the total abundance. This help to account for collinearity between pollinator metrics by starting with a null model and adding, step by step (forward selection), pollinators with the largest effect on OSR yield (all pollinators with a significant or marginally significant effect were kept in the model). Correlations between pollinator's genera are given in Fig S.C.3.

We then investigated, at plant scale, the plant fecundity traits that were affected by insect pollinators. The traits were: the fruiting success, the average number of seeds per pod, the averaged seed unit weight measured on control branches, for all four years, as well as the total seed biomass per plant, only available in 2015 and 2016. Total seed biomass per plant was strongly correlated to plant biomass (Appendix D, Zhang and Flottmann, 2016), thus we adjusted the seed biomass for the plant total biomass using a linear regression between seed biomass and plant biomass, both of which were *log(x+1)* transformed (Appendix D). Positive

residuals of this model showed those OSR plants that produced more seed biomass than expected for their total biomass. The residuals (the seed biomass adjusted for plant biomass) of the model were then used in further analyses. All these traits were averaged for each position in the field. Then we used mixed linear models to explain fecundity traits as a function of bee abundance estimated by pan traps, accounting for year (four values), and plant position in the field (edge *vs.* core), and their two-way interactions with bee abundance, all as fixed factors, and field ID as a random factor.

To quantify the relative contributions of the different pollination processes (i.e. insect, wind and self-pollination), we used paired branch comparisons of OSR fecundity traits (Wragg and Johnson, 2011), using fruiting success as the trait for calculation since this was shown to be positively affected by pollinators (see results below). Fruiting success was hierarchically averaged per treatment and then per field to obtain contributions at field level. The contribution of wind pollination was estimated as the difference between the traits for "W+SF" ("W": Wind pollination, "SF": self-pollination) and "SF" treatments while the contribution of self-pollination was based on "SF" alone (N=57). In 2013 and 2014, there was no Osmolux treatment so the contribution of wind plus self-pollination was based on "W+SF" (N=44). The contribution of pollination by small insects was estimated as the difference between "SP+W+SF" ("SP": Small-bodied pollinators) and "W+SF" (N=72) and for large insects by the difference between "LP+SP+W+SF" ("LP": Large-bodied pollinators) and "SP+W+SF" (N=72). In 2014, there was no large mesh treatment, hence the contribution of all insects was estimated as the difference between "LP+SP+W+SF" and "W+SF" (N=29). The relative contributions of each of the pollination processes were then obtained as the % of the traits measured for the control branches (Bartomeus et al., 2014; Bommarco et al., 2012). In some cases, the difference in fecundity traits between treatments was negative, when, for example, fruiting success was higher in "W+SF" than in "SF". Since a negative contribution cannot theoretically exist, negative values were arbitrarily set to 0 where such negative contributions exceeded -5% (16.5% of 332 fruiting success values, see Appendix E). Additionally as the fruiting success could be biased by the treatment protocol (e.g., mechanical effects), we also adjusted for this bias (as detailed in Appendix E) and checked for the difference between unadjusted (uncorrected data, underestimating self-pollination) and adjusted values (corrected data, Appendix E).

In all analyses, pollinator abundance was *log(x+1)* transformed and fruiting rate was arcsine transformed to ensure that the distributions were normal and homoscedastic. All analyses were performed using R (R Core team, 2015). The "stats" package was used for linear modelling, predicting values, model selection and stepwise multiple regression. The "lmerTest" package was used for linear mixed model (Kuznetsova et al., 2014).

3. Results

3.1. Pollinator diversity

A total of 23,744 pollinators were caught over the four years in pan traps (average 6.7 ind/trap, range 0-136) within or near the focal fields. As expected, there was a strong variation between fields in the number of pollinators caught, from 0.33 to 43.19 individuals per pan trap, a 131-fold variation. Similarly, there was a ten-fold variation in genera diversity. Wild bees were the main guild caught (81.3%), followed by hoverflies (14.4%), honeybees (3.2%)

and bumblebees (1.1%). The most abundant pollinator genera were *Lasioglossum* (62.9%), *Halictus* (9.2%) and *Andrena* (7.8%). The complete list is given in Appendix C. In all, 19 genera of bees and 23 genera of hoverflies were caught. The sweep net method captured 1,110 pollinators (average 6.5 ind/transect, range: 0–68) in 2015 and 2016 (n = 71 fields), with mainly honeybees (73.5%), hoverflies (19.3%), wild bees (4.6%) including, *Lasioglossum* (1.34%), *Andrena* (2.6%) and *Halictus* (0.25%), and Bumblebees (2.5%), see Appendix C. The capture profiles of the pan traps and the sweep nets were completely different and gave uncorrelated results (Appendix C). They were, therefore, considered separately.

3.2. Effect of fertilizers and pesticides inputs on OSR yield

The OSR yield at field scale (as declared by the farmers) was, on average, 3.14 tons/ha (range 1.9-5.2, n = 151) and varied between years ($F_{3,147}$ = 6.39, p < 0.001). Yield was significantly affected by phosphorus fertilizer ($F_{1,149}$ = 6, p = 0.015**),** while **t**he other fertilizers (nitrogen, potassium and sulphur), pesticides (herbicides, insecticides and fungicides), and OSR type (see Appendix G, for interaction with pollinator metrics), had no significant effect on OSR yield (all P > 0.11, see Appendix F for model selection).

3.3. Contribution of pollinators at field scale

Once the main farming practices had been identified, we found that OSR yield was significantly and positively correlated with pollinator diversity measured using pan traps (Table 1), especially bee diversity (Table 1, Fig 2.a), but not with hoverfly diversity (Table 1). There were no significant interactions between farming practices and pollinator metrics in any of our models (Table 1). An increasing the number of bee genera from 1 to 10, was associated with an increase in yield of 37.5% (range: 27.7-47.5%), about 1 $t.ha^{-1}$. Each additional genus was, therefore associated with an average increase of 0.11 $t.ha^{-1}$ in OSR yield. Restricting the analysis to years 2015 and 2016, when bees were identified at species level, species richness had a similar, but non-significant, effect (Appendix G). The number of genera was, therefore, a better predictor of OSR yield than species richness. Total pollinator abundance also increased the yield (Table 1), with bee abundance having a greater effect than hoverfly abundance (Table 1, Fig 2.b). Bee abundance had slightly less effect (slope 0.16 +/-0.05) than bee diversity (slope 0.18, +/-0.05): i.e. an increase of yield of one ton/ha would require nine more genera but 29.4 more bees. Multiple stepwise regression using the nine most abundant genera indicated that *Lasioglossum* was the probable main contributor ($F_{1,147}$=10.27, P = 0.0016, Fig 2.c), followed by bumblebees ($F_{1,147}$=3.44, P = 0.066) and the hoverfly *Eupeodes* ($F_{1,147}$=2.83, P = 0.095).

There was also a significant positive correlation between yield and bee abundance measured using sweep nets (Table 1) with an overall increase of 0.8 $ton.ha^{-1}$ (28.6%, range: 15.6-41.6%, Fig 2.e), but the effect of bee diversity (species or genus level) was far less pronounced and varied with the year (Table 1, Fig 2.d, Appendix G). Multiple stepwise regression suggested that honeybees were the main contributor to yield ($F_{1,42}$=6.51, P = 0.015, Fig 2.f), rather than *Lasioglossum* as found for pan traps. This is likely to be an artefact of the low effectiveness of pan traps for catching honeybees: honeybees and *Lasioglossum* accounted for 3.2% and 62.9% of catches in pan traps, and 73.5% and 1.3% of catches in

sweep nets. Restricting the analyses to fields where exclusion experiments were carried out (66 fields instead of 151) did not change any of the conclusions (see Appendix G).

3.4. Effect of pollinators on OSR fecundity traits at plant scale

For the control branches, a model taking into account bee abundance, plant position and year (and their two-way interactions with bee abundance), showed that bee abundance measured by pan traps increased fruiting success ($F_{1,184}$=10.67, P = 0.002, Fig 3.a) while the year had an equally strong effect ($F_{3,184}$=10.02, P < 0.001; see Appendix H for additional statistical models). The number of seeds per pods was negatively correlated ($F_{3,184}$=5.98, P = 0.016, Fig 3.b) with bee abundance, but seed unit weight was not affected ($F_{3,184}$=0.003, P = 0.96, Fig 3.c). However, the increase in fruiting rate was sufficient to increase the seed biomass adjusted for plant biomass ($F_{1,130}$= 6.86, P = 0.011, Fig 3.d). In addition the seed biomass adjusted for plant biomass averaged per field was positively correlated to yield (r_s = 0.31, P = 0.04, n = 43). This suggested that OSR plants increase their investment in grain production in preference to vegetative biomass production in presence of pollinators. No significant interaction was found between bee abundance and plant position or year (P > 0.19 for both interactions) for any fecundity trait. The results were the same when farming practices were taken into account in the models (Appendix H).

3.5. Experimental quantification of insect pollination

Insect pollinators were estimated to have contributed 30% of the fruiting success (Fig 4.a) and this contribution increased with increasing bee abundance (Table 2, Fig 4.b). Wind and self-pollination accounted for 70% of fruiting success (Fig 4.a). In 2015 and 2016, wind and self-pollination rates were separated and self-pollination was found to have a far greater contribution (66 %) than wind (4.2%) (Fig 4). A positive correlation between pollinator contribution and yield (r_s = 0.24, P = 0.05, n = 66) confirmed that an increase in pollinators increased the yield at field scale. We found that large-bodied insect species (abdomen wider than 3 mm) had a similar contribution (15.6%) to small-bodied insects (12%). Bee diversity (for both pan traps and sweep nets), *Lasioglossum* (pan traps), and honeybee (sweep net) abundances all had a significant positive effect on the contribution of insects to pollination (Fig 4.b, Table 2), confirming that honeybees were the main large pollinators while *Lasioglossum* were the main wild bee pollinators genus.

4. Discussion

Determining the role of insect pollinators is a central question for managing pollination services in crop production (Kremen, 2005). Previous studies have already emphasised the role of insect pollinators in OSR yields, usually in fields with or without pollinators (Araneda Durán et al., 2010; Bommarco et al., 2012; Hudewenz et al., 2014; Marini et al., 2015; Stanley et al., 2013) or correlating OSR yields with pollinator abundance (Bartomeus *et al.* 2014; Woodcock *et al.* 2016; Zou *et al.* 2017). In most studies however, the contribution of pollinators was calculated for small area (except Lindström et al. 2016) which may have under-estimated pollinator contribution, especially for OSR, a plant that shows high ability to compensate for flower loss (Pinet et al. 2015). Here we combined empirical and experimental data collected over four years in farm fields to estimate pollinators' contribution at two

different scales, field and plant. Our study shows that bees have a major effect on OSR yields, with 35.7% higher yields in pollinator rich landscapes than in landscapes with almost no pollinators.

4.1. Contribution of insect pollination to OSR yield

Oilseed rape is a crop showing a modest dependence on pollinators, between 10% and 40% (Klein *et al.*, 2007), and self-pollination is dominant in OSR (Becker et al., 1992). Using genetic inheritance tests, self-crossing has been shown to be 53% to 87% depending on the field (Becker et al., 1992). In our study, we found that self-pollination accounted for approximately 66% of total pollination, but varied between fields (95% CI = 30.8% to 100%). Self-pollination and self-crossing are not directly comparable and we cannot infer whether an increase in the contribution by pollinators replaced or supplemented the contribution of self-pollination, although pollinators have been shown to increase the out-crossing rate (Brunet and Weet, 2006). Wind pollination contributed about to 4.2%. Only one other study has quantified wind pollination in OSR and the values ranged from 3% to 12% (Mesquida and Renard, 1982). Weak wind pollination in OSR has been linked to both the pollen and the flower structures, which are more adapted to insect dispersal than wind dispersal (Hayter and Cresswell, 2006). Using pollinator exclusion, we estimated that pollinator contribution was 30%, close to the 37.5% increase in yield at field scale corresponding to the highest pollinator diversity in our study site. Pollinator contribution was independent of plant variety or farmer's practices. Conventional OSR has been shown to be more dependent on pollinators than hybrid OSR (Lindström et al., 2016; Marini et al., 2015), but Hudewenz et al. (2014) analysed a large number of varieties and found that the contribution of pollinators depend more on the OSR varieties themselves rather than the OSR type (conventional *versus* hybrid). Studies including farming practices have not agreed on whether farming practices affect the contribution of pollinators: some authors found no interaction with pollinators (van Gils et al., 2016), as in our study, while others found interactions between practices and pollinators (Marini et al., 2015).

Our results therefore clearly demonstrate that insect pollinators are an important component of OSR yield for farmers in our study area, increasing yields by up to 0.8 to 1 ton.ha^{-1}, depending on the method used to sample the pollinators (pan traps or sweep nets). The net effect of pollinators in our study is thus slightly higher than that found in other studies (Lindström et al., 2016; Woodcock et al., 2016), from 0.4 to 0.6 ton.ha^{-1}, but far less than the 2.5 tons.ha^{-1} found by Araneda Durán et al. (2010). In our study, the increase in yield, between 29% and 37.5%, depending on the method for sampling pollinators and the scale (plant *versus* field), is generally higher than increases reported so far: between 12% and 20% (Bartomeus et al., 2014; Bommarco et al., 2012; Samnegard et al., 2016; Zou et al., 2017b) up to 30% (Stanley et al., 2013). This discrepancy may arise from differences in the pollinator communities, since our study site has a very rich wild bee community, with more than 250 species (Rollin et al., 2015). Bartomeus *et al.* (2014) and Woodcock *et al.* (2016) found that OSR seed production was positively correlated with pollinator visiting rate, a parameter that we did not measure here. It should also be noted that we used partial plant bags rather than entire caged plants (Bartomeus et al., 2014; Zou et al., 2017b), which may also account for part of the differences between this and other studies.

We were able to identify which fecundity traits were affected by pollinators, and at which scale (branch or plant), and were thus responsible for the increase of yield at the field level. Two main traits benefited from insect pollinators: fruiting success and seed biomass adjusted for plant biomass. As expected, pollinators increased fruiting success, potentially due to more pollen brought by pollinators (Hayter and Cresswell, 2006) and better pollen transfer that may increase out-crossing rates (Brunet and Weet, 2006) compared to wind or self-pollination. We also detected a trade-off between the number of seeds per pod and the fruiting rate, the number of seeds per pods decreasing with increasing presence of pollinators, suggesting that the plant may not maximise all fecundity traits simultaneously. Other trade-offs have already been identified, e.g. seed unit weight *vs.* number of pods per plant (Araneda Durán *et al.*, 2010), or number of seeds per pod *vs.* seed unit weight (Zou *et al.* 2017). Interestingly, total seed mass per plant adjusted for plant biomass was positively correlated with the presence of pollinators and field yield. Zou *et al.* (2017) found a very similar result: plant yield divided by straw (similar to plant biomass) was correlated with wild bee abundance. Our adjusted seed biomass per plant is actually fairly close to the harvest index (ratio of seed total biomass divided by plant biomass), which has been found to be more closely correlated with OSR field yield than with OSR plant yield (Degenhart & Kondra 1984). We found no effect of the position in the field on the pollination by insects, however the distance into the field tested in our study was relatively small. Woodcock et al. (2016), for instance, the effect of the position with a higher distance (maximum of 200m), and found that visits to OSR flowers strongly decreased with distance but only for bumblebee and hoverflies (no effects were found for wild bees and honeybees). Interestingly, bumblebee and hoverflies were not identified as main pollinators in our study.

4.2. Which insects contribute to OSR pollination?

We found that higher bee diversity (genus level) resulted in higher OSR yields, possibly as a result from niche complementarity since bees show different foraging temporal preferences, or forage on different flowers according to the position of the flower on the plant (Hoehn et al., 2008). The effect of bee species diversity on OSR yield has been reported recently (Zou et al., 2017b) and 20 of the most common bee species were found to forage in OSR (Kleijn et al., 2015). Large bees, such as honeybees, are known to pollinate OSR and visit more flowers than any other pollinators (Garratt et al., 2014). We found that honeybees were the most important pollinators, but unlike other studies, did not find that bumblebees had any effect (Garratt et al., 2014). This is perhaps because bumblebees were scarce during oilseed rape blooming in our site, as already reported by Rollin *et al.* (2013). Although wild bees are usually less abundant than honeybees in OSR (Rollin *et al.*, 2013), they spend longer on flowers (Woodcock et al., 2013) and, therefore, transfer more pollen during flower visits than honeybees. Among wild bees, *Lasioglossum* (from *Halictidae* family) had a fairly strong effect, which is surprising since, unlike *Osmia*, this genus has never been identified as an important OSR pollinator, (Garratt et al., 2014). *Lasioglossum* is however known to forage extensively on OSR (Le Féon et al., 2013; Woodcock et al., 2013). Hoverflies were also present in our pollinator community, however we did not find that hoverflies had any effect. This can be explained by the fact that hoverflies are less effective pollinators for OSR (Garratt et al., 2014).

4.3. Conclusions

We show here that OSR fields in our study area are pollinator limited, both in terms of bee (genus) diversity, and honeybee and wild bee abundances. Given the increase of OSR fields worldwide and the pollination service supply limitations that have already been identified (Breeze et al., 2014) and with the current decline in pollinators (Potts et al., 2010) improving pollinator richness or abundance in general is becoming urgent, though problematic (Bretagnolle and Gaba, 2015). Simplification of agricultural landscapes leads to poor pollination services (Connelly et al., 2015), intensive farming practices are either directly (Henry et al., 2012) or indirectly (Requier et al., 2015) harmful to bees, and the maintenance of semi-natural habitats in the landscape is critical for wild bees (Kennedy et al., 2013). However, plans for reducing pesticide use, improving or restoring semi-natural habitats in farming landscapes and establishing wild flower strips (Blaauw and Isaacs, 2014) have, so far, remained limited. All these measures, whether they are implemented through Agri-environmental Schemes or as greening components of direct payments under the Common Agriculture Policy, still have costs. The merit of our study is that it demonstrates that increasing pollinator abundance at landscape level also has financial benefits for farmers, since increase in production can be directly translating into gross margins or revenue. By accurately quantifying the yield increase as a function of pollinator abundance, we pave the way for a monetary evaluation of the pollination service in OSR farming systems that can be balanced against the cost of managing landscapes to maintain bee diversity and pollinator abundance within a land sharing framework, i.e. at the cost of reducing the area under crops. Most public policies targeting wild bees aim to exchange crop area for semi-natural habitats, and use, therefore land sharing strategies (Green et al., 2005). However, sharing land for bees may not necessarily mean that farmer's revenue will decrease, since crop yields (hence income) will increase as shown by our study and another recent study (Pywell *et al.* 2015).

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Appendices

Appendix A. Study sites and summary of the data that were collected for this study for each year.

Appendix B. OSR yield at field scale and pollinator community metrics for different time periods and spatial windows.

Appendix C. Effect of pan trap position in field on pollinator catch and list of the pollinators caught using pan traps and sweep nets

Appendix D. Adjustment of the total seed biomass using the total plant biomass.

Appendix E. Detecting and accounting for possible systematic bias effect of mesh and Osmolux on fruiting success.

Appendix F. Effect of farming practices on OSR yield

Appendix G. Effect of pollinators on OSR yield: supplementary models

Appendix H. Effect of pollinator diversity and abundance, caught by pan traps, and farming practices on OSR fertility traits

Table 1. Linear models of OSR yield as a function of pollinator diversity or pollinator abundance (obtained by pan traps in 151 fields or sweep nets in 44 fields), year, phosphorus fertilizer and their two way interactions with pollinator metrics. All abundances are *log (x+1)* transformed. Significant effects ($P > 0.05$) are in bold.

	Pan trap		Sweep net			Pan trap		Sweep net	
	F	*P*	*F*	*P*		F	P	F	P
Total diversity	**3.99**	**0.048**	1.40	0.25	Total abundance	**7.75**	**0.006**	**4.52**	**0.042**
Year	**6.93**	**< 0.001**	0.01	0.92	Year	**4.85**	**0.003**	0.01	0.92
Phosphorus fertilizer	**7.07**	**0.009**	**7.09**	**0.011**	Phosphorus fertilizer	**7.28**	**0.008**	**8.04**	**0.007**
Total diversity *x* year	0.24	0.87	**4.68**	**0.037**	Total abundance x year	0.35	0.79	3.07	0.088
Total diversity *x* phosphorus fertilizer	0.70	0.4	0.13	0.72	Total abundance x phosphorus fertilizer	0.54	0.47	0.03	0.85
Bee diversity	**14.93**	**< 0.001**	0.17	0.68	Bee abundance	**12.06**	**0.001**	**5.63**	**0.023**
Year	**4.55**	**0.004**	0.02	0.88	Year	**3.58**	**0.016**	0.01	0.9
Phosphorus fertilizer	**10.20**	**0.002**	**6.84**	**0.013**	Phosphorus fertilizer	**7.54**	**0.007**	**6.72**	**0.013**
Bee diversity x year	0.18	0.9	**6.97**	**0.012**	Bee abundance x year	0.12	0.95	3.58	0.066
Bee diversity x phosphorus fertilizer	0.48	0.49	1.02	0.32	Bee abundance x phosphorus fertilizer	0.38	0.54	0.20	0.66
Hoverfly diversity	0.01	0.99	1.85	0.18	Hoverfly abundance	3.76	0.055	0.40	0.53
Year	**6.96**	**< 0.001**	0.01	0.91	Year	**5.49**	**0.001**	0.03	0.87
Phosphorus fertilizer	**6.73**	**0.010**	**7.94**	**0.008**	Phosphorus fertilizer	**7.98**	**0.005**	**9.71**	**0.003**
Hoverfly diversity x year	0.14	0.94	0.37	0.55	Hoverfly abundance x year	2.07	0.11	0.78	0.38
Hoverfly diversity x phosphorus fertilizer	0.19	0.66	0.00	0.96	Hoverfly abundance x phosphorus fertilizer	0.01	0.93	2.81	0.1

Table 2. Effect of bee diversity, bee abundance and *Lasioglossum* caught by pan traps and sweep nets on the contribution of all pollinators, large pollinators and small pollinators, respectively, to fruiting success. A linear model was used. All abundances are *log (x+1)* transformed. Significant effects ($P < 0.05$) are in bold.

		Pollinator contribution			Large pollinators contribution			Small pollinators contribution		
		Value	*F*	*P*	Value	*F*	*P*	Value	*F*	*P*
Pan trap	Bee diversity	**0.033**	**7.52**	**0.007**	0.01	0.89	0.37	**0.026**	**5.03**	**0.028**
	Bee abundance	**0.23**	**10.47**	**0.0017**	**0.14**	**5.3**	**0.024**	0.073	1.27	0.26
	Lasioglossum	**0.2**	**10.93**	**0.0013**	0.11	3.78	0.056	0.087	2.14	0.15
	Sample size (Field)			101			72			72
Sweep net	Bee diversity	**0.057**	**5.62**	**0.021**	**0.066**	**20.88**	**<0.001**	-0.009	0.026	0.61
	Bee abundance	0.11	2.8	0.01	**0.15**	**13.61**	**<0.001**	-0.039	0.71	0.44
	Honeybee	0.1	2.27	0.14	**0.13**	**11.45**	**0.0019**	-0.035	0.59	0.45
	Sample size (Field)			55			55			55

Fig 1. (a) The study site, the LTSER Zone Atelier “Plaine & Val de Sèvre” showing OSR crops and the monitored OSR fields in 2015 as an example. (b) The study design, showing the plant, pan trap and sweep net transect locations within the field. (c) Design of pollinator exclusion experiment for OSR plants, showing the position and types of pollinator exclusion treatments.

Fig 2. Effect of pollinator community metrics estimated from pan traps (a-c) and sweep nets (d-e) on OSR crop yield. All abundances are *log (x+1)* transformed. The colour lines indicate the linear regressions between yield and pollinator for 2013 (red, square dot, dashed line), 2014 (green, round dot, solid line), 2015 (blue, triangle dot, dot-dashed line) and 2016 (purple, diamond dot, dotted line). The black line shows the relationship averaged over the four years. The black line is not drawn where the regressions are not significant.

Fig 3. Effect of bee abundance estimated from pan traps on different OSR fertility traits, averaged at field scale. The traits were measured for the control branch (a-c) and whole plant (d). The coloured lines show the linear regressions between OSR fertility traits and bee abundance (*log (x+1)* transformed) for 2013 (red, square dot, dashed line), 2014 (green, round dot, solid line), 2015 (blue, triangle dot, dot-dashed line) and 2016 (purple, diamond dot, dotted line) where these are significant. The black line shows the relationship averaged over the four years. Lines are not drawn where the regressions are not significant.

Fig 4. (a) Relative contributions of different pollination processes over the four years on fruiting success. Boxes show upper and lower quartiles, horizontal line is the median. (b) Effect of bee abundance (*log (x+1)* transformed) on contribution of pollinators. The black line is the linear regression.

Fig 1.

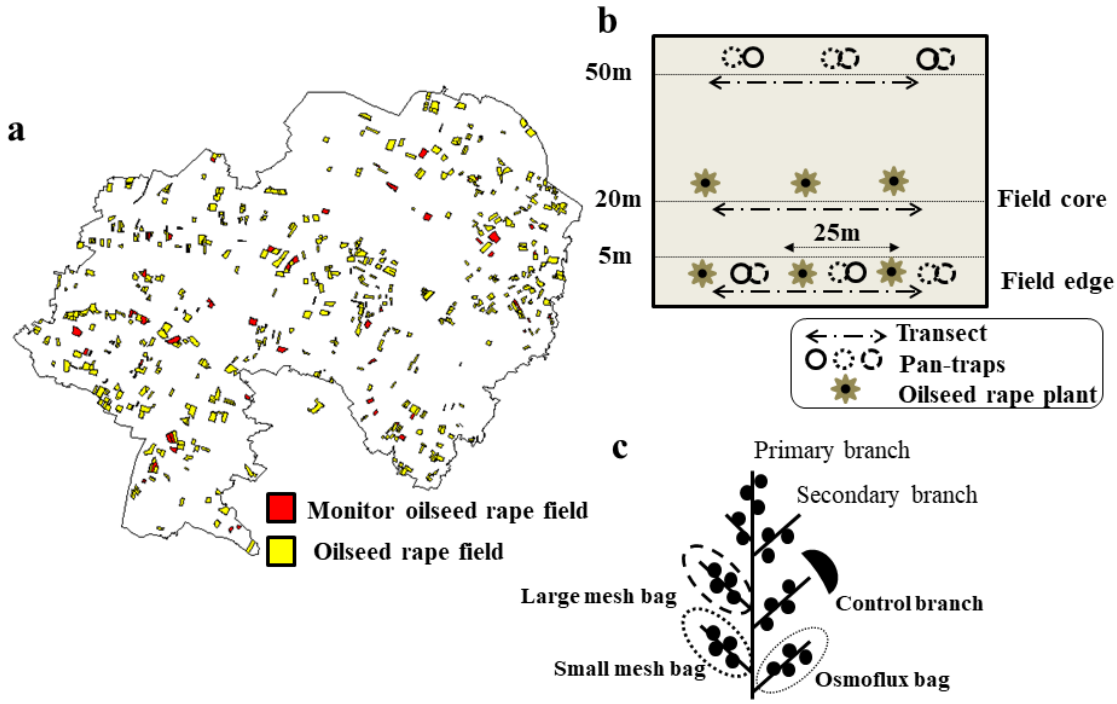

a
Monitor oilseed rape field
Oilseed rape field
b
50m
20m
5m
25m
Field core
Field edge
Transect
Pan-traps
Oilseed rape plant
c
Primary branch
Secondary branch
Large mesh bag
Control branch
Small mesh bag
Osmoflux bag

Fig 2.

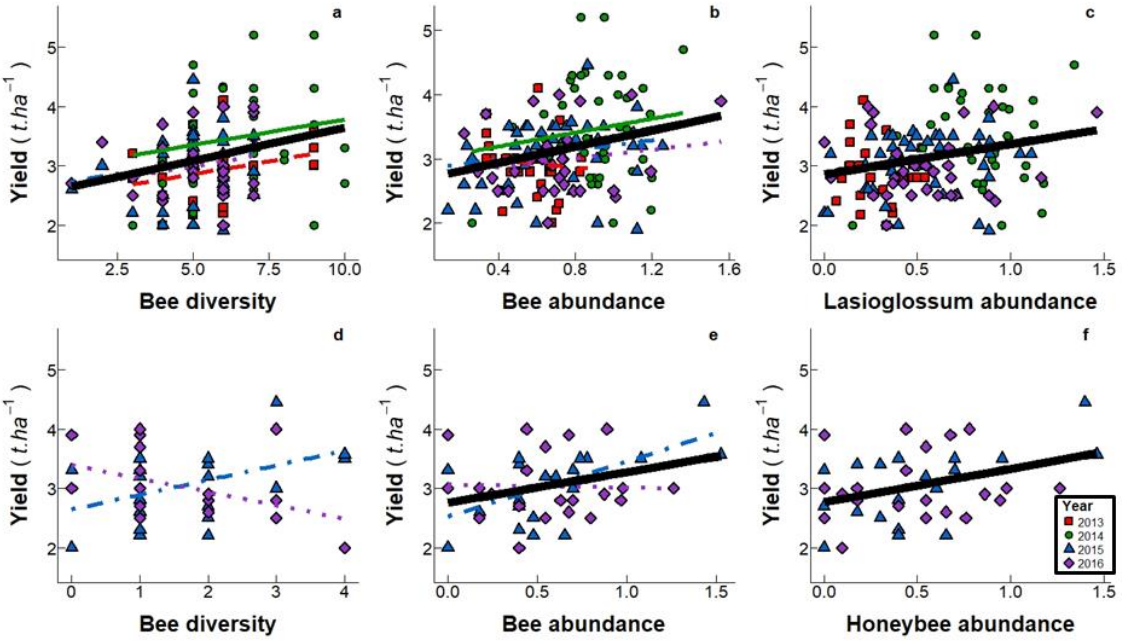

a
b
c
d
e
f
Yield (t.ha^{-1})
Bee diversity
Bee abundance
Lasioglossum abundance
Honeybee abundance
Year
2013
2014
2015
2016

Fig 3.

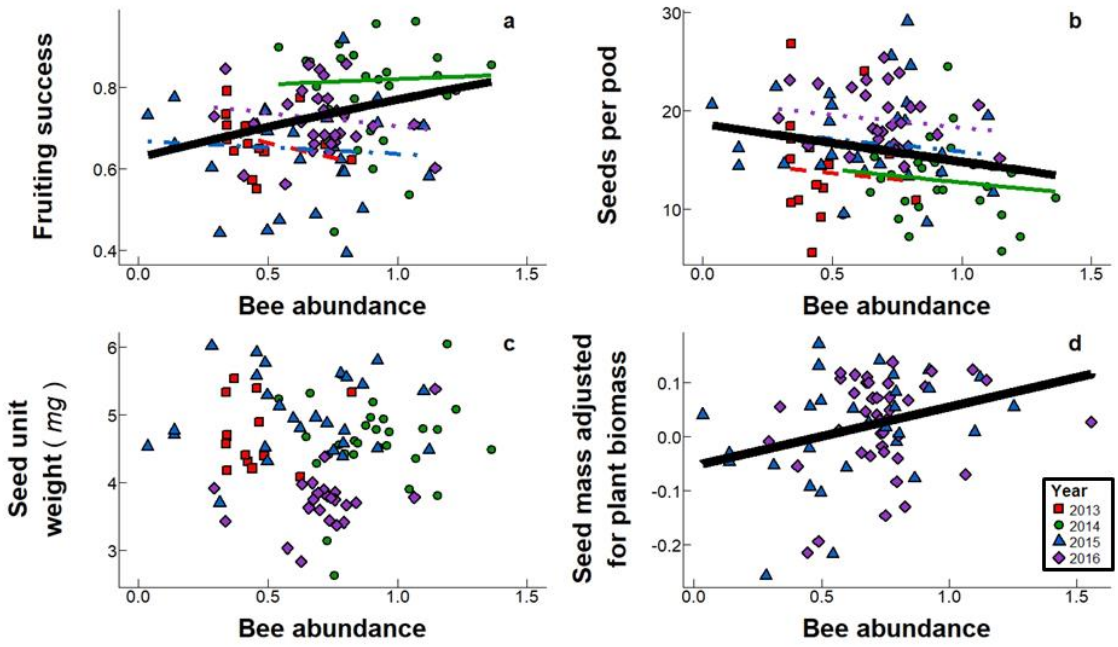
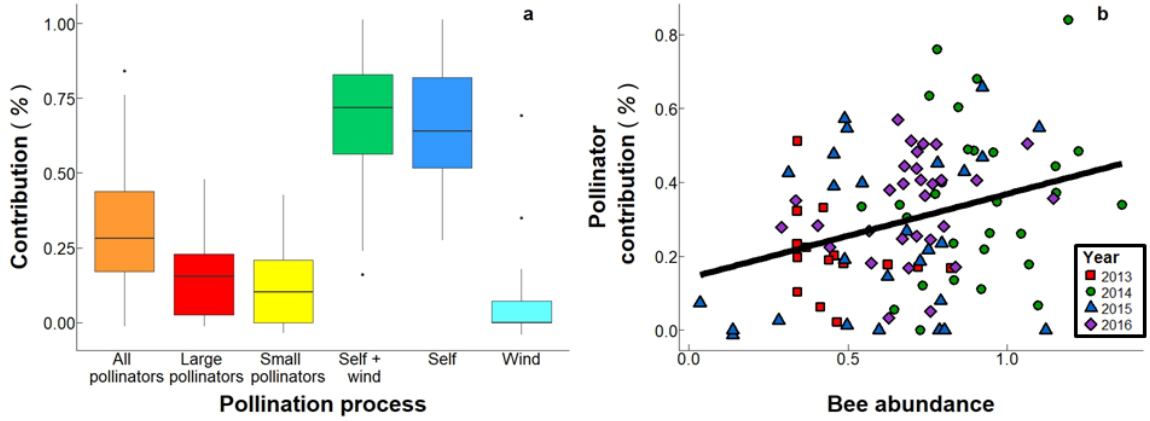

a
Fruiting success
0.4
0.6
0.8
0.0
0.5
1.0
1.5
Bee abundance
b
Seeds per pod
10
20
30
0.0
0.5
1.0
1.5
Bee abundance
c
Seed unit weight (mg)
3
4
5
6
0.0
0.5
1.0
1.5
Bee abundance
d
Seed mass adjusted for plant biomass
-0.2
-0.1
0.0
0.1
0.0
0.5
1.0
1.5
Bee abundance
Year
2013
2014
2015
2016

Fig 4.


a
Contribution (%)
1.00
0.75
0.50
0.25
0.00
All pollinators
Large pollinators
Small pollinators
Self + wind
Self
Wind
Pollination process
b
Pollinator contribution (%)
0.8
0.6
0.4
0.2
0.0
0.0
0.5
1.0
Bee abundance
Year
2013
2014
2015
2016

Appendix

Appendix A. Study sites and summary of the data that were collected for this study for each year.

Fig S.A. gives the location of the study site in France.

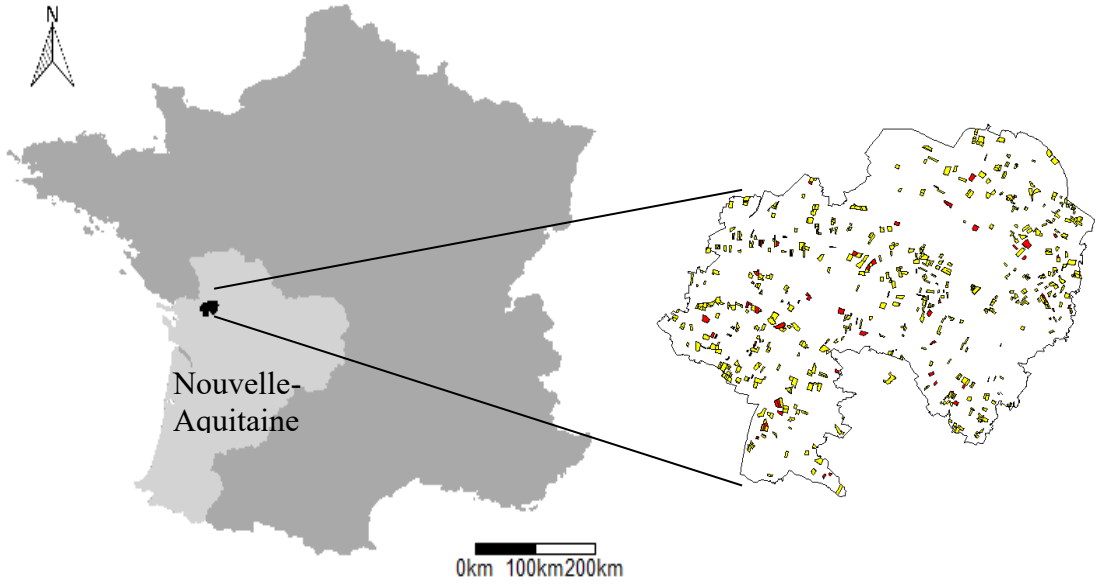


Fig S.A. Geographical location of Zone Atelier « Plaine & Val de Sèvre » in the Nouvelle Aquitaine region, France.

Table S.A. Summary of the data collected for each year, where a treatment was not applied or a measurement was not made for a given year, the cell is shaded.

		Year			
		2013	2014	2015	2016
	Farm survey	27	45	48	31
OSR manipulation	Control branch	126	148	118	178
	Large mesh branch	124		107	172
	Small mesh branch	100	132	112	173
	Osmolux branch			107	165
Plant measurements	Plant measurements			172	419
	Branch count				420
Pan trap	Edge	6	6	6	
	Core	6	6	6	3
	Number of sessions per field	1	1	1	2
Sweep net	Edge			Yes	Yes
	20 m				Yes
	50 m			Yes	Yes

Appendix B. OSR yield at field scale and pollinator community metrics for different time periods and spatial windows.

We explored the effect of the time period and spatial window, that was used to estimate pollinator community metrics, on the effect of these metrics on yield. Three time periods were tested with pollinator data from pan traps. Pan traps were first set up from the day 90 each year (30/31 March) to day 180 (28/29 June). Each year, this period covered the entire flowering period of oilseed rape and beyond. Three time periods were tested, i.e. pollinators caught by pan traps were estimated with captures starting from day 90 until day160 (end of flowering), until day 170 (10 days after the end of flowering), and until day 180 (20 days after the end of flowering). The effect of the spatial window used to estimate pollinator community metrics was tested using four buffer areas with radii 1000, 1250, 1500 and 2000 m. The effect of pollinators on the yield was also tested for pollinator metrics estimated by pan traps in the OSR field only (0m). 20 linear models were used to investigate the effect of bee and hoverfly diversity and bee and hoverfly abundance (*log(x+1)* transformed) on OSR yield at field scale.

The effect of bee diversity was stronger at 1250m, for periods to day160 and to day 170 and was weaker or absent for other radii and the period to day 180 (see Table S.B). Bee abundance had an effect for radii from 1000 to 2000 m and this effect was significant for the periods to day 160 and day 170 (Table S.B). The abundance and diversity of bees detected with pan traps only in the OSR fields had no effect, showing the importance of estimating bee abundance and bee diversity at landscape scale. Hoverfly diversity and abundance had no effect for any period and buffer size (Table S.B). We, therefore present results for a radius of 1250 m around the focal field for a period between day 90 and day 170.

Table S.B. Effect of bee and hoverfly diversities and bee and hoverfly abundances on OSR yield for different spatial buffers and time periods. All abundances are *log(x+1)* transformed. *F*-value are given as negative if the coefficient is negative thus R^2 (percentage of variance explained) are given. Significant effects are in bold and represent as follows: + $P < 0.01$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

	Time period of 160 days				
Spatial radius	0m	1000m	1250m	1500m	2000m
OSR focus field	78	125	144	150	151.00
Average total number of pan traps in buffer	8.32	24.98	28.04	33.30	44.12
Average number of fields surveyed in buffer	1	2.85	3.26	3.87	5.13
Bee diversity	1.49	**9.02****	**12.89*****	**5.05***	1.45
r²	1.92	6.83	8.32	3.30	0.97
Hoverfly diversity	0.44	0.98	1.12	0.07	0.09
r²	0.57	0.79	0.79	0.05	0.06
Bee abundance	0.77	**7.87****	**9.23****	**12.60****	**16.47*****
r²	1	6.02	6.10	7.85	9.95
Hoverfly abundance	0.02	-0.06	-0.31	-0.65	-1.57
r²	0.02	0.05	0.22	0.43	1.04

	Time period of 170 days				
Spatial radius	0m	1000m	1250m	1500m	2000m
OSR focus field	78	132	151	151	151
Average total number of pan traps in buffer	8.43	26.93	30.35	36.70	48.87
Average number of fields surveyed in buffer	1	3.01	3.44	4.17	5.58
Bee diversity	0.99	**7.94****	**13.41*****	**5.67***	0.86
r²	1.28	5.76	8.26	3.67	0.57
Hoverfly diversity	0.02	-0.20	0.00	-0.91	-2.28
r²	0.02	0.15	0.00	0.61	1.51
Bee abundance	0.45	**8.88****	**11.34****	**13.76*****	**16.57*****
r²	0.47	6.40	7.07	8.46	10.01
Hoverfly abundance	-0.14	-2.86+	-3.30+	**-3.98***	**-8.62****
r²	0.19	2.16	2.17	2.60	5.47

	Time period of 180 days				
Spatial radius	0m	1000m	1250m	1500m	2000m
OSR focus field	78	135	151	151	151
Average total number of pan traps in buffer	9.83	31.24	35.46	43.35	58.74
Average number of fields surveyed in buffer	1	3.15	3.64	4.48	6.07

Bee diversity	0.23	1.99	**6.53***	1.74	0.00
r^2	0.3	1.47	4.20	1.15	0.00
Hoverfly diversity	**-3.45***	**-4.83***	-2.60	**-5.46***	**-6.04***
r^2	4.35	3.50	1.72	3.53	3.90
Bee abundance	0.22	2.48	3.65+	**5.39***	**7.83****
r^2	0.29	1.83	2.39	3.49	5.00
Hoverfly abundance	**-5.39***	**-9.46****	**-10.37****	**-10.03****	**-16.30*****
r^2	6.62	6.64	6.50	6.31	9.86

Appendix C. Effect of pan trap position in field on pollinator catch and list of the pollinators caught using pan traps and sweep nets.

We explored the difference in pollinator abundance and diversity between pan traps at the edge of fields and in the core for 2013, 2014 and 2015. Pollinators were averaged for each position (edge or core) and pollinator abundance and diversity were calculated (as described in Material & Methods). Linear models were used with total pollinator abundance and richness as dependent variables, year and position in field and their two-term interaction as explanatory variables. Only the year had a significant effect on either pollinator abundance or diversity ($P < 0.001$). The position of the pan traps had no effect on total pollinator abundance ($F_{1,864} = 1.42$, $P = 0.23$, Fig S.C.1.A) or diversity ($F_{1,864} = 2.62$, $P = 0.13$, Fig S.C.1.B). The interaction between year and position in the field had no significant effect ($P > 0.28$).

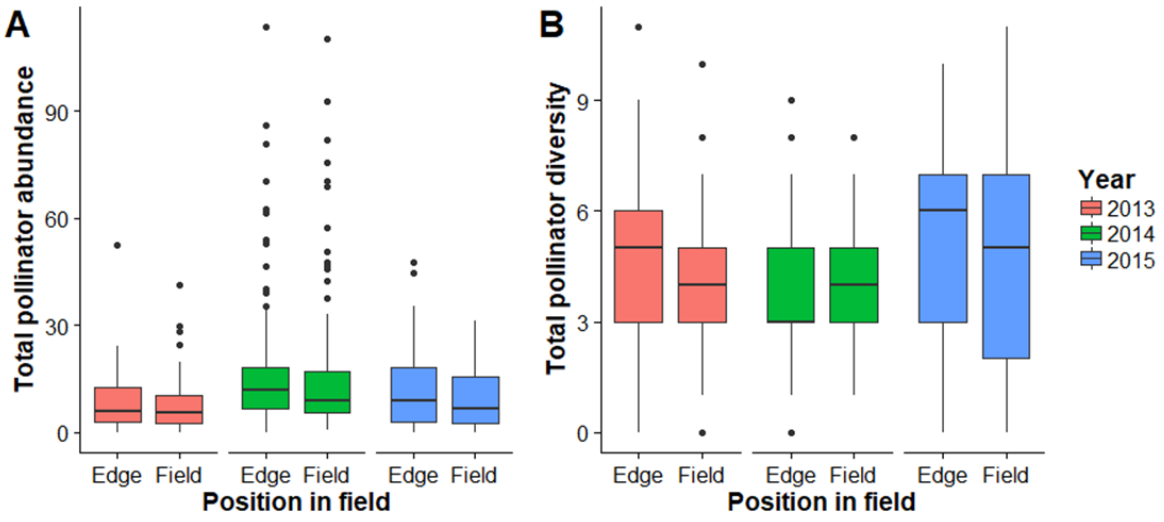


Fig S.C.1. Total pollinator abundance (A) and diversity (B) for pan traps placed at the edge of field and those in the field core. Boxes show upper and lower quartiles, horizontal line indicates the median.

This table (Table S.C.1) lists the pollinators caught in pan traps and sweep nets.

Table S.C.1. List of pollinator genera caught using pan traps and sweep nets between 2013 and 2016.

Pan trap		Sweep net	
Genus	Catch	Genus	Catch
Lasioglossum	*14927*	Honeybee	*878*
Halictus	*2188*	*Episyrphus*	*71*
Andrena	*1863*	*Eristalis*	*34*
Eupeodes	*1192*	*Andrena*	*31*
Honeybee	*750*	Bumblebee	*30*
Sphaerophoria	*737*	*Melanostoma*	*17*
Episyrphus	*599*	*Lasioglossum*	*16*
Melanostoma	*422*	*Eupeodes*	*14*
Bumblebee	*260*	*Epistrophe*	*5*
Eristalis	*245*	*Halictus*	*3*
Nomada	*124*	*Chrysotoxum*	*3*
Eucera	*86*	*Meliscaeva*	*3*
Pipizella	*59*	*Bombyle*	*1*
Sphecodes	*46*	*Eucera*	*1*
Scaeva	*45*	*Melitta*	*1*
Osmia	*30*	*Nomada*	*1*
Cheilosia	*28*	*Osmia*	*1*
Melitta	*17*		
Merodon	*14*		
Rhingia	*12*		
Helophilus	*11*		
Syrphus	*10*		
Chrysotoxum	*9*		
Hylaeus	*6*		
Anthophora	*5*		
Eristalinus	*5*		
Xylocopa	*4*		
Meliscaeva	*4*		
Paragus	*3*		
Xylota	*3*		
Colletes	*2*		
Eumerus	*2*		
Ferdinandea	*2*		
Chelostoma	*1*		
Hoplitis	*1*		
HoplOsmia	*1*		
Megachile	*1*		
Trachusa	*1*		
Myathropa	*1*		
Neoascia	*1*		
Platycheirus	*1*		
Xanthogramma	*1*		

Table S.C.2. Pearson correlation coefficient between the pollinator communities caught by pan traps and sweep nets in the OSR focal fields.

	Pearson correlation	P
Pollinator diversity	0.086	0.8
Bee diversity	0.09	0.41
Hoverfly diversity	<0.001	0.98
Total pollinator abundance	0.007	0.95
Wild bee abundance	0.21	0.085
Hoverfly abundance	0.1	0.93
Honeybee abundance	0.27	0.046
Bumblebee abundance	0.13	0.29

Fig S.C.2 shows the correlation between the total pollinator abundances (*log(x+1)* transformed) caught by pan trap and sweep nets each year (coloured dashed lines) and for all years (black dashed lines). Total pollinator abundance caught by sweep nets is the dependent variable, and total pollinator abundance caught by pan traps, year (two levels) and their interaction are the explanatory variables.

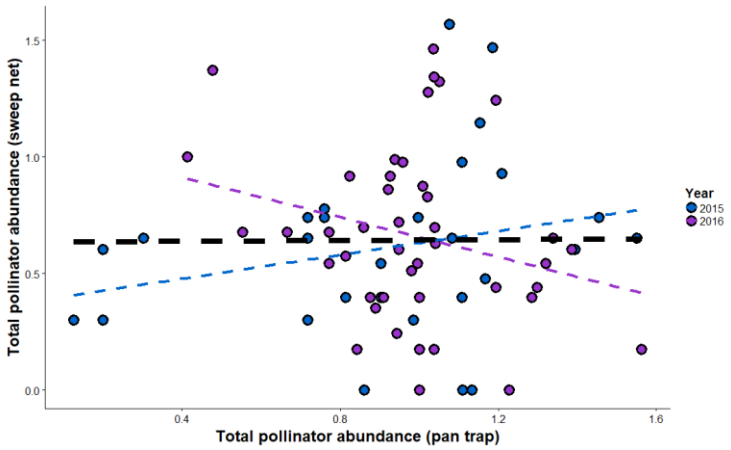


Fig S.C.2. Correlation between total pollinator abundance estimated using sweep nets and total pollinator abundance estimated using pan traps and linear regressions for 2015 (blue) and 2016 (purple) and both years (black). The regressions are not significant.

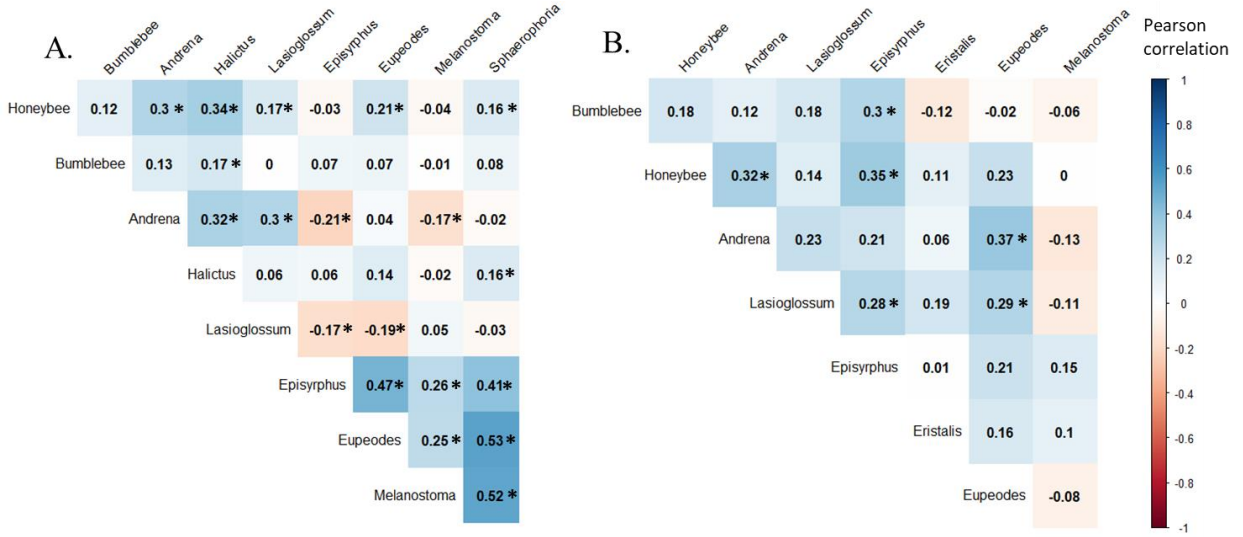


Fig S.C.3 shows the Pearson correlation matrices between the nine most common genera (*log(x+1)* transformed) caught by pan-traps (left) and between the eight most common genera caught by sweep nets (right). The Pearson correlation coefficients are shown by colour gradient. Positive correlations are presented in blue and negative correlations in red. * shows that the correlation was significant.

Appendix D. Adjustment of the total seed mass using the total plant biomass

We used a linear model to adjust the total seed mass using the total plant biomass and year (2 levels: 2015 and 2016) as explanatory variables. Total seed mass and total plant biomass were *log(x+1)* transformed. Fig S.D.1 shows a strong linear correlation between total seed mass and total plant biomass ($F_{1,590}$ = 1618.28 , P < 0.001, R^2 = 0.75, slope = 0.98).

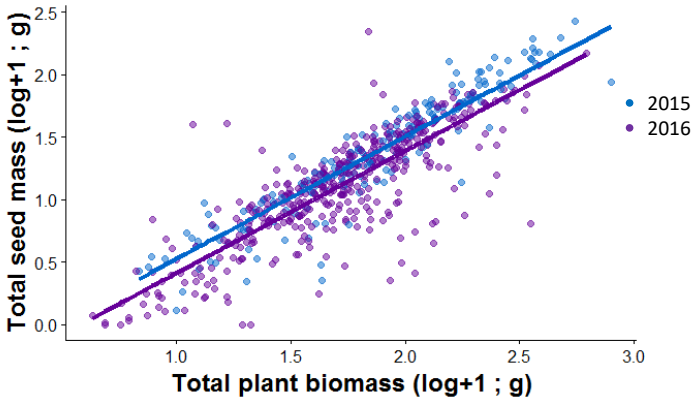


Fig S.D.1. Total seed mass as a function of total plant biomass and year.

The distribution of the residuals and standardised residuals of the model revealed (i) outliers (Fig S.D.2.A) and (ii) a fat-tailed distribution (Fig S.D.2.B). We therefore kept only values with residuals between 0.5 and -0.5 (between the red lines in Fig S.D.2.A) for further investigation. 4.97 % plants were thus removed from the analysis.

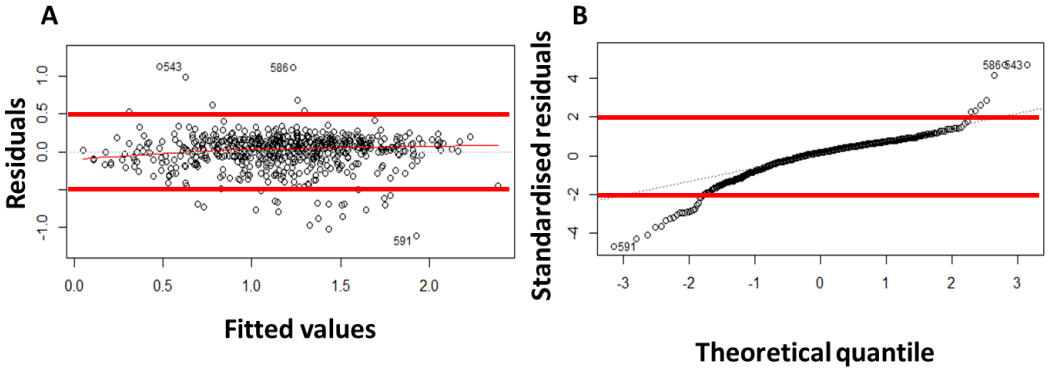


Fig S.D.2. Diagnostic plot of total seed mass model. (A) shows the plot of the residuals against the fitted values and (B) shows the normal probability plot of the standardised residuals (Q-Q plot). The dashed lines represent the relationships expected (A) between the residuals and the fitted values and (B) between the standardised residuals and theoretical quantiles of a normal distribution.

Appendix E. Detecting and accounting for possible systematic bias effect of mesh and Osmolux on fruiting success.

Mesh bags are known to have potentially negative effects on phytometer plants (Howpage et al., 2001; Martin et al., 2013; Sacchi and Price, 1988; Wragg and Johnson, 2011). These effects are usually due to mechanical constraints that affect, in the case of OSR plants, pod development. In our case, for instance, the additional weight of the mesh bag after rain could bend the pods. Alternatively, the mesh may limit pollen transfer, even if the mesh size is large enough to allow pollen transfer, as the mesh screens the flowers. Such artefacts are inherent in the use of mesh bags around flowers in pollination exclusion experiments (Howpage et al., 2001; Sacchi and Price, 1988; Wragg and Johnson, 2011).

To detect potential treatment biases, we first averaged fruiting success according to treatment at the field scale, and plotted it against bee abundance (Fig S.E.1A). We expected that the control branches (pollinated by self-pollination (SF), wind-pollination (W), small pollinators (SP) and large pollinators (LP)) would show higher fruiting success than large mesh (pollinated by "SP+W+SF"), followed by small mesh ("W+SF") and Osmolux ("SF"). The control branches had a higher fruiting success than the bagged branches in all years (Fig.S.E.1.A), but the order of the treatments was not always as expected. For instance, in several cases Osmolux gave higher success than small mesh (Fig S.E.1A). This would indicate a negative pollinator contribution, though it is typically an artefact of using a mesh bag. Such negative contributions were set to zero by replacing, for example, the small mesh values by the Osmolux values when small mesh was less than Osmolux (flooring) unless the difference was less than 5% which was considered to be within the measurement error. A total of 17 small mesh (i.e. 16.8% of all small mesh values) and 28 large mesh values (i.e. 38.4% of all large mesh values) were thus set to Osmolux or small mesh respectively, but no Osmolux value was changed. The results after flooring are given Fig S.E.1.B.

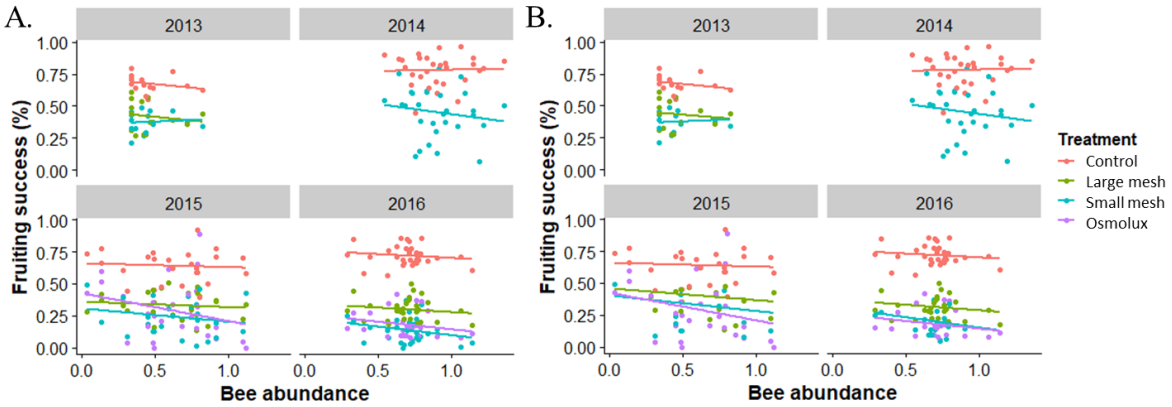


Fig. S.E.1. Effect of bee abundance (*log(x+1)* transformed) on fruiting success for all years (2013-16) and for all treatments (red= control; green=large mesh; blue=small mesh; purple= Osmolux) for (A) raw data and (B) floored corrected data.

Even in the absence of pollinators, self and wind pollination should result in some fruiting success. Therefore, the relationship between bee abundance and fruiting success for the control plants should have a positive intercept. In the same way, since our results showed that

insect pollination had a positive effect on fruiting success, the slope of this relationship should be positive when all years are taking into account. As expected, a positive relationship was found between fruiting success and bee abundance with a positive intercept estimate at 0.65 (red line in Fig. S.E.2).

In absence of insect pollination (i.e. treatments that restricts pollinator access), the intercept of the relationship between bee abundance (*log(x+1)* transformed) and fruiting success (green line, Fig. S.E.2) should be equal to the intercept of the relationship for the control plants. A difference in the intercept would indicate a systematic bias resulting from the treatment. As shown in Fig. S.E.2, we detected a difference between the two intercepts. Differences were also detected between the intercepts of the large mesh treatment and small mesh treatment, between the intercepts of the large mesh treatment and the Osmolux treatment, and between the intercepts of the small mesh treatment and the OS treatment. However, none of these differences were significant. Differences were however found in the intercepts of the relationships between years for a given treatment. We therefore used the difference between the intercepts of the control (evaluated for all year) and large mesh relationships each year as a measure of the bias (difference between control and large mesh intercept: 0.49, 0.06, 0.45, 0.37 for 2013-14-15-16). All values for all treatments were therefore corrected by adding this difference, except for data collected in 2014 when small mesh was used as it was the only treatment.

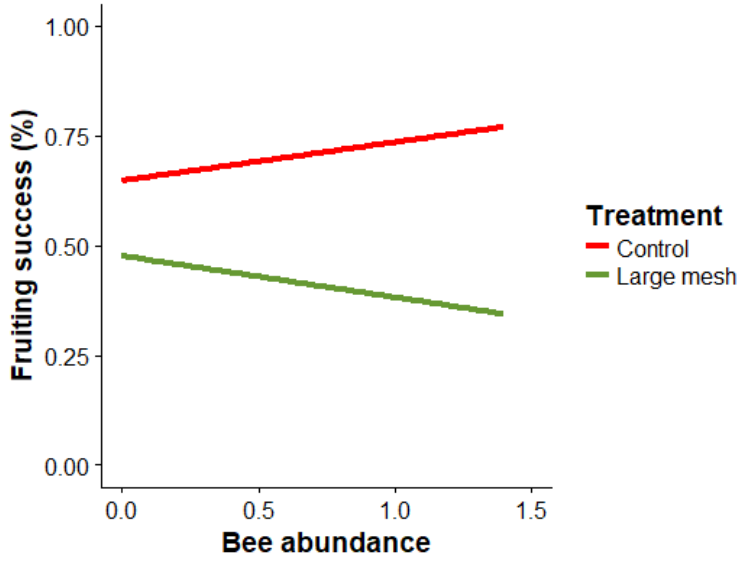


Fig. S.E.2. Fruiting success as a function of bee abundance (*log(x+1)* transformed) for controls (red line) for all year and large mesh branches (green line) for 2013.

The values with intercept adjustment are shown in Fig. S5.E.A. In some cases, adding the difference in intercept resulted in large mesh values being higher than control values (ten control values, 9.9% of all control values). The control values were, therefore floored to large mesh (Fig. S5.E.B).After intercept adjustment, a total of 55 values were floored (16.5 % of all results).

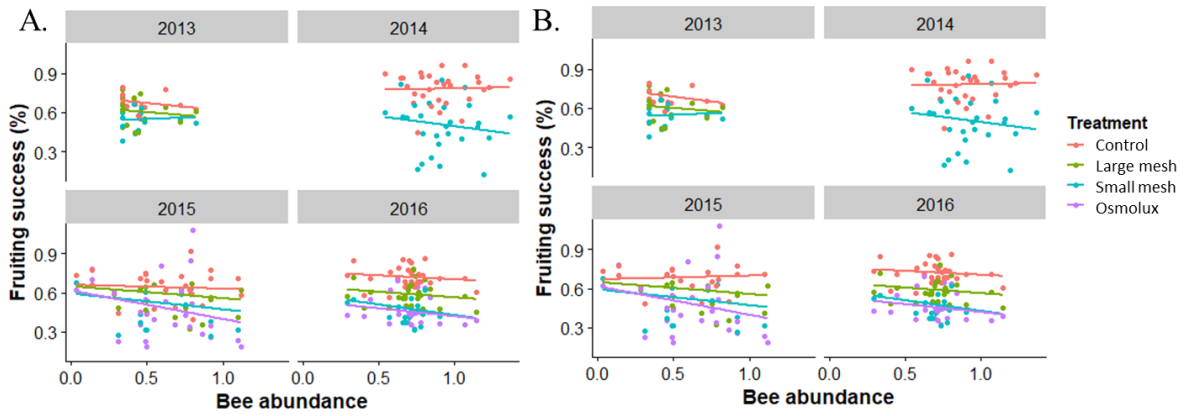


Fig. S.E.3. Fruiting success for all years and all treatments for (A) values adjusted by the intercept correction and (B) values adjusted by the intercept correction and floored

The relative contributions of the different pollination processes to the fruiting success were 30% for insect-pollination and 66% for self-pollination when the corrections were applied (Fig. S.E.4A). Without any correction, relative contributions were estimated to be 59% for insect pollination (Fig. S.E.4A) and 41% for self-pollination (Fig. S5.4A). These values are higher (for insect) or lower (for self-pollination) than is generally found in literature (Bartomeus et al., 2014; Becker et al., 1992; Zou et al., 2017). These relatively high discrepancies suggest that correcting for potential mechanical bias is required. To ensure that our corrections gave consistent results, the contributions of the pollination process were also calculated for the number of seeds per pod (Fig. S.E.4C). As expected for a fertility trait negatively affected by pollinators, insect contribution was insignificant (4.9%, Fig. S.E.4C) compared to self-contribution (90.7%, Fig. S.E.4C).

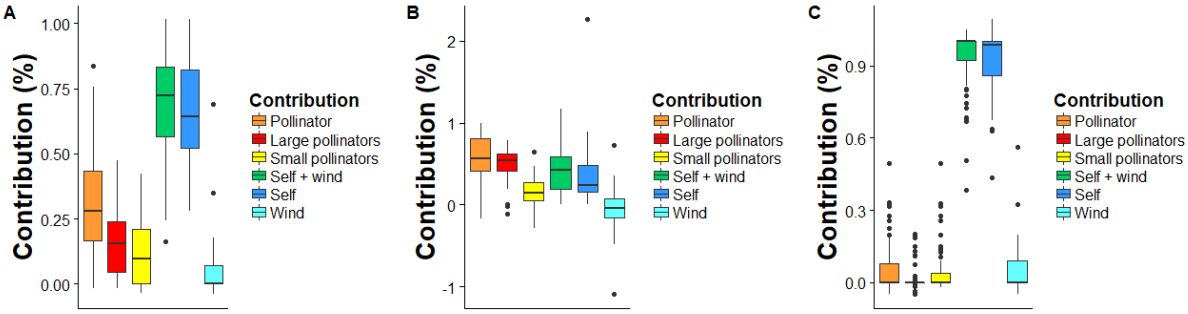


Fig. S.E.4. Contribution of different pollination processes to fruiting success for each year with (A) intercept adjustment and flooring, (B) no adjustment, and (C) for seeds per pod with adjustment.

We then explored how the effect of insect pollination on pollination success was affected by keeping or removing all negative values (Fig S.E.5). We found that results were similar whether or not the negative values were kept, with a pollinator contribution to pollination success estimated as 28.1% when keeping negative values and 32% when they were removed. Similar, we found similar results for estimating the contribution of self-pollination: 80.1 % when negatives values were kept (Fig S.E.5.A) and 70.8% when negative values were removed (Fig S.E.5.B).

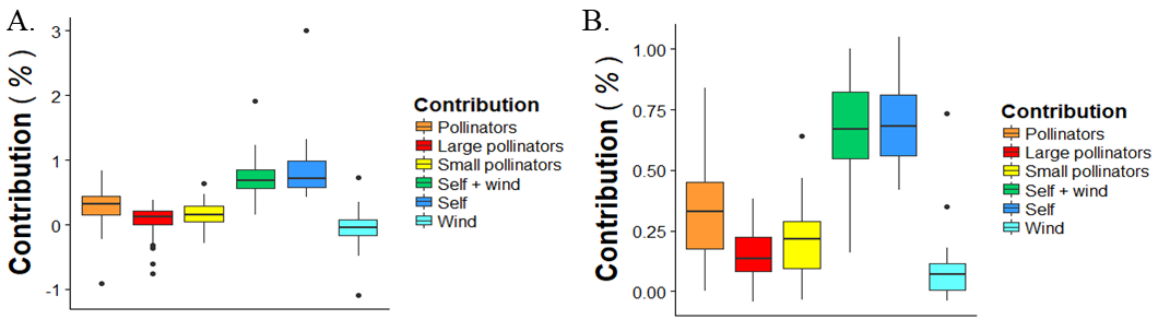


Fig. S.E.5. Contribution of different pollination processes to fruiting success for each year with (A) intercept adjustment and without flooring and (B) with intercept adjustment and all negative values removed.

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Appendix F. Effect of farming practices on OSR yield

We used a stepwise (backward and forward) model selection procedure (based on *p-value* criterion to identify farming practices having significant or marginal effect on yield ($P < 0.1$). OSR yield was used as the dependent variable, and main fertilizers (nitrogen, phosphorus, sulphur and potassium), pesticides (frequency of insecticide, herbicide, and fungicide treatments) and OSR variety type (hybrid *versus* conventional) as explanatory variables. Only phosphorus fertilizer had a significant effect on OSR yield (Table S.F). Other variables were not kept in model.

Table S.F. Summary of model selection for the effect of main fertilizer, pesticide and OSR variety type on OSR yield. Sorted in order of elimination of explanatory variables with associated *p*-value. Only explanatory variables with marginal or significant effect were kept ($P < 0.1$).

Explanatory variable	Order of elimination	*P*
Frequency of insecticide treatment	1	0.68
Nitrogen fertilizer	2	0.69
Sulphur fertilizer	3	0.49
Frequency of fungicide treatment	4	0.28
OSR variety type	5	0.26
Potassium fertilizer	6	0.14
Frequency of herbicide treatment	7	0.11
Phosphorus fertilizer	kept	0.015

Appendix G. Effect of pollinators on OSR yield: supplementary models

A set of linear models was used to check whether the OSR variety type modified the effect of pollinators on yield, even though the type had no direct effect on yield (see Appendix F). We therefore used all models presented under the section "*Contribution of pollinators at field scale"* adding the OSR type and its interaction with pollinator metrics. The interactions between pollinator metrics and OSR type had no effect (Table S.G.1) meaning that the effect of pollinator metrics on yield was independent of the OSR variety type.

Table S.G.1. Results of linear models of OSR yield as a function of pollinator diversity or pollinator abundance (obtained by pan traps in 151 fields or sweep nets in 44 fields), year, phosphorus fertilizer, OSR variety type (hybrid *versus* conventional) and their two-way interactions with pollinator metrics. Significant effects ($P > 0.05$) are in bold. All abundances are *log(x+1)* transformed.

	Pan trap		Sweep net			Pan trap		Sweep net	
	F	*P*	*F*	*P*		F	P	F	P
Total diversity	**4.01**	**0.047**	1.33	0.26	Total abundance	**7.73**	**0.006**	**4.44**	**0.042**
Year	**6.98**	**< 0.001**	0.01	0.92	Year	**4.84**	**0.003**	0.01	0.92
Phosphorus fertilizer	**7.12**	**0.009**	**6.74**	**0.014**	Phosphorus fertilizer	**7.26**	**0.008**	**7.91**	**0.008**
OSR variety type	2.82	0.095	0.03	0.86	OSR variety type	2.29	0.13	0.01	0.94
Total diversity *x* year	0.38	0.77	**4.42**	**0.043**	Total abundance x year	0.21	0.89	3.02	0.091
Total diversity *x* phosphorus fertilizer	0.36	0.55	0.13	0.72	Total abundance x phosphorus fertilizer	0.36	0.55	0.03	0.87
Total diversity x OSR variety type	0.02	0.88	0.14	0.71	Total abundance x OSR variety type	0.07	0.79	1.35	0.25
Bee diversity	**15.11**	**< 0.001**	0.17	0.68	Bee abundance	**12.05**	**0.001**	**5.64**	**0.023**
Year	**4.60**	**0.004**	0.02	0.88	Year	**3.57**	**0.016**	0.01	0.9
Phosphorus fertilizer	**10.32**	**0.002**	**6.69**	**0.014**	Phosphorus fertilizer	**7.54**	**0.007**	**6.74**	**0.014**
OSR variety type	1.91	0.17	0.10	0.75	OSR variety type	2.11	0.15	0.03	0.87
Bee diversity x year	0.20	0.89	**6.82**	**0.013**	Bee abundance x year	0.09	0.97	3.56	0.067
Bee diversity x phosphorus fertilizer	0.57	0.45	1.00	0.33	Bee abundance x phosphorus fertilizer	0.20	0.66	0.23	0.63
Bee diversity x OSR variety type	1.65	0.2	1.11	0.3	Bee abundance x OSR variety type	0.05	0.82	2.05	0.16
Hoverfly diversity	0.01	0.99	1.75	0.19	Hoverfly abundance	3.76	0.055	0.38	0.54
Year	**7.03**	**< 0.001**	0.01	0.91	Year	**5.50**	**0.001**	0.03	0.87
Phosphorus fertilizer	**6.80**	**0.010**	**7.53**	**0.009**	Phosphorus fertilizer	**7.99**	**0.005**	**9.21**	**0.004**
OSR variety type	2.80	0.097	0.01	0.99	OSR variety type	2.55	0.11	0.00	0.94
Hoverfly diversity x year	0.18	0.91	0.35	0.56	Hoverfly abundance x year	1.92	0.13	0.81	0.37
Hoverfly diversity x phosphorus fertilizer	0.02	0.9	0.00	0.95	Hoverfly abundance x phosphorus fertilizer	0.08	0.78	2.63	0.11
Hoverfly diversity x OSR variety type	0.73	0.39	0.06	0.81	Hoverfly abundance x OSR variety type	0.00	0.95	0.01	0.93

A second set of models was used for only the 66 fields with both farm surveys and pollinator exclusion experiments to check if relation between pollinator metrics and OSR yield were still significant using this reduced data set, common to both parts of the study. As can be seen in Table S.G.2, the significance levels are lower (as can be expected because of smaller sample size), but all the effects have a similar sign and magnitude. In particular, there are still positive correlations between the abundance and diversity of bees and the OSR yield (Fig S.G.1).

Table S.G.2. Results of linear models of OSR yield as a function of pollinator diversity or pollinator abundance (obtained by pan traps in 66 fields or sweep nets in 34 fields), year, phosphorus fertilizer, OSR variety type (hybrid *versus* conventional) and their two-way interactions with pollinator metrics. All abundances are *log(x+1)* transformed. Significant effects ($P > 0.05$) are in bold.

	Pan trap		Sweep net			Pan trap		Sweep net	
	F	*P*	*F*	*P*		F	P	F	P
Total diversity	2.74	0.104	**5.18**	**0.031**	Total abundance	2.59	0.113	**9.59**	**0.004**
Year	1.94	0.133	0.71	0.407	Year	1.35	0.267	0.83	0.371
Phosphorus fertilizer	1.63	0.208	**4.67**	**0.039**	Phosphorus fertilizer	2.24	0.140	**7.11**	**0.013**
Total diversity *x* year	0.72	0.547	0.05	0.819	Total abundance x year	0.97	0.414	0.25	0.624
Total diversity *x* phosphorus fertilizer	2.03	0.160	0.06	0.813	Total abundance x phosphorus fertilizer	0.40	0.530	0.00	0.964
Bee diversity	**6.58**	**0.013**	1.68	0.205	Bee abundance	**3.90**	**0.05**	**10.49**	**0.003**
Year	0.74	0.534	0.46	0.504	Year	0.92	0.435	0.85	0.364
Phosphorus fertilizer	2.85	0.097	3.93	0.057	Phosphorus fertilizer	2.41	0.126	**5.04**	**0.033**
Bee diversity x year	0.86	0.469	3.01	0.094	Bee abundance x year	0.89	0.450	0.67	0.420
Bee diversity x phosphorus fertilizer	1.85	0.179	0.37	0.546	Bee abundance x phosphorus fertilizer	0.37	0.543	0.05	0.826
Hoverfly diversity	0.17	0.683	**4.72**	**0.038**	Hoverfly abundance	1.17	0.285	2.58	0.119
Year	2.38	0.080	0.78	0.384	Year	1.81	0.155	0.92	0.346
Phosphorus fertilizer	1.49	0.227	**6.72**	**0.015**	Phosphorus fertilizer	2.33	0.133	**12.16**	**0.002**
Hoverfly diversity x year	0.68	0.566	0.31	0.580	Hoverfly abundance x year	2.08	0.114	0.01	0.909
Hoverfly diversity x phosphorus fertilizer	0.36	0.549	0.13	0.724	Hoverfly abundance x phosphorus fertilizer	0.00	0.954	**6.39**	**0.017**

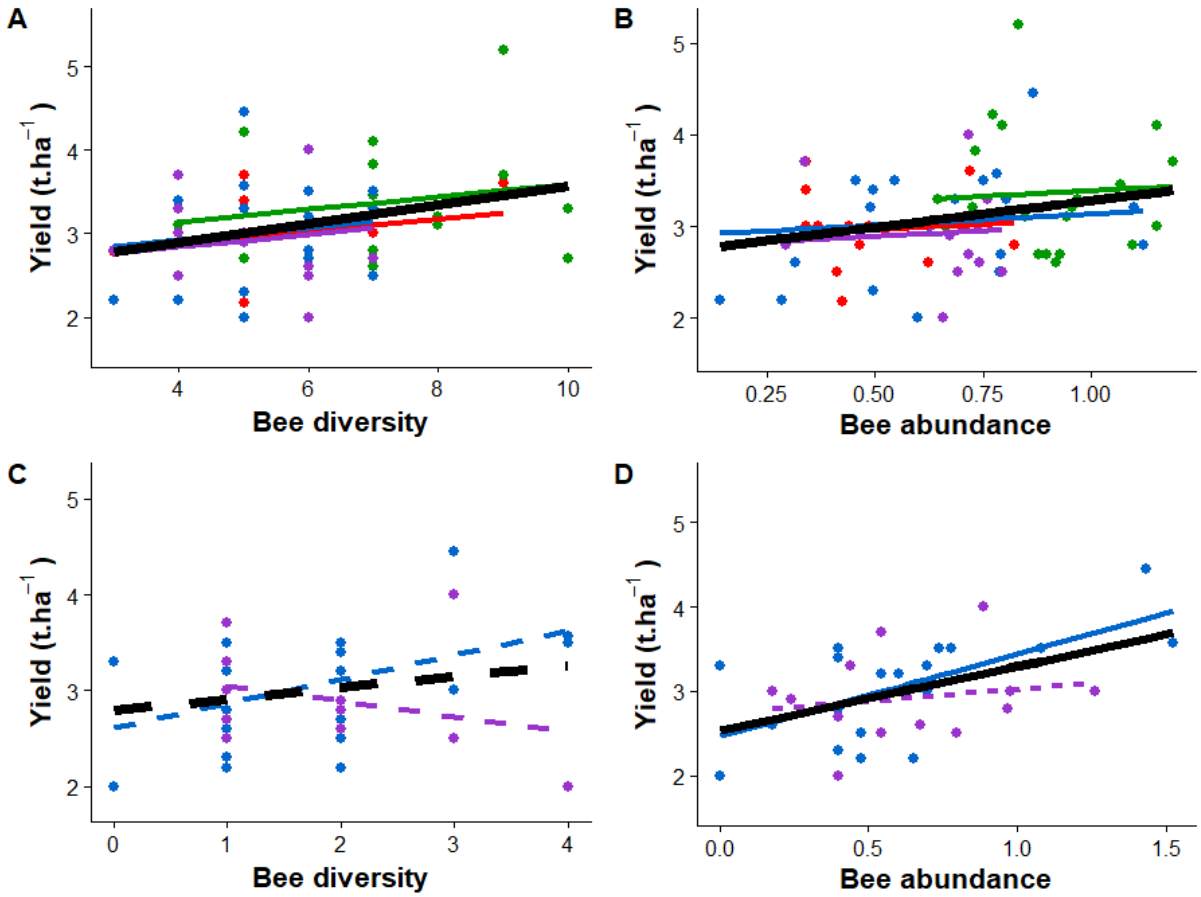

Fig S.G.1. Effect of pollinator community metrics estimated from pan traps (A-B) and sweep nets (C-D) on OSR crop yield. The coloured lines show the linear regressions between yield and pollinators for 2013 (red), 2014 (green), 2015 (blue) and 2016 (purple). The black line shows the relationship averaged over the four years. Lines are dashed where the regressions are not significant. All abundances are *log(x+1)* transformed.

Finally, we tested the effect of the number of bee species on OSR yield for 2015-2016 when identification at species level was available. Bee species richness did not affect OSR yield significantly, either with pan-traps ($F_{1,73}$ = 1.11, P = 0.29, Fig S.G.2) or sweep net ($F_{1,38}$ = 0.47, P = 0.5, Fig S.G.2).

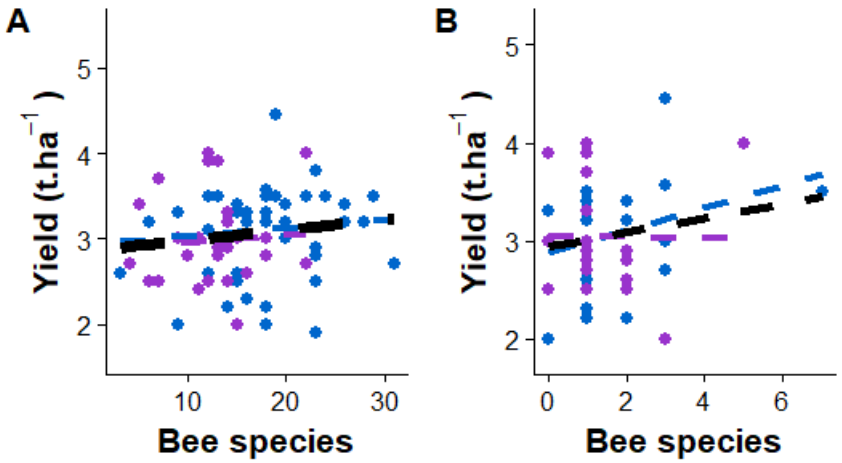

Fig S.G.2. Effect of the number of bee species estimated from pan traps (A) and sweep nets (B) on OSR crop yield. The colour lines indicate the linear regressions between yield and pollinators for 2015 (blue) and 2016 (purple). The black line shows the relationship averaged over the two years. Lines are dashed where the regressions are not significant.

Appendix H. Effect of pollinator diversity and abundance, caught by pan traps, and farming practices on OSR fertility traits

We used 6 linear mixed models to determine the effect of pollinator diversity (total, bee and hoverfly diversity) and pollinator abundance (total, bee and hoverfly abundance, *log(x+1)* transformed) estimated by pan traps on the fruiting success of the control branch (averaged by plant position) accounting for year and the plant position in the field as well as their two terms interaction with pollinator metrics. Field ID was used as a random factor. Bee abundance had a stronger positive effect on fruiting success than bee diversity and total pollinator abundance (Table S.H). Hoverfly abundance had an effect on fruiting success which varied with the year (Table S.H), while increased hoverfly diversity reduced fruiting success (Table S.H).

Table S.H. Fruiting success of control branches depending on pollinator diversity and pollinator abundance evaluated by pan trap, taking account of year and plant position (and their two-way interactions with pollinator metrics). The *F*-values of the linear models are given as negative if the coefficient is negative. Significant effects are in bold. Apart from total diversity, only significant single effects and interactions are shown ($P < 0.05$). All abundances are *log(x+1)* transformed.

	F	*P*
Total diversity	-1.68	0.2
Bee diversity	**4.22**	**0.043**
Hoverfly diversity	**-10.98**	**0.001**
Total pollinator abundance	**6.85**	**0.01**
Bee abundance	**10.67**	**0.002**
Hoverfly abundance	**-8.19**	**0.005**
Hoverfly abundance *x* year	**2.84**	**0.04**
N	194	

We then used 4 linear models to determine the effect of bee abundance estimated by pan traps on the fruiting success, seeds per pods, seed unit weight for the control branch and seed mass per plant adjusted for plant biomass (averaged for each position in the field) accounting for year, phosphorus fertilizer (the only farmers practices with significant effect on OSR yield) and the plant position in the field as well as their two-term interactions. Field ID was used as a random factor. Bee abundance had a significant positive effect on fruiting success ($F_{1,112} = 16$, $P < 0.001$, Fig S.H) and a marginally significant positive effect on seed mass adjusted for plant biomass ($F_{1,71} = 3.27$, $P = 0.078$, Fig S.H). Bee abundance had a marginally significant negative effect on seeds per pod ($F_{1,112} = 3.08$, $P = 0.085$, Fig S.H) and bee abundance had no effect on seed unit weight ($F_{1,110} = 0.18$, $P = 0.68$, Fig S.H). No interactions were found between bee abundance and year, phosphorus fertilizer, or plant position (all $P > 0.2$). The effect of bee abundance on OSR fertility was similar to the models not using farming practices (see results). Only *p*-value was different but this was mainly due to the smaller dataset as farming practices were not available for all fields with pollinator exclusion experiments.

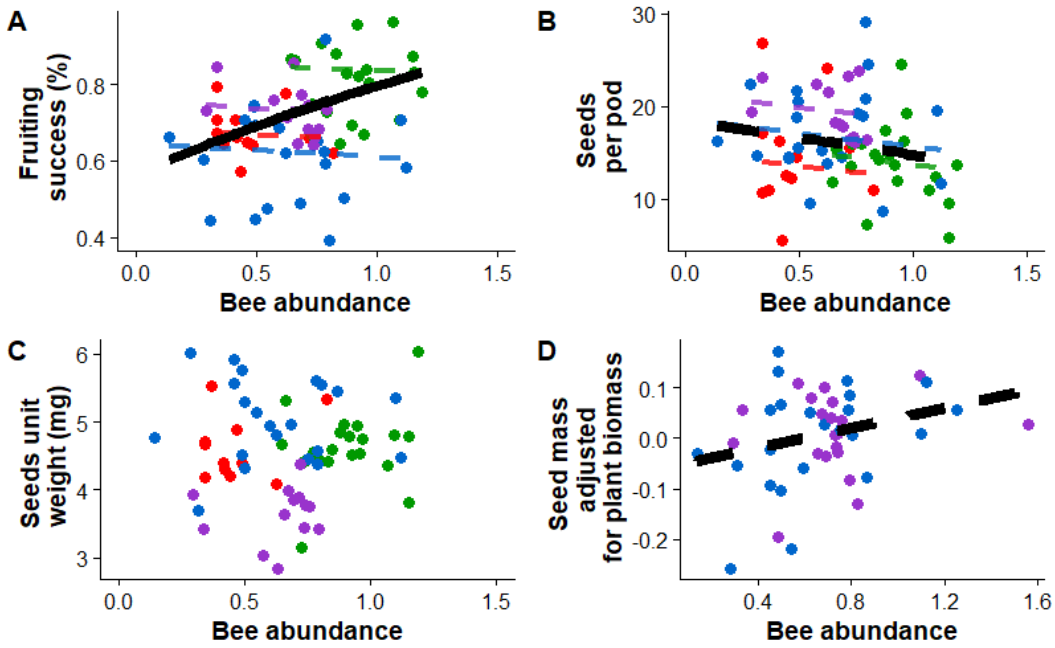

Fig S.H. Effect of bee abundance (*log(x+1)* transformed) estimated from pan traps on different OSR fertility traits, averaged at field scale. The traits were measured for the control branch (A-C) and the whole plant (D). The colour lines show the linear regressions between OSR fertility traits and bee abundance for 2013 (red), 2014 (green), 2015 (blue) and 2016 (purple) where these are significant. The black line shows the relationships averaged over the four years. Lines are dashed where the regressions are not significant.

Chapitre II :

Quantification du bénéfice des pollinisateurs dans les rendements de tournesol par une approche expérimentale: réconcilier les estimations à l'échelle de la plante à celles de la parcelle

Avant-propos et résumé du chapitre 2 :

Le tournesol est une culture dont les rendements sont dépendants des pollinisateurs. Cette culture est la troisième en termes de surface en Europe et a donc un intérêt économique fort. Cependant la contribution des pollinisateurs dans les rendements de tournesol reste incertaine ; les pollinisateurs peuvent augmenter la production de graines de 20% ou la doubler selon les études. De plus, la majorité des études qui ont évalué la contribution des pollinisateurs ont été réalisées en condition contrôlée et sur des petites surfaces pouvant ne pas refléter le bénéfice des pollinisateurs en condition réelle. Finalement comme pour le colza, les pollinisateurs impliqués restent en débat entre les études et particulièrement l'importance des pollinisateurs sauvages dans la production de tournesol. Dans cette étude, nous avons donc cherché à évaluer la contribution des pollinisateurs dans la production de tournesol directement dans les parcelles agricole à la fois à l'échelle de la parcelle et celle de la plante tout en déterminant les pollinisateurs impliqués dans la pollinisation du tournesol. Cette contribution est évaluée le long d'un gradient de pollinisateurs et en utilisant des filets. Dans cette étude, nous nous sommes intéressés plus particulièrement à deux composantes du rendement du tournesol que sont le diamètre des têtes de tournesol et la densité de plante. Ces deux composantes peuvent augmenter les rendements et la présence des pollinisateurs, mais sont négativement corrélées entre elles.

Notre étude montre que les pollinisateurs peuvent augmenter les rendements de tournesols de 40% à l'échelle de la parcelle et entre 32.5% et 35.4% à l'échelle de la plante selon la méthode utilisée (respectivement le gradient de pollinisateurs et l'exclusion des pollinisateurs par les filets). Cette contribution est égale à celle de l'autopollinisation mais est plus importante que celle du vent (22.2%). Les abeilles domestiques sont les principaux pollinisateurs impliqués dans la pollinisation du tournesol alors que les pollinisateurs sauvages contribuent peu. La présence des abeilles domestiques est en partie déterminée par la densité de plantes mais pas par le diamètre des têtes de tournesol. A l'échelle de la plante, les abeilles domestiques augmentent le nombre de graines par tournesol ainsi que le poids des graines par m², une fois la densité de plante prise en compte, malgré un compromis entre le nombre de graines et le poids moyen des graines.
Cette étude confirme l'importance des abeilles domestiques dans la production de tournesol et l'intérêt de les préserver dans les milieux agricoles.

Experimental quantification of insect pollination on sunflower yield, reconciling plant and field scale estimates

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Abstract
Most crops grown in Europe, including sunflower (*Helianthus annulus L.*), benefit from insect pollination. However, valuing this benefit is not straightforward since estimates for the increase sunflower yield vary from 18% up to 100%. Most estimates have, moreover, been performed at plant scale, a scale that is not relevant for farmers who reason at field scale. In this four-year study, we quantified the contribution of insect pollination to sunflower yield at field and plant scales in working farm fields distributed along a gradient of pollinator diversity and abundance. Pollinators were found to increase field yield up to 40% (i.e. 0.7 t/ha) and by 31.3% at plant scale; the magnitude of effect on yield being therefore similar at both scales. The pollinators increased the yield by increasing the number of fertilized seeds per plant with no significant effect on the unit mass of the seeds although there was a trade-off between number of seeds and unit mass. Among pollinators, honeybees were the main taxon impacting sunflower yield. Sunflower plant density was a strong determinant of yield, with higher densities attracting increased numbers of honeybees. Using pollinator and wind exclusion, we finally quantified the relative contributions of self-pollination (~40%), insect pollination (~35%) and wind pollination (~20%). Our results show, to the best of our knowledge, the first evidence of the key role of pollinators in sunflower production at field scale in real farming conditions, and underscore the need to maintain suitable conditions for pollinators in agricultural landscapes.

Keywords
Agroecology, Pollination service, Honeybee, Wild pollinators, Biodiversity, Wind pollination, Sunflowers, Self-pollination

Introduction

Ecological intensification of agriculture has been promoted as a way of reducing chemical inputs by relying on pest control and pollination as ecosystem functions, rather than on agrochemicals (Bommarco, Kleijn, & Potts, 2013). Up to 70% of crops and 35% of agriculture production depend on insect pollination (Klein et al., 2007), that involve domesticated pollinators such as honeybees (*Apis mellifera*) and many wild bees (Garibaldi et al., 2013; Kleijn et al., 2015). However, recent declines of wild bees and honeybees and in the same time the increase of pollinated dependent crop area may lead to pollination limitation at continental scale (Aizen & Harder, 2009). Despite strong evidence that pollinators are critical for agriculture production, insect pollination is still ignored in the selection of farming practices, farming systems and crops (Chen, Zhang, Liu, & Yu, 2017; Misganaw, Mengesha, & Awas, 2017). One reason may be a mismatch between the viewpoints of farmers, who measure yield at field scale, and researchers who quantify the contribution of insect pollination using proxies at small field part (Garibaldi et al., 2016), plant scale (Bartomeus et al., 2014), or even smaller scales (Bos et al., 2007; Garibaldi et al., 2013). Such proxies may not accurately account for the capacity of crop plants to compensate for a pollination deficit (Bos et al., 2007), nor for intra- or inter- field in yield (Kayad et al., 2016). An estimate of the contribution of pollinators will only be meaningful for farmers if the yield is measured at field scale along a pollinator gradient (Vaissière, Freitas, & Gemmill-Herren, 2011). Such studies are rare (Gaines-Day & Gratton, 2016; Lindström et al., 2016).

Sunflower (*Helianthus annulus L.*), the major oil seed crop in Europe (FAOSTAT, 2014), is highly dependent on pollinators whose contribution to yield is controversial and has been estimated from 18% up to 100% (i.e. doubling the yield). The dependence of the yield on pollinators has been found to be weak (Degrandi-Hoffman & Chambers, 2006; Tamburini, Lami, & Marini, 2017), medium (Aslan, Yavuksuz, & Asian, 2010) or strong (Carvalheiro et al., 2011; Garibaldi et al., 2016, Greenleaf & Kremen, 2006). The variability may be the result of the different methods that were used to estimate the pollinators' contribution, e.g. using cages enclosing pollinators (Aslan et al., 2010), that may force plant-pollinator interactions seldom occurring naturally (Banda & Paxton, 1991), or using experimental fields that may not be representative of farming practices (Degrandi-Hoffman & Chambers, 2006; Tamburini et al., 2017). Direct estimates of the contribution of insect pollination to sunflower yield in working farm fields are very rare (Carvalheiro et al., 2011, Garibaldi et al., 2016; Greenleaf & Kremen, 2006), and rarely consider the effect of plant density within (Garibaldi et al., 2016,Carvalheiro et al., 2011; Greenleaf & Kremen, 2006). The variability may also due to the pollinator metrics used: honeybee abundance (Greenleaf & Kremen, 2006; Pisanty, Klein, & Mandelik, 2013), wild pollinator diversity (Carvalheiro et al., 2011), wild bee abundance (Greenleaf & Kremen, 2006; Hevia et al., 2016) or total pollinator abundance (Garibaldi et al., 2016). Variability also arises from the method of estimating the pollinators' contribution: flower pollination success (Carvalheiro et al., 2011; Greenleaf & Kremen, 2006) or seed mass (Carvalheiro et al., 2011). These metrics do not take into account the trade-off between number of seeds and their unit mass (Tamburini et al., 2017). At the field scale, yield is the product of plant density, unit mass and number of seeds per flower head. The latter depends on pollination success, with the head diameter (Marinkovic, 1992) being a confounding variable since its average has been reported as decreasing with plant density (Ibrahim, 2012) while larger heads attract more pollinators (Pisanty et al., 2013). Finally, sunflower is also pollinated by self-pollination (Javed & Medhi, 1992) and wind pollination, though their contributions have never been differentiated (e.g. Degrandi-Hoffman & Chambers, 2006; Javed & Medhi, 1992).

Our study aimed to fill those gaps by assessing the effect of insect pollination on yield at plant and field scales in real farming conditions over four years using a single experimental design . Yield may depend on both pollinator abundance and diversity, which are very different between fields. In our study, fields were selected along gradients of landscapes with different densities of semi-natural

habitats, meadows and organically farmed fields to ensure a wide range of pollinator abundances and diversities (Kennedy et al., 2013). In each field, we performed pollination exclusion experiments to determine the effectiveness of each type of pollination. We first assessed, at plant and field scales, the relationships between the various components of yield to test for potential trade-offs, especially between plant density, head diameter, number of seeds per head and seed unit mass. Then we investigated whether pollinators (wild or domestic measured as abundance or diversity) increased yield at field and plant scales, accounting for the trade-offs identified. Finally, we evaluated the relative contributions of insect pollination, wind pollination and self-pollination on sunflower yields for a range of pollinator abundances and diversities.

Material and methods

Study area and field selection

Pollinator exclusion experiments and farm surveys were conducted between 2013 and 2017 in the Long-Term Social Ecological Research site (LTSER) "Zone Atelier Plaine & Val de Sèvre", a 450 km² study site located in the south of *Deux-Sèvres* district, central western France (Bretagnolle et al., 2018). Sunflower represents about 10% of the agricultural area. Experiments were conducted directly in working farm fields. Each year, we randomly selected 40 to 60 1 km² squares in the LTSER distributed along three gradients of landscape features: semi-natural habitats (hedges and forest fragments), meadows and organically farmed fields. All these landscape features have been shown to strongly influence pollinators (Kennedy et al., 2013). We used a moving window to select the squares (see Fahrig et al., 2011 for the procedure used) to minimize inter-gradient correlations. Within each square, one sunflower focus field was then selected when present. On average, the sunflower fields were 350 m apart (102 m to 1250 m). Field size ranged from 0.3 ha to 20.7 ha (mean 5.8 ha).
A first set of 97 sunflower fields (17, 5, 38 and 37 in 2013, 2014, 2015 and 2016 respectively) was used for an empirical assessment of pollinators on sunflower yield at the field scale. A second set of 67 fields (23, 27 and 17 from 2015, 2016 and 2017 respectively), of which half were also in the first set, was used for pollinator exclusion experiments. The two sets differed because not all farmers accepted either surveys or experiments in their fields in 2015 and 2016 (i.e. years where both surveys and experiments were carried out). No field was used in two different years. Experiments were carried out on 44 different hybrid restored varieties of sunflower, all of which were self-fertile. Most fields were cultivated using conventional practices (98%), the others being organically farmed.

Measurement of yield components

Information on farming practices (fertilizers, pesticides, sowing density, crop variety) and yield, for the 97 fields of the first set, were collected at the end of each cropping season by farm surveys. In 2016 and 2017, just prior to harvest, the number of sunflower plants was measured in 1 m² quadrats in the field border and at 15 m and 75 m from the field edge. Plant density at field scale was then estimated by averaging the number of plants over the three quadrats. Sunflower plants (see below) were collected five days before harvest. In the laboratory, head diameter (in mm) was measured twice and averaged for analyses and then heads were stored in individual bags and left into a heat chamber at 60°C for 48 hours. Seeds were removed mechanically from the heads, and fertilized seeds were separated from empty seeds (arbitrary threshold of 9 mg) by seed density with a wind machine (Batteuse petites graines, ATID, France). Then fertilized seeds were counted twice with a seed counter (Contador 2, Pfeuffer, Germany). The repeatability between the two measurements was extremely high (less than 0.1% difference), so we used the average. Total seed mass (using only fertilized seeds) was measured (nearest 0.1 mg) and three individual fertilized seeds were randomly chosen and weighed to provide the individual unit mass (average of the three weights).

Pollination exclusion experiments

In 2015, twenty sunflower plants were selected per field in rows of four plants at five different positions (Table 1). In 2016 and 2017, only 12 sunflowers were selected at three positions (Table 1). The distance from the edge was studied because insect pollination in sunflower has been shown to decrease with distance from the edge (Hevia et al., 2016). The four plants within a row were chosen to be at the same growth stage (same overall height, same head flower diameter). Each plant within a given row was subject to a different treatment to estimate the contributions of large pollinators (LP), small pollinators (SP), wind pollination (W) and self-pollination (SF) at plant scale. We also used manual (hand) pollination (HP) in some rows, with or without insect pollinator exclusion, to estimate the effect of bagging sunflower heads (Wragg & Johnson, 2011).

Within each row, one plant was used as a control (Table 1) with the flowers accessible to all pollination process (LP+SP+W+SF). The head of a second plant was bagged with a large mesh (3 mm mesh size), preventing large insect pollination but allowing small pollinators (SP), wind-pollination (W) and self-pollination (SF), while a third plant was bagged with small mesh bag (0.6 mm mesh size; Table 1), preventing all insect pollination (W+SF). The fourth plant on the row was treated differently depending on the year and plant position. Experimental design evolved throughout years to improve our ability to estimate pollinator contribution. Thus in 2015, it was bagged with osmolux, a tissue allowing only gas exchange thus excluding all types of pollination but self-pollination (SF). In 2016, only the plant in middle position (15 m) was bagged with osmolux (Table 1): one of the other two was left open and hand pollinated (HP) with pollen from a neighbouring plant, while the other was bagged with small mesh and hand pollinated. The bagged plant was either at the edge (0m) or the centre of the field (75m) depending on the field. In 2017, the fourth plants in the edge (0m) and centre rows (75m) were bagged with osmolux, while in the row 15 m from the edge, the fourth plants were left open and hand pollinated and a fifth plant was bagged with osmolux and hand pollinated (Table 1). The plants were bagged at the very beginning of flowering and removed after the last flowers faded, to avoid the bag affecting seed formation. Sample size varied slightly because some sunflower plants died and some bags, especially osmolux, were found open or torn.

Pollinator sampling

We sampled the pollinators using two complementary methods. Firstly, they were trapped in pan traps (Westphal et al., 2008), these were plastic bowls of 12cm diameter and 10cm deep filled with c. 600 ml of water with drops of soap and left in the field during 4 days per fields. Pan traps were three different colours (yellow, blue or left white) to catch pollinators by colour preference (Westphal et al., 2008): The traps were mounted on wooden stakes, in the vegetation height (Westphal et al., 2008) and installed during summer to covering the sunflower flowering period (~15th June to 22th August). Given that bees, in particular honeybees but also bumblebees and at least some wild bees (Zurbuchen et al., 2010), forage over large distances, we used other surrounding fields as well as the focal field to estimate the pollinator community around the focal field, thus avoiding dilution, spill over or attraction effects (Holzschuh et al., 2016). Traps were set in fields with sunflowers, maize and meadows. The number of fields surveyed at a given buffer distance was quite variable (e.g. 1-10 fields at 2000m from the focal field), with on average 28.8 pan traps in 4.0 fields. As pollinator abundance and diversity did not differ statistically between field edge and field core for 2013-2015 (Fig.A), in 2016 and 2017, the sampling effort was reduced to the field core with three pan traps placed twice during the season.

We used sweep-nets to complement the pan traps, since pan traps may underestimate some pollinators (e.g. honeybee (Westphal et al., 2008). In 2015, we swept two transects per field: one at the edge and one in the field core. In 2016 and 2017, we swept three transects: at the edge, 20 m from the edge and in the field core. All transects were 50m in length and lasted 10 minutes measured with a

chronometer to ensure approximately equal sampling effort. Honeybee was visually counted and other pollinators were caught by sweep net. We stopped the chronometer each time an insect (except for honeybee) was caught to remove it from the sweep-net, identify it visually or put it into a tube for later identification. We swept the transects between 8.30am and 5.30pm, when the air temperature was above 15°C and the weather sunny.

Professional entomologists identified all insects caught in the pan traps at genera level for wild bees and species level for hoverflies. For 2015-2017 only, we identified bees at species level. Abundance per guild was obtained by a hierarchical average procedure, starting with mean count per bowl colour and position in the field (core *vs*. edge), then averaging for each position in the field, and finally for each field. This was then averaged with all other fields within a radius of 2000m from the 25st of June (day 175 of year) to the 30th of August (day 240), covering the full sunflower flowering period each year. The diversity was represented either at genera or species level. A similar procedure was used for the sweep net captures. See Appendix A. for a description of the pollinator community.

Statistical analyses

We used linear models or linear mixed models (LM or LMM) for all analyses. As we expected sunflower yield to be influenced by farming practices, we first assessed the effects these practices on yield. Unexpectedly, none of the farming practices analysed here significantly affected yield (Table C.2), hence they were not included further in the analyses. We then analysed the relationships between yield (and various components of yield such as average head diameter), plant density (only available in 2016 and 2017) and sowing density. In these models, we accounted for the effects of year and distance to edge as fixed effects. Distance to edge was nested within the field ID, and the field ID was nested within year to account for the sampling design (the distance to edge varied between years and no field was sampled in different years). Next we investigated yield, with head diameter, plant density and year as explanatory variables.

We also examined the relationship between yield components at plant scale to check for potential trade-offs. Since the head diameter was expected to be the main driver of plant yield, we analysed relationships between the head diameter and three plant yield components, the number of fertilized seeds, the seed mass and the total seed mass per head. We used an asymptotic model to test whether the yield components saturated with head diameter. We used LMM since the field ID was included as a random effect as repeated measurements (i.e., different individual plants) were available for each field. Distance to edge and year were also included as fixed effects.

To analyse the effects of pollinators on yield at field scale, we built several LMs with different pollinator metrics, year and their interactions as explanatory variables. Pollinator metrics included pollinator diversity (bees and hoverflies at genera and species levels), abundance per guild (honeybees estimated by sweep nets, and wild bees, hoverflies and bumblebees estimated by pan traps) and total abundance. We used regression to quantify the effects of various pollinator metrics on yield, with the confidence interval obtained from the standard error of the model estimates, and compared the predicted yield at the lowest and highest values of each pollinator metric. The most relevant pollinator metric (honeybee abundance, see results) was then used to determine which sunflower plant yield component was most influenced by insect pollination. We built LMs with each sunflower yield component (number of fertilized seeds, seed unit mass and seed mass per m²) as successive dependent variables, and honeybee abundance, distance to edge, year and the interactions with honeybee abundance as explanatory variables. Given the predominant effect of the sunflower head diameter, it was added as an covariate in the model. To explore whether number of pollinators could saturate or decrease yield, we confronted a linear, a saturation and a humped model to analyse how sunflower yield changes with pollinator abundance. The asymptotic model, i.e. saturation hypothesis, was found to be the best model (data not shown) and therefore kept for the analysis.

To quantify the contribution of the different types of pollination, we used the number of fertilised seeds per head as a measurement of yield per plant for each experimental treatment, since this parameter was the most affected by pollinator abundance. The use of bags as an exclusion treatment may potentially bias the estimated yield. We performed a preliminary analysis to check for such bias and corrected the number of fertilised seeds to take into account the effects of the bias. (Appendix B.). We then estimated the contribution of wind pollination as the difference between the number of fertilized seeds (corrected values) in the treatment which excluded all pollinators and the treatment allowing only self-pollination (SF). The contribution of pollination by small insects was estimated as the difference in the number of fertilized seeds between the large pollinator exclusion treatment and the treatment which excluded all pollinators, while the contribution of pollination by large insects was the difference in the number of fertilized seeds between the control and the large pollinator exclusion treatment. The overall pollinator contribution was the sum of the small and large pollinator contributions. The relative contributions of each of the pollination types were then obtained as the % of the total contributions (Bartomeus et al., 2014). In a few cases, the difference in the number of fertilised seeds between treatments was negative. Since a negative contribution cannot theoretically exist, negative values were arbitrarily set to 0 when the magnitude of the negative contribution exceeded 10% (Appendix B.). Setting these negative contributions did not affect the result (Fig G.5). Differences in the contribution of the different types of pollination processes were tested using a LM and post-hoc test, with pollination type, year and their interaction as explanatory variables.

In all analyses, pollinator metrics ,head diameter and plant density were used as predictor were *log(x+1)* transformed. Honeybee abundance and seed mass per m² were *log(x+1)* transformed when used as response variable to meet normality and homoscedasticity assumptions. All analyses were performed with R software (R Core team, 2015), using "stat" package for linear models, multiple stepwise regression and post hoc tests and "lmertest" for linear mixed models (Kuznetsova, Brockhoff, & Christensen, 2014). F and p-values of the LM (LMM) models are provided when we were interested in the relevance of the model for all variables. Otherwise, these values are provided only for the variable of interest.

Results

Components of sunflower yield at field and plant scales

Sunflower yield in farmers' fields was on average 2.08 tons.ha^{-1} (range: 0.9-3.0, n = 97), and did not statistically differ between years (LM, $F_{3,93}$=1.87, p = 0.14). We observed a high variation of average head diameter between fields (17.7 cm, range 12.0-25.4), a smaller variation between years but not with distance from the edge of the field (Table 2). Average head diameter was not correlated with plant density (only available in 2016 and 2017) when accounting for year and distance to edge ($F_{6,116}$=0.57, p = 0.45), unlike previously published studies. Sunflower plant density was also highly variable between fields (7.6 plants/m², range 3.3-10.7), slightly higher in 2017 than in 2016 (8.5 *vs.* 7 plants/m²) and increasing, though not significantly, from edge to core (Table 2). Plant density was unrelated to sowing density and other farming practices (Table C.3). Similar results were found for head diameter (Table C.3). Finally, field yield did not depend neither on plant density ($F_{1,20}$ = 2.49, p = 0.13) in 2016 nor on head diameter ($F_{1,34}$=0.0.72, P=0.48) in 2015-16.

At the plant level, strong and positive relations were found between head diameter and number of fertilised seeds, seed mass, or seed mass per head (LMM, *all* p < 0.001, Fig.1.a.b.c).The relationships were saturating for the number of fertilized seeds and head diameter and between seed mass per head and fertilized seeds (Fig.1). At the plant level therefore, larger heads yielded higher

total seed mass (Fig.1.c), but there was also a trade-off between the number of fertilized seeds and the seed mass (Table 3, Fig.1.d) after accounting for head diameter.

Effect of pollinator abundance and diversity on sunflower yield at field and plant scales

Sunflower yield at field scale was significantly increased by honeybee abundance, for both pollinator sampling methods (Fig. 2a,c; see Table D.2 for statistical tests), with saturation for sweep net data. The yield increase between fields with lowest honeybee abundance (0.5 honeybees/transect for sweep net) to fields with highest abundance (116 honeybees/transect) was 41.1% (range 30.5- 51.2), i.e. 0.72 t/ha yield increase. Similar value was obtained with pan trap data (41.5% increase, range 30.4-52.6, Fig.2*c*). Given that the abundance data were obtained within a predefined buffer zone and period (2000m radius and 65 days), we checked the robustness of our results with varying spatial and temporal ranges: at 2000m, the relationships were independent of the time, but the relationships were slightly weaker with a smaller buffer zone (Table D.1). Among the other pollinators, only hoverflies increased sunflower yield, though this was due to 2013, a year where hoverflies were particularly abundant (Fig.2.e; Table D.2). Wild pollinator abundance and richness (either at genera or species levels), did not contribute to yield (Fig. 2.b,d; Table D.2). According to our results, therefore, among bees, only honeybees affected sunflower yield at field level.

Next, we investigated which plant yield components were influenced by honeybee abundance. At field scale, honeybee abundance was not correlated with average head diameter ($F_{1,65}$ = 1.19, p = 0.28) for 2015-16-17, but honeybee abundance was correlated with plant density ($F_{1,42}$ = 4.52 , p = 0.039, Fig.1.e) for 2016-17. At plant scale, accounting for head diameter as a proxy of total number of flowers, honeybee abundance was significantly correlated with the total number of fertilized seeds per head ($F_{1,218}$=32.45, $p < 0.001$) with an increase of 31.3% between fields with 0.5 honeybees/transect and 116 honeybees/transect. This relationship was unaffected by distance of the plant from the edge (interaction between honeybee and plant position: $F_{1,218}$= 0.2 , p=0.65). As expected from the trade-off between the number of seeds and the individual seed mass (Fig.1.d), seed mass was negatively correlated with honeybee abundance although not significantly ($F_{1,217}$ = 3.56, p = 0.06). However, the positive correlation between honeybee abundance and total number of fertilized seeds was strong enough to result in a positive correlation with seed mass per m² with a similar saturation to that observed for the yield at field scale ($F_{1,116}$= 14.82, $p < 0.001$, Fig.1.f). Overall therefore, honeybees increase yield by increasing the number of fertilised seeds per plant which saturates with an excess of honey.

Pollination processes and their contribution to yield

The contributions of the various pollination processes were significantly different ($F_{4,312}$ = 58.36, $p < 0.001$). Self-pollination (42.5%) and insect pollination (34.5%) were the main contributors to the number of fertilized seeds per head (Fig.3.*a*). Large pollinators (30.6%) such as honeybees and bumblebees had more effect than small pollinators (4% Fig.3.a). Only 23% of pollination was attributed to the wind (Fig.*3*.a). The contribution of insect pollinators varied between years (18% in 2015, 43% in 2016 and 2017), as did that of other pollination processes ($F_{2,312}$=4.85, p = 0.008) except small pollinators (interaction year-pollination process, $F_{8,312}$=14.15, $p < 0.001$). Honeybee abundance (sweep net data) varied between years (2.44, 22.7 and 29.8 honeybees/transect, $F_{2,64}$ = 43.32, $p < 0.001$), and this variation significantly affected the insect pollinators' contribution to pollination ($F_{1,64}$ = 35.4, $p < 0.001$, Fig.3.b). The contribution of pollinators was marginally correlated with the yield estimated at field scale ($F_{1,35}$ = 3.5, p = 0.07, Fig.3.c), confirming that the increase of pollinators contribution at plant scale resulted in an increase in yield at field scale.

Discussion

Our study revealed that honeybees were the main insect pollinator involved in sunflower yield: increasing the honeybee abundance improved the relative contribution of insect pollination over other pollination mechanisms, and increased the number of fertilized seeds independently of the head diameter. Barros et al. (2004) also found that yield increased with the number of seeds per m² rather than seed unit mass. Seed unit mass decreased non-significantly with increasing honeybee abundance, as a consequence of the trade-off between the mass and the number of fertilized seeds (see Barros et al., 2004; Tamburini et al., 2017). Such a trade-off is commonly found in plants (Jakobsson & Eriksson, 2000). Our results also showed that plant density was positively correlated with honeybee abundance, while head diameter was not, suggesting that honeybees were more attracted by plant density than plant size. Moreover, higher honeybee abundance still increased seed mass per m² independently of the plant density. Increasing plant density was also shown to increase yield at field scale, in agreement with Barros et al. (2004). Plant density is thus a key feature that must be considered when studying sunflower yield and our results show that the contribution of pollinators cannot be directly estimated from pollination success or seed unit mass on their own.

Sunflower head diameter was found to be a strongly correlated with the number of fertilized seeds and seed mass (see also Marinkovic, 1992). Allowing for the effect of head diameter, we found that pollinators had a positive effect on the number of fertilised seeds, which was potentially due to the increase of pollination success with increasing pollinator abundance (Carvalheiro et al., 2011; Greenleaf & Kremen, 2006; Pisanty et al., 2013), though this was not directly estimated in our study. Honeybee abundance was not positively correlated with head diameter, conversely to Pisanty et al. (2013), although they studied honeybee visits between small and large flowers within the same field. Surprisingly, we found that plant density was not negatively correlated with head diameter unlike Ibrahim (2012) who found a negative correlation for plant densities between 4.5 and 9 plants per m². Another study found that the number of flowers per head did not decrease with increasing density above about four plants per m² (Villalobos, Sadras, Soriano, & Fereres, 1994), well below the average value (7.6 plants per m²) we found in our study. Possibly, as there was no correlation between fertilizer dose and yield, soil resources were not limiting for sunflower development in our study. In addition, we found that fields with a high density of plants had a higher pollinator abundance, being probably more attractive due to an increase in resource availability, as found for other plants (Delmas, Fort, Escaravage, & Pornon, 2016).

The contribution of insect pollination was about the same level as self-pollination, confirming that modern hybrid sunflowers are highly self-fertile unlike wild sunflower species (Gandhi et al., 2005). Other studies found similar results of 26% to 70 % (Degrandi-Hoffman & Chambers, 2006; Javed & Medhi, 1992). Since we estimated a relative contribution we cannot determine if the self-pollination rate is fixed or varies with pollinator abundance, which may increase outcrossing rate (Wang, Yamasue, Itoh, & Kusanagi, 1998). We also found that wind pollination contributed about 20%. Our study is the first to differentiate wind pollination from self-pollination. Wind pollination has not previously been demonstrated for sunflowers as they are particularly adapted to insect pollination (Wojtaszek & Maier, 2014). Wind tunnel experiments would be necessary to confirm our result (Cresswell & Osborne, 2004).

The increase in yield was up to 40%, close to the pollinators' contribution estimated at plant scale (34.5%), i.e. an additional gain of 0.7 $t.ha^{-1}$, slightly depending on the method used to sample the pollinators (pan traps or sweep nets). This estimate is, to our knowledge, the first at field scale. It demonstrates the essential role of pollinators for farmers, though it is slightly lower than the increase in yield estimated from plant (Carvalheiro et al. 2011) or small scale experiments (Garibaldi et al., 2016), even those were directly assessed in working farm fields. In plant scale studies, the increases were 47% to 74% similar to Garibaldi et al. 2016 , depending on the sunflower variety. However, in

the Carvalheiro et al. (2011), wild bees had a positive effect. Other studies performed in farm fields have evaluated the pollinator contribution for male sterile lines (Greenleaf & Kremen, 2006) where pollination entirely depends on insect or wind. Finally we found that sunflower yield depended mainly on honeybee abundance, as already shown (Aslan et al., 2010; Degrandi-Hoffman & Chambers, 2006; Greenleaf & Kremen, 2006; Pisanty et al., 2013). Hoverflies were found to improve yield in only one out of the four years. Though such effect has not been found in other studies, hoverflies are known to pollinate other oil crops, such as oilseed rape (Jauker & Wolters, 2008). Wild bees were sometimes found to affect sunflower yield indirectly, by increasing the efficiency of honeybees in pollinating sunflower (Carvalheiro et al., 2011; Greenleaf & Kremen, 2006), but the direct effect of wild bees was found to be fairly low compared to that of honeybees (Greenleaf & Kremen, 2006; Pisanty et al., 2013).

In conclusion, although the importance of insect pollination for sunflower production has been already demonstrated using exclusion experiments (Aslan et al., 2010) or experimentally managed fields (Degrandi-Hoffman & Chambers, 2006; Tamburini et al., 2017), our study is the first to quantify how insect pollination effects at plant scale translate into yield at field scale in real farming conditions. In addition, our results show that sunflower yield can be increased through the management of honeybee hives and plant density without resorting to agrochemicals.

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Table 1. Summary of numbers of sunflowers per position and per treatment for 2015, 2016 and 2017. There were four sunflowers per position except for the 15m position in 2017 which had five sunflowers. ^{H} indicates that the plants were hand pollinated

Treatment	**Description**	**Plant position** (distance from field edge in m)	**2015**	**2016**	**2017**	**Total**
Control	Flowers are accessible to all pollination process	0	21	27+12^{H}	14	234 +40^{H}
		5	20			
		15	22	27	16+13^{H}	
		35	23			
		75	20	27+15^{H}	17	
Large pollinator exclusion	Large mesh bag (3mm), preventing large insect pollination but allowing small pollinators , wind pollination and self-pollination	0	19	27	15	233
		5	21			
		15	19	27	16	
		35	23			
		75	22	27	17	
All insect pollination exclusion	Small mesh bag (0.6mm), preventing all insect pollination but allowing wind pollination and self-pollination	0	16	26+15^{H}	15	223 +27^{H}
		5	19			
		15	19	27	17	
		35	22			
		75	21	24+12^{H}	17	
Self-pollination only	Osmolux bag excluding all types of pollination but self-pollination.	0	17		11	120 +13^{H}
		5	12			
		15	12	27	13^{H}	
		35	10			
		75	16		14	

Table 2. Summary statistics of linear models investigating variation of plant density and head diameter for field, year and plant position. *P*-value significant ($p < 0.05$) are bold.

	Head diameter (N = 227)		Plant density (N = 123)	
	F	*P*	*F*	*P*
Year	**7.75**	**< 0.001**	**3.75**	**0.06**
Plant position	2.85	0.095	2.99	0.092
Year : field ID	**2.21**	**< 0.001**	**1.75**	**0.04**
Field ID: plant position	0.81	0.82	0.68	0.88

Table 3. Summary statistics of linear mixed models investigating the trade-off seed mass per plant and fertilized seeds, accounting for plant position and year. Field ID is used as random variable. *P*-value significant ($p < 0.05$) are bold.

	F	*P*
log(Head diameter+1)	**203.57**	**< 0.001**
Plant position	0.79	0.375
Year	**4.27**	**0.015**
log(Fertilized seeds+1)	**20.46**	**< 0.001**
log(Head diameter+1) *x* year	**4.02**	**0.019**
log(Fertilized seeds+1) *x* year	1.81	0.166

Fig.1. Effect of head diameter on (a) fertilized seeds, (b) seed mass and (c) total seed mass per head. (d) Trade-off between seed mass (allowing for head diameter) and number of fertilized seeds. (e) Effect of plant density on honeybee abundance. (f) Effect of honeybee abundance on the total seed mass per m² (accounting for by head diameter). The black lines show the relationship averaged over the three years. 95% confidence bands are in grey. Lines for individual years are shown when year effect is significant ($p < 0.05$).

Fig.2. Effect of different pollinators estimated by (a-b) sweep net or (c-e) pan trap method on sunflower yield. The black lines show the relationship averaged over the four years. 95% confidence bands are in grey.

Fig.3. (a) Mean (± 95% confidence interval) of contributions of different pollination processes. Bars with the same letter are not significantly different at 5% significance. (b) Effect of honeybee abundance (estimated by sweep net) on pollinators' contribution. (c) Effect of pollinators' contribution on yield. The black lines show the relationship averaged over the three years. 95% confidence bands are in grey. The dashed lines indicates a marginally significant relationship ($0.1 > p > 0.05$)

Fig.1.

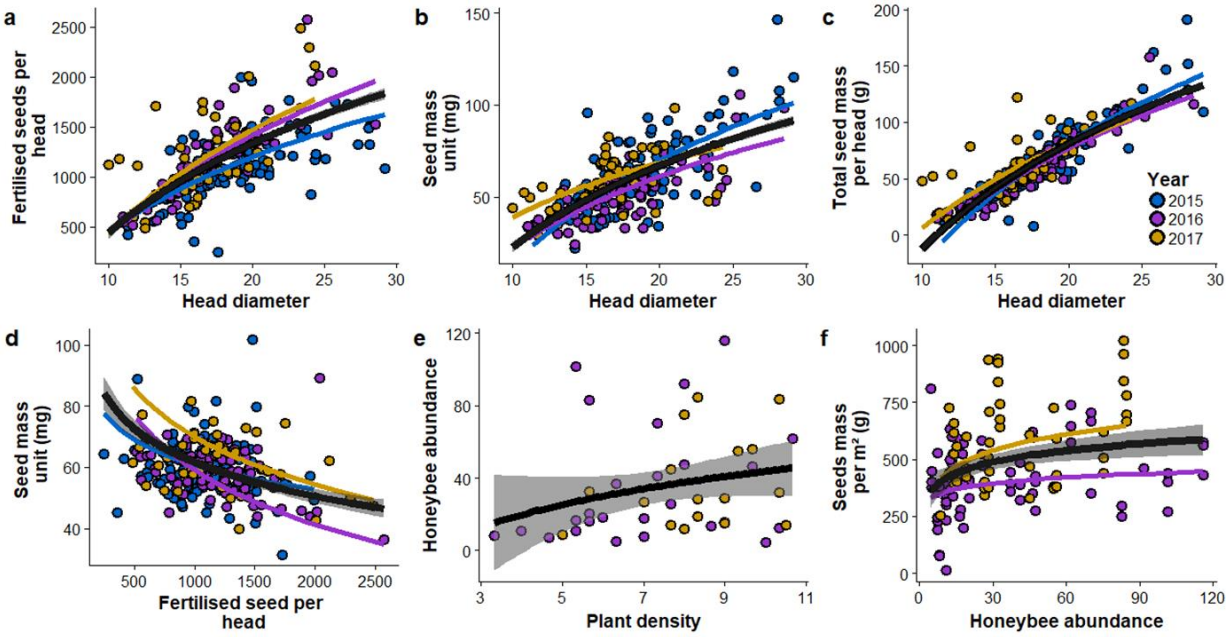

a
Fertilised seeds per head
Head diameter
b
Seed mass unit (mg)
Head diameter
c
Total seed mass per head (g)
Head diameter
Year
2015
2016
2017
d
Seed mass unit (mg)
Fertilised seed per head
e
Honeybee abundance
Plant density
f
Seeds mass per m² (g)
Honeybee abundance

Fig.2.

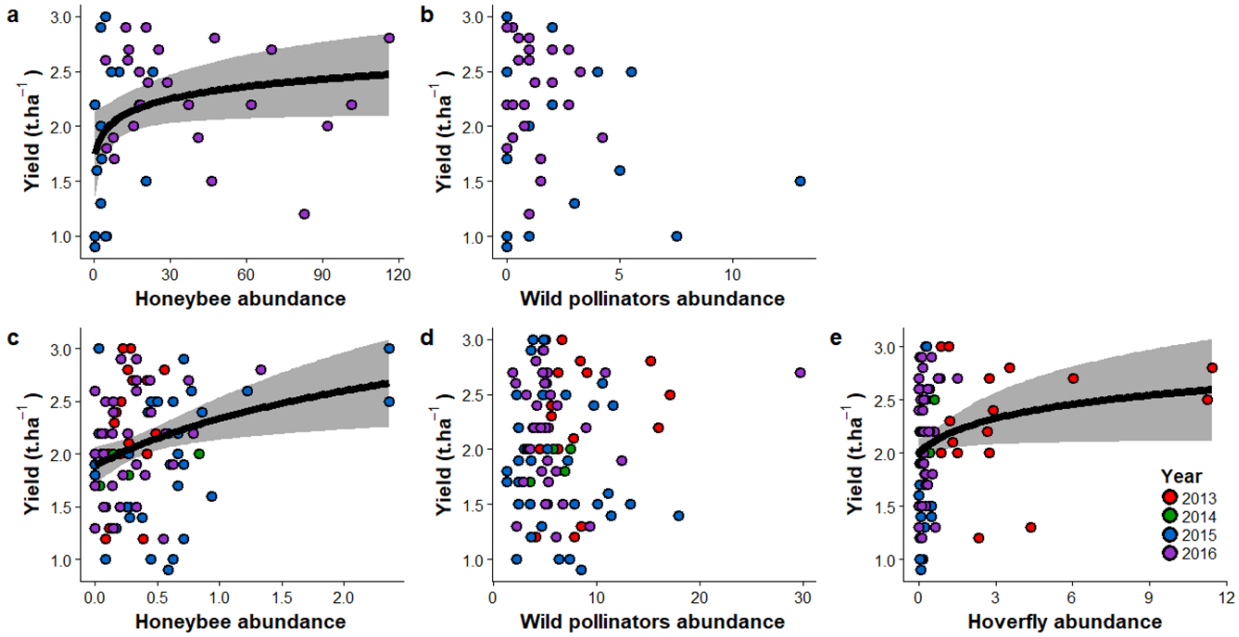
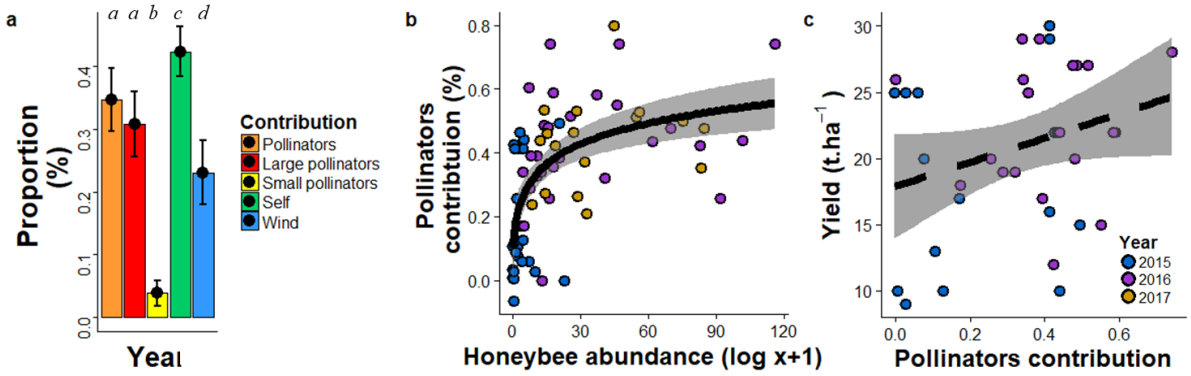

a
b
c
d
e
Yield (t.ha^{-1})
Honeybee abundance
Wild pollinators abundance
Hoverfly abundance
Year
2013
2014
2015
2016

Fig.3.


a
a a b c d
Proportion (%)
0.0
0.1
0.2
0.3
0.4
Yeal
Contribution
Pollinators
Large pollinators
Small pollinators
Self
Wind
b
Pollinators contribtuion (%)
0.0
0.2
0.4
0.6
0.8
0
30
60
90
120
Honeybee abundance (log x+1)
c
Yield (t.ha^{-1})
10
15
20
25
30
0.0
0.2
0.4
0.6
Pollinators contribution
Year
2015
2016
2017

Appendix

Appendix A. Effect of pan trap position in the field on pollinator abundance and diversity and description of pollinators community

In 2013, 2014 and 2015, pollinator abundance and diversity at genera level were estimated using pan traps placed at the edge and in the core of the fields. To investigate the effect of position within the fields, we analysed the effect of the year, the pan trap position in the field and their interaction on pollinator abundance (log x +1 transformed) and diversity at genera level (i.e. the number of genera) with a linear model. Both abundance and diversity were significantly affected by the year (Fig.A.a, Fig.A.b), but the position in the field, and the interaction with the year, did not have a significant effect. The diversity was higher in 2013 with 2.48 genera per pan trap against 1.78 in 2014 and 2.16 in 2015.

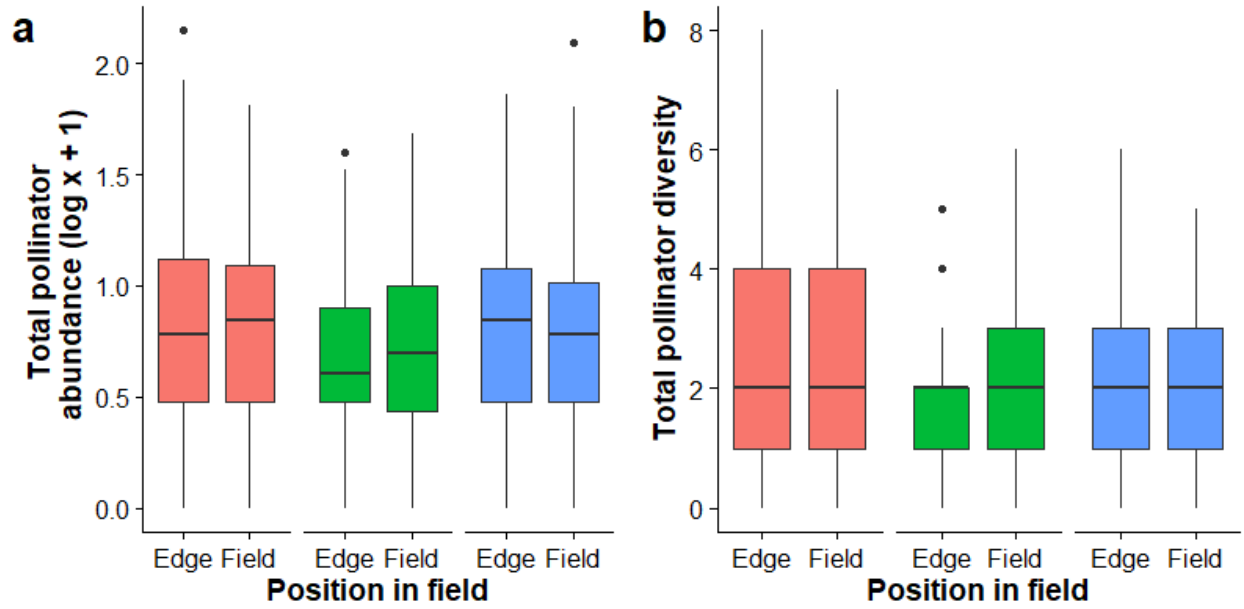


Fig. A. Pollinator abundance (a) and diversity at genera level (b) for pan traps placed at the edge and in the core of the fields in 2013 (red), 2014 (green) and 2015 (blue). Boxes show upper and lower quartiles, horizontal line indicates the median. The year had a significant effect on both pollinator metrics, but with a very low explanatory power (for abundance, adjusted R^2= 0.009, $F_{5,1518}$= 2.74, P = 0.018 and, for diversity, adjusted R^2= 0.028, $F_{5, 1518}$= 8.59, P < 0.0001).

For 2013-2017, a total of 14,745 pollinators were captured in pan traps (mean 7.5 ind/trap, range 0-209, *n* =1965) in a radius of 2 km around the focal fields over 65 days (from 25th June to 27th August). Wild bees were the main guild (76% of all captures), followed by hoverflies (16.4%), honeybees (5.2%) and bumblebees (2.4%). *Lasioglossum* (62.5%) and *Halictus* (9.9%) were the main genera among the 26 wild bee genera caught. In 2016-2017, when we identified bees to species level, 76 bee species were caught with *Lasioglossum subhirtum* (36.2%) and *L. maluchurum* (15.6%) being the most common. As expected, the sweep net (2015-2017) provided a different picture: 6,191 pollinators were caught (mean 31.4 ind/transect, range: 0–200, N=197), mainly honeybees (93.8%; Table A lists the pollinators caught).

Table A. List of pollinator genera caught with pan-traps from 2013 to 2017 and sweep-nets from 2015 to 2017.

Pan-trap		Sweep-net	
Genus	Catch	Genus	Catch
Lasioglossum	*9213*	Honeybee	*5807*
Halictus	*1463*	Bumblebee	*189*
Eupeodes	*990*	*Lasioglossum*	*83*
Episyrphus	*897*	*Sphaerophoria*	*56*
Honeybee	*764*	*Eristalis*	*21*
Bumblebee	*351*	*Halictus*	*14*
Andrena	*338*	*Andrena*	*11*
Sphaerophoria	*309*	*Melitta*	*3*
Melanostoma	*97*	*Eupeodes*	*2*
Melitta	*59*	*Osmia*	*1*
Scaeva	*38*	*Panurgus*	*1*
Eristalis	*36*	*Chrysotoxum*	*1*
Hylaeus	*30*	*Episyrphus*	*1*
Panurgus	*23*	*Helophilus*	*1*
HoplOsmia	*20*		
Eristalinus	*17*		
Osmia	*11*		
Ferdinandea	*11*		
Sphecodes	*9*		
Megachile	*6*		
Hoplitis	*5*		
Eucera	*4*		
Lithurgus	*4*		
Nomada	*4*		
ProtOsmia	*3*		
Syrphus	*3*		
Chelostoma	*2*		
Heriades	*2*		
Stelis	*2*		
Xylocopa	*2*		
Chrysotoxum.y	*2*		
Helophilus	*2*		
Meliscaeva	*2*		
Neoascia	*2*		
Paragus	*2*		
Pipizella	*2*		
Anthidium	*1*		
Anthophora	*1*		
Coelioxys	*1*		
Tetralonia	*1*		
Trachusa	*1*		
Cheilosia	*1*		
Eumerus	*1*		
Heringia	*1*		
Merodon	*1*		
Platycheirus	*1*		
Syritta	*1*		
Xylota	*1*		

Appendix B. Detecting and adjusting for bias in the number of fertilised seeds per head

The effect of pollinators on the fruiting rate is often assessed using mesh around the flowers (Bartomeus et al., 2014; Carvalheiro et al., 2011; Degrandi-Hoffman & Chambers, 2006). However, the mesh may interfere mechanically with fruiting (Jacobs et al., 2009; Martin, Reineking, Seo, & Steffan-Dewenter, 2013; Wragg & Johnson, 2011). We first analysed whether the mesh had an effect on our results, and, if so, we adjusted for it to reduce the effect on the quantification of the contribution of the various pollination processes (Jacobs et al., 2009; Wragg & Johnson, 2011).

If the mesh bags do not introduce bias or artefacts, then we should expect that the pollinator abundance and the fruiting rate of bagged flowers to be independent, since pollinators have no access to the flowers. We checked whether the pollinator abundance (here represented by honeybee abundance estimated using sweep-nets) affected the number of fertilised seeds per head for any of the three bagging treatments: small mesh and Osmolux, that should exclude all insects, as well as large mesh that should exclude honeybees that are too large to pass through. A linear model was used to examine the effect of honeybee abundance (log x+1 transformed), year, plant position, the interaction between honeybee abundance and year and between honeybee abundance and plant position. We also included the head diameter (log x+1 transformed), to allow for its positive relationship with the number of fertilised seeds. As expected, honeybee abundance did not significantly affect the number of fertilised seeds when the plants were bagged with Osmolux (Table B.1). However, there was a significant correlation between honeybees and the number of fertilised seeds with large or small mesh bags and this depended on the year. In 2016 and 2017 the correlation was positive and in 2015 it was negative (Fig.B.1). A possible explanation for the positive correlation may be that, when honeybee abundance was very high, there was "airborne" pollination, the release of pollen during honeybee visits (Pierre et al., 2010). This is similar to wind pollination and so the Osmolux bagged flowers were not affected. To test if the effect of honeybee abundance was similar for small and large mesh bagged flowers in 2016-2017, a second model was used with the number of fertilised seeds as the dependent variable and honeybee abundance, treatment (small and large mesh), year (2016 and 2017), and the interactions between honeybee abundance and treatment, honeybee abundance and year, and honeybee abundance, year and treatment as explanatory variables. The effect of honeybee abundance did not depend on either the treatment or the year (Table B.2), so the adjustments made this bias were the same for both mesh bags and all years (see below).

Table B.1. Summary of linear model testing the honeybee abundance effect on the number of fertilised seeds in plants with Osmolux, little and large meshes. All significant effects ($p < 0.05$) are in bold.

	Large mesh		Little mesh		Osmolux	
	F	*P*	*F*	*P*	*F*	*P*
log(Head diameter+1)	**55.54**	**< 0.001**	**46.51**	**< 0.001**	**17.92**	**< 0.001**
log(Honeybee abundance+1)	3.12	0.079	**9.32**	**0.003**	0.10	0.753
Plant position	0.01	0.921	1.45	0.230	3.16	0.079
Year	1.44	0.240	0.38	0.686	**11.15**	**< 0.001**
log(Honeybee abundance+1) : plant position	0.41	0.522	0.81	0.369	0.01	0.909
log(Honeybee abundance+1) : year	**11.52**	**< 0.001**	**9.88**	**< 0.001**	0.08	0.920

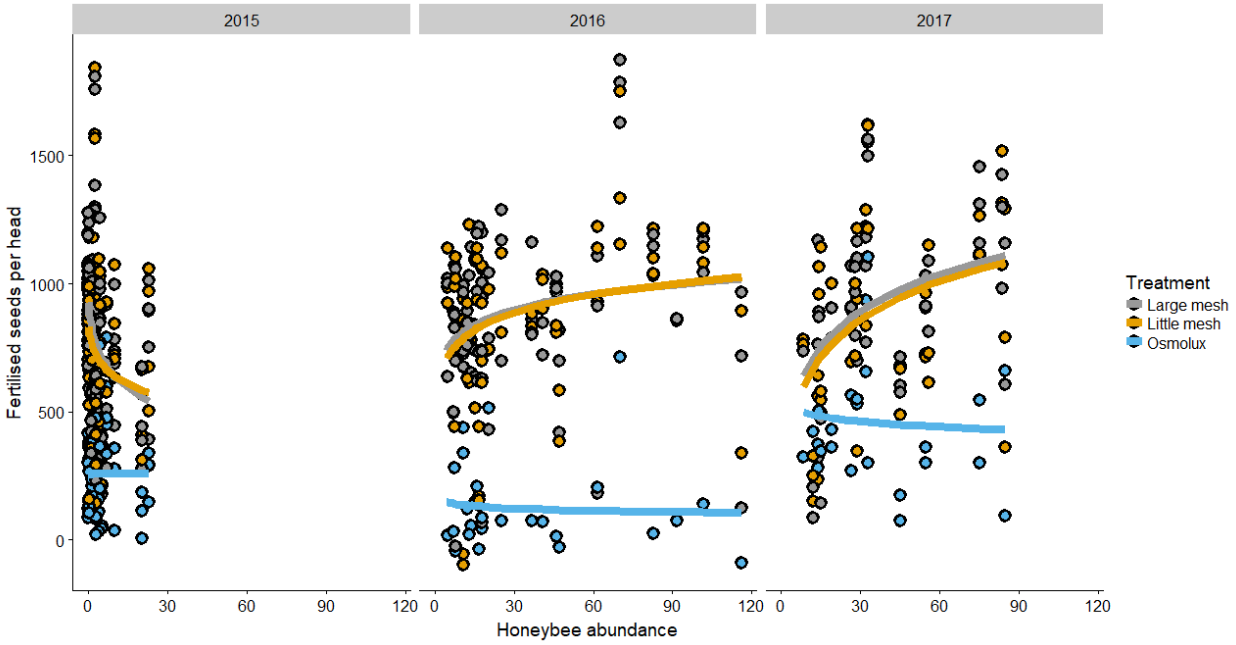


Fig.B.1. Effect of honeybee abundance estimated by sweep net captures, on the number of fertilised seeds per head (accounting for head diameter) for the three exclusion treatments: grey for large mesh, yellow for small mesh, and blue for Osmolux for 2015, 2016 and 2017. Lines represent the asymptotic relationship between pollinators and fertilised seeds for each treatment.

Table B.2. Summary of the linear model testing the effect of honeybee abundance on the number of fertilised seeds in flowers bagged with large or small mesh (treatment) taking account of the year (2016 and 2017), treatment and sunflower head diameter. All significant effects ($p < 0.05$) are in bold.

	F	*P*
log(Head diameter+1)	**57.21**	< **0.001**
log(Honeybee abundance+1)	**24.27**	< **0.001**
Treatment	0.08	0.772
Year	0.25	0.614
log(Honeybee abundance+1) : treatment	0.02	0.895
log(Honeybee abundance+1): year	3.41	0.066
log(Honeybee abundance+1) : year: treatment	0.04	0.836

Another type of bias is the mechanical effect of the exclusion bag on fruit development. We used hand pollination treatments to quantify this bias with two analyses considering the effect of mesh bags and Osmolux bags. To estimate the effect of the bags, we tested the difference of number of fertilised seeds between hand pollinated sunflower and sunflowers hand pollinated and bagged with small mesh (2016 data) and Osmolux (2017 data). We excluded head diameter from the analyses because the mechanical stress may affect the head diameter: within each field sunflowers with similar head diameter were selected at the beginning of the experiment. Although the number of fertilised seeds was lower for bagged heads (149.3, 14.1%, fewer fertilised seeds with small mesh bags and 172.8, 25.8%, fewer fertilised seeds with Osmolux bags, Fig.B.2) this was not significant for either small mesh bags ($F_{1,51} = 3.17$, $P = 0.12$) or Osmolux bags ($F_{1,24} = 0.97$, $P = 0.34$).

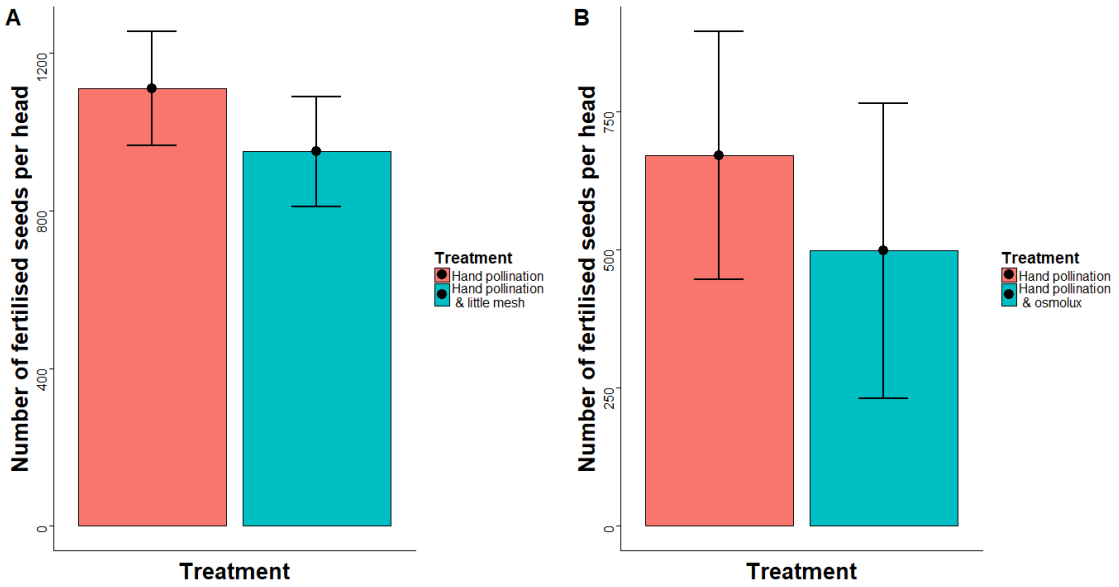


Fig.B.2. Mean (± confidence interval at 95%) of number of fertilised seeds per head in the different treatments in (A) 2016 and (B) 2017.

Overall therefore, we detected two types of bias in the bag experiments: bagging increased fruiting rate with increasing honeybees abundance and bagging decreased fruiting due to mechanical stress (though this was not significant). In both cases, the magnitude of the artefact was about 25% change in the number of fertilised seeds, a moderate value (see also Jacobs et al. 2009, Wragg and Johnson 2011), but high enough to be taken into account. We therefore adjusted for these when quantifying the effect of insect pollination on sunflower yield.

In order to account for the bias proportional to the honeybee abundance, we used a correction factor for the number of fertilised seeds in the flows bagged with small and large mesh. This correction factor was the intercept of the linear models (Fig.B.1), i.e. the number of fertilised seeds in the absence of honeybees. We used data from 2016 and 2017: the data from 2015 were not included as no positive effect of honeybee abundance was detected on the number of fertilised seeds. In the LMs, the number of fertilised seeds in the small and large mesh treatments was explained by head diameter and honeybee abundance which had been shown to have a significant effect on the number of fertilised seeds (Table B.2). The model intercepts were 401 and 390 fertilised seeds per head in 2016 and 2017 for an average head diameter each year. These were added to the residuals for the small and large mesh treatments (Table B.2, Fig.B.3). There was no correction for Osmolux or for 2015.

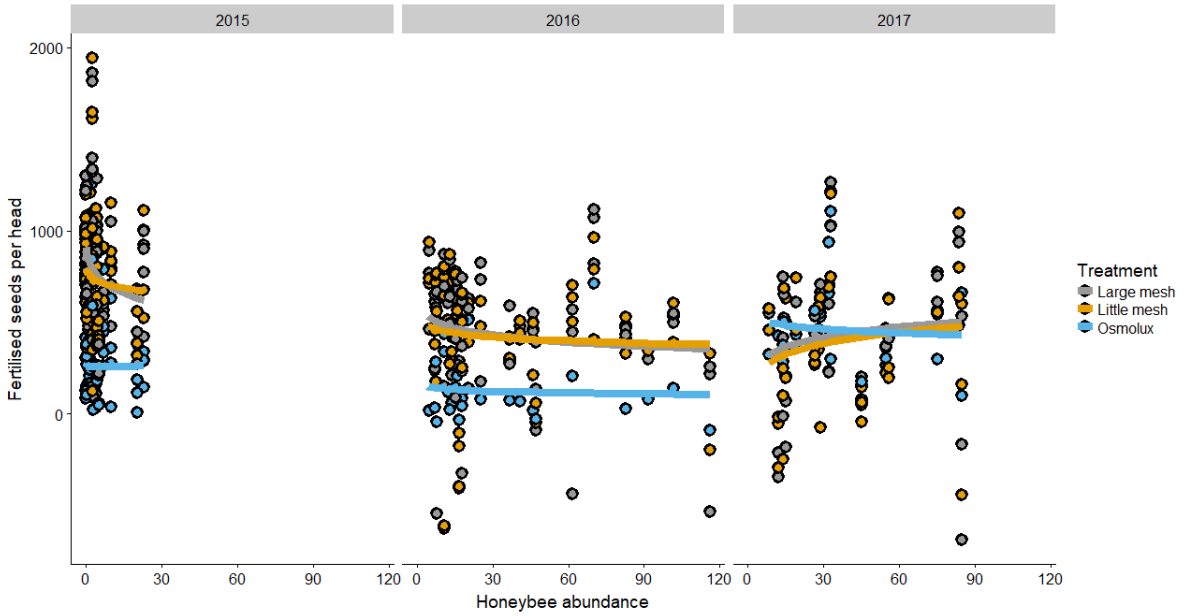


Fig.B.3. Effect of honeybee abundance, estimated by sweep net captures, on the number of fertilised seeds per head in the three exclusion treatments: large mesh bag (in grey), small mesh (in yellow) and Osmolux (in blue) for 2015, 2016 and 2017. The numbers of fertilised seeds in the large and small mesh exclusion treatments were corrected to take account of the bias introduced by the honeybee abundance. Lines represent the asymptotic relationship between honeybee abundance and the number of fertilised seeds for each treatment.

To correct for the bias due to mechanical stress, we first averaged the number of fertilised seeds per head for each treatment in each field and then corrected those average values by the impact of the mesh bags (14.1%) and Osmolux bags (25.8%). 14.1% of the fertilised seed count for the control treatment was added to the fertilised seed counts of the small and large mesh bagged heads and 25.8% of the fertilised seed count for the control treatment was added to the Osmolux bagged heads. We assumed that the effect of small and large mesh would be similar, as we did not test the large mesh.

We expected that the controls (pollinated by self-pollination (SF), wind pollination (W), small pollinators (SP) and large pollinators (LP) would have more fertilised seeds per head than large mesh (pollinated by "SP+W+SF"), followed by small mesh ("W+SF") and Osmolux ("SF") treatments. The controls had more fertilised seeds per head than other treatments in all years (Fig.B.4.a), but ranking of the treatments was not always as expected. For example, in several cases Osmolux had higher fertilised seed counts than small mesh (Fig.B.4.a). This would indicate a negative pollinator contribution, though it is most likely an artefact of using a mesh bag. When the difference was higher than 10%, we considered it as a measurement error and discarded the value. When the difference was less than 10%, the negative contributions were set to zero equalizing the number of fertilised seeds between the two treatments. For example, the Osmolux counts were attributed to the small mesh counts when the fertilised seed count for small mesh was less than that for Osmolux (flooring). Overall, 5 control (7.5% of the total), 12 small mesh (17.9% of the total) and 18 large mesh (26.9% of the total) counts were floored. None of the osmolux values were changed. The results after flooring are given Fig.B.4.b.

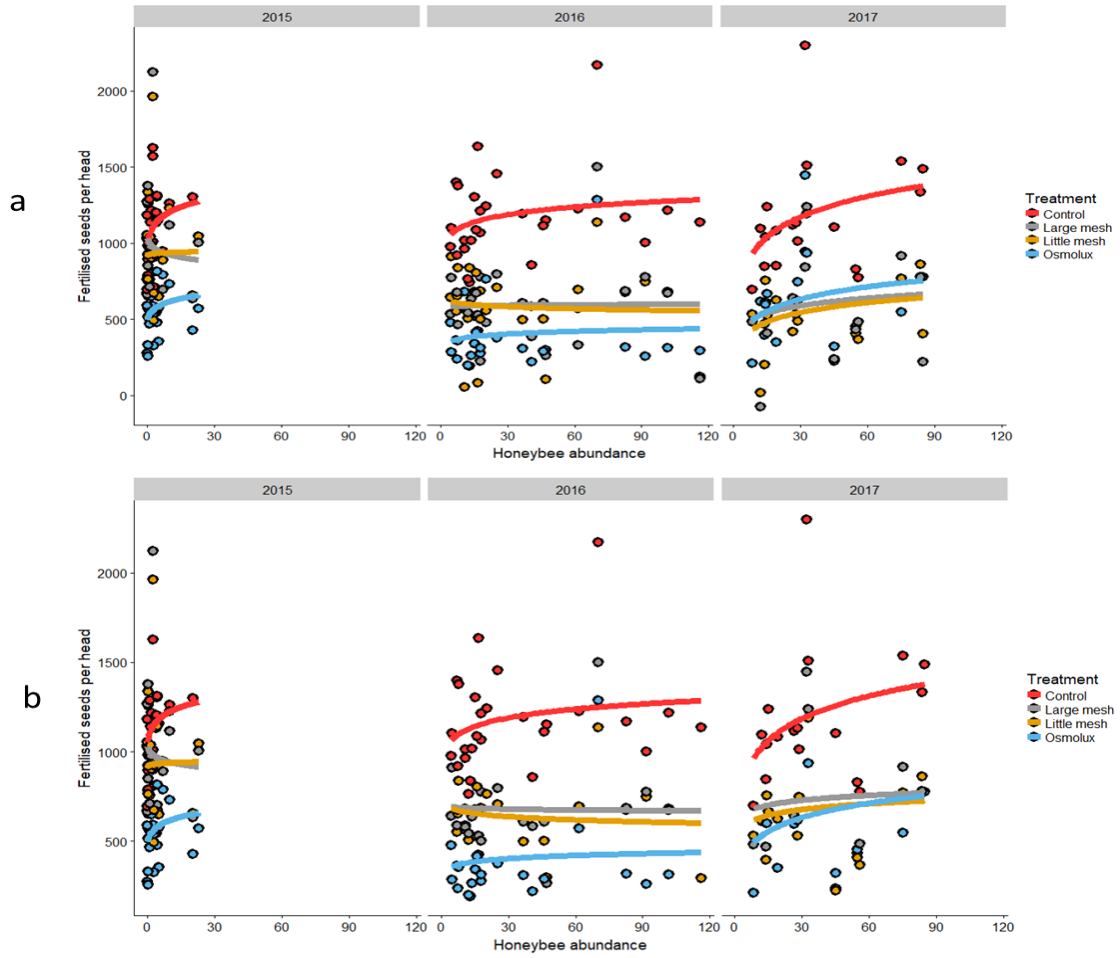


Fig.B.4. Effect of honeybee abundance estimated by sweep net captures on the number of fertilised seeds per head (averaged by field) (a) corrected for the two biases (honeybee abundance and mechanical effects) for small and large mesh bags, and (b) after flooring, with colours indicating the treatment: red for control, green for large mesh, blue for little mesh, and purple for Osmolux for 2015, 2016 and 2017. Lines represent the asymptotic relationships between honeybee abundance and the number of fertilised seeds in each treatment.

We then explored how the different pollination contribution process was affected by keeping or removing all negative values (Fig B.5). We found that results were similar whether or not the negative values were kept, with a pollinator contribution to pollination success estimated as 37.6% when keeping negative values and 34.5% when they were removed. Similar, we found similar results for estimating the contribution of self-pollination: 43.1 % when negatives values were kept (Fig B.5) and 42.5% when negative values were removed (Fig B.5) or wind, 18.6% when negative values were kept and 23% when negative values were removed. .

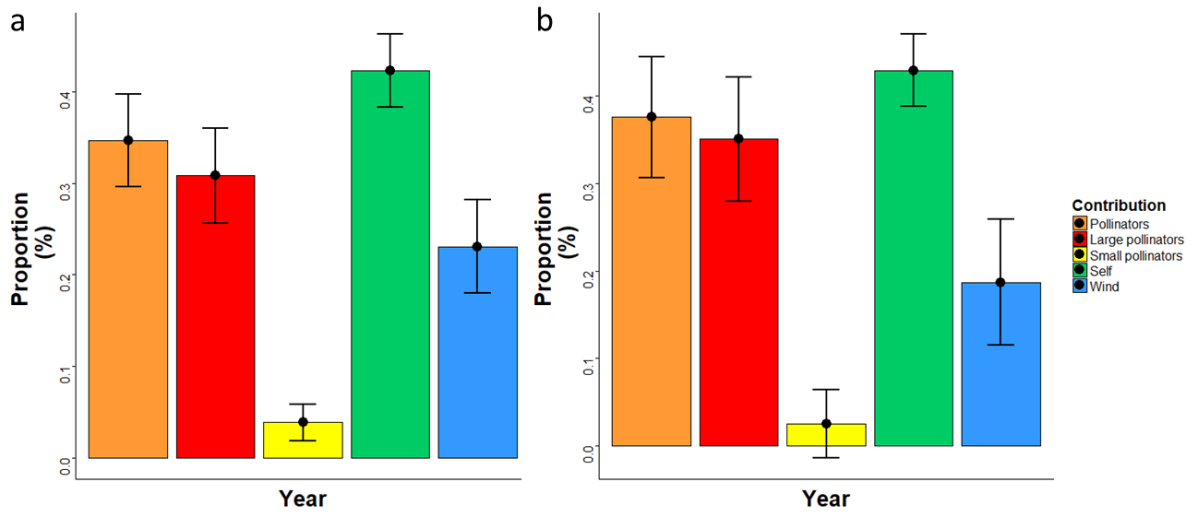


Fig.B.5. Mean (± 95% confidence interval) of contributions of different pollination processes with (a) strong negative values removed or (b) kept.

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Appendix C. Effect of farmers' practices on sunflower yield

We used a linear model to test the effects of all the main fertilisers (nitrogen, phosphorus and potassium), herbicide treatments (others pesticides were rarely sprayed on sunflower fields), type of agriculture (organic *versus* conventional), field size, sowing density and year on sunflower yield at field scale (Table C.1).

Table C.1. Mean of farmers' practice parameters and standard deviation (SD).

Farmers practices	**Average (± SD)**
Field size (ha)	5.6 (± 4.6)
Nitrogen fertiliser (Kg/ha)	37.9 (± 31.2)
Phosphorus fertiliser (Kg/ha)	31.8 (± 38.5)
Potassium fertiliser (Kg/ha)	26.3 (± 27.9)
Frequency of herbicide treatment	1.2 (± 0.78)
Sowing density (Seeds per ha)	71381 (± 4637)

We performed both univariate analysis and multiple stepwise regression to account for collinearity. None of the parameters was significant in the multiple stepwise regression (Table C.2). Similarly, none of the individual parameters had a significant effect on yield (Table C.2).

Table C.2. The effect of farmers' practice parameters and year on sunflower yield with multiple stepwise regression and with each parameter tested independently. (-) indicated that the parameter was not selected from the multiple stepwise regression.

	Mutliple stepwise regression		Univariate analysis	
	F	*P*	*F*	*P*
Agriculture type	-	-	0.23	0.63
Nitrogen fertiliser	-	-	0.18	0.68
Phosphorus fertiliser	-	-	0.28	0.59
Potassium fertiliser	-	-	0.96	0.33
Frequence of herbicide treatment	-	-	0.11	0.74
Sowing density	-	-	0.19	0.67
Field size	-	-	0.06	0.81
Year	-	-	1.87	0.14

We then test the correlation of main fertilizer (nitrogen, phosphorus, potassium), pesticide (herbicide) and sowing density on head diameter (n=37) and plant density (n=21). Pearson correlation tests were realised. No significant relation was found between farming practice and head diameter or plant density (Table C.3).

Table C.3. Pearson correlation between main fertilizers, pesticide and sowing density on head diameter and plant density. r_p is the Pearson coefficient.

	Sowing density		Nitrogen input		Phosphorus input		Potassium input		Frequence of herbicide treatment	
	r_p	*P*	r_p	*P*	r_p	*P*	r_p	*P*	r_p	*P*
Head diameter	0.09	0.59	-0.07	0.7	-0.2	0.24	-0.23	0.18	-0.27	0.1
Plant density	0.08	0.71	0.19	0.4	0.18	0.43	0.31	0.15	-0.08	0.74

Appendix D. Relationship between sunflower yield and pollinator metrics within different temporal and spatial windows.

We explored the effect of the time period and spatial window used to estimate pollinator community metrics on the effect of these metrics on sunflower yield. Pan traps were installed from 15th June (165th day of the year) to 27th August (day 240) covering the whole of the sunflower flowering period. Three time periods were tested, starting from day 165 (15th June, i.e. 15 days before flowering), day 175 (25th June, i.e. 5 days before flowering) and day 185 (3rdJuly, i.e. at the beginning of flowering). Five buffer radii were also tested: 0 m (pan traps only in the focal field), 500 m, 1000 m, 1500 m, and 2000 m. We explored the effect of wild bee, honeybee, bumblebee and hoverfly abundances (all log x+1 transformed) as well as bee diversity (honeybee, wild bee and bumblebee genera) and hoverfly diversity (genera) on sunflower yield using linear models.

Honeybee abundance had a significant effect on sunflower yield for the largest radius (2000m) for all time periods and for 1500 m radius for the period starting from day 185 (Table D.1). Hoverfly abundance had a positive effect for 1500 m and 2000 m from day 175. Other pollinator metrics had no significant effect for any time period or buffer radius. Consequently, we used the pollinator metrics for pan traps within a buffer of radius 2000m around the focal fields from 25th June (day 175) to 27th August (day 240).

Table D.1. *F*-values and r^2 for the effect of pollinator metrics on sunflower yield for various spatial and temporal windows. The sign indicates the sign of estimate. Significant results are highlighted in bold with the significance:: * P < 0.05; ** P < 0.01; *** P < 0.001.

	Time period of 165 days							
Spatial radius	0m		1000m		1500m		2000m	
Sunflowers focus field		44.00		80.00		90.00		97.00
Average total number of pan traps in buffer		7.34		17.99		25.80		39.18
Average number of field surveyed in buffer		1.00		2.37		3.33		5.10
Bee diversity	-	**6.08***	-	0.8	-	0.16	+	0.04
r^2		12.64		1.03		0.18		0.04
Hoverfly diversity	-	0.47	-	0.05	+	0.64	+	1.58
r^2		1.10		0.07		0.72		1.64
Wilbee abundance	-	0.01	-	0.03	-	0.05	+	0.51
r^2		0.03		0.04		0.06		0.53
Bumblebee abundance	-	2.34	-	3.81	-	1.26	-	1.27
r^2		5.28		4.66		1.41		1.32
Honeybee abundance	+	0.08	+	0.90	+	1.44	+	**5.65***
r^2		0.18		1.14		1.61		5.61
Hoverfly abundance	-	0.25	-	0.12	+	1.05	+	2.16
r^2		0.59		0.15		1.18		2.22

	Time period of 175 days							
Spatial radius	0m		1000m		1500m		2000m	
Sunflowers focus field		43.00		77.00		88.00		97.00
Average total number of pan traps in buffer		6.86		14.01		19.43		29.50
Average number of field surveyed in buffer		1.00		1.90		2.64		4.06
Bee diversity	-	**6.26***	-	0.56	-	0.08	+	0.29
r^2		13.25		0.75		0.10		0.30
Hoverfly diversity	+	0.24	-	0.04	+	0.94	+	1.49
r^2		0.57		0.06		1.08		1.54
Wilbee abundance	-	0.16	-	1.51	-	2.87	-	0.44
r^2		0.38		1.98		3.23		0.46
Bumblebee abundance	-	3.24	-	**4.47***	-	1.62	-	2.07
r^2		7.32		5.62		1.85		2.13
Honeybee abundance	+	0.30	+	2.44	+	**4.18***	+	**8.35****
r^2		0.73		3.15		4.64		8.08
Hoverfly abundance	+	0.90	+	0.95	+	**4.64***	+	**4.67***
r^2		2.15		1.24		5.12		4.68

	Time period of 185 days

Spatial radius	0m		1000m		1500m		2000m	
Sunflowers focus field		40.00		70.00		82.00		94.00
Average total number of pan traps in buffer		6.38		11.85		15.46		22.39
Average number of field surveyed in buffer		1.00		1.70		2.25		3.26
Bee diversity	-	**5.06***	-	0.50	-	0.32	+	0.36
r^2		11.75		0.73		0.40		0.39
Hoverfly diversity	-	0.61	-	0.58	-	0.03	+	0.44
r^2		1.59		0.85		0.04		0.47
Wilbee abundance	-	0.07	-	0.20	-	0.44	+	0.57
r^2		0.20		0.29		0.55		0.62
Bumblebee abundance	-	2.65	-	**4.90***	-	**8.26****	-	3.79
r^2		6.52		6.73		9.36		3.96
Honeybee abundance	+	0.30	+	1.68	+	2.18	+	**6.06***
r^2		0.78		2.42		2.66		6.18
Hoverfly abundance	-	0.49	+	0.00	+	0.18	+	0.78
r^2		1.28		0.00		0.22		0.84

Then we investigated the effects on sunflower yield of pollinator metrics, estimated either from pan trap (for a radius of 2000 m, between 185 days and 240 days) or sweep net captures: the abundance of each pollinator group (wild pollinators, wild bees, hoverflies, honeybee, and bumblebee; all log x+1 transformed) and pollinator diversity at genera or species level considering all pollinators, bees (wild bees, bumblebees, honeybee) and hoverflies. We built linear models with each of the pollinator metrics, linear and quadratic terms, year and the interaction between the pollinator metric and year. There were 97 fields for pan traps and 40 fields for sweep nets.

Table D.2. Output of linear models. Significant results ($p < 0.05$) highlighted in bold.

		Pan trap		Sweep net	
		F	*P*	*F*	*P*
Abundance	log(Honeybee+1)	**8.92**	**0.004**	**4.97**	**0.032**
	Year	**3.97**	**0.010**	1.31	0.260
	Year : log(honeybee+1)	0.21	0.887	1.93	0.174
	log(Wild pollinators+1)	0.08	0.781	0.78	0.384
	Year	1.79	0.155	4.64	0.038
	Year : log(wild pollinators+1)	0.39	0.757	0.00	0.970
	log(Wild bee+1)	0.44	0.511	0.37	0.548
	Year	1.73	0.167	**5.36**	**0.026**
	Year : log(wild bee+1)	0.02	0.997	2.37	0.133
	log(Hoverfly+1)	**4.59**	**0.035**	0.05	0.833
	Year	1.21	0.309	**5.32**	**0.027**
	Year : log(hoverfly+1)	0.27	0.850	0.00	0.993
	log(Bumblebee+1)	2.06	0.155	3.50	0.069
	Year	1.71	0.170	3.12	0.086
	Year : log(bumblebee+1)	0.14	0.933	2.03	0.163
Diversity (genera)	log(All pollinator+1)	1.45	0.232	0.21	0.649
	Year	2.16	0.098	**5.16**	**0.029**
	Year : log(all pollinator+1)	0.04	0.988	0.05	0.818
	log(Bee+1)	0.71	0.401	0.00	0.979
	Year	**3.01**	**0.034**	**5.33**	**0.027**
	Year : log(bee+1)	0.59	0.624	0.01	0.907
	log(Hoverfly+1)	0.86	0.355	0.84	0.366
	Year	1.55	0.207	**5.34**	**0.027**
	Year : log(hoverfly+1)	0.64	0.593	0.00	0.959
Diversity (species)	log(All pollinator+1)	<0.01	0.988	0.33	0.569
	Year	**5.81**	**0.018**	**5.31**	**0.027**
	Year : log(all pollinator+1)	0.01	0.906	0.02	0.880
	log(Bee+1)	0.00	0.955	1.21	0.279
	Year	**5.80**	**0.019**	**5.07**	**0.031**
	Year : log(bee+1)	0.04	0.847	0.07	0.790
	log(Hoverfly+1)	0.05	0.826	0.82	0.372
	Year	3.78	0.056	**5.26**	**0.028**
	Year : log(hoverfly+1)	0.56	0.456	0.00	0.990

Chapitre III :

Une solution basée sur la nature en pratique : une modélisation écologique et économique montre que les pollinisateurs sont plus efficaces que les produits agrochimiques dans la production de colza

Avant-propos et résumé du chapitre III :

Nous avons montré dans les chapitres I et II que les pollinisateurs sont d'importants contributeurs du rendement agricole pour deux oléo-protéagineux. Cependant les pollinisateurs ne sont pas les seuls contributeurs des rendements. Plusieurs pratiques agricoles parmi lesquelles les fertilisants ou les pesticides, ont aussi un effet positif sur la production agricole. De plus, l'effet bénéfique des pratiques et des pollinisateurs sur les rendements ne sont pas forcément additifs. Plusieurs pratiques peuvent réduire la contribution des pollinisateurs, soit en compensant en partie les pertes de production en absence de pollinisateurs ou en modifiant directement la contribution des pollinisateurs. Néanmoins, les pratiques agricoles ainsi que leurs possibles interactions avec les pollinisateurs sont rarement pris en compte dans les études voulant estimer la contribution des pollinisateurs dans la production agricole. Le but de ce troisième chapitre est d'estimer et de comparer la contribution des pratiques agricoles par rapport à celle des pollinisateurs tout en identifiant leurs potentielles interactions, à la fois sur le rendement à l'échelle de la parcelle et sur le bénéfice monétaire (revenu, approximé par la marge brute) que les agriculteurs retirent de la vente de leur production pour la culture de colza.

Notre étude montrent que plusieurs pratiques (herbicide, phosphore, fongicide,…) augmentent les rendements de colza alors que certaines autres pratiques n'ont pas d'effets (azote, insecticide,..) malgré leur forte utilisation dans les parcelles. L'effet bénéfique des pollinisateurs est additif pour la majorité des pratiques excepté pour les insecticides qui réduisent la contribution des pollinisateurs aux rendements. Ce résultat est en accord avec de précédentes études qui montrent que les insecticides réduisent l'efficacité pollinisatrice des insectes. En termes de bénéfices monétaires, les principaux déterminants sont les pratiques agricoles les principaux déterminants. En effet, la majorité des pratiques (excepté le phosphore) sont très coûteuses par rapport à leur effet bénéfique sur les rendements de colza et par conséquent réduisent la marge brute de l'agriculteur. Au contraire, les pollinisateurs augmentent le revenu des agricultures de plus de 250 € par hectare.

De manière plus générale, notre étude montre que pour le colza, l'utilisation intensive d'intrants (pesticides et fertilisants), qui a été identifié comme un frein pour une agriculture durable, pourrait être réduit sans pour autant avoir d'impact sur le rendement (azote etinsecticide) ainsi que sur les revenus des agriculteurs (herbicide, fongicide) voire dans certains cas les augmenter. De plus, la promotion des pollinisateurs dans les milieux agricoles pourrait permettre d'assurer de meilleurs rendements et revenus aux agriculteurs et est donc un moyen d'intensifier écologiquement et durablement la production de colza.

Relative importance of bees and farming practices for yield and farmers' income

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Abstract

There is growing evidence that insect pollination can support higher yield and reduced its variability for a wide range of insect pollinated crops. However, little is known about how insect pollination and agricultural inputs interactively affect crop production and in turn farmers' economic benefits. Especially, the relationships between pollinators, fertilizer and pesticides, whether they synergically or negatively affect crop yield and farmers' income, remain to be established. This information is however crucial to optimize management strategies to reconcile food production, farmers' profitability and biodiversity conservation. Here, we investigate the interactive effect of insect-pollination and agricultural inputs on oilseed rape (*Brassica napus* L.) yield and farmers' income. We show that bees increase yield and profitability by c. 25% between fields with smaller and larger bee abundance. This effect is however decreased by farming practices, especially insecticides applications. Our results also show that both production and profitability reached higher values in fields with high bee abundance than in high input fields. Our analysis indicates that environmental friendly management strategies that support ecosystem services benefit both to food production and farmers' profitability.

Keywords

Pollination service, oilseed rape, agroecology, farming practices, ecological intensification, insecticides, herbicides, honey bee, wild bee

Introduction

Achieving world food production objective with current human population growth and meat protein dietary trajectories is key but a challenging priority (Godfray et al. 2010, Gerland et al. 2014, Tilman and Clark 2014). Modern agriculture may lie on a tipping point (Barnosky et al. 2012), with nature's supporting system fading out and anthropogenic inputs, such as fertilizers and pesticides, being either inefficient or used inefficiently (Vitousek et al. 2009, Gaba et al. 2016). There is also growing recognition that ecosystem services (ES) degradation is not only an environmental problem but has huge economic consequences (Sandhu et al. 2016). The key challenge is, therefore, to stabilize in western countries and increase in developing countries, crop yields while decreasing the dependence on external inputs of agrochemicals in agriculture (Tittonell 2014). Agro-ecology, although not new is now a paradigm of utmost importance or next generation agriculture (Bommarco et al. 2013), with part of solution lying on nature-based solutions (Foley et al. 2011, Tittonell 2014). This paradigm shift requires forwarding ecological principles for the management and design of sustainable agro-ecosystems that balance ecological soundness, economic viability and social justice (Altieri 1983). One critical aspect of using this framework relies on the possibility and conditions under which agro-chemicals may be replaced by nature-based solutions, while minimizing yield loss (if any), hence increasing economic returns to farmers.

Insect pollination is a key ecosystem function (i.e., intermediate ecosystem service) as a third of human food consumed benefits directly or indirectly from it (Klein et al. 2007). The annual global value of insect-mediated crop pollination, as for 2015, was estimated to be between $235 and $577 billion (Potts et al. 2016). However in recent years, substantial declines in the abundance, diversity and efficiency of insect pollinators have been reported worldwide (Steffan-Dewenter et al. 2005, Garibaldi et al. 2009, Potts et al. 2010). Oilseed rape (OSR, *Brassica napus*), appears as a case in point. Driven by increasing demand (e.g., for biofuels), the area of OSR is rapidly growing over Europe, becoming a crop of global significance (Aizen and Harder 2009). Pesticides are largely consumed in intensive farming to mitigate the direct impact of pests on OSR yield (Bijanzadeh et al. 2010, Zhang et al. 2017) in order to increase its yield (Bijanzadeh et al. 2010, Sutter et al. 2017). However, insecticides may increase pollinators' mortality rates (Henry et al. 2012) or reduce their pollination efficiency as found in apple crop (Stanley et al. 2015) and in OSR (Sutter and Albrecht 2016). OSR production is indeed now limited by pollination in Europe (Breeze et al. 2014). Although a self- and wind-pollinating crop (Hudewenz et al. 2014), the economic value of insect pollination to OSR was estimated as €3.9 million per annum (Stanley et al. 2013), with yield gains between 20 and 35% due to insect pollination (Bommarco et al. 2012, Perrot et al. in review and references herein).

Estimating yield gain from pollinators is however less easy than usually thought (Breeze et al. 2016). Firstly, the mesh method used to measure pollination services, i.e. the proportion of yield lost without pollination, excludes both other ecosystems services and the plant response to stress(Bos et al. 2007). Second, benefits of pollination services to crop yield are often implicitly considered as independent from the level of external inputs (Bartomeus et al. 2014, Breeze et al. 2016). However, crop production (yield) depends on a complex multi-scale system (Seppelt et al. 2011) which involves external inputs applied by the farmers potentially interacting with biodiversity and the functions it support. If the crop or yield is limited by pollinators, farmers can react and improve their yield by practices. Soil fertilization reduces pollination contribution but compensates yield losses from poor insect pollination (Marini et al. 2015), though in some cases no such interaction was detected (van Gils et al. 2016). Recent studies have demonstrated that the value of insect pollination is contingent of farming practices; soil fertility (Tamburini et al. 2016), pest control levels (Sutter and Albrecht 2016), field size (Holzschuh et al. 2016) and cultivar (Hudewenz et al. 2014). Third, pollinator abundance and pollination vary with the composition of the surrounding landscape. Landscape with large quantity of semi-natural elements (forest, grassland) can have a positive effect on pollinators

(Bartomeus et al. 2014) though the reverse may also occur (Zou et al. 2017). Dilution effects have also been demonstrated in larger fields (Holzschuh et al. 2016) as the foraging ranges of pollinators is limited in space, especially for wild bees (Zurbuchen et al. 2010). Overall the degree to which pollinators and other farming practices interact or limit OSR production remains controversial and poorly studied (Burkle and Irwin 2009, Seppelt et al. 2011), and is actually a multidimensional problem (Breeze et al. 2016).

Despite there is evidence that farming practices potentially modify pollinators, very few studies were performed in real farmers' field conditions (but see Lindström et al. 2016), and rarely more than one farming practice was tested in interaction with pollinators (but see Marini et al. (2015)). Here, we study possible trade-offs and synergies among fertilizer supply, pesticide use, soil quality and pollinators, and how they affect yield and farmers' income. We collected data from 296 OSR fields situated along landscape gradients with contrasting proportions of arable and semi-natural elements, ensuring for a wide variation in pollinator abundance and diversity. We specifically address two questions: i) what is the actual relationship between the use of agrochemicals (fertilizers and pesticides), landscape features and pollinators on one hand and yield and profitability on the other hand? and ii) At which point the positive relationships between the effect of insect-pollination, fertilizer and pesticides on yield and income will level off ?

Material & methods

Study area

The study took place in the LTSER "Zone Atelier Plaine & Val de Sèvre", a long term social-ecological research site of 450 km² (Bretagnolle et al. 2018) located in central western France (46.23°N, 0.41W). It is an agricultural landscape dominated by intensive cereal crop production (44% winter cereals, most of which winter wheat, 8-12% rape seed, sunflower or maize, and 14% meadows and alfalfa, 4% woods and 9% villages; 2016), with an average field size of 4-5 ha. For this study, the periods of interest were the winter farming seasons between October 2011 and October 2016. Information about crop yields and farming practices (pesticide and fertilizer use, ploughing and mechanical weed control system) and general information about the farm (number of crops, agricultural equipment) were collected by means of interviews with all the individual farmers after harvests. The sample comprises a total of 144 farmers with 296 fields. Two oilseed rape types, hybrid (277 fields) and pure line (24 fields), were used by farmers. Surveyed fields were selected through a random sampling scheme: the first step consisted in obtaining 1-km² squares that were randomly selected to represent density gradients of three environmental features: semi-natural habitats (hedges and forest fragments), meadows, and organically farmed fields. All these landscape features are known to influence strongly pollinator presence (Kennedy et al. 2013), and were mapped onto the GIS LTSER (Bretagnolle et al. 2018). We used a moving window to select the squares (Fahrig et al. 2011). Within the selected squares, an OSR focus field was then chosen if present (usually, there was only one OSR field. Field size ranged from 0.5 ha to 28 ha (mean 6.6 ha). Soil type varied from very poor dry soil 20 cm deep or even less, to 50 cm silt.

Then the % of OSR outside the focal field and of semi-natural elements (SNE) were tabulated over eight buffer radius, from 250m to 2000m. We consider as SNE the sum of landscape composed by grasslands, forest and hedges.

Insect pollinators surveys

Between 2013 and 2016, the abundance and diversity of the major groups of flower-visiting insects, including bees (Hymenoptera, Apoidea, Apiformes) and hoverflies (Diptera, Syrphidae) were surveyed. A total of 75 fields (7, 20, 22 and 31 in 2013, 2014, 2015 and 2016) were sampled. Pollinators were sampled by two complementary methods. First, colored pan traps were used

(Westphal et al. 2008), consisting in bowls of 12cm diameter, 10cm deep plastic sprayed fluorescent yellow (RAL 1026, Euro industry Supply, Stuttgart, Germany), sprayed fluorescent blue (Sparvar 3107, Euro industry Supply, Stuttgart, Germany) or left white. Different colors capture different pollinators by their color preferences (Westphal et al. 2008). The traps were mounted on wooden stakes, with the height of the bowls being adjusted so that they were at the vegetation canopy (Westphal et al. 2008). The bowls were filled with about 600 ml of water with drops of soap to catch insects. For a given field, pan traps were settled only once, left for 4 days and removed afterwards. Across all fields, pan traps were installed during OSR flowering period. For each field, we put 12 pan traps (four of each of the three colors), six at the edge and six 50 m inside the field (core field). For each position, the pan traps were grouped in pairs of two randomly selected different colors, with the pairs spaced 25 m apart (Perrot et al. in review). In 2016, pan traps were only installed at the center of the field (Perrot et al. in review). In addition, we used sweep netting in the focal OSR fields in 2013 and 2014 and visual counting in 2015 and 2016, since pan traps are known to be selective with respect to the bees caught, e.g. honeybees are rarely caught by pan traps (Westphal *et al.*, 2008). Both sweep netting and visual counting were done in two transects, one at the edge and one 50 meters from the edge of the field. Transects were done between 8.30am and 5.30pm when air temperature was > 15°C and the weather was sunny. Sweep netting was limited to 50 catches attempts, while visual counting lasted for ten minutes, measured with a chronometer to ensure equal sampling effort. All insects caught were identified in the laboratory, at genera or species level for wild bees and species level for hoverflies, by professional entomologists.

Bee abundance per field was estimated from both pan-traps and sweep-nets. We derived a pollinators index (from now: bees) by first averaging wild pollinators and honeybees independently per field. Since the two averages were of similar magnitude (0-122 wild bees in pan-traps, vs. 0-78 honeybees in sweep-net), we then scaled pollinators abundance per sampling method, and finally summed them.

Farmer interviews

The general farm statistics, including use of inputs, obtained from the questionnaires is presented for the entire sample, each soil type and year in Table 1. From the farm surveys we derived pesticide, fertilizer and pollinators indicators, i.e. the Treatment Frequency Indicator (TFI), per pesticide type (Herbicides, Insecticides and Fungicides) which quantifies the number of recommended doses applied to each unit of cropped area. TFI per hectare is expressed as:

$$TFI_k = \sum_{j=1}^{k} \left(\sum_{i=1}^{n} \frac{D_i . S_i}{Dh_i . S_t} \right) \qquad (1)$$

where D_i, Dh_i and S_i, i=1, …, n are, respectively, the applied dose, the national recommended dose, and the treated surface area for the n spraying operations; k the respective pesticide; and St is the total field area (see Lechenet et al. (2017)). This includes all the pesticides treatments applied in a given crop field except for seed treatment. The reference dose is provided for a given pesticide commercial product and corresponds to the minimum registered dose for a given crop. Over our sample of farms, total TFI varied from 0.9 to 13.5 (mean: 5.2±2.1, N=296). The fertilizer used by farmers can be divided in inorganic and organic fertilizers. Since inorganic nitrogen is rapidly available to plants, the quantity of nitrogen used was directly calculated according to the fertilizer composition and the respective quantity applied. Conversely, organic nitrogen is a relatively stable compound and it has to go through mineralization in order to be converted into its inorganic forms. Thus, quantity of nitrogen mineralized in the organic fertilizers was calculated accordingly (see Jeuffroy and Recous (1999) for a detailed description).

Evaluating profitability

The gross margin (GM) per hectare was calculated accounting for the final grain yield revenue plus CAP Pillar 1 and Pillar 2 (if Agri-environmental Measures were adopted) subsidies minus variable costs (VC; details below) associated with OSR production. It was calculated as follows:

$$GM = [g.GY] + CAP - VC \quad (2)$$

where g is the price of OSR (€ t^{-1}), GY is the grain yield (t ha^{-1}) and VC are the variable costs (€ ha^{-1}).

Grain prices were set equal to the annual average market values: 450.5, 480.3, 413.7, 353.2, 369.9 and 373.9 €/ton from 2011 to 2016, respectively (Finances.net 2017). Fertilizers costs per hectare were directly calculated according to their total composition in nitrogen (0.9 € ha^{-1}), phosphorus (0.95 € ha^{-1}), potassium (0.65 € ha^{-1}), sulphur (0.76 € ha^{-1}) and *magnesium* (0.2 € ha^{-1}), the quantity applied and cost of each respective application. Pesticide costs per hectare were calculated according to their market price, obtained from cooperative prices, the quantity applied and cost of each respective application. Variable costs (VC) include all input costs that vary with one crop production cycle, such as seeds variety, soil tillage, fertilizers and pesticides (including application costs). Although the VC is not a measure of the overall profitability, it allows a valid comparison across the diverse farmers' management strategies since VC ignores any fixed costs. That is, for the same quantity of output, VC can fluctuate depending upon the amount or type of inputs used (e.g. the large range of weed management options).

Statistical analyses

The model selection procedure used throughout is based on model averaging using the dredge function in package MuMin (Barton 2018). The model averaging approach allowed studying the uncertainty when quantifying the precision of a given coefficient (Johnson and Omland 2004). We kept all models with ΔAIC from the best model <2.0 (Burnham and Anderson 2002). Relative importance was calculated as the sum of the Akaike weights over all of the models in which the parameter of interest appears (Johnson and Omland 2004). The resulting model was considered to be the best explanatory model. To improve normality, bees, fertilizer inputs and field size area were log + 1 transformed prior to analyses. The relative importance of the predictor variables of the full model was calculated as the proportion of the total variance explained by each variable using increments of multiple R^2 squared (i.e. percentage type 2 sum of squares) of the model predictors. The calculated percentages were used as measures of effect sizes. All variables were centered beforehand to make the interactions easier to interpret (Schielzeth 2010).

The effect of farmers practices of farmers practices, soil class (red, deep, medium and superficial soils), bees and landscape on yield and GM were independently estimated by selecting the best explanatory linear model, using a sequential approach for model selection. First, using the complete data-set (296 fields), we analyzed relationship between observed yield and farming practices (fertilizer and pesticides) accounting for direct and interactive between farming practices and soil class. Single effect variables that although not significant showed an interaction with another variable were also kept. We included interactions between practices (fertilizers and pesticides) and soil to account for farmers' adjustment of practices concerning soil quality. Then we added bees as a pollinator metric and its two-way interactions with the selected farming practice variables. Field size and soil class were also added as explanatory variables. Finally, landscape metrics (% of OSR and % of semi-natural elements, SNE) in eight radius (from 250m to 2000m) buffer counting from the focus field border were added to the best model. This analysis could however be carried out only from years 2013 to 2016, since bee were not sampled with pan traps or sweep net before, with a sample size of 75 fields. All models were visually inspected for normality of errors and heteroscedasticity and results were compared.

Results

Impact of farming practices on OSR yield and farmers' economic returns

We first assessed the direct effects of farming practices (fertilization and pesticides use) on yield using the complete data set consisting in 296 OSR fields surveyed between 2011 and 2016. Overall, crop yield averaged 3.1 t ha-1 (± 0.6), red soils showing a statistically higher yield (c. 26% in average, respectively) compared with the three other soils (Fig. 1). We then investigated which farming practices affected yield, with soil type as covariate as well as two-way interactions between practices (fertilizers and pesticides) and soil. The best model (25.7% deviance explained, $F_{10,285} = 10.37$, $P < 0.01$) indicated that phosphorus, herbicide and fungicide positively affected yield (see values in Table 12a). Nitrogen only affected yield through a significant interaction with soil, with a higher effect in the richest soils (Table 2a). Economic return was first analysed with the best farming practices predictors obtained in the previous model ($P < 0.01$; $F_{10,285}=26.51$; deviance explained 39.2 %; see Table 2b). In order to check that the best GM model was not improved by using other parameters (i.e., those not retained by the model selection procedure), we ran another model selection procedure starting with the full model (including all two-way interactions). Results indicated a shift between phosphorus in yield to potassium in GM. All inputs had negative effects on gross margin while they had slight positive effects on yield (fertilizers, herbicides and fungicides). Similarly to yield, nitrogen had a significant effect on GM when interacting with soil (Table 2b).

Additive effects of insect pollinators on yield and gross margin

Next, we investigated whether the best yield and income models would be significantly improved by adding to the model, bee abundance. We restricted the analyses here to the data set in which all parameters were available simultaneously (i.e., 75 fields). We detected a positive and highly significant effect of bees on yield (Table 3a). To check the robustness of this result, a complete model selection using all variables (plus the bees) was run again from the start to check whether new variables may be kept. This was the case, with the inclusion of a significant and negative effect of insecticides through its interaction with bees (Table 3b), slightly improving % of deviance explained from 26.4% ($P =0.10$; $F_{15,59}=1.589$;Table 3a) to 29.5% ($P<0.01$, $F_{5,69}=5.077$; Table 3b). Based on slope comparison, after phosphorus, bees' abundance had the second larger effect of yield. We finally incorporated in the best yield model the possible further effects of two landscape metrics, i.e. % of OSR surrounding the focal field, and % of SNE at the same buffer area ($P<0.01$, $F_{7,67}=4.687$; Table 3c). The % OSR at 250 meters (see Supplementary Table 2 for analysing other radii) entered significantly the model, improving the deviance explained by 6.9%. SNE in the same buffer radius had no effect.

The same approach was used for the gross margin, by now including bees to the previous best model based on practices. Contrary to yield, bees showed a marginally significant impact on GM (Table 4a). When starting from the full model set of variables, the new model selection ($P<0.01$, $F_{6,68}=8.759$; 38.6% deviance explained) excluded all farming practices in interaction with bees, thus retaining only single negative effects (nitrogen, insecticides and herbicides) with a marginally significant effect of bees (Table 4b). As for yield, including both % of OSR and % of SNE at 250 meters (see Supplementary Table 2 for analysis other radii) to the previous model improved the % of deviance explained by c.9% ($F_{8,66}=8.146$, $P < 0.01$; Table 4c). It further displayed a significant positive effect of bees, and showed that the % of OSR in the surrounding landscape at 250m buffer radius had a significant positive effect on GM. As for yield, soil effect vanished. With this final model, almost 50% of the deviance was explained, and suggested that bees increased GM by c.0.75t.ha-1 and c.250€ per ha between field with smallest to highest bee abundance (Fig 2b).

Trading pollinators with pesticides to improve profits

Finally, since there were opposed effects between pollinators abundance and insecticide or herbicide uses on yield and GM, we explored to which extent, based on our empirical data, reducing pesticides use could be balanced by improving bees, and their resulting effects on yield and/or GM. To this end, we set all others parameters (and their effects) at their mean, and only varied herbicides, insecticides (both by their TFI) and bee abundance, measuring their interacting effects on yield and GM using 3D plots with farming practices (X-axis), bee abundance (Y-axis) and their interaction, and yield and profit (Z-axis). The most interesting feature emerged with the trade-off between insecticides intensity and bee abundance (Fig. 3a-c). This indicates that farmers can maximise yield through two options: one, by maximising TFI (insecticides), presumably reducing pests, and the other one consisting in spraying no insecticides, which maximises bee abundance. But unsurprisingly, in regard to gross margin, only the latter strategy improved economic benefits. A similar, though less extreme, pattern appeared with herbicide use (Fig. 3b-d). Finally, we investigated a cross strategy between herbicide and insecticide use. The results suggest that a strategy in which both herbicides and insecticides are reduced would increase yield and simultaneously gross margins.

Discussion

Crop yield results from various and complex combinations of biotic and abiotic factors. OSR showed improved production with insect pollination. We report here that insect pollination enhances crop yield and farmers economic benefits, that these benefits overweight those of farming practices. Bee abundance was a strong determinant of OSR production supporting previous studies (*Perrot et al. in review*, Bommarco et al. 2012, Bartomeus et al. 2014). Effect of bees was less predominant on GM mostly due to the strong negative effect of farming practices on GM. Our analysis revealed different type of interaction between farming practices and bee abundance on yield. The absence of interaction between the amount of fertilisers and bee abundance suggests an additive effect of bees and fertiliser benefits on yield. This is in opposition with Marini et al. (2015) but in accordance with van Gils et al. (2016). We observed a significant interaction between insecticide and bee abundance on yield but not on GM. While the effect on yield could be due to the decrease of pollinators individual performance by reducing the number of flowers visits (Gill and Raine 2014, Stanley et al. 2015), the absence of effect on GM is most likely due to the expensive cost of insecticide. We also found a positive effect of quantity of neighbouring OSR fields. Previous studies have found that similar surrounding OSR can reduce pest in focus field as pollen beetles or stem weevils larvae (Zaller et al. 2008b). By reducing the pest damage, the percentage of OSR in surrounding landscape can increase OSR yield (Zaller et al. 2008a). However, pest damage was not follow on field and more investigations were needed to confirm this effect.

Although nitrogen is the most common fertilizer found in crops around the world, no effect of high fertilizer amount on OSR yield was found in our study. N input may be used in saturating quantity (N-input mean was c.157 kg.ha-1). Climatic (lixiviation) or ecophysiological (low assimilation by the plants) reasons may also explain this absence of relationship. N-input was found similar between soil type (respectively 139, 151, 158, 168 kg.ha-1 for red, deep, intermediate and superficial soils). Research has shown that the effect of N-input on yield can strongly vary between a positive effect (Rathke et al. 2005, Marini et al. 2015), no effect (Stahl et al. 2017,Colnenne et al. 2002) or even negative effect (Hocking et al. 1997, Cheema et al. 2001, Ozturk 2010, Khan et al. 2018). Efficiency of N fertilization could also vary between varieties (Bouchet et al. 2016), but in our study we could not evaluate that, since c. 93% of the farmers used hybrid seed. K-input showed also no effect on yield, potentially due to the lower quantity used in field. Phosphorus was the only fertilizer found as a strong determinant of both yield and gross margins as found by (Lickfett et al. 1999) potentially by increasing pods per plant and seed per pod (Rose et al. 2008). For pesticides,

there is a growing incertitude concerning the positive effect of pesticides on yield (Furlan et al. 2017, see also Gaba et al. (2016) on wheat). On the larger dataset, we found a weak positive effect of fungicide and herbicide as found in previous studies (Balodis et al. 2006, Bijanzadeh et al. 2010). These pesticide reduce potentially pest damage and competition with weeds and permit the increase of OSR yield (Bankina et al. 2010, Bijanzadeh et al. 2010). However, these treatments are very expensive compare to their potential benefits, thus the negative observed effect on gross margins. The direct effect of insecticide, although its high use was surprisingly not found on yield, yet it decreases gross margin. Different results have been obtained by Sutter et al. (2017). The absence of relation yield-insecticide may likely be due to the inefficient use insecticide (Furlan et al. 2017), i.e. insecticide were applied even in absence of pest as a prophylactic method. In addition, small pest population may not necessary affect OSR yields (Pinet et al. 2015) or they can even increase seed yield through a compensate mechanism (Gagic et al. 2016).

Over-application of nutrients is a challenge facing intensive farming. New modes of agriculture are necessary to promote sustainable crop production (Tittonell 2014) and reducing dependency to chemicals inputs. Here, we identified for OSR production several ways to limit inputs and increase the contribution of pollinators, while maintaining yield and simultaneously increase farmers' gross margins. Thus, it is likely that these inputs are either being over or inefficiently applied (Lassaletta et al. 2014, Furlan et al. 2017). We show here that it is economically feasible to reduce one of the largest environmental source of agriculture pollution, nitrogen. Although OSR is a crop highly demanding on N fertilizer to build up efficient photosynthetic leaf tissue (Hegewald et al. 2016), our results demonstrate that there is a space for a significant reducing it without harming yields, while benefiting farmers economics returns. N reduction leads as well to a lower N, not taken up by the crop, leaching rates during periods of heavy rainfall (Rathke et al. 2006). The reduction of N-input can as well lead to increase in oil content (Rathke 2005).

Pollinating insects despite their proven economic contribution to crop are rarely considered in farming planning. Besides, the actual value of insect pollination has often been studied in isolation from crop management interactions. Through our economic valuation of the ecosystem services provided by domestic and wild bees we have shown an antagonist interaction with insecticides. These results can be used as an incentive for a better use of harmful pesticides, benefiting biodiversity, agricultural production and ecosystem processes as a whole. The consequences of shifts in bee abundance caused by agriculture landscape can be severe. We have shown that OSR in the surrounding landscape up to 250m buffer has a positive effect on pollinator abundance possible due to a dilution in pest abundance, hence damage. Pollinator depended crops will certainly benefit from a pollinator-friendly management of agricultural landscapes which supports ecosystem services, in which a potential optimum should be found between OSR area and natural element which provide bee abundance (Morandin and Winston 2006). This study provides a clear demonstration that an environmental friendly management which supports ecosystem services is compatible with high crop yields, and can even increase farmers' economic returns. We have here showed, Pywell et al. (2015) did for the northwest Europe, that the concept of ecological intensification of agriculture is achievable on large commercial arable farms, with a "win-win" strategy between crop production, farmers economic returns and the environment.

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Table 1- General statistics obtained from the questionnaires for OSR cropping (N=296). OSR area and yield values were obtained directly from the farm questionnaires. The remaining values were calculated as described in the Methods.

	mean (±SD)	min	max
OSR area (ha)	6.9 (±5)	0.4	28.5
Yield (kg ha^{-1})	3089.4 (±632.1)	1600	5200
N input (kg ha^{-1})	158.7 (±55.2)	20.9	333.8
P input (kg ha^{-1})	53.3 (±37.7)	0	183.2
K input (kg ha^{-1})	32.3 (±54.7)	0	311
TFI_{Herb} (ha^{-1})	1.6 (±1)	0	5.8
TFI_{Inst} (ha^{-1})	2.3 (±1.2)	0	7.2
TFI_{Fong} (ha^{-1})	1 (±0.6)	0	4
Total Revenue (€ ha^{-1})	1210.9 (±249.9)	702.8	1937
Profit (€ ha^{-1})	628.6 (±300.2)	-104.9	1727.3
Total cost (€ ha^{-1})	901.4 (±197.7)	388.9	1514.7
Cost N (€ ha^{-1})	150 (±53.8)	18.8	359.8
Cost P (€ ha^{-1})	57 (±40.6)	0	190.9
Cost K (€ ha^{-1})	27 (±43.7)	0	237.2
Cost Herb (€ ha^{-1})	112.9 (±57.2)	0	314.6
Cost Inst (€ ha^{-1})	23.8 (±14.3)	0	98.5
Cost Fong (€ ha^{-1})	43 (±22.6)	0	127.3

Table 2 – Model averaging results for yield and gross margin responses to farming practices. Estimated coefficients (β), their 95% confidence intervals (CI) and importance values (w) are given per model parameter for yield and profit model averaging of LM analyses. β and CI are not present for the categorical variables. Significant terms with confidence intervals not overlapping with zero are in bold.

a) Yield as a function of Farmer practices (N, P, H, F, soil; and their two-way interactions)

	w	β	Lower CI	Upper CI	var Exp	p-val
N dose	1	-130.1	-279.8	19.6	0.7%	0.11
P dose	**1**	**93.4**	**29.2**	**157.5**	**2.1%**	**<0.01**
H TFI	**1**	**74.5**	**9**	**139.9**	**1.3%**	**0.04**
F TFI	**1**	**88.3**	**23.5**	**153.1**	**1.8%**	**<0.01**
Soil	1				17.3%	<0.01
N dose:Soil	1				2.6%	0.02

b) Gross margin as a function of Farmer practices from model above

	w	β	Lower CI	Upper CI	var Exp	p-val
N dose	**1.00**	**-180.7**	**-240.7**	**-120.8**	**0.081**	**<0.01**
K dose	**1.00**	**-52.5**	**-78.2**	**-26.7**	**0.178**	**<0.01**
H TFI	**1.00**	**-89.5**	**-116.5**	**-62.5**	**0.471**	**<0.01**
F TFI	**1.00**	**-53.1**	**-79.7**	**-26.6**	**0.172**	**<0.01**
Soil	1.00				0.677	<0.01
N dose:Soil	1.00				0.142	<0.01

Table 3 – Model averaging results for yield response to farming practices, bees and Semi-natural elements. Estimated coefficients (β), their 95% confidence intervals (CI) and importance values (w) are given per model parameter for yield and profit model averaging of LM analyses. β and CI are not present for the categorical variables. Significant terms with confidence intervals not overlapping with zero are in bold.

a) Best yield model including Bees

	w	β	Lower CI	Upper CI	var Exp	p-val
Yield ~ Bees + N dose + P dose + H TFI + F TFI + Soil + Bees: N dose + Bees: P dose + Bees: H TFI + Bees: F TFI + N dose:Soil						
Bees		92.8	-11.0	196.6	0.064	0.03
N dose		-57.0	-428.5	314.4	0.030	0.12
P dose		**176.2**	**12.3**	**340.1**	**0.058**	**0.03**
H TFI		93.8	-76.0	263.7	0.021	0.20
F TFI		39.4	-119.8	198.5	0.001	0.78
Soil					0.045	0.31
Bees: N dose		68.4	-71.3	208.1	0.012	0.33
Bees: P dose		-57.5	-182.3	67.3	0.011	0.36
Bees: H TFI		-13.3	-146.3	119.7	0.000	0.84
Bees: F TFI		56.3	-48.6	161.2	0.014	0.29
N dose:Soil					0.007	0.91

b) Yield as a function of Farmer practices & Bees

	w	β	Lower CI	Upper CI	var Exp	p-val
Yield ~ Bees + N dose + P dose + I TFI + Bees:I TFI						
Bees	**1.00**	**107.4**	**2970.2**	**3210.7**	**0.080**	**<0.01**
N dose	0.55	-99.9	17.8	197.1	0.023	0.14
P dose	**1.00**	**229.1**	**-232.3**	**32.5**	**0.121**	**<0.01**
I TFI	1.00	-85.4	95.8	362.4	0.012	0.29
Bees: I TFI	1.00	-108.7	-211.0	40.1	0.056	0.02

c) Yield as a function of farmer practices & Bees & Landscape

	w	β	Lower CI	Upper CI	var Exp	p-val
Yield ~ Bees + N dose + P dose + I TFI OSR250 + SNE250 + Bees: I TFI						
Bees		**122.3**	**31.5**	**213.1**	**0.089**	**<0.01**
N dose		-120.4	-252.2	11.3	0.032	0.07
P dose		**238.0**	**106.4**	**369.7**	**0.124**	**<0.01**
I TFI		-104.3	-227.6	19	0.021	0.14
OSR250		**15.1**	**2.6**	**27.6**	**0.056**	**0.02**
SNE250		2.4	-10	14.8	0.001	0.70
Bees: I TFI		-90.6	-182.5	1.3	0.037	0.05

Parameters N, P, K, H, I, F indicate respectively Nitrogen, Phosphorus, Potassium, Herbicide, Insecticide and Fungicide. Dose is the quantity of fertilizer applied (logged) and TFI is the Treatment frequency index. Soil represents the different soil types. OSR250 and SNE250 indicate the percentage of OSR and percentage of semi-natural elements in a buffer radius of 250m outside the focal field.

Table 4 – Model averaging results for gross margin response to farming practices, bees and Semi-natural elements. Estimated coefficients (β), their 95% confidence intervals (CI) and importance values (w) are given per model parameter for yield and profit model averaging of LM analyses. β and CI are not present for the categorical variables. Significant terms with confidence intervals not overlapping with zero are in bold.

a) Best gross margins model including Bees

	w	β	Lower CI	Upper CI	var Exp	p-val
Yield ~ Bees + N dose + P dose + H TFI + F TFI + Soil + Bees: N dose + Bees: P dose + Bees: H TFI + Bees: F TFI + N dose:Soil						
Bees		24.6	-14.5	63.7	0.028	0.10
N dose		**-28.1**	**-168.1**	**111.9**	**0.132**	**<0.01**
P dose		36.9	-24.8	98.7	0.015	0.23
H TFI		-61.2	-125.2	2.9	0.072	0.01
F TFI		-17.1	-77.1	42.9	0.010	0.33
Soil					0.058	0.14
Bees: N dose		15.1	-37.5	67.8	0.003	0.57
Bees: P dose		-14.6	-61.6	32.5	0.004	0.54
Bees: H TFI		30.7	-19.4	80.8	0.015	0.23
Bees: F TFI		37.9	-1.6	77.5	0.038	0.06
N dose:Soil					0.021	0.57

b) Gross margin as a function of Farmer practices & Bees

	w	β	Lower CI	Upper CI	var Exp	p-val
Gross Margin ~ Bees + N dose + P dose + K dose + I TFI + H TFI						
Bees	0.78	31.9	-2.0	65.8	0.032	0.06
N dose	**1.00**	**-91.2**	**-143.4**	**-39.0**	**0.109**	**<0.01**
P dose	1.00	59.7	7.7	111.7	0.047	0.03
K dose	0.81	-48.5	-98.1	1.1	0.034	0.06
I TFI	**1.00**	**-83.8**	**-133.1**	**-34.6**	**0.104**	**<0.01**
H TFI	**1.00**	**-65.6**	**-114.7**	**-16.5**	**0.064**	**<0.01**

c) Gross margin as a function of farmer practices & Bees & Landscape

	w	β	Lower CI	Upper CI	var Exp	p-val
GM ~ Bees + N dose + P dose + K dose + I TFI + H TFI + OSR250 + OSR250						
Bees		**35.7**	**1.9**	**69.6**	**0.035**	**0.04**
N dose		**-102.7**	**-153.9**	**-51.6**	**0.126**	**<0.01**
P dose		**64.7**	**14**	**115.3**	**0.051**	**0.01**
K dose		-33.7	-82.5	15	0.015	0.17
H TFI		**-97.8**	**-146.1**	**-49.6**	**0.128**	**<0.01**
I TFI		**-70.2**	**-117.5**	**-22.9**	**0.069**	**<0.01**
OSR250		**6.6**	**1.7**	**11.4**	**0.058**	**<0.01**
SNE250		0.1	-4.6	4.8	0.000	0.97

Parameters N, P, K, H, I, F indicate respectively Nitrogen, Phosphorus, Potassium, Herbicide, Insecticide and Fungicide. Dose is the quantity of fertilizer applied (logged) and TFI is the Treatment frequency index. Soil represents the different soil types. OSR250 and SNE250 indicate the percentage of OSR and percentage of semi-natural elements in a buffer radius of 250m outside the focal field.

Fig 1. Effect of nitrogen input on yield (a) and gross margins (c), herbicide on yield (b) and Gross Margins (d). Black lines reprentes linear regression as predicted by linear model. Lines are dashed when they are not signifncant.

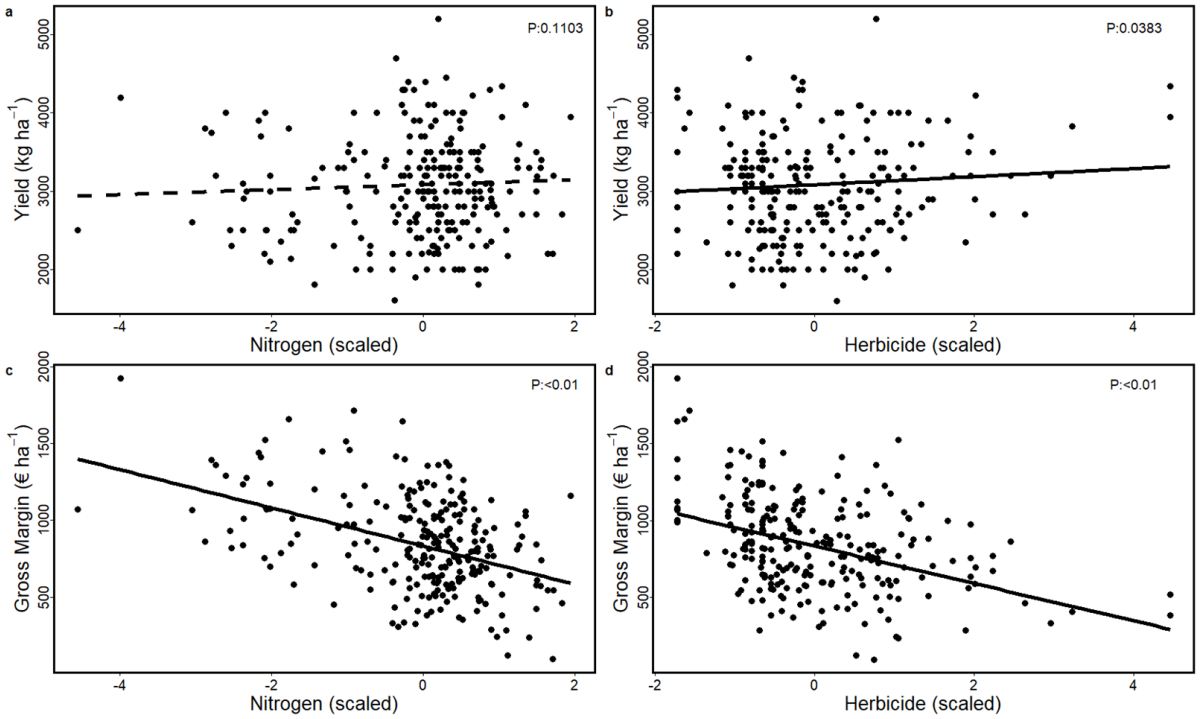


Fig 2. Effect of bees index on yield (a) and gross margins (b). Black lines reprentes linear regression as predicted by linear model.

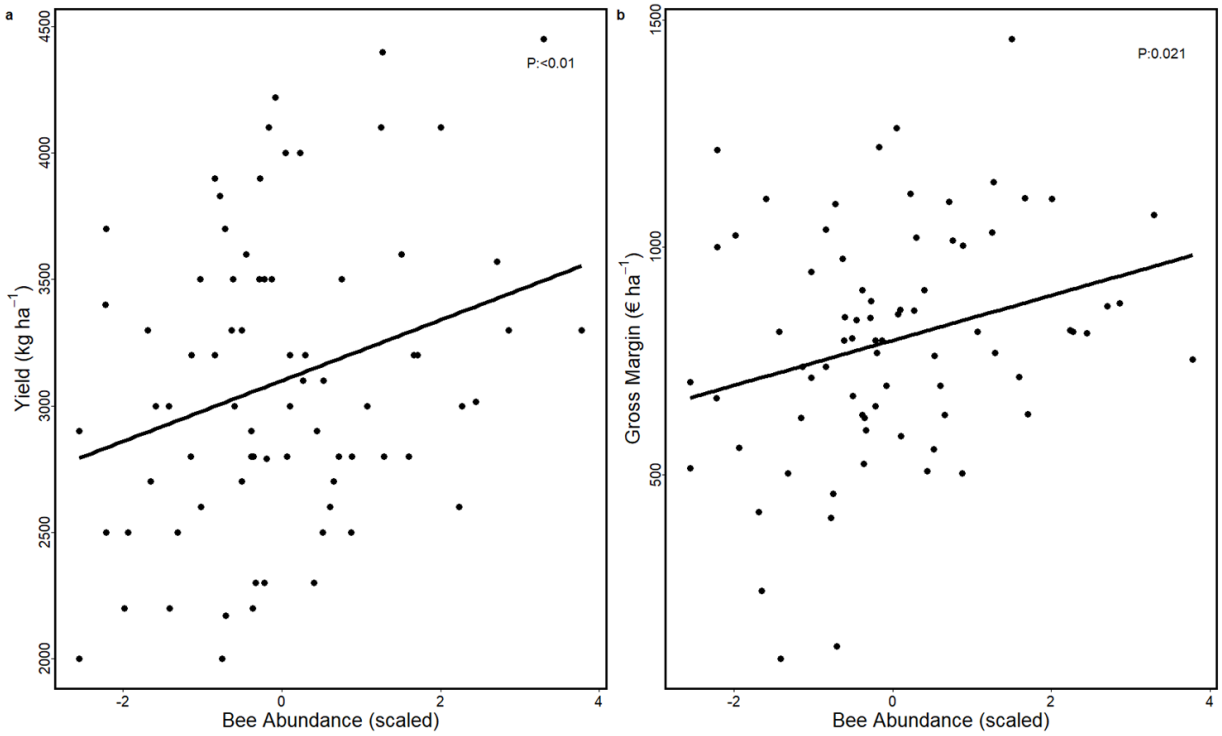
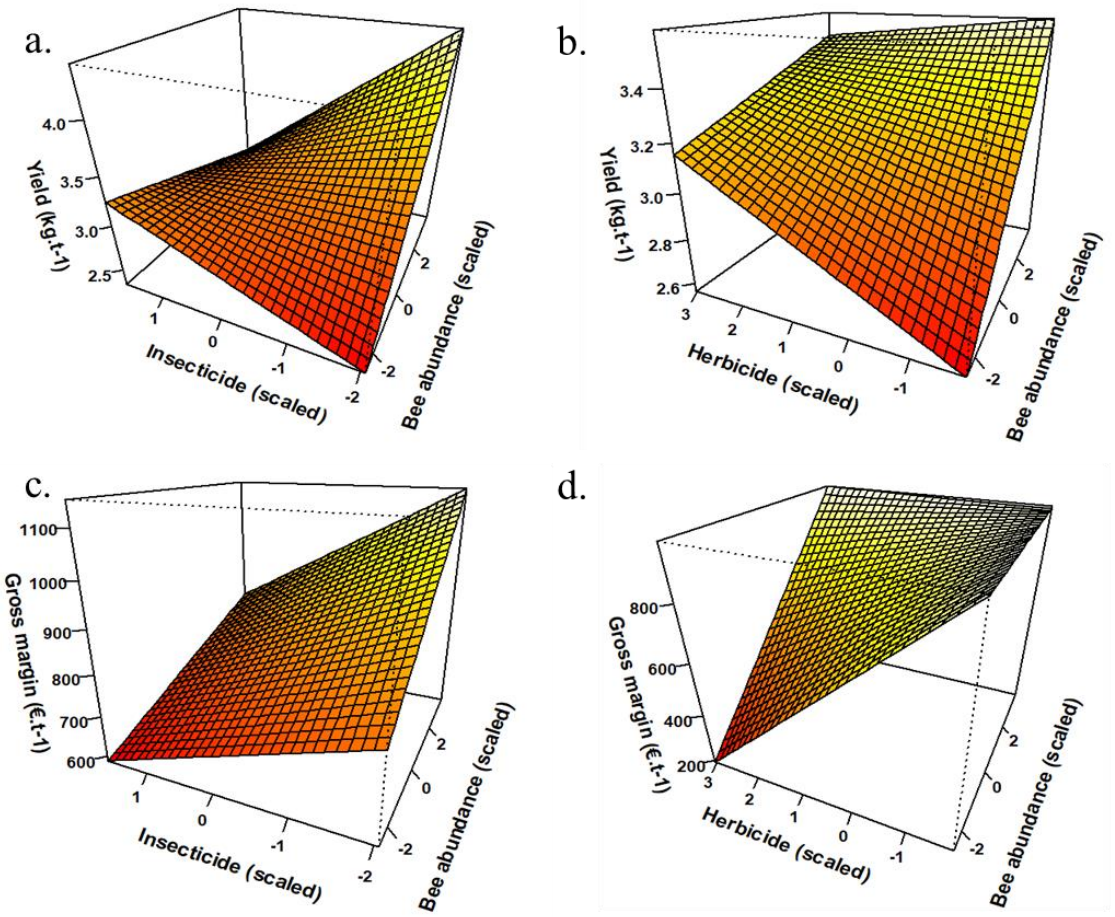


Fig 3. Effect of the interaction between bees and insecticides on yield (a) and gross margins (b), and the effect of the interaction between bees and herbicides on yield (c) and gross margins (d)



Supplementary Tables

Supplementary table 1. Selection of buffer radius for the effect of landscape element and farmers practices on Yield. Effect of local and landscape management on bee abundance for different buffer radius. Variable presents are those keeping by the respective best model. Coefficient (β), F value and P value are given. Also R2 and F stat for model is provided.

	Buffer zone											
	250m			500m			750m			1000m		
	β	F	P	β	F	P	β	F	P	β	F	P
OSR	15.1	5.8	0.02	16.4	3.8	0.06	16.8	2.4	0.13	12.2	0.8	0.38
SNE	2.4	0.2	0.70	6.1	0.6	0.44	0.8	0.0	0.92	-1.4	0.0	0.85
Bees	122.3	9.4	<0.01	126.6	9.6	<0.01	114.5	8.1	0.01	106.6	7.3	0.01
N dose	-120.4	3.3	0.07	-128.2	3.7	0.06	-122.2	3.2	0.08	-108.8	2.4	0.12
P dose	238.0	13.0	<0.01	255.9	14.2	<0.01	246.8	13.2	<0.01	233.2	11.6	<0.01
TFI I	-104.3	2.2	0.14	-106.8	2.0	0.16	-90.9	1.3	0.26	-84.8	1.1	0.29
Bees:												
TFI I	-90.6	3.9	0.05	-104.7	5.1	0.03	-110.4	5.6	0.02	-109.5	5.4	0.02
R2	0.361			0.308			0.295			0.280		
F stat	4.6878 on 7,67			4.2697 on 7,67			4.0006 on 7,67			3.7203 on 7,67		

	1250m			1500m			1750m			2000m		
	β	**F**	**P**	**β**	**F**	**P**	**β**	**F**	**P**	**β**	**F**	**P**
OSR	2.2	0.0	0.89	8.9	0.2	0.62	10.3	0.3	0.59	7.8	0.2	0.69
SNE	-3.5	0.2	0.64	-2.6	0.1	0.73	-2.9	0.2	0.69	-4.4	0.4	0.54
Bees	101.9	6.8	0.01	101.1	6.7	0.01	99.0	6.7	0.01	97.4	6.6	0.01
N dose	-95.0	1.8	0.19	-100.7	2.0	0.16	-98.6	2.0	0.16	-91.9	1.7	0.19
P dose	225.1	10.8	<0.01	227.8	11.1	<0.01	225.9	11.0	<0.01	223.0	10.8	<0.01
TFI I	-81.1	1.0	0.32	-82.5	1.1	0.30	-81.9	1.1	0.30	-79.2	1.0	0.32
Bees:												
TFI I	-109.9	5.4	0.02	-109.6	5.3	0.02	-111.6	5.5	0.02	-113.8	5.7	0.02
R2	0.272			0.275			0.275			0.276		
F stat	3.5823 on 7,67			3.6217 on 7,67			3.6377 on 7,67			3.653 on 7,67		

Parameters N, P, H and I indicate respectively Nitrogen, Phosphorus, Herbicide and Insecticide. Dose is the quantity of fertilizer applied (logged) and TFI is the Treatment frequency index. Soil represents the different soil types. OSR and SNE indicate the percentage of OSR and percentage of semi-natural elements in the buffer radius outside the focal field.

Supplementary table 2. Selection of buffer radius for the effect of landscape element and farmers practices on Gross Margins. Effect of local and landscape management on bee abundance for different buffer radius. Variable presents are those keeping by the respective best model. Coefficient (β), F value and P value are given. Also R2 and F stat for model is provided.

	Buffer zone											
	250m			500m			750m			1000m		
	β	F	P	β	F	P	β	F	P	β	F	P
OSR	6.6	7.3	<0.01	6.00	3.19	0.08	6.60	2.40	0.13	6.40	1.40	0.24
SNE	0.1	0.0	0.97	-1.50	0.24	0.63	-4.00	1.80	0.18	-4.30	2.33	0.13
Bees	35.7	4.4	0.04	33.20	3.60	0.06	28.90	2.80	0.10	26.70	2.45	0.12
N dose	-102.7	16.1	<0.01	-103.40	15.28	<0.01	-99.00	14.00	<0.01	-94.00	12.57	<0.01
P dose	64.7	6.5	0.01	72.30	7.53	0.01	62.40	5.76	0.02	55.80	4.61	0.04
K dose	-33.7	1.9	0.17	-36.50	2.11	0.15	-32.50	1.66	0.20	-32.70	1.68	0.20
H TFI	-97.8	16.4	<0.01	-95.30	14.47	<0.01	-90.20	13.33	<0.01	-87.40	12.30	<0.01
I TFI	-70.2	8.8	<0.01	-67.20	7.58	0.01	-60.20	6.17	0.02	-58.00	5.70	0.02
R2	0.482			0.471			0.478			0.479		
F stat	8.1456 on 8,66			7.3459 on 8,66			7.5605 on 8,66			7.5757 on 8,66		
	1250m			1500m			1750m			2000m		
	β	**F**	**P**	**β**	**F**	**P**	**β**	**F**	**P**	**β**	**F**	**P**
OSR	3.7	0.4	0.56	4.3	0.4	0.55	4.3	0.3	0.59	4.1	0.3	0.62
SNE	-4.9	2.8	0.10	-4.3	2.1	0.15	-4.1	1.9	0.18	-4.2	2.0	0.16
Bees	25.2	2.1	0.15	24.8	2.1	0.16	24.8	2.0	0.16	25.1	2.1	0.15
N dose	-89.1	11.1	<0.01	-90.1	11.4	<0.01	-89.3	11.4	<0.01	-87.6	11.1	<0.01
P dose	51.5	3.8	0.05	52.7	3.9	0.05	52.2	3.8	0.05	51.8	3.8	0.05
K dose	-32.8	1.6	0.21	-31.4	1.4	0.24	-31.2	1.3	0.25	-31.0	1.3	0.26
H TFI	-83.1	10.7	<0.01	-83.9	10.2	<0.01	-83.9	9.6	<0.01	-85.3	9.9	<0.01
I TFI	-58.1	5.6	0.02	-58.4	5.6	0.02	-58.2	5.5	0.02	-57.2	5.3	0.03
R2	0.471			0.463			0.459			0.459		
F stat	7.3329 on 8,66			7.1091 on 8,66			7.0035 on 8,66			6.9995 on 8,66		

Parameters N, P,K, H and I indicate respectively Nitrogen, Phosphorus, Potassium, Herbicide and Insecticide. Dose is the quantity of fertilizer applied (logged) and TFI is the Treatment frequency index. Soil represents the different soil types. OSR and SNE indicate the percentage of OSR and percentage of semi-natural elements in the buffer radius outside the focal field.

Chapitre IV :

Les abeilles domestiques améliorent la qualité de la production de colza

Avant-propos et résumé du chapitre 4 :

Les 3 premières études ont évalué l'effet bénéfique des pollinisateurs sur les rendements. Cependant, le rendement n'est pas le seul paramètre qui détermine la valeur d'une récolte ; la qualité des graines en fait aussi partie. Dans cette quatrième étude, nous nous intéresserons à l'effet des pollinisateurs sur la qualité des graines de colza qui est déterminée par la quantité d'huile par graine et sa composition en acide gras. De précédentes études ont montré un effet positif de la pollinisation entomophile sur le pourcentage de lipides dans les graines, mais aucune étude ne s'est intéressée à l'effet des pollinisateurs sur la composition en acides gras. Le but de cette étude va être d'étudier l'effet des pollinisateurs sur la composition en acide gras et sur le pourcentage en lipides des graines. Pour cela, nous utiliserons à la fois le gradient de pollinisateurs ainsi que la méthode d'exclusion des processus de pollinisation. L'étude prendra aussi en compte les pratiques agricoles (fertilisants, pesticides, variétés) qui peuvent modifier la qualité des graines ainsi que l'effet des pollinisateurs.

Notre étude montre que les abeilles domestiques améliorent la qualité des graines de colza en augmentant le pourcentage des acides gras insaturés et en diminuant le pourcentage d'acides gras trans et saturés. Une augmentation du pourcentage de lipides par graine est aussi observée mais pour une seule année. Cet effet n'est pas observé pour les abeilles sauvages. Nous montrons aussi que cet effet est indépendant des variétés et des autres pratiques agricoles mêmes si plusieurs pratiques modifient la composition en acide gras. L'utilisation de filet met en évidence un effet important des abeilles domestiques sur la quantité de lipides. Aucune différence significative de composition d'acides gras n'est observée entre les traitements contrôle, grande maille (exclusion des gros pollinisateurs) et petite maille (exclusion des petites pollinisateurs). A l'inverse, une différence importante de composition d'acides gras est observée entre le le traitement osmolux (qui ne permet que l'autofécondation) et les autres traitements. Les résultats observés supportent des résultats précédemment observés chez l'amande où l'autofécondation se traduit par une augmentation d'acide linoléique et une diminution d'acide oléique.

Plusieurs mécanismes semblent par conséquent jouer dans la production d'acides gras. L'augmentation du pourcentage d'acides gras insaturés observé lorsque l'abeille domestique est abondante pourrait s'expliquer par une réallocation des ressources. En effet, les acides gras insaturés sont moins coûteux à produire pour la plante que les acides gras trans et saturés. Maintenir des fleurs en floraison est coûteux pour la plante de colza, mais ce coût est réduit en présence d'abeilles domestiques. La réduction de coût liée au maintien des fleurs pourrait alors compenser le coût de production des acides gras insaturés. L'allofécondation est également un mécanisme probable puisque nous avons observé des différences importantes en son absence. Cette étude met également en évidence que les abeilles domestiques augmentent à la fois les rendements et la qualité de la récolte sans compromis entre ces deux variables.

Honeybees improve oil quality of oilseed rape

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Summary

Oilseed rape (OSR) is a predominant crop in European Union. OSR nutritional value, i.e. OSR quality is determined by seed oil content and fatty acids (FAs) composition. OSR production show improved production quantity and seed oil content with insect pollination, however the benefit of insect pollination on FAs composition remained unknown. In this study, we address this gap by investigating the effect of pollinators on OSR seed oil content and FAs composition in farmers' fields during four years. We first examined the relationships between wild bee and honeybee abundances and OSR quality, and found that OSR quality was only responsive to honeybees. Honeybee improved OSR quality, by increasing the amount of unsaturated FAs and decreasing the amount of saturated and trans-saturated FAs. Honeybee also increased seed oil content but not all years. The effect of honeybee was unrelated to plant cultivar or farming practices. We then assess the potential effect of insect pollination on oil content and FAs composition using an exclusion experiment to disentangle the contribution of pollination processes. Seeds pollinated by honeybee showed higher amount of oil content (48% in average). FA profile was strongly influenced by the experimental treatments, which mainly result from differences between self-pollinated seeds and cross-pollinated ones. Our study show, to the best of our knowledge, the first evidence that honeybee enhances the quality value of OSR oil. Further investigations need to be conducted to find explanations for this increase of quality in OSR insect pollinated seeds. Our results highlight potential negative consequences of any pollinator decline, compromising crop yields and provoking risks to food security.

Keywords
Agroecosystem, Crop pollination, Ecosystem service, Fatty acid, Oil content, Pollinator

Introduction

Balancing biodiversity conservation with food security and the preservation of a broader set of ecosystem services, in a context of global change, is among the greatest challenges of the century (Crist et al., 2017; Godfray et al., 2010). Crop pollination is a clear example of the contributions of nature to people within ecosystems that provide services valued by society (Millenium Ecosystem Assessment, 2005). Crops, as diverse as strawberries, tomatoes, cacao, coffee, sunflowers and oilseed rape show improved production quantity (yield) with animal pollination (Klein et al., 2007). Indeed, 70% of crops worldwide depend on pollinators for the yield (Klein et al., 2007). In a context of higher food demands, pollination service may thus improve food security. This need is even accentuated by recent evidences revealing higher quality in crop production when plants are pollinated by insect pollinators (e.g. Bommarco, Marini & Vaissière 2012; Bartomeus *et al.* 2014; Klatt *et al.* 2014). Strawberry fruits pollinated by bees show less malformation, greater fruit weight and long shelf life (Klatt et al., 2014), oilseed rape plants allocate more oil resources to insect pollinated seeds (Bartomeus et al., 2014; Bommarco et al., 2012) and Gala apples showed significant improvement in concentration of micronutrients (Garratt et al., 2014). However, not all crops benefit from insect pollinators: Bartomeus et al. (2014) did not found any effect of insect pollination on the nitrogen content in the seeds of field beans, and Garratt et al. (2014a) revealed differential response among apple varieties. Finally, few studies have investigated how insect pollination affects crop quality, hence the basic information on the effectiveness of insect pollination in improving crop quality is lacking for many crops and varieties.

Oilseed crops are highly valuable crops used in human food and to produce bioenergy. Presently oilseed rape (*Brassica napus*) is the predominant oil crop in European union (FAOSTAT, 2014), mainly grown as a winter crop, and the world's total acreage of oilseed rape (and canola) along with related oilseed brassicas (e.g. mustards) is about 34.4 M ha, with a production of around 69.5 M t (FAOSTAT, 2014). Oilseed rape (OSR) seeds are rich in oil (42-48%; (Bommarco et al., 2012; Rathke et al., 2005) and represented one-third of oil consumed in Europe for 2013 (www.oilworld.biz). Insect pollination have been shown to increase in oilseed rape yield (Perrot *et al.in review*; Bommarco, Marini & Vaissière 2012; Bartomeus *et al.* 2014; Marini *et al.* 2015). The dependence of OSR for insect pollination, however, differ among varieties (Hudewenz et al., 2014) or cultivar type (hybrid versus open, Lindström *et al.* 2016). The effect of insect pollination on oil content has however received little attention. Only a handful studies have so far investigated this effect (Bartomeus et al., 2014; Bommarco et al., 2012; Marini et al., 2015; Oz et al., 2008; Sutter and Albrecht, 2016), and demonstrated an increase of oil content per seed between 1.28-6% when comparing seeds from flowers with and without access to pollinators. However, the nutritional value of OSR oil, i.e. OSR quality, is determined by seed oil content and the fatty acids (FAs) composition. High nutritional value oils are defined by low percentage of trans-saturated and saturated fatty acids (Anderson et al., 2010; de Souza et al., 2015), a high percentage of unsaturated fatty acid composed by monounsaturated and polyunsaturated fatty acids (Carrillo et al., 2012; Ruxton et al., 2004) and a low ω6-ω3 ratio (lower than 5, Simopoulos 2002). OSR FAs composition results from a mixture of saturated FAs (10%) and unsaturated FAs (90%) with a higher proportion of monounsaturated FAs (60%) than polyunsaturated FAs (30%). On average, OSR contains high amounts of oleic acid (C18:1, ~50-60%), along with moderate amounts oflinoleic acid (C18:2, ~15-20%) and alpha-linolenic acid (C18:3, ~5-10%) (Adamska et al., 2004; Jahreis and Schäfer, 2011; Orsavova et al., 2015). OSR FAs composition also have low trans-saturated FAs percentage (<1%) and ω6-ω3 ratio (~2, (Jahreis and Schäfer, 2011; Orsavova et al., 2015). Understanding how insect pollination affects FAs composition (including the ω6-ω3 ratio) is therefore mandatory to determine its contribution to the nutritional value of OSR.

In this study, we test the hypothesis that OSR quality benefits from insect pollination by increasing seed oil content and the percentage of unsaturated FAs. We therefore examined OSR seed

oil content, the percentage of FAs group (unsaturated, saturated and trans-saturated FAs) and of the main FAs (especially oleic, linoleic and alpha-linoleic) of OSR plants from for 72 farmers' fields in 2013, 2014, 2015 and 2016. Fields were located along a gradient of wild bee and honeybee abundances (Perrot *et al.in review*). First, we examined the relationship between pollinators on one hand and either yield, oil content or FAs composition on the other hand. Because fertilisers and pesticides are known to affect seed oil content and FA composition (Cogdill, 2013; Lickfett et al., 1999; Rathke et al., 2005; Zhang et al., 2012), we included these farming practices in the analysis. Second, we focused on the effect of the role of OSR cultivar and cultivar types on OSR quality. Two main plant cultivars are commonly cultivated in France: the restored hybrids, which represent more than 80% of the French OSR growing area in 2013, and the open cultivar (18%) (https://www.terre-net.fr/). The newest generation of winter OSR hybrids should display both high yield and high oil contents (Wittkop et al., 2009). Therefore, we predict a higher amount of oil content in hybrids than open varieties. We also assume variation in pollinator abundance among OSR varieties because they may differentially attract pollinators by offering heterogeneous nectar rewards (Ouvrard et al., 2017). Therefore to ensure for an effect of cultivar, we explored the effect of pollinator abundance on OSR quality within the two most frequent OSR varieties in our dataset. Finally, we assess the potential effect of insect pollination on oil content and FAs composition using an exclusion experiment to disentangle the contribution of pollination processes. Oilseed rape can be self- (Becker et al., 1992), wind- (Mesquida and Renard, 1982) and insect-pollinated (Bommarco et al., 2012). In each field, we used bags to prevent large pollinators, all pollinators or wind from having access to flowers. We show, to the best of our knowledge, the first evidence that honeybee improves the nutritional value of OSR oil independently of OSR cultivar by increasing the amount of unsaturated FAs and decreasing the amount of saturated and trans-saturated FAs.

Material and methods

Study site, experimental fields and landscape context

Experimentation was conducted between 2013 and 2016 in the LTSER "Zone Atelier Plaine & Val de Sèvre" (ZA-PVS, 450 km²), a study site located in the south of *Deux-Sèvres* district, central western France (Bretagnolle et al., 2018). Only winter OSR is cultivated in the LTSER, representing 8%-10% of the agricultural surface. Experiments were conducted directly on working farm fields, without requesting modifications to the farming practices. All selected fields were cultivated using conventional agriculture. Fields were picked out by random selection within 1-km² selected to represent density gradients of three environmental features: semi-natural habitats (hedges and forest fragments), meadows, and organically farmed fields. All these features are known to influence pollinators abundance (Kennedy et al., 2013) and were mapped onto the GIS database of the LTSER ZA-PVS (Bretagnolle et al., 2018). We used a moving window to select squares (see Fahrig et al., 2011). Within the selected squares, an OSR field was chosen if present (usually, there was only one OSR field). On average, OSR fields were at 357.4 m (65.4 m to 1147.3 m) distance from the nearest OSR neighbour. Field size ranged from 1 to 20.2 ha (mean 6.1 ha).

Study design

72 OSR farmers' fields were used for experimental studied (11/21/24/16 in 2013, 2014, 2015 and 2016, respectively). Information on practices (yield, plant cultivar, fertiliser and pesticides) were obtained by means of farmers' enquiries at the end of each cropping season.

In fields, six individual OSR plants were selected at two different positions: at edge of field (between 0 and 5m into field) and 20m in core field (see Perrot et al. *in review* for further details). On each individual plant, three (2013), two (2014) and four (2015-16) secondary branches were selected on which we implemented pollination exclusion treatments. For each individual plant, branches were

selected so as to be at the same flowering stage, and close (adjacent) to each other. Various treatments allowed for self-pollination (SF), wind-pollination (W), small-bodied (SP) and large-bodied (LP) insect pollinators. One of the branches was used as a control (N=372 branches in total), i.e. all its flowers were accessible to all pollination media (insects, wind and self-pollination: "SF+W+SP+LP"). A second branch was caged with a small mesh bag (mesh size=0.6 mm, N=260 branches), flowers could only be pollinated by self- or wind pollination ("SF+W"). In 2013, 2015 and 2016, a third branch was caged with a large mesh (mesh size=3mm, N=227 branches), thus allowing self-, wind and small-insects pollination ("SF+W+LP"). Finally, in 2015 and 2016 a fourth treatment was added, using an osmolux bag (Pantek, France, N=142 branches), allowing only gas exchange and thus excluding all types but self-pollination ("SF"). In 2013 only, each treatment was replicated for each plant (i.e. two controls, large and little mesh branches per plant), but not in other years. For all treatments, bags were installed before onset of flowering. Plants were visited weekly to adjust bags, i.e. bags were lifted upwards to cover new or future flowers leaving outside flowers that were faded. Bags were completely removed after the last flower had faded. All manipulations were made gently to avoid effect on seed development (Jacobs et al., 2009). We collected the branches five days before harvest by separating experimental (caged) and control branches from the rest of the plant and stored in individual paper bags.

Seed weight, oil extraction, identification and calculation of fatty acid

Once branches back to the laboratory, all bags were left 48 hours into a heat chamber at 60°C. Then for each treatment three seeds per branch and per treatment were selected, individually weighted, and ground together with a grinder mixed with 7ml of isopropanol:hexane. The resulting was evaporated at 40-50°C during one night. Oil extracted was weighted and the total oil content was expressed on the basis of the dry weight of the three seeds. Oil was then stored at -20°C with chloroform to FA analysis.

FA composition was analysed in 66 of the 72 fields (16-19-24-12 for 2013-16) by mixing, for each field, oil samples per treatment to reduce economic cost of the analysis. Gas chromatography was used to determine FA composition. Lipid was prepared for gas chromatography follow the method of Morrison and Smith (1964) for 3 mg of oil. Then, gas chromatography was realised on a Hewlett Packard Model 5890 chromatograph (Palo Alto, CA, USA) using a CPSIL-88 column (100m 9 0.25 mm i.d. film thickness 0.2 µm, Varian, Les Ulis France) equipped with a flame ionisation detector. Hydrogen was used as a carrier gas (inlet pressure, 210 kPA). FA was identified by comparison with commercial synthetic standards. The data were processed using the EZChrom Elit software (Agilent Technologies, Massy, France). FA relative percentage was expressed one the peak of a FA to the total peak of all FA.

Pollinator sampling

Wild bees and honeybees were sampled during OSR flowering by two different methods i.e; pan-trap and sweep net. 12 pan-traps in 2013-15 and 6 pan-traps in 2016 filled by water and soap were put into OSR fields and in neighbourhood field (maximum of 1.25 km) during 4 days (Perrot & al. in review) at two different position in 2013-2015 (field and core field) and only in core field in 2016 (Perrot & al. in review). Sweep net were only carried in OSR field and were only available in for 2015-2016. Sweep consists in transect at two different positions in 2015 (field and core field), and three positions in 2016 (a supplementary transect in core field) during 10 minutes (Perrot et al. in review). All pollinators catch were then identified at the laboratory (at genera or species level according to year (Perrot et al. in review). Wild bee abundance was found better estimated by pan-traps than honeybee by sweep net in this study sites (Perrot & al. in review) as found for Westphal *et al.* (2008). Honeybee abundance was estimated by the average of honeybee abundance catch by field

(averaged on the two or three transect per field). Wild bee was estimated by a hierarchical average procedure, starting with mean count per bowl colour and position in the field (core *vs*. edge), then averaging per position in field, and finally per field (in 2016, pan traps were settled twice for a same field, and were thus further averaged). For each focal field, this final average per genus was averaged with all other fields within a radius of 1250m (Perrot et al. in review).

407 honeybees were caught by sweep net for 2015-2016 (average 4.3 bees per transect, range = 0-52) with in averaged 4.1 honeybees by field (range = 0-28), thus 12473 wild bees were caught by pan-traps over the four years (average 5.68 wild bee per pan trap, range: 0-117), and strongly varied between fields from 0.3 to 21.7 individuals per field (see Perrot & al. in review).

Statistical analyses

We first examined the relationship between pollinators and seed mass, oil content and FAs composition in control branches. Seed mass was averaged per branch. Oil content and FAs composition were averaged per branch in 2013. We studied FA composition by investigating the variation in the proportion of saturated, trans-saturated and unsaturated FAs (hereafter FA groups), the ω3-ω6 ratio as well as the proportion of each FAs (hereafter FA profile). We used linear model for the ω6-ω3 ratio and linear mixed models (LMM) for seed mass and oil content with field ID as random factor to account for repeated measures per field. We also included either wild bee or honeybee abundance, and year (4 or 2 levels according to pollinators ID), plant position (2 levels) and their interactions with pollinators (either wild bee or honeybee abundance). Plant position was not included when analysing FA composition metrics, which were estimated at the field level (see methods). We applied a Redundandy Analysis (RDA,Ter Braak 1986) to estimate the total variation in FA composition (for both FA groups and FA profile) which can be explained by pollinator abundance. We included in the models and in the RDA farming practices to account for confounding effects on seed mass and the quantity and quality of oil of OSR. We included the effect of four main practices expected to affect the effect of insect pollination on OSR yield and quantity and quality of oil, namely N and P inputs, and the treatment frequency intensity (TFI) of insecticides and herbicides. Details on farming practices are presented in Table S1.

A positive relationship between pollinator abundance and quantity and quality of oil can suggest a benefit from insect pollination. However, we cannot discard a confounding effect due to a cultivar effect since quantity and quality of oil and nectar rewards amount vary among varieties. We therefore investigated the effect of plant cultivar ID or cultivar type (hybrid and open cultivar) on honeybee abundance (i.e. the main pollinator affecting OSR nutritional value from the previous analysis, see Result section) and seed nutritional value. We test the null hypothesis that plant cultivar ID (or cultivar type) has no significant effect on honeybee abundance or nutritional value of oilseed rape by computing the sampling distribution for *F stat* (explained variance on unexplained variance) using a permutation test. 20000 samples were generated and *p-values* were computed (Higgins, 2004). To disentangle between an attractive effect and the benefit of insect pollination, we restrained the dataset to the two most common varieties, Dk Exstorm and Dk Expertise, present in respectively 12 and 11 fields. For each cultivar, we built LMs to explain the variation of each FA groups amount with honeybee abundance as explanatory variables.

Finally, we assessed the role of insect pollination on seed oil content and FAs composition using an exclusion experiment to disentangle the contribution of pollination processes on OSR quality. We built LMMs including honeybee abundance, year and treatment (4 levels) and their interaction with honeybee abundance. We also included the farming practices. A post-hoc test was then applied to evaluate the differences between treatment modalities. We also applied a RDA to estimate the total variation in FA groups and FA profile explained by honeybee abundance, farming practices and the exclusion treatments. We also included year and its interaction with honeybee abundance.

All analyses were performed using the software R (R Core team, 2015). In models, all non-significant interactions terms were removed from final model. Wild bee and honeybee abundances were *log(x+1)* transformed for linear mixed model to ensure for normal distribution and homoscedasticity. We used the "stats" package for linear modelling, "nlme" package for linear mixed model (Pinheiro et al., 2016) and "lsmeans" package associated post-hoc tests (Lenth, 2016). RDAs were realised with "vegan" package (Oksanen et al., 2013) and "jmuOutlier" package was used for permutation test (Higgins, 2004).

Results

Effect of pollinators on oilseed rape seeds nutritional value

Over the four years, control seeds weighted in average 4.5 mg (range: 1.6-.7.9) and contained 2.2 mg lipids (0.5-4.2) which represented 48 % (15.8-98%) of seed unit weight. We observed a high inter-field and intra-field variation in seed mass and seed oil content (Appendix S2). Open-pollinated OSR seeds were mainly composed of 7.7% saturated FAs and 90.6% of unsaturated FAs among which 63.7% monounsaturated FAs and 26.9% polyunsaturated FAs (Fig 1. Table 1). The levels of trans-saturated FAs was very low, i.e. 1.7 % which corresponds to the amount of trans-oleic acid (Fig 1). The major monounsaturated FAs present was oleic acid (C18:1) which was particularly high (58.4%). Linoleic acid was the most abundant polyunsaturated FAs (18.4%) and alpha-linolenic acid, the second most abundance i.e. 8.4 % (Fig 1. Table 1). Eruric acid was rarely found (0.18%). The ω6-ω3 ratio was close to 2.2 (Table 1).

Using the pan trap data, which mainly account for the wild bee component of the bee assemblage, we did not find any effect of (wild) bee on seed unit weight, seed oil content, or FA composition (all $p > 0.07$, ESM 3, Table S3). Similarly, using sweep net data (available for 2015-2016), no effects of honeybee and farming practices were found on seed mass and oil content except in 2016 where a significant effect of honeybee abundance was observed on oil content (Fig. 2 A-B, Table 2). However when FA composition was split down into groups (saturated unsaturated and trans-saturated FAs), we found that FA composition was strongly determined by honeybee abundance, N and P inputs and year. UFA decreased significantly with the first RDA axis (increasing herbicide and insecticide TFI, decreasing honeybee abundance and P-input, Table 2, Fig 2.C). The opposite pattern was observed for saturated FAs and trans-saturated FAs (Table 2, Fig 2.C). Nonetheless, honeybee abundance and farming practices (except herbicide treatment index) did not significantly modified FA profile (i.e. FA composition described by the percentage of each FAs; Table 2). Finally, no effect of honeybee or farming practices was found on the ratio of w6 on w3 (LM, all $p > 0.6$).

Effect of OSR cultivar

OSR fields belonged to 19 different varieties, mainly restored hybrid (86.7%) and conventional (14.3%), including five fields cultivated with more than one cultivar ID. The permutation test showed significant differences in seed mass and seed oil content among the 19 varieties (Table 3) but only a significant difference in seed unit weight when varieties were grouped in cultivar types (Table 3). Open pollinated cultivars had generally higher seed unit weight (4.9 mg +/- SD) than hybrids (4.45 mg +/-). No significant differences in FA groups, in the main FAs or in ω6-ω3 ratio were observed among cultivar ID or cultivar type (Table 3). A permutation test was also used to test the hypothesis that crop cultivar (or cultivar type) affected honeybee abundance (Fig. 3). No significant differences in honeybee abundance was observed among the 12 varieties (i.e. only data for 2015 and 2016 were

used; Table 3), suggesting that an absence in difference in pollinator attractiveness among varieties In addition, we found that similar effect of honeybee on oil content and unsaturated FAs within the two main cultivars in our dataset, although these relationships were not significant (Fig. 3.B).

Effect of pollinator exclusion treatments

We finally assessed the role of insect pollination on seed oil content and FAs composition using an exclusion experiment. Oil content for 2015-2016 was on average lower in seeds when pollinators were partially (45.1+/-0.87 in large- mesh treatments) or totally excluded (44.6%+/-0.93 and 45% +/-0.92 in small-mesh and osmolux treatments respectively) than in insect-pollinated seeds (48%+/-0.83) (Table S4.1). Significant differences were, however, only observed between control and treatments (Table S4.1), suggesting a positive effect of honeybee pollination on OSR oil content. Exclusion treatments had however no effect on seed mass (Table 2), which results in an overall significantly higher seed lipid mass in open pollinated seeds (2.1mg +/- 0.062 in control seeds *versus* 1.93mg +/- 0.065, 1.97mg +/- 0.07, and 2.0).

Adding the experimental treatment in the RDA to investigate the effect of honeybee abundance, farming practices and year on FA groups, did not modify the effects of these variables on the proportion of each FA groups in OSR seeds (Table 2). Surprisingly, although, we found significant differences in oil content, we did not find any effect of the pollinator exclusion treatments on the amount of each FA groups in OSR seeds. Conversely, FA profile was strongly and significantly influenced by the experimental treatments (Table 2 and Fig. 3). The main differences were observed when both insect- and wind pollination (osmolux treatment) were excluded. OSR seeds in osmolux treatment showed higher amount of linoleic and alpha-linoleic FAs and lower amount of oleic FA than insect- and wind- pollinated seeds (Fig. 3, Table S4.2). The first ordination RDA axis (horizontal) was negatively correlated to insecticide and positively correlated with honeybee abundance. The amount of linoleic and alpha-linoleic acids were found to be strongly positively influenced by honeybee abundance and negatively by insecticide applications, although no significant relationships were found (Appendix S4). Opposite pattern was observed for the amount of oleic, trans-oleic and stearic acids, which were more abundant in OSR in fields with lower honey abundance and high TFI insecticides, although the latter has no significant effect (Fig. 3). The RDA analysis also revealed a significant effect of herbicides on FA profile.

Discussion

We found insect pollination, which was mainly conducted by honey bees, to play a key role for OSR quality. Seeds pollinated by insects showed higher oil content, supporting previous studies that showed higher oil content in the insect-pollinated treatment (Bartomeus et al., 2014; Bommarco et al., 2012; Marini et al., 2015). Seed mass was unrelated to honeybee abundance. This is in agreement with a previous study in the same study site, which revealed a positive effect of honey on yield at field scale, through improved fruiting success and plant seed mass after adjusting for plant biomass (Perrot et al. in review). The nutritional value of OSR is attributed to their FA composition, which was affected by both honeybee gradient and the pollination exclusion treatment. Honeybee increased unsaturated FAs and decreased trans-saturated and saturated FA. In addition, self-pollinated seeds had lower amount of oleic acid (C18:1) and higher amount of in linoleic (C18:2) and alpha-linolenic acid (C18:3). The results, to the best of our knowledge, are the first evidence that honeybee improves the nutritional value of OSR oil independently of OSR cultivar.

Our results showed OSR quality to be almost responsive to honeybees. This is consistent with earlier findings, where honeybee were the most common pollinators of OSR (Bartomeus et al., 2014; Bommarco et al., 2012). Honeybee have already been shown to be effective crop pollinators affecting both OSR yield and oil content (Oz et al., 2008). Contrary to our expectation, honeybee abundance did not varied between OSR cultivars ID. OSR varieties show offering heterogeneous nectar rewards (Ouvrard et al., 2017), hence they may differentially attract pollinators. The absence of relationship between honeybee abundance and OSR cultivar may suggest that nectar resources provided by this set of cultivars in the selected farmers' fields may slightly vary. External factors can also affect the presence of honeybees in OSR fields such as the distance of hives to fields (not available in our study) (Cunningham et al., 2016), the presence of other flowering resources (Bretagnolle and Gaba, 2015) or the quantity of OSR fields in the surrounding landscape (i.e. dilution effect, (Holzschuh et al., 2016). Annual variation also affects honey abundance (Gordo and Sanz, 2006). Our results revealed strong inter-annual variation in the effect of honey abundance on oil content and FAs composition. We also found inter-annual variation in FAs composition which could be explained by annual variation in water availability (Champolivier and Merrien, 1996) or in temperature (Baux et al., 2013), both known to modify OSR quality.

Honeybee pollination modified FAs composition in a way that enhance OSR quality. High nutritional value OSR oils are defined by a high percentage of unsaturated FAs. In open pollinated seeds (control), higher amount of unsaturated FAs and oil content, and lower amount of of saturated and trans-saturated FAs were related to higher honeybee abundance. Honeybee pollination may affect plant resource allocation. On a per carbon basis, unsaturated FAs cost more to produce and yield less energy when oxidized than saturated FAs (Linder, 2000), but unsaturated FAs rich seeds may have a competitive advantage by being able to germinate earlier and grow more rapidly at low temperatures (Linder, 2000). Honeybee has been shown to reduce the number of flowers produced by the canola plant (Sabbahi et al., 2006). Consequently, plants pollinated by honeybees may invest less in producing flowers, which would allow allocating resourcing in the production of unsaturated FAs. OSR may also benefit from cross-pollination induced by honeybees (Brittain et al., 2014; Negussie et al., 2015). Cross-pollination may indeed support the increase of OSR quality. In the exclusion experiment, insect- and wind- pollinated seeds had higher amount of oleic acid and lower amount of linoleic acid then self-pollinated seeds. Such pattern was previously shown in almonds (Brittain et al., 2014) or in *Jatropha curcas* L (Negussie et al., 2015). However, higher amount of polyunsaturated FAS such as linoleic acid in oil may contribute to chronic diseases in developed countries (Jandacek, 2017) and is associated with lower combustion quality when oil is used as biofuel (Ramos et al., 2009).

Our study shows that OSR nutritional value can be improved by increasing honeybee abundance in OSR fields. This could in turn economically benefit to farmers (Bommarco et al., 2012). In the very same farmers' fields than the ones studied here, Perrot et al. (in revision) has shown that honeybees increases OSR crop production at the field scale by 800 kg/ha, which represents an increase of 384 kg/ha of OSR oil. In average, seed pollinated by honeybee increase 2.9% (range: 2.07-3.71) percentage unit of additional oil content. This would represent an increase of price of 4.4% (3.1-5.6) according to Bommarco et al. 2012.

Oil content and FAs composition of OSR seeds found here were similar than the ones described in literature (Table 1). Oil content varied significantly among OSR cultivars, but not between the two OSR cultivar types i.e. hybrid and open cultivars. This is in agreement with previous findings showing similar oil content in hybrid and open cultivars (Han-zhong et al., 2009; Marini et al., 2015). Contrary to Liersch et al. (2013), we found no modification of FAs composition between varieties ID or between cultivar types. Since the amount of differences between cultivars found in Liersch et al. (2013) was pretty small (less than 1.24%), the unbalanced representation of varieties ID

in our dataset may not prevent the detection of any differences in FAs composition among cultivars (due to a lack of statistical power). Several management factors influence OSR oil content. Increasing rate of nitrogen(N)-fertilizer results can result in a decrease in oil content (Rathke et al., 2005) or have no effect (Dreccer et al., 2000) while phosphorus(P)-fertilizer positively affect it (Lickfett et al., 1999). Similarly to Dreccer et al. (2000), the effect of N-supply on the oil content of winter oilseed rape was not significant. However, N-supply increased the amount of linoleic acid as previously reported by (Rathke et al., 2006)) The absence of effect of phosphorus on oil content in our study is most probably related to the low quantity applied as well as soil type in the selected fields (in average 53.15 kg/ha in farmers' fields compared to 74 kg/ha in experimental pots in Lickfett et al. 1999). We also found a significant effect of herbicide on FA profile. Herbicide treatments may directly affect the synthesis of FAs as previously revealed in canola (Codgill 2013). More investigations are therefore needed to understand mechanisms underlying the effect of these farming practices on FAs composition.

Conclusion

Our study shows that only estimated the importance of pollinators on their contribution on yield could grandly underestimate their total contribution to crop production, hence benefits for food production and farmers. Maintaining pollination service may therefore be a way to balance biodiversity conservation and food production in agricultural landscapes. Incentive monetary values could be proposed by agricultural cooperative to farmers, which promotes honeybee in their fields as the harvest which finally received has a better quality. Further investigations need to be conducted to find explanations for the increase of unsaturated FAs and the decrease of saturated and trans-saturated FAs with honeybee abundance.

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Table 1. Fatty acids composition of oilseed rape seeds collected in the 72 farmers' fields on plants with or without access to insect-pollination. Results are the mean value ± standard error for the four treatments in the exclusion experiment. Mean, minimum and maximum values of FAs groups and main FAs from Adamska & al. 2004, Jahreis & al. 2011, Lierch & al. 2014, Orsavova & al. 2015 are also given for comparison.

	Control	Large mesh	Small mesh	Osmolux	Litterature
Saturated FAs	7.71 (± 0.1)	8.04 (± 0.12)	8.22 (± 0.14)	8.02 (± 0.15)	10.7
Palmitic	4.53 (± 0.04)	4.75 (± 0.06)	4.78 (± 0.06)	4.67 (± 0.08)	4.65 (4.48-4.86)
Stearic	2.15 (± 0.08)	2.12 (± 0.11)	2.29 (± 0.10)	2.24 (± 0.14)	1.64 (1.6-1.7)
Trans-saturated FAs	1.69 (± 0.12)	1.50 (± 0.14)	1.78 (± 0.13)	1.87 (± 0.16)	0.14
Unsaturated FAs	90.59 (± 0.20)	90.46 (± 0.23)	89.99 (± 0.23)	90.10 (± 0.27)	93.1 (92.46-93.7)
Monounsaturated FAs	63.69 (± 0.27)	62.72 (± 0.41)	62.73 (± 0.3)	61.09 (± 0.59)	66 (60.9-71.1)
Oleic acid (C18 :1)	58.43 (± 0.29)	57.01 (± 0.51)	57.20 (± 0.36)	55.96 (± 0.61)	62.27 (60.9-63.3)
Polyunsaturated FAs	26.90 (± 0.31)	27.75 (± 0.44)	27.26 (± 0.35)	29.01 (± 0.63)	28.53 (20.9-32)
Linoleic acid (C18:2) …	18.44 (± 0.23)	19.28 (± 0.34)	18.88 (± 0.25)	20.01 (± 0.46)	20.54 (19.6-20.94)
Alpha-linoleic acid (C18:3)	8.36 (± 0.11)	8.36 (± 0.16)	8.27 (± 0.13)	8.89 (± 0.2)	7.96 (1.2-10,67)
ω6- ω3 ratio	2.23 (± 0.02)	2.34 (±0.05)	2.31 (± 0.03)	2.27 (± 0.04)	2

Table 2. Output of linear mixed models and RDA investigating the effect of honeybee abundance and farming practices on seed mass and oil content (LMM) and FAs group (i.e. unsaturated, trans saturated and saturated FAs) and FAs profile using (A) control seeds or (B) all seeds (control and treatment seeds). R^2m and R^2c refer to marginal R^2 and conditional R^2. (-) indicates that the variable was not included in the model.

	Seed mass (mg)		Oil content (%)		FAs group		FAs Profile	
	Linear mixed models				RDA			
A	R^2 m	R^2 c	R^2 m	R^2 c	R^2		R^2	
	0.349	0.425	0.157	0.360	0.55		0.55	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Honeybee abundance	0.4	0.53	1.81	0.19	**5.8**	**0.02**	1.28	0.26
Plant position	0.17	0.68	0.001	0.98	**-**	**-**	**-**	**-**
N-input	0.7	0.41	0.57	0.46	**7.28**	**0.01**	1.33	0.25
P-input	0.17	0.68	1.61	0.21	**8.71**	**0.005**	1.67	0.19
Herbicide	3.29	0.09	1	0.33	2.05	0.16	**3.46**	**0.041**
Insecticide	0.14	0.71	0.05	0.82	0.81	0.38	1.27	0.27
Year	**44.21**	**< 0.001**	0.84	0.37	**6.25**	**0.016**	**18.25**	**< 0.001**
Honeybee abundance x Year	-	-	**6.45**	**0.02**	-	-	-	-
B	R^2 m	R^2 c	R^2 m	R^2 c	R^2		R^2	
	0.296	0.445	0.154	0.360	0.48		0.49	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Honeybee abundance	0.04	0.85	3.96	0.06	**14.59**	**< 0.001**	**3.83**	**0.04**
Exclusion treatment	1.35	0.26	**9.14**	**< 0.001**	1	0.4	**3.4**	**0.01**
Plant position	**2.11**	**0.15**	0.22	0.64			-	-
N-Input	0.65	0.43	1.56	0.22	**10.54**	**0.001**	1.82	0.16
P-Input	0.45	0.51	1.51	0.23	**14.6**	**< 0.001**	1.98	0.14
Herbicide	3.3	0.08	1.29	0.26	**5.95**	**0.013**	**6.38**	**0.007**
Insecticide	0.28	0.6	0.13	0.72	0.25	0.66	1.28	0.25
Year	**34.04**	**< 0.001**	2.02	0.17	**32.95**	**< 0.001**	**74.64**	**< 0.001**
Honeybee abundance x Year	-	-	**9.36**	**0.004**	-	-	-	-

Table 3. Summary of permutation test of effect plant cultivar ID and plant cultivar type on OSR seed quality and honeybee abundance. F and P values were given thus the number of fields for each test.

	Cultivar ID		Cultivar type (Open versus hybrid)		Field
	F	P	F	P	N
Seed mass	**2.68**	**<0.001**	**7.24**	**0.008**	72
Lipid mass	**2.35**	**0.001**	2.71	0.1	
Oil content	**2.27**	**0.004**	0.18	0.66	
Saturated FAs	0.63	0.84	0.19	0.67	66
Trans-saturated FAs	1.15	0.33	0.04	0.85	
Unsaturated FAs	0.89	0.58	0.12	0.73	
Monounsaturated FAs	0.93	0.57	2.78	0.1	
Oleic acid (C18 :1)	1.01	0.47	3.76	0.06	
Polyunsaturated FAs	0.78	0.72	1.55	0.22	
Linoleic acid (C18:2)	0.5	0.93	0.74	0.4	
Alpha-linoleic acid (C18:3)	1.87	0.06	3.1	0.09	
ω6-ω3 ratio	1.64	0.1	1.78	0.19	
Honeybee abundance	0.57	0.63	0.19	0.73	40

Figure 1. FAs composition of control OSR seeds.

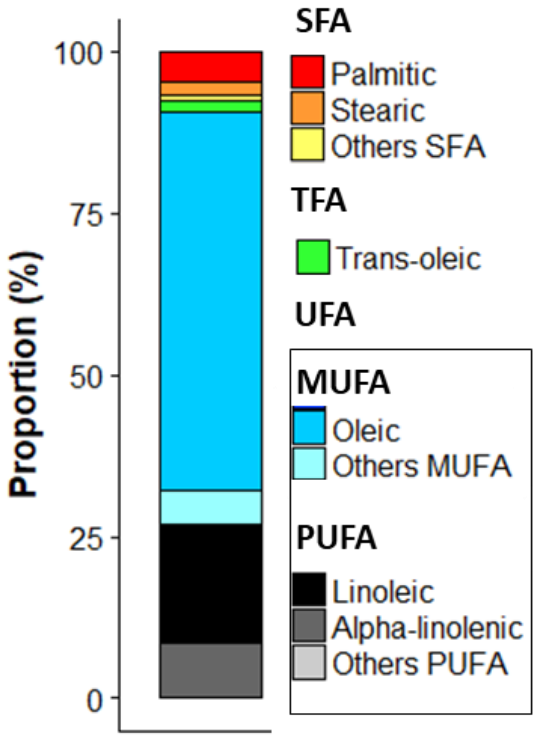


Figure 2. Relationship between honeybee abundance and (a) seed mass or (b) oil content. Colored lines represent linear relationships as predicted by linear mixed models for each year (blue for 2015 and purple for 2016). (c) Redundancy analysis (RDA) ordination diagram (triplot) showing explanatory variables (black-colour arrows) and FAs group (grey solid arrows, saturated FAs (SFA), trans-saturated FAs (TFA), unsaturated FAs (UFA) for 2015 (blue) and 2016 (purple). Diamond dots represented centroids of data by year. Smaller angles of the arrows indicate stronger correlation between the individual variables.

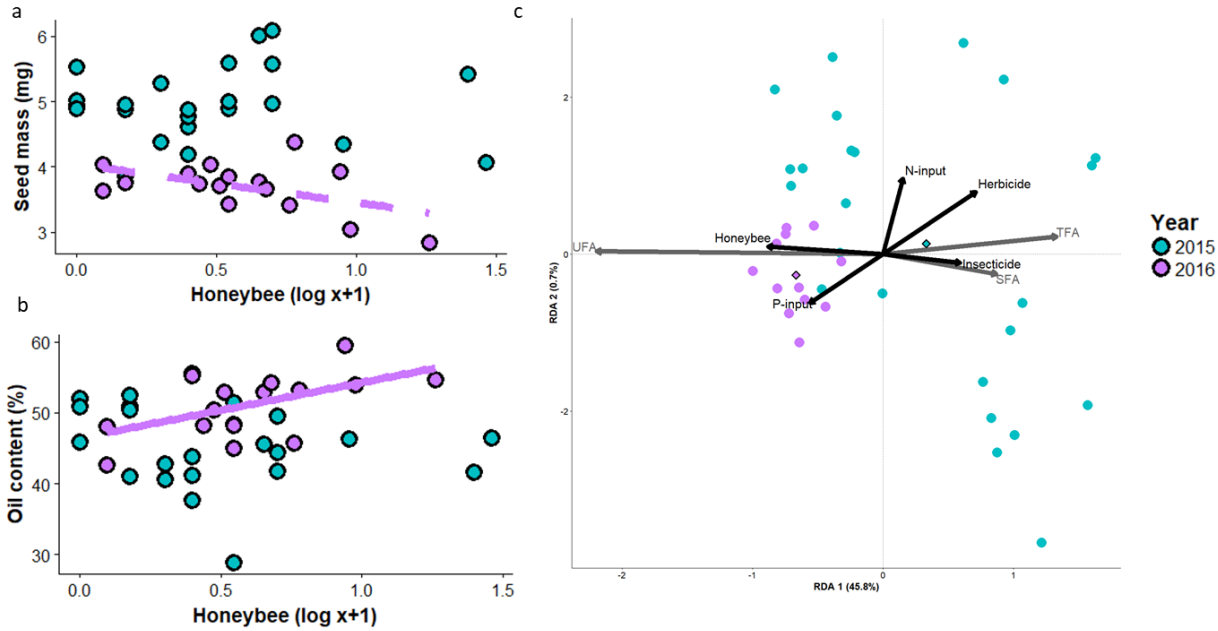


Figure 3. (A.a) Attractive effect of plant cultivar on honeybee abundance. Boxes show upper and lower quartiles, horizontal line is the median. B. (a-c) Linear models between honey abundance and saturated FAs (SFA), trans-saturated FAs (TFA), unsaturated FAs (UFA) in the control seeds in the 34 OSR fields. The p-value of linear relation is given in graph (d-f) Relationships between honey abundance and saturated FAs, trans-saturated FAs, unsaturated FAs in the control seeds of DK Expertise and DK Exstorm cultivars. Cultivar ID and linear relation are indicated by colour (blue for 2015 and red for 2016). The p-value of the linear relationship is given for each cultivar in graph (p_{exp}= p-value for DK Expertise and p_{exs} = p-value for DK Exstorm).

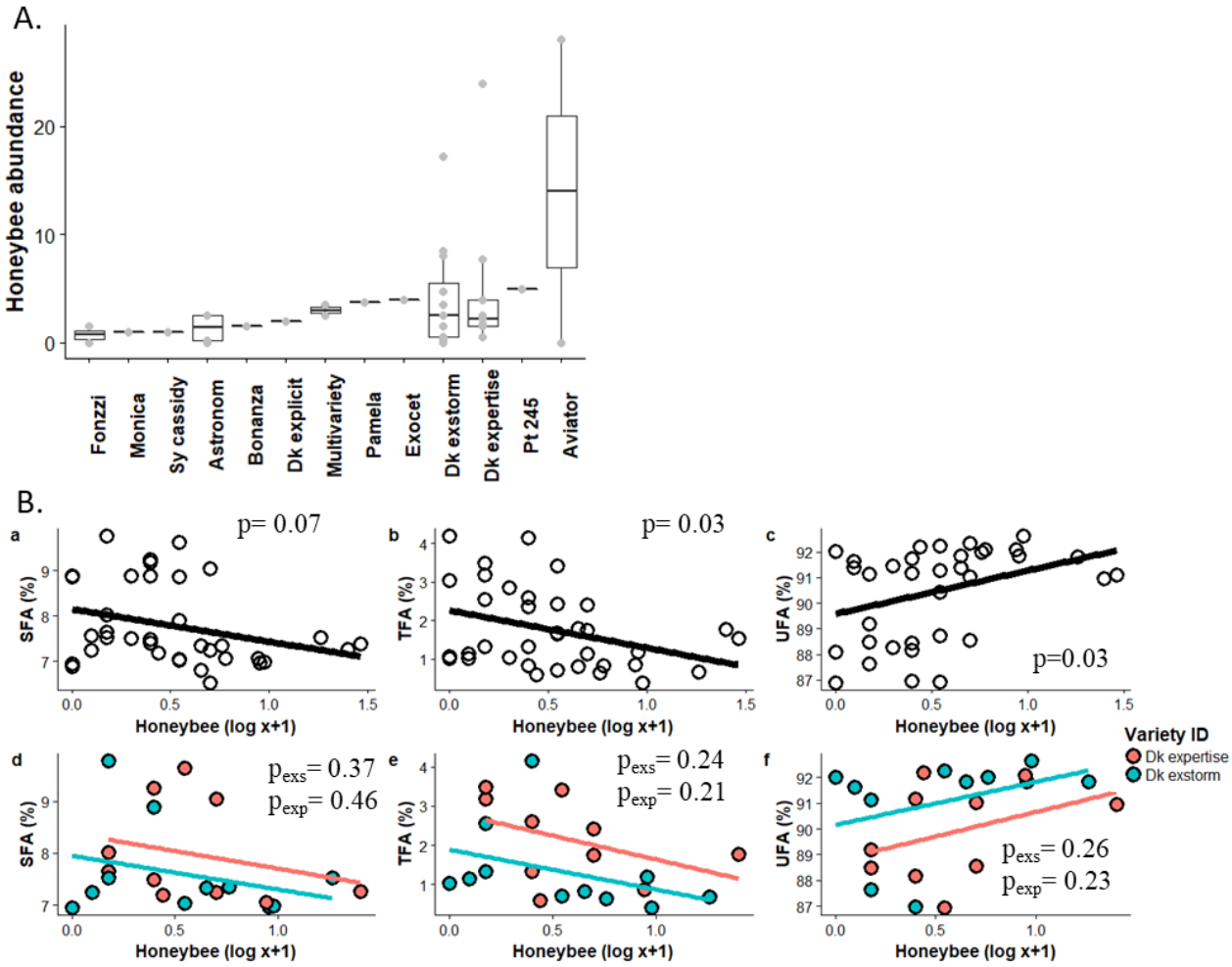
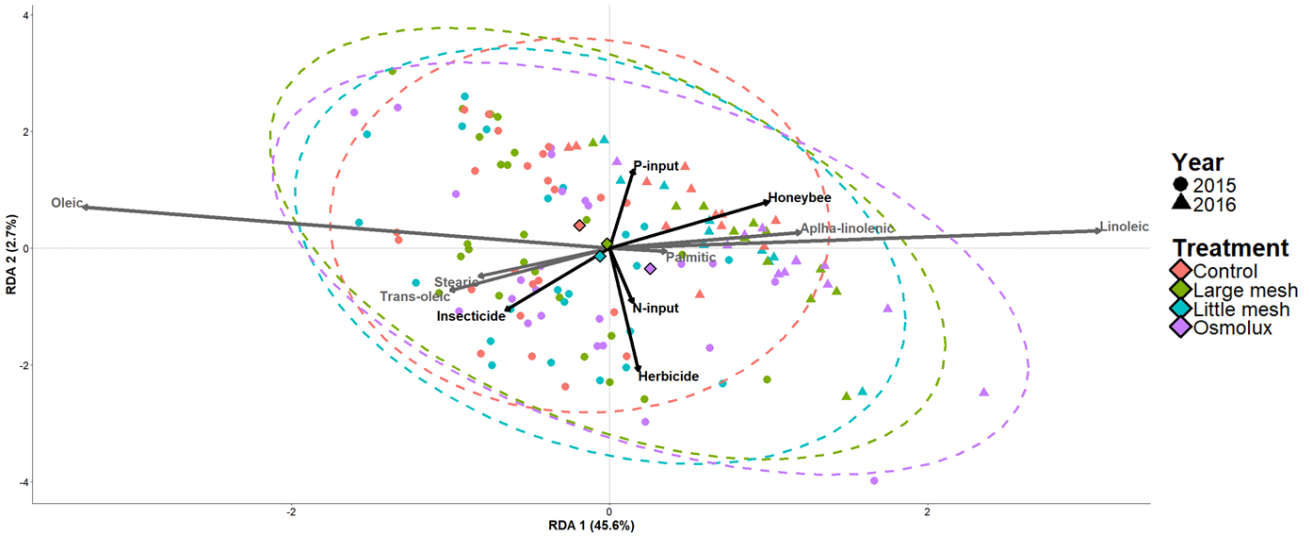


Figure 4: Redundancy analysis (RDA) ordination diagram (triplot) showing explanatory variables (black-colour arrows) and FAs profile (grey solid arrows, only the more important FAs were represented) for 2015 (round dots) and 2016 (triangles) and for the different treatments (red: control, green: large.mesh, blue: small mesh and purple: osmolux). Confidence ellipse (95%) was also drawn for each treatment and diamond dots represented centroids of data for each treatment. Smaller angles of the arrows indicate stronger correlation between the individual variables.



Appendix

Appendix S1. Summary of farming practices in the 72 farmers' fields

Table S1. Summary of the main farming practices expected to affect the influence of insect-pollination on oilseed rape (OSR) quality.

	Mean	Minimum	Maximum
Nitrogen (kg.ha^{-1})	173.9	97.5	302.2
Phosphorus (kg.ha^{-1})	53.15	0	145
Treatment Frequency Index of insecticides	2.3	0	7.2
Treatment Frequency Index of herbicides	1.81	0	5.79

Appendix S2. Analyse of variance of seed mass and oil content

We examine the intra-field and intra-individual variation in seed unit weight and the intra-field in oil content in the control seeds. Seed mass was estimated on three seeds per control branch on each of the six OSR plants per field. Seed oil content was estimated at the plant scale because of measurement constraints i.e. the amount of oil in one seed is not enough to estimate oil content (minimum = 3 seeds). We built a linear model (LM) with field ID and plant ID to assess the part of variation in seed unit weight due to inter-field and inter-individual variation. Residual variance of this model represents the intra individual variation of seed mass. The intra-field variation in oil content was assessed using a LM with field ID as explanatory variable which represents the inter field variation. Residual variance of this model represents the intra field variation of seed mass. The variance explained by each variable is defined as the ratio of the sum of its squares to the total sum of squares.

Seed mass was very stable into a same plant (only 14.4% of variance explained). Inter-field variation of seed mass was similar to intra-field variation (respectively 38% and 47.5%). For oil content, we also found inter-field variation in seed oil content since field ID explained 46.6% of variance, however this was quite similar to the intra-field variance (53.3%).

Appendix 3. Effect of wild bee abundance on seed quality

Table S3 presents the output of the linear mixed models and redundancy analyses (RDA) investigating the effect of wild bee abundance (estimated by the pan trap method) on OSR quality for complete dataset (2013-2016, Table S3A) and dataset restricted to fields in which the sweep net was also applied. Wild bee abundance had no significant effect on OSR oil content or FA composition whatever the dataset used.

Table S3. Output of linear mixed models and RDA investigating the effect of wild bee abundance and farming practices on seed unit weight and oil content (LMM) and FA group (i.e. UFA, TFA, SFA) and FA profile using (A) the complete dataset or (B) the dataset restricted to the fields in which the sweep net was also applied. R^2m and R^2c refer to marginal R^2 and conditional R^2. (-) indicates that the variable was not included in the model.

A	Seed mass (mg)		Oil content (%)		FAs group		FA Profile	
	Linear mixed models				RDA			
	R^2 m	R^2 c	R^2 m	R^2 c	R^2		R^2	
	0.232	0.330	0.071	0.375	0.41		0.38	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Wildbee	0.248	0.620	0.452	0.504	0.909	0.346	1.265	0.265
Plant position	0.013	0.908	0.137	0.712			-	-
N-input	1.643	0.205	0.323	0.572	**3.945**	**0.048**	0.734	0.491
P-input	0.289	0.593	0.268	0.607	**4.238**	**0.040**	0.699	0.511
Herbicide	0.173	0.679	1.710	0.196	0.674	0.423	0.951	0.374
Insecticide	0.020	0.889	1.645	0.204	0.694	0.417	2.048	0.118
Year	**19.429**	**< 0.001**	2.252	0.091	**7.736**	**< 0.001**	**6.691**	**< 0.001**
B	Seed mass (mg)		Oil content (%)		FAs group		FA Profile	
	Linear mixed models				RDA			
	R^2 m	R^2 c	R^2 m	R^2 c	R^2		R^2	
	0.369	0.435	0.113	0.366	0.54		58.7	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Wildbee	0.039	0.845	1.172	0.287	1.202	0.283	2.722	0.076
Plant position	2.977	0.086	0.001	0.981			-	-
Year	**49.314**	**0.000**	**6.226**	**0.018**	**6.367**	**0.015**	**21.649**	**<0.000**
N-input	0.167	0.686	0.019	0.892	**8.181**	**0.006**	1.861	0.149
P-input	0.259	0.614	2.316	0.138	**9.354**	**0.003**	2.212	0.109
Herbicide	**5.957**	**0.020**	0.470	0.498	3.077	0.084	**5.337**	**0.011**
Insecticide	0.056	0.815	0.297	0.590	1.515	0.222	0.854	0.407
Year	**49.314**	**0.000**	**6.226**	**0.018**	**6.367**	**0.015**	**21.649**	**<0.000**
Wildbee *x* Position	**3.980**	**0.048**	-	-	-	-	-	-

Appendix S4. **Effect of the exclusion treatments on seed quality**

We assessed the role of insect pollination on seed oil content using an exclusion experiment to disentangle the contribution of pollination processes on OSR quality. We built LMMs including honeybee abundance, year, treatment (4 levels), N and P inputs, IFT insecticides and herbicides. Field ID was used as random factor. A tukey post-hoc test was then applied to evaluate the differences between treatment modalities. We found significant differences in seed oil content between control on one hand and the treatments on the other hand. Conversely, no significant differences were found between exclusion treatments. These results suggest a positive effect of the largest pollinator, i.e. honey bees, on the amount of oil in OSR seeds.

Table S4.1 Summary of post hoc test.

	Oil content (%)		
Difference	Estimate	t ratio	P
Control - Large mesh	**2.890**	**3.995**	**< 0.001**
Control - Small mesh	**3.370**	**4.244**	**< 0.001**
Control - Osmolux	**3.047**	**3.922**	**0.001**
Large mesh - Small mesh	0.480	0.580	0.938
Large mesh - Osmolux	0.157	0.193	0.997
Small mesh - Osmolux	-0.324	-0.371	0.983

A linear mixed model was then realized to understand the effect of honeybee abundance on the three main FAs (oleic, linoleic and alpha-linolenic acid). Honeybee abundance, the main fertilizers (nitrogen, phosphorus) and pesticides (TFI Herbicide, TFI Insecticide), and year were put as explanatory variable. We also included treatment and its interaction with honeybee abundance and removed if not significant. Post-hoc_tests were performed to identify which treatment modality(ies) significantly affect the percentage of the three main FAs.

No significant effect of honeybee abundance was found on the three main FAs (Table S4.2,Fig S4). Seeds in osmolux treatment which were only self-pollinated showed significantly lower amount of oleic acid and higher amount of linoleic and alpha-linolenic acid than control, large mesh and small mesh seeds.

Table S4.2. Output of linear mixed models on the effect of honeybee abundance on the three main FAs (oleic, linoleic and alpha-linolenic acids), accounting for the main fertilizers (nitrogen, phosphorus) and pesticides (Herbicide, Insecticide), year as well as treatment.

	Oleic acid		Linoleic acid		Alpha-linolenic acid	
	F	P	F	P	F	P
Honeybee abundance	0.842	0.367	3.963	0.056	0.467	0.500
Treatment	**8.262**	**< 0.001**	**6.729**	**< 0.001**	**8.810**	**< 0.001**
Year	**20.874**	**< 0.001**	**53.611**	**< 0.001**	**27.594**	**< 0.001**
N-input	3.153	0.086	0.759	0.391	0.000	0.994
P-input	0.102	0.751	0.422	0.521	0.059	0.810
Herbicide	0.646	0.428	1.081	0.307	0.016	0.900
Insecticide	**4.217**	**0.049**	1.757	0.195	0.299	0.589

Table S4.3. Summmary of post-hoc test of treatment on the three main FAs (oleic, linoleic and alpha-linolenic acids)

	Oleic acid			Linoleic acid			Alpha-linolenic acid		
	Estimate	t ratio	P	Estimate	t ratio	P	Estimate	t ratio	P
Control - Large mesh	0.834	2.068	0.171	-0.416	-1.658	0.351	0.018	0.125	0.999
Control - Small mesh	0.971	2.362	0.091	-0.431	-1.688	0.335	0.141	0.970	0.767
Control - Osmolux	**1.999**	**4.955**	**< 0.001**	**-1.111**	**-4.431**	**< 0.001**	**-0.537**	**-3.765**	**0.002**
Large mesh - Small mesh	0.136	0.331	0.987	-0.015	-0.060	1.000	0.123	0.848	0.831
Large mesh - Osmolux	**1.165**	**2.887**	**0.024**	**-0.695**	**-2.773**	**0.033**	**-0.555**	**-3.889**	**< 0.001**
Small mesh - Osmolux	1.029	2.503	0.065	**-0.680**	**-2.663**	**0.044**	**-0.678**	**-4.667**	**< 0.001**

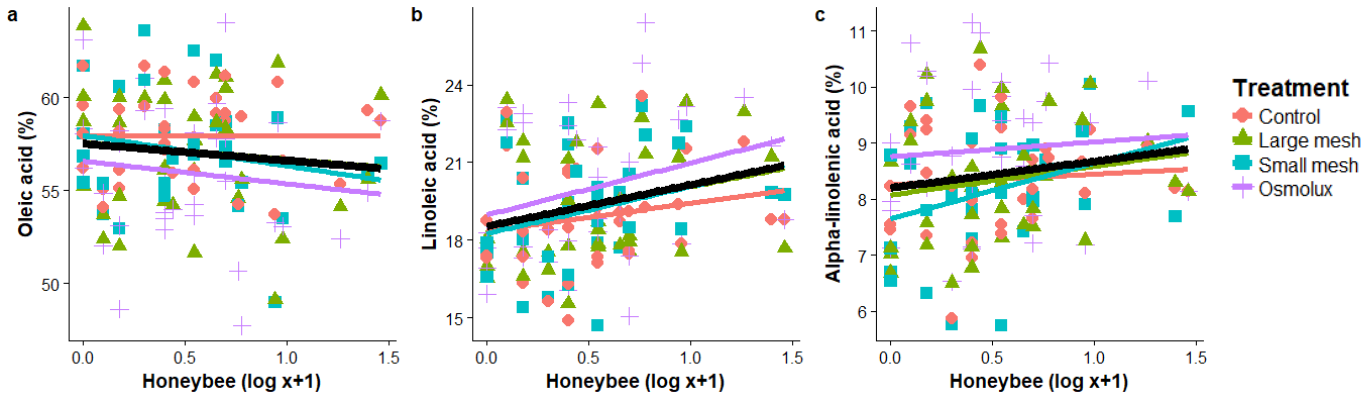


Fig S4. Effect of honeybee abundance on the three main FA (oleic, linoleic and alpha-linolenic acid) for each treatment (red and round for control, green and triangle dot for large mesh, blue and square dot for small mesh and purple and cross dot for osmolux). Each line represents the linear relation colored by treatment. The black line represents the linear model averaged for the four treatments.

Discussion générale

L'objectif principal de cette thèse a été de quantifier les bénéfices apportés par les pollinisateurs dans la production de colza (Chapitre I, III, IV) et de tournesol (Chapitre II) en condition de plein champs, directement dans les cultures des agriculteurs. Les bénéfices de la pollinisation ont été mesurés à deux échelles (parcelle et plante) avec différentes méthodologies (gradients de pollinisateurs et pose de filet). Ces études ont aussi permis d'identifier les traits à l'échelle de la plante, qui sont modifiées par les pollinisateurs et permettent l'augmentation de la production à l'échelle de la parcelle (Chapitre I, III & IV). Le bénéfice à la production a été évalué en terme de rendement (Chapitre I & II), de qualité (Chapitre IV), et monétairement (Chapitre III).

Nos résultats montrent que les pollinisateurs augmentent le rendement à l'échelle de la parcelle, de 28 à 38% pour le colza (selon les pollinisateurs, Tableau 1, Chapitre I) et de 40% pour le tournesol (Tableau 1, Chapitre IV) entre les parcelles avec les plus faibles et les plus hautes abondances ou diversité de pollinisateurs (Tableau 1). Cette contribution est réduite par l'utilisation d'insecticides dans les parcelles de colza (Chapitre III). Ces résultats sont en accord avec Klein *et al*. (2007) qui classent ces cultures moyennement dépendantes des pollinisateurs pour leur production (entre 10-40%). Les pollinisateurs augmentent les rendements entre 0.8-1 $t.ha^{-1}$ pour le colza et 0.7 $t.ha^{-1}$ pour le tournesol (Tableau 1). Cela correspond à un gain monétaire important pour les agriculteurs, chiffré à plus de 250 € par ha pour le colza (Chapitre III, non évalué pour le tournesol). De plus, les pollinisateurs améliorent la qualité des graines de colza (non évalué pour le tournesol) en augmentant la quantité d'acide gras insaturés ainsi que le pourcentage de lipide par graine et en réduisant la quantité d'acides gras trans et saturés (Chapitre IV).

L'utilisation de filets pour calculer la contribution des pollinisateurs à l'échelle de la plante a permis de montrer que plusieurs biais (réduction du succès de pollinisation, augmentation du nombre de graines sous les filets par les pollinisateurs, Chapitre I & II) pouvaient mener à une mauvaise estimation de la contribution des pollinisateurs dans la production agricole. Cependant, une fois ces biais pris en compte dans le calcul des contributions, les estimations obtenues sont plus faibles que celles obtenues à l'échelle de la parcelle mais sont du même ordre de grandeur : 30% pour le colza et 35% pour le tournesol (Chapitre I & II, Tableau 3). Cette différence entre les estimations peuvent venir en partie de la non prise en compte de plusieurs compromis entre différents traits à l'échelle la plante (succès de pollinisation *versus* nombre de graines par silique pour le colza, nombre de graines *versus* poids des graines pour le tournesol, chapitre I & II) ou d'autres facteurs non dépendants des pollinisateurs (la densité de plante par exemple pour le tournesol, Chapitre II), mais qui sont nécessaires à l'élaboration du rendement à l'échelle de parcelle.

Finalement, nous avons identifié les principaux insectes impliqués dans la pollinisation du colza. Ce sont les abeilles domestiques et les abeilles sauvages avec principalement le genre *Lasioglossum*. Pour le tournesol, les principaux pollinisateurs sont les abeilles domestiques. La diversité des genres d'abeilles a aussi un effet bénéfique sur les rendements de colza mais pas sur ceux de tournesols.

Tableau 4. Résumé des bénéfices des pollinisateurs dans la production de colza et de tournesol en fonction des différents traits de production, de la métrique de pollinisateurs (A ; Abondance ; D ; Diversité des genres), de l'échelle et des méthodes utilisés (pose de filet ou gradient de pollinisateurs (GrP)) pour calculer ce bénéfice. La méthode utilisée pour estimer le gradient de pollinisateurs est précisée (pan trap ou sweep net). Certaines contributions ne sont pas indiquées dans les chapitres et sont calculées pour ce tableau.

Culture	Traits	Echelle	Pollinisateurs	Méthode	Contribution (%)	Augmentation rendement (t/ha)
Colza	Rendement	Parcelle	Abeilles (A)	GrP (pan trap)	**32.4**	0.9
	Rendement	Parcelle	Abeilles (D)	GrP (pan trap)	**37.5**	1
	Rendement	Parcelle	Abeilles (A)	GrP (sweep net)	**28.6**	0.8
	Succès de pollinisation	Plante	Abeilles (A)	GrP (pan trap)	**28.4**	
	Succès de pollinisation	Plante	Abeilles (D)	GrP (pan trap)	**19.8**	
	Succès de pollinisation	Plante	Abeilles (A)	GrP (sweep net)	**12.5**	
	Succès de pollinisation	Plante		Filet	**30**	
	Contribution pollinisateurs	Plante	Abeilles (A)	GrP (pan trap)	**30.2**	
	Contribution pollinisateurs	Plante	Abeilles (D)	GrP (pan trap)	**30**	
	Contribution pollinisateurs	Plante	Abeilles (A)	GrP (sweep net)	**16.5**	
Tournesol	Rendement	Parcelle	Abeilles domestiques (A)	GrP (sweep net)	**40**	0.7
	Nombre de graines	Plante	Abeilles domestiques (A)	GrP (sweep net)	**32.3**	
	Nombre de graines	Plante		Filet	**35.4**	
	Contribution pollinisateurs	Plante	Abeilles domestiques (A)	GrP (sweep net)	**35.6**	

A. Mécanismes de pollinisation

1. Les déterminants du succès de pollinisation

Les pollinisateurs augmentent les rendements en améliorant le succès de pollinisation des fleurs de colza et tournesol, ce qui a pour conséquence d'augmenter la production à l'échelle de la plante (Chapitre I & II). Des résultats similaires ont été trouvés dans d'autres études pour le colza (Bartomeus et al., 2014; Zou et al., 2017b), et pour le tournesol (Degrandi-Hoffman and Chambers, 2006; Tamburini et al., 2017). Le succès de pollinisation peut être augmenté par la quantité de pollen (Dogterom et al., 2000) ou par la qualité du pollen reçue par la plante qui est définie par l'origine du pollen (autopollinisation ou allopollinisation, Wang et al., 1998). Nos études ne nous permettent pas de déterminer quel est le paramètre déterminant (quantité ou qualité) du succès de pollinisation du colza et du tournesol. Néanmoins, la contribution de l'autopollinisation à la production de graines (obtenus par les

filets) pour le tournesol est plus faible que pour le colza (42% *versus* 67%, Chapitre I & II). Ce résultat pourrait indiquer que le colza est moins dépendant de la qualité du pollen que le tournesol. De précédentes études ont identifié qu'à la fois la quantité et la qualité du pollen augmentent le succès de pollinisation des fleurs de tournesol mais que l'importance de ces deux facteurs pouvaient varier entre les variétés de tournesol (Chamer et al., 2015), alors que le succès de pollinisation des fleurs de colza ne semble pas dépendre de l'origine du pollen (Ouvrard et al., 2017). D'autres paramètres, comme des structures florales avec une importante quantité de fleurs par plante, proches les unes des autres et une forte synchronie de floraison pourraient indiquer des plantes dont le succès de pollinisation dépend principalement de la quantité de pollen comme la myrtille arbustive (*Vaccinium corymbosum*, Fig 18.A, Dogterom et al., 2000). Ces structures pourraient favoriser le passage du pollen d'une fleur à l'autre au sein d'une même plante par les pollinisateurs (Devaux et al., 2014). Au contraire, des structures florales où le nombre de fleurs est moindre comme chez *Monochoria korsakowii*, pourrait indiquer des plantes dont la qualité du pollen est plus importante que la quantité (Fig 18.B, Wang *et al.* 1998). Les structures florales du colza et du tournesol se rapprochent de celle de la myrtille arbustive avec un nombre important de fleurs et une forte synchronie de ces fleurs (Fig 18.C & D). Ceci indiquerait que le colza et le tournesol dépendent plus de la quantité de pollen reçue que de sa qualité.

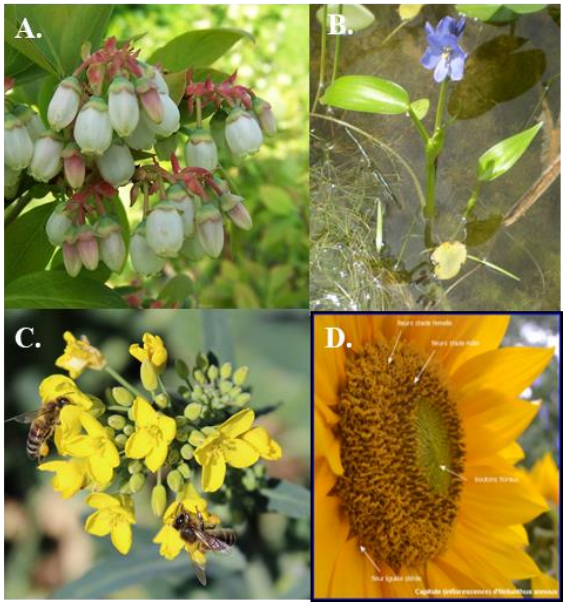


Fig. 18. Floraison de (A) *la myrtille arbustive (issue de commons.wikimedia.org)*, (B) *Monochoria korsakowii (issue de commons.wikimedia.org)*, (C) du colza *(photo prise par Quentin Van Hecke)* et (D) du tournesol *(issue de www.svtauclairjj.fr/)*

2. Les compromis d'allocation de ressources:

Plusieurs compromis ont été trouvés entre différents traits liés à la production de graines par plante pour le colza et pour le tournesol. Pour le tournesol, le nombre de graines est corrélé négativement au poids de ses graines. Ces deux traits sont respectivement positivement et négativement (mais significativement pour ce dernier) corrélés à l'abondance de pollinisateurs (Chapitre II). Ce compromis est souvent observé entre différentes espèces de plantes, qu'elles soient sauvages (Jakobsson and Eriksson, 2000) ou domestiques (Gambín and Borrás, 2010),

mais plus rarement étudié au sein d'une même espèce (Aniszewski, 2001). Cette corrélation revient à un compromis entre le nombre de descendants et la qualité des descendants car les graines plus légères ont généralement un taux de germination plus faible (Jakobsson and Eriksson, 2000; Updhaya et al., 2007). Une seule autre étude a trouvé que les pollinisateurs diminuent le poids moyen des graines de tournesol (Tamburini et al., 2017). La majorité des études a trouvé un effet positif des pollinisateurs sur le poids moyen des graines de tournesol (Carvalheiro et al., 2011; Degrandi-Hoffman and Chambers, 2006; Oz et al., 2009). Pour le colza, ce compromis entre nombre de graines et poids des graines n'est pas observé. En effet, les pollinisateurs n'ont aucun effet sur le poids moyen des graines de colzas alors qu'ils affectent le nombre de graines par plante en augmentant le succès de pollinisation des fleurs malgré une corrélation négative avec le nombre de graines par siliques (Chapitre 1). Contrairement à notre étude, la majorité des autres publications montrent une augmentation du nombre de graines par silique et du succès de pollinisation avec la pollinisation entomophile, et une diminution du poids moyen des graines (Hudewenz et al., 2014; Marini et al., 2015; Zou et al., 2017b). Ces différences d'allocations de ressources en fonction de l'abondance des pollinisateurs, pourraient venir d'une modification de la stratégie d'allocation des ressources entre variété (Chamer et al., 2015; Hudewenz et al., 2014). Le compromis entre nombre de graines et qualité des graines ne semble donc pas être détecté pour le colza. De plus, les pollinisateurs augmentent la quantité d'acides gras insaturés. Ces acides gras augmentent le taux de germination des graines à des températures basses (Linder, 2000) et expliqueraient l'augmentation du taux de germination observé par Kevan & Eisikowitch (1990) lorsque les graines de colza sont issues de fleurs pollinisées par les abeilles domestiques. En outre, ces acides gras insaturés sont beaucoup plus coûteux à produire que les acides gras saturés (Linder, 2000), qui eux diminuent avec l'abondance des pollinisateurs. Le colza semble donc capable d'augmenter à la fois le nombre de ses graines et leur qualité.

D'autres compromis pourraient exister par exemple entre la durée de floraison et la qualité ou le nombre de graines. Maintenir une fleur en floraison est coûteux pour la plante (Castro et al., 2008). Ce coût pourrait être très important pour le colza qui compte plus de 300 fleurs par plante (Hudewenz et al., 2014; Zou et al., 2017b), ce qui expliquerait la corrélation négative entre le nombre de fleurs et le poids moyen des graines observé par Hudewenz *et al.* (2014). Cependant, cette durée de floraison diminue avec la pollinisation des abeilles domestiques (Sabbahi et al., 2006) et permettrait un investissement à la fois dans le nombre et la qualité des graines. Le taux de visites par minute et par fleur est plus important chez les abeilles domestiques que chez les autres pollinisateurs (Garratt et al., 2014b; Rader et al., 2009). Ce facteur pourrait être déterminant dans la réduction du temps de floraison et expliquerait pourquoi l'effet des pollinisateurs sur la qualité des graines de colza n'est observé que pour l'abeille domestique (Chapitre III).

La modification de la qualité des graines de tournesol par la pollinisation des insectes n'a pas été étudiée dans cette thèse. Étant donné que la stratégie de reproduction du tournesol est d'investir dans la quantité de graines plutôt que dans leur poids (Chapitre II), on pourrait s'attendre à une diminution de la qualité des graines en termes d'acide gras ou de pourcentage de lipides. Cela irait à l'inverse de précédentes études qui ont montré que la pollinisation

entomophile augmentait la quantité de lipides par graine de tournesol (Aslan et al., 2010; Nderitu et al., 2008). De futures expérimentations sont nécessaires pour étudier ces potentiels compromis entre durée de floraison, qualité de graines, nombre des graines et comment les pollinisateurs peuvent les affecter, que ce soit pour le colza ou le tournesol.

B. Implication pour l'intensification écologique de la production de colza et de tournesol :

Cette thèse a montré l'importance du rôle des pollinisateurs dans la production de colza et de tournesol. Augmenter l'abondance des pollinisateurs ainsi que leur diversité dans les milieux agricoles permettrait d'augmenter voire de stabiliser les rendements ainsi que les revenus des agricultures (Garibaldi et al., 2014; Lucas A Garibaldi et al., 2011). Ceci permettrait donc d'intensifier écologiquement la production de colza et de tournesol (Bommarco et al., 2013). Cependant, avant de pouvoir promouvoir les pollinisateurs dans les milieux agricoles, l'identité des principaux pollinisateurs doit être connue ainsi que les éléments du paysage et les pratiques agricoles qui déterminent leur présence et leur abondance (Kremen, 2005).

1. Les pollinisateurs du colza et du tournesol :

Déterminer de rôle de chaque insecte dans les cultures est une question centrale dans la gestion du service de pollinisation dans les milieux agricoles (Kremen, 2005). En effet, de nombreux insectes visitant les fleurs de colza ou tournesol ne sont pas des pollinisateurs ou sont peu efficaces pour polliniser la culture en question (Chifflet et al., 2011; Pisanty et al., 2013). Dans les colzas ou les tournesols de cette étude, comme pour la majorité des autres cultures, ce sont les pollinisateurs les plus abondants (dits « dominant ») qui sont responsables de la majorité de la pollinisation de ces plantes (Kleijn et al., 2015; Winfree et al., 2015). Les abeilles domestiques augmentent à la fois les rendements de colza et de tournesol (Chapitre I & II) confirmant leur rôle essentiel dans la production agricole. En effet, les abeilles domestiques augmentent les rendements de nombreuses autres cultures (ex. : les myrtilles, la féverole, la pastèque, Cunningham and Le Feuvre, 2013; Garantonakis et al., 2016; Rogers et al., 2014). Les rendements de colzas sont aussi augmentés par l'abondance des abeilles du genre « *Lasioglossum* », ainsi que par la diversité de genre des abeilles (Chapitre I). L'importance des abeilles du genre *Lasioglossum* dans la production agricole est peu étudiée, à l'instar d'autres genres d'abeilles sauvages comme le genre « *Osmia* » ou les bourdons (Garratt et al., 2014b; Jauker et al., 2012; Vergara and Fonseca-Buendia, 2014). Pourtant ce genre d'abeille pourrait être important dans la production agricole. Le genre *Lasioglossum* augmente les rendements de piments (Landaverde-González et al., 2017) et est retrouvé dans de nombreuses autres cultures (ex. : les fraises, les pastèques les pommes, Földesi et al., 2016; Grab et al., 2017; Mallinger and Gratton, 2015). L'effet positif de la diversité des abeilles a été montré pour de nombreuses cultures : le café (Klein et al., 2003), les pastèques (Mallinger and Gratton, 2015), les myrtilles (Rogers et al., 2014) et dans une autre étude pour le colza (Zou et al., 2017b). Le mécanisme à la base de cet effet positif de la diversité des genres sur les rendements de colza n'est pas identifié dans nos études. Il pourrait découler soit d'une complémentation spatiale entre genres d'abeilles avec des genres butinant sur les fleurs hautes du colza et d'autres sur les fleurs basses (Brittain et al., 2013a; Hoehn et al., 2008), soit d'une complémentation temporelle des genres sur la journée (des genres présents

en début de journée et d'autres en fin de journée, Hoehn et al., 2008; Pisanty et al., 2016) ou sur la durée de floraison du colza (des genres présent en début de floraison de colza et d'autres en fin de floraison, Ellis et al., 2017). Cet effet de la diversité n'est pas observé dans le tournesol, possiblement parce que les autres pollinisateurs se trouvent en trop faible abondance par rapport aux abeilles domestiques dans les cultures de tournesol (Chapitre II, Pisanty et al., 2013; Rader et al., 2015).

Étonnamment, les traits fonctionnels qui déterminent l'importance d'une espèce de pollinisateurs dans une production agricole sont peu étudiés (mais lire Albrecht *et al.* 2012; Munyuli 2014). Les abeilles domestiques et les abeilles du genre *Lasioglossum* sont des pollinisateurs eusociaux avec de nombreux individus par colonie (Rollin et al., 2015; Torne-́Noguera et al., 2014). Ce trait est souvent retrouvé dans les pollinisateurs de colza et de tournesol (Halinski et al., 2015; Rollin et al., 2015; Sardiñas and Kremen, 2015) tout comme pour la majorité des pollinisateurs retrouvés dans les cultures (De Palma et al., 2015; Pisanty and Mandelik, 2015; Rader et al., 2014). Ce trait pourrait déterminer, en partie, l'importance d'une espèce d'abeilles dans les productions agricoles (Munyuli, 2014). Les espèces eusociales, du fait de leur très grand nombre d'individus, visent un nombre de fleurs plus important par plante que les pollinisateurs avec un comportement solitaire (Albrecht et al., 2012). D'autres traits comme la longueur de la langue (Garibaldi et al., 2015) ou la taille du corps (Garibaldi et al., 2015; Munyuli, 2014) pourraient modifier le succès de pollinisation en fonction de la morphologie florale de la plante (Garibaldi et al., 2015). Ce qui expliquerait pourquoi les abeilles de petite taille du genre *Lasioglossum*, qui sont aussi des pollinisateurs à langue courte (Torne-́Noguera et al., 2014), ne sont pas efficaces pour polliniser les fleurs de tournesol à longues corolles (Mallinger and Prasifka, 2017; Pisanty et al., 2013).

2. L'effet du paysage et des pratiques agricoles sur les pollinisateurs et leurs contributions aux rendements:

Les éléments du paysage qui influencent les pollinisateurs dans nos cultures n'ont pas été étudiés dans les différents chapitres de cette thèse. Parmi les éléments du paysage, c'est principalement l'effet des éléments semi-naturels (haie, prairie forêt) sur les pollinisateurs qui est étudié (Cariveau et al., 2013; Lucas A. Garibaldi et al., 2011; Kennedy et al., 2013). Néanmoins, dans cette thèse, les principaux pollinisateurs pourraient ne pas dépendre de ces éléments.

Pour les abeilles domestiques, on peut s'attendre à ce que la densité (Cunningham et al., 2016) et la distance des ruches aux parcelles agricoles (Cunningham and Le Feuvre, 2013) soient les principaux déterminants de leur abondance dans les cultures. En effet, les populations sauvages d'abeilles domestiques dites « férales » sont très peu présentes dans les milieux agricoles (Oleksa et al., 2013).

Les abeilles du genre *Lasioglossum* sont principalement des espèces nichant dans les sols (Torne-́Noguera et al., 2014). Les études ont montré que la quantité de surface en agriculture ainsi que la quantité de zone rudérale (espaces nus avec peu de végétation) augmenteraient la quantité de ce genre d'abeille dans les parcelles (Brandt et al., 2017; Zou et al., 2017a). Ces zones servent de sites de nidification pour ces abeilles comme cela a été montré dans les parcelles de tournesols (Sardiñas et al., 2016). Le type de sol pourrait aussi déterminer la

présence de ces pollinisateurs (Geslin et al., 2016; Kim et al., 2006). Potentiellement, l'effet de ces variables va être similaire sur la diversité des pollinisateurs puisque les principaux genres capturés, *Lasioglossum*, *Halictus*, et *Andrena*, (Chapitre I & II) sont connus pour nicher dans les sols (Torne-Noguera et al., 2014).

La densité de plantes au m², qui est en partie déterminée par la densité de semis, a un effet attractif sur les pollinisateurs pour le tournesol (Chapitre II). Cet effet est souvent observé pour des plantes sauvages comme le rhododendron ferrugineux (*Rhododendron ferrugineum*, Delmas et al., 2016) ou la digitale pourpre (*Digitalis purpurea*, Grindeland et al., 2005). L'augmentation de la densité de plantes pourrait augmenter la quantité de ressources par m² et donc l'attractivité des plantes pour les pollinisateurs. D'autres pratiques sont susceptibles de modifier l'abondance des pollinisateurs. Les insecticides, en réduisant l'impact des ravageurs sur le colza, permettent la production de plus de nectar par fleurs de colza et donc augmentent l'abondance des pollinisateurs visitant les parcelles (Lindstrom et al., 2017). Plusieurs autres études ont montré que les parcelles ayant reçu des traitements pesticides (insecticide, herbicide, fongicide) sont beaucoup plus attractifs pour les abeilles (Kessler et al., 2015; Liao et al., 2017). Ces substances ont un effet addictif sur les pollinisateurs (Johnson et al., 2013; Kessler et al., 2015). Cependant, ces substances sont nocives pour les abeilles (Henry et al., 2012; Johnson et al., 2013; Ben A. Woodcock et al., 2016) et peuvent réduire la contribution des pollinisateurs comme trouvé pour le colza dans nos études (Chapitre III). En effet, les pesticides réduisent l'efficacité pollinisatrice des insectes (Gill and Raine, 2014; Stanley et al., 2015). D'autres pratiques, comme l'utilisation de fertilisants (azote, phosphore…), ou le type de variétés (hybride ou conventionnelle), peuvent modifier la contribution des pollinisateurs (Lindström et al., 2016; Marini et al., 2015). Dans nos études, ces effets ne sont pas observés (Chapitre I, II, III). Les pollinisateurs ont un effet additifs aux fertilisants (van Gils et al., 2016) et ils sembleraient que la contribution des pollinisateurs varieraient plutôt entre variétés qu'entre type de variété (Hudewenz et al., 2014).

3. Les possibles freins et solutions :

L'abondance des pollinisateurs et la magnitude du service de pollinisation pourraient être augmentées par la présence de certains types d'habitat (zones rudérales) et par la réduction des insecticides. Cependant réduire la surface utilisée pour l'agriculture au profit de zones rudérales ou réduire l'utilisation de pesticides peut être vu comme une stratégie risquée par les agriculteurs (Smith and Sullivan, 2014). Des incitations économiques pourraient orienter les agriculteurs vers ces pratiques comme la promotion de mesures agro-environnementales (MAE). Les MAEs ont été mises en place à l'échelle de l'union européenne pour promouvoir des pratiques agricoles moins intensives en fournissant un soutien financiers aux agriculteurs (Batáry et al., 2015, lire Villien and Claquin, 2012 pour une liste de MAEs mise en place en France). Toutefois, aucune MAE n'a pour objectif de préserver les pollinisateurs et augmenter le service de pollinisation. Les pollinisateurs pourraient bénéficier indirectement d'autres MAEs comme celles qui promeuvent la réduction de pesticides, ou l'installation de boisement dans le paysage (Villien and Claquin, 2012) mais l'effet indirect de ces mesures sur les pollinisateurs reste inconnu et dans plusieurs cas les MAEs se sont montrées inefficaces pour

promouvoir la biodiversité et leurs services associés dans les milieux agricoles (Batáry et al., 2015; Dicks et al., 2014; Kleijn et al., 2001; Kleijn and Sutherland, 2003). De plus, ces mesures sont coûteuses pour l'Union Européenne et les pays qui les mettent en œuvre (Batáry et al., 2015) ; ce qui pose la question de la durabilité de ce système sur le long terme.

C. Limites & Perspectives:

La contribution des pollinisateurs est ici calculée sur une seule zone, très riches en espèces d'abeilles sauvages (plus de 300, Rollin et al., 2015) avec une très forte densité d'abeilles domestiques (Rollin et al., 2013). Il serait intéressant de répliquer cette étude sur d'autres zones (France ou Europe) avec d'autres communautés de pollinisateurs (Westphal et al., 2008). Il est possible que dans certaines zones moins riches en pollinisateurs, la contribution des pollinisateurs dans les rendements soit moindre pour le colza, à moins que certaines espèces dominantes de pollinisateurs soient capables de compenser cette perte de diversité. Dans le cas du tournesol, de trop fortes densités d'abeilles domestiques sont capable d'exclure les autres pollinisateurs (Hudewenz and Klein, 2015) et pourraient expliquer en partie l'absence d'autres pollinisateurs importants pour les rendements dans nos études (Chapitre II). Des zones avec des densités moindres d'abeilles domestiques pourraient permettre d'identifier d'autres pollinisateurs du tournesol. L'étude de la contribution des pollinisateurs entre ces différentes zones pourrait s'élargir aux diptères qui ne sont pas étudiés dans cette thèse (excepté les syrphes). En effet, ces insectes peuvent être d'importants contributeurs de la pollinisation dans les milieux agricoles (Orford et al., 2015; Rader et al., 2015; Tiusanen et al., 2016). De plus, les diptères sont souvent retrouvés dans les colzas de cette zone, dont principalement le genre *Empis* (observation personnelle).

D'autres facteurs externes pourraient modifier la contribution des pollinisateurs entre ces différentes zones mais restent peu étudiées. Plusieurs variables météorologiques (pluie, température,..) sont connues pour modifier l'activité des pollinisateurs (Fijen and Kleijn, 2017; Westphal et al., 2008). Les différences de ces variables entre sites pourraient moduler le service de pollinisation en augmentant ou en diminuant les plages horaires où les pollinisateurs sont actifs (Nielsen et al., 2017; Tuell and Isaacs, 2010). De plus, ces variables pourraient aussi modifier la durée de floraison d'une même culture entre sites et modifier le succès de pollinisation des plantes (Alonso, 2004). En effet, cette durée de floraison pourrait déterminer en partie la probabilité de rencontre entre une fleur et un pollinisateur avec une augmentation de cette probabilité avec l'augmentation de la durée de floraison.

Identifier les éléments du paysage et les pratiques agricoles qui déterminent la richesse et l'abondance des pollinisateurs dans les parcelles est d'une importance cruciale pour promouvoir les pollinisateurs dans les milieux agricoles, mais outre l'effet des éléments semi-naturels, d'autres éléments du paysage doivent être pris en compte.

Les cultures à fleurs (ou « *mass flowering crops* » en anglais) pourraient avoir une forte influence sur l'abondance ou la richesse des pollinisateurs. En effet, la quantité de cultures à fleurs peut avoir un effet attractif (Isaacs and Kirk, 2010) ou un effet de dilution (Holzschuh et al., 2016) sur les pollinisateurs présents. Ces cultures peuvent aussi modifier la pollinisation des autres cultures à fleurs retrouvés dans les saisons suivantes. En effet, plusieurs études ont montré que le colza peut augmenter la quantité de pollinisateurs comme les bourdons dans les

tournesols de la même année (Riedinger et al., 2014) ainsi que l'abondance des abeilles sauvages dans les colzas de l'année suivante (Riedinger et al., 2015). L'effet du tournesol sur les pollinisateurs du colza de l'année suivante n'a jamais été étudié mais potentiellement les ressources florales de fin de saison seraient capables d'augmenter les pollinisateurs dans les premières cultures à fleurs de l'année suivante (Häussler et al., 2017). Les adventices sont des plantes sauvages qui sont retrouvées dans les parcelles agricoles. Ce sont des ressources très importantes pour les pollinisateurs surtout entre la période de floraison du colza et du tournesol (Requier et al., 2016, 2015). Des paysages riches en adventices pourraient être des paysages plus riches en pollinisateurs visitant les parcelles (Bretagnolle and Gaba, 2015) mais ces adventices pourraient réduire les rendements par compétition que ce soit du colza, du tournesol ou d'autres cultures (Bretagnolle and Gaba, 2015). Un potentiel optimal pourrait exister entre quantité d'adventices, pollinisateurs et rendements (Bretagnolle and Gaba, 2015).

L'effet des ressources florales et de certains éléments du paysage sur l'abondance et la richesse des pollinisateurs pourrait être aussi évalué expérimentalement en rajoutant par exemple des bandes fleuries ou des zones rudérales à la place de la culture (Pywell et al., 2015) ou dans des zones non cultivées (Blaauw and Isaacs, 2015). Cette méthode permettrait d'identifier à la fois la quantité de ces éléments, ainsi que leur répartition spatiale pour maximiser la pollinisation du colza et du tournesol. En effet, la répartition spatiale de ces éléments est la clé pour la réussite de ces expérimentations. Les abeilles sont des « *central foragers* », c.à.d. qu'elles établissent un nid et butinent aux alentours de leur nid. Cette distance de butinage est restreinte, en dessous de 1000 m pour la majorité des abeilles (Greenleaf *et al.* 2007; Zurbuchen *et al.* 2010). L'ajout des éléments qui augmentent potentiellement la présence des pollinisateurs dans les parcelles doit être à proximité des cultures. Par conséquent une stratégie « *wildlife friendly* », où la biodiversité et les agriculteurs se partagent le paysage semblent être préférable pour la production agricole du colza et du tournesol à une stratégie « *land sparing* » où la biodiversité est regroupée dans une même zone et séparée de la production agricole (Fischer et al., 2008; Green et al., 2005). Il est à noter que des travaux similaires pourraient être réalisés pour les abeilles domestiques en fonction de la densité de ruches et de leur distance aux cultures (Cunningham et al., 2016; Cunningham and Le Feuvre, 2013). Une fois ces relations connues, cela permettrait de savoir la quantité de surfaces agricoles ou la quantité de pesticides à réduire pour augmenter leur abondance (leur richesse) et maximiser le profit des agriculteurs (exemple dans Fig. 19). Il serait intéressant d'évaluer l'impact de ces mesures sur les espèces rares de pollinisateurs pour déterminer si une stratégie « gagnant-gagnant » est possible entre production et biodiversité dans les milieux agricoles (Sutter et al., 2017).

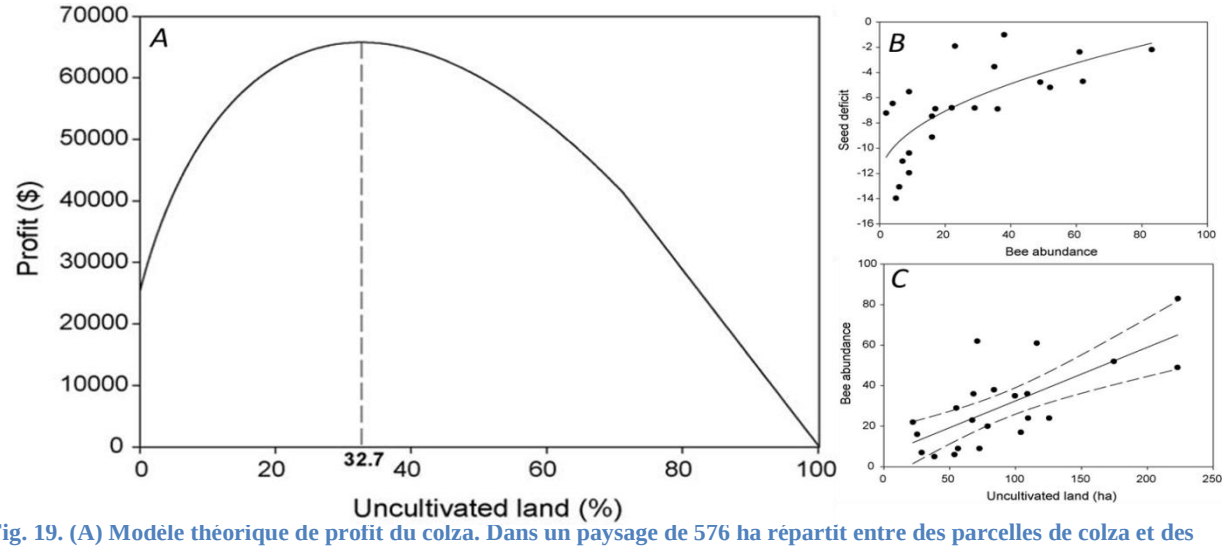


Fig. 19. (A) Modèle théorique de profit du colza. Dans un paysage de 576 ha répartit entre des parcelles de colza et des surfaces non cultivées, les auteurs cherchent à déterminer la quantité optimale de surface non cultivées qui maximise le profit suite à la vente de la production de colza tout en connaissant (B) la relation entre abondance des pollinisateurs et production de graines et (C) la relation entre abondance des pollinisateurs et surface non cultivée (issue de Morandin & Winston 2006)**.**

Finalement, l'ensemble de ces expérimentations doit se faire sous forme de collaborations entre les chercheurs et les agriculteurs (Batáry et al., 2015; Geertsema et al., 2016) et réfléchies en termes de coût-bénéfice permettant une démonstration directe de l'efficacité de ces pratiques et donc du succès de l'implémentation de ces méthodes. Ces collaborations permettent un échange plus rapide de connaissances entre les agriculteurs et les chercheurs et pourraient augmenter l'engagement des agriculteurs vers une agriculture moins intensive (de Snoo et al., 2013; Doré et al., 2011; Herzon and Mikk, 2007)..

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