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THÈSE

Présentée par : Maxime Ragué

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Discipline : Biologie de l'environnement, des populations, écologie

**Dynamiques spatiale et temporelle des paysages agricoles : conséquences
sur les interactions plantes-pollinisateurs et la pollinisation**

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INRAE



Zones
Ateliers
LYSER FRANCE PLAINES ET VALS DE SÈVRE



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Liste des abréviations

<u>Anglais</u>	<u>Français</u>
ANOVA: Analysis of variance	
Df: degree of freedom	
GAM: Generalized additive models	
ha: hectare	
MFC: Mass flowering crop	CFM : Culture à floraison massive
OF: Organic farming	AB : Agriculture biologique
OSR: Oilseed rape	
Sd: standard deviation	
Se: standard error	
SNH: Semi-natural habitats	HSN : Habitats semi-naturels
	ZAPVS : Zone Atelier Plaine et Val de Sèvre

INTRODUCTION GENERALE

I. Conciliation entre la société humaine et la biodiversité dans les milieux agricoles

1. Vers l'étude de la biodiversité dans les espaces anthropisés

L'espèce humaine et les activités qui lui sont associées se sont intégrées à l'ensemble des écosystèmes. L'**anthropocène** définit cette période où l'Humain est devenu une force structurante des écosystèmes et est notamment caractérisée par la perturbation des cycles biogéochimiques et le déclin de la **biodiversité** (Corlett, 2015; Dirzo et al., 2014). La crise de la biodiversité est majeure, l'abondance¹ et la diversité² de nombreux groupes taxonomiques déclinent sur l'ensemble du globe (IUCN, 2021; WWF, 2018). A titres d'exemples, respectivement 41% et 32% des populations d'insectes et de mammifères ont décliné au cours du dernier siècle (Ceballos et al., 2017; Sánchez-Bayo & Wyckhuys, 2019).

La science de l'écologie, d'abord centrée sur l'étude des interactions écologiques au sein des communautés naturelles et avec leur environnement, s'est depuis intéressée aux interactions entre la société humaine et la biodiversité avec pour principal objectif de comprendre la façon dont maintenir les espèces malgré la présence de l'Humain (Mace, 2014). Cela s'est traduit par la compréhension des facteurs d'impacts des activités humaines sur la biodiversité (Crutzen, 2006), par exemple à travers la fragmentation et la dégradation des habitats (Fahrig, 2003), ou la surexploitation des ressources (Rosser & Mainka, 2002). Les études concluent que l'atteinte des objectifs de conservation de la biodiversité repose sur la modification de la société humaine et des activités associées. Mais restreints à certaines disciplines scientifiques et ne touchant qu'une partie de la société, les objectifs de conservation de la biodiversité pour ce qu'est la biodiversité intrinsèquement se révèlent complexes. D'autres arguments, notamment économiques et sociétaux et, impliquant des études interdisciplinaires, apparaissent nécessaires pour atteindre les objectifs de conservation de la biodiversité.

Les études scientifiques se sont alors tournées vers les écosystèmes les plus anthropisés, par exemple les milieux agricoles. Et elles se sont concentrées sur les nombreux bénéfices que tire la société humaine de la biodiversité : ce sont les **services écosystémiques** (Millennium Ecosystem Assessment, 2005). A travers un effet en cascade, la biodiversité contribue à des flux d'informations, de matière et d'énergie sur lesquels reposent les **fonctions des écosystèmes**³ (Brockhoff et al., 2017), puis les services écosystémiques (Daily, 1997) et finalement les activités humaines (Cardinale et al., 2012). La société humaine et la biodiversité montrent ainsi un degré de dépendance fort l'un envers l'autre à travers des liens complexes. L'intégration de la société humaine à la biodiversité de par leurs interactions et interdépendances a été conceptualisée à travers le cadre des socio-écosystèmes (Bretagnolle et al., 2019; Collins et al., 2011).

2. La biodiversité dans les milieux agricoles

La quantité et la diversité des espaces agricoles notamment dans les conditions du sol, le climat et les pratiques font des espaces agricoles des zones à haut potentiel de conservation de la biodiversité

¹ Le nombre d'individus.

² Le nombre d'espèces et la répartition de leur abondance.

³ Les mécanismes écologiques qui supportent l'intégrité et le maintien des écosystèmes.

(Henle et al., 2008). Les espaces agricoles occupent environ 50% et 40% des surfaces française et européenne (Chatellier & Delame, 2007; Neron, 2018). Ce sont des espaces façonnés par l'Humain pour son alimentation, où des espèces domestiquées ont été implantées, en particulier des plantes cultivées (culture) et du bétail (élevage). Aujourd'hui ces espèces occupent une place majeure sur le globe, les plantes cultivées couvrent environ 11% de la surface terrestre (Ritchie & Roser, 2013) et les mammifères domestiqués représentent 93% de la masse totale des mammifères non-humains (Bar-On et al., 2018). Malgré la place considérable occupée par les espèces domestiquées, les espaces agricoles abritent des communautés sauvages dans les espaces non cultivés, i.e. les habitats semi-naturels (HSN) tels que les bois ou les haies (Duelli & Obrist, 2003; Söderström et al., 2001) mais également dans les espaces cultivés. Les parcelles agricoles peuvent en effet abriter des insectes (Dufлот et al., 2017; Rollin et al., 2015), des plantes (Henckel et al., 2015; Petit et al., 2011), des mammifères (Butet et al., 2006; Fuentes-Montemayor et al., 2020) ou des oiseaux (Kumar & Sahu, 2020; Redlich et al., 2018).

Les espaces cultivés ne sont pas simplement une zone de cooccurrence mais plutôt une zone d'interactions entre les espèces domestiquées et sauvages. La stratégie adoptée par le modèle agricole d'après-guerre a cherché à augmenter la production agricole en s'appuyant sur l'utilisation d'intrants notamment de pesticides, pour limiter les interactions négatives entre la production agricole et la biodiversité. Les interactions visées sont la compétition pour les ressources entre les plantes sauvages et cultivées, ou encore la prédation et le parasitisme de ces dernières. L'augmentation de la taille des parcelles combinée à la diminution de la surface couverte par les HSN (Brown & Schulte, 2011; Hooftman & Bullock, 2012) ont également contribué à isoler les espèces domestiquées des espèces sauvages. Cette isolation spatiale de la biodiversité du système agricole révèle un conflit entre les objectifs de conservation et de production agricole. L'intensification et la diffusion du système d'agriculture conventionnelle se placent en effet comme l'un des principaux facteurs de déclin de la biodiversité (Maxwell et al., 2016). Le système agricole conventionnel contribue au déclin des populations, que ce soit d'espèces ciblées, par exemple les plantes sauvages (Fried et al., 2009) ainsi que d'espèces non ciblées comme les oiseaux (Stanton et al., 2018) ou les insectes pollinisateurs (Le Féon et al., 2010). Ce déclin de la biodiversité dans les milieux agricoles semble fragiliser la production agricole car les rendements des grandes cultures plafonnent malgré l'utilisation de plus en plus massive d'intrants chimiques et des outils de précision utilisés de plus en plus performants (Grassini et al., 2013; Wiesmeier et al., 2015). Ce plafonnement est particulièrement observé pour les cultures qui dépendent d'autres espèces, par exemple des insectes pollinisateurs, pour leur production (Garibaldi, et al., 2011). Les systèmes agricoles interviennent indirectement sur l'ensemble de la biodiversité en perturbant les réseaux trophiques, provoquant une diminution de l'intensité des fonctions écologiques essentielles à la production agricole menaçant ainsi leur propre productivité.

3. Soutenir la production agricole par la biodiversité

La biodiversité des paysages agricoles assure des fonctions essentielles à la production agricole. Parmi les plus déterminantes et les plus étudiées, le **contrôle biologique**⁴ assurée par des prédateurs et parasitoïdes, la **pollinisation**⁵, fonction assurée notamment par des insectes hyménoptères, diptères et lépidoptères, et la **conservation des sols**⁶ supportée notamment par des invertébrés ou microorganismes

⁴ La prédation et le parasitisme d'organismes causant des dégâts aux cultures.

⁵ Etape nécessaire à la reproduction des plantes, en particulier cultivées, assurant la production de nourriture à travers les graines, les fruits ou les légumes.

⁶ La protection du sol face à sa dégradation en termes d'érosion ou de perte de fertilité.

du sol. Deux composantes des communautés sont essentielles dans le maintien d'une fonction écologique. La première est l'abondance des organismes impliqués dans la fonction, à mesure que l'abondance des individus augmente, les flux de matière ou d'énergie sous-jacents à la fonction s'intensifient (Steffan-dewenter, 2003). La seconde composante est la diversité, notamment spécifique, à savoir le nombre d'espèces et leur équitabilité⁷, et sa relation avec le niveau d'une fonction a été largement étudiée. De nombreuses études montrent ainsi une relation positive entre la diversité des espèces et le niveau d'une fonction. Des effets de complémentarité, i.e. l'augmentation de l'efficacité des flux dans l'espace et dans le temps (processus déterministe), et d'échantillonnage, i.e. l'augmentation de la probabilité d'inclure une espèce qui contribue fortement à la fonction (processus stochastique), sont impliqués (Loreau & Hector, 2001; Tilman et al., 2014). D'autres études suggèrent un effet de la diversité biologique sur la stabilité et la résilience des fonctions, qui sont respectivement la capacité d'un écosystème à fonctionner de manière similaire au cours du temps, et à retourner à son niveau de fonctionnement initial après une perturbation (Loreau, 2000; Tilman et al., 2006).

Une alternative au modèle agricole conventionnel a émergé et propose une voie intéressante pour concilier la biodiversité et la production agricole. L'**agroécologie** repose sur la valorisation de la biodiversité et des services écosystémiques sous-jacents, en particulier le contrôle biologique et la pollinisation dans les parcelles agricoles pour assurer de manière durable la production agricole (Wezel et al., 2014). L'idée sous-jacente est donc d'intégrer la biodiversité à la production agricole et non plus de séparer les activités agricoles de la biodiversité et de sa conservation. Au vu de la diversité d'espèces peuplant encore les systèmes agricoles, la conciliation entre la conservation de la biodiversité et la production agricole reste possible. Il faut déterminer les moyens de maintenir des communautés abondantes et diversifiées de microorganismes du sol, de prédateurs ou parasites des ravageurs de cultures ou encore d'insectes pollinisateurs dans les paysages agricoles pour maintenir les fonctions écologiques essentielles au maintien de la production agricole (Dainese et al., 2019).

II. Etude de la dynamique des paysages agricoles

1. Enjeux de l'étude des paysages agricoles

La parcelle agricole est l'échelle spatiale de gestion concernant le type de culture ou les pratiques agricoles à mettre en œuvre. A cette échelle, des études se sont intéressées à la réponse de la biodiversité et des fonctions écologiques aux caractéristiques des parcelles agricoles. Les études sont nombreuses et montrent que certaines pratiques ou systèmes de production sont compatibles avec le maintien de la biodiversité et des fonctions dans les parcelles agricoles. Parmi les systèmes de production, l'agriculture biologique (AB), qui se passe d'intrants chimiques, ou l'agriculture de conservation des sols, à travers l'arrêt du labour, permettent d'augmenter la diversité et l'abondance de divers groupes taxonomiques (plantes, insectes, oiseaux et microorganismes du sol), et fonctions écologiques (Briones & Schmidt, 2017; Lichtenberg et al., 2017; Martin et al., 2020; Tuck et al., 2014). Néanmoins, les parcelles agricoles sont des systèmes ouverts ce qui implique que les organismes peuvent disperser d'une parcelle à une autre. Les conditions en dehors de la parcelle agricole peuvent ainsi moduler la biodiversité présente dans cette parcelle (Tschardt et al., 2012). Donc, selon les conditions paysagères, une parcelle en agriculture conventionnelle peut supporter une biodiversité plus importante qu'une parcelle en AB (Gabriel et al., 2010). Cela suggère qu'il peut y avoir des décalages entre l'échelle de gestion (la parcelle agricole) et l'échelle à laquelle les processus écologiques interviennent (Cumming et al., 2013).

⁷ La répartition de l'abondance des espèces.

L'hétérogénéité des parcelles forme à l'échelle du km² une **mosaïque** d'éléments cultivés où sont intercalés en plus ou moins grande quantité des habitats semi naturels (des bois, des haies, des prairies ou encore des jachères) et des infrastructures humaines (Pickett & Cadenasso, 1995) : ce sont les **paysages agricoles**. Bien que ceux-ci tendent à être uniformisés, une diversité importante de pratiques agricoles peut encore être observée à différentes échelles spatiales. L'écologie des paysages s'intéresse aux processus écologiques qui interviennent à des échelles plus larges que celles communément étudiées en écologie. Cette discipline a en effet pour objectif de comprendre les flux d'énergie, de nutriments ou d'espèces entre les éléments du paysage et de caractériser les échelles spatiales et temporelles auxquelles ces processus écologiques surviennent (Turner, 2005). Cette discipline offre ainsi un cadre d'étude cohérent pour la mise en place de pratiques agroécologiques (Tittonell, 2014), sa mobilisation dans les milieux agricoles peut permettre de mieux comprendre les flux d'organismes et les fonctions écologiques entre éléments des paysages agricoles (parcelles cultivées ou HSN), et à caractériser les échelles auxquelles ces flux se produisent. Cela passe par la caractérisation de l'hétérogénéité des paysages agricoles et de ses conséquences de cette hétérogénéité sur la biodiversité et les fonctions écologiques.

2. Méthodes d'étude des paysages agricoles

Déterminer les conséquences de l'hétérogénéité des paysages agricoles sur la biodiversité et les fonctions écologiques associées requiert des méthodes robustes pour décrire les patrons spatiaux. La première étape consiste en la description des types d'occupation du sol (types de cultures ou autres variables d'intérêts) dans un site d'étude. L'idée est de grouper les unités du paysage, les parcelles agricoles, dans des catégories. Différentes méthodes peuvent être utilisées, parmi elles l'utilisation de photos satellites ou la cartographie sur le terrain (Turner, 2005). Dans, une seconde étape, des suivis de la biodiversité ou des mesures de fonctions écologiques sont effectuées dans des parcelles placées dans des contextes paysagers variés. La troisième étape consiste en la caractérisation de l'hétérogénéité spatiale du paysage. L'approche classique dite des "buffers" repose sur la caractérisation de variables paysagères dans des rayons définis autour des points d'observations. Deux principales catégories de variables paysagères sont couramment utilisées. La **composition du paysage** caractérise les types d'occupations du sol dans le paysage et inclut notamment la surface couverte par un type d'habitat (par exemple la quantité d'HSN dans le buffer) mais également la diversité des habitats (nombre d'habitats différents et équitabilité). La configuration rend compte de la complexité de l'agencement des différents habitats dans le paysage, un proxy intéressant est la taille des parcelles dans le paysage (Fahrig et al., 2011). Finalement, les variables réponses mesurées dans différentes parcelles sont confrontées aux gradients de composition et de configuration du paysage avec des procédures statistiques appropriées (e.g. modèles linéaires).

L'échelle à laquelle les variables paysagères influencent les processus écologiques varie avec le taxon impliqué ou la variable paysagère elle-même (Miguet et al., 2016). Une méta analyse a révélé que les échelles de travail était rarement justifiées (Jackson & Fahrig, 2015). Afin de pallier à la difficulté de choisir une échelle d'étude *a priori*, il est intéressant de définir l'**échelle d'influence** du paysage, c'est-à-dire l'échelle d'étude parmi d'autres qui a le plus d'effet sur une variable observée (voir Steffan-Dewenter et al., (2002) par exemple). Cette échelle d'influence est néanmoins souvent mal estimée car la gamme d'échelles testées est trop faible, ou l'écart entre les valeurs d'échelles testées trop important (Jackson & Fahrig, 2015).

3. La dynamique temporelle : un aspect rarement inclus dans l'étude des paysages agricoles

Les **habitats** peuvent être définis comme un type d'occupation du sol dans les paysages agricoles (Lindenmayer et al., 2007). Néanmoins, l'hétérogénéité des occupations du sol décrite par un observateur humain n'est pas forcément indicative d'une hétérogénéité perçue par un organisme donné (Fahrig et al., 2011). Il semble ainsi nécessaire de faire le lien entre les types d'occupation du sol et la quantité ou la qualité des **ressources** qu'ils fournissent pour les organismes d'intérêt (Fahrig et al., 2011). Les ressources sont des entités biotiques (vivantes) ou abiotiques (non vivantes) qui contribuent positivement à la croissance des populations et sont exploitées dans ce but (Grover, 1997). Ainsi la vision dichotomique de l'habitat où les habitats favorables à un organisme sont entourés d'une matrice inhospitalière a été abandonnée aux dépens d'une vision quantitative de l'habitat, où l'habitat fournit en plus ou moins grande quantité des ressources (Turner, 2005). Les ressources peuvent ainsi être accessibles en différentes quantité ou qualité à différents endroits de la mosaïque agricole avec des conséquences sur la dispersion des organismes. Comprendre comment les organismes utilisent les ressources à travers la mosaïque agricole est primordial pour optimiser les fonctions écologiques.

Une littérature abondante existe quant aux effets de l'hétérogénéité du paysage sur les organismes et les fonctions écologiques. Parmi les patrons les plus décrits dans les paysages agricoles, celui de l'augmentation de la diversité ou de l'abondance de groupes taxonomiques et de fonctions écologiques avec la quantité d'HSN dans le paysage est le plus étudié (Holland et al., 2017; Rusch et al., 2010; Steffan-Dewenter et al., 2002). Les HSN sont connus pour fournir des ressources abondantes et diversifiées pour de nombreux organismes, par exemple des ressources florales pour les pollinisateurs (Cole et al., 2017), ou des insectes pour les oiseaux (Pffner & Luka, 2000). Les populations qui bénéficient localement des ressources exploitées pour leur survie et leur reproduction dispersent vers les habitats adjacents, c'est le processus de **spillover** (Blitzer et al., 2012; Tschardtke et al., 2012). La majorité des études paysagères repose sur des observations de la biodiversité ou des fonctions écologiques que l'on peut qualifier d'instantanées, car conduites dans un habitat donné et à un moment donné de la saison. Par exemple, les études sur la pollinisation sont souvent conduites dans des cultures dépendantes de la pollinisation par les insectes au moment de leur floraison (voir par exemple Bartomeus et al., 2014; Nicholson et al., 2017).

Une contrainte évidente au fait de ne pas répliquer des observations dans différents habitats et moments de la saison est la multiplication de l'effort d'échantillonnage. Néanmoins, cela pose question car la disponibilité des ressources peut varier au cours du temps au sein des habitats et donc potentiellement modifier la dispersion des organismes dans la mosaïque agricole au cours de la saison. Cette dynamique peut impliquer la phénologie des cultures ou le calendrier cultural (dates et types de pratiques agricoles). Augmenter temporairement la disponibilité des ressources dans un habitat peut avoir pour effet de concentrer temporairement les organismes dans cet habitat. Des perturbations (une diminution de la quantité de ressource par exemple) dans des habitats du paysage peuvent également contraindre les organismes à se concentrer dans des habitats fournissant encore des ressources (Tschardtke et al., 2012). La **dynamique temporelle** est un concept clé en écologie du paysage mais qui est beaucoup moins étudiée que la dynamique spatiale alors qu'elle peut avoir des implications cruciales dans le maintien des organismes et des fonctions écologiques des paysages agricoles. Par exemple, au lieu de concentrer les efforts de conservation d'organismes sur un habitat (par exemple les HSN), une combinaison d'habitats fournissant des ressources à différents moments de la saison est une stratégie supposée efficace pour conserver la biodiversité et les fonctions écologiques (Aguilera et al., 2020). Cet **effet de complémentarité** a déjà été suggéré par des études indiquant que des paysages

agricoles abritant une diversité d'habitats importante supportent efficacement certains groupes taxonomiques et fonctions écologiques (Gardiner et al., 2009; Petersen & Nault, 2014). La complémentarité des habitats n'est néanmoins pas garantie par ce patron. A cela s'ajoute la difficulté d'évaluer l'échelle spatiale à laquelle caractériser cette complémentarité des habitats, car la dispersion des organismes entre habitats peut changer au cours de la saison. Des études sur la capacité des habitats à supporter les organismes et les fonctions à travers la saison culturale à de multiples échelles spatiales sont notamment requises pour valider cette hypothèse.

III. Dynamiques de la disponibilité des ressources florales, pollinisateurs et pollinisation dans les paysages agricoles

1. Les pollinisateurs des espaces agricoles

Les **pollinisateurs sauvages** regroupent des centaines d'espèces d'insectes appartenant en particulier aux ordres des diptères (e.g. les syrphes), des lépidoptères (e.g. les papillons rhopalocères) et des hyménoptères (e.g. les abeilles) dans les zones tempérées (Rollin et al., 2016) avec leur singularité morphologique, phénologique et d'exigence en termes d'habitats (Forrest et al., 2015; Westrich et al., 1996). Ces insectes mobiles visitent successivement des fleurs afin d'y récolter des **ressources florales**, le nectar consommé principalement pour les sucres, et le pollen principale source de protéines, qui sont essentielles à leur survie et à leur reproduction (Roulston & Goodell, 2011). D'autres ressources sont également essentielles à leur reproduction, notamment des cavités par exemple dans le bois ou un sol nu pour les abeilles (Potts et al., 2005). Les pollinisateurs et les plantes sont impliqués dans une interaction mutualiste car les plantes visitées tirent également parti de cette interaction pour leur reproduction via la **pollinisation** entomophile⁸. Tous les insectes qui visitent les fleurs des plantes ne sont pas des pollinisateurs. Ces derniers possèdent des caractéristiques comportementales et morphologiques propres aux pollinisateurs leur permettant de transporter et déposer le pollen (Rader et al., 2009). D'autres processus peuvent contribuer à la pollinisation à différents niveaux, la pollinisation anémophile quand le vent est le vecteur de transfert du pollen, et l'autopollinisation quand le pollen provient de la même plante. La contribution des différents processus varie d'une espèce de plante à l'autre, au final c'est presque 90% des plantes sauvages et plus de 70% des cultures qui bénéficient de la pollinisation entomophile (Klein et al., 2007; Ollerton et al., 2011).

Un pollinisateur particulier, l'**abeille domestique** *Apis mellifera* peuple également les paysages agricoles. Cet insecte a été domestiqué il y a des milliers d'années pour la production de miel et vit ainsi dans des ruches disposées dans les paysages agricoles (Cunningham et al., 2016), certaines populations sauvages et férales⁹ sont également encore présentes (Kohl & Rutschmann, 2018; Requier et al., 2019). Chaque ruche abrite des milliers d'individus de cet insecte social (Geslin et al., 2017) ce qui en fait l'insecte pollinisateur le plus abondant des paysages agricoles (Perrot et al., 2019; Rollin et al., 2013). En plus de son effectif conséquent, son important degré de généralisme (Geslin et al., 2017; Requier et al., 2015), sa période d'activité qui s'étend sur l'ensemble de la saison (Becher et al., 2014), la coopération entre individus de la même ruche (Seeley, 1986), ainsi que sa capacité de dispersion importante (Beekman & Ratnieks, 2000), font de l'abeille domestique le principal insecte pollinisateur des espaces agricoles. Pour ces raisons, mais également pour sa facilité de gestion, l'optimisation du service de pollinisation des cultures repose essentiellement sur l'abeille domestique (Rollin & Garibaldi,

⁸ Le transfert de pollen par des insectes des anthères vers les stigmates qui contiennent les ovules

⁹ Population retournée à l'état sauvage après domestication.

2019). On peut citer son rôle essentiel par exemple dans la pollinisation du tournesol (Perrot et al., 2019), ou du colza (Perrot et al., 2018), deux cultures d'intérêt économique majeur en Europe. Néanmoins, une stratégie d'optimisation de la fonction de pollinisation basée sur une unique espèce est risquée, il est alors nécessaire de considérer également la diversité des pollinisateurs sauvages pour assurer la stabilité du service de pollinisation (Garibaldi, Steffan-Dewenter, et al., 2011).

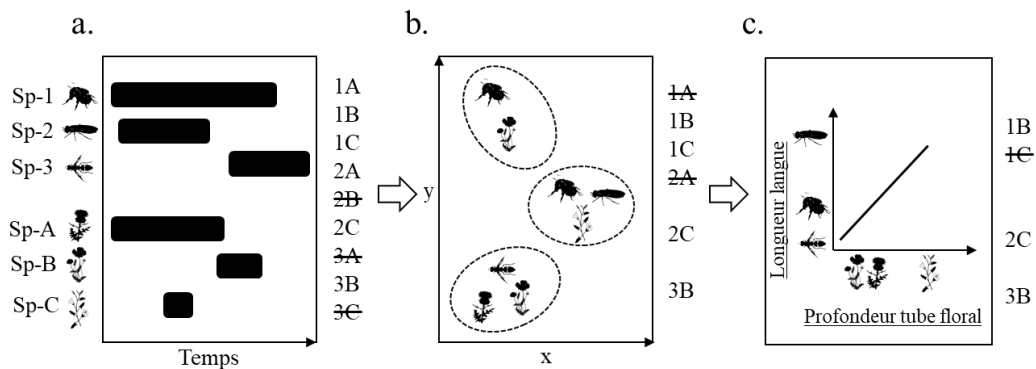


Fig. 0.1 : Représentation schématique des conditions nécessaires à la mise en place d'une interaction entre un pollinisateur (Sp-1, Sp-2, Sp-3) et une plante (Sp-A, Sp-B, Sp-C). Les interactions 2B, 3A et 3C sont impossibles car la phénologie (les barres noires représentent les moments auxquelles les espèces sont présentes) de ces binômes ne se recoupe pas au contraire des autres binômes (a). Les interactions 1A et 2A ne peuvent pas se produire car ces espèces ne se croisent pas dans l'espace (elles peuvent se rencontrer dans l'espace si dans les mêmes cercles pointillés) (b). L'interaction 1C n'est pas possible car la longueur de la langue de Sp-1 et la profondeur du tube floral de Sp-C ne correspondent pas. Dans notre exemple, sur les 9 interactions possibles, seulement 3 ont lieu.

Malgré leur rôle dans la pollinisation des cultures et des plantes sauvages, les pollinisateurs sauvages (Hallmann et al., 2017, 2021) et l'abeille domestique (Potts, Roberts, et al., 2010) déclinent. Différents facteurs semblent impliqués dans ce déclin : l'usage de pesticides, la diminution de la disponibilité en sites de reproduction, les parasites ainsi que le réchauffement climatique (Goulson et al., 2015; Potts, Biesmeijer, et al., 2010). Le rôle de la diminution des **ressources florales**, et donc des ressources alimentaires, dans le déclin des insectes pollinisateurs est largement admis car ce sont leur ressource alimentaire (Baude et al., 2016; Roulston et al., 2007). Il a ainsi été montré expérimentalement qu'augmenter la quantité de ressources maintient les insectes pollinisateurs (Blaauw & Isaacs, 2014; Ebeling et al., 2008). La diversité des ressources florales semble également essentielle au maintien des pollinisateurs, en effet différentes conditions sont requises pour qu'une interaction se mette en place entre une plante et un pollinisateur (Fig. 0. 1). La première est liée à la correspondance dans la phénologie des espèces¹⁰ : un binôme de plante et de pollinisateur peut interagir si leur période de floraison et d'activité se recoupe (Manincor et al., 2020; Peralta et al., 2020). La deuxième condition est la rencontre dans l'espace de la plante et du pollinisateur, ce facteur semble déterminant à la vue du renouvellement spatial important des communautés de plantes et de pollinisateurs dans les paysages agricoles (Fried et al., 2019; Rollin et al., 2015). Mais, tandis que les plantes sont immobiles (excepté au stade graine), les insectes pollinisateurs sont capables de disperser sur de plus ou moins grandes distances pour accéder aux ressources florales (Greenleaf et al., 2007). Finalement, la compatibilité morphologique définit la possibilité d'interagir entre une espèce de plante et de pollinisateur s'ils se rencontrent. La littérature fait état de corrélations entre traits des plantes et des pollinisateurs, notamment entre la profondeur du tube floral des plantes et la longueur de la langue des pollinisateurs (Corbet, 2000;

¹⁰ La variation temporelle des stades des vie des organismes.

Klumpers et al., 2019) : c'est le syndrome de pollinisation (Ollerton et al., 2009). Maintenir les communautés de pollinisateurs semble ainsi reposer sur le maintien d'une diversité de ressources florales capable de fournir des ressources à différents moments, endroits et à différents pollinisateurs selon leurs traits morphologiques.

2. (Dis)continuité spatiale et temporelle des ressources florales dans les paysages agricoles

Dans les paysages des grandes cultures, le **colza** (*Brassica napus* L.) et le **tournesol** (*Helianthus annuus*) sont des **cultures dites à floraison massive** (CFM) qui représentent respectivement une surface de 10% et 4% des surfaces cultivées en France (données FAO pour une période allant de 2015 à 2019). Concentrées dans les parcelles agricoles, elles fournissent jusqu'à plusieurs millions de fleurs selon la taille des parcelles (Geslin et al., 2017) et respectivement 10 et 0,08 L de nectar ainsi que 3,5 et 1,8 kg de pollen par hectare et par jour (Horn et al., 2021). D'autres cultures fournissent également des ressources florales dans les paysages agricoles : la luzerne (*Medicago sativa*), le maïs (*Zea mays*), le féverole (*Vicia faba*), le lin (*Linum usitatissimum*) et le pavot (*Papaver somniferum*) mais de façon relativement peu importante du fait de leur faible abondance et/ou faible capacité nutritive. Du fait de la faible diversité des CFM et des périodes de floraison restreintes à quelques semaines au début du printemps (colza) et au milieu de l'été (tournesol), la disponibilité des ressources florales fournies par les CFM est discontinue le temps. Les paysages agricoles sont ainsi marqués par une période sans ressources florales fournies par les CFM entre les périodes de floraison du colza et du tournesol.

La singularité des interactions plantes pollinisateurs suggère que la fourniture de ressources florales de façon continue dans l'espace et dans le temps est une stratégie prometteuse pour la persistance des pollinisateurs qu'ils soient sauvages ou domestiqués et donc pour la pollinisation. Les ressources florales dites sauvages sont diversifiées dans les espaces agricoles. Les HSN sont les habitats abritant l'abondance et la diversité des ressources florales la plus importante. Parmi eux, les bois ou les haies fournissent des ressources de façon stable dans le temps à travers les arbres et arbustes, et les jachères et les friches à travers les plantes herbacées (Cole et al., 2017; Steffan-Dewenter & Tschardt, 2001). Une flore spontanée diversifiée peuple également les parcelles agricoles, ce sont les **plantes adventices** (Bourgeois et al., 2020). Des milliers d'espèces de plantes adventices sont trouvées dans les parcelles agricoles en France et fournissent en plus ou moins grande quantité des ressources florales de façon continue (Jauzein, 1995; Pacini et al., 2003). Parmi les espèces emblématiques on peut citer le coquelicot *Papaver rhoeas* ou le bleuet *Centaurea cyanus* L. (Bosch et al., 1997; Nichols et al., 2019) qui fournissent une grande quantité de nectar accessible pour une diversité de pollinisateurs. Parmi les cultures dominantes des paysages de grandes cultures, il y a en moyenne 19, 28, 18 et 14 espèces en culture de céréale, de colza, de tournesol et de maïs (Bourgeois et al., 2020), la diversité et l'abondance des plantes qu'elles abritent est moins importante qu'en prairie (Gaba et al., 2020) et elles fournissent une quantité moins importante de nectar (Baude et al., 2016). Les parcelles en AB abritent une quantité et une diversité plus importante de plantes adventices (Henckel et al., 2015), d'autres facteurs tels que le paysage ou les pratiques agricoles peuvent également affecter la disponibilité en plantes adventices (Bourgeois et al., 2020; Mahaut et al., 2018).

Ainsi, selon la composition des paysages agricoles, i.e. la surface couverte par les différents types d'habitats, la **continuité spatiale et temporelle** des ressources florales dans les paysages agricoles pourra être assurée ou non. En Fig. 0.2, nous présentons quatre types de paysages. Deux paysages n'assurent pas la continuité spatiale et temporelle de la disponibilité des ressources florales : ce sont des paysages avec peu d'habitats abritant des plantes sauvages, et notamment des HSN ou des parcelles en

AB. La présence de colza et de tournesol dans le paysage augmente la disponibilité des ressources florales dans le paysage mais qu'à certaines périodes (Fig 0.2 a, b). Au contraire, des paysages avec une forte quantité d'HSN ou d'AB, que ce soit des CFM ou non (cultures riches en plantes sauvages), assurent la continuité spatiale et temporelle de disponibilité en ressources florales, tandis que la présence de colza et de tournesol supplémente les paysages en ressources florales (Fig. 0. 2 c, d).

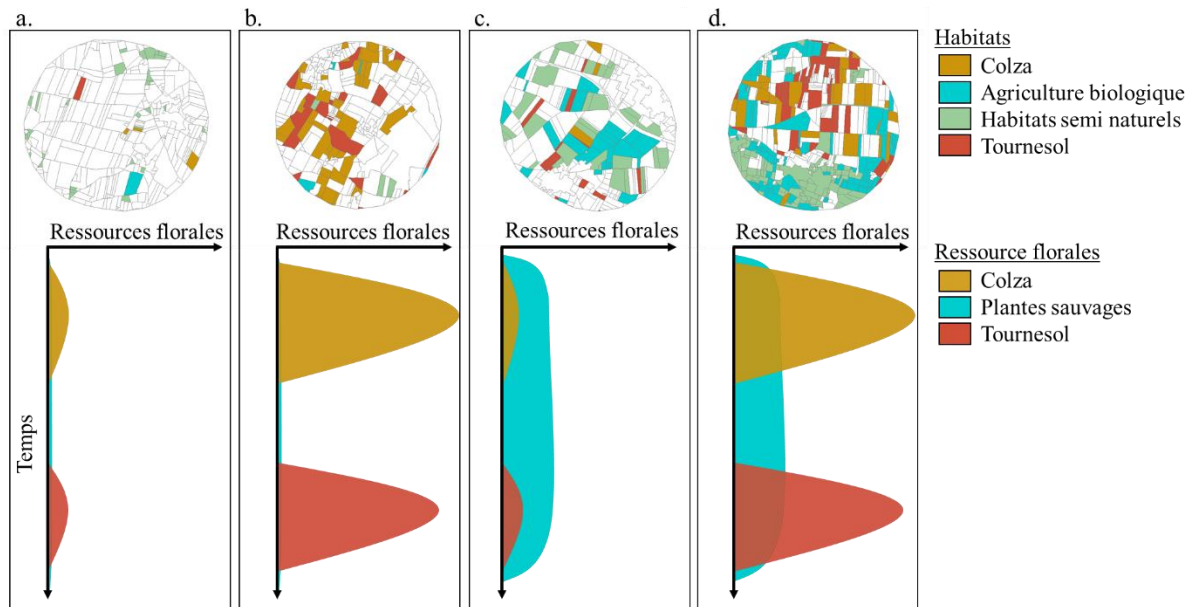


Fig. 0.2 : Présentation de quatre paysages agricoles hypothétiques et de la quantité de ressources florales qu'ils fournissent à travers la saison. Inspiré de Iuliano & Gratton, (2020).

3. Dynamique des interactions plantes-pollinisateurs dans les paysages agricoles

Les HSN et les parcelles en AB, en fournissant une quantité importante de ressources florales abritent une diversité et une abondance importantes en insectes pollinisateurs sauvages (Cole et al., 2017; Sidemo-Holm et al., 2021). Leur capacité à maintenir la diversité et l'abondance des pollinisateurs sauvages, notamment dans le cas des HSN, augmente avec la diversité et l'abondance des ressources florales qu'ils abritent (Fründ et al., 2010; Rollin et al., 2019). Une augmentation de la quantité d'HSN (Bommarco et al., 2012; Steffan-Dewenter et al., 2002) et d'AB (Holzschuh et al., 2008; Lichtenberg et al., 2017) dans le paysage est associée à une augmentation de la diversité et de l'abondance des pollinisateurs sauvages à travers un processus de spillover largement documenté. Ce renforcement de la diversité et de l'abondance des pollinisateurs conduit à une augmentation de l'efficacité de pollinisation par exemple des CFM comme le colza (Bartomeus et al., 2014) ou des plantes sauvages telles que la primevère *Primula veris* (Lindgren et al., 2018). Néanmoins, la quantité d'HSN dans le paysage n'a d'effet sur les pollinisateurs qu'à certaines échelles spatiales, par exemple 250m pour les petites abeilles et 750m pour les bourdons (Steffan-Dewenter et al., 2002). Aussi, la distance aux HSN diminue le taux de visites des fleurs par les abeilles (Jauker et al., 2009; Ricketts et al., 2008). Des fleurs peuvent ainsi ne pas être visitées car trop éloignées des HSN, cela indique que la distance à laquelle les insectes pollinisateurs butinent est limitée dans les paysages agricoles. La dépendance de certains insectes à leur site de nidification (Potts et al., 2005) et la taille des pollinisateurs (Greenleaf et al., 2007) sont impliquées. La distance de butinage des insectes pollinisateurs varie ainsi de quelques centaines de mètres pour les plus petits pollinisateurs à quelques kilomètres pour les plus gros (Greenleaf et al., 2007). Cette limitation de la dispersion a également été observée au sein des parcelles, où les insectes sauvages semblent cantonnés aux bordures des parcelles (Garratt et al., 2018; MacInnis & Forrest, 2019). Même

l'abeille domestique qui disperse surtout à partir des ruches, semble butiner majoritairement sur les bords de parcelles malgré sa grande capacité de dispersion, jusqu'à 10 kms (Beekman & Ratnieks, 2000; Sáez et al., 2012).

Les **pulses de ressources florales** fournies par les CFM attirent les insectes pollinisateurs. Pendant la floraison de ces cultures, l'abeille domestique y est l'insecte le plus abondant (Rollin et al., 2013). Les ressources fournies par les CFM représentent ainsi 35% et surtout 80% de ses besoins annuels en pollen et nectar respectivement (Requier et al., 2015). Une diversité de pollinisateurs sauvages sont également attirés par les CFM (Rasheed et al., 2015; Stanley and Stout, 2014), il y sont néanmoins trois et 20 fois moins abondants que l'abeille domestique dans les cultures de colza et de tournesol respectivement (Rollin et al., 2013). Les insectes pollinisateurs des CFM proviennent majoritairement du paysage alentour et notamment des habitats riches en ressources florales. Un **processus d'attraction** des insectes pollinisateurs des HSN par les CFM a ainsi été mis en évidence (Nicholson et al., 2017). Ce processus d'attraction bénéficie aux espèces cultivées en étant pollinisées par les insectes (Bartomeus et al., 2014) mais au détriment de la pollinisation des plantes sauvages des habitats adjacents. Il a ainsi été montré que l'efficacité de la pollinisation de la primevère officinale *Primula veris* dans les HSN diminue avec la quantité de CFM dans le paysage (Holzschuh et al., 2011) : c'est l'**effet de dilution** (Holzschuh et al., 2016). Ces études ne tiennent néanmoins pas compte du décalage temporel qui peut survenir entre les CFM d'une même parcelle, alors qu'il est suspecté que seules les parcelles à leur pic de floraison contribuent à l'effet de dilution. Aussi, la plupart des études se sont concentrées sur l'effet des pulses de ressources florales fournies par les CFM aux pics de floraison, mais d'autres beaucoup plus rares ont étudié l'effet des CFM dans le paysage après leur floraison. Ainsi, après la floraison du colza, il a été montré que la diversité des pollinisateurs et l'efficacité de la pollinisation du fraisier sont plus importantes dans des prairies placées dans des paysages qui fournissaient quelques semaines plus tôt une grande quantité de colza (Diekötter et al., 2014; Herbertsson et al., 2017). Ces effets paysagers semblent liés aux bénéfices d'une grande consommation de ressources dans les colzas pour la reproduction des insectes (Jauker, Peter, et al., 2012; Westphal et al., 2003).

Les interactions entre pollinisateurs, et notamment entre l'abeille domestique, très abondante, et les pollinisateurs sauvages semblent modifier les interactions plantes-pollinisateurs. De nombreuses études reportent un effet négatif de l'abeille domestique sur les pollinisateurs sauvages (Mallinger et al., 2017; Wojcik et al., 2018) à travers la compétition pour les ressources. La compétition fait référence soit à la réduction de la disponibilité en ressources florales (nectar et/ou pollen) pour une espèce après sa déplétion par une autre espèce : c'est la **compétition par exploitation** (Mittelbach, 2012; Henry and Rodet, 2018), soit à la restriction de l'accès aux ressources florales via des contacts directs entre espèces : c'est la **compétition par interférence** (Gross et al., 2019). En milieu agricole, 40% des ressources utilisées par les pollinisateurs sauvages en HSN le sont également par l'abeille domestique (Steffan-Dewenter & Tschamntke, 2000) mais, sa faible abondance dans ces habitats (Rollin et al., 2013) semble insuffisante pour réduire le taux de visites des plantes sauvages par les pollinisateurs sauvages. C'est l'attraction des pollinisateurs par les CFM qui semble concentrer la pression de compétition pour les ressources. Il a ainsi été suggéré que l'abeille domestique exclut les pollinisateurs sauvages des CFM car les parcelles de colza (Lindström et al., 2016), et de citrouilles (Artz et al., 2011) qui abritent une plus forte abondance en abeille domestique sont aussi celles qui sont les moins visitées par les pollinisateurs sauvages.

IV. Objectifs de la thèse

1. Problématique

La diversité et l'abondance des insectes pollinisateurs déclinent dans les milieux agricoles malgré leur implication dans la pollinisation des plantes sauvages et cultivées (Klein et al., 2007; Ollerton et al., 2011). Les systèmes de production relevant des principes de l'agroécologie, c'est-à-dire valorisant notamment les pollinisateurs et la pollinisation entomophile, s'affiche comme une stratégie efficace pour concilier les insectes pollinisateurs et la production agricole dans les espaces agricoles (Wezel et al., 2014). La disponibilité des ressources florales, c'est-à-dire des ressources alimentaires des insectes pollinisateurs, est un facteur clé dans le maintien de ces insectes et de la pollinisation. Ainsi, l'augmentation de la disponibilité en ressources florales à l'échelle de la parcelle et du paysage agricole est favorable au maintien des pollinisateurs et de la pollinisation (Cole et al., 2017; Holzschuh et al., 2008; Steffan-Dewenter et al., 2002). Néanmoins la dimension temporelle a été peu incluse dans les études alors que les paysages agricoles sont marqués par des pulses de ressources florales fournies par les CFM. Par conséquent, le rôle de la continuité spatio-temporelle de la disponibilité des ressources florales dans le maintien des pollinisateurs et de la pollinisation est un aspect jusqu'à présent peu connu, et dont une meilleure connaissance est indispensable pour la mise en œuvre de stratégies de gestion.

Mon travail de thèse vise donc à comprendre le rôle de la disponibilité des ressources florales dans le maintien des pollinisateurs et de la pollinisation en tenant compte de manière explicite de la dynamique spatiale et temporelle des ressources dans le paysage agricole.

Le premier axe de recherche de mon travail de thèse porte sur la caractérisation de l'effet attractif des CFM sur l'utilisation des ressources florales par les pollinisateurs, les interactions entre l'abeille domestique et les pollinisateurs sauvages pour les ressources, et des conséquences sur la fonction de pollinisation au sein de ces habitats. Nous étudions (i) la structuration spatio-temporelle de la fourniture de ressources florales, plus précisément du nectar ainsi que le patron de butinage de l'abeille domestique au sein d'une CFM à travers la journée à l'échelle de la parcelle agricole et (ii) l'efficacité de la pollinisation au sein d'une CFM, plus particulièrement de la pollinisation par les insectes. Nous analysons ensuite leurs variations en fonction des périodes de floraison des CFM et du contexte paysager. Les effets de la quantité de CFM dans le paysage et du décalage temporel dans la floraison des CFM sont approfondis. Des facteurs paysagers connus pour affecter l'abondance en abeille domestique (e.g. nombre de ruches) ou en pollinisateurs sauvages (e.g. quantité d'AB ou d'HSN qui fournissent des fleurs sauvages) sont également visés. Enfin, nous déterminons si la capacité des CFM à être visitées par les pollinisateurs sauvages à travers la diversité et l'abondance des plantes adventices qu'ils abritent est modifiée par l'abondance en abeille domestique.

Le deuxième axe de recherche concerne l'étude de la complémentarité des autres habitats, les céréales et les prairies, avec les CFM dans l'espace et dans le temps, à travers la compréhension du rôle de ces habitats et des ressources florales qu'ils fournissent dans le maintien des insectes pollinisateurs et de la pollinisation. Nous étudions d'abord l'efficacité de la pollinisation par les insectes en culture de céréale et en prairie à différentes périodes de floraison d'une CFM et après sa floraison et cela le long de gradient de quantité de CFM dans le paysage. Dans ces deux habitats, nous nous intéressons plus particulièrement au rôle de la diversité et de l'abondance des plantes adventices qu'ils abritent dans le maintien des pollinisateurs sauvages en période de floraison des CFM ou en dehors mais également le long de gradients paysagers.

Un axe de recherche transversale aux deux premiers axes porte sur la caractérisation des échelles

d'influence du paysage sur les pollinisateurs et la pollinisation. Pour cela, nous mobilisons la méthode 'siland' développée par Carpentier & Martin, (2021) qui estime les effets et échelle d'influence par maximum de vraisemblance sans faire aucun *a priori* sur l'échelle d'influence.

2. Présentation des chapitres

Les deux axes de recherche sont développés à travers trois chapitres rédigés sous la forme d'articles scientifiques.

Chapitre 1 – Etude multi-échelles de la structuration spatio-temporelle de la déplétion du nectar par l'abeille domestique en culture de tournesol. Dans ce chapitre, nous caractérisons les distributions de la quantité de nectar et de l'abondance en abeille domestique à différentes distances de la bordure en culture de tournesol et cela à différentes heures de la journée et périodes de la saison. Nous déterminons ensuite si ces distributions sont modifiées par la quantité de ressources florales et le nombre de ruches dans le paysage. Ce chapitre est rédigé sous forme d'un article qui sera soumis dans le journal *Apidologie*.

Chapitre 2 - L'efficacité de la pollinisation dans les paysages agricoles : explorer le rôle de la dispersion, de la dilution, et de la complémentarité entre habitats. Nous étudions les variations de la pollinisation entomophile en fonction des ressources florales dans la parcelle et dans le paysage en tenant compte de la période de floraison d'une CFM. Nous utilisons des plantes phytomètres disposées dans des parcelles de différentes cultures distribuées dans des paysages plus ou moins riches en ressources florales. Cet article a été soumis le 15 avril 2021 puis resoumis après révision majeure le 8 août 2021 dans le journal *Landscape Ecology*.

Chapitre 3 - Mise en évidence du rôle complémentaire des cultures à floraison massive et des plantes adventices pour le maintien des pollinisateurs sauvages dans les paysages agricoles. Nous étudions la relation entre les plantes adventices et les pollinisateurs sauvages à l'échelle de la parcelle agricole et sa variation avec l'indicateur utilisé pour caractériser les communautés (diversité, abondance). Nous déterminons également l'effet de la disponibilité en fleurs cultivées dans la parcelle, le paysage, et la saison, de la quantité de fleurs sauvages dans le paysage et de l'abondance en abeille domestique dans la parcelle sur cette relation. Cet article sera soumis au journal *Journal of Applied Ecology*.

A travers ces chapitres, mon travail de thèse apporte des connaissances sur l'utilisation des habitats et des ressources florales par les insectes pollinisateurs et les conséquences de cette utilisation sur la fonction de pollinisation à de multiples échelles spatiales et temporelles dans la mosaïque agricole. L'ensemble de nos résultats devrait contribuer aux réflexions de stratégies de conservation des insectes pollinisateurs et de la pollinisation qu'ils supportent dans les paysages agricoles en intégrant le rôle des pulses de ressources florales fournies par les CFM, le rôle des plantes sauvages, la place de l'abeille domestique et les effets de la taille des parcelles agricoles.

METHODE GENERALE

I. La Zone Atelier Plaine & Val de Sèvre

Le réseau des 14 Zones Ateliers en France tend à comprendre (i) les relations entre biodiversité, activités humaines et fonctions écologiques et (ii) les leviers d'actions d'optimisation des fonctions écologiques, et cela dans des socio-écosystèmes variés (milieux urbains, agricoles, montagnards, fluviaux ; Bretagnolle et al., 2019). Parmi elles, la Zone Atelier Plaine & Val de Sèvre (ZAPVS ; Bretagnolle et al., 2018) est une zone agricole intensive de 435 km² située dans les Deux-Sèvres dans le nord de la région Nouvelle Aquitaine. Chaque année, l'occupation du sol est cartographiée à l'échelle de la parcelle agricole. Cette zone est occupée par plus de 70% de cultures, surtout des cultures céréalières (50%), également des CFM tels que le colza (8%) et le tournesol (12%) et où subsiste une quantité importante de bois, jachères, prairies et haies (22%). Aujourd'hui presque 16% de la surface cultivée est en agriculture biologique. La ZAPVS est caractérisée par une très forte diversité en termes de pratiques agricoles, de comportement des acteurs (agriculteurs, citoyens) ou de paysages. Cette hétérogénéité représente une opportunité pour l'étude de la biodiversité ou du fonctionnement des écosystèmes le long de gradients sociaux et écologiques (Gaba & Bretagnolle, 2020). Des recherches interdisciplinaires et transdisciplinaires sont menées sur ce territoire afin de produire les connaissances nécessaires pour transformer le système agri-alimentaire actuel vers un système agri-alimentaire résilient. Pour ce faire, plusieurs approches sont mobilisées : suivi à long terme de la biodiversité, des fonctions écologiques, de la production agricoles, des paysages, des pratiques agricoles et alimentaires ; expérimentations pour explorer des solutions dans le cadre de l'agroécologie et approches de modélisation pour tester des scénarios d'agencement des paysages ou d'implémentation de politiques publiques.

II. Suivi des plantes, des pollinisateurs, de leurs interactions et de la pollinisation

Des suivis des plantes adventices, des insectes pollinisateurs, et de leurs interactions ainsi que des approches semi-expérimentales permettant la quantification de la fonction de pollinisation sont effectués dans plus d'une centaine de parcelles appartenant à des agriculteurs de la ZAPVS. Les parcelles dans lesquelles les suivis sont faits sont sélectionnées de manière à couvrir des gradients d'intensité de gestion : quantités d'AB, de prairies et d'habitats boisés (haie, forêt). Les suivis sont effectués dans les principales cultures de la ZAPVS et cela à différents moments de la saison. Ceux en colza et en tournesol couvrent majoritairement leur période de floraison, alors que ceux en prairie et en céréales sont effectués pendant et en dehors de la floraison du colza et du tournesol. En parallèle de ces suivies, nous déterminons la phénologie des CFM à travers des observations des taux de couverture des fleurs cultivées à l'échelle de la parcelle agricole et cela à différents moments de la saison. Les données de différents suivis ont été mobilisés pendant la thèse (Fig. 0.3).

Les plantes adventices. Un botaniste échantillonne et détermine les plantes adventices dans 25 quadrats de 1m² dans les parcelles agricoles, cinq sont placés en bordure et 20 en plein champ. Chaque quadrat est divisé en quatre sous quadrats de 0,25m² dans lesquelles les occurrences des espèces de plantes adventices sont enregistrées.

Suivi des insectes pollinisateurs sauvages. Nous échantillonnons les pollinisateurs sauvages avec un ensemble de trois bols de différentes couleurs (bleu, jaune, blanc), remplis d'eau savonneuse. Ceux-

ci sont placés en plein champ pendant quatre jours à hauteur de culture. Les espèces de pollinisateurs capturées sont déterminées par un entomologiste.

Suivi de l'abeille domestique. Le long de trois transects de 50m × 5m (deux en plein champ, et un en bordure), les abeilles domestiques en activité de butinage sont dénombrées.

Suivi de la pollinisation. Pour quantifier l'efficacité de la pollinisation, nous plaçons deux pieds de colza en pots qui correspondent à des plantes phytomètres (une en bordure et une en plein champ) pendant quatre jours dans les parcelles. Nous utilisons comme proxy de l'efficacité de la pollinisation le taux de fructification à l'échelle de la branche des fleurs ouvertes pendant les quatre jours. Les plantes phytomètres sont supplémentées de traitements expérimentaux consistant en la pose de sacs de différents maillages pour séparer les effets des insectes à l'efficacité de la pollinisation, de ceux du vent et de l'autopollinisation.

Plus spécifiquement, nous avons élaboré et mis en place en 2020 un suivi des ressources florales et de l'abeille domestique en culture de tournesol et à l'échelle de la tête de tournesol. Le côté innovant de l'échantillonnage reposait sur la répétition des suivis à différentes positions dans la parcelle, ainsi qu'à différents moments de la journée et de la saison accompagné d'un suivi fin de la phénologie des parcelles suivies, et d'une caractérisation fine de la quantité de ressources florales et du nombre de ruches abrités dans les paysages.

Suivi du butinage de l'abeille domestique Pendant cinq minutes, toutes les 15 secondes, nous avons indiqué les événements correspondant à l'activité de butinage de l'abeille domestique sur la tête de tournesol.

Suivi du nectar Nous avons quantifié la quantité de nectar fourni par la tête de tournesol en plaçant un micro capillaire de 1 µL pendant cinq seconds sur le réceptacle de cinq fleurs pistillées choisies aléatoirement.

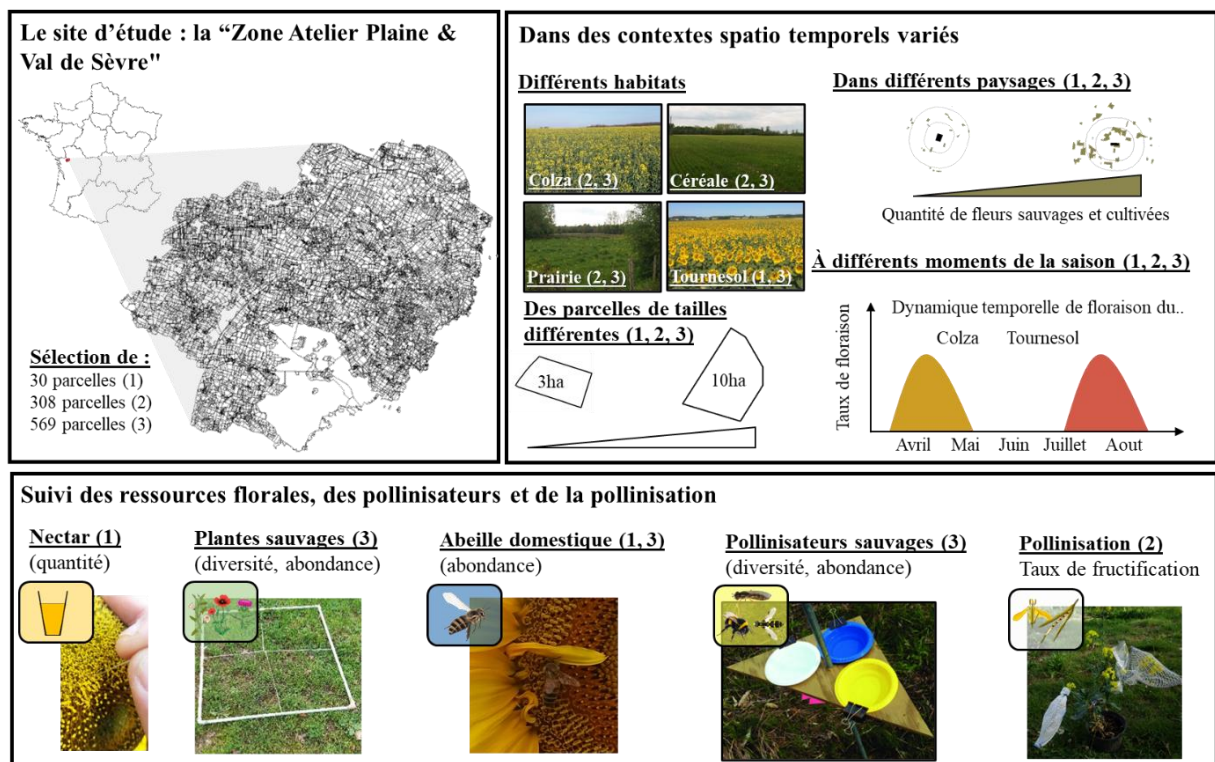


Fig. 0.3 : Vue d'ensemble des observations et design expérimentaux mis en place dans la Zone Atelier Plaine & Val de Sèvre dans le cadre de la thèse. Les chiffres entre parenthèse correspondent aux numéros de chapitres.

CHAPITRE 1 - ÉTUDE MULTI-ECHELLES DE LA STRUCTURATION SPATIO-TEMPORELLE DE LA DEPLETION DU NECTAR PAR L'ABEILLE DOMESTIQUE EN CULTURE DE TOURNESOL

Avant-propos. Avant d'étudier la complémentarité entre les CFM et les autres habitats et ressources qu'ils abritent dans le maintien des insectes pollinisateurs et la fonction de pollinisation, nous nous sommes concentrés sur le patron de butinage de l'abeille domestique pendant le pulse de ressources florales fournies par une culture à floraison massive afin d'appréhender le lien particulier entre ces pulses de ressources florales et le patron de butinage de l'abeille domestique.

Contexte. L'abeille domestique, *Apis mellifera*, est le principal insecte pollinisateur du tournesol, en retour elle consomme le nectar fourni par les fleurs de tournesol pour satisfaire ses besoins alimentaires. Des tournesols éloignés de la bordure de la parcelle peuvent souffrir d'un manque d'abeille domestique car leur visite implique une distance importante à parcourir pour accéder au nectar. Mais, ces dynamiques saisonnière et journalière de la fourniture en nectar au sein des parcelles et le contexte paysager, connu pour affecter l'abondance en abeille domestique, rendent complexe la compréhension de la distribution du nectar et de l'abeille domestique au sein des parcelles de tournesol.

Objectif. Nous avons pour objectifs de (i) caractériser la distribution spatiale du nectar et de l'abeille domestique au sein des cultures de tournesol à travers la journée et la saison et (ii) déterminer comment le nombre de ruches et la quantité de ressources florales dans le paysage modifient ces dynamiques.

Méthode. Nous avons suivi la quantité de nectar et l'abondance en abeille domestique du bord au centre de 30 parcelles de tournesol de tailles différentes et cela à travers la journée et la saison. Les parcelles variaient également dans le nombre de ruches et la quantité de tournesol à différentes périodes de floraison dans le paysage.

Résultats. L'abeille domestique visitait les fleurs de tournesol en période de sécrétion du nectar. La quantité de nectar augmentait avec la distance à la bordure dans les premières heures de la journée, suggérant que l'abeille domestique consomme d'abord le nectar en bordure de parcelle. Plus tard dans la journée, ce patron persistait dans des parcelles placées dans des paysages abritant une faible quantité de ruches et une grande quantité de tournesol à des stades de floraison fournissant du nectar. Nous suggérons que le délai pour que l'abeille domestique disperse vers le centre des parcelles dans la journée est moins important dans des parcelles entourées par une grande quantité de ruches et une quantité limitée de nectar.

Conclusion. Des tournesols à des distances importantes de la bordure peuvent souffrir d'un déficit en abeilles domestique dans certaines conditions paysagères. Pour optimiser la pollinisation du tournesol par l'abeille domestique, nous proposons de conserver des petites parcelles, ou d'augmenter l'abondance en abeille domestique en ajoutant des ruches ou en augmentant la distance spatiale ou temporelle des parcelles de tournesol en fleurs dans le paysage.

Mots clés. *Apis mellifera* | Dynamiques spatiale et temporelle | Patron de butinage | Ressources florales | Taille des parcelles

Multi-scales study of spatio-temporal structuration of nectar depletion by the honeybee in sunflower crop

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I. Abstract

Context. The honeybee, *Apis mellifera*, is the main pollinating insect of sunflower, in return it forages for nectar to meet its dietary requirements. Sunflowers that are far from the field border may suffer from a lack of honeybees because of a high distance to travel to access the nectar. But the seasonal and daily dynamics of nectar supply within the field and landscape context that affect honeybee abundance challenges the understanding of the distribution of nectar and honeybee within the sunflower field.

Aims. We aimed at (i) characterizing the spatial dynamic of nectar and honeybee within sunflower fields throughout the day and the season and (ii) determining how the number of hives and the amount of floral resources in the landscape modify those dynamics.

Method. We surveyed nectar amount and honeybee abundance from the border to the center of 30 sunflower fields varying in their sizes and throughout the day and the season. The fields also varied in the number of hives and in the amount of sunflower at different flowering stages in the landscape.

Results. Honeybees visited the sunflower in period of nectar secretion. The nectar amount increased with the distance from the field border early in the day, suggesting that the honeybee first depleted nectar in the field border. Later in the day, this pattern persisted in fields placed in landscapes sheltering a low number of hives and a high amount of sunflowers at flowering stages providing nectar. The time needed for the honeybee to move from the field border to the field center was suggested to be lower in fields surrounded by a high amount of hives and a limited amount of nectar.

Conclusion. The sunflowers that are far from the field borders may suffer from a deficit in honeybee visitation under certain landscape conditions. To optimize sunflower pollination by the honeybee, we recommend preserving small fields or increasing honeybee abundance by adding hives or by increasing the spatial distance or the temporal mismatch of flowering between the sunflower fields in the landscape.

Key words. *Apis mellifera* | Field size | Floral resource | Foraging pattern | Temporal and spatial dynamics

II. Introduction

Agricultural landscapes consist in mosaics of cultivated fields and semi-natural elements. The role of semi-natural habitats in maintaining biodiversity and ecological functions is largely accepted (Holland et al., 2017; Steffan-Dewenter et al., 2002). But, less is known about the influence of field size on biodiversity, even if it is supposed to constrain the access to the resources for numerous organisms at the most central positions of the fields (Fahrig et al., 2015; E. A. Martin et al., 2019). The honeybee, *Apis mellifera*, is a key species in farmland landscapes as it is the main pollinating insect of crops (Klein et al., 2007), in particular for sunflower crop *Helianthus annuus* of which the seed production benefits from insect pollination up to an increase of 30% (Perrot et al., 2019). In sunflower fields, the honeybee mainly forages for nectar resources on sunflower plants (Requier et al., 2015) while wildflowers are very few visited (Carvalho et al., 2011). The honeybee has a great dispersal ability as it can forage until 10kms in agricultural landscapes (Beekman & Ratnieks, 2000). But, this high foraging distance may be associated to a lack of floral resource (Bänsch et al., 2020) suggesting that the honeybee preferentially forages on flowers at low distances. Within sunflower fields, previous studies have shown that the honeybee decreased in abundance when going away from the field border (Lajos et al., 2021; Sáez et al., 2012). Those studies were however restricted to few meters in the fields while the consideration of the entire border-center gradient in relation to the field size appears essential to highlight potential spatial disparity in sunflower crop pollination.

In addition, variation in nectar amount has an obvious potential to influence honeybee foraging as suggested by the positive relationship detected between the nectar amount and the sunflower visitation rate by the honeybee (Mallinger & Prasifka, 2017). Two factors may affect the availability of nectar in the fields: nectar secretion and nectar depletion. First, nectar secretion by the sunflower is temporally discontinuous within the season (Horn et al., 2021). Nectar secretion occurs at the staminate stage and stops as soon as the pistillate stage begins (Maier, 2014). It may explain the honeybee abundance peak detected in the season in sunflower crop (Chambó et al., 2011). Secondly, nectar depletion mainly involves the honeybee itself as wild pollinators such as bees, bumblebees or hoverflies are less frequently observed visiting sunflowers (Greenleaf & Kremen, 2006; Skinner, 1987). The flower visitation by the honeybee was for example shown to rapidly decrease the amount of nectar available on wildflowers through the day (Hansen et al., 2002). The foraging pattern of the honeybee in the sunflower fields is however rather constant from the morning to the afternoon (Pisanty et al., 2014). As the honeybee seems to preferentially forage in the borders of the sunflower fields, nectar depletion is first expected to be more important in this field position which may then constrain the honeybee to disperse far from the field border to forage. There is thus a need to explore the spatial distribution of nectar amount and honeybee foraging at different time periods to better understand the complexity of the relationship between honeybee foraging and nectar availability in sunflower fields.

Landscape factors affecting honeybee abundance may modify spatial and temporal distributions of nectar and honeybee foraging. The fields sheltering a high honeybee abundance have a higher honeybee visitation rate far from the borders than the fields with a low honeybee abundance (Garratt et al., 2018). Thus, as the intensity of nectar depletion increases with honeybee abundance (Torné-Noguera et al., 2016), one may expect nectar depletion of the most distant flowers to be more important in sunflower fields visited by a high honeybee abundance. Two main factors modify the abundance of the honeybee in the sunflower fields. First, a greater number of hives, sheltering thousands of honeybee workers, in the landscape is known to affect the visitation rate of crop flowers (Cunningham et al., 2016; Rollin & Garibaldi, 2019). Secondly, the increasing amount of floral resources in the landscape, especially those

provided by sunflower is known to reduce honeybee abundance through a dilution effect (Holzschuh et al., 2011). Sunflower or, more generally, mass flowering crops in the landscape are generally considered as a whole providing a homogeneous amount of floral resource (Holzschuh et al., 2016; Lajos et al., 2021). But, variations in sowing dates or cultivar may create a phenological mismatch of few days between sunflower fields leading to a gap between the area covered by sunflower in the landscape and the provision of nectar in the landscape, while the dilution process is expected to occur only when the sunflower provides nectar. Thus, a fine description of the landscapes and the floral resources they shelter is needed, which may have constrained such studies in the past.

In the present study, we aimed to (i) characterize the spatio-temporal distribution of nectar amount and honeybee abundance within sunflower fields and (ii) determine how the amount of sunflower and the number of hives in the surrounding landscape modify those distributions. Improving our understanding of the distribution of honeybee and nectar in sunflower is a methodological challenge as it requires a quasi-simultaneous time-based monitoring on daily and seasonal bases, a spatial monitoring at the field scale, and a survey at the landscape scale to quantify the number of hives and the amount of floral resources. Therefore, we surveyed the nectar and the honeybees in foraging activity in 30 sunflower fields in an intensive agricultural plain during the sunflower flowering period. Fields were of different sizes and were placed along two landscape gradients known to affect honeybee abundance in the fields: the amount of sunflowers and the number of hives in the landscape. In each field, surveys were performed on six sunflower plants distributed by pair at three distances from the field border. Surveys were repeated thrice during the day and five times during the flowering season. We first determined the distribution of the nectar amount and the honeybee abundance during the day and the season. Then, we investigated their spatial distribution within fields through the day and the season. We finally examined how the amount of sunflowers at different flowering stage, thus providing different amount of nectar, and the number of hives in the landscape modified the spatial distribution of nectar amount and honeybees in the fields.

III. Methods

1. Sunflower fields selection

We selected 30 sunflower fields of the LTSER “Zone Atelier Plaine & Val de Sèvre”, an intensive agricultural plain that covers 435km² in western France (Bretagnolle et al., 2018). The pollinator community in the study site is dominated by the honeybee, especially in sunflower fields (>90% of total pollinating insect observations; Rollin et al., 2013). The sunflower covered 14% of the study site, its flowering period was from the end of June to the beginning of September in this temperate area. Among the 30 sunflower fields that were studied in summer 2020, the onset of flowering was on average the 10th of July \pm 7sd days and the average period of flowering was 24 days \pm 5. Sunflower crops belonged to 13 cultivars; field size ranged from 1.2ha to 15.5ha.

2. Nectar amount and honeybee visitation abundance at the sunflower head scale

In each field, we surveyed the amount of nectar and the abundance of foraging honeybees on six sunflower plants (Fig. 1.1a). The plants were randomly selected among those having the main phenology of the field to avoid mismatch effects within the fields.

We first quantified the number of honeybees in foraging activity on each sunflower head through visual observation. The observer stood at 50 cm of the sunflower head. A visual observation lasted five minutes, and the number of honeybees in foraging activity on a sunflower head (i.e., feeding on flowers

or flying around the sunflower head at a distance < 15 cm) was noted each 15 seconds (20 repetitions). **Honeybee abundance** on a sunflower head was the sum of the number of honeybees in foraging activity for the 20 repetitions.

Then, we quantified the **amount of nectar** provided by each of the six sunflower heads. We placed a 1 μ L microcapillary during five seconds on the receptacle of a pistillate floret randomly selected on the sunflower head. This was replicated on five different pistillate florets. The amount of nectar provided by the sunflower head was determined by multiplying the averaged amount of nectar per floret by the number of opened florets on the sunflower head. Indeed, previous studies showed that staminate and pistillate florets provide similar amount of nectar within the sunflower head (Chaudhary & Poonia, 2018; Fazekas et al., 2019). The number of opened florets at the time of the nectar sampling was determined using a constant value of the area covered by an individual floret and an estimation of the area covered by opened florets. This latter estimation was based on three measures of radius on the sunflower head and repeated through the season: the head radius, the head radius occupied by staminate flowers and the head radius occupied by pistillate flowers (see Appendix 1A for details).

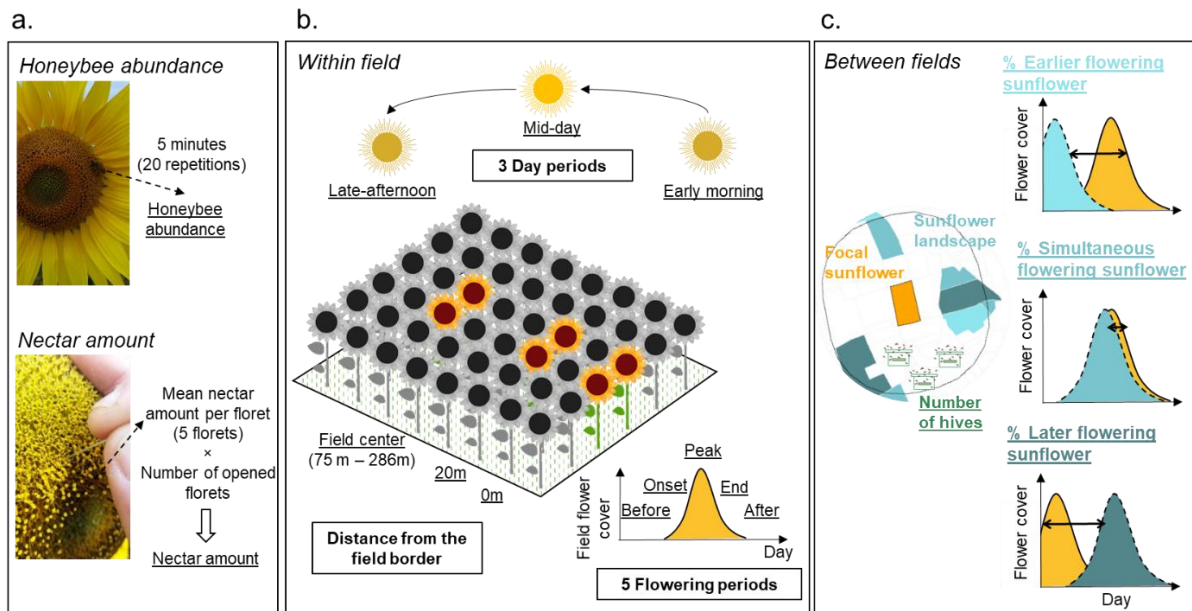


Fig. 1.1: Surveys of honeybee abundance and nectar amount at the sunflower head scale (a) The surveys were repeated through the day period (Early-morning, Mid-day, and Late-afternoon), the flowering period (before, the onset, the peak the end, and after the flowering period), and the distance from the field border (from the field border to the center of the field in field varying in field size). Sunflower fields varied in the number of hives and of %Sunflower (either earlier or simultaneous, later flowering sunflower as compared to the focal sunflower field).

Surveys of the amount of nectar and honeybee abundance on sunflowers were repeated through time and space (Fig. 1.1b). They were performed between 14°C and 39°C in rainless conditions, which are favorable conditions for the honeybee to forage (Abou-Shaara, 2014; Puškadija et al., 2007).

(i) The **distance from the field border**. We selected six focal sunflower plants per field at a continuous distance from the field border. Two were in the field edge (about 1 m from the field border), two were at 20m from the field border, and two were in the center of the fields at a distance ranging from 74m to 286m from the field border due to the variation in field size.

(ii) The **flowering period**. Surveys were repeated at five flowering periods corresponding to five weeks of survey: before, the onset, the peak, the end, and after the flowering. Each week, we surveyed the flower cover in the fields (visual observation taking values from 0% in absence of opened flowers to 100% when all sunflowers of the fields were flowering). The peak period was the week of survey

with the highest flower cover, other flowering periods were assigned relatively to the peak period (e.g. the onset flowering was a week before the peak). The survey was performed on average during 4.43 ± 0.50 sd weeks, observations were lacking for the periods ‘before’ or ‘after the flowering’ in respectively 66% and 33% of the cases.

(iii) The **day periods**. We repeated the survey thrice during each of the five flowering periods: in the early morning (10% and 90% quantiles of hours: 7:45, 9:30), in the mid-day (10:30-17:30) and in the late afternoon (18:30-20:30). Surveys of the three-day periods were performed during different days within the flowering period to avoid any confounding effects between field sampling and weather conditions, one or two days separated two surveys within the same field.

3. Hives and sunflowers in the landscapes

We estimated two variables at the landscape scale expected to influence honeybee abundance and nectar amount in the fields. The variables were characterized in buffer of 500m radius outside the fields. This spatial scale was lower than the average distance of foraging of the honeybee estimated at a thousand of meters (Danner et al., 2016; Hagler et al., 2011) but allowed to finely characterize the landscape context (Fig. 1.1c).

(i) The **number of hives** was the total number of hives in the *a priori* determined 500m buffer area outside the fields. Once during the sunflower flowering period, we explored the whole buffer zone of each studied field in search of hives. By car, we took all the paths and roads, stopped to explore behind the hedges, above the walls, and to visualize the open areas (fields) with binoculars. We referenced the groups of hives and the number of hives per group.

(ii) The **landscape amount of sunflower**. Land cover was monitored at the field scale and recorded in a GIS database (Bretagnolle et al., 2018). The amount of sunflower was the area cropped with sunflower in the buffer zone of 500m radius outside the fields. To consider the heterogeneity between sunflower fields in the landscape in the provision floral resource, we estimated the **%earlier flowering sunflower**, **%simultaneous flowering sunflower**, and the **%later flowering sunflower** in the landscape relatively to the focal sunflower field. We first determined the temporal dynamic of each focal field by explaining the flower cover (visual estimations taking values from 0% in absence of opened flowers to 100% when all sunflowers of the fields were flowering, 12 ± 1.8 observations per field) by the date using GAMs (Generalized Additive Models) estimated for each field. Secondly, one day during the flowering period of the focal field, we visually determined the flower cover and the flowering stage (either before or after the peak flowering) of all sunflower fields occurring in the landscape. Thirdly, those punctual observations in the landscape were compared to the temporal dynamic of flower cover of the focal field. The fields in the landscape whose flower cover was reached with more than 3 days in advance on the predicted flower cover of the focal field were considered as earlier flowering sunflower while those flowering with more than 3 days late on the predicted flower cover of the focal field were later flowering sunflowers. Otherwise, fields in the landscape were considered in the same week of flowering and were thus classified as simultaneous flowering sunflower as compared to the focal field (See Appendix 1B for additional information).

4. Statistical analyses

For all the analyses, the nectar amount and the honeybee abundance were analyzed by linear mixed models and were $\log_{10}(x+1)$ transformed to meet the condition of homoscedasticity of the residuals. We also included for the whole statistical procedure the field identity and the Julian day as random effect

factors to account for repeated observations in the fields and variations in the climatic conditions between days.

Seasonal and daily distributions of nectar amount and honeybee abundance. We first used linear mixed models with the nectar amount and the honeybee abundance as explained variables. We focused on three flowering periods: the onset, the peak, and the end of the flowering, we excluded the data from ‘before’ and ‘after’ flowering as the nectar amount and the honeybee abundance tended toward zero at these periods (Appendix 1C). For each field, we cumulated the six observations of nectar amount and honeybee abundance for each flowering period and each day period ($n = 270$). The explaining variables were the flowering period (a qualitative variable with three levels), the day period (a qualitative variable with three levels) and their interaction.

Spatial distribution of nectar and honeybee through the day and the season. We investigated the distribution of nectar and honeybee along the distance from the field border to the field center. We focused on the periods with the highest amount of nectar and honeybee abundance i.e., the onset and the peak flowering periods. We performed six linear mixed models, one for each flowering period and each day period ($n = 90$), to account for heteroscedasticity between these periods. The two observations of nectar amount and honeybee abundance were cumulated for each flowering period, each day period and each distance from the field border per field. The nectar amount and the honeybee abundance were explained by the distance from the field border, a quantitative variable that we \log_{10} transformed to account for its nonlinear effects. We also included the field size in the models to account for differences in attractiveness between fields.

Spatial distribution related to the landscape context. As in the previous step, we run six linear mixed models, one for each flowering and day periods ($n = 90$). We explained the nectar amount and the honeybee abundance by the distance from the field border, the number of hives, the %Sunflower and their interaction with the distance from the field border. The %Sunflower was measured in the buffer zone of 500m radius outside the fields and included three quantitative variables: % earlier flowering, % simultaneous flowering and %later flowering sunflower as compared to the focal field which allowed to disentangle which flowering lag, through its amount in the landscape, influenced the most the nectar amount and the honeybee abundance.

The analyses were performed with R software, version 4.1.0 (R Core team, 2021). We used the ‘lme4’ package for linear mixed models (Bates et al., 2021), the ‘car’ package (Fox et al., 2020) for type II analyses of variance and the ‘emmeans’ package for the estimations of the effect sizes (Lenth et al., 2020). For all analyses we looked at the diagnostic plots to confirm the hypotheses of normality and homoscedasticity required for linear mixed models. We measured the variance inflation factors of the models to ensure for the absence of multicollinearity.

IV. Results

Together, the six sunflower individuals in the fields provided over the entire survey period (9 observations per individual) on average $198.71\mu\text{L} \pm 184.39\text{sd}$ of nectar and were visited by 69.80 ± 55.46 honeybees. The variation in nectar amount and honeybee abundance was high between and within the sunflower cultivars in the fields (see Appendix 1D). In the buffer zone of 500m radius outside the

focal fields, the number of hives varied from 0 to 65, and %sunflower from 0% to 35%. We found a slight non-significant positive correlation between %Sunflower and the number of hives in the landscape (mean and 95IC of Pearson correlation coefficient: 0.30[-0.07; 0.59], $p = 0.11$). Among the sunflower in the landscape, %earlier, %simultaneous and %later flowering sunflower as compared to the focal field varied from 0% to 34%, 0% to 26% and 0% to 33% respectively. During the peak flowering of the focal field, the fields in the landscape classified as earlier, simultaneous, or later flowering were respectively at the end, the peak, and the onset of the flowering.

1. Temporal distribution of nectar amount and honeybee visitation abundance

The sum of the nectar amount for six sunflower individuals per sampling event was on average $22.50\mu\text{L} \pm 59.47\text{sd}$. The variation of the nectar amount in the fields was mainly explained by the flowering period ($\chi^2 = 47.62$; $df = 2$; $p < 0.001$). The provision of nectar by sunflower was more important at flowering onset and at peak flowering as compared to the end of the flowering period (Fig. 1.2a). During these two flowering periods, we observed the highest proportion of staminate flowers on the sunflower head, $10.44\% \pm 6.19$, $8.93\% \pm 5.42$, and $0.96\% \pm 2.20$ respectively in the onset, the peak, and the end of the flowering period (see Appendix 1A). The nectar amount also varied with the day period although to a lesser extent than with the flowering period ($\chi^2 = 33.03$; $df = 2$; $p < 0.001$); it was higher in the early-morning than in the mid-day or in the late-afternoon (Fig. 1.2a). We did not detect any significant interaction between the flowering and the day periods ($\chi^2 = 5.53$; $df = 4$; $p = 0.24$).

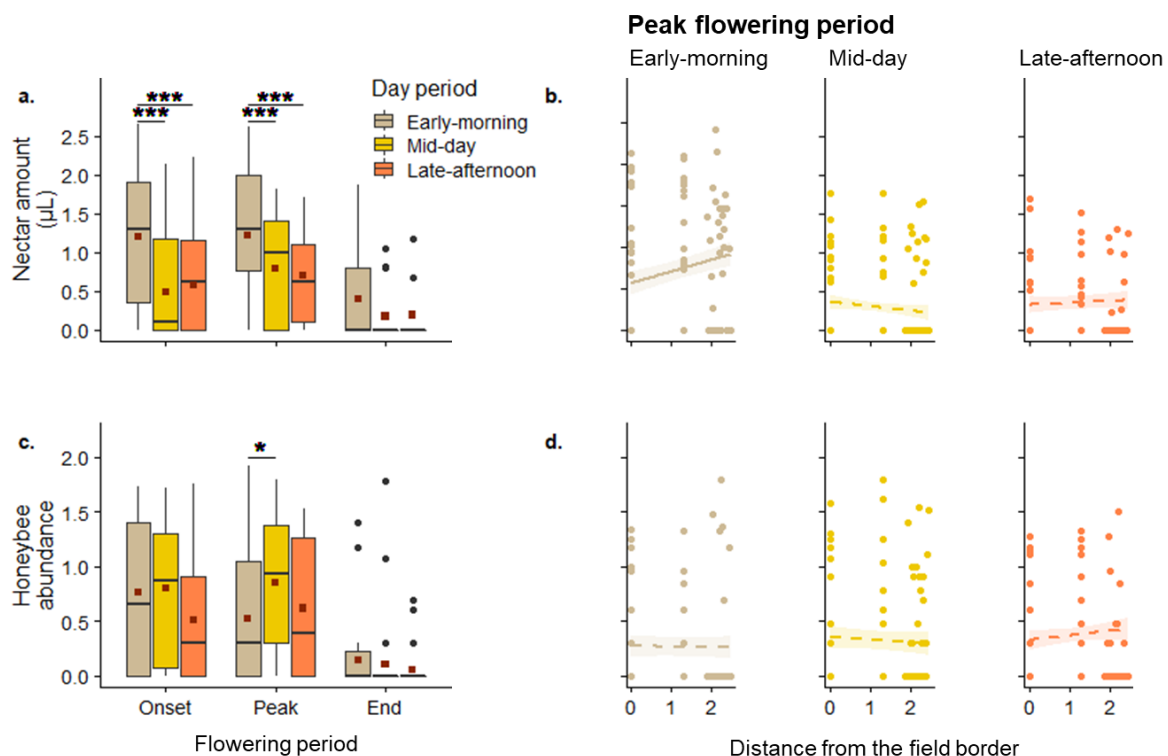


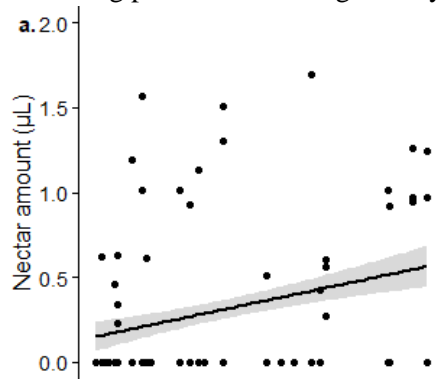
Fig. 1.2: Variation of nectar amount (a, b) and honeybee abundance (c, d) with the flowering and the day periods (a, c) and with the distance from the field border (\log_{10}) during the three-day periods (early morning, mid-day, and late afternoon) at the peak flowering period. Both explained variables were $\log_{10}(x+1)$ transformed. We represented (a, c) the raw data (boxplot) and the predicted means (red square) and indicated significant differences between the levels of the day period within the flowering period (p -value: *** < 0.001 ; ** < 0.01 and * < 0.05). Then, we presented (b, d) the raw data (dots), the predicted relationships and the standard errors (solid lines if significant, dashed lines if non-significant effects).

During the five minutes visual observation, the abundance of honeybee foraging on the six sunflower heads per field was on average 7.90 ± 14.29 . The seasonal foraging pattern of the honeybee

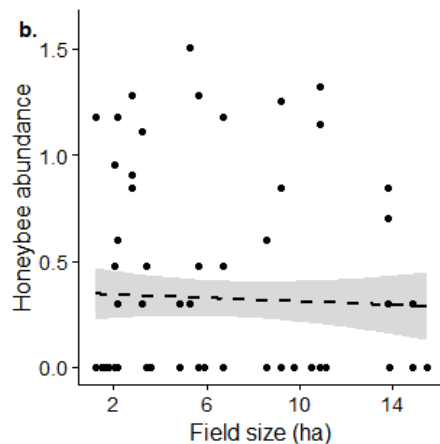
was similar to this of the nectar amount with strong variations of honeybee abundance during the flowering period ($\chi^2 = 69.90$; $df = 2$; $p < 0.001$): the honeybees were more abundant at the flowering onset and at peak flowering than at the end of the flowering period (Fig. 1.2c). The daily pattern of honeybee abundance was however less pronounced as compared to this of the nectar amount ($\chi^2 = 5.96$; $df = 2$; $p = 0.05$). The honeybees were more abundant in the mid-day, followed by the early-morning and the late-afternoon (Fig. 1.2c). We found no significant interaction between the day period and the flowering period ($\chi^2 = 6.08$; $df = 4$; $p = 0.19$).

2. Within field distributions of nectar amount and honeybee abundance

The effect of the distance from the field border on the nectar amount was studied throughout the flowering periods and during the day. The spatial distribution of the nectar amount in the day was quite



different between the flowering periods. At flowering onset, we did not find any effect of the distance from the field border whatever the day period. In the peak flowering period, in the early morning the nectar amount was higher in the farthest sunflowers from the field border ($\chi^2 = 4.46$; $df = 1$; $p = 0.03$). In the mid-day and late afternoon, there was no effect of the distance from the field border (Fig. 1.2b). The amount of nectar was significantly higher in larger fields as compared to smaller ones, but only in the late afternoon ($\chi^2 = 5.71$; $df = 1$; $p = 0.02$; Fig 1.3a).



Our analyses revealed that the honeybee abundance did not vary with the distance from the field border whatever the flowering period and the day period (Fig. 1.2d). Also, the field size had no effect on the honeybee abundance (Fig. 1.3b).

Fig. 1.3: Variation of the nectar amount (a), and the honeybee abundance (b) with the field size. The raw data of nectar and honeybee surveyed in the late afternoon at peak flowering period are presented as well as the predicted relationships (solid lines if significant, dashed lines if non-significant effects) and the corresponding standard errors.

3. Variation in nectar amount and honeybee visitation abundance with the landscape context

At flowering onset, the number of hives and the %Sunflower in the surrounding landscape of the focal fields had no effect on the nectar amount (Appendix 1E). By contrast, at peak period, the patterns of nectar distribution significantly varied with the number of hives and %Sunflower especially at mid-day (Table 1.1a). The amount of nectar was significantly higher in fields surrounded by a high amount of sunflower flowering earlier or simultaneously than the focal field. This pattern was enhanced on plants located at the most important distances from the field border (Fig. 1.4a). The number of hives in the surrounding landscape also affected the nectar, with a higher nectar amount far from the field border in fields with a low number of hives in their landscapes (Fig. 1.4b). In the early morning, we also observed a significant higher amount of nectar in fields with higher amount of later flowering sunflower in the landscape, but without interaction with the distance to the field border. In the late afternoon, the

nectar amount increased with the distance from the field border in the fields surrounded by a high amount of sunflower flowering earlier or simultaneously, while the number of hives had no effect (Table 1.1a).

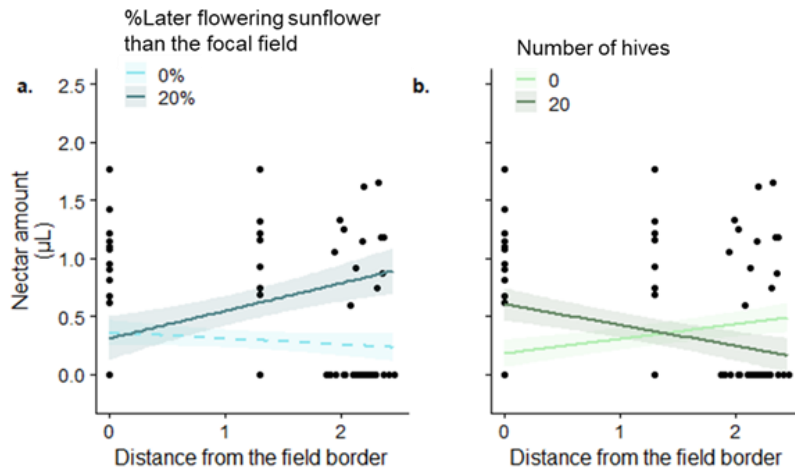


Fig. 1.4: Variation in the nectar amount with the distance to the field border in landscapes varying in % of later flowering sunflower than the focal field (a) and in the number of hives (b) in mid-day of the peak flowering period. The raw data are presented (dots) as well as the predicted relationships and their standard errors. Solid lines represent significant relationships, while dashed ones represent non-significant relationships. We predicted the nectar amount in relation to the distance to the field border for low (10% quantiles) and high (90% quantiles) amounts of %Sunflower and numbers of hives.

At the onset of flowering, the honeybee abundance, as well as the nectar amount, were not modified by the number of hives and %Sunflower (Appendix 1E) but they were at the peak period (Table 1.1b). In the early morning, the honeybee abundance was significantly higher in the fields surrounded by a high number of hives (Fig. 1.5a) and by a high %earlier flowering sunflower (Fig. 1.5b). In early morning and mid-day, we also found a higher honeybee abundance at the most important distances from the field border in the fields surrounded by a high amount of later flowering sunflower than the focal field (Fig. 1.5c).

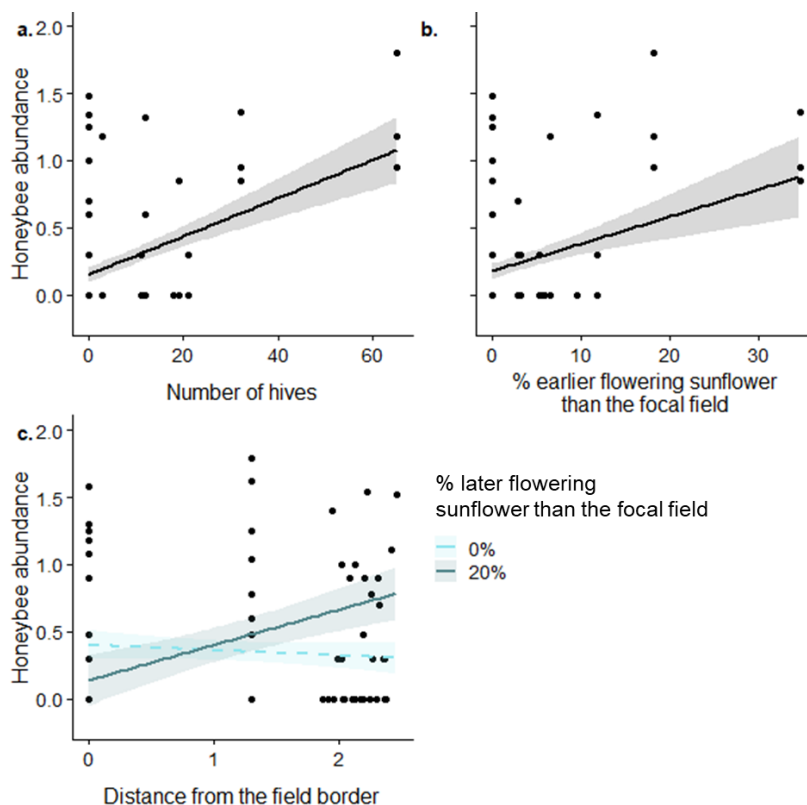


Fig. 1.5: The effect of the number of hives (a), the %earlier flowering sunflower (b) and the distance from the field border (c) on the honeybee abundance at the pea flowering period. Raw data are represented by dots and the predicted relationships by lines (solid if significant, else dashed), the shaded areas represent the standard errors. The represented %later flowering sunflower correspond to the 10% and 90% quantiles.

Table 1.1: Summary statistics of the models explaining the nectar amount (a) and the honeybee abundance (b) with the distance from the field border, the number of hives, %Sunflower in the landscape of either earlier, simultaneous, or later flowering sunflower than the focal field and field size (see step iii of the statistical analyses) as explanatory variables. We present the models performed on the peak flowering period at the three-day periods (in the early-morning, the mid-day and the late-afternoon). We indicated X² and p-value from type II analyses of variance and mean \pm se of effect size (slopes).

		Peak flowering period									
		Early-morning			Mid-day			Late-afternoon			
		df	X ²	p	Effect	X ²	p	Effect	X ²	p	Effect
a. Nectar amount	Distance to field border	1	4.41	0.04	0.144 \pm 0.068	0.15	0.70	0.023 \pm 0.057	1.13	0.29	-0.057 \pm 0.053
	Number of hives	1	0.55	0.46	-0.007 \pm 0.011	3.66	0.06	0.010 \pm 0.006	0.02	0.89	0.001 \pm 0.006
	%Later sunflower	1	4.21	0.04	0.028 \pm 0.014	4.11	0.04	0.014 \pm 0.007	2.10	0.15	0.010 \pm 0.008
	%Simultaneous sunflower	1	0.05	0.82	0.005 \pm 0.021	4.43	0.04	0.021 \pm 0.011	0.13	0.72	0.004 \pm 0.010
	%Earlier sunflower	1	0.91	0.34	0.019 \pm 0.022	2.95	0.09	-0.018 \pm 0.011	1.19	0.27	-0.011 \pm 0.011
	Field size	1	1.49	0.22	-0.033 \pm 0.030	0.30	0.58	0.008 \pm 0.016	3.22	0.07	0.026 \pm 0.016
	Distance \times Number of hives	1	0.14	0.71	-0.002 \pm 0.006	5.05	0.02	-0.011 \pm 0.005	0.10	0.75	0.001 \pm 0.005
	Distance \times %Later sunflower	1	0.01	0.93	-0.001 \pm 0.008	4.23	0.04	0.015 \pm 0.007	4.86	0.03	0.015 \pm 0.007
	Distance \times %Simultaneous sunflower	1	1.25	0.26	0.013 \pm 0.012	3.50	0.06	0.019 \pm 0.010	5.54	0.02	0.021 \pm 0.009
	Distance \times %Earlier sunflower	1	0.06	0.81	-0.003 \pm 0.012	0.89	0.34	0.009 \pm 0.010	0.84	0.36	-0.008 \pm 0.009
b. Honeybee abundance	Distance to field border	1	0.02	0.89	-0.009 \pm 0.038	0.50	0.48	0.039 \pm 0.058	0.31	0.58	-0.024 \pm 0.042
	Number of hives	1	4.64	0.03	0.010 \pm 0.005	0.27	0.60	0.003 \pm 0.006	1.13	0.29	0.006 \pm 0.006
	%Later sunflower	1	1.56	0.21	0.008 \pm 0.007	0.35	0.55	0.004 \pm 0.008	4.56	0.03	0.017 \pm 0.008
	%Simultaneous sunflower	1	0.10	0.76	0.003 \pm 0.010	0.48	0.49	-0.007 \pm 0.011	2.72	0.10	0.017 \pm 0.012
	%Earlier sunflower	1	4.47	0.03	0.020 \pm 0.010	0.10	0.75	0.004 \pm 0.012	0.79	0.37	0.010 \pm 0.012
	Field size	1	0.01	0.93	-0.001 \pm 0.014	1.18	0.28	0.016 \pm 0.015	0.75	0.39	-0.013 \pm 0.016
	Distance \times Number of hives	1	2.29	0.13	0.005 \pm 0.003	0.35	0.55	0.003 \pm 0.005	2.57	0.11	0.006 \pm 0.004
	Distance \times %Later sunflower	1	4.73	0.03	0.010 \pm 0.005	4.50	0.03	0.015 \pm 0.007	3.23	0.07	-0.009 \pm 0.005
	Distance \times %Simultaneous sunflower	1	1.84	0.17	0.009 \pm 0.007	2.55	0.11	0.016 \pm 0.010	2.66	0.10	0.011 \pm 0.007
	Distance \times %Earlier sunflower	1	0.25	0.62	0.003 \pm 0.007	0.03	0.87	-0.002 \pm 0.010	1.63	0.20	0.009 \pm 0.007

V. Discussion

We studied the spatio-temporal distributions of the nectar amount and the honeybee foraging within sunflower fields and along the day, and the way the landscape context modified these distributions. We first showed that the honeybee intensively foraged at the onset and at the peak flowering periods on sunflower plants (Fig. 1.2). This seasonal pattern of the honeybee foraging on sunflower, already described (Chambó et al., 2011; Pisanty et al., 2014), matched with the periods of high availability of nectar, that is in periods of nectar secretion when pistillate flowers are available on sunflower heads (Maier, 2014). At this period, the sunflowers continuously secrete nectar (Chabert et al., 2020), but secretion appeared to be rapidly compensated by nectar depletion in the day as high amounts of nectar were mainly available in the first hours of the day (Fig. 1.2). We suggest that the nectar resource renews in the night and is depleted as the honeybee forages in the day. The honeybee was already shown to deplete nectar on rosemary crop (Torné-Noguera et al., 2016) or on wild plants as bramble (Wignall et al., 2020). Also, the decreasing amount of nectar along the day was already highlighted on two species of trees (Hansen et al., 2002). The authors in the latter study attributed this pattern to nectar depletion by the honeybee for two reasons. First, the daily pattern was less marked for flowers with insect exclusion indicating the minor contribution of nectar evaporation to the decrease in the nectar amount throughout the day. Secondly, the honeybee accounted for more than 90% of the total number of visits of the flowers. Although wild insects visit sunflower for nectar resource (Jadhav et al., 2011), their contributions to nectar depletion may be minor according to their relative low abundance in sunflower in our study site, less than 5% of the visits (Rollin et al., 2013). As in the study of Hansen et al., (2002), when depletion overpassed nectar secretion and that sunflower sheltered few nectar, we showed the honeybee to still abundantly visit the sunflowers (Fig. 1.2) suggesting that the nectar provided by the sunflowers stayed the privileged floral resource for the honeybee probably due to the continuous nectar secretion. Later in the season, as soon as the nectar is no longer produced, the honeybee may move toward other sunflower fields with a later phenology. Indeed, we found the honeybee abundance to increase in the fields when surrounded in the landscape by a high amount of sunflower flowering earlier, that did not provide nectar anymore (Fig. 1.5b). The honeybee may also disperse to other habitats providing wildflowers to support their dietary needs (Magrath et al., 2017; Requier et al., 2015). We also detected variations in nectar amount and honeybee abundance from a cultivar to another, while variation in nectar quality was less important (Appendix 1D). But the number of cultivars in our study (13 cultivars for 30 fields), which is representative of the high number of cultivars used in farmland, did not allow us to explore this effect in our study. Some cultivars were already shown to secrete more nectar than others (Cerrutti & Pontet, 2016) while nectar depletion may be less important for some cultivars as the depth of florets constrains the access to the nectar for pollinating insects (Prasifka et al., 2018).

Our results suggested that the honeybee modified the spatio-temporal structuration of nectar depletion and in turn its own foraging pattern. There was a higher nectar amount in sunflowers far from the field border in the morning (Fig. 1.3b) suggesting that the honeybee traveled few distances to forage in the first hours of the day. This pattern confirms previous studies showing the honeybee to be more abundant in the most peripheral positions of the sunflower fields (Lajos et al., 2021; Sáez et al., 2012), we however did not detect any spatial structuration of the honeybee abundance. Such a spatial structuration in nectar depletion may require a full bloom in the field as the lower amount of nectar in the field border was only detected in peak flowering period. A few hours after having detected spatial

structuration in nectar depletion, we showed the nectar amount to be low and homogeneously distributed within the field (Fig. 1.2a, Fig. 1.3b, c) suggesting that the honeybee dispersed to the most important distances from the field border where a high amount of nectar was still abundantly provided. The day period may thus explain discrepancies between studies showing either neutral (Pisanty et al., 2014) or negative effects (Lajos et al., 2021) of the distance from the field border on the honeybee abundance. Our results also suggested that the honeybee moved from the field border to the field center later in time in fields with a low honeybee abundance as compared to the fields sheltering a higher honeybee abundance. We indeed showed that a high amount of nectar persisted in the day far from the field border when the fields were surrounded by a low number of hives and a high amount of floral resources (Fig. 1.4). The persistence of nectar in the fields was also more important in the largest fields (Fig. 1.3). The honeybee was also shown to visit the sunflowers more abundantly at more important distances from the field border in the spatial contexts in which the nectar provided by the sunflower persisted far from the field border (Fig. 1.5c). These results differ from those of Garratt et al., (2018) who showed the honeybee to forage far from the border of oilseed rape fields when the honeybee abundance was high in the fields, i.e. supplemented in hives. This suggests different foraging behaviors of the honeybee between sunflower and OSR that may result from a lower honeybee abundance (Rollin et al., 2013) or a higher amount of nectar provided per unit area in oilseed rape than in sunflower (Horn et al., 2021). Intraspecific exploitative competition is suspected to constrain the honeybee to forage at most important distances within the fields in OSR and faster at these positions in sunflowers when honeybee abundance was high. Other factors such as cooperation (Seeley, 1986) or interference behavior (Cairns et al., 2005) may also modify the foraging pattern of the honeybee within the sunflower fields and have to be disentangled from exploitative competition.

Previous studies indicated that there were several potential limitations for agroecological practices in agricultural landscapes involving large fields as this kind of landscape shelters a lower biodiversity of weeds, pollinators or predators (Fahrig et al., 2015) and a lower level of ecosystem services (E. A. Martin et al., 2019). Considering the positive relationship between the honeybee visitation abundance and the sunflower pollination (Pisanty et al., 2014), the main strategy of sunflower pollination optimization relied on the increase of the honeybee abundance through the deposition of hives in the landscape (Cunningham et al., 2016; Perrot et al., 2019; Rollin & Garibaldi, 2019). Although large fields in our study are relatively small compared to those in other study sites, e.g. our larger field was seven times smaller than the larger field in the study of Lajos et al., (2021), our results suggested that increasing field size was linked to a higher degree of dependence of the most central positions to the landscape context. The deficit in honeybee pollination far from the field border may be compensated by adding hives or by increasing the temporal lag between the flowering of sunflowers in the landscape, by modulating the sowing date for example. Despite the high availability of the honeybee to pollinate sunflowers, the maintenance of the diversity of wild pollinators in agricultural landscapes seems necessary for two reasons. First, the deficit of honeybee pollination far from the field border may be compensated by the bumblebees thanks to their high dispersal ability (Greenleaf et al., 2007). The honeybee may also constrain the bumblebees to forage at important distances from the field border as suggested by Lindström et al., (2016) thus allowing spatial complementation in crop pollination (Miñarro & García, 2018; Pisanty et al., 2016). Secondly, the conservation of wild pollinators is critical considering the decline of honeybees (Potts, Roberts, et al., 2010) as they are able to efficiently pollinate sunflower crop (Mallinger et al., 2019). Their efficiency in pollinating crops seems however restricted to small fields, as they are mainly observed foraging near the field border due to their low dispersal

ability and their dependence to nidification sites (Sardiñas et al., 2016). To disentangle if wild pollinators are able to replace and/or complement the honeybee in pollinating sunflower crop, more studies are needed on the foraging behavior of wild pollinators in sunflower crop in fields with high or low honeybee abundance.

Authors contributions. MR, SG and LC conceived and planned the field work. MR and LC collected and entered the data. MR, SG and FC conceived the study. MR analyzed the data with significant contributions of SG, FC and OM. MR, SG and FC discussed and interpreted the results. MR, SG and FC wrote the paper with significant contributions of OM.

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Conflict of Interest. The authors declare that they have no conflict of interest.

Data availability statement. The datasets generated and used during the study are available from the corresponding author on reasonable request.

CHAPITRE 2 - L'EFFICACITE DE LA POLLINISATION DANS LES PAYSAGES AGRICOLES : LE ROLE DU SPILLOVER, DE LA DILUTION ET DE LA COMPLEMENTARITE ENTRE HABITATS

Avant-propos. Nous avons constaté dans le chapitre précédent que l'abeille domestique visite largement les cultures à floraison massive pendant que celles-ci fournissent du nectar. Le processus de dilution de l'abeille domestique est également suspecté d'intervenir car la consommation du nectar par l'abeille domestique en culture de tournesol est moins importante dans des paysages fournissant une quantité importante de ressources florales via les tournesols. Aussi, dès lors que les cultures à floraison massive fournissent moins de ressources, l'abeille domestique disperse vers d'autres habitats du paysage. Nous avons donc étudié ici la capacité d'une CFM (le colza), des prairies et des cultures de céréales à soutenir la pollinisation, et plus particulièrement la pollinisation par les insectes à travers différents contextes passagers et à différentes périodes de la floraison du colza.

Contexte. Reconnu comme un service écosystémique essentiel dans les paysages agricoles, la pollinisation est menacée par le déclin des pollinisateurs, notamment dû à l'homogénéisation du paysage et le déclin des ressources florales. Cependant, il y a une compréhension encore limitée de l'interaction entre les éléments du paysage et le pulse de ressources florales fourni par les cultures à floraison massive sur la pollinisation.

Objectifs. Les objectifs de l'étude étaient de (i) déterminer comment l'efficacité de la pollinisation varie avec la quantité de ressources florales dans la parcelle et dans le paysage à travers la période de floraison du colza et (ii) de quantifier la magnitude des processus de pollinisation.

Méthodes. Nous avons mesuré l'efficacité de la pollinisation (le succès de fructification) en utilisant des plantes de colza phytomètres déposées dans des prairies, céréales et colza, qui varient dans la quantité de ressources florales à l'échelle de la parcelle et du paysage (quantités de colza, d'habitats semi-naturels et d'agriculture biologique utilisées comme proxy). La contribution des différents processus de pollinisation était déterminée en utilisant une expérimentation d'ensachement sur les plantes phytomètres.

Résultats. L'efficacité de la pollinisation était améliorée dans les périodes et les paysages avec une grande quantité de fleurs de colza, et d'habitats semi-naturels via une plus forte abondance en pollinisateurs. Notre expérimentation d'ensachement révèle également une complémentarité entre habitats pour les pollinisateurs, car la pollinisation par les insectes dans les prairies et les céréales était plus importante après la floraison du colza, en particulier dans des paysages riches en colza en ce qui concerne la pollinisation par les gros insectes.

Conclusion. La disponibilité en ressources florales guide la pollinisation par les insectes à travers des processus d'attraction, de spillover et de complémentarité spatiale et temporelle entre habitats. Ces résultats suggèrent que pour maximiser l'efficacité de la pollinisation dans les paysages agricoles qui abritent des cultures de colza, il faut inclure une combinaison d'habitats qui fournissent des ressources florales de façon continue dans le temps.

Mots clés. Composition du paysage | Correspondance temporelle | Pollinisation par les insectes | Habitats semi-naturels

Pollination efficiency in farmland landscapes: exploring the relative roles of spillover, dilution and complementarity between habitats

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I. Abstract

Context Recognized as a critical ecosystem service in farmland, pollination is threatened by the decline of pollinators, notably due the homogenization of the landscape and the decline of floral resources. However, there is still limited understanding of the interplay between landscape features and the pulses of floral resources provided by mass-flowering crops.

Objective The goals of this study were to (i) determine how pollination efficiency varies with the amount of floral resources at field and landscape scales through the oilseed rape (OSR) flowering period and (ii) quantify the magnitude of the pollination processes involved.

Methods We measured pollination efficiency (fruiting success) using OSR plant phytometers placed in grassland, cereal and OSR fields varying in quantity of floral resources at both field and landscape scales (amount of OSR, SNH and OF). The individual contributions of different processes to pollination were determined using a bagging experiment on plant phytometers.

Results Pollination efficiency was enhanced during both the temporal period and in landscapes with a high amount of OSR flowers, and SNH as a result of higher pollinator presence. Our bagging experiment also supported a complementarity between habitats for pollinators, as insect-pollination in grassland and cereals was higher after OSR flowering, especially in OSR-rich landscapes, in regard to large-insect-pollination.

Conclusions The floral resource availability drives insect-pollination through attraction, spillover, and spatial and temporal complementarities between habitats. These results suggest that maximizing pollination efficiency in farmland landscapes partly consisting of OSR fields should include a combination of habitats that provide continuous floral resources.

Key words. Insect-pollination | Landscape composition | Semi-natural habitats | Temporal matching

II. Introduction

Agricultural landscapes are temporally and spatially highly dynamic mosaics of annual crops and semi-natural elements. Landscape features such as crop diversity, or semi-natural habitat (SNH) surrounding fields, are increasingly recognized as key factors determining biodiversity and its associated ecosystem services (Dainese et al., 2019; Fahrig et al., 2011, 2015; E. A. Martin et al., 2019). However, despite the presumably strong effects of crop phenology or temporal changes in land use on the availability of resources and nesting habitats for species (Schellhorn et al., 2015), few studies have investigated the role of landscape features on biodiversity or ecosystem services at different times, either on an annual basis or at the crop rotation level (Le Féon et al., 2013; Rusch et al., 2011; Vasseur et al., 2013). Maintaining pollinating insects is critical because of their key role in agroecosystem functioning through the pollination of both crops and wild plants (Klein et al., 2007; Ollerton et al., 2011). Yet, these insects may be particularly sensitive to temporal resource limitation since they rely exclusively on nectar and pollen (Roulston & Goodell, 2011), both available only for a few days in individual flowers (Elzinga et al., 2007; Rathcke & Lacey, 1985).

Blooms of mass-flowering crops largely exceed the amount of floral resources provided by wild plants, and are therefore highly attractive to bees (Holzschuh et al., 2011). However, this high amount of floral resources occurs only during a limited period of time, a temporal pattern that may have cascading shortage effects on bees and pollination over the season in agricultural landscapes (Diekötter et al., 2014; Requier et al., 2017). Given that bees are optimal foragers and highly mobile organisms, temporal lags between flowering peaks either in a particular field or at the landscape scale may result in a mismatch between the local number of flowers to be pollinated and the number of available pollinating insects (Fijen et al., 2019; Herbertsson et al., 2017). Hence, sustaining pollinator populations in agricultural landscapes requires maintaining spatial and temporal continuity of floral resources as suggested by Mallinger et al. (2016). Ways to enhance the provision of complementary floral resources in space and time include increasing the amount of SNH (Rollin et al. 2013) and organically farmed (OF) fields that host higher density of wild plants (Requier et al., 2015; Wintermantel et al., 2019), or diversifying landscape composition (Meyer et al., 2007; Petersen & Nault, 2014). However, increasing the diversity of flower availability may have considerable effects on pollinators and pollination. For instance, mass-flowering crops may attract pollinators from surrounding SNH and/or OF fields. These movements can negatively affect wild plant species that have overlapping flowering periods with crops, but at the same time may increase seed production in crops due to higher pollination efficiency (Holzschuh et al., 2011). A high density of mass-flowering crops can also have potential negative consequences on crop pollination (reduced seed production due to lower pollinator abundance) through the dilution of available pollinators during their flowering period (Holzschuh et al., 2011, 2016).

While a number of studies have explored the relationships between bees and landscape features, the efficiency of insect pollination related to landscape elements while considering temporal variation in floral resource availability has been little studied. This study attempted to address this gap by exploring how pollination efficiency, in particular insect pollination, varies with landscape composition both throughout the season, including the flowering period of a mass-flowering crop, and afterwards. Pollination efficiency was measured with a standardized metric, using the fruiting success of oilseed rape (*Brassica napus* L., OSR hereafter) plant phytometers as a proxy to allow comparisons in space and time. Several studies have used crop species as plant phytometers to estimate pollination efficiency: for example strawberry in SNH (Castle et al., 2019) or sunflower or radish in crop fields (Bennett & Isaacs, 2014; Hass et al., 2018). Our OSR plant phytometers were placed in three different crop types

(grassland, cereal and OSR fields), in fields varying in the amount of local floral resources, as well as in their surrounding landscapes, and at different times during OSR flowering periods. The focal fields thus differed both in the amount and duration of floral resource availability, e.g., high local floral resources in OSR fields during OSR blooming, and much lower after OSR flowering. Floral resources provided by wild plants were rather constant over time, moderate in grasslands, and lower in cereal and OSR fields (Bourgeois et al., 2020; Cole et al., 2017; Frankl et al., 2005).

The focal fields were distributed along three landscape gradients determined by the amount of SNH, OF and OSR crops. The amount of floral resources around fields thus differed, with a presumably high and constant availability of wildflowers in landscapes rich in OF (Hardman et al. 2016) and SNH (Cole et al., 2017), but a more heterogeneous availability of floral resources in landscapes with a high level of OSR, from a very high amount during OSR flowering to reduced resources outside the flowering period.

OSR is a mass-flowering crop that is mainly self-pollinated, however insect pollination – involving both large insects such as honeybees (Lindström et al., 2016; Perrot et al., 2018) and smaller insects such as wild bees (Perrot et al., 2018; Zou et al., 2017) or, to a lesser extent hoverflies (Jauker, Bondarenko, et al., 2012) – also contributes to yield (Perrot et al., 2018). Therefore, to disentangle the contribution of the pollination processes involved (pollination via large or small insects, wind, or self-pollination), we supplemented the phytometers with a bagging experiment (using bags of different mesh sizes on selected phytometer branches). When placed in OSR fields, especially during peak OSR flowering, OSR phytometers were expected to show higher pollination efficiency because of higher OSR pollen availability and/or higher abundance of pollinators attracted to the flowering OSR field. The bagging experiment allowed differentiating between these two processes: no difference in fruiting success between control flowers compared to bagged flowers (excluding insects) would suggest higher levels of OSR pollen leading to higher pollination, while higher fruiting success in control flowers compared to bagged flowers would suggest a higher number of insect pollinators. We also predicted a lower pollination efficiency of OSR phytometers in landscapes with high amounts of OSR as compared to those with lower amounts of OSR, based on the hypothesis of the dilution of insect pollinators. Similarly, we predicted higher pollination efficiency in landscapes with high amounts of SNH and OF as a result of higher pollinator abundance and attraction of insects to OSR. Finally, positing complementarity between habitats we predicted a higher pollination efficiency of OSR phytometers placed in cereals and grasslands after the peak OSR flowering than during this peak, further predicting that the pattern would be enhanced in OSR-rich landscapes by a spillover effect.

III. Materials & methods

1. Study site

The study was carried out in spring from 2015 to 2019 in the Zone Atelier Plaine & Val de Sèvre (hereafter ZA-PVS; Fig. 2.1a), a research site of 435 km² in central-western France (46°14'N 0°28'W) that is part of the Long-Term Social-Ecological Research (LTSER) network. Land cover was monitored each year at the field scale by field workers and recorded in a GIS database (Bretagnolle et al., 2018). The study site was dominated by annual crops (almost 75% on average during the five years of study) that include more than 30 crop types. In the cultivated area, the most dominant crops during the study period were cereals as wheat or barley (54%) followed by sunflower (12%) and maize (12%) which flower in summer, then OSR (8%) and peas (4%). For this study, the amount of OF was calculated,

including all organically farmed fields. These covered between 6% (2015) and 9% (2019) of the cultivated area. These OF fields consisted mainly of cereals (about 50%), followed by sunflower (10%) while less than 1% were OSR fields. We excluded grasslands because these were included in the amount of SNH, together with hedgerows and fallow and set-aside land. We considered as grasslands, meadows (permanent grasslands >6 years old) and alfalfa, clover, or mixed leguminous/grass (temporary grasslands, generally <5 years old).

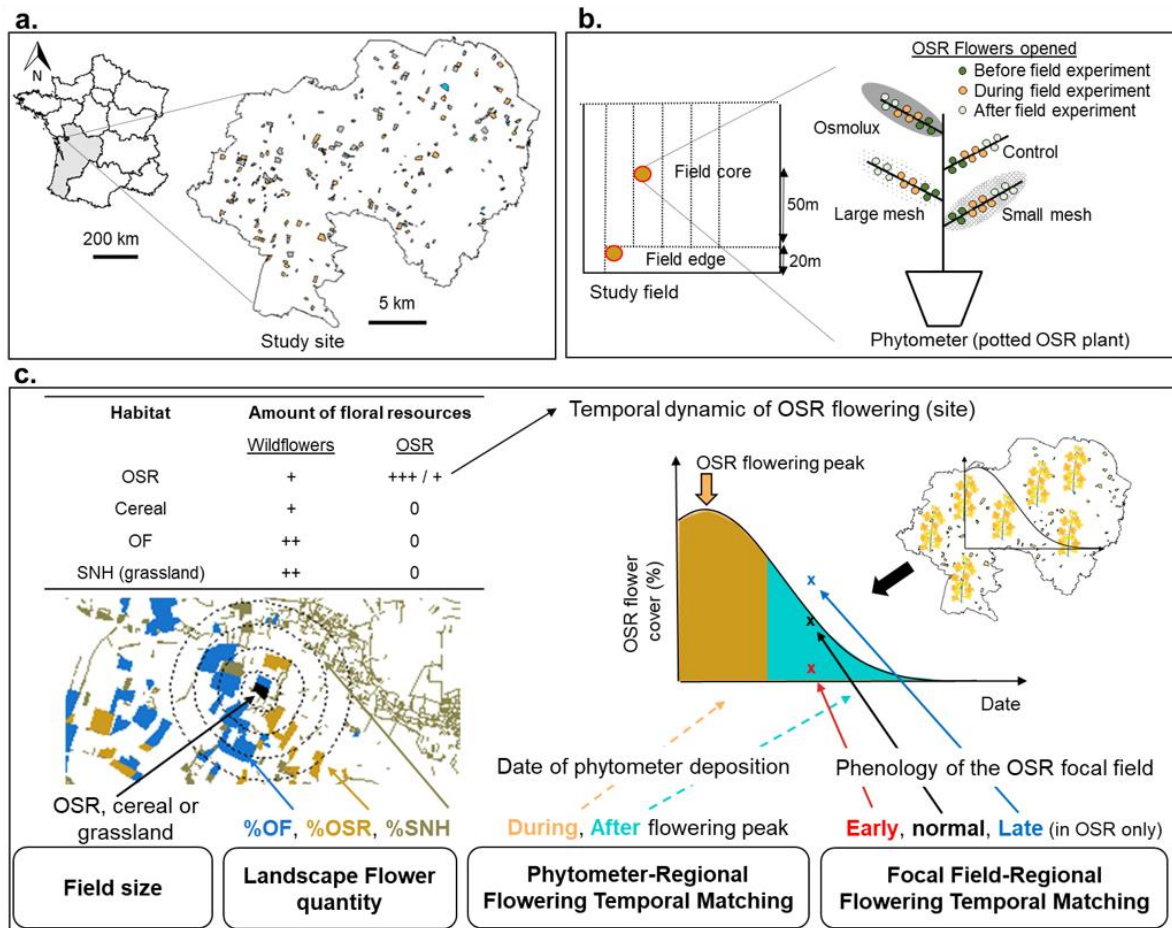


Fig. 2.1: (a) The experimental design was set up in the LTSER Zone Atelier Plaine & Val de Sèvre, a study area situated in central western France. Oilseed rape plant phytometers were placed in OSR fields (yellow), cereal fields (grey) and grasslands (blue) from 2015 to 2019. (b) In each farmer's field, we placed two OSR phytometers (circles), one at the edge and one in the core of the field. Four branches were tested, one with a control treatment, one with a large mesh treatment, one with a small mesh treatment and one with an Osmolux treatment. In OSR, the flowering sequence goes from the base to the apex. We discriminated between flowers that opened during the experiment from flowers that opened before or after the field experiment. (c) Plant phytometers were deposited in OSR, cereals or grasslands; field size was used as a proxy of the amount of floral resources at the field scale. %OSR (oilseed rape), %SNH (semi-natural habitats) and %OF (organic farming) were used to estimate 'Landscape Flower Quantity'. We provided information about the amount and type of floral resources provided by the habitats (focal or landscape ones) based on literature (Bourgeois et al., 2020; Gaba et al., 2020; Hardman et al., 2016; Hegland & Boeke, 2006; Sidemo-Holm et al., 2021): +++: flower cover > 50%, ++: flower cover > 10%, +: flower cover > 0%, 0: flower cover = 0%) The amount of flowers provided by wild plants is rather constant (Cole et al., 2017). To account for the temporal variation of OSR flower cover we developed two variables: 'Phytometer-Regional Flowering Temporal Matching' described the period of OSR flowering during which phytometers were placed in the fields (during or after OSR flowering peak) and 'Focal Field-Regional Flowering Temporal Matching' defined the temporal deviation between flowering in the OSR focal field and OSR flowering in the study site and was thus designed only for OSR fields in contrast to the other three variables.

2. OSR plant phytometers

We used OSR plants as phytometers to measure pollination efficiency. Phytometers allow pollination efficiency to be studied independently of resource availability (e.g. water, nutrients) so that variation is only influenced by insect abundance and pollen availability (Castle et al., 2019; T. S.

Woodcock et al., 2014). We used fruiting success as a proxy of pollination efficiency. Following Jauker et al. (2012), fruiting success was measured by the ratio of pods and flowers on an OSR plant branch (Fig. 2.1b). We collected individual OSR plants in cultivated fields at the end of March each year. Plants were transplanted in 3 L pots and placed in an insect-proof greenhouse to avoid any insect pollination. Potted plants were watered as needed and no fertilizer was added. A total of 616 OSR plant phytometers were used over the study period (198 in 2015, 196 in 2016, 94 in 2017, 58 in 2018 and 70 in 2019).

From OSR peak flowering (the beginning of April, though this depends on the year) to post-flowering (mid-May), phytometers were placed in OSR fields (124 fields in total over the five years), cereal fields (110 fields in four years) and grasslands (46 fields in three years; Fig. 2.1a) for four days, corresponding to the average flowering period of an individual OSR flower (Mesquida & Renard, 1981). Two plant phytometers were placed per field, one in the field core and one at the edge (Fig. 2.1b), to account for variation in pollinator communities between these two field compartments (i.e. small pollinators are generally more abundant at field borders; Ricketts et al. 2008; Garratt et al. 2018), and therefore potential differences in the magnitude of small-insect pollination. On each OSR phytometer, we selected four branches of similar size and flowering stage, one of which became a control branch. On this branch, open flowers were tagged with two colour rings, delineating along the branch the portion in open flower stage. After four days, we counted the number of flowers that further opened in the field and identified them using another colour mark on the branch (Fig. 2.1b). Plants were then placed back in the insect-proof greenhouse for pod ripening. When plant phytometers reached maturity (i.e. after seed maturation), we collected all pods on each experimental branch, either under treatment or control (see below and Appendix 2A for details on experimental protocols). Fruiting success was obtained by counting the number of flowers that produced pods on each branch between the marks and then calculating their proportion. We excluded 12.3% of the phytometers from the study because of missing data, e.g. broken or dried branches that did not produce pods (7.9% of fields were without data).

Pollinator exclusion by bagging

For each OSR phytometer, the three other branches apart from the control branch were selected for exclusion treatments. Exclusion was used to assess the relative magnitude of large and small insect, wind, and self-pollination (Fig. 2.1b) and to separate from the effects of higher pollinator abundance from effects of higher amounts of OSR pollen. The exclusion treatments consisted of covering a branch with bags of different mesh sizes depending on the study target: (i) an Osmolux bag allowing air but not pollen flow (Osmolux treatment: OS) thus permitting only self-pollination, (ii) a mesh of 0.6 mm allowing only wind or self-pollination (small mesh treatment: SM), and (iii) a mesh of 3.0 mm allowing wind, self-pollination and pollination by small insects (small wild bees and hoverflies) with an abdomen thinner than 3 mm (large mesh treatment: LM). The absence of a bag on the control branches allowed self-, wind and insect pollination by small or large insects (honeybees and bumblebees with an abdomen larger than 3 mm). To assess the magnitude of each pollination process, we computed dimensionless effect sizes (varying between -1 and 1) between paired treatments as the ratio of the difference in fruiting success between treatments from their sum. A positive value indicated that fruiting success was higher in the first treatment compared to the second. Paired treatments included (1) control versus SM (complete exclusion of insects) to assess the magnitude of insect-pollination; (2) control versus LM (exclusion of large insects) to assess the magnitude of large insect-pollination; (3) LM versus SM to assess the magnitude of small insect-pollination; and (4) SM versus OS (exclusion of wind-pollination) to assess the magnitude of wind-pollination. Self-pollination magnitude (5) was estimated using the fruiting success in the OS treatment.

Four measures of OSR floral seasonality and availability in focal fields

To account for spatial and temporal variations in floral resource quantity at both local and landscape scales, we derived four measures of floral resources from our data (Fig. 2.1c).

(i) **Field Size.** Field size was used as a proxy of the quantity of available flowers at field scale, assuming that the amount of flowers was proportional to the field size, i.e. larger fields had more floral resources than smaller ones. Floral resources referred to OSR flowers in OSR fields, as wildflowers were minor compared to OSR flowers in this crop, and to wildflowers (mainly weed species) in grasslands and cereals. Previous studies in our site indicated a higher diversity and abundance of weeds in grasslands (average \pm sd: 22 ± 10 species and 308 ± 128 plants/m² respectively) than in cereals (12 ± 10 and 153 ± 176) or in OSR (17 ± 4 and 153 ± 83 ; Gaba et al. 2020; Bourgeois et al. 2020). By using field size as a proxy, we assumed that the quantity of flowers depended more on the field area than on the local flower density. In our study, field size varied from 1.1 to 27.6 ha for OSR, from 0.7 to 33.7 ha for cereals and from 0.2 to 24.1 ha for grasslands. By contrast, flower density generally varies from 6.75 to 12.75 OSR plants/m² (Momoh & Zhou, 2001), from 1% to 5% of wildflower density in cereal fields (Sidemo-Holm et al. 2021), and 1% to 13% in grasslands (Hegland & Boeke, 2006), i.e. five to ten times less than the variation in field size.

(ii) **Landscape Flower Quantity.** Floral resource quantity at the landscape scale varied with the amount of OSR, SNH and OF in the surrounding landscape at a given radius. Our phytometers were placed along gradients of OSR flowers provided by OSR crops (%OSR), and wildflowers provided by SNH and OF (Cole et al., 2017; Sidemo-Holm et al., 2021). These were estimated in buffer zones excluding the focal fields (distances between focal field centroids and borders were 165.7 ± 58.9 m in OSR, 167.5 ± 59.4 m in cereals, and 116.7 ± 62.8 m in grasslands). For each crop type, fields were selected to maximize gradients of %OSR (min–max values in 250 m and 1000 m buffer radii: 0–55%; 0–25%), %SNH (0–72%; 0–38%) and %OF (0–76%; 0–53%). The landscape gradients were uncorrelated with crop type. The Landscape Flower Quantity provided by OSR, SNH and OF was estimated in buffer zones with various radii, specific for each type of pollination process and each crop type. At their respective buffer scales of maximum effect, %OSR, %SNH and %OF were then used as proxies of total floral resource availability.

(iii) **Phytometer–Regional Flowering Temporal Matching.** Temporal matching between phytometer setting and regional OSR flowering in the study site that year was used to characterize the temporal lag between the flowering period of OSR and the deposition date of plant phytometers in the fields. This metric was calculated differently for plant phytometers placed in OSR fields and those placed in the other two crop types. First, we used generalized additive models (GAMs) to derive, separately for each year, the temporal dynamic of OSR flowering in the study site using % of OSR flower cover collected in OSR fields across the study site (from 0% when no OSR flowers were open in the field to 100% when OSR flowers covered the total area of the field; see Appendix 2B). For phytometers placed in OSR, we identified the period of OSR peak flowering from the fitted GAMs for each year as the range between the maximal estimated OSR flower cover and a relative 20% reduction of OSR flower cover. The choice of a 20% threshold was determined in order to balance the sampling dates with equal representation in both categories. The time period in days (ranging from 100 to 118 Julian days depending on the year) thus defined the peak flowering period. Phytometers placed in OSR fields during that period were considered to be placed at the peak flowering period, and those placed outside this range were considered to be placed after the peak flowering period. For phytometers placed in cereals and grasslands, we used a different threshold: a 60% reduction of OSR flower cover indicated

the end of flowering (rather than 20% as in OSR fields). This difference in threshold accounted for the fact that the phytometers were placed later (on average 12 days) than in OSR fields, thus balancing sample sizes between the two categories required delaying the threshold value later in the season (Appendix 2B).

(iv) **Focal Field–Regional Flowering Temporal Matching.** Temporal matching between OSR focal field flowering and OSR regional flowering in the study site for a given year referred to the temporal lag between the flowering of the focal OSR fields and the flowering of OSR at the site scale. This parameter was calculated only for plant phytometers placed in OSR fields. Here we used the % of OSR flower cover collected in OSR fields. Cumulating all data for a given year, we used a GAM to derive the deflowering pattern according to date and its intra-year variability. Using two quantiles (33% and 66%), for any given date we defined three categories based on % of flower coverage in a given focal field: OSR fields were either relatively early, i.e. below 33% deflowered compared to average kinetics, relatively late (over 66%), or normal, i.e. within the range (33–66%; Appendix 2B).

3. Statistical analyses

In a first step, we conducted preliminary analyses to investigate the potential effect of the position of the plant phytometers in the field (core *versus* edge). As no significant differences were detected, the two values were averaged per treatment, field, and date (Appendix 2C). The sample size in our study was thus $n = 308$ fields. We then explored differences in pollination efficiency between crop types by using a subset of the data in which all crops were investigated the same year. We used a linear model to test the effect of crop type (three levels) and year (three levels in common between crops) on phytometer fruiting success. For this first set of analyses, we used data only from the control branches.

In a second step, we investigated the effects of ‘Phytometer–Regional Flowering Temporal Matching’ and the amount of floral resources at both field and landscape scales on the fruiting success of plant phytometers. Again, we only used data from the control branches. We built three models, one for each crop type, because (i) ‘Phytometer–Regional Flowering Temporal Matching’ was estimated differently for phytometers in OSR fields than for those in cereal fields and grasslands and (ii) we assumed the scales of influence of the landscape variables to vary with the focal crop type. We considered fruiting success of OSR phytometers as the dependent variable, and ‘Field Size’, ‘Landscape Flower Quantity’ (%OSR, %SNH and %OF) and ‘Phytometer–Regional Flowering Temporal Matching’ as explanatory variables. We also included the interaction of ‘Field Size’ and ‘Landscape Flower Quantity’ with ‘Phytometer–Regional Flowering Temporal Matching’ (except in grasslands due to a smaller sample size) as a way to identify spillover and dilution processes. Year was included as a fixed effect factor with five, four and three levels respectively in OSR fields, cereal fields and grasslands to account for interannual dynamics of pollinating insects (Perrot et al., 2018; Rollin et al., 2015). For phytometers placed in OSR fields, the models also included ‘Focal Field–Regional Flowering Temporal Matching’ (a qualitative variable with three levels), in interaction with ‘Field Size’ and ‘Phytometer–Regional Flowering Temporal Matching’. The models were estimated using the ‘siland’ method (Carpentier & Martin, 2021) which enables the simultaneous estimation of the effect of all explanatory variables and the buffer radii of landscape variables i.e. radii of ‘Landscape Flower Quantity’ (%OSR, %SNH and %OF) without any prior assumption on the spatial scales of influence. The model residuals were assumed to be Gaussian (see details in Appendix 2D).

Finally, based on the bagging treatments, we investigated how the magnitude of each pollination process (large and small insect, wind, and self-pollination) varied with local, temporal and landscape

factors for each crop type. We built a total of 15 linear models (three crop types with five pollination processes) to explore the effects of the amount of floral resources in the fields and in the landscape as well as ‘Phytometer–Regional Flowering Temporal Matching’. Explanatory variables were the same as those used for the study of fruiting success of the control treatment. As the scale of effects of landscape features was expected to change with the pollination process, we used the ‘siland’ method.

All the analyses were performed using R software (version 3.6.2; R Core team 2019) with the ‘siland’ package (Carpentier & Martin, 2020), ‘car’ for Type II analyses of variance (Fox et al. 2020), ‘emmeans’ (Lenth et al. 2020) for the estimations of effect sizes and ‘BSDA’ for unilateral sign tests (Arnholt and Evans 2017). For each model we looked at residual diagnostics to check for normal hypothesis (quantile-quantile plots) and homoscedasticity (spread of residual did not change with predicted values; Kozak and Piepho 2018). We also confirmed the absence of spatial autocorrelation of residuals with variogram visualization (Dormann et al., 2007). Finally, we verified that the landscape scales of influence were well estimated, i.e. being the global rather than the local maximum of likelihood (profile likelihood visualization) and that the metrics of landscape composition did not correlate to each other at the estimated spatial scales (see Appendix 2E).

IV. Results

The fruiting success of the phytometer control branch (proportion of flowers producing a pod, ranging from 0 to 1) varied with crop type ($F = 10.23$; $df = 2$; $p < 0.001$). Fruiting success was higher for phytometers in OSR fields (mean \pm sd: 0.49 ± 0.28 , $n = 135$) than for phytometers in cereals (0.38 ± 0.28 ; $n = 100$) or grasslands (0.36 ± 0.27 ; $n = 43$). Year ($df = 2$; $F = 13.74$; $p < 0.001$) also had significant effect on fruiting success, but not its interaction with crop type ($df = 4$; $F = 0.16$; $p = 0.96$).

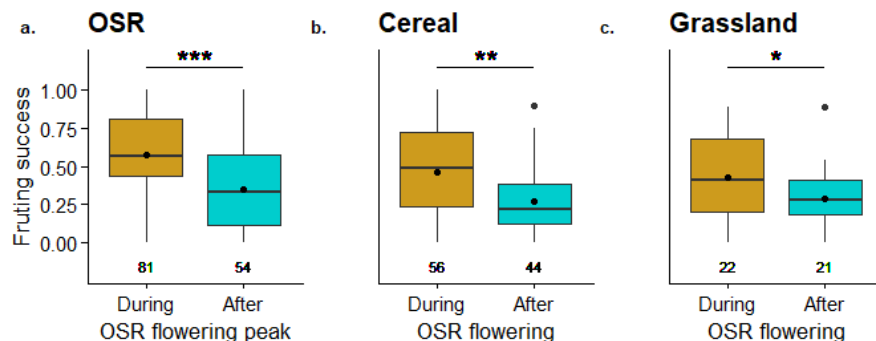


Fig. 2.2: Variation in OSR fruiting success with ‘Phytometer–Regional Flowering Temporal Matching’ in OSR (a), cereals (b) and grasslands (c). Thresholds discriminating ‘Phytometer–Regional Flowering Temporal Matching’ (i.e. during and after OSR flowering / flowering peak) were defined differently for phytometers in OSR fields and for phytometers placed in cereals and grasslands (see ‘Methods’ for details). Quantiles and means (black dots) of raw data are represented and numbers show the sample sizes. Significant differences between levels of ‘Phytometer–Regional Flowering Temporal Matching’ are indicated by asterisks (p-value: *** < 0.001; ** < 0.01 and * < 0.05). Effect sizes: fruiting success was on average greater during OSR peak flowering than after in OSR (0.21 ± 0.05 se; from Table 2.1a model), in cereals (0.15 ± 0.05 ; from Table 2.1b model) and in grasslands (0.19 ± 0.07 ; from Table 2.1c model).

1. Factors affecting the fruiting success of OSR plant phytometers in OSR fields

Using ‘Field Size’ and ‘Focal Field–Regional Flowering Temporal Matching’, as two measures of floral resource availability at field scale, ‘Landscape Flower Quantity’ (measured by %SNH, %OF and %OSR) as a measure of landscape floral resource availability, and ‘Phytometer–Regional Flowering Temporal Matching’ as a measure of temporal deviation in flowering, as well as the interactions between these variables and the year (fixed effect factor), 44.3% of the variance in the fruiting success of phytometers placed in OSR fields was explained (Table 2.1a). Fruiting success strongly varied with year

(15.2% of explained variance), ‘Phytometer–Regional Flowering Temporal Matching’ (14.0%), ‘Landscape Flower Quantity’ (8.7% cumulated for %OSR, %SNH and %OF), and the interaction between ‘Phytometer–Regional Flowering Temporal Matching’ and ‘Field Size’ (2.3%). ‘Focal Field–Regional Flowering Temporal Matching’ had no effect on fruiting success (Table 2.1a).

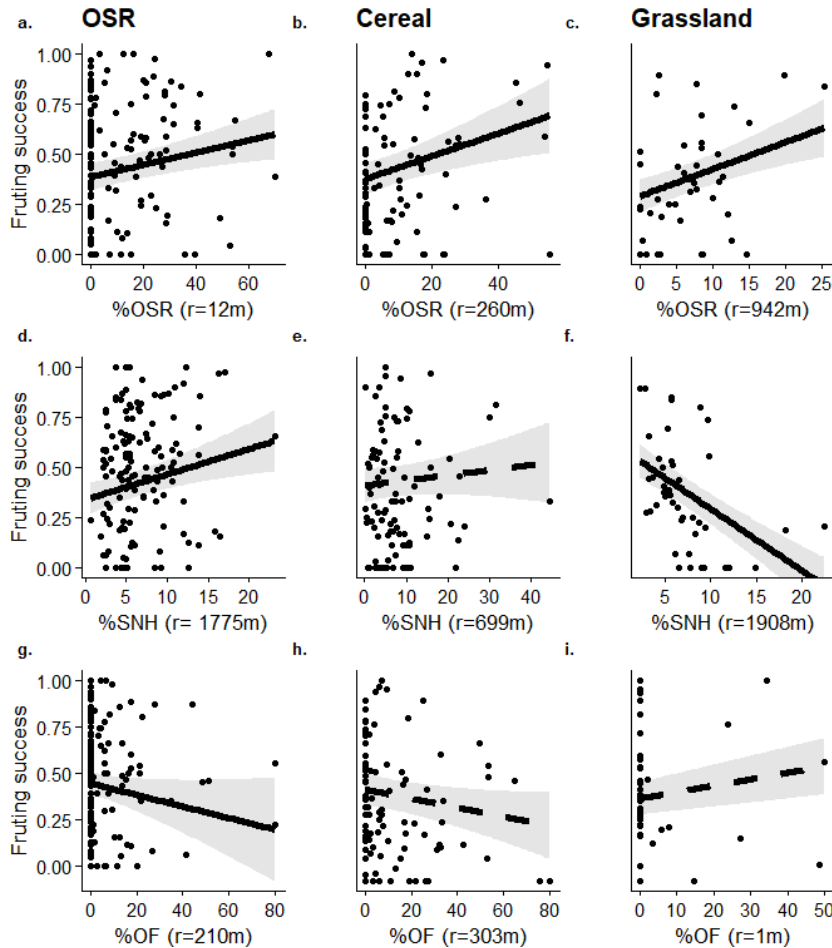


Fig. 2.3: Effect of ‘Landscape Flower Quantity’ on fruiting success of plant phytometers. The effects of %OSR (a, b, c), %SNH (d, e, f) and %OF (g, h, i) were quantified in buffer radii (r value in brackets) estimated by optimization of likelihood outside the OSR fields (a, d, g), cereal fields (b, e, h) and grasslands (c, f, i) in which the phytometers were placed. Dots of different shapes show raw data for each year. The lines show the adjusted relationships and the shaded area the standard error (based on models presented in Table 2.1). Lines in bold show significant effects (p -value < 0.05) and dotted lines non-significant effects. Effect sizes: in OSR, fruiting success increased with %OSR (mean \pm se: 0.0030 ± 0.0013 per %OSR) and %SNH (0.0126 ± 0.0057 per %SNH) and decreased with %OF (-0.0034 ± 0.0015 per %OF). Fruiting success increased with %OSR (0.0057 ± 0.0026 per %OSR) in cereals and in grasslands (0.0134 ± 0.0065 per %OSR), while it decreased with %SNH (-0.0305 ± 0.0080 per %SNH) in grasslands.

Fruiting success was on average higher for phytometers in OSR fields during OSR peak flowering than after (Fig. 2.2a). The effect of ‘Field Size’ differed significantly between the two categories of ‘Phytometer–Regional Flowering Temporal Matching’ (Table 2.1a): during OSR peak flowering, fruiting success tended to decrease with ‘Field Size’, while post-peak it tended to increase (Appendix 2G). The fruiting success of phytometers was significantly modified by %OSR, %SNH and %OF (Table 2.1a): %OSR (Fig. 2.3a) and %SNH (Fig. 2.3d) had a positive effect on fruiting success while fruiting success decreased with %OF (Fig. 2.3g). The estimated scale of effect differed between landscape features, being small for %OSR (12 m outside the fields, meaning that considering the presence of an adjacent OSR field was enough to explain increased fruiting success in the focal field), high for %SNH (1772 m) and intermediate for %OF (210 m outside the fields).

2. Fruiting success of OSR plant phytometers in cereal fields and grasslands

In cereal fields and grasslands, the statistical models explained respectively 35.8% and 54.6% of the variance in OSR phytometer fruiting success (Table 2.1b, c). As with phytometers in OSR fields, the fruiting success in cereal fields and grasslands varied with year, ‘Phytometer–Regional Flowering

Table 2.1: Summary statistics of the models investigating the effects of ‘Phytometer–Regional Flowering Temporal Matching’ and floral resources in the fields (field size as a proxy) and ‘Focal Field–Regional Flowering Temporal Matching’ only for OSR fields) and in the surrounding landscapes (%OSR: % oilseed rape, %SNH: % semi-natural habitats and %OF: % organic farming) on fruiting success in the control treatment in OSR fields (a), cereal fields (b) and grasslands (c). We performed type II analyses of variance. The coefficients of determination of the three models (R^2), the variance explained by each variable (%Var; sum of squares associated to a variable divided by the total sum of squares), the degrees of freedom (df), the F-value (F) and the p-value (p) are presented. Significant values are bold. Estimations of landscape effects and scale of effects were similar without local \times landscape interactions (Appendix 2F).

	a. OSR				b. Cereal				c. Grassland				
	R^2	df	% Var	F	p	df	% Var	F	p	df	% Var	F	p
			44.3%				35.8%				54.6%		
Year		4	15.2	7.13	< 0.001	3	18.1	6.34	< 0.001	2	18.4	7.08	< 0.01
Field size		1	0.0	0.07	0.79	1	0.3	0.27	0.60	1	0.5	0.35	0.56
Phytometer–Regional Flowering Temporal Matching		1	14.0	26.36	< 0.001	1	7.9	8.34	< 0.01	1	9.0	6.97	0.01
Focal Field–Regional Flowering Temporal Matching		2	1.1	1.00	0.37	-	-	-	-	-	-	-	-
%OSR (Landscape Flower Quantity)		1	2.9	5.45	0.02	1	4.6	4.82	0.03	1	5.6	4.31	0.05
%SNH (Landscape Flower Quantity)		1	3.0	5.65	0.02	1	0.4	0.46	0.50	1	19.1	14.73	< 0.001
%OF (Landscape Flower Quantity)		1	2.8	5.32	0.02	1	2.4	2.51	0.12	1	1.7	1.29	0.26
Field size x Phytometer–Regional Flow. Temp. Matching		1	2.3	4.32	0.04	1	0.2	0.20	0.65	-	-	-	-
Focal Field–Reg. Flow. Temp. Matching x Phytometer–Reg. Flow. Temp. Matching		2	1.5	1.41	0.25	-	-	-	-	-	-	-	-
Field size x Focal Field–Reg. Flow. Temp. Matching		2	0.8	0.71	0.50	-	-	-	-	-	-	-	-
%OSR x Phytometer–Reg. Flow. Temp. Matching		1	0.1	0.26	0.61	1	0.5	0.48	0.49	-	-	-	-
%SNH x Phytometer–Reg. Flow. Temp. Matching		1	0.7	1.23	0.27	1	1.0	1.07	0.30	-	-	-	-
%OF x Phytometer–Reg. Flow. Temp. Matching		1	0.0	0.02	0.89	1	0.4	0.39	0.53	-	-	-	-

Temporal Matching’ and the amount of floral resources in the surrounding landscape; however, ‘Field Size’ had no effect (Table 2.1b, c). In cereals, we observed the same pattern as in OSR (Fig. 2.2b, Fig. 2.3b, e, h): fruiting success was higher during OSR flowering than after (Fig. 2.2b), increased with %OSR (Fig. 2.3b) and %SNH, but decreased with %OF, although non-significantly for %SNH and %OF (Fig. 2.3e, h). A strikingly different pattern emerged with grasslands: as in OSR and cereals, the fruiting success of phytometers was higher during OSR flowering, though only slightly (Fig. 2.2c), increased with %OSR at landscape scale (Fig. 2.3c), but decreased with %SNH (Fig. 2.3f). The spatial extent of the effect of landscape differed between crop types, %OSR acted for example at higher spatial scale in grasslands (942 m) than in cereals (260 m) or in OSR (12 m; Appendix 2E).

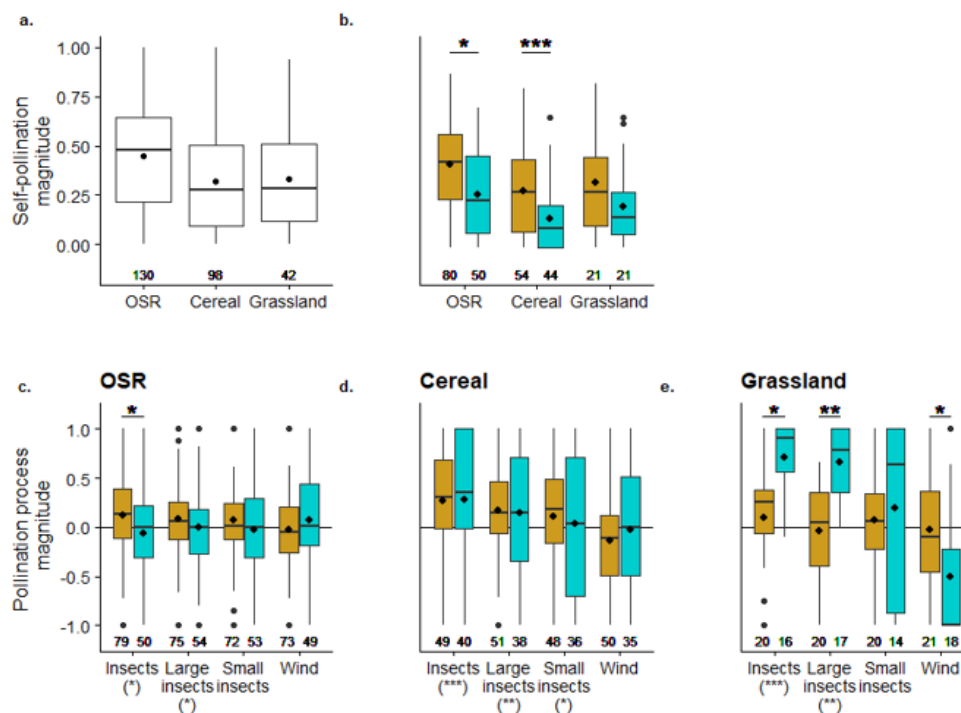


Fig. 2.4: Magnitude of self-pollination between crops (a, b) and other pollination processes in OSR fields (c), cereal fields (d) and grasslands (e) and the variation between categories of ‘Phytometer–Regional Flowering Temporal Matching’: during (orange boxes) versus after (green boxes) OSR peak flowering. The magnitude of pollination processes was estimated using effect sizes, their superiority to zero was tested using unilateral sign tests (p-value: *** < 0.001; ** < 0.01 and * < 0.05 in brackets). Asterisks (p-value: *** < 0.001; ** < 0.01 and * < 0.05) also indicate significant differences between categories of ‘Phytometer-Regional Flowering Temporal Matching’ (see Table 2.2; c-e). Quantiles and means (black dots) of raw data are presented, numbers indicate the sample sizes. Effect sizes: self-pollination was 0.11 ± 0.05 SE greater during OSR peak flowering than after in OSR fields, and 0.16 ± 0.04 (estimation from Table 2.2a model) greater during OSR flowering than after in cereals (from Table 2.2b model). Insect-pollination was 0.27 ± 0.11 SE greater during OSR peak flowering than after in OSR (from Table 2.2a model). Insect-pollination (0.92 ± 0.18) and large insect-pollination (0.88 ± 0.17) were greater after OSR flowering than during, while wind-pollination was 0.73 ± 0.23 greater during OSR flowering than after in grasslands (from Table 2.2c model).

3. Pollination processes of OSR plant phytometers

The magnitude of the various pollination processes affecting the fruiting success of plant phytometers differed slightly between the three crop types. Self-pollination was the main pollination process of OSR phytometers whatever the crop type where they were set in, while wind pollination was low (Fig. 2.4a, c–e). The magnitude of self- and, to a lesser extent, of wind pollination were higher in OSR fields (Fig. 2.4c–e). The second most dominant process of pollination was insect-pollination (Fig. 2.4c–e). In contrast to wind and self-pollination, insect pollination was lower in OSR fields (Fig. 2.4c) than in cereals and grasslands (Fig. 2.4d, e). Of insects, large insects had the greatest effect in all crops,

while the magnitude of small insects was greater than zero only in cereals (Fig. 2.4). Pollination processes also differed quite strongly according to the OSR flowering period during which the phytometer was placed, in addition to the crop in which it was placed (Fig. 2.4c-e). In OSR fields, higher fruiting success (Fig. 2.2a) in the peak flowering period resulted in significantly higher insect pollination (Fig. 2.4c). In contrast, insect pollination dramatically increased in grasslands after the OSR flowering period (Table 2.2c; Fig. 2.4e). No such marked difference was detected for insect pollination in cereals, which was high in both periods (Fig. 2.4d). The relative importance of wind pollination *versus* insect pollination differed between crops, with wind pollination decreasing in grasslands after the OSR flowering period while remaining similar in OSR and cereals throughout the two periods (Table 2.2c; Fig. 2.4c, d, e). Self-pollination was higher during OSR flowering than after in all crops (Fig. 2.4b). Supplementary analyses also showed that self-pollination linearly decreased with the Julian date (Appendix 2H).

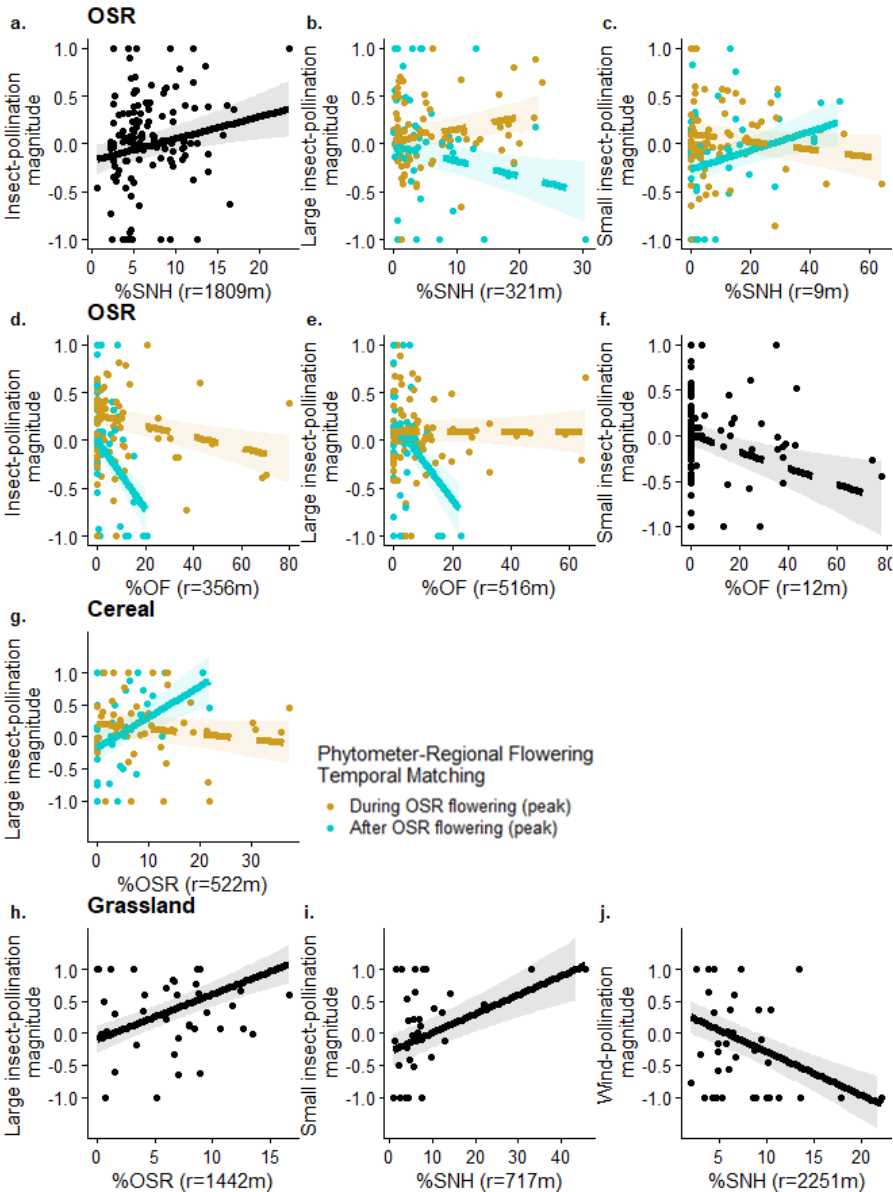


Fig. 2.5: Variation in the magnitude of pollination processes with 'Landscape Flower Quantity' (%OSR: % oilseed rape, %SNH: % semi-natural habitats and %OF: % organic farming) and 'Phytometer-Regional Flowering Temporal Matching' in OSR fields (a-f), cereals (g) and grasslands (h-j). The scale of effects was estimated by likelihood optimizations. Raw data is shown for each year, the predicted relationships are based on models presented in Table 2.2 (bold if a significant effect, or else dotted) and their standard errors.

Insect pollination was higher than wind pollination whatever the crop and season (though not necessarily significantly, e.g., in OSR), suggesting that the abundance of pollinators, rather than the abundance of pollen, was involved in the higher observed fruiting success (Fig. 2.4c–e). In addition, insect pollination often responded in the same way as fruiting success to landscape features (Fig. 2.3, Fig. 2.5). In OSR fields, insect pollination increased with %SNH (Fig. 2.5a) and decreased with %OF (Fig. 2.5d). There was an interaction between landscape composition and ‘Phytometer–Regional Flowering Temporal Matching’ on small- and large-insect pollination (Table 2.2a): increasing %SNH improved small insect pollination after OSR peak flowering (Fig. 2.5c), while large-insect pollination was negatively related to %OF only after OSR peak flowering (Fig. 2.5e). The increase in fruiting success with %OSR resulted from a joint increase of insect, wind, and self-pollination (Appendix 2I). However, the increase in fruiting success in cereals and grasslands resulted from an increase in large-insect pollination with %OSR, although this was the case only after OSR flowering in cereals (Fig. 5g, h; Table 2.2b, c). Small-insect pollination also increased with %SNH in grasslands (Fig. 2.5i), as opposed to the pattern observed for fruiting success (Fig. 3f), and wind pollination diminished with %SNH (Table 2.2c; Fig. 2.5j).

The spatial extent of the effects of landscape varied with the pollination processes, being in general lower for wind than for insect pollination (e.g., 3 m and 747 m for %OSR in OSR crops). For insects, the spatial scales of landscape features were greater for large than for small insects (e.g., 321 m and 9 m for %SNH in OSR crops). Large-insect pollination was also shown to respond at different spatial scales depending on the focal crop type, as %OSR acted on large-insect pollination at a higher spatial scale in grasslands (1442 m) than in cereals (522 m; Appendix 2E). Self-pollination, which was expected to be constant across the conditions, was also modified by the amount of local and landscape floral resources in OSR, cereals and grasslands (Appendix 2H).

V. Discussion

The results of our study showed that fruiting success of plant phytometers placed in OSR crop was higher in OSR peak flowering period, i.e., when OSR flower resources are highest, and was improved by neighbouring OSR fields. The pulse of OSR flowers was especially attractive for small insects that lead to an increase of fruiting success in OSR crops surrounded by a high amount of SNH. A temporal spillover occurred after the period of OSR flowering and involved large insects that dispersed from OSR to grasslands and cereal crops.

Our phytometer approach revealed high heterogeneity in fruiting success rates (used as a proxy of pollination efficiency) even within crop types, suggesting that there may be a strong spatial and temporal variation in pollen limitation in our study site. Fruiting success of our OSR phytometers (0.49 on average) was within the range (from 0.31 to 0.75) found in other studies on *Brassica* plant phytometers (Hudewenz et al., 2014; Palmer & Zimmerman, 1994), though slightly lower than those estimated directly on OSR plants in crop fields (0.70; Zou et al. 2017), including in our study site (0.65; Perrot et al. 2018). Such pollination rates indicate a rather high abortion rate of flowers, i.e. from 51% in OSR fields to up to 62% and 64% in cereals and grasslands. Although other factors may also contribute to abortion, such as lack of water or nutrients that may physiologically limit plant phytometers (Marini et al., 2015), this is more likely to result, at least partly, from pollen limitation. Indeed, OSR pollen availability strongly varies between crop types (i.e. higher in OSR fields than in cereals and grassland), in the surrounding landscape of focal fields and throughout the flowering period of OSR. This lack of pollen in the air can reduce wind pollination (McCartney & Lacey, 1991) at a low spatial scale, since

Table 2.2: Effects of ‘Phytometer–Regional Flowering Temporal Matching’ and availability of floral resources in the fields and in the surrounding landscapes (%OSR: % oilseed rape, %SNH: % semi-natural habitats and %OF: % organic farming) on the magnitude of each pollination process in (a) OSR fields, (b) cereal fields and (c) grasslands. For each of 15 models, we applied type II analyses of variance. Coefficients of determination of the models (R^2), degree of freedom (df), F-value (F) and p-value (p) for each explained variable are indicated. Significant values are in bold.

	d f	Insects		Large insects		Small insects		Wind		Self	
		F	p	F	p	F	p	F	p	F	p
a. OSR		$R^2 = 32.0\%$		$R^2 = 22.3\%$		$R^2 = 16.7\%$		$R^2 = 28.4\%$		$R^2 = 47.8\%$	
Year	4	2.84	0.03	1.57	0.19	0.98	0.42	5.20	<0.001	13.60	<0.001
Field size	1	2.76	0.10	0.02	0.88	1.39	0.24	2.55	0.11	0.01	0.93
Phytometer–Regional Flowering Temporal Matching	1	4.89	0.03	0.49	0.49	1.12	0.29	0.17	0.68	12.96	<0.001
Focal Field–Regional Flowering Temporal Matching	2	2.87	0.06	0.96	0.39	0.62	0.54	1.44	0.24	2.65	0.08
%OSR (Landscape Flower Quantity)	1	1.20	0.28	0.06	0.81	1.07	0.30	1.60	0.21	3.47	0.07
%SNH (Landscape Flower Quantity)	1	4.81	0.03	0.21	0.64	0.14	0.71	0.78	0.38	5.81	0.02
%OF (Landscape Flower Quantity)	1	6.65	0.01	0.85	0.36	3.71	0.06	1.50	0.22	0.36	0.55
Field size x Phytometer–Regional Flow. Temp. Matching	1	0.69	0.41	1.44	0.23	0.03	0.86	1.53	0.22	7.58	0.01
Focal Field–Reg. Flow. Temp. Matching x Phytometer–Reg. Flow. Temp. Matching	2	3.35	0.04	0.16	0.85	0.82	0.44	1.20	0.31	0.53	0.59
Field size x Focal Field–Reg. Flow. Temp. Matching	2	2.68	0.07	1.05	0.35	0.29	0.75	1.09	0.34	3.90	0.02
%OSR x Phytometer–Reg. Flow. Temp. Matching	1	3.02	0.09	1.87	0.17	3.10	0.08	0.41	0.52	1.18	0.28
%SNH x Phytometer–Reg. Flow. Temp. Matching	1	0.37	0.54	4.42	0.04	4.29	0.04	0.69	0.41	0.00	0.99
%OF x Phytometer–Reg. Flow. Temp. Matching	1	5.76	0.02	7.39	0.01	1.45	0.23	0.02	0.89	6.79	0.01
b. Cereal		$R^2 = 15.7\%$		$R^2 = 18.5\%$		$R^2 = 11.6\%$		$R^2 = 15.2\%$		$R^2 = 39.2\%$	
Year	3	1.24	0.30	0.51	0.68	0.20	0.90	0.61	0.61	10.13	<0.001
Field size	1	0.04	0.84	0.01	0.91	0.07	0.79	2.77	0.10	0.95	0.33
Phytometer–Regional Flowering Temporal Matching	1	0.11	0.74	0.02	0.89	1.13	0.29	0.94	0.34	13.06	<0.001
%OSR (Landscape Flower Quantity)	1	0.03	0.87	0.03	0.87	1.55	0.22	0.36	0.55	0.10	0.75
%SNH (Landscape Flower Quantity)	1	2.14	0.15	0.71	0.40	0.92	0.34	0.40	0.53	1.64	0.20
%OF (Landscape Flower Quantity)	1	0.17	0.68	2.69	0.11	1.95	0.17	0.20	0.65	1.10	0.30
Field size x Phytometer–Reg. Flow. Temp. Matching	1	0.09	0.77	1.09	0.30	0.16	0.69	0.30	0.58	0.02	0.88
%OSR x Phytometer–Reg. Flow. Temp. Matching	1	1.88	0.17	6.35	0.01	0.54	0.46	2.78	0.10	5.14	0.03
%SNH x Phytometer–Reg. Flow. Temp. Matching	1	1.47	0.23	1.54	0.22	0.73	0.39	1.37	0.25	2.80	0.10
%OF x Phytometer–Reg. Flow. Temp. Matching	1	1.64	0.20	0.11	0.74	0.22	0.64	3.29	0.07	3.68	0.06
c. Grassland		$R^2 = 57.4\%$		$R^2 = 56.5\%$		$R^2 = 51.4\%$		$R^2 = 42.7\%$		$R^2 = 38.4\%$	
Year	2	2.56	0.10	1.15	0.33	7.01	<0.01	3.71	0.04	2.74	0.08
Field size	1	0.04	0.85	0.49	0.49	0.23	0.64	0.15	0.70	0.42	0.52
Phytometer–Regional Flowering Temporal Matching	1	25.17	<0.001	26.54	<0.001	3.89	0.06	10.13	<0.01	0.40	0.53
%OSR (Landscape Flower Quantity)	1	1.72	0.20	10.34	<0.01	1.64	0.21	2.76	0.11	9.35	<0.01
%SNH (Landscape Flower Quantity)	1	10.38	<0.01	1.48	0.23	6.35	0.02	7.90	0.01	1.33	0.26
%OF (Landscape Flower Quantity)	1	1.88	0.18	1.34	0.26	1.90	0.18	0.34	0.56	3.73	0.06

wind-carried pollen rarely exceeds 50 m dispersion from OSR fields (Popławska et al., 2013).

Pollen limitation can also lower self-pollination later in the season. Lower airborne pollination may, however, be balanced out by higher insect-mediated pollination, as has been shown with radish or strawberry when used as plant phytometers in semi-natural habitats or crop fields (Castle et al., 2019; Hass et al., 2018). Pollinating insects carry pollen over long distances (Chifflet et al., 2011) and/or directly from opened flowers of plant phytometers by successively visiting different flowers (Rader et al., 2009). Our bagging experiment confirmed that insect pollination was a major process in OSR pollination after self- and before wind pollination (Hudewenz et al., 2014; Perrot et al., 2018). The high insect pollination rate found in cereals and grasslands suggests that this pollination process may compensate for low OSR pollen availability. As expected, we detected a strong variation in the magnitude of insect pollination according to the spatial and temporal conditions of the focal fields under study. In our site, pollinator richness ranged from 0 to 25 species (Rollin et al., 2015) and abundance from 0 to 68 individuals per 100 m² (Perrot et al., 2018). Moreover, pollinator richness and abundance strongly vary across years (Perrot et al., 2018), thus directly affecting the magnitude of insect pollination.

We found that pollination efficiency in OSR fields was higher in periods and landscapes characterized by high availability of OSR flowers (Fig. 2.2a, 2.3a) in sharp contrast to predictions of the dilution hypothesis. This conflicts from most previous studies, which have detected such a dilution effect, finding that increasing the amount of mass-flowering crops in the landscape decreases large-pollinator abundance, e.g. honeybees and bumblebees (Bänsch, Tschardtke, Gabriel, et al., 2020; Holzschuh et al., 2016), hence decreasing pollination efficiency in these crops (Shaw et al., 2020) or adjacent crops (Grab et al., 2017) and grasslands (Holzschuh et al., 2011). The gradients of %OSR used in our study (from 0% to 26% in a buffer of 747 m outside OSR fields) were similar to those used in other studies (e.g. from 0% to 30% in a buffer of 1000 m; Holzschuh et al. 2011), thus other factors must explain this discrepancy. One possible reason may be the plant phytometer itself: dilution was found when plant phytometers used was not the blooming crop (e.g. strawberry plants with the blooming of apple flowers in Grab et al., 2017), or *Primula veris* with the blooming of OSR flowers (Holzschuh et al. 2011). Two other possible factors may also be involved in explaining the difference with our study. First, the rich and abundant pollinator community in our study site (Bretagnolle et al., 2018; Rollin et al., 2013) may avoid such a dilution effect more likely to be detected in depauperate pollinator communities (Tschardtke et al., 2012). Second, OSR accounted for about 8% of crops, and therefore a high load of OSR pollen in the air may have balanced out any dilution of pollinator insects (Cavallero et al., 2018; Waser & Price, 2016). We also found an increase in pollination efficiency with higher amount of OSR fields in the landscape, but at a small scale (12 m), a distance consistent with the distance at which pollen disperses with wind (about 50 m; Popławska et al., 2013). Conversely, the spatial extent of the effect of %OSR on insect pollination was at much larger scale (e.g. 747 m for plant phytometers in OSR fields), underlying the ability of insect pollinators to forage over hundreds of metres (Greenleaf et al., 2007).

While our results did not support a dilution effect, we detected patterns consistent with a reverse pattern, in the form of an attractive effect of the bloom of OSR flowers. During peak OSR flowering, this was detected in the attraction of insects from SNH to OSR, as there was higher pollination efficiency of phytometers placed in OSR fields surrounded by a high amount of SNH (Fig. 2.3d), particularly for small pollinators (indicated by the bagging experiment; Fig. 2.5a, b, c). Such attraction operated at a larger scale for large pollinators (321m) than for small ones (9m), in accordance with the ability of large

pollinators to forage at greater distances (Jackson & Fahrig, 2012; Miguet et al., 2016). Semi-natural habitats are well-known sources of pollinators in agricultural landscapes, including bees (Steffan-Dewenter et al., 2002), hoverflies (Bommarco et al., 2012) and bumblebees (Hopfenmüller et al., 2014). Our results thus confirm that SNH benefit wild pollinators in adjacent OSR fields (Bommarco et al., 2012), hence reducing pollen limitation (Cusser et al., 2016) and increasing pollination efficiency in insect-dependent crops (Bukovinszky et al., 2017; Raderschall et al., 2021) such as OSR (Bartomeus et al., 2014).

Finally, we found a temporal spillover mechanism that occurs later in the flowering season, when insects disperse from OSR fields after peak flowering to other crops and SNH, which become attractive (Fig. 2.4c, d, e; Fig. 2.5g). This process, already suggested, is related to the fact that pollinating insects follow the temporal pattern of floral resource availability in the landscape (Bretagnolle & Gaba, 2015; Mandelik et al., 2012). At a seasonal scale, different habitats are therefore sequentially used, corroborating that the presence of OSR in a landscape benefits pollinator diversity (Diekötter et al., 2014; Kovács-Hostyánszki et al., 2013) and pollination of wild plants (Herbertsson et al., 2017) in adjacent grasslands. Such a spillover effect was also detected in cereal fields, as large-insect pollination was higher in cereals surrounded by a high amount of OSR, but only after peak OSR flowering. In contrast to our predictions however, a negative effect of organic farming was detected in small-bodied insects whatever the OSR flowering period, and in larger insects only outside OSR flowering. We suggest this effect may result from pollinator attraction to organic fields. Organically farmed cereal fields support a high diversity of wild plants (Henckel et al., 2015) which are visited by both wild pollinators (Sidemo-Holm et al. 2021) and honeybees (Wintermantel et al., 2019). Our study was inconclusive in regard to the possible effect of the amount of floral resources at the field scale possibly because of our crude measure of local availability of floral resources (we used field size as a proxy), which did not consider variation in the composition of floral resources.

VI. Conclusion

Our study revealed complex and interacting mechanisms (i.e. attraction, spillover and temporal complementarity between habitats) through space and time, between crops, and between crops and semi-natural elements, depending on insect types. The amount of SNH in the landscape appeared to play a key role in pollination efficiency: it provided pollinating insects – especially small insects – to OSR crops, with a reverse spillover effect after OSR peak flowering. These results suggest that grasslands and cereals may act complementarily to OSR fields in supporting insects (and hence pollination) throughout the season in a landscape. Therefore, farmland landscapes that combine habitats providing nesting sites and floral resources after OSR flowering or, even better, continuous flowering resources across the seasons over the entire landscape, would contribute to supporting large pollinator populations and therefore improve pollination.

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Conflicts of interest/Competing interests. The authors declare that they have no conflict of interest.

Availability of data and material. The datasets generated and used for the study are available (except confidential data such as landscape information) from the corresponding author on reasonable request.

Code availability. The code performed to analyse the dataset is available from the corresponding author on reasonable request.

Ethics approval. Not applicable

Consent to participate. Not applicable

Consent for publication. Not applicable

Authors' contributions. VB and SG conceived the study and were in charge of overall direction. VB and SG designed and planned the field work. JG worked in the field and in the laboratory for yield component quantification with the help of TP and MR. JG entered the data. MR analysed the data. SG, FC, OM, VB and TP provided feedback and helped improve analyses. MR, SG, VB, FC, OM and TP discussed and interpreted the results. MR, SG, VB and FC wrote the paper. TP and OM commented and helped shape the manuscript. All authors approved the final version of the manuscript.

CHAPITRE 3 - MISE EN EVIDENCE DU ROLE COMPLEMENTAIRE DES CULTURES A FLORAISON MASSIVE ET DES PLANTES ADVENTICES POUR LE MAINTIEN DES POLLINISATEURS SAUVAGES DANS LES PAYSAGES AGRICOLES

Avant-propos. Nous avons identifié deux étapes dans la dynamique spatio temporelle de la fonction de pollinisation impliquant la dispersion des insectes pollinisateurs dans la mosaïque agricole : les insectes pollinisateurs (i) dispersent des HSN vers les cultures de colza (ii) puis redispersent vers les HSN et vers les cultures de céréales en période de faible disponibilité en fleurs de colza montrant ainsi le rôle complémentaire des cultures à floraison massive, des HSN et céréales dans le maintien des insectes pollinisateurs et de la fonction de pollinisation. Nous avons également vu que les ressources florales fournies par les cultures à floraison massive sont largement exploitées par l'abeille domestique. Ici nous avons donc étudié la façon dont les cultures à floraison massive et l'abeille domestique modifient les relations entre les plantes adventices et les pollinisateurs sauvages.

Contexte. Les plantes sauvages des parcelles agricoles (les adventices) peuvent jouer un rôle important dans le maintien des pollinisateurs sauvages. Mais certains facteurs freinent la compréhension de leurs effets sur les pollinisateurs dans les parcelles agricoles comme le rôle respectif de la diversité et de l'abondance des adventices sur les pollinisateurs, ou la compétition par exploitation qui intervient à travers les cultures à floraison massive (CFM), les fleurs sauvages dans le paysage et l'abeille domestique.

Objectif. Nous avons étudié la "relation plantes adventices – pollinisateurs sauvages" et sa variation (i) suivant que la diversité ou alors l'abondance des adventices et des pollinisateurs soient caractérisées et (ii) avec la disponibilité en CFM dans la parcelle, dans le paysage et dans le temps, avec l'abondance en abeille domestique dans la parcelle, et avec la disponibilité en fleurs sauvages dans le paysage.

Méthode. Nous avons échantillonné les adventices et les pollinisateurs sauvages et caractérisé leur diversité (indices de Hill) et abondance dans 569 parcelles. Les échantillonnages étaient effectués en colza et tournesol avec une forte disponibilité en fleurs cultivées ainsi que dans des céréales et prairies, à différentes périodes de la floraison des CFM. Les parcelles variaient dans l'abondance en abeille domestique, et la disponibilité en CFM (quantité de colza et de tournesol) et en fleurs sauvages (quantité d'habitats semi-naturels, et d'agriculture biologique) dans le paysage.

Résultats. Les adventices supportaient les pollinisateurs sauvages dans des contextes de faible disponibilité en CFM (e.g. dans les céréales et en dehors de la floraison des CFM) et dans des CFM avec une forte abondance en abeille domestique. La relation augmentait avec la disponibilité en fleurs sauvages dans le paysage. Aussi, l'effet des adventices était mieux décrit par l'abondance ou la diversité suivant le type de culture.

Synthèses et applications. Les plantes sauvages et les CFM à travers un effet de complémentarité peuvent supporter les pollinisateurs sauvages. Nous suggérons de combiner des parcelles abritant des adventices avec une diversité de cultures incluant les CFM pour augmenter la capacité des paysages agricoles à supporter les pollinisateurs sauvages.

Mots clés. Abeille domestique | Composition du paysage | Correspondance temporelle | Nombre de Hill | Ressources florales

Highlighting the complementary role of mass flowering crops and weeds for maintaining wild pollinators in farmland

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I. Abstract

Context. Wild plants in the agricultural fields (weeds) are suggested as a key element for maintaining wild pollinators. Several factors hampered the understanding of the relationship between weeds and wild pollinators at the field scale as the respective role of the amount and diversity of weeds on wild pollinators, or the exploitative competition in which the mass flowering crops (MFC), the wildflowers in the landscape and the honeybee may be involved.

Aims. We studied the “weed – wild pollinator relationship” and its variation (i) depending on whether weeds and wild pollinators were characterized through their diversity or abundance and (ii) with the availability of MFC in the field, in the landscape and in time, with honeybee abundance in the field and with the availability of wildflowers in the landscape.

Method. We surveyed weeds and wild pollinators in 569 fields and characterized their diversity with several indexes and their abundances. Surveys were performed in oilseed rape and sunflower with high crop flowering supply and cereal, and grassland and at different periods of the MFC flowering. The fields varied in the honeybee abundance, the availability of MFC in the landscape (amount of oilseed rape or sunflower) and in wildflowers (amount of semi-natural habitats and organic farming).

Results. Weeds positively influenced the wild pollinators in contexts of low availability of MFC (e.g., in cereal fields and outside the flowering period of MFC) and in MFC with a high honeybee abundance. The relationship also increased with the availability of wildflowers in the landscape. Weed effect was better described by the diversity or the abundance depending on the crop type.

Synthesis and applications. Weeds and MFC, through complementary effects, may support the wild pollinators. We recommend combining fields with high weed availability, with a diversity of crops including MFC to improve the ability of agricultural landscapes to support wild pollinators.

Key words: Floral resource | Hill numbers | Honeybee | Landscape composition | Temporal matching

II. Introduction

Biodiversity loss is one of the major concerns in the Anthropocene (Dirzo et al., 2014; Tilman et al., 2014). On-going losses have been demonstrated especially for insects which have experienced declines of 75% of biomass over the past 30 years (Hallmann et al., 2017) and 34% of richness over the past 10 years (Seibold et al., 2019). Insect pollinators contribute to the maintenance of pollination services ensuring the production of crops worldwide (Klein et al., 2007) and the maintenance of almost 90% of insect-dependent plants (Ollerton et al., 2011). The stake in farmland is to halt this loss for ensuring food security as well as biodiversity conservation.

There is now a consensus on the importance of floral resources for the maintenance of pollinators through the fulfilling of their pollen and nectar requirements (Nicholls & Altieri, 2013; Roulston & Goodell, 2011). Floral resource enhancement was reported to support pollinators in experimental studies (Biella et al., 2019; Ebeling et al., 2008) and in natural conditions through the establishment of habitats which are rich in floral resources such as fallow strips (Haaland et al., 2011) or hedgerows (Kremen et al., 2018). The role of flower abundance and diversity are often discussed (Neumüller et al., 2020). On one side, abundance involves an increase in the amount of floral resources and, in the other side, diversity may increase the number of different morphologies and phenologies of flowers and therefore the matching with pollinators (Peralta et al., 2020). However, the respective contributions of flower abundance and diversity in the support of pollinators remains to be established.

Spontaneous flora within the agricultural fields (hereafter weeds) represents a high potential to support pollinators thanks to their high abundance and diversity (Bretagnolle & Gaba, 2015). Previous studies reported an increase of pollinators diversity or abundance with weed diversity or abundance but were restricted to semi-natural habitats (Fründ et al., 2010; Rollin et al., 2019) or to an unique crop (Rosa García & Miñarro, 2014; Sidemo-Holm et al., 2021). But, both weeds and pollinators display high levels of spatial and temporal diversity in agricultural landscapes due to habitat requirements and specific traits (Mahaut et al., 2018; Rollin et al., 2015). For example semi-natural habitats (hereafter SNH) such as grasslands shelter a greater diversity and abundance of wild pollinators (Rollin et al., 2013) and weeds (Gaba et al., 2020) compared to arable crops. There is also a high variability in species diversity and abundance among crops with for instance a higher diversity of weeds in oilseed rape (hereafter OSR) as compared to cereal and sunflower (Bourgeois et al., 2020). These variations may affect the relationship between weeds and wild pollinators. Therefore, the role of weeds in maintaining pollinators as well as the relationship between weed diversity and abundance and pollinator diversity and abundance in different crop types remain to be established. This gap of knowledge limits our ability to implement efficient conservation or management actions, a better understanding of this relationship in real world conditions is therefore needed.

The presence of domestic plant and pollinator species in the agricultural areas, generally at high abundance, complexifies the understanding of the relationship between weeds and wild pollinators. First, although, floral resources are mainly provided by weeds in farmland (Timberlake et al., 2019), mass-flowering crops (MFC) such as OSR *Brassica napus L.* and sunflower *Helianthus annuus* also provided important resources on short duration in early spring (OSR) and in the summer (sunflower; Requier et al., 2015). Nectar and pollen supplies are respectively 10 and 0.08 L and 3.5 et 1.8 kg per hectare and per day in OSR and sunflower (Horn et al., 2021). By providing abundant floral resources, MFC may reduce pollinator visitation of weeds during their flowering periods (Diekötter et al., 2010). Second, the mechanism of exploitation competition (Geslin et al., 2017) can also occur at the landscape scale as wild pollinators disperse over hundreds of meters to forage (Greenleaf et al., 2007). MFC in the

landscape can attract wild pollinators (Bartomeus et al., 2014; Holzschuh et al., 2016); such an attractive effect can also be exerted by fields organically farmed (hereafter OF; Sidemo-Holm et al., 2021) or SNH (Cole et al., 2017) which shelter a high amount of wildflowers. However, as SNH and OF affect locally both weeds (Bourgeois et al., 2020; Henckel et al., 2015) and wild pollinators (Holzschuh et al., 2008; Steffan-Dewenter et al., 2002), how they affect the relationship between weeds and wild pollinators is difficult to disentangle. Finally, the honeybee *Apis mellifera*, the dominant pollinator in agricultural landscapes, is involved in a competition for floral resources with wild pollinators (Geslin et al., 2017; Mallinger et al., 2017). The availability of MFC guides the type and the intensity of the competition as the honeybee concentrates in MFC in their flowering periods (Rollin et al., 2013) and is suggested to exclude wild pollinators from crop flowers (Lindström et al., 2016) which can make weeds more attractive. Despite the central role of domestic species and landscape composition in plant-pollinator interactions in agricultural landscapes, their effects on the support of wild pollinators by weeds has not been studied yet in farmers' fields.

We aimed at providing a general understanding of the role of weeds in supporting wild pollinators in real field conditions by analyzing the “weed - wild pollinator relationship”. We characterized the diversity and abundance of weeds and wild pollinators in 569 farmers' fields. Fields were selected to differ in the amount and type of floral resources locally (MFC versus herbaceous grasslands and cereals), in their surrounding landscape (amount of MFC providing crop flowers and amounts of SNH and OF providing wildflowers) and in time (during and outside MFC flowering period) as well as in their abundance of honeybees. We first examined the weed - wild pollinator relationship in OSR, cereals, grasslands, and sunflowers. We expected weeds to affect positively wild pollinators except in OSR and sunflower because of the high amount of crop flowers they supply. As we had no *a priori* on the components of weeds and wild pollinators best describing the weed-wild pollinator relationship, we studied several measures of diversity using Hill numbers and the abundance of weeds and wild pollinators. Second, we focused on MFC crops and assessed the effect of honeybee abundance on the weed-wild pollinator relationship. Under the hypothesis that the honeybee increases the attractivity of weeds through competition for crop flowers, we predicted weeds to favor wild pollinators in MFC fields sheltering a high honeybee abundance. Then we explored the weed - wild pollinator relationship through time by studying this relationship during and outside MFC flowering periods. We predicted weeds to positively influence wild pollinators outside MFC flowering periods as weeds are the unique floral resources at these time periods. Finally, we examined how the amount of floral resources in the landscape affect the relationship. We expected weeds to have a positive effect on wild pollinators in landscapes poor in floral resources as weeds in the fields are the main floral resources for wild pollinators.

III. Materials and methods

1. Study site

The study took place during spring and summer seasons from 2015 to 2019 in the LTSER “Zone Atelier Plaine & Val de Sèvre”, an intensive farming plain in the west of France. Land cover was monitored each year at the field scale and recorded in a GIS database (Bretagnolle et al., 2018). Annual crops almost occupied three quarters of the site, the dominant crop type was winter cereal i.e., wheat or barley (50% on average during the five studied years) followed by MFC including 8% of OSR and 12% of sunflower that flowered respectively in spring (April-May) and summer (July-August). Arable fields

organically farmed covered from 6% (in 2015) to 9% (in 2019) of the cultivated area, most of them were cereal fields (about 50%). SNH occupied an important area, 7% were herbaceous habitats (grasslands, fallows, and wastelands) and 15% were ligneous habitats (hedges and forests). Grasslands included permanent (>6 years old) and temporary grasslands for grazing or hay making. 140 OSR fields, 257 cereal fields, 90 grasslands and 93 sunflower fields were selected for the surveys of weeds and wild pollinators. OSR and cereal surveys were performed in spring, OSR survey covered entirely the period of OSR flowering while cereal survey overlapped it in part (>50%). Surveys in grasslands and sunflowers were performed latter in the season (during summer), mostly during sunflower flowering period (>80% for sunflower and >50% for grasslands). Field size was on average 6.03 ha \pm 4.99 sd. Details are given in Appendix 3A.

2. Sampling of weeds and wild pollinators in the farmer's fields

In each field, we surveyed weeds in 25 plots of one m², among which 20 plots were located in field core (20 plots) and five in field margin. Each plot was divided into four 0.25m² subplots (100 subplots) in which weed species occurrence was recorded (Bourgeois et al., 2020). We identified 96.7% of the individuals at the species level. The protocol performed in 2015 in grasslands was different (smaller plots), we thus excluded these data from our dataset.

We sampled wild pollinators, i.e., wild bees, hoverflies, and butterflies (suborder Rhopalocera), by pan-traps. Pan-traps were a set of three colored plastic bowls of 12cm diameters (blue, white and yellow) filled with soap solution placed in fields at crop canopy height during four days (Perrot et al., 2018; Westphal et al., 2008). One pan-trap (in field core) from 2016 and 2019 while four in 2015 (two in field margin and two in field core) were deposited in the fields. We identified 99.9% of the individuals at the species level (see Appendix 3A for more information).

Weeds and wild pollinators community indexes

We characterized the abundance and diversity of weeds and wild pollinators at the field scale. We evaluated **abundance** through the total number of wild pollinators trapped, and through the sum of weed species occurrence in the 100 subplots (proxy of the abundance). To quantify diversity, we used Hill numbers qD , that refer to the effective number of species and differ according to the order entropy (q), the sensibility of the index to the relative abundance of species in the sample increasing with q (Hill, 1973). We used (i) **Species richness** (where $q = 0$), the number of species independently of their abundances, (ii) the exponential of **Shannon diversity** (where $q = 1$) which weights species in relation to their frequency in the field, i.e. this is the effective number of “typical” species and (iii) the inverse of **Simpson diversity** (where $q = 2$) which weighs more the abundant species with large frequencies in the field and corresponds to the number of “dominant” species in the field (Chao et al., 2014).

To consider the higher number of pan-traps deposited in the fields in 2015 compared to the other years, we performed a resampling procedure of wild pollinators this given year. We used the two pan-traps deposited in field core (six bowls). We randomly assembled wild pollinators from three bowls of different colors, and quantified wild pollinator abundance and diversity of the resulting “species assemblage”. We repeated the step 1000 times, wild pollinator abundance and diversity in 2015 were the averaged 1000 values of abundance and diversity, respectively.

Alternative floral resource availability

We characterized the availability of crop plants flowers (i.e., alternative floral resources than weeds) in the fields at both local, landscape and temporal scales (Fig. 3.1). Because of the temporal

dynamic of crops and because of the timing of surveys (OSR and cereals in spring during OSR flowering period, and sunflowers and grasslands in summer during sunflower flowering period), we investigated the effect of OSR as a MFC when focusing on OSR and cereals, and of sunflower as a MFC when focusing on for grasslands and sunflowers. Availability of crop plants flowers was thus explored using three variables.

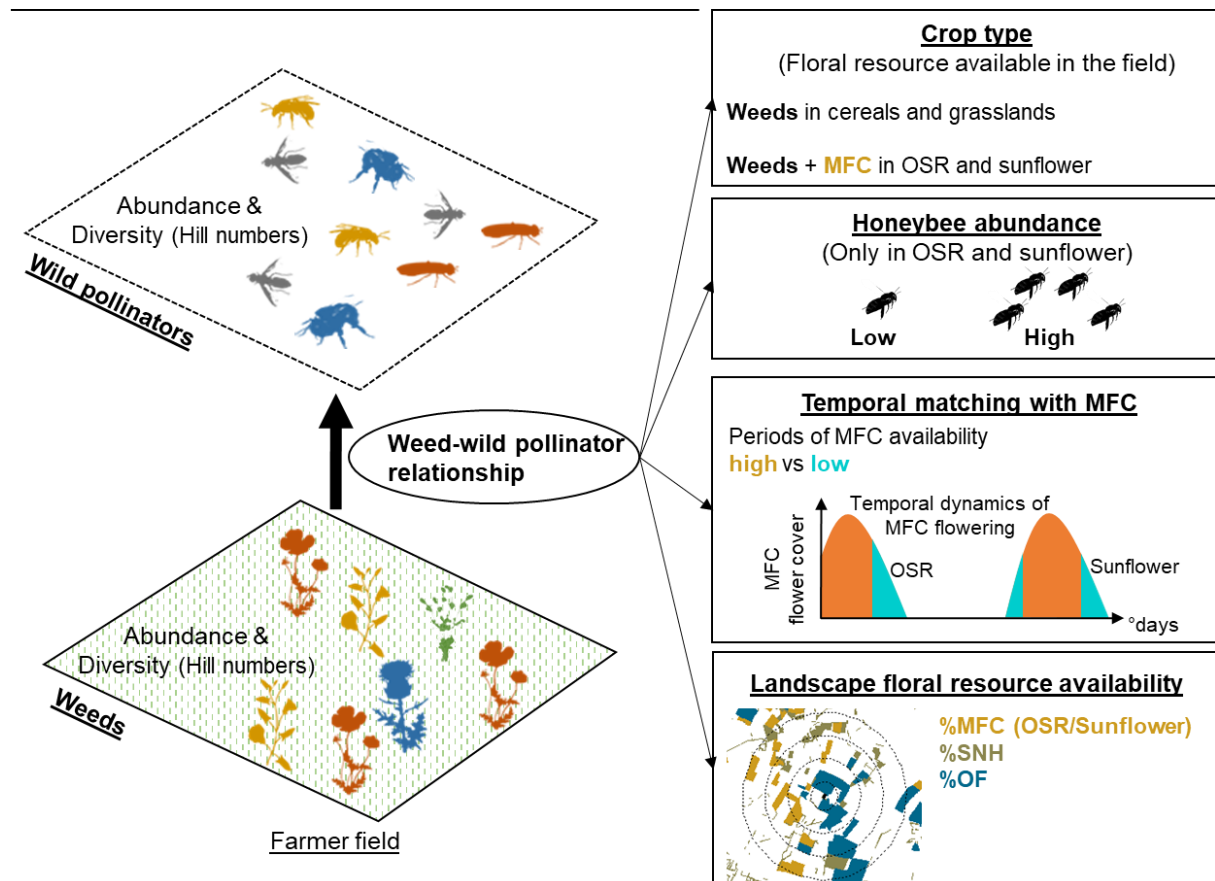


Fig 3.1. The study reposed on the estimation of the “weed-wild pollinator relationship” in real field conditions in four crop types varying in floral resource supply and on its variation with honeybee abundance in the field, Temporal matching with mass flowering crop (MFC) and Landscape floral resource availability (%MFC, %Semi-natural habitats: %SNH and %Organic farming: %OF). Oilseed rape (OSR) and cereals were surveyed in spring and overlap OSR flowering period, while grasslands and sunflower were monitored in summer overlapping sunflower flowering period. MFC refer to OSR for OSR and grassland and to sunflower for grassland and sunflower.

Local availability of crop plant flowers was assessed using crop type that enables to discriminate between MFC (OSR and sunflower) on one hand and cereal and grassland on the other hand. At the landscape scale, we quantified the floral resource availability providing by MFC and SNH and OF fields in buffers excluding the fields. We estimated the buffer radii for each landscape feature and crop type without any *a priori* on the spatial extent of their effects (see statistical analyses for details). Finally, to account for variation in the amount of floral resources during MFC flowering period (being higher at the peak and the before and after), we estimated the temporal lag between the flowering period of MFC (OSR or sunflower) and the sampling date of wild pollinators. This temporal matching with MFC flowering variable was characterized for each crop type and included two levels: the periods of high and low MFC flower availability. We predicted the temporal dynamics of OSR and sunflower flower cover at the study site scale using quadratic regressions with flower cover in OSR ($n = 158$ fields) or sunflower ($n = 182$) as the explained variable and cumulative degree-days as the explanatory variable. Crop flower

cover ranged from 0% in absence of opened crop flowers to 100% when all crop flowers were opened in the field. We used data from Niort weather station (Météo France) for the matching between dates and cumulative degree days (from the 1st of January of the year). We considered the amount of MFC floral resources to be higher when fields were sampled during a high amount of predicted crop flower cover (i.e., higher than an estimated threshold; see Appendix 3B) and to be lower when fields were sampled during periods of low amount of predicted crop flower cover (i.e., lower than the threshold).

Honeybee abundance

Honeybees in foraging activity were counted along 50m × 5m transects walks in OSR and sunflower fields (Perrot et al., 2018; Westphal et al., 2008). Two transect walks per field were performed in 2015 (one in field margin and one in field core) while three were performed from 2016 to 2019 (with an additional transect in field core). We ran a linear model on data from 2016 to 2019 to predict the number of honeybees observed along a hypothetical third 50m transect walk in 2015 by those along the first transect walk in field core (Appendix 3C).

3. Statistical analyses

We performed a sequential analysis in four steps. We first investigated the response of wild pollinator diversity and abundance to weed diversity and abundance (step 1). Then, we examined how the abundance of honeybee (step 2) and the temporal matching with MFC flowering (step 3) affect this relationship. Finally, we explored the effect of landscape floral resource availability on the “weed-wild pollinator relationship” (step 4). Each step was characterized by a specific procedure, either variable selection (step 1), determination of levels of categorical variables (steps 2 to 3), or estimation of landscape scales of influence (step 4). As diversity and abundance for wild pollinators and weeds varied with crop type (see results), and to avoid collinearity between sampling dates and crop types, the following analyzes were carried independently in each crop type. All wild pollinator community indexes were $\log_{10}(x + 1)$ transformed to satisfy the condition of homoscedasticity of the residuals.

In the first step, we used 16 linear models per crop type with wild pollinators as explained variable and weeds as explanatory variable to explore all possible combinations between wild pollinators and weeds community indexes (diversity indexes and abundance). The studied year (five levels except in grassland with four levels), the cumulative degree days through the year and its squared term were added as covariates to take into account the inter and intra annual dynamics of wild pollinators (Balfour et al., 2018; Perrot et al., 2018). We selected among of the 16 models per crop type, the one in which the combination “pollinators and weeds community indexes” yielded to the highest percentage of variance in pollinators explained by weeds (models 1).

In the second step, we explored how domesticated species (honeybee and crop plants) affect the “weeds - wild pollinators relationship”. We first focused on the effect of honeybees in OSR and sunflower and added in the best models of step 1 honeybee abundance (two levels: high and low) and its interaction with weeds community selected index (models 2). In the third step, in all crop types, we added in models (i.e., models 1 for cereal and grassland and models 2 for OSR and sunflower) temporal matching with MFC (two levels: high and low) in interaction with weeds community index (models 3). Independently in each crop type, the thresholds for levels of honeybee abundance and temporal matching with MFC were values yielding to maximal likelihoods for models 2 and 3 respectively among a gradient of tested thresholds (Appendix 3B).

Finally, we added %SNH, %MFC and %OF to account for Landscape floral resource availability and their interaction with weeds (models 4). The models were estimated using the ‘siland’ method that

allows estimating the effect of explanatory variables and the buffer radii of landscape features without any *a priori* on these scales (Carpentier & Martin, 2021).

We performed all analyses with R software (R Core team, 2021). We used the ‘car’ package for type II ANOVA (Fox et al., 2020), ‘emmeans’ package for effect size estimation (Lenth et al., 2020) and ‘siland’ package for landscape analyses (Carpentier & Martin, 2020). To detect possible violations of standard regression assumptions, we look at residual diagnostics to verify normal hypothesis (quantile-quantile plots) and homoscedasticity (spread of residual did not change with predicted values). We also confirmed the absence of spatial autocorrelation of residuals with variograms visualization and absence of multicollinearity between the variables by measuring variance inflation factors of models.

IV. Results

1. Effects of weeds on wild pollinators

The abundance and diversity of weeds and wild pollinators varied with crop type, but not conjointly. Weed species richness was higher in OSR (mean number of weed species per field \pm sd: 29.32 ± 8.92) and grasslands (31.57 ± 11.95) than in cereals (22.94 ± 13.34) and sunflowers (19.91 ± 8.09). Weed abundance was maximal in grassland (mean number of total weed species occurrence in the fields \pm sd: 463.08 ± 190.88), intermediary in OSR (279.62 ± 148.23) and cereal (266.41 ± 267.04) and minimal in sunflower (209.62 ± 118.61). On the contrary, wild pollinator diversity was less important in OSR compared to the three other crops as shown by species richness in OSR (mean number of wild pollinator species per field \pm sd: 2.97 ± 2.53), cereals (6.48 ± 2.99), grasslands (5.64 ± 2.87) and sunflowers (6.42 ± 3.41). Wild pollinator abundance was lower in OSR (mean number of individuals per field \pm sd: 7.19 ± 2.53), compared to grassland (21.69 ± 2.87) and sunflower (23.26 ± 3.40) and slightly greater in cereal (32.49 ± 2.99).

Weeds effect greatly depended on crop type, as shown by the contrasted variances of wild pollinators explained by weeds obtained from the combinations of wild pollinator and weed community indexes (Fig. 3.2a, c, e, g). The variance of wild pollinators explained by weeds was low in all crop types (generally less than 3%) except in sunflower (up to 10%). In OSR and sunflower, the effect of weeds was greatest when combining the diversity of weeds and wild pollinators, more specifically the exponential of Shannon diversity (Hill1) and the inverse of Simpson diversity (Hill2) (Fig. 3.2a, d). In cereal, weeds, in particular weed abundance, had a stronger effect on the diversity (Hill1 and Hill2) than on the abundance of wild pollinators (Fig. 3.2c). Differently, weeds in grassland had more effects on wild pollinator abundance, in particular through species richness, (Fig. 3.2e).

When considering the metrics combination that best explained the weed-wild pollinator relationship (Fig. 3.2), we found positive relationships between weeds and wild pollinators in all crops except in sunflower. Weed abundance had a significant positive effect on wild pollinator diversity in cereal (Type II ANOVA; $F = 9.46$; $p < 0.01$; Fig. 3.2d), the effects of weed diversity were non-significant on wild pollinator diversity in OSR ($F = 2.51$; $p = 0.12$; Fig. 3.2b) and on wild pollinator abundance in grassland ($F = 3.86$; $p = 0.053$; Fig. 3.2f). In the contrary, weed diversity had a significant negative effect on wild pollinator diversity in sunflower ($F = 8.10$; $p < 0.01$; Fig. 3.2h).

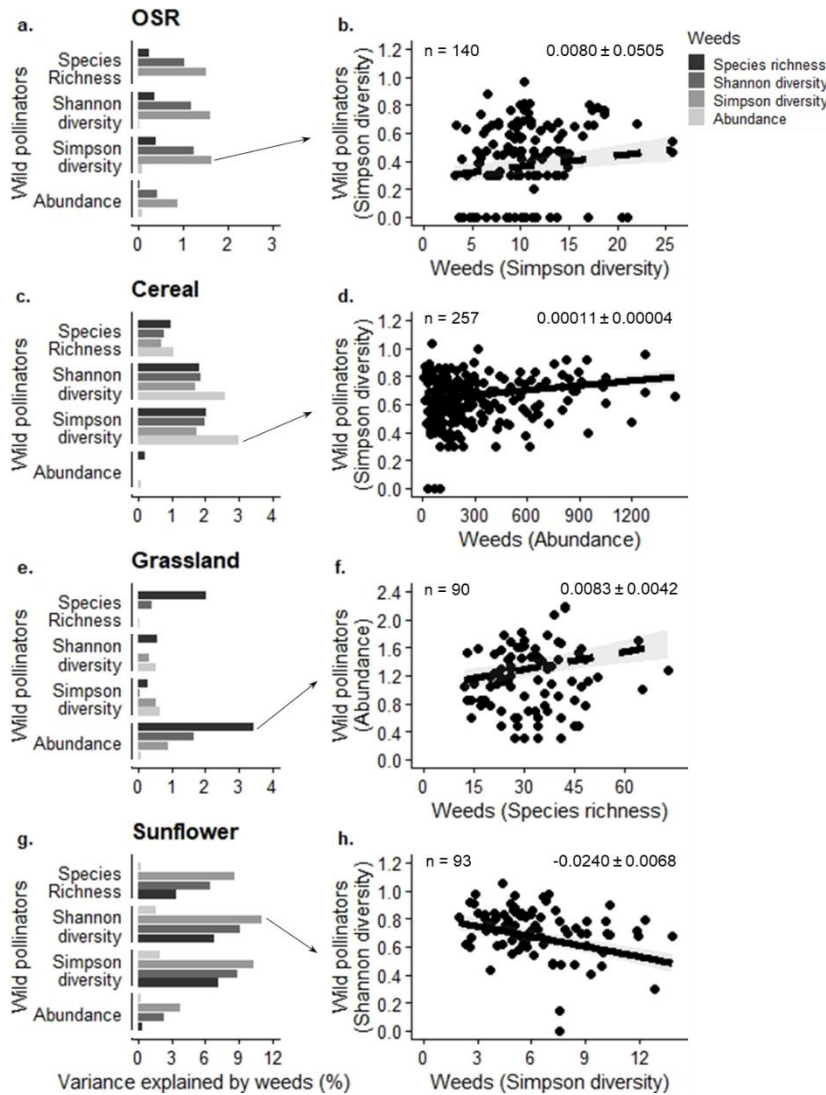


Fig. 3.2: Relationship between wild pollinator diversity and abundance ($\log_{10}(x+1)$) and weed diversity and abundance in OSR (a-b), cereal (c-d), grassland (e-f) and sunflower (g-h). The first column shows the percentage of variance of wild pollinator diversity and abundance explained by weed diversity and abundance. The second column shows the relationship between wild pollinators and weeds using the metrics that give the highest contribution of weeds to variance of wild pollinators as indicated by an arrow. Lines are the adjusted significant relationships and dashed non-significant ones. Shade areas are the standard errors. Equations indicated the effects sizes (slope \pm standard error) estimated from models 1 (see section “statistical analyses”). The sample sizes are indicated for each crop type (n).

2. Effect of honeybee abundance on the “weed - wild pollinator relationship” in MFC.

Honeybees were more abundant in sunflower (109.36 ± 162.23) than in OSR (15.80 ± 24.41). In both MFC, we found a positive effect of the interaction between “weed and honey abundance” on wild pollinator. This suggests that weed diversity sustained a higher wild pollinator diversity in fields with a high honeybee abundance (Fig. 3.3). This effect was however only significant in OSR ($F = 8.25$; $p < 0.01$).

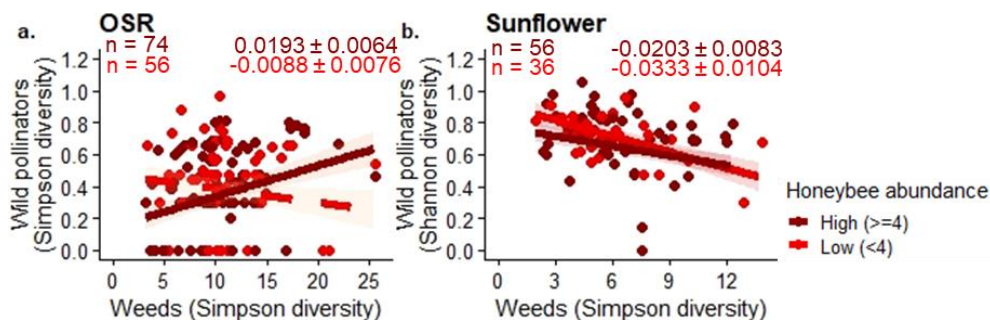


Fig 3.3: Relationship between wild pollinator diversity and weed diversity in presence of low and high honeybee abundance in OSR (a) and sunflower (b). Dark and light red show the relationship in presence of high and low honeybee abundance in OSR and sunflower fields (n is the sample size by level of honeybee abundance). The threshold that best discriminates the two categories of honeybee abundance was respectively five and 11 honeybees in OSR and sunflower (Appendix 3B). The effect sizes (slopes \pm se) are estimated from models 2. Solid lines show significant relationship.

3. Crop floral resources strongly affect the “weed - wild pollinator relationship”.

The effect of the interaction between weeds and Temporal Matching with MFC described changes in the “weed - wild pollinator relationship” between periods of high and low availability of MFC. This interaction effect was high and positive in OSR ($F = 13.60$, $p < 0.001$), cereal ($F = 13.38$, $p < 0.001$), grassland ($F = 4.25$; $p = 0.04$), and sunflower ($F = 22.75$; $p < 0.001$). Weed diversity in OSR and weed abundance in cereal had a positive effect on wild pollinator diversity only in period of low availability of OSR flowers, while these effects were non-significant in period of high availability of OSR (Fig. 3.4a, b). Similarly, in grassland, weed diversity had a positive effect on wild pollinator abundance in period of low availability of sunflower flowers, while in sunflower, the negative effects of weed diversity on wild pollinator diversity was less pronounced in period of low availability of sunflower flowers (Fig. 3.4c, d).

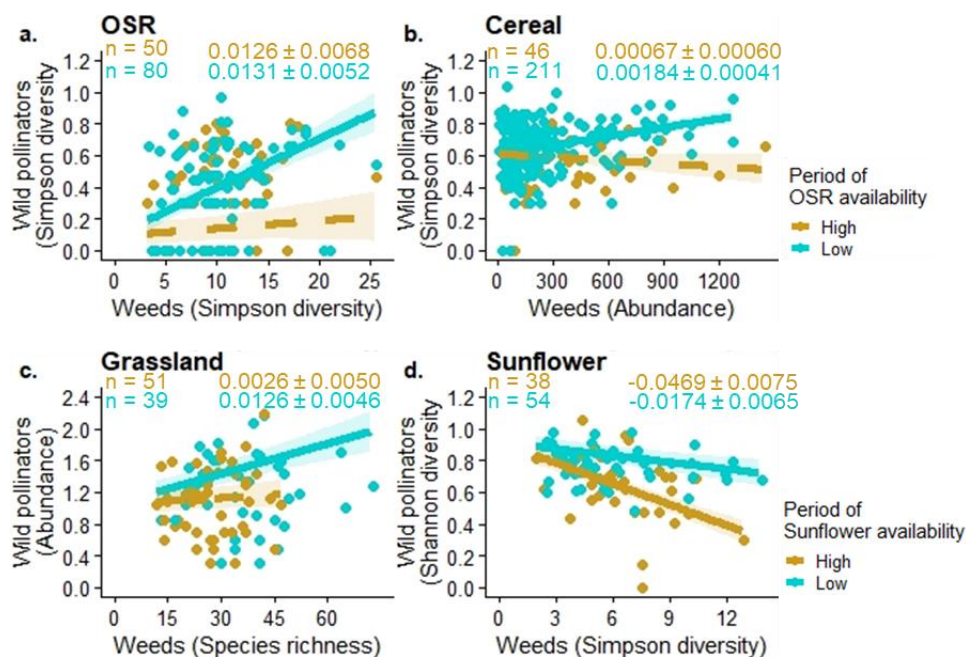


Fig. 3.4: Relationship between wild pollinators and weeds in period of high and low availability of MFC in OSR (a), cereal (b), grassland (c) and sunflower (d). MFC corresponds to OSR in OSR and cereal, and to sunflower in grassland and sunflower. The threshold that best discriminates the periods of low (flower cover in the study site during the sampling < threshold) and high availability (flower cover during the sampling ≥ threshold) of OSR/Sunflower correspond to flower cover of 64% and 28% in OSR and cereal, and of 16% and 24% in grassland and sunflower. Raw data are colored according to the levels of the period of MFC flower availability (sample size is indicated for each category). Lines show significant relationship and dashed lines non-significant ones. The effect sizes (slope ± standard error) were estimated from models 3, we fixed honeybee abundance at “High” in OSR and sunflower (note that the relationship was non-different from zero in OSR fields with low honeybee abundance even in period of low availability of OSR).

4. High effect of landscape floral resource availability on the “weed - wild pollinator relationship” in cereal and grassland.

Landscape floral resource availability had a greater influence on the “weed - wild pollinator relationship” in cereal and grassland than in OSR and sunflower. %OF and %SNH in the landscape had similar influences on the “weed - wild pollinator relationship”. %OF significantly accentuated the positive effect of weed abundance on wild pollinator diversity in cereal ($F = 11.63$; $p < 0.001$; Fig. 3.5a), the effect was similar in organically and conventionally farmed fields (Appendix 3D). Similarly, %SNH increased the effect of weed diversity on wild pollinator diversity in grassland ($F = 6.14$; $p = 0.02$; Fig.

3.5b) but at a smaller spatial scale (122m outside focal fields instead of 1322m for %OF). On the contrary, %sunflower in a buffer radius of 1236m decreased the effect of weed diversity on wild pollinator abundance in grassland ($F = 5.29$; $p = 0.02$; Fig. 3.5c).

Landscape floral resource availability also modified wild pollinator diversity in the field through direct effects of %SNH and %OSR in both OSR and cereal, no such effects were detected in grassland and sunflower. The effects were all negative and generally acted at high spatial scales (scales of effects estimated at >1400m except for the effect of %SNH in cereal estimated at 44m; Appendix 3E).

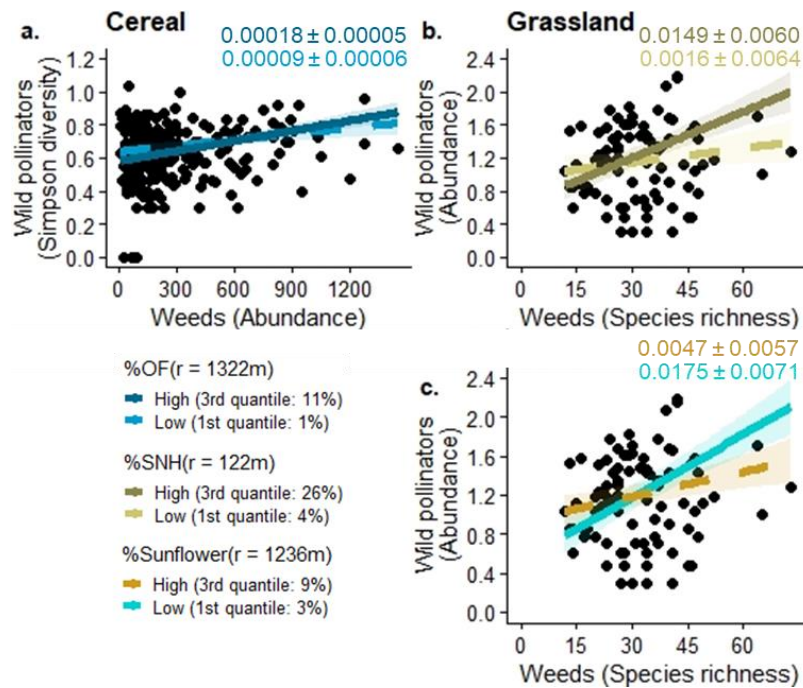


Fig. 3.5: Relationship between wild pollinator and weed (diversity or abundance) in landscape varying in amount of Organic Farming (%OF) in cereals (a), in amount of semi-natural habitats (%SNH) and sunflower (%Sunflower) in grasslands (b, c). “Low” and “high” correspond to the first and third quantiles of the amount of each landscape feature at the estimated scales of influence. The effect sizes (slope \pm se) were estimated from models 4, we fixed Temporal matching with MFC flowering at “period of low availability of OSR/Sunflower” as it greatly influenced the “weed – wild pollinator relationship” (the relationship in cereal was non significantly different from zero in period of high availability of MFC even when surrounded by a high amount of OF).

V. Discussion

The massive decline of pollinators requires finding solutions to maintain these different species as well as the pollination service in agricultural landscapes. Here, we explored the “weed - wild pollinator relationship” in 569 farmers’ fields (oilseed rape: OSR, sunflower, cereal, and grassland) to highlight whether a high weed diversity or abundance may relate to higher diversity or abundance of wild pollinators. We also examined how the relationship varies with the honeybee abundance in the fields, the availability of mass flowering crop (MFC) in the field and through the spatial and temporal contexts as well as with the availability of wildflowers in the landscape. We found a positive relationship between weeds and wild pollinators in cereal fields, in periods of low availability of MFC and in landscapes with a low amount of MFC. A positive relationship was also observed in oilseed rape fields sheltering a high honeybee abundance. The effects of weeds on wild pollinators vary with the way communities of weeds and wild pollinators were characterized (diversities and abundance) depending on crop type. A surprising negative relationship between weeds and wild pollinators was observed in sunflower. We finally highlighted a synergic effect between local and landscape availability of wildflowers as the

positive relationship between weeds and wild pollinators was more important in cereals surrounded by a high amount of OF, and in grasslands surrounded by high amount of SNH.

Spatial and temporal complementarity between floral resources provided by MFC and by weeds contributes to the persistence of wild pollinators in farmland. First, weeds did not increase wild pollinators in periods of MFC flowering in MFC and in other habitats (Fig 3.4), i.e., in grasslands and cereal fields, in particular in MFC rich landscapes (Fig. 3.5c). This suggests a strong attractive effect of wild pollinators by crop flowers and confirms previous studies showing MFC to contribute to the maintenance of wild pollinators (Diekötter et al., 2014; Westphal et al., 2003). The temporal window of availability of MFC is however restrained to few weeks, contrary to weeds that contribute to the spatio-temporal continuity of floral resource availability in farmland (Requier et al., 2015; Timberlake et al., 2019). Previous studies showed that weeds support wild pollinators in cereals and grasslands (Rollin et al., 2019; Sidemo-Holm et al., 2021). As the increase of wild pollinators with weeds in cereals and grasslands was observed only in period of low availability of MFC (Fig. 3.4b, c), our results indicated that weeds increase wild pollinators in these habitats as the exploitative competition with MFC decreases. A spatio-temporal complementarity was expected since pollinators were shown to follow the temporal dynamics of floral resource in the landscape (Bretagnolle & Gaba, 2015; Mandelik et al., 2012).

Interestingly, weed effect was better described by abundance or diversity depending on cereals and grasslands. Cereals sheltered relatively few weeds but were visited by high abundance and diversity of wild pollinators, so that the competition for floral resources may be strong. As suggested by Yamamoto et al., (2007), the interspecific competition in cereal fields may be released by floral resource amount (weed abundance) allowing a higher diversity of wild pollinators to visit cereals. In grasslands, there was a relative high weed abundance and diversity and we showed weed effect to occur through their species richness rather than through their abundance, suggesting the floral resource limitation to be less intense than in cereals. Weeds species richness may increase the attractivity of weed communities through sampling effect, i.e. by increasing the probability to include a species with a great attractive ability (Nichols et al., 2019), or through complementary effect, i.e. by including flowers with various morphology or phenology in the communities (Loreau & Hector, 2001; Peralta et al., 2020).

Beyond complementarity between MFC and weeds in farmland, we suggest weeds to provide alternative floral resources within fields especially in OSR, when competition for crop flowers with the honeybee is strong. As expected, we observed a positive relationship between weed diversity and wild pollinator diversity in OSR fields when honeybee abundance was high (Fig. 3.3a). The facets of weeds and wild pollinators involved in this relationship showed different patterns from those in cereals and grasslands, maybe because weed diversity and abundance were relatively high and wild pollinator diversity and abundance were relatively low, or because the relationship involved wild pollinators probably excluded by the honeybee from OSR flowers. Honeybee is the main forager in MFC (Rollin et al., 2013) and was already shown to compete for floral resources with wild pollinators (Mallinger et al., 2017; Wojcik et al., 2018). A competitive exclusion of wild pollinators from crop flowers by the honeybee in a diversity of MFC was already suggested (Angelella et al., 2021; Artz et al., 2011; Lindström et al., 2016). Weeds in the fields may therefore allow the honeybee and wild pollinators to cooccur in MFC, extra floral nectaries of some crops may play a similar role (Jeavons et al., 2020). Such a mechanism may however decrease the fitness of wild pollinators, by foraging on floral resources that are less abundant. While nectar quality does not vary between crops and weeds (Pamminger et al., 2019), the nectar amount provided by OSR : 10L per hectare and per day (Horn et al., 2021), largely overpassed

nectar amount provided by weeds in OSR fields. A recent study in mesocosms highlighted that wild bees better reproduce when they forage both on crops and wildflowers (Klaus et al., 2021). As the foraging activity of the honeybee is temporally discontinuous in MFC within the day and the season (Pisanty et al., 2014), temporal segregation may allow wild pollinators to use both type of floral resources in MFC.

Surprisingly, we found a negative relationship between weeds and wild pollinators in sunflower fields (Fig. 3.2h). As in OSR, weed and wild pollinator diversity were implied in the relationship, but the relationship showed contrasting pattern in the two crops. In comparison to OSR, the sunflowers were seven times more visited by the honeybee, and sheltered on average 10 weed species less, while a study reported that it provides an amount of nectar 125 times less important (Horn et al., 2021). Moreover, a bias may emerge from the correlative method we performed and that differed from previous studies focusing on the relationships between flower availability and wild pollinators on flowers (Rollin et al., 2019; Sidemo-Holm et al., 2021). A first bias could occur from the use of the amount of weeds as a proxy of the floral resources provided by weeds to the pollinators. It seems minor as entomophilous and non-entomophilous weeds were highly correlated in our data (see Appendix E), and weed diversity was already shown to correlate with flower cover (Sutter et al., 2017) although no study explored this link in sunflower. The second bias involves a gap between wild pollinator sampling (by pan-traps) and wild pollinators effectively visiting the fields. The pan-trap method is not very efficient in sampling large pollinators (Westphal et al., 2008) such as bumblebees known to abundantly visit sunflower fields (Rollin et al., 2013). Also, Roulston et al., (2007) suggested that the efficiency of pan-traps in sampling pollinators may be affected by a competitive effect with floral resource, which is expected to be high in sunflower. No such bias seemed however involved at the field scale on wild bees and hoverflies (Westerberg et al., 2021), the two dominant pollinator groups in our study.

The amount of wildflowers in the landscape increases the ability of weeds to support wild pollinators in the fields. We showed that the positive relationships between weeds and wild pollinators in cereals and grasslands increased when they were respectively surrounded by high amounts of OF and SNH. Interactive effects between local and landscape floral resource availability are rarely studied, and the few studies show negative, null or positive interactive patterns (Kennedy et al., 2013; Knapp et al., 2019; Nayak et al., 2015). At least in our study site, the grasslands, and the cereals the most visited by wild pollinators were those with a high availability of weeds (richness or abundance) and surrounded by a high amount of wildflowers provided by SNH or OF. However, SNH in the nearby landscape negatively affected wild pollinators in cereal fields (Appendix 3E), potentially because SNH attracted wild pollinators as they are their main place of foraging in agricultural landscapes (Cole et al., 2017; Rollin et al., 2013).

VI. Synthesis and implications

Our study suggests that weeds complement mass flowering crops in the maintenance of wild pollinators in farmland by ensuring the spatio-temporal continuity of floral resource availability and by allowing resource partitioning in MFC with the honeybee. The conservation of weeds in cereals is particularly targeted as cereals cover the major part of European agricultural area, until 52% in France (Neron, 2018). It needs to be combined with a diversity of crop type (including MFC) and SNH (including grasslands) in the agricultural landscapes. But a strategy that optimizes wild pollinators in all the habitats of the agricultural matrix seems difficult to implement as complex mechanisms involving floral resources at multiple spatial scales (from field to landscape) guide the diversity and abundance of

wild pollinators in the habitats. The attractive effect of SNH combined with the synergic effect between weeds in the fields and wildflowers in the landscape suggest that a mixed strategy between land sharing, through the increase of weeds in the fields, and land sparing, through the increasing amount of SNH, appears to be the best strategy to support wild pollinators in agricultural landscapes.

Authors contributions. SG contributed to the design of the field work. SG, MR and FC conceived the study. MR analyzed the data with the help of SG, FC and OM. MR, SG, FC interpreted the results. MR, SG and FC wrote the manuscript with substantial contributions of OM. All authors approved the final version of the manuscript.

Statement on inclusion: Our study took place in the “Zone Atelier Plaine & Val de Sèvre, an open-air laboratory in which biodiversity, ecological functions and agricultural practices are surveyed for several years. Our study, by providing implications for the maintenance of wild pollinators, takes part in the broader aim of increasing the knowledge on interaction between farming practices, biodiversity and ecosystem services to provide keys to develop new agroecological practices in the territory. We regularly provide feedbacks to stakeholders of the territory (farmers, beekeepers, or citizens) during events in different forms.

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Conflict of Interest. The authors declare that they have no conflict of interest.

Data availability statement. The datasets generated and used for the study are available from the corresponding author on reasonable request. Confidential information such as crop cover cannot be transmitted.

DISCUSSION GENERALE & PERSPECTIVES

I. Synthèse & limites des résultats

A travers trois chapitres, cette thèse avait pour objectif de comprendre comment la distribution des ressources florales dans l'espace et dans le temps modifie les interactions plantes-pollinisateurs et la pollinisation dans la mosaïque agricole.

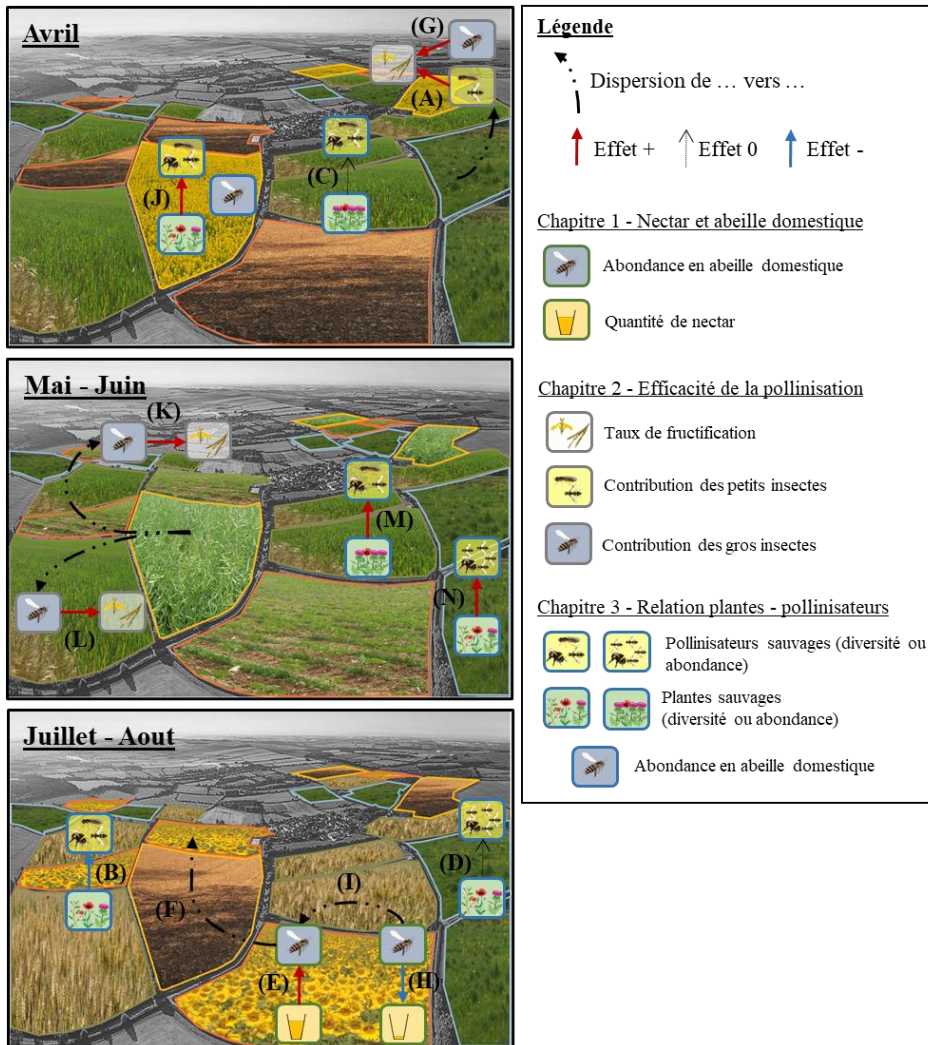


Fig. 4. 1 : Résumé des résultats de la thèse. Les résultats du chapitre 1 sont représentés par des figurés à bordure verte, ceux du chapitre 2 sont à bordures grises, et ceux du chapitre 3 sont à bordure bleues. Les lettres (A), (B), (C), etc, correspondent à des résultats de la thèse discutés dans le corps du texte.

1. Processus d'attraction et de dilution par les cultures à floraison massive

Les résultats de la thèse indiquent que les pulses de ressources florales fournis par les CFM, à travers un processus d'**attraction**, modifient l'utilisation des habitats et des ressources florales par les insectes pollinisateurs avec des conséquences fonctionnelles dans l'ensemble de la mosaïque agricole (Chapitres 1, 2, 3).

Nous montrons d'abord que les HSN sont favorables aux petits pollinisateurs, probablement des abeilles sauvages, qui dispersent et contribuent à la pollinisation en culture de colza (Chapitre 2) (A). Les bénéfices de la quantité d'HSN dans le paysage sur les pollinisateurs et la pollinisation ont été

largement étudiés (Bartomeus et al., 2014; Bukovinszky et al., 2017). En mobilisant l'approche 'siland' pour estimer les échelles d'effets (Carpentier & Martin, 2021), nos résultats indiquent que cette dispersion des abeilles sauvages intervient quand les HSN et les colzas sont adjacents (Chapitre 2), probablement dû à leur faible capacité de dispersion (Greenleaf et al., 2007). Cet effet attractif n'implique pas les plantes sauvages présentes dans les CFM mais bien les fleurs cultivées. Ainsi, dans le chapitre 3 nous montrons que les CFM qui abritent une quantité ou une diversité importante de plantes adventices ne sont pas plus visitées par les pollinisateurs sauvages (**B**). Aussi, ce chapitre, nos résultats suggèrent qu'à travers un processus de **compétition par exploitation**, les CFM pendant leur floraison restreignent l'importance des fleurs sauvages pour les pollinisateurs sauvages dans l'ensemble de la mosaïque agricole. En période de floraison des CFM, nous mettons en évidence une absence de relation entre plantes adventices et pollinisateurs sauvages dans l'ensemble de la mosaïque agricole, en céréale (**C**) et en prairie (**D**) et en particulier dans des paysages abritant une grande quantité de CFM (Chapitre 3).

Les CFM sont particulièrement **attractifs pour l'abeille domestique**, celle-ci étant très abondante en colza et plus encore en tournesol (Chapitre 3). En tournesol, l'abondance en abeille domestique augmente avec le nombre de ruches placées à proximité (Chapitre 1) ce qui confirme des études précédemment conduites dans différentes CFM (Cunningham et al., 2016; Rollin & Garibaldi, 2019). Néanmoins cet effet d'attraction semble important uniquement quand la quantité de nectar est maximale dans les parcelles, c'est-à-dire aux premières heures de la journée au pic de floraison des cultures (Chapitre 1). De plus, nous montrons que l'abeille domestique visite les CFM uniquement en **période de sécrétion** du nectar (**E**). Le nectar étant rapidement consommé, très probablement par l'abeille domestique, dès que la sécrétion du nectar s'arrête, l'abeille domestique visite des CFM qui fleurissent plus tard (**F**) ou d'autres habitats pour satisfaire ses besoins alimentaires. Cette dispersion de l'abeille domestique implique que les CFM, et notamment le colza, ont une capacité à supporter la pollinisation plus faible en fin de floraison qu'au pic de floraison (Chapitre 2) (**G**).

Nous montrons que l'augmentation de la quantité de ressources florales fournie par les CFM dans le paysage peut diminuer l'abondance en abeille domestique, confirmant ainsi l'**hypothèse de dilution** (Holzschuh et al., 2016). En effet, la déplétion du nectar par l'abeille domestique en culture de tournesol est moins importante dans des paysages qui fournissent une grande quantité de ressources florales par le tournesol (Chapitre 1). Néanmoins si les parcelles d'un même paysage montrent un **décalage temporel dans leur floraison**, celles-ci peuvent être successivement visitées par l'abeille domestique (Chapitre 1). Cet effet de dilution semble avoir peu de conséquences sur la fonction de pollinisation (Chapitre 2). Nous avons testé l'hypothèse de dilution associée à l'augmentation de la quantité de colza dans le paysage sur l'efficacité de la pollinisation du colza, alors que les études qui rapportent un effet de dilution sur la pollinisation s'intéressent à la pollinisation de plantes différentes de celles impliquées dans le pulse de ressources florales (Grab et al., 2017; Holzschuh et al., 2011). Nos résultats indiquent ainsi que l'augmentation de la quantité de pollen de colza dans le paysage peut compenser la dilution des pollinisateurs.

2. Déplétion du nectar et partitionnement des ressources dans les cultures à floraison massive

L'attraction des insectes pollinisateurs par les CFM semble favoriser les interactions interspécifiques et notamment la compétition pour les ressources entre les pollinisateurs sauvages et l'abeille domestique (Chapitres 1, 3).

Nos résultats suggèrent que l'abeille domestique consomme les ressources florales en culture de

tournesol de façon structurée dans l'espace (Chapitre 1). Nous montrons que l'abeille domestique épuise le nectar fourni en tournesol d'abord en périphérie des parcelles (**H**). Ce résultat s'accorde avec des études précédentes indiquant que l'abeille domestique butine préférentiellement sur le bord des CFM (Lajos et al., 2021; Lindström et al., 2016). Mais la dynamique spatiale et temporelle de disponibilité en nectar au sein des parcelles modifie ce patron car dès lors que la persistance du nectar est plus importante loin de la bordure des parcelles, l'abeille domestique y butine abondamment (Chapitre 1) (**I**). Cette **dispersion temporelle vers le centre des parcelles** semble intervenir avec un délai dans la journée dans les parcelles placées dans des conditions paysagères qui ne favorisent pas une forte abondance en abeilles domestiques. Ces résultats suggèrent que les plantes au centre des parcelles sont moins efficacement pollinisées car moins visitées par les insectes pollinisateurs. Mais, dans le Chapitre 2, l'efficacité de la pollinisation n'était pas significativement liée à la distance à la bordure, s'opposant ainsi avec d'autres études (Carvalho et al., 2010; Stanley et al., 2013), nos mesures de pollinisation étant probablement trop proches l'une de l'autre au sein des parcelles (20m vs 50m de la bordure).

Nos résultats indiquent également que l'abondance en abeille domestique modifie l'utilisation des ressources florales par les pollinisateurs sauvages en CFM et plus particulièrement en colza (Chapitre 3). Nous montrons en effet que la diversité des plantes sauvages augmente la diversité des pollinisateurs sauvages en colza, uniquement quand l'abondance en abeille domestique est importante (**J**). Dans ce cas, il semblerait ainsi y avoir un **partitionnement des ressources** entre l'abeille domestique qui butine les fleurs de colza, et les pollinisateurs sauvages qui butinent les plantes adventices. L'exclusion des pollinisateurs sauvages des plantes cultivées par l'abeille domestique est un processus qui a déjà été suggéré dans diverses CFM (Angelella et al., 2021; Artz et al., 2011; Lindström et al., 2016). Nous montrons que les plantes adventices à travers leur diversité dans les parcelles peuvent fournir une alternative locale à une diversité de pollinisateurs sauvages en cas d'exclusion des fleurs cultivées.

3. Complémentarités spatiale et temporelle des habitats et des ressources florales

Les CFM fournissent des ressources florales de façon limitée dans le temps. Nous montrons qu'à travers un processus de dispersion, une succession d'habitats et de ressources florales sont ainsi utilisées par les insectes pollinisateurs avec des conséquences sur la pollinisation que les habitats supportent dans les paysages agricoles (Chapitres 2, 3).

Nous montrons que les insectes pollinisateurs, en particulier l'abeille domestique, quittent les parcelles de colza pour visiter d'autres habitats dès la fin de la floraison du colza. En effet, la pollinisation par l'abeille domestique est plus importante après la floraison du colza dans les prairies (**K**) et dans les céréales (**L**) en particulier dans les paysages riches en colza (Chapitre 2). De façon intéressante, nous montrons que la dispersion vers les prairies intervient à plus large échelle que la dispersion vers les céréales, probablement parce que ces habitats fournissent une quantité plus importante de ressources florales. Différents habitats sont ainsi successivement visités par les insectes pollinisateurs dans la saison pour satisfaire leurs besoins alimentaires. Nous confirmons ainsi l'hypothèse de **complémentarité spatio-temporelle** des habitats dans le maintien des pollinisateurs suggérée dans des études précédentes (Mallinger et al., 2016; Mandelik et al., 2012) et montrée sur une unique espèce d'abeille *Osmia bicornis* (Yourstone et al., 2021). Nos résultats confirment également que les CFM sont des ressources qui bénéficient aux insectes pollinisateurs et à la pollinisation des plantes dans les espaces agricoles (Diekötter et al., 2014; Herbertsson et al., 2017).

Finalement, nos résultats indiquent qu'en dehors des périodes de floraison des CFM, la capacité des prairies et des céréales à supporter les insectes pollinisateurs sauvages augmente avec la diversité

ou la quantité de ressources florales qu'ils abritent (Chapitre 3). Cela confirme que les fleurs cultivées et sauvages sont successivement visitées dans les paysages agricoles révélant ainsi une sorte de complémentarité entre ces deux types de ressources dans le maintien des insectes pollinisateurs sauvages déjà suggérée chez l'abeille domestique (Requier et al., 2015). Les relations entre les ressources florales et les pollinisateurs sauvages ont déjà été explorées en céréales et en prairies (Rollin et al., 2019; Sidemo-Holm et al., 2021). Nos résultats indiquent que les plantes adventices supportent les pollinisateurs sauvages à travers différents mécanismes dans ces deux habitats. L'abondance des plantes adventices augmente la diversité des pollinisateurs sauvages en céréale (**M**). Une augmentation de la diversité des pollinisateurs sauvages à travers un assouplissement de la **compétition interspécifique** est suggérée comme le principal processus en jeu dans ces habitats. A cette même période, la diversité des plantes sauvages augmente l'abondance des pollinisateurs sauvages en prairie (**N**). Nous suggérons ici que la compétition interspécifique est faible dans les prairies, et que la diversité des plantes supporte les pollinisateurs à travers des **effets d'échantillonnage** ou de **complémentarité**.

4. Limites des études

La caractérisation des échelles d'effet du paysage était un objectif majeur de la thèse, c'est un point qui n'a néanmoins pas été abordé dans le Chapitre 1. Dans cette étude l'échelle à laquelle nous avons caractérisé le paysage (500m) était plus faible que l'échelle d'effet attendue selon la capacité de dispersion de l'abeille domestique (Beekman & Ratnieks, 2000; Jackson & Fahrig, 2012). Mais il existe des compromis entre la finesse de la description des paysages et l'échelle spatiale à laquelle les paysages sont décrits. En effet, dans le Chapitre 1 nous avons décrit finement les ressources fournies par les paysages à travers l'observation du décalage temporel dans la floraison des parcelles, et avons recherché activement les ruches à la même échelle spatiale. Alors que dans les Chapitres 2 & 3, les échelles d'influence étaient précisément déterminées, en contrepartie le décalage temporel dans la floraison des CFM était caractérisé de façon moins précise et nous avons utilisé la quantité d'AB et d'HSN dans le paysage comme proxy de la quantité de fleurs sauvages dans le paysage. Bien que ces deux habitats abritent une quantité de ressources florales importante (Cole et al., 2017; Sidemo-Holm et al., 2021), il existe une variabilité importante entre parcelles dans la fourniture de ressources dont nous avons montré l'importance dans la capacité à maintenir localement les pollinisateurs (Chapitre 3). Une description fine des paysages et des ressources qu'ils abrite à large échelle spatiale pourrait reposer sur l'utilisation d'images aériennes par exemple (Herman, 2021).

La mobilisation de méthodes d'échantillonnages différentes peut fournir des résultats contradictoires, nous en avons un exemple dans cette thèse. En culture de colza, la quantité d'HSN dans le paysage favorise la pollinisation par les petits pollinisateurs à une faible échelle spatiale (Chapitre 2) alors que dans la même culture, la diversité des pollinisateurs sauvages capturés par bols colorés diminue avec la quantité d'HSN à une échelle bien plus large (Chapitre 3). Les deux méthodes d'échantillonnage utilisées sont certainement toutes deux associées à des biais donnant lieu à des représentations différentes d'une même communauté de pollinisateurs. Nous étions focalisés sur les petits insectes qui visitent et pollinisent les fleurs de colza dans le Chapitre 3, et donc à une fraction des pollinisateurs (Senapathi et al., 2015), et à l'ensemble des pollinisateurs sauvages dans le Chapitre 2, bien que les plus gros pollinisateurs soient capturés de manière peu efficace par bols colorés (Westphal et al., 2008). Appliquer différentes méthodes de suivi et confronter les résultats obtenus à partir des différentes méthodes est une pratique cohérente, bien que coûteuse, pour vérifier la robustesse des résultats. Il pourrait ainsi être intéressant dans le cadre de cette thèse, de valider les relations observées entre la

diversité et l'abondance des plantes et des pollinisateurs sauvages dans le chapitre 3 avec des données d'interactions réalisées (observations des insectes pollinisateurs sur les fleurs).

L'ensemble de nos études étaient conduites dans la ZAPVS qui abrite une diversité importante d'insectes pollinisateurs sauvages, par exemple, plus d'un quart des espèces d'abeilles sauvages présentes en France y sont observées (Bretagnolle et al., 2018). Il est suspecté que les patrons d'utilisation des ressources florales par les insectes pollinisateurs ainsi que la pollinisation dans les paysages agricoles varient d'une zone à une autre suivant les communautés de pollinisateurs qu'elles abritent. De plus, les études présentées dans les chapitres 2 et 3 indiquent un fort effet de l'année sur la diversité et l'abondance des insectes pollinisateurs et sur la pollinisation. Cet effet de l'année est difficile à comprendre car de nombreux paramètres peuvent intervenir, il pourrait être intéressant dans un premier temps de quantifier la contribution des conditions climatiques, connues pour affecter les communautés de pollinisateurs (Miñarro & García, 2018; Nderitu et al., 2008) à la dynamique interannuelle des communautés de pollinisateurs. Mais, cela repose sur des suivis des pollinisateurs sur des dizaines d'années pour avoir suffisamment de puissance statistique et de variations dans les conditions climatiques. Le Chapitre 1 repose sur des données collectées sur une année d'étude avec une anomalie positive de température dans notre site d'étude pendant la période de suivi (données Météo France). Nous suggérons de répéter les suivis sur d'autres années d'étude pour valider les patrons mis en évidence dans ce chapitre.

II. Maintenir les pollinisateurs et la pollinisation dans les paysages agricoles

1. Supplémenter les paysages en ressources avec les cultures à floraison massive

Les CFM en supplémentant les paysages agricoles en ressources florales participent au maintien de l'abeille domestique, des pollinisateurs sauvages et de la pollinisation dans les paysages agricoles (Chapitres 1, 2 et 3). **Augmenter la quantité de CFM** semble être favorable aux pollinisateurs à large échelle spatiale (Chapitre 2) mais peut engendrer des effets de dilution qui peuvent limiter l'exploitation des ressources florales (Chapitre 1). Nos résultats suggèrent qu'un décalage temporel dans la floraison des parcelles peut augmenter l'efficacité d'exploitation des ressources fournies par les CFM, notamment par l'abeille domestique (Chapitre 1). L'accumulation de degrés jours guide la phénologie des cultures (Miller et al., 2018), une méthode pour **étaler la floraison des parcelles** pourrait être de semer les CFM à différentes dates dans un même paysage. Le risque est d'affecter la production agricole en semant à une date non optimale (Ozer, 2003) et en étalant la disponibilité en pollen dans la saison (Chapitre 2). Une stratégie alternative pour augmenter la disponibilité en CFM en évitant les effets de dilution pourrait reposer sur le développement d'une **diversité de cultures** fournissant des ressources florales. Des cultures telles que le lin (floraison d'avril à mai), le pois (mai à juin), le pavot (juillet) ou le sarrasin (juin à septembre) sont ciblées par les insectes pollinisateurs et pourraient être successivement visitées dans la saison. Il a par exemple été montré que des cultures de fraises était largement visitées par les insectes pollinisateurs après la floraison de vergers de pommes (Grab et al., 2017).

Pour aller plus loin dans la compréhension du rôle des CFM, nous proposons d'étudier leur effet sur le long terme, et notamment à une échelle pluri-annuelle, sur les communautés de pollinisateurs. Les communautés ne répondent pas instantanément à un changement de pratiques ou de paysages, les pratiques et paysages passés peuvent avoir des répercussions sur la biodiversité et les fonctions écologiques (Alignier & Aviron, 2017; Mahaut et al., 2018). Récemment, Beyer et al., (2021) ont montré que la quantité de CFM dans le paysage sur les trois années précédentes impacte positivement

l'abondance des pollinisateurs sauvages et l'efficacité de la pollinisation en culture de colza. Cela indique un décalage temporel dans la réponse des pollinisateurs à la quantité de ressources fournies par les CFM à travers des bénéfices pour leur survie et leur reproduction (Westphal et al., 2009). Ces bénéfices semblent néanmoins restreints à certaines populations généralistes visitant les fleurs cultivées, les espèces rares étant peu observées dans les cultures (Kleijn et al., 2015). Les CFM pourraient fournir un avantage aux espèces généralistes par rapport aux espèces rares en termes de survie et de reproduction et modifier durablement les communautés de pollinisateurs.

2. Assurer la continuité spatio-temporelle de disponibilité en ressources florales

Nos résultats assurent que la continuité spatiale et temporelle dans la disponibilité des ressources florales est essentielle pour maintenir les insectes pollinisateurs et la pollinisation dans les paysages agricoles. Les HSN sont ainsi des éléments centraux des paysages agricoles car les insectes pollinisateurs dispersent des HSN vers les CFM pendant la floraison de ces derniers puis, après leur floraison, redispersent vers les HSN (Chapitre 2). En accord avec de nombreuses études, nous recommandons de conserver une surface en HSN importante pour supporter les pollinisateurs et la pollinisation (Bartual et al., 2018; Steffan-Dewenter et al., 2002). La première étape de dispersion a lieu à une faible échelle spatiale alors que la seconde a lieu à bien plus large échelle, nous proposons alors de **maintenir des HSN à proximité des CFM** pour favoriser l'utilisation complémentaire des ressources florales dans la mosaïque agricole. La conservation d'habitats ligneux (bois, haies), de jachères et de prairies est alors ciblée (Haaland et al., 2011; Mallinger et al., 2016). La capacité des prairies à supporter les pollinisateurs sauvages augmente avec la **diversité des plantes sauvages** qu'elles supportent (Chapitre 3). Les prairies dans les paysages agricoles sont fauchées pour le foin ou pâturées par le bétail. En accord avec l'hypothèse de perturbation intermédiaire¹¹ (Mackey & Currie, 2001), la diminution de l'intensité de leur usage à travers la réduction du nombre de fauches ou de la densité du bétail conduit à une augmentation de la diversité des plantes sauvages dans les prairies (Blüthgen et al., 2012) et permet finalement d'augmenter la capacité de ces habitats à maintenir les pollinisateurs et la pollinisation (Albrecht et al., 2007).

Nos résultats indiquent également que les plantes adventices, en contribuant à la continuité spatio-temporelle de disponibilité en ressources florales, sont essentielles pour la persistance des insectes pollinisateurs et de la pollinisation (Chapitres 2 et 3). L'augmentation de la disponibilité en **plantes adventices en culture de céréale** est à privilégier car cette culture couvre plus de 50% de la surface agricole française (Neron, 2018). L'abondance, plus que la diversité des plantes adventices semble déterminante dans le maintien des pollinisateurs (Chapitre 3), celle-ci est guidée par un ensemble complexe de processus impliquant la dispersion, les pratiques agricoles et la compétition avec la culture. Atteindre une abondance importante en plantes adventices en culture céréalière peut reposer sur la diminution de l'intensité du désherbage à travers l'AB notamment (Sidemo-Holm et al., 2021), la diminution de la quantité d'engrais connue pour augmenter la compétition entre la culture et les plantes adventices (Gaba et al., 2018) et l'augmentation de la quantité d'AB dans le paysage (Bourgeois et al., 2020).

Pour aller plus loin dans la compréhension de la complémentarité spatio-temporelle des habitats dans la persistance des pollinisateurs, nous proposons de mobiliser la méthode développée par Marini et al., (2019), plus intégrative que celle des buffers, et qui permet d'étudier la façon dont les

¹¹ Hypothèse qui établit que la diversité est maximale à des niveaux intermédiaires de perturbation.

communautés sont liées à de multiples habitats dans les paysages. Cette méthode repose sur des suivis, par exemple des pollinisateurs, dans différents habitats d'un même paysage. En liant les espèces de pollinisateurs à différents habitats, les méthodes et outils d'analyses des réseaux d'interactions bipartites entre les espèces de pollinisateurs et les habitats peuvent être utilisés. Nous proposons de répéter les suivis dans des paysages plus ou moins hétérogènes et à différentes périodes de la saison, la variation de la forme des réseaux pourrait ainsi renseigner sur l'importance d'un habitat et des ressources qu'il fournit pour certaines espèces à travers les conditions paysagère et temporelle. Deux limites majeures à l'application de cette méthode émergent, la première est liée à l'effort d'échantillonnage conséquent engendré par la répétition des suivis au sein d'un même paysage, la seconde est liée à la définition *a priori* de l'échelle d'échantillonnage qui fait prendre le risque de travailler à une échelle non optimale.

3. Réduire la taille des parcelles agricoles

Nos résultats indiquent que l'abeille domestique exploite préférentiellement les ressources florales à proximité de la bordure des parcelles agricoles, en particulier dans les CFM (Chapitre 1). Ce patron semble plus marqué chez les pollinisateurs sauvages (Geslin et al., 2016; MacInnis et al., 2020) qui ont généralement une capacité de dispersion moins importante que l'abeille domestique (Greenleaf et al., 2007). Pour faciliter la consommation des ressources par les pollinisateurs et ainsi maintenir la pollinisation, **favoriser des petites parcelles** semble être une stratégie cohérente. Les petites parcelles maintiennent en effet plus efficacement les pollinisateurs sauvages (Artz et al., 2011; Muljar et al., 2010) alors que des plus grosses parcelles en CFM sont principalement visitées par l'abeille domestique (Isaacs & Kirk, 2010). A l'échelle paysagère, diminuer la taille des parcelles entraîne une augmentation de l'hétérogénéité configurationnelle connue pour favoriser la diversité et l'abondance des insectes pollinisateurs (Hass et al., 2018; Hopfenmüller et al., 2014 mais voir Holzschuh et al., 2010). En favorisant le mouvement des organismes et le transfert de pollen, l'efficacité de la pollinisation augmente également avec l'hétérogénéité configurationnelle des paysages (Hass et al., 2018).

Pour aller plus loin, il pourrait être intéressant d'étudier le rôle de l'hétérogénéité configurationnelle sur la complémentarité spatio-temporelle des habitats dans le maintien des insectes pollinisateurs. En facilitant le mouvement des organismes entre habitats, l'hétérogénéité configurationnelle est suspectée d'augmenter la complémentarité entre habitats dans le maintien des pollinisateurs et de la pollinisation. Jusqu'ici les études s'intéressant aux interactions entre la configuration et la composition du paysage sont rares (mais voir Martin et al., 2019), probablement dû à des contraintes méthodologiques liées par exemple à la corrélation entre certaines variables décrivant la composition du paysage et des variables décrivant la configuration du paysage (Fahrig et al., 2011).

4. Concilier l'abeille domestique et les pollinisateurs sauvages

Nos résultats suggèrent que l'abeille domestique exclut les pollinisateurs sauvages des fleurs cultivées (Chapitre 3) questionnant ainsi le rôle de l'abeille domestique dans les paysages agricoles. En effet, les fleurs cultivées représentent une ressource préférentielle pour de nombreux pollinisateurs sauvages (Westphal et al., 2009), la survie et la reproduction de ces espèces peut diminuer en présence de l'abeille domestique et ainsi contribuer à leur déclin (Hudewenz & Klein, 2015). Ce déclin menace la pollinisation des cultures par les pollinisateurs sauvages (Garibaldi et al., 2013), la pollinisation des cultures par l'abeille domestique dont l'efficacité peut être guidée par les interactions avec les pollinisateurs sauvages (Greenleaf & Kremen, 2006), et la résilience du service de pollinisation qui repose sur la diversité des pollinisateurs (Senapathi et al., 2015; Winfree et al., 2007). Mais, bien que

l'abeille domestique soit en compétition pour les ressources avec les pollinisateurs sauvages, sa conservation est essentielle, c'est en effet une espèce emblématique des milieux agricoles qui supporte la production de certaines cultures et du miel (Catarino, Bretagnolle, et al., 2019; Faure et al., 2021). Nous proposons de **maintenir les plantes adventices dans les CFM pour concilier les pollinisateurs sauvages et l'abeille domestique**. Nos résultats suggèrent en effet que l'augmentation de la diversité des plantes adventices en culture de colza permet le partitionnement des ressources entre l'abeille domestique sur les fleurs cultivées et les pollinisateurs sauvages sur les plantes adventices (Chapitre 3). Dans ce cas, l'abeille domestique participe à la pollinisation et les pollinisateurs sauvages se nourrissent des ressources fournies par les plantes adventices et peuvent visiter les fleurs cultivées en cas d'absence de l'abeille domestique.

Pour aller plus loin dans la compréhension des mécanismes de cooccurrence entre l'abeille domestique et les pollinisateurs sauvages en CFM, nous suggérons d'étudier leur ségrégation dans l'espace, dans le temps¹², et le partitionnement des ressources¹³. Alors que les aspects temporels, notamment journaliers et saisonniers (Pisanty et al., 2014), spatiaux (Miñarro & García, 2018) et des ressources consommées (Jeavons et al., 2020) ont été explorés, l'étude du Chapitre 1 suggère qu'il est nécessaire de prendre en compte ces dimensions simultanément car l'abeille domestique exploite les ressources à différents emplacements des parcelles au cours de la journée (Chapitre 1). Nous suggérons d'étudier les mécanismes de cooccurrence dans différentes cultures, par exemple en tournesol, mais aussi en colza où l'abondance en abeille domestique y est plus faible et le nectar fourni de manière plus importante (Horn et al., 2021; Rollin et al., 2013). Nous proposons également de séparer le rôle de la compétition par exploitation de la compétition par interférence, l'idée étant de comprendre si le patron de butinage des pollinisateurs sauvages se fixe sur la quantité de nectar ou sur l'abeille domestique.

III. Compatibilité avec la productivité des paysages agricoles

Pour favoriser la persistance des pollinisateurs et de la pollinisation dans les paysages agricoles, à partir de nos résultats nous avons proposé de maintenir les HSN et les plantes adventices, d'étaler la floraison des CFM et, de réduire la taille des parcelles agricoles (Fig. 4. 2). La mise en place de ces mesures peut être freinée par des conflits que ces mesures entraînent avec la conservation d'autres groupes taxonomiques ou la production agricole.

1. Les plantes adventices : pilier de la multifonctionnalité vs compétition avec les cultures

Les plantes adventices par leur diversité ou leur abondance permettent de maintenir les pollinisateurs et la fonction de pollinisation en particulier en dehors des périodes de floraison des CFM (Chapitre 2, 3). Les plantes adventices se placent comment le pilier de la multifonctionnalité¹⁴ dans les milieux agricoles en étant à la base de nombreux réseaux trophiques. Ainsi, dans une étude expérimentale consistant à manipuler la diversité des plantes dans des quadrats expérimentaux de 40m², Scherber et al., (2010) ont montré que la diversité des plantes augmente la diversité et l'abondance des parasitoïdes, des carnivores, des herbivores, des omnivores et des décomposeurs du sol. Plus récemment, dans des parcelles agricoles, Gaba et al., (2020) ont montré que l'abondance des plantes adventices supporte la multifonctionnalité des parcelles agricoles (activité enzymatique du sol, pollinisation, contrôle biologique) dans différents types de cultures.

¹² Utilisation de ressource à différents endroits et moments.

¹³ Utilisation de ressources distinctes (par exemple les fleurs cultivées et les plantes adventices).

¹⁴ Le fonctionnement moyen d'un écosystème (Hector & Bagchi, 2007).

La préservation des plantes adventices dans les parcelles agricoles s'apparente à la stratégie "land sharing" où les objectifs de conservation de la biodiversité sont élaborés dans les zones productives (Phalan et al., 2011). Les plantes adventices, les "mauvaises herbes" sont néanmoins mal perçues par les acteurs du secteur agricole car elles peuvent favoriser des organismes qui impactent négativement les cultures (Barbercheck & Wallace, 2021) mais surtout parce qu'elles sont en compétition pour les ressources avec les plantes cultivées (Cousens, 1985; Ryan et al., 2009). Cette compétition est suspectée d'être impliquée dans la perte de rendements dans les parcelles en AB par rapport à celles en agriculture conventionnelle. Néanmoins, accompagnée de pratiques agroécologiques, la perte de rendement en AB est moins importante (Seufert et al., 2012) ce qui suggère que des méthodes peuvent favoriser la biodiversité sans impacter les rendements. A titre d'exemple, diminuer la densité de semis en culture de céréale, dans une certaine mesure, peut augmenter la couverture en fleurs adventices dans les parcelles sans affecter les rendements des cultures, probablement à travers une diminution de la compétition au sein de la plante cultivée (Sidemo-Holm et al., 2021). Une autre étude en champ montre également que la réduction de la quantité d'herbicides ne conduit pas à un déclin de rendement en culture de céréales (Catarino, Gaba, et al., 2019).

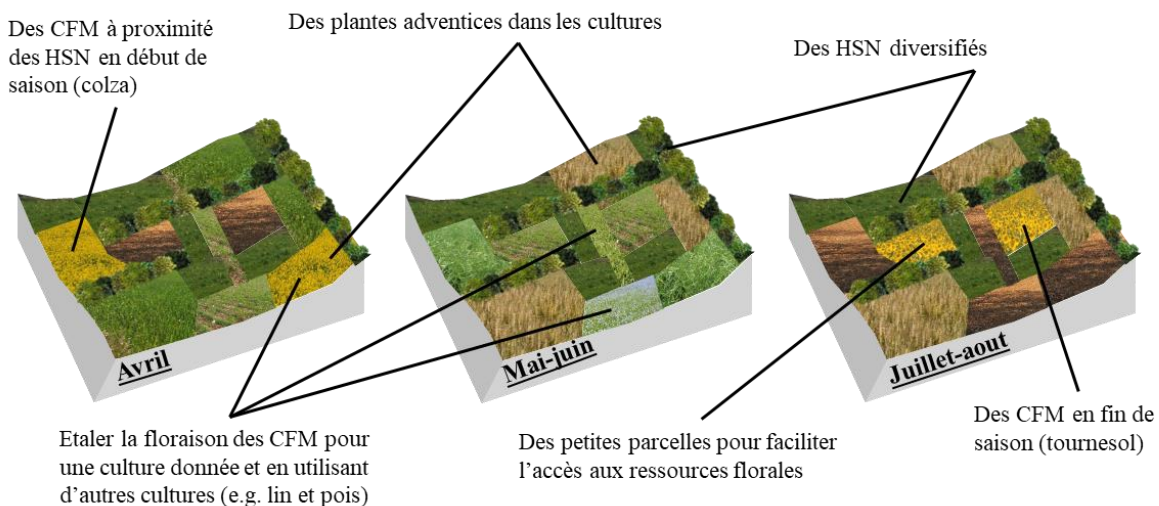


Fig. 4. 2. Représentation d'un paysage agricole du printemps à l'été en milieu tempéré qui favorise le maintien des pollinisateurs et de la fonction de pollinisation.

2. Les habitats semi naturels : source de biodiversité vs perte de surface cultivable

Les HSN sont essentiels pour supporter les pollinisateurs et la pollinisation des espaces agricoles en favorisant l'utilisation des ressources fournies par les CFM et en assurant la continuité spatiale et temporelle de disponibilité en ressources florales. Ces habitats apparaissent également efficaces pour maintenir de nombreux groupes taxonomiques et fonctions écologiques (e.g. contrôle biologique, conservation des sols ; Holland et al., 2017) et donc la multifonctionnalité dans les paysages agricoles (Resch et al., 2021). Par exemple une méta-analyse a révélé que la quantité d'HSN favorise les agents du contrôle biologique mais pas les ravageurs de culture (Chaplin-Kramer et al., 2011), les ravageurs peuvent bénéficier des ressources présentes dans les HSN mais semblent aussi prédatées de façon plus intense.

La quantité d'HSN dans les paysages agricoles augmente également les rendements agricoles, c'est notamment le cas dans les cultures dépendantes de la pollinisation entomophile (Raderschall et al., 2021; B. A. Woodcock et al., 2019) alors que les études sont moins claires dans les céréales par exemple (Raatz

et al., 2021; Redlich et al., 2021). Augmenter la quantité d’HSN dans le paysage est donc une stratégie favorable à la conservation de la biodiversité, et aux agriculteurs dont l’optimisation des rendements sur la surface qui leur est disponible est souvent visée (Montoya et al., 2020). Il y a aussi une demande de la part des agriculteurs plus importante d’HSN quand ceux-ci cultivent une quantité importante de CFM qui dépendent de la pollinisation par les insectes (Montoya et al., 2020). Augmenter la quantité de CFM dans le paysage peut donc indirectement favoriser la conservation de la biodiversité. Mais, évidemment, dédier l’ensemble de l’espace aux HSN n’est pas compatible avec la production agricole à l’échelle du territoire dont l’optimisation est visée par les syndicats agricoles (Montoya et al., 2020). Il faut ainsi trouver le(s) juste(s) compromis, maintenir et restaurer les HSN pour qu’ils couvrent une surface modérée, aux alentours de 20%, pourrait permettre de maintenir les rendements et leur stabilité des cultures dépendantes et non dépendantes de la pollinisation par les insectes (Montoya et al., 2019).

3. Des petites parcelles : accessibilité des ressources vs efficacité de la mécanisation

Les ressources florales sont préférentiellement exploitées à de faibles distances de la bordure des parcelles (Chapitre 1), des petites parcelles favorisent donc localement les pollinisateurs mais également à l’échelle du paysage en favorisant la dispersion des organismes entre habitats. De nombreux groupes taxonomiques et fonctions écologiques répondent positivement à la diminution de la taille des parcelles. C’est notamment le cas des plantes adventices (Alignier et al., 2020) dont la diversité et l’abondance en plein champ découlent d’un processus de dispersion à partir des bords de parcelle (Bourgeois et al., 2020). Des grosses parcelles fournissent ainsi relativement peu de ressources par unité de surface à travers les plantes adventices aux insectes pollinisateurs, granivore, herbivores ou décomposeurs. D’autres études montrent qu’une augmentation de la taille des parcelles entraîne une diminution de la diversité ou de l’abondance de nombreux organismes tels que les oiseaux, les papillons, les araignées, les carabes (Fahrig et al., 2015) et des fonctions écologiques telles que la pollinisation et le contrôle biologique (Martin et al., 2019).

Diminuer la taille des parcelles favorise également les rendements. Une synthèse de 118 études réalisées dans des contextes variés révèlent que des petites parcelles affichent des rendements plus importants (dans 79% des études) que des parcelles de tailles plus importantes (Ricciardi et al., 2021). Il semble ainsi possible à travers la diminution de la taille des parcelles de maintenir la biodiversité tout en augmentant ou maintenant la production agricole. La diminution de la taille des parcelles peut néanmoins entraîner une augmentation des coûts de production en augmentant le temps passé pour les pratiques agricoles et la consommation d’essence par unité de surface due aux performances moins importantes des machines agricoles en bord de parcelles (Clough et al., 2020). Néanmoins, le gain d’efficacité des machines agricoles plafonne à partir de 2ha (Rodríguez & Wiegand, 2009) ce qui suggère qu’une réduction de la taille des parcelles à 2ha est un compromis intéressant pour maintenir la biodiversité, les rendements et les coûts associés aux pratiques agricoles. Cet objectif semble plus ou moins réalisable en fonction des zones géographiques. Dans notre zone d’étude dans l’ouest de la France, cela reviendrait à diviser la taille des parcelles en moyenne par trois, mais dans d’autres régions du monde, par exemple dans le sud-ouest des Etats-Unis les parcelles devraient être divisées par 16 en moyenne (Larsen & Noack, 2021).

IV. Conclusion

Nous avons montré que la dynamique spatiale et temporelle des paysages agricoles conduisait les pollinisateurs à visiter différents habitats et à butiner différents types de ressources florales (fleurs cultivées et sauvages) au cours de la saison. La dispersion spatiale et temporelle, les interactions trophiques, et la compétition semblent être des facteurs déterminants dans la mise en place des interactions entre plantes et pollinisateurs. Une diversité d'habitats doit être conservée pour assurer la conservation des pollinisateurs et de la fonction de pollinisation. Cela peut passer par le maintien d'habitats semi-naturels et de plantes adventices dans les cultures pour assurer la continuité spatiale et temporelle des ressources florales, de cultures à floraison massive pour compléter les paysages agricoles en ressources florales, et par la réduction de la taille des parcelles pour favoriser l'accessibilité des ressources pour les pollinisateurs. Ces mesures sont compatibles avec le maintien de nombreux groupes taxonomiques et avec la multifonctionnalité dans les paysages agricoles. Afin de maintenir à la fois la biodiversité et la production agricole, certains compromis dans l'agencement des paysages agricoles doivent être trouvés, notamment quant à la surface à allouer aux habitats semi-naturels, à la place à laisser aux plantes adventices dans les parcelles ou à la taille des parcelles. La transition vers un système agricole s'appuyant sur des pratiques agroécologiques permettrait la mise en place de stratégies gagnantes-gagnantes pour le maintien de la biodiversité et de la productivité dans les paysages agricoles (Tamburini et al., 2020).

BIBLIOGRAPHIE

- Abou-Shaara, H. (2014). The foraging behaviour of honey bees, *Apis mellifera*: A review. *Veterinari Medicina*, 59, 1–10. <https://doi.org/10.17221/7240-VETMED>
- Aguilera, G., Roslin, T., Müller, K., Tamburini, G., Birkhofer, K., Caballero-Lopez, B., Lindström, S. A.-M., Öckinger, E., Rundlöf, M., Rusch, A., Smith, H. G., & Bommarco, R. (2020). Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. *Journal of Applied Ecology*, 57(11), 2170–2179. <https://doi.org/10.1111/1365-2664.13712>
- Ahrenfeldt, E. J., Klatt, B. K., Arildsen, J., Trandem, N., Andersson, G. K. S., Tschardtke, T., Smith, H. G., & Sigsgaard, L. (2015). Pollinator communities in strawberry crops – variation at multiple spatial scales. *Bulletin of Entomological Research*, 105(4), 497–506. <https://doi.org/10.1017/S000748531500036X>
- Albrecht, M., Duelli, P., Müller, C., Kleijn, D., & Schmid, B. (2007). The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland: Agri-environment schemes and pollination. *Journal of Applied Ecology*, 44(4), 813–822. <https://doi.org/10.1111/j.1365-2664.2007.01306.x>
- Alignier, A., & Aviron, S. (2017). Time-lagged response of carabid species richness and composition to past management practices and landscape context of semi-natural field margins. *Journal of Environmental Management*, 204, 282–290. <https://doi.org/10.1016/j.jenvman.2017.08.054>
- Alignier, A., Solé-Senan, X. O., Robleño, I., Baraibar, B., Fahrig, L., Giralt, D., Gross, N., Martin, J.-L., Recasens, J., Sirami, C., Siriwardena, G., Bøsem Baillod, A., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Badenhausser, I., Baudry, J., ... Batáry, P. (2020). Configurational crop heterogeneity increases within-field plant diversity. *Journal of Applied Ecology*, 57(4), 654–663. <https://doi.org/10.1111/1365-2664.13585>
- Angelella, G. M., McCullough, C. T., & O'Rourke, M. E. (2021). Honey bee hives decrease wild bee abundance, species richness, and fruit count on farms regardless of wildflower strips. *Scientific Reports*, 11(1), 3202. <https://doi.org/10.1038/s41598-021-81967-1>
- Arnholt, A. T., & Evans, B. (2017). *BSDA: Basic Statistics and Data Analysis* (1.2.0). <https://CRAN.R-project.org/package=BSDA>
- Artz, D. R., Hsu, C. L., & Nault, B. A. (2011). Influence of Honey Bee, *Apis mellifera*, Hives and Field Size on Foraging Activity of Native Bee Species in Pumpkin Fields. *Environmental Entomology*, 40(5), 1144–1158. <https://doi.org/10.1603/EN10218>
- Balfour, N. J., Ollerton, J., Castellanos, M. C., & Ratnieks, F. L. W. (2018). British phenological records indicate high diversity and extinction rates among late-summer-flying pollinators. *Biological Conservation*, 222, 278–283. <https://doi.org/10.1016/j.biocon.2018.04.028>
- Bänsch, S., Tschardtke, T., Gabriel, D., & Westphal, C. (2020). Crop pollination services: Complementary resource use by social vs solitary bees facing crops with contrasting flower supply. *Journal of Applied Ecology*, n/a(n/a). <https://doi.org/10.1111/1365-2664.13777>
- Bänsch, S., Tschardtke, T., Ratnieks, F. L. W., Härtel, S., & Westphal, C. (2020). Foraging of honey bees in agricultural landscapes with changing patterns of flower resources. *Agriculture, Ecosystems & Environment*, 291, 106792. <https://doi.org/10.1016/j.agee.2019.106792>
- Barbercheck, M. E., & Wallace, J. (2021). Weed–Insect Interactions in Annual Cropping Systems. *Annals of the Entomological Society of America*, 114(2), 276–291. <https://doi.org/10.1093/aesa/saab002>
- Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. *Proceedings of the National Academy of Sciences*, 115(25), 6506–6511. <https://doi.org/10.1073/pnas.1711842115>
- Bartomeus, I., Potts, S. G., Steffan-Dewenter, I., Vaissière, B. E., Woyciechowski, M., Krewenka, K. M., Tscheulin, T., Roberts, S. P. M., Szentgyörgyi, H., Westphal, C., & Bommarco, R. (2014). Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. *PeerJ*, 2, e328. <https://doi.org/10.7717/peerj.328>
- Bartual, A., Bocci, G., Marini, S., & Moonen, A. C. (2018). Local and landscape factors affect sunflower pollination in a Mediterranean agroecosystem. *PLOS ONE*, 13(9), e0203990. <https://doi.org/10.1371/journal.pone.0203990>
- Bates, D., Maechler, M., Bolker, J., Runkler, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., Bauer, A., & simulate.formula, P. N. K. (shared copyright on. (2021). *lme4: Linear Mixed-Effects Models using "Eigen" and S4* (1.1-27.1). <https://CRAN.R-project.org/package=lme4>
- Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A. K., Morton, R. D., Smart, S. M., & Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, 530(7588), 85–88. <https://doi.org/10.1038/nature16532>
- Becher, M. A., Grimm, V., Thorbek, P., Horn, J., Kennedy, P. J., & Osborne, J. L. (2014). BEEHAVE: A systems model of honeybee colony dynamics and foraging to explore multifactorial causes of colony failure. *Journal of Applied Ecology*, 51(2), 470–482. <https://doi.org/10.1111/1365-2664.12222>
- Beekman, M., & Ratnieks, F. L. W. (2000). Long-range foraging by the honey-bee, *Apis mellifera* L. *Functional Ecology*, 14, 490–496. <https://doi.org/10.1046/j.1365-2435.2000.00443.x>
- Bennett, A. B., & Isaacs, R. (2014). Landscape composition influences pollinators and pollination services in perennial biofuel plantings. *Agriculture, Ecosystems & Environment*, 193, 1–8. <https://doi.org/10.1016/j.agee.2014.04.016>
- Beyer, N., Gabriel, D., & Westphal, C. (2021). Contrasting effects of past and present mass-flowering crop cultivation on bee pollinators shaping yield components in oilseed rape. *Agriculture, Ecosystems & Environment*, 319, 107537. <https://doi.org/10.1016/j.agee.2021.107537>

- Biella, P., Akter, A., Ollerton, J., Tarrant, S., Janeček, Š., Jersáková, J., & Klecka, J. (2019). Experimental loss of generalist plants reveals alterations in plant-pollinator interactions and a constrained flexibility of foraging. *Scientific Reports*, 9(1), 7376. <https://doi.org/10.1038/s41598-019-43553-4>
- Blaauw, B. R., & Isaacs, R. (2014). Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wildflowers. *Basic and Applied Ecology*, 15(8), 701–711. <https://doi.org/10.1016/j.baee.2014.10.001>
- Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A.-M., Rand, T. A., & Tscharntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agriculture, Ecosystems & Environment*, 146(1), 34–43. <https://doi.org/10.1016/j.agee.2011.09.005>
- Blüthgen, N., Dormann, C. F., Prati, D., Klaus, V. H., Kleinebecker, T., Hölzel, N., Alt, F., Boch, S., Gockel, S., Hemp, A., Müller, J., Nieschulze, J., Renner, S. C., Schöning, I., Schumacher, U., Socher, S. A., Wells, K., Birkhofer, K., Buscot, F., ... Weisser, W. W. (2012). A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic and Applied Ecology*, 13(3), 207–220. <https://doi.org/10.1016/j.baee.2012.04.001>
- Bommarco, R., Marini, L., & Vaissière, B. E. (2012). Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia*, 169(4), 1025–1032. <https://doi.org/10.1007/s00442-012-2271-6>
- Bosch, J., Retana, J., & Cerdá, X. (1997). Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia*, 109(4), 583–591. <https://doi.org/10.1007/s004420050120>
- Bourgeois, B., Gaba, S., Plumejeaud, C., & Bretagnolle, V. (2020). Weed diversity is driven by complex interplay between multi-scale dispersal and local filtering. *Proceedings of the Royal Society B: Biological Sciences*, 287(1930), 20201118. <https://doi.org/10.1098/rspb.2020.1118>
- Bretagnolle, V., Benoit, M., Bonnefond, M., Breton, V., Church, J. M., Gaba, S., Gilbert, D., Gillet, F., Glatron, S., Guerbois, C., Lamouroux, N., Lebouvier, M., Mazé, C., Mouchel, J.-M., Ouin, A., Pays, O., Piscart, C., Ragueneau, O., Servain, S., ... Fritz, H. (2019). Action-orientated research and framework: Insights from the French long-term social-ecological research network. *Ecology and Society*, 24(3), art10. <https://doi.org/10.5751/ES-10989-240310>
- Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhauer, I., Monceau, K., Allier, F., Monestiez, P., & Gaba, S. (2018). Towards sustainable and multifunctional agriculture in farmland landscapes: Lessons from the integrative approach of a French LTSER platform. *Science of The Total Environment*, 627, 822–834. <https://doi.org/10.1016/j.scitotenv.2018.01.142>
- Bretagnolle, V., & Gaba, S. (2015). Weeds for bees? A review. *Agronomy for Sustainable Development*, 35(3), 891–909. <https://doi.org/10.1007/s13593-015-0302-5>
- Briones, M. J. I., & Schmidt, O. (2017). Conventional tillage decreases the abundance and biomass of earthworms and alters their community structure in a global meta-analysis. *Global Change Biology*, 23(10), 4396–4419. <https://doi.org/10.1111/gcb.13744>
- Brockerhoff, E. G., Barbaro, L., Castagneyrol, B., Forrester, D. I., Gardiner, B., González-Olabarria, J. R., Lyver, P. O., Meurisse, N., Oxbrough, A., Taki, H., Thompson, I. D., van der Plas, F., & Jactel, H. (2017). Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity and Conservation*, 26(13), 3005–3035. <https://doi.org/10.1007/s10531-017-1453-2>
- Brown, P. W., & Schulte, L. A. (2011). Agricultural landscape change (1937–2002) in three townships in Iowa, USA. *Landscape and Urban Planning*, 100(3), 202–212. <https://doi.org/10.1016/j.landurbplan.2010.12.007>
- Bukovinszky, T., Verheijen, J., Zwerver, S., Klop, E., Biesmeijer, J. C., Wäckers, F. L., Prins, H. H. T., & Kleijn, D. (2017). Exploring the relationships between landscape complexity, wild bee species richness and reproduction, and pollination services along a complexity gradient in the Netherlands. *Biological Conservation*, 214, 312–319. <https://doi.org/10.1016/j.biocon.2017.08.027>
- Butet, A., Paillat, G., & Delettre, Y. (2006). Seasonal changes in small mammal assemblages from field boundaries in an agricultural landscape of western France. *Agriculture, Ecosystems & Environment*, 113(1), 364–369. <https://doi.org/10.1016/j.agee.2005.10.008>
- Cairns, C. E., Villanueva-Gutierrez, R., Koptur, S., & Bray, D. B. (2005). Bee Populations, Forest Disturbance, and Africanization in Mexico. *Biotropica*, 37(4), 686–692. <https://doi.org/10.1111/j.1744-7429.2005.00087.x>
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486(7401), 59–67. <https://doi.org/10.1038/nature11148>
- Carpentier, F., & Martin, O. (2020). *siland: Spatial Influence of Landscape* (2.0). <https://CRAN.R-project.org/package=siland>
- Carpentier, F., & Martin, O. (2021). Siland a R package for estimating the spatial influence of landscape. *Scientific Reports*, 11(1), 7488. <https://doi.org/10.1038/s41598-021-86900-0>
- Carvalho, L. G., Seymour, C. L., Veldtman, R., & Nicolson, S. W. (2010). Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *Journal of Applied Ecology*, 47(4), 810–820. <https://doi.org/10.1111/j.1365-2664.2010.01829.x>
- Carvalho, L. G., Veldtman, R., Shenkute, A. G., Tesfay, G. B., Pirk, C. W. W., Donaldson, J. S., & Nicolson, S. W. (2011). Natural and within-farmland biodiversity enhances crop productivity: Weeds maximize nature benefits to crops. *Ecology Letters*, 14(3), 251–259. <https://doi.org/10.1111/j.1461-0248.2010.01579.x>
- Castle, D., Grass, I., & Westphal, C. (2019). Fruit quantity and quality of strawberries benefit from enhanced pollinator abundance at hedgerows in agricultural landscapes. *Agriculture, Ecosystems & Environment*, 275, 14–22. <https://doi.org/10.1016/j.agee.2019.01.003>
- Catarino, R., Bretagnolle, V., Perrot, T., Vialoux, F., & Gaba, S. (2019). A Nature-based solution in practice: Ecological and economic modelling shows pollinators outperform agrochemicals in oilseed crop production. *BioRxiv*, 628123. <https://doi.org/10.1101/628123>

- Catarino, R., Gaba, S., & Bretagnolle, V. (2019). Experimental and empirical evidence shows that reducing weed control in winter cereal fields is a viable strategy for farmers. *Scientific Reports*, *9*(1), 9004. <https://doi.org/10.1038/s41598-019-45315-8>
- Cavallero, L., Morales, C. L., Montero-Castaño, A., Gowda, J. H., & Aizen, M. A. (2018). Scale-dependent effects of conspecific flower availability on pollination quantity and quality in an invasive shrub. *Oecologia*, *188*(2), 501–513. <https://doi.org/10.1007/s00442-018-4239-7>
- Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, *114*(30), E6089–E6096. <https://doi.org/10.1073/pnas.1704949114>
- Cerrutti, N., & Pontet, C. (2016). Differential attractiveness of sunflower cultivars to the honeybee *Apis mellifera* L. *OCL*, *23*(2), D204. <https://doi.org/10.1051/ocl/2016005>
- Chabert, S., Sénéchal, C., Fougereux, A., Pousse, J., Richard, F., Nozières, E., Geist, O., Guillemard, V., Leylavergne, S., Malard, C., Benoist, A., Carré, G., Caumes, É., Cenier, C., Treil, A., Danflous, S., & Vaissière, B. E. (2020). Effect of environmental conditions and genotype on nectar secretion in sunflower (*Helianthus annuus* L.). *OCL*, *27*, 51. <https://doi.org/10.1051/ocl/2020040>
- Chambó, E. D., Garcia, R. C., Oliveira, N. T. E. de, & Duarte-Júnior, J. B. (2011). Honey bee visitation to sunflower: Effects on pollination and plant genotype. *Scientia Agricola*, *68*(6), 647–651. <https://doi.org/10.1590/S0103-90162011000600007>
- Chao, A., Chiu, C.-H., & Jost, L. (2014). Unifying Species Diversity, Phylogenetic Diversity, Functional Diversity, and Related Similarity and Differentiation Measures Through Hill Numbers. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 297–324. <https://doi.org/10.1146/annurev-ecolsys-120213-091540>
- Chaplin-Kramer, R., O'Rourke, M. E., Blitzer, E. J., & Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity: Pest and natural enemy response to landscape complexity. *Ecology Letters*, *14*(9), 922–932. <https://doi.org/10.1111/j.1461-0248.2011.01642.x>
- Chatellier, V., & Delame, N. (2007). *Les exploitations agricoles européennes et françaises*. 15.
- Chaudhary, O. P., & Poonia, R. (2018). Nectar production and nectar secretion rhythms in sunflower populations and hybrids. *Journal of entomology and zoology studies*, *5*.
- Chifflet, R., Klein, E. K., Lavigne, C., Féon, V. L., Ricroch, A. E., Lecomte, J., & Vaissière, B. E. (2011). Spatial scale of insect-mediated pollen dispersal in oilseed rape in an open agricultural landscape. *Journal of Applied Ecology*, *48*(3), 689–696. <https://doi.org/10.1111/j.1365-2664.2010.01904.x>
- Clough, Y., Kirchweber, S., & Kantelhardt, J. (2020). Field sizes and the future of farmland biodiversity in European landscapes. *Conservation Letters*, *13*(6). <https://doi.org/10.1111/conl.12752>
- Cole, L. J., Brocklehurst, S., Robertson, D., Harrison, W., & McCracken, D. I. (2017). Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. *Agriculture, Ecosystems & Environment*, *246*, 157–167. <https://doi.org/10.1016/j.agee.2017.05.007>
- Collins, S. L., Carpenter, S. R., Swinton, S. M., Orenstein, D. E., Childers, D. L., Gragson, T. L., Grimm, N. B., Grove, J. M., Harlan, S. L., Kaye, J. P., Knapp, A. K., Kofinas, G. P., Magnuson, J. J., McDowell, W. H., Melack, J. M., Ogdén, L. A., Robertson, G. P., Smith, M. D., & Whitmer, A. C. (2011). An integrated conceptual framework for long-term social-ecological research. *Frontiers in Ecology and the Environment*, *9*(6), 351–357. <https://doi.org/10.1890/100068>
- Corbet, S. A. (2000). Butterfly nectaring flowers: Butterfly morphology and flower form. *Entomologia Experimentalis et Applicata*, *96*(3), 289–298. <https://doi.org/10.1046/j.1570-7458.2000.00708.x>
- Corlett, R. T. (2015). The Anthropocene concept in ecology and conservation. *Trends in Ecology & Evolution*, *30*(1), 36–41. <https://doi.org/10.1016/j.tree.2014.10.007>
- Cousens, R. (1985). An empirical model relating crop yield to weed and crop density and a statistical comparison with other models. *The Journal of Agricultural Science*, *105*(3), 513–521. <https://doi.org/10.1017/S0021859600059396>
- Crutzen, P. J. (2006). The “Anthropocene.” In E. Ehlers & T. Krafft (Eds.), *Earth System Science in the Anthropocene* (pp. 13–18). Springer. https://doi.org/10.1007/3-540-26590-2_3
- Cumming, G. S., Olsson, P., Chapin, F. S., & Holling, C. S. (2013). Resilience, experimentation, and scale mismatches in social-ecological landscapes. *Landscape Ecology*, *28*(6), 1139–1150. <https://doi.org/10.1007/s10980-012-9725-4>
- Cunningham, S. A., Fournier, A., Neave, M. J., & Feuvre, D. L. (2016). Improving spatial arrangement of honeybee colonies to avoid pollination shortfall and depressed fruit set. *Journal of Applied Ecology*, *53*(2), 350–359. <https://doi.org/10.1111/1365-2664.12573>
- Cusser, S., Neff, J. L., & Jha, S. (2016). Natural land cover drives pollinator abundance and richness, leading to reductions in pollen limitation in cotton agroecosystems. *Agriculture, Ecosystems & Environment*, *226*, 33–42. <https://doi.org/10.1016/j.agee.2016.04.020>
- Daily, G. C. (Ed.). (1997). *Nature's services: Societal dependence on natural ecosystems*. Island Press.
- Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L. G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L. A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D. S., Kennedy, C. M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D. K., ... Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances*, *5*(10), eaax0121. <https://doi.org/10.1126/sciadv.aax0121>
- Danner, N., Molitor, A. M., Schiele, S., Härtel, S., & Steffan-Dewenter, I. (2016). Season and landscape composition affect pollen foraging distances and habitat use of honey bees. *Ecological Applications*, *26*(6), 1920–1929. <https://doi.org/10.1890/15-1840.1>
- Diekötter, T., Kadoya, T., Peter, F., Wolters, V., & Jauker, F. (2010). Oilseed rape crops distort plant-pollinator interactions. *Journal of Applied Ecology*, *47*(1), 209–214. <https://doi.org/10.1111/j.1365-2664.2009.01759.x>
- Diekötter, T., Peter, F., Jauker, B., Wolters, V., & Jauker, F. (2014). Mass-flowering crops increase richness of cavity-nesting

- bees and wasps in modern agro-ecosystems. *GCB Bioenergy*, 6(3), 219–226. <https://doi.org/10.1111/gcbb.12080>
- Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345(6195), 401–406. <https://doi.org/10.1126/science.1251817>
- Dormann, C. F., McPherson, J. M., Araújo, M. B., Bivand, R., Bolliger, J., Carl, G., Davies, R. G., Hirzel, A., Jetz, W., Kissling, W. D., Kühn, I., Ohlemüller, R., Peres-Neto, P. R., Reineking, B., Schröder, B., Schurr, F. M., & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, 30(5), 609–628. <https://doi.org/10.1111/j.2007.0906-7590.05171.x>
- Duelli, P., & Obrist, M. K. (2003). Regional biodiversity in an agricultural landscape: The contribution of seminatural habitat islands. *Basic and Applied Ecology*, 4(2), 129–138. <https://doi.org/10.1078/1439-1791-00140>
- Duflot, R., Ernoult, A., Aviron, S., Fahrig, L., & Burel, F. (2017). Relative effects of landscape composition and configuration on multi-habitat gamma diversity in agricultural landscapes. *Agriculture, Ecosystems & Environment*, 241, 62–69. <https://doi.org/10.1016/j.agee.2017.02.035>
- Ebeling, A., Klein, A.-M., Schumacher, J., Weisser, W. W., & Tschamtko, T. (2008). How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*, 117(12), 1808–1815. <https://doi.org/10.1111/j.1600-0706.2008.16819.x>
- Elzinga, J. A., Atlan, A., Biere, A., Gigord, L., Weis, A. E., & Bernasconi, G. (2007). Time after time: Flowering phenology and biotic interactions. *Trends in Ecology & Evolution*, 22(8), 432–439. <https://doi.org/10.1016/j.tree.2007.05.006>
- Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 487–515. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132419>
- Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., Sirami, C., Siriwardena, G. M., & Martin, J.-L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes: Heterogeneity and biodiversity. *Ecology Letters*, 14(2), 101–112. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>
- Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., King, D., Lindsay, K. F., Mitchell, S., & Tischendorf, L. (2015). Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems & Environment*, 200, 219–234. <https://doi.org/10.1016/j.agee.2014.11.018>
- Faure, J., Mouysset, L., & Gaba, S. (2021). Combining incentives for pollination with collective action to provide a bundle of ecosystem services in farmland. *ArXiv:2104.12640 [Econ, q-Fin]*. <http://arxiv.org/abs/2104.12640>
- Fazekas, C., Péntek, A., & Vojnich, V. J. (2019). Effect of foliar fertilizers applications on the nectar production of Sunflower (*Helianthus Anuus* L.) and on the foraging behaviour of honeybees (*Apis mellifera* L.). *International Journal of Engineering*, 8.
- Fijen, T. P. M., Scheper, J. A., Boekelo, B., Raemakers, I., & Kleijn, D. (2019). Effects of landscape complexity on pollinators are moderated by pollinators' association with mass-flowering crops. *Proceedings of the Royal Society B: Biological Sciences*, 286(1900), 20190387. <https://doi.org/10.1098/rspb.2019.0387>
- Forrest, J. R. K., Thorp, R. W., Kremen, C., & Williams, N. M. (2015). Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. *Journal of Applied Ecology*, 52(3), 706–715. <https://doi.org/10.1111/1365-2664.12433>
- Fox, J., Weisberg, S., Price, B., Adler, D., Bates, D., Baud-Bovy, G., Bolker, B., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., Graves, S., Heiberger, R., Krivitsky, P., Laboissiere, R., Maechler, M., Monette, G., Murdoch, D., Nilsson, H., ... R-Core. (2020). *car: Companion to Applied Regression* (3.0-8). <https://CRAN.R-project.org/package=car>
- Frankl, R., Wanning, S., & Braun, R. (2005). Quantitative floral phenology at the landscape scale: Is a comparative spatio-temporal description of “flowering landscapes” possible? *Journal for Nature Conservation*, 13(4), 219–229. <https://doi.org/10.1016/j.jnc.2004.10.002>
- Fried, G., Cordeau, S., Metay, A., & Kazakou, E. (2019). Relative importance of environmental factors and farming practices in shaping weed communities structure and composition in French vineyards. *Agriculture, Ecosystems & Environment*, 275, 1–13. <https://doi.org/10.1016/j.agee.2019.01.006>
- Fried, G., Petit, S., Dessaint, F., & Reboud, X. (2009). Arable weed decline in Northern France: Crop edges as refugia for weed conservation? *Biological Conservation*, 142(1), 238–243. <https://doi.org/10.1016/j.biocon.2008.09.029>
- Fründ, J., Linsenmair, K. E., & Blüthgen, N. (2010). Pollinator diversity and specialization in relation to flower diversity. *Oikos*, 119(10), 1581–1590. <https://doi.org/10.1111/j.1600-0706.2010.18450.x>
- Fuentes-Montemayor, E., Ferryman, M., Watts, K., Macgregor, N. A., Hambly, N., Brennan, S., Coxon, R., Langridge, H., & Park, K. J. (2020). Small mammal responses to long-term large-scale woodland creation: The influence of local and landscape-level attributes. *Ecological Applications*, 30(2), e02028. <https://doi.org/10.1002/eap.2028>
- Gaba, S., & Bretagnolle, V. (2020). Designing Multifunctional and Resilient Agricultural Landscapes: Lessons from Long-Term Monitoring of Biodiversity and Land Use. In C. Hurford, P. Wilson, & J. Storkey (Eds.), *The Changing Status of Arable Habitats in Europe* (pp. 203–224). Springer International Publishing. https://doi.org/10.1007/978-3-030-59875-4_14
- Gaba, S., Caneill, J., Nicolardot, B., Perronne, R., & Bretagnolle, V. (2018). Crop competition in winter wheat has a higher potential than farming practices to regulate weeds. *Ecosphere*, 9(10), e02413. <https://doi.org/10.1002/ecs2.2413>
- Gaba, S., Cheviron, N., Perrot, T., Piutti, S., Gautier, J.-L., & Bretagnolle, V. (2020). Weeds Enhance Multifunctionality in Arable Lands in South-West of France. *Frontiers in Sustainable Food Systems*, 4. <https://doi.org/10.3389/fsufs.2020.00071>
- Gabriel, D., Sait, S. M., Hodgson, J. A., Schmutz, U., Kunin, W. E., & Benton, T. G. (2010). Scale matters: The impact of organic farming on biodiversity at different spatial scales: Scale matters in organic farming. *Ecology Letters*, 13(7), 858–869. <https://doi.org/10.1111/j.1461-0248.2010.01481.x>
- Gardiner, M. M., Landis, D. A., Gratton, C., DiFonzo, C. D., O'Neal, M., Chacon, J. M., Wayo, M. T., Schmidt, N. P., Mueller, E. E., & Heimpel, G. E. (2009). Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecological Applications*, 19(1), 143–154. <https://doi.org/10.1890/07-1265.1>

- Garibaldi, L. A., Aizen, M. A., Klein, A. M., Cunningham, S. A., & Harder, L. D. (2011). Global growth and stability of agricultural yield decrease with pollinator dependence. *Proceedings of the National Academy of Sciences*, *108*(14), 5909–5914. <https://doi.org/10.1073/pnas.1012431108>
- Garibaldi, L. A., Steffan-Dewenter, I., Kremen, C., Morales, J. M., Bommarco, R., Cunningham, S. A., Carvalheiro, L. G., Chacoff, N. P., Dudenhöffer, J. H., Greenleaf, S. S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M. M., Morandin, L. A., Potts, S. G., Ricketts, T. H., Szentgyörgyi, H., ... Klein, A. M. (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits: Habitat isolation and pollination stability. *Ecology Letters*, *14*(10), 1062–1072. <https://doi.org/10.1111/j.1461-0248.2011.01669.x>
- Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., Kremen, C., Carvalheiro, L. G., Harder, L. D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N. P., Dudenhöffer, J. H., Freitas, B. M., Ghazoul, J., Greenleaf, S., ... Klein, A. M. (2013). Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. *Science*, *339*(6127), 1608–1611. <https://doi.org/10.1126/science.1230200>
- Garratt, M. P. D., Brown, R., Hartfield, C., Hart, A., & Potts, S. G. (2018). Integrated crop pollination to buffer spatial and temporal variability in pollinator activity. *Basic and Applied Ecology*, *32*, 77–85. <https://doi.org/10.1016/j.baae.2018.06.005>
- Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Fontaine, C., Henry, M., Ropars, L., Rollin, O., Thébault, E., & Vereecken, N. J. (2017). Chapter Four—Massively Introduced Managed Species and Their Consequences for Plant–Pollinator Interactions. In D. A. Bohan, A. J. Dumbrell, & F. Massol (Eds.), *Advances in Ecological Research* (Vol. 57, pp. 147–199). Academic Press. <https://doi.org/10.1016/bs.aecr.2016.10.007>
- Geslin, B., Oddie, M., Folschweiller, M., Legras, G., Seymour, C. L., van Veen, F. J. F., & Thébault, E. (2016). Spatiotemporal changes in flying insect abundance and their functional diversity as a function of distance to natural habitats in a mass flowering crop. *Agriculture, Ecosystems & Environment*, *229*, 21–29. <https://doi.org/10.1016/j.agee.2016.05.010>
- Goulson, D., Nicholls, E., Botias, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957–1255957. <https://doi.org/10.1126/science.1255957>
- Grab, H., Blitzer, E. J., Danforth, B., Loeb, G., & Poveda, K. (2017). Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. *Scientific Reports*, *7*(1), 45296. <https://doi.org/10.1038/srep45296>
- Grassini, P., Eskridge, K. M., & Cassman, K. G. (2013). Distinguishing between yield advances and yield plateaus in historical crop production trends. *Nature Communications*, *4*(1), 2918. <https://doi.org/10.1038/ncomms3918>
- Greenleaf, S. S., & Kremen, C. (2006). Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences*, *103*(37), 13890–13895. <https://doi.org/10.1073/pnas.0600929103>
- Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, *153*(3), 589–596. <https://doi.org/10.1007/s00442-007-0752-9>
- Gross, C. L., Whitehead, J. D., Mackay, E. S. G., Mackay, K. D., Andrew, N. R., & Paini, D. (2019). Interactions between two species of recently-sympatric invasive honeybees: *Apis cerana* induces aggression in *Apis mellifera* during foraging. *Biological Invasions*, *21*(12), 3697–3706. <https://doi.org/10.1007/s10530-019-02081-y>
- Grover, J. P. (1997). *Resource Competition*. Springer US.
- Haaland, C., Naisbit, R. E., & Bersier, L.-F. (2011). Sown wildflower strips for insect conservation: A review. *Insect Conservation and Diversity*, *4*(1), 60–80. <https://doi.org/10.1111/j.1752-4598.2010.00098.x>
- Hagler, J. R., Mueller, S., Teuber, L. R., Machtley, S. A., & Van Deynze, A. (2011). Foraging range of honey bees, *Apis mellifera*, in alfalfa seed production fields. *Journal of Insect Science*, *11*(1). <https://doi.org/10.1673/031.011.14401>
- Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE*, *12*(10), e0185809. <https://doi.org/10.1371/journal.pone.0185809>
- Hallmann, C. A., Ssymank, A., Sorg, M., Kroon, H. de, & Jongejans, E. (2021). Insect biomass decline scaled to species diversity: General patterns derived from a hoverfly community. *Proceedings of the National Academy of Sciences*, *118*(2). <https://doi.org/10.1073/pnas.2002554117>
- Hansen, D. M., Olesen, J. M., & Jones, C. G. (2002). Trees, birds and bees in Mauritius: Exploitative competition between introduced honey bees and endemic nectarivorous birds? *Journal of Biogeography*, *29*(5–6), 721–734. <https://doi.org/10.1046/j.1365-2699.2002.00720.x>
- Hardman, C. J., Norris, K., Nevard, T. D., Hughes, B., & Potts, S. G. (2016). Delivery of floral resources and pollination services on farmland under three different wildlife-friendly schemes. *Agriculture, Ecosystems & Environment*, *220*, 142–151. <https://doi.org/10.1016/j.agee.2016.01.015>
- Hass, A. L., Kormann, U. G., Tscharntke, T., Clough, Y., Baillod, A. B., Sirami, C., Fahrig, L., Martin, J.-L., Baudry, J., Bertrand, C., Bosch, J., Brotons, L., Burel, F., Georges, R., Giralt, D., Marcos-García, M. Á., Ricarte, A., Siriwardena, G., & Batáry, P. (2018). Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1872), 20172242. <https://doi.org/10.1098/rspb.2017.2242>
- Hector, A., & Bagchi, R. (2007). Biodiversity and ecosystem multifunctionality. *Nature*, *448*(7150), 188–190. <https://doi.org/10.1038/nature05947>
- Hegland, S. J., & Boeke, L. (2006). Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecological Entomology*, *31*(5), 532–538. <https://doi.org/10.1111/j.1365-2311.2006.00812.x>
- Henckel, L., Börger, L., Meiss, H., Gaba, S., & Bretagnolle, V. (2015). Organic fields sustain weed metacommunity dynamics in farmland landscapes. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1808), 20150002. <https://doi.org/10.1098/rspb.2015.0002>

- Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R. F. A., Niemelä, J., Rebane, M., Wascher, D., Watt, A., & Young, J. (2008). Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe—A review. *Agriculture, Ecosystems & Environment*, *124*(1–2), 60–71. <https://doi.org/10.1016/j.agee.2007.09.005>
- Herbertsson, L., Rundlöf, M., & Smith, H. G. (2017). The relation between oilseed rape and pollination of later flowering plants varies across plant species and landscape contexts. *Basic and Applied Ecology*, *24*, 77–85. <https://doi.org/10.1016/j.baae.2017.08.001>
- Herman, V. (2021). *Application de la télédétection à la quantification de la ressource mellifère d'un paysage en relation avec la dynamique d'un rucher d'Apis mellifera L. Approche méthodologique*. <https://matheo.uliege.be/handle/2268.2/12971>
- Hill, M. O. (1973). Diversity and Evenness: A Unifying Notation and Its Consequences. *Ecology*, *54*(2), 427–432. <https://doi.org/10.2307/1934352>
- Holland, J. M., Douma, J. C., Crowley, L., James, L., Kor, L., Stevenson, D. R. W., & Smith, B. M. (2017). Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agronomy for Sustainable Development*, *37*(4), 31. <https://doi.org/10.1007/s13593-017-0434-x>
- Holzschuh, A., Dainese, M., González-Varo, J. P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., Scheper, J., Wickens, J. B., Wickens, V. J., Bommarco, R., Kleijn, D., Potts, S. G., Roberts, S. P. M., Smith, H. G., Vilà, M., Vujić, A., & Steffan-Dewenter, I. (2016). Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecology Letters*, *19*(10), 1228–1236. <https://doi.org/10.1111/ele.12657>
- Holzschuh, A., Dormann, C. F., Tschardtke, T., & Steffan-Dewenter, I. (2011). Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1723), 3444–3451. <https://doi.org/10.1098/rspb.2011.0268>
- Holzschuh, A., Steffan-Dewenter, I., & Tschardtke, T. (2008). Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos*, *117*(3), 354–361. <https://doi.org/10.1111/j.2007.0030-1299.16303.x>
- Holzschuh, A., Steffan-Dewenter, I., & Tschardtke, T. (2010). How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology*, *79*(2), 491–500. <https://doi.org/10.1111/j.1365-2656.2009.01642.x>
- Hoofman, D. A. P., & Bullock, J. M. (2012). Mapping to inform conservation: A case study of changes in semi-natural habitats and their connectivity over 70 years. *Biological Conservation*, *145*(1), 30–38. <https://doi.org/10.1016/j.biocon.2011.09.015>
- Hopfenmüller, S., Steffan-Dewenter, I., & Holzschuh, A. (2014). Trait-Specific Responses of Wild Bee Communities to Landscape Composition, Configuration and Local Factors. *PLoS ONE*, *9*(8), e104439. <https://doi.org/10.1371/journal.pone.0104439>
- Horn, J., Becher, M. A., Johst, K., Kennedy, P. J., Osborne, J. L., Radchuk, V., & Grimm, V. (2021). Honey bee colony performance affected by crop diversity and farmland structure: A modeling framework. *Ecological Applications*, *31*(1), e02216. <https://doi.org/10.1002/eap.2216>
- Hudewenz, A., & Klein, A.-M. (2015). Red mason bees cannot compete with honey bees for floral resources in a cage experiment. *Ecology and Evolution*, *5*(21), 5049–5056. <https://doi.org/10.1002/ece3.1762>
- Hudewenz, A., Pufal, G., Bögeholz, A.-L., & Klein, A.-M. (2014). Cross-pollination benefits differ among oilseed rape varieties. *The Journal of Agricultural Science*, *152*(5), 770–778. <https://doi.org/10.1017/S0021859613000440>
- Isaacs, R., & Kirk, A. K. (2010). Pollination services provided to small and large highbush blueberry fields by wild and managed bees: Field size and blueberry pollination. *Journal of Applied Ecology*, *47*(4), 841–849. <https://doi.org/10.1111/j.1365-2664.2010.01823.x>
- IUCN. (2021). *IUCN Green Status of Species* (1st ed.). IUCN, International Union for Conservation of Nature. <https://doi.org/10.2305/IUCN.CH.2021.02.en>
- Iuliano, B., & Gratton, C. (2020). Temporal Resource (Dis)continuity for Conservation Biological Control: From Field to Landscape Scales. *Frontiers in Sustainable Food Systems*, *4*, 127. <https://doi.org/10.3389/fsufs.2020.00127>
- Jackson, H. B., & Fahrig, L. (2012). What size is a biologically relevant landscape? *Landscape Ecology*, *27*(7), 929–941. <https://doi.org/10.1007/s10980-012-9757-9>
- Jackson, H. B., & Fahrig, L. (2015). Are ecologists conducting research at the optimal scale?: Is research conducted at optimal scales? *Global Ecology and Biogeography*, *24*(1), 52–63. <https://doi.org/10.1111/geb.12233>
- Jadhav, J. A., Sreedevi, K., & Prasad, P. R. (2011). Insect pollinator diversity and abundance in sunflower ecosystem. *Current Biotica*, *5*(3), 344–350.
- Jauker, F., Bondarenko, B., Becker, H. C., & Steffan-Dewenter, I. (2012). Pollination efficiency of wild bees and hoverflies provided to oilseed rape. *Agricultural and Forest Entomology*, *14*(1), 81–87. <https://doi.org/10.1111/j.1461-9563.2011.00541.x>
- Jauker, F., Diekötter, T., Schwarzbach, F., & Wolters, V. (2009). Pollinator dispersal in an agricultural matrix: Opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology*, *24*(4), 547–555. <https://doi.org/10.1007/s10980-009-9331-2>
- Jauker, F., Peter, F., Wolters, V., & Diekötter, T. (2012). Early reproductive benefits of mass-flowering crops to the solitary bee *Osmia rufa* outbalance post-flowering disadvantages. *Basic and Applied Ecology*, *13*(3), 268–276. <https://doi.org/10.1016/j.baae.2012.03.010>
- Jauzein, P. (1995). *Flore des champs cultivés*. INRA.
- Jeavons, E., van Baaren, J., & Le Lann, C. (2020). Resource partitioning among a pollinator guild: A case study of monospecific flower crops under high honeybee pressure. *Acta Oecologica*, *104*, 103527. <https://doi.org/10.1016/j.actao.2020.103527>
- John, H., Nyamasyo, G., Kasina, M., & Oronje, M. (2008). Diversity of sunflower pollinators and their effect on seed yield in

- Makueni District, Eastern Kenya. *Spanish Journal of Agricultural Research*, 6. <https://doi.org/10.5424/sjar/2008062-318>
- Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., Bommarco, R., Brittain, C., Burley, A. L., Cariveau, D., Carvalheiro, L. G., Chacoff, N. P., Cunningham, S. A., Danforth, B. N., Dudenhöffer, J.-H., Elle, E., Gaines, H. R., Garibaldi, L. A., Gratton, C., ... Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, 16(5), 584–599. <https://doi.org/10.1111/ele.12082>
- Klaus, F., Tschardt, T., Bischoff, G., & Grass, I. (2021). Floral resource diversification promotes solitary bee reproduction and may offset insecticide effects – evidence from a semi-field experiment. *Ecology Letters*, 24(4), 668–675. <https://doi.org/10.1111/ele.13683>
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L. G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L. K., Rader, R., Ricketts, T. H., Williams, N. M., Lee Adamson, N., Ascher, J. S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J. C., Blitzer, E. J., ... Potts, S. G. (2015). Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, 6(1), 7414. <https://doi.org/10.1038/ncomms8414>
- Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tschardt, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), 303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Klumpers, S. G. T., Stang, M., & Klinkhamer, P. G. L. (2019). Foraging efficiency and size matching in a plant–pollinator community: The importance of sugar content and tongue length. *Ecology Letters*, 22(3), 469–479. <https://doi.org/10.1111/ele.13204>
- Knapp, J. L., Shaw, R. F., & Osborne, J. L. (2019). Pollinator visitation to mass-flowering courgette and co-flowering wild flowers: Implications for pollination and bee conservation on farms. *Basic and Applied Ecology*, 34, 85–94. <https://doi.org/10.1016/j.baae.2018.09.003>
- Kohl, P. L., & Rutschmann, B. (2018). The neglected bee trees: European beech forests as a home for feral honey bee colonies. *PeerJ*, 6, e4602. <https://doi.org/10.7717/peerj.4602>
- Kovács-Hostyánszki, A., Haenke, S., Batáry, P., Jauker, B., Báldi, A., Tschardt, T., & Holzschuh, A. (2013). Contrasting effects of mass-flowering crops on bee pollination of hedge plants at different spatial and temporal scales. *Ecological Applications*, 23(8), 1938–1946. <https://doi.org/10.1890/12-2012.1>
- Kozak, M., & Piepho, H.-P. (2018). What's normal anyway? Residual plots are more telling than significance tests when checking ANOVA assumptions. *Journal of Agronomy and Crop Science*, 204(1), 86–98. <https://doi.org/10.1111/jac.12220>
- Kremen, C., M'Gonigle, L. K., & Ponisio, L. C. (2018). Pollinator Community Assembly Tracks Changes in Floral Resources as Restored Hedgerows Mature in Agricultural Landscapes. *Frontiers in Ecology and Evolution*, 6, 170. <https://doi.org/10.3389/fevo.2018.00170>
- Kumar, P., & Sahu, S. (2020). Composition, diversity and foraging guilds of avifauna in agricultural landscapes In Panipat, Haryana, India. *Journal of Threatened Taxa*, 12(1), 15140–15153. <https://doi.org/10.11609/jott.5267.12.1.15140-15153>
- Lajos, K., Samu, F., Bihaly, Á. D., Fülöp, D., & Sárospataki, M. (2021). Landscape structure affects the sunflower visiting frequency of insect pollinators. *Scientific Reports*, 11(1), 8147. <https://doi.org/10.1038/s41598-021-87650-9>
- Larsen, A. E., & Noack, F. (2021). Impact of local and landscape complexity on the stability of field-level pest control. *Nature Sustainability*, 4(2), 120–128. <https://doi.org/10.1038/s41893-020-00637-8>
- Le Féon, V., Burel, F., Chifflet, R., Henry, M., Ricoch, A., Vaissière, B. E., & Baudry, J. (2013). Solitary bee abundance and species richness in dynamic agricultural landscapes. *Agriculture, Ecosystems & Environment*, 166, 94–101. <https://doi.org/10.1016/j.agee.2011.06.020>
- Le Féon, V., Schermann-Legionnet, A., Deletre, Y., Aviron, S., Billeter, R., Bugter, R., Hendrickx, F., & Burel, F. (2010). Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. *Agriculture, Ecosystems & Environment*, 137(1–2), 143–150. <https://doi.org/10.1016/j.agee.2010.01.015>
- Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2020). *emmeans: Estimated Marginal Means, aka Least-Squares Means* (1.4.6) [Computer software]. <https://CRAN.R-project.org/package=emmeans>
- Lichtenberg, E. M., Kennedy, C. M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-Pérez, N. A., Carvalheiro, L. G., Snyder, W. E., Williams, N. M., Winfree, R., Klatt, B. K., Åström, S., Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekötter, T., ... Crowder, D. W. (2017). A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Global Change Biology*, 23(11), 4946–4957. <https://doi.org/10.1111/gcb.13714>
- Lindenmayer, D., Hobbbs, R. J., Montague-Drake, R., Alexandra, J., Bennett, A., Burgman, M., Cale, P., Calhoun, A., Cramer, V., Cullen, P., Driscoll, D., Fahrig, L., Fischer, J., Franklin, J., Haila, Y., Hunter, M., Gibbons, P., Lake, S., Luck, G., ... Zavaleta, E. (2007). A checklist for ecological management of landscapes for conservation. *Ecology Letters*, 0(0), 071010211025003-??? <https://doi.org/10.1111/j.1461-0248.2007.01114.x>
- Lindgren, J., Lindborg, R., & Cousins, S. A. O. (2018). Local conditions in small habitats and surrounding landscape are important for pollination services, biological pest control and seed predation. *Agriculture, Ecosystems & Environment*, 251, 107–113. <https://doi.org/10.1016/j.agee.2017.09.025>
- Lindström, S. A. M., Herbertsson, L., Rundlöf, M., Bommarco, R., & Smith, H. G. (2016). Experimental evidence that honeybees depress wild insect densities in a flowering crop. *Proceedings of the Royal Society B: Biological Sciences*, 283(1843), 20161641. <https://doi.org/10.1098/rspb.2016.1641>
- Loreau, M. (2000). Biodiversity and ecosystem functioning: Recent theoretical advances. *Oikos*, 91(1), 3–17. <https://doi.org/10.1034/j.1600-0706.2000.910101.x>
- Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412(6842),

- 72–76. <https://doi.org/10.1038/35083573>
- Mace, G. M. (2014). Whose conservation? *Science*, *345*(6204), 1558–1560. <https://doi.org/10.1126/science.1254704>
- MacInnis, G., Buddle, C. M., & Forrest, J. R. K. (2020). Small wild bee abundance declines with distance into strawberry crops regardless of field margin habitat. *Basic and Applied Ecology*, *44*, 14–23. <https://doi.org/10.1016/j.baae.2020.02.007>
- MacInnis, G., & Forrest, J. R. K. (2019). Pollination by wild bees yields larger strawberries than pollination by honey bees. *Journal of Applied Ecology*, *56*(4), 824–832. <https://doi.org/10.1111/1365-2664.13344>
- Mackey, R. L., & Currie, D. J. (2001). The Diversity–Disturbance Relationship: Is It Generally Strong and Peaked? *Ecology*, *82*(12), 3479–3492. [https://doi.org/10.1890/0012-9658\(2001\)082\[3479:TDDRII\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[3479:TDDRII]2.0.CO;2)
- Magrach, A., González-Varo, J. P., Boiffier, M., Vilà, M., & Bartomeus, I. (2017). Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. *Nature Ecology & Evolution*, *1*(9), 1299–1307. <https://doi.org/10.1038/s41559-017-0249-9>
- Mahaut, L., Fried, G., & Gaba, S. (2018). Patch dynamics and temporal dispersal partly shape annual plant communities in ephemeral habitat patches. *Oikos*, *127*(1), 147–159. <https://doi.org/10.1111/oik.04415>
- Maier, C. (2014). A Microscopic Review of the Sunflower and Honeybee Mutualistic Relationship. *International Journal of AgriScience*, *4*, 272–282.
- Mallinger, R. E., Bradshaw, J., Varenhorst, A. J., & Prasifka, J. R. (2019). Native Solitary Bees Provide Economically Significant Pollination Services to Confection Sunflowers (*Helianthus annuus* L.) (Asterales: Asteraceae) Grown Across the Northern Great Plains. *Journal of Economic Entomology*, *112*(1), 40–48. <https://doi.org/10.1093/jee/toy322>
- Mallinger, R. E., Gaines-Day, H. R., & Gratton, C. (2017). Do managed bees have negative effects on wild bees?: A systematic review of the literature. *PLoS ONE*, *12*(12). <https://doi.org/10.1371/journal.pone.0189268>
- Mallinger, R. E., Gibbs, J., & Gratton, C. (2016). Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees’ foraging periods. *Landscape Ecology*, *31*(7), 1523–1535. <https://doi.org/10.1007/s10980-015-0332-z>
- Mallinger, R. E., & Prasifka, J. (2017). Benefits of Insect Pollination to Confection Sunflowers Differ Across Plant Genotypes. *Crop Science*, *57*(6), 3264–3272. <https://doi.org/10.2135/cropsci2017.03.0148>
- Mandelik, Y., Winfree, R., Neeson, T., & Kremen, C. (2012). Complementary habitat use by wild bees in agro-natural landscapes. *Ecological Applications*, *22*(5), 1535–1546. <https://doi.org/10.1890/11-1299.1>
- Manincor, N. de, Hautekeete, N., Piquot, Y., Schatz, B., Vanappelghem, C., & Massol, F. (2020). Does phenology explain plant–pollinator interactions at different latitudes? An assessment of its explanatory power in plant–hoverfly networks in French calcareous grasslands. *Oikos*, *129*(5), 753–765. <https://doi.org/10.1111/oik.07259>
- Marini, L., Bartomeus, I., Rader, R., & Lami, F. (2019). Species–habitat networks: A tool to improve landscape management for conservation. *Journal of Applied Ecology*, *56*(4), 923–928. <https://doi.org/10.1111/1365-2664.13337>
- Marini, L., Tamburini, G., Petrucco-Toffolo, E., Lindström, S. A. M., Zanetti, F., Mosca, G., & Bommarco, R. (2015). Crop management modifies the benefits of insect pollination in oilseed rape. *Agriculture, Ecosystems & Environment*, *207*, 61–66. <https://doi.org/10.1016/j.agee.2015.03.027>
- Martin, E. A., Collins, S. J., Crowe, S., Girard, J., Naujokaitis-Lewis, I., Smith, A. C., Lindsay, K., Mitchell, S., & Fahrig, L. (2020). Effects of farmland heterogeneity on biodiversity are similar to—Or even larger than—The effects of farming practices. *Agriculture, Ecosystems & Environment*, *288*, 106698. <https://doi.org/10.1016/j.agee.2019.106698>
- Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M. P. D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S. G., Smith, H. G., Al Hassan, D., Albrecht, M., Andersson, G. K. S., Asís, J. D., Aviron, S., Balzan, M. V., ... Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, *22*(7), 1083–1094. <https://doi.org/10.1111/ele.13265>
- Maxwell, S. L., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). Biodiversity: The ravages of guns, nets and bulldozers. *Nature*, *536*(7615), 143–145. <https://doi.org/10.1038/536143a>
- McCartney, H. A., & Lacey, M. E. (1991). Wind dispersal of pollen from crops of oilseed rape (*Brassica napus* L.). *Journal of Aerosol Science*, *22*(4), 467–477. [https://doi.org/10.1016/0021-8502\(91\)90005-3](https://doi.org/10.1016/0021-8502(91)90005-3)
- Mesquida, J., & Renard, M. (1981). Pollinisation du colza d’hiver mâle-fertile et mâle-stérile (*Brassica napus* L var. Oleifera Metzger) par l’abeille domestique (*Apis mellifica* L.). Effets sur la phénologie et le rendement. *Apidologie*, *12*(4), 345–362. <https://doi.org/10.1051/apido:19810404>
- Meyer, B., Gaebeler, V., & Steffan-Dewenter, I. D. (2007). Patch Size and Landscape Effects on Pollinators and Seed Set of the Horseshoe Vetch, *Hippocrepis comosa*, in an Agricultural Landscape of Central Europe. *Entomologia Generalis*, *173*–185. <https://doi.org/10.1127/entom.gen/30/2007/173>
- Miguet, P., Jackson, H. B., Jackson, N. D., Martin, A. E., & Fahrig, L. (2016). What determines the spatial extent of landscape effects on species? *Landscape Ecology*, *31*(6), 1177–1194. <https://doi.org/10.1007/s10980-015-0314-1>
- Millennium Ecosystem Assessment (Ed.). (2005). *Ecosystems and human well-being: Synthesis*. Island Press.
- Miller, P., Lanier, W., & Brandt, S. (2018). *Using Growing Degree Days to Predict Plant Stages*. 8.
- Miñarro, M., & García, D. (2018). Complementarity and redundancy in the functional niche of cider apple pollinators. *Apidologie*, *49*(6), 789–802. <https://doi.org/10.1007/s13592-018-0600-4>
- Mittelbach, G. G. (2012). *Community ecology*. Sinauer Associates.
- Momoh, E. J. J., & Zhou, W. (2001). Growth and Yield Responses to Plant Density and Stage of Transplanting in Winter Oilseed Rape (*Brassica napus* L.). *Journal of Agronomy and Crop Science*, *186*(4), 253–259. <https://doi.org/10.1046/j.1439-037x.2001.00476.x>
- Montoya, D., Gaba, S., de Mazancourt, C., Bretagnolle, V., & Loreau, M. (2020). Reconciling biodiversity conservation, food production and farmers’ demand in agricultural landscapes. *Ecological Modelling*, *416*, 108889. <https://doi.org/10.1016/j.ecolmodel.2019.108889>

- Montoya, D., Haegeman, B., Gaba, S., de Mazancourt, C., Bretagnolle, V., & Loreau, M. (2019). Trade-offs in the provisioning and stability of ecosystem services in agroecosystems. *Ecological Applications*, 29(2), e01853. <https://doi.org/10.1002/eap.1853>
- Muljar, R., Viik, E., Marja, R., Svilponis, E., Jõgar, K., Karise, R., & Mänd, M. (2010). *The effect of field size on the number of bumble bees*. 8, 357–360.
- Nayak, G. K., Roberts, S. P. M., Garratt, M., Breeze, T. D., Tscheulin, T., Harrison-Cripps, J., Vogiatzakis, I. N., Stirpe, M. T., & Potts, S. G. (2015). Interactive effect of floral abundance and semi-natural habitats on pollinators in field beans (*Vicia faba*). *Agriculture, Ecosystems & Environment*, 199, 58–66. <https://doi.org/10.1016/j.agee.2014.08.016>
- Nderitu, J., Nyamasyo, G., Kasina, M., & Oronje, M. L. (2008). Diversity of sunflower pollinators and their effect on seed yield in Makueni District, Eastern Kenya. *Spanish Journal of Agricultural Research*, 6(2), 271. <https://doi.org/10.5424/sjar/2008062-318>
- Neron, F. (2018). *Petit précis d'agriculture* (3e édition). France Agricole.
- Neumüller, U., Burger, H., Krausch, S., Blüthgen, N., & Ayasse, M. (2020). Interactions of local habitat type, landscape composition and flower availability moderate wild bee communities. *Landscape Ecology*, 35(10), 2209–2224. <https://doi.org/10.1007/s10980-020-01096-4>
- Nicholls, C. I., & Altieri, M. A. (2013). Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agronomy for Sustainable Development*, 33(2), 257–274. <https://doi.org/10.1007/s13593-012-0092-y>
- Nichols, R. N., Goulson, D., & Holland, J. M. (2019). The best wildflowers for wild bees. *Journal of Insect Conservation*, 23(5–6), 819–830. <https://doi.org/10.1007/s10841-019-00180-8>
- Nicholson, C. C., Koh, I., Richardson, L. L., Beauchemin, A., & Ricketts, T. H. (2017). Farm and landscape factors interact to affect the supply of pollination services. *Agriculture, Ecosystems & Environment*, 250, 113–122. <https://doi.org/10.1016/j.agee.2017.08.030>
- Ollerton, J., Alarcón, R., Waser, N. M., Price, M. V., Watts, S., Cranmer, L., Hingston, A., Peter, C. I., & Rotenberry, J. (2009). A global test of the pollination syndrome hypothesis. *Annals of Botany*, 103(9), 1471–1480. <https://doi.org/10.1093/aob/mcp031>
- Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120(3), 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Ozer, H. (2003). Sowing date and nitrogen rate effects on growth, yield and yield components of two summer rapeseed cultivars. *European Journal of Agronomy*, 19(3), 453–463. [https://doi.org/10.1016/S1161-0301\(02\)00136-3](https://doi.org/10.1016/S1161-0301(02)00136-3)
- Pacini, E., Nepi, M., & Vesprini, J. L. (2003). Nectar biodiversity: A short review. *Plant Systematics and Evolution*, 238(1), 7–21. <https://doi.org/10.1007/s00606-002-0277-y>
- Palmer, T. M., & Zimmerman, M. (1994). Pollen Competition and Sporophyte Fitness in *Brassica campestris*: Does Intense Pollen Competition Result in Individuals with Better Pollen? *Oikos*, 69(1), 80–86. <https://doi.org/10.2307/3545286>
- Pamminger, T., Becker, R., Himmelreich, S., Schneider, C. W., & Bergtold, M. (2019). The nectar report: Quantitative review of nectar sugar concentrations offered by bee visited flowers in agricultural and non-agricultural landscapes. *PeerJ*, 7, e6329. <https://doi.org/10.7717/peerj.6329>
- Peralta, G., Vázquez, D. P., Chacoff, N. P., Lomáscolo, S. B., Perry, G. L. W., & Tylianakis, J. M. (2020). Trait matching and phenological overlap increase the spatio-temporal stability and functionality of plant–pollinator interactions. *Ecology Letters*, 23(7), 1107–1116. <https://doi.org/10.1111/ele.13510>
- Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.-L., & Bretagnolle, V. (2018). Bees increase oilseed rape yield under real field conditions. *Agriculture, Ecosystems & Environment*, 266, 39–48. <https://doi.org/10.1016/j.agee.2018.07.020>
- Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.-L., Saintilan, A., & Bretagnolle, V. (2019). Experimental quantification of insect pollination on sunflower yield, reconciling plant and field scale estimates. *Basic and Applied Ecology*, 34, 75–84. <https://doi.org/10.1016/j.baae.2018.09.005>
- Petersen, J. D., & Nault, B. A. (2014). Landscape diversity moderates the effects of bee visitation frequency to flowers on crop production. *Journal of Applied Ecology*, 51(5), 1347–1356. <https://doi.org/10.1111/1365-2664.12287>
- Petit, S., Boursault, A., Le Guilloux, M., Munier-Jolain, N., & Reboud, X. (2011). Weeds in agricultural landscapes. A review. *Agronomy for Sustainable Development*, 31(2), 309–317. <https://doi.org/10.1051/agro/2010020>
- Pfiffner, L., & Luka, H. (2000). Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. *Agriculture, Ecosystems & Environment*, 78(3), 215–222. [https://doi.org/10.1016/S0167-8809\(99\)00130-9](https://doi.org/10.1016/S0167-8809(99)00130-9)
- Phalan, B., Onial, M., Balmford, A., & Green, R. E. (2011). Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. *Science*, 333(6047), 1289–1291. <https://doi.org/10.1126/science.1208742>
- Pickett, S. T. A., & Cadenasso, M. L. (1995). Landscape Ecology: Spatial Heterogeneity in Ecological Systems. *Science*, 269(5222), 331–334. <https://doi.org/10.1126/science.269.5222.331>
- Pisanty, G., Afik, O., Wajnberg, E., & Mandelik, Y. (2016). Watermelon pollinators exhibit complementarity in both visitation rate and single-visit pollination efficiency. *Journal of Applied Ecology*, 53(2), 360–370. <https://doi.org/10.1111/1365-2664.12574>
- Pisanty, G., Klein, A.-M., & Mandelik, Y. (2014). Do wild bees complement honeybee pollination of confection sunflowers in Israel? *Apidologie*, 45(2), 235–247. <https://doi.org/10.1007/s13592-013-0242-5>
- Popławska, W., Liersch, A., Jędryczka, M., Kaczmarek, J., Wolko, J., Ogródowczyk, M., & Bartkowiak-Broda, I. (2013). Wind-mediated pollen dispersal of oilseed rape—An estimation using pollen traps. *Geography*.
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, 25(6), 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Potts, S. G., Roberts, S. P. M., Dean, R., Marris, G., Brown, M. A., Jones, R., Neumann, P., & Settele, J. (2010). Declines of managed honey bees and beekeepers in Europe. *Journal of Apicultural Research*, 49(1), 15–22. <https://doi.org/10.3896/IBRA.1.49.1.02>

- Potts, S. G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G., & Willmer, P. (2005). Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, *30*(1), 78–85. <https://doi.org/10.1111/j.0307-6946.2005.00662.x>
- Prasifka, J. R., Mallinger, R. E., Portlas, Z. M., Hulke, B. S., Fugate, K. K., Paradis, T., Hampton, M. E., & Carter, C. J. (2018). Using Nectar-Related Traits to Enhance Crop-Pollinator Interactions. *Frontiers in Plant Science*, *9*, 812. <https://doi.org/10.3389/fpls.2018.00812>
- Puškadija, Z., Štefanić, E., Mijić, A., Zdunić, Z., Paradiković, N., Florijančić, T., & Opačak, A. (2007). Influence of weather conditions on Honey bee visits (*Apis mellifera carnica*) during sunflower (*Helianthus annuus*) blooming period. *Poljoprivreda*, *13*(1), 230–233.
- R Core team. (2021). *A language and environment for statistical computing* (4.1.0) [Computer software]. R Foundation for Statistical Computing.
- Raatz, L., Pirhofer Walzl, K., Müller, M. E. H., Scherber, C., & Joshi, J. (2021). Who is the culprit: Is pest infestation responsible for crop yield losses close to semi-natural habitats? *Ecology and Evolution*, *n/a*(*n/a*). <https://doi.org/10.1002/ece3.8046>
- Rader, R., Howlett, B. G., Cunningham, S. A., Westcott, D. A., Newstrom-Lloyd, L. E., Walker, M. K., Teulon, D. A. J., & Edwards, W. (2009). Alternative pollinator taxa are equally efficient but not as effective as the honeybee in a mass flowering crop. *Journal of Applied Ecology*, *46*(5), 1080–1087. <https://doi.org/10.1111/j.1365-2664.2009.01700.x>
- Raderschall, C. A., Bommarco, R., Lindström, S. A. M., & Lundin, O. (2021). Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield. *Agriculture, Ecosystems & Environment*, *306*, 107189. <https://doi.org/10.1016/j.agee.2020.107189>
- Rasheed, M. T., Inayatullah, M., Shah, B., Ahmed, N., Huma, Z., & Ahmed, S. (2015). *Identification and record of insect pollinators on two cultivars of sunflower*.
- Rathcke, B., & Lacey, E. P. (1985). Phenological Patterns of Terrestrial Plants. *Annual Review of Ecology and Systematics*, *16*(1), 179–214. <https://doi.org/10.1146/annurev.es.16.110185.001143>
- Redlich, S., Martin, E. A., & Steffan-Dewenter, I. (2021). Sustainable landscape, soil and crop management practices enhance biodiversity and yield in conventional cereal systems. *Journal of Applied Ecology*, *58*(3), 507–517. <https://doi.org/10.1111/1365-2664.13821>
- Redlich, S., Martin, E. A., Wende, B., & Steffan-Dewenter, I. (2018). Landscape heterogeneity rather than crop diversity mediates bird diversity in agricultural landscapes. *PLOS ONE*, *13*(8), e0200438. <https://doi.org/10.1371/journal.pone.0200438>
- Requier, F., Garnery, L., Kohl, P. L., Njovu, H. K., Pirk, C. W. W., Crewe, R. M., & Steffan-Dewenter, I. (2019). The Conservation of Native Honey Bees Is Crucial. *Trends in Ecology & Evolution*, *34*(9), 789–798. <https://doi.org/10.1016/j.tree.2019.04.008>
- Requier, F., Odoux, J.-F., Henry, M., & Bretagnolle, V. (2017). The carry-over effects of pollen shortage decrease the survival of honeybee colonies in farmlands. *Journal of Applied Ecology*, *54*(4), 1161–1170. <https://doi.org/10.1111/1365-2664.12836>
- Requier, F., Odoux, J.-F., Tamic, T., Moreau, N., Henry, M., Decourtye, A., & Bretagnolle, V. (2015). Honey bee diet in intensive farmland habitats reveals an unexpectedly high flower richness and a major role of weeds. *Ecological Applications*, *25*(4), 881–890. <https://doi.org/10.1890/14-1011.1>
- Resch, M. C., Schütz, M., Buchmann, N., Frey, B., Graf, U., van der Putten, W. H., Zimmermann, S., & Risch, A. C. (2021). Evaluating long-term success in grassland restoration: An ecosystem multifunctionality approach. *Ecological Applications*, *31*(3), e02271. <https://doi.org/10.1002/eap.2271>
- Ricciardi, V., Mehrabi, Z., Wittman, H., James, D., & Ramankutty, N. (2021). Higher yields and more biodiversity on smaller farms. *Nature Sustainability*, *4*(7), 651–657. <https://doi.org/10.1038/s41893-021-00699-2>
- Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., Mayfield, M. M., Morandin, L. A., Ochieng', A., & Viana, B. F. (2008). Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters*, *11*(5), 499–515. <https://doi.org/10.1111/j.1461-0248.2008.01157.x>
- Ritchie, H., & Roser, M. (2013). Land Use. *Our World in Data*. <https://ourworldindata.org/land-use>
- Rodríguez, C., & Wiegand, K. (2009). Evaluating the trade-off between machinery efficiency and loss of biodiversity-friendly habitats in arable landscapes: The role of field size. *Agriculture, Ecosystems & Environment*, *129*(4), 361–366. <https://doi.org/10.1016/j.agee.2008.10.010>
- Rollin, O., Benelli, G., Benvenuti, S., Decourtye, A., Wratten, S. D., Canale, A., & Desneux, N. (2016). Weed-insect pollinator networks as bio-indicators of ecological sustainability in agriculture. A review. *Agronomy for Sustainable Development*, *36*(1), 8. <https://doi.org/10.1007/s13593-015-0342-x>
- Rollin, O., Bretagnolle, V., Decourtye, A., Aptel, J., Michel, N., Vaissière, B. E., & Henry, M. (2013). Differences of floral resource use between honey bees and wild bees in an intensive farming system. *Agriculture, Ecosystems & Environment*, *179*, 78–86. <https://doi.org/10.1016/j.agee.2013.07.007>
- Rollin, O., Bretagnolle, V., Fortel, L., Guilbaud, L., & Henry, M. (2015). Habitat, spatial and temporal drivers of diversity patterns in a wild bee assemblage. *Biodiversity and Conservation*, *24*(5), 1195–1214. <https://doi.org/10.1007/s10531-014-0852-x>
- Rollin, O., & Garibaldi, L. A. (2019). Impacts of honeybee density on crop yield: A meta-analysis. *Journal of Applied Ecology*, *56*(5), 1152–1163. <https://doi.org/10.1111/1365-2664.13355>
- Rollin, O., Pérez-Méndez, N., Bretagnolle, V., & Henry, M. (2019). Preserving habitat quality at local and landscape scales increases wild bee diversity in intensive farming systems. *Agriculture, Ecosystems & Environment*, *275*, 73–80. <https://doi.org/10.1016/j.agee.2019.01.012>
- Rosa García, R., & Miñarro, M. (2014). Role of floral resources in the conservation of pollinator communities in cider-apple

- orchards. *Agriculture, Ecosystems & Environment*, 183, 118–126. <https://doi.org/10.1016/j.agee.2013.10.017>
- Rosser, A. M., & Mainka, S. A. (2002). Overexploitation and Species Extinctions. *Conservation Biology*, 16(3), 584–586. <https://doi.org/10.1046/j.1523-1739.2002.01635.x>
- Roulston, T. H., & Goodell, K. (2011). The Role of Resources and Risks in Regulating Wild Bee Populations. *Annual Review of Entomology*, 56, 293–312. <https://doi.org/10.1146/annurev-ento-120709-144802>
- Roulston, T. H., Smith, S. A., & Brewster, A. L. (2007). A Comparison of Pan Trap and Intensive Net Sampling Techniques for Documenting a Bee (Hymenoptera: Apiformes) Fauna. *Journal of the Kansas Entomological Society*, 80(2), 179–181. [https://doi.org/10.2317/0022-8567\(2007\)80\[179:ACOPTA\]2.0.CO;2](https://doi.org/10.2317/0022-8567(2007)80[179:ACOPTA]2.0.CO;2)
- Rusch, A., Valantin-Morison, M., Sarthou, J.-P., & Roger-Estrade, J. (2010). Chapter six - Biological Control of Insect Pests in Agroecosystems: Effects of Crop Management, Farming Systems, and Seminatural Habitats at the Landscape Scale: A Review. In D. L. Sparks (Ed.), *Advances in Agronomy* (Vol. 109, pp. 219–259). Academic Press. <https://doi.org/10.1016/B978-0-12-385040-9.00006-2>
- Rusch, A., Valantin-Morison, M., Sarthou, J.-P., & Roger-Estrade, J. (2011). Multi-scale effects of landscape complexity and crop management on pollen beetle parasitism rate. *Landscape Ecology*, 26(4), 473–486. <https://doi.org/10.1007/s10980-011-9573-7>
- Ryan, M. R., Smith, R. G., Mortensen, D. A., Teasdale, J. R., Curran, W. S., Seidel, R., & Shumway, D. L. (2009). Weed-crop competition relationships differ between organic and conventional cropping systems: Weed-crop competition in organic and conventional systems. *Weed Research*, 49(6), 572–580. <https://doi.org/10.1111/j.1365-3180.2009.00736.x>
- Sáez, A., Sabatino, M., & Aizen, M. A. (2012). Interactive Effects of Large- and Small-Scale Sources of Feral Honey-Bees for Sunflower in the Argentine Pampas. *PLOS ONE*, 7(1), e30968. <https://doi.org/10.1371/journal.pone.0030968>
- Sánchez-Bayo, F., & Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, 232, 8–27. <https://doi.org/10.1016/j.biocon.2019.01.020>
- Sardiñas, H. S., Tom, K., Ponisio, L. C., Rominger, A., & Kremen, C. (2016). Sunflower (*Helianthus annuus*) pollination in California's Central Valley is limited by native bee nest site location. *Ecological Applications*, 26(2), 438–447. <https://doi.org/10.1890/15-0033>
- Schellhorn, N. A., Gagic, V., & Bommarco, R. (2015). Time will tell: Resource continuity bolsters ecosystem services. *Trends in Ecology & Evolution*, 30(9), 524–530. <https://doi.org/10.1016/j.tree.2015.06.007>
- Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-D., Roscher, C., Weigelt, A., Allan, E., Beßler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L. W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., ... Tschamtker, T. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, 468(7323), 553–556. <https://doi.org/10.1038/nature09492>
- Seeley, T. D. (1986). Social foraging by honeybees: How colonies allocate foragers among patches of flowers. *Behavioral Ecology and Sociobiology*, 19(5), 343–354. <https://doi.org/10.1007/BF00295707>
- Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, 574(7780), 671–674. <https://doi.org/10.1038/s41586-019-1684-3>
- Senapathi, D., Biesmeijer, J. C., Breeze, T. D., Kleijn, D., Potts, S. G., & Carvalheiro, L. G. (2015). Pollinator conservation—The difference between managing for pollination services and preserving pollinator diversity. *Current Opinion in Insect Science*, 12, 93–101. <https://doi.org/10.1016/j.cois.2015.11.002>
- Seufert, V., Ramankutty, N., & Foley, J. A. (2012). Comparing the yields of organic and conventional agriculture. *Nature*, 485(7397), 229–232. <https://doi.org/10.1038/nature11069>
- Shaw, R. F., Phillips, B. B., Doyle, T., Pell, J. K., Redhead, J. W., Savage, J., Woodcock, B. A., Bullock, J. M., & Osborne, J. L. (2020). Mass-flowering crops have a greater impact than semi-natural habitat on crop pollinators and pollen deposition. *Landscape Ecology*, 35(2), 513–527. <https://doi.org/10.1007/s10980-019-00962-0>
- Sidemo-Holm, W., Carrié, R., Ekroos, J., Lindström, S. A. M., & Smith, H. G. (2021). Reduced crop density increases floral resources to pollinators without affecting crop yield in organic and conventional fields. *Journal of Applied Ecology*, 1365-2664.13887. <https://doi.org/10.1111/1365-2664.13887>
- Skinner, J. A. (1987). Abundance and Spatial Distribution of Bees Visiting Male-sterile and Male-fertile Sunflower Cultivars in California. *Environmental Entomology*, 16(4), 922–927. <https://doi.org/10.1093/ee/16.4.922>
- Söderström, B., Svensson, B., Vessby, K., & Glimskär, A. (2001). Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity & Conservation*, 10(11), 1839–1863. <https://doi.org/10.1023/A:1013153427422>
- Stanley, D. A., Gunning, D., & Stout, J. C. (2013). Pollinators and pollination of oilseed rape crops (*Brassica napus* L.) in Ireland: Ecological and economic incentives for pollinator conservation. *Journal of Insect Conservation*, 17(6), 1181–1189. <https://doi.org/10.1007/s10841-013-9599-z>
- Stanley, D., & Stout, J. (2014). Pollinator sharing between mass-flowering oilseed rape and co-flowering wild plants: Implications for wild plant pollination. *Plant Ecology*, 215, 315–325. <https://doi.org/10.1007/s11258-014-0301-7>
- Stanton, R. L., Morrissey, C. A., & Clark, R. G. (2018). Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. *Agriculture, Ecosystems & Environment*, 254, 244–254. <https://doi.org/10.1016/j.agee.2017.11.028>
- Steffan-dewenter, I. (2003). Seed set of male-sterile and male-fertile oilseed rape (*Brassica napus*) in relation to pollinator density. *Apidologie*, 34(3), 227–235. <https://doi.org/10.1051/apido:2003015>
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., & Tschamtker, T. (2002). Scale-Dependent Effects of Landscape Context on Three Pollinator Guilds. *Ecology*, 83(5), 1421–1432. [https://doi.org/10.1890/0012-9658\(2002\)083\[1421:SDEOLC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2)

- Steffan-Dewenter, I., & Tscharntke, T. (2000). Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia*, *122*(2), 288–296. <https://doi.org/10.1007/s004420050034>
- Steffan-Dewenter, I., & Tscharntke, T. (2001). Succession of bee communities on fallows. *Ecography*, *24*(1), 83–93. <https://doi.org/10.1034/j.1600-0587.2001.240110.x>
- Sutter, L., Jeanneret, P., Bartual, A. M., Bocci, G., & Albrecht, M. (2017). Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. *Journal of Applied Ecology*, *54*(6), 1856–1864. <https://doi.org/10.1111/1365-2664.12907>
- Tamburini, G., Bommarco, R., Wanger, T. C., Kremen, C., van der Heijden, M. G. A., Liebman, M., & Hallin, S. (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science Advances*, *6*(45), eaba1715. <https://doi.org/10.1126/sciadv.aba1715>
- Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and Ecosystem Functioning. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 471–493. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>
- Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, *441*(7093), 629–632. <https://doi.org/10.1038/nature04742>
- Timberlake, T. P., Vaughan, I. P., & Memmott, J. (2019). Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*, *56*(7), 1585–1596. <https://doi.org/10.1111/1365-2664.13403>
- Tittonell, P. (2014). Ecological intensification of agriculture—Sustainable by nature. *Current Opinion in Environmental Sustainability*, *8*, 53–61. <https://doi.org/10.1016/j.cosust.2014.08.006>
- Torné-Noguera, A., Rodrigo, A., Osorio, S., & Bosch, J. (2016). Collateral effects of beekeeping: Impacts on pollen-nectar resources and wild bee communities. *Basic and Applied Ecology*, *17*(3), 199–209. <https://doi.org/10.1016/j.baae.2015.11.004>
- Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., ... Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes—Eight hypotheses. *Biological Reviews*, *87*(3), 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Tuck, S. L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L. A., & Bengtsson, J. (2014). Land-use intensity and the effects of organic farming on biodiversity: A hierarchical meta-analysis. *Journal of Applied Ecology*, *51*(3), 746–755. <https://doi.org/10.1111/1365-2664.12219>
- Turner, M. G. (2005). Landscape Ecology: What Is the State of the Science? *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 319–344. <https://doi.org/10.1146/annurev.ecolsys.36.102003.152614>
- Vasseur, C., Joannon, A., Aviron, S., Burel, F., Meynard, J.-M., & Baudry, J. (2013). The cropping systems mosaic: How does the hidden heterogeneity of agricultural landscapes drive arthropod populations? *Agriculture, Ecosystems & Environment*, *166*, 3–14. <https://doi.org/10.1016/j.agee.2012.08.013>
- Waser, N. M., & Price, M. V. (2016). Drought, pollen and nectar availability, and pollination success. *Ecology*, *97*(6), 1400–1409. <https://doi.org/10.1890/15-1423.1>
- Westerberg, L., Berglund, H., Jonason, D., & Milberg, P. (2021). Color pan traps often catch less when there are more flowers around. *Ecology and Evolution*, *11*(9), 3830–3840. <https://doi.org/10.1002/ece3.7252>
- Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S. G., Roberts, S. P. M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B. E., Woyciechowski, M., Biesmeijer, J. C., Kunin, W. E., Settele, J., & Steffan-Dewenter, I. (2008). Measuring Bee Diversity in Different European Habitats and Biogeographical Regions. *Ecological Monographs*, *78*(4), 653–671. <https://doi.org/10.1890/07-1292.1>
- Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale: Flowering crops enhance pollinator densities. *Ecology Letters*, *6*(11), 961–965. <https://doi.org/10.1046/j.1461-0248.2003.00523.x>
- Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2009). Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, *46*(1), 187–193. <https://doi.org/10.1111/j.1365-2664.2008.01580.x>
- Westrich, P., Association, I. B. R., & London, L. S. of. (1996). The conservation of bees. In *Habitat requirements of central European bees and the problems of partial habitats* (pp. 1–16). Academic press.
- Wezel, A., Casagrande, M., Celette, F., Vian, J.-F., Ferrer, A., & Peigné, J. (2014). Agroecological practices for sustainable agriculture. A review. *Agronomy for Sustainable Development*, *34*(1), 1–20. <https://doi.org/10.1007/s13593-013-0180-7>
- Wiesmeier, M., Hübner, R., & Kögel-Knabner, I. (2015). Stagnating crop yields: An overlooked risk for the carbon balance of agricultural soils? *Science of The Total Environment*, *536*, 1045–1051. <https://doi.org/10.1016/j.scitotenv.2015.07.064>
- Wignall, V. R., Brolly, M., Uthoff, C., Norton, K. E., Chipperfield, H. M., Balfour, N. J., & Ratnieks, F. L. W. (2020). Exploitative competition and displacement mediated by eusocial bees: Experimental evidence in a wild pollinator community. *Behavioral Ecology and Sociobiology*, *74*(12), 152. <https://doi.org/10.1007/s00265-020-02924-y>
- Wintermantel, D., Odoux, J., Chadœuf, J., & Bretagnolle, V. (2019). Organic farming positively affects honeybee colonies in a flower-poor period in agricultural landscapes. *Journal of Applied Ecology*, *1365-2664.13447*. <https://doi.org/10.1111/1365-2664.13447>
- Wojcik, V. A., Morandin, L. A., Davies Adams, L., & Rourke, K. E. (2018). Floral Resource Competition Between Honey Bees and Wild Bees: Is There Clear Evidence and Can We Guide Management and Conservation? *Environmental Entomology*, *47*(4), 822–833. <https://doi.org/10.1093/ee/nvy077>
- Woodcock, B. A., Garratt, M. P. D., Powney, G. D., Shaw, R. F., Osborne, J. L., Soroka, J., Lindström, S. A. M., Stanley, D., Ouvrard, P., Edwards, M. E., Jauker, F., McCracken, M. E., Zou, Y., Potts, S. G., Rundlöf, M., Noriega, J. A.,

- Greenop, A., Smith, H. G., Bommarco, R., ... Pywell, R. F. (2019). Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. *Nature Communications*, *10*(1), 1481. <https://doi.org/10.1038/s41467-019-09393-6>
- Woodcock, T. S., Pekkola, L. J., Dawson, C., Gadallah, F. L., & Kevan, P. G. (2014). Development of a Pollination Service Measurement (PSM) method using potted plant phytometry. *Environmental Monitoring and Assessment*, *186*(8), 5041–5057. <https://doi.org/10.1007/s10661-014-3758-x>
- WWF. (2018). *Living Planet Report 2018: Aiming Higher* (Grooten, N. & Almond, R. E. A.).
- Yamamoto, N., Yokoyama, J., & Kawata, M. (2007). Relative resource abundance explains butterfly biodiversity in island communities. *Proceedings of the National Academy of Sciences*, *104*(25), 10524–10529. <https://doi.org/10.1073/pnas.0701583104>
- Yourstone, J., Karlsson, M., Klatt, B. K., Olsson, O., & Smith, H. G. (2021). Effects of crop and non-crop resources and competition: High importance of trees and oilseed rape for solitary bee reproduction. *Biological Conservation*, *261*, 109249. <https://doi.org/10.1016/j.biocon.2021.109249>
- Zou, Y., Xiao, H., Bianchi, F. J. J. A., Jauker, F., Luo, S., & van der Werf, W. (2017). Wild pollinators enhance oilseed rape yield in small-holder farming systems in China. *BMC Ecology*, *17*(1), 6. <https://doi.org/10.1186/s12898-017-0116-1>

ANNEXES

I. Informations supplémentaires du chapitre 1

1. Appendix 1A. Estimation of the number of opened florets at the sunflower head scale.

To determine the amount of nectar provided at the sunflower head scale, we combined our measures of nectar amount per floret with an estimation of the number of opened florets at the time of nectar sampling. At each flowering period and for all surveyed sunflowers (180 sunflower heads), we measured with a tape measure the radius of the head (which extends from the base of the petals to the center of the head), and the radius occupied by staminate in one hand and pistillate florets in the other hand.

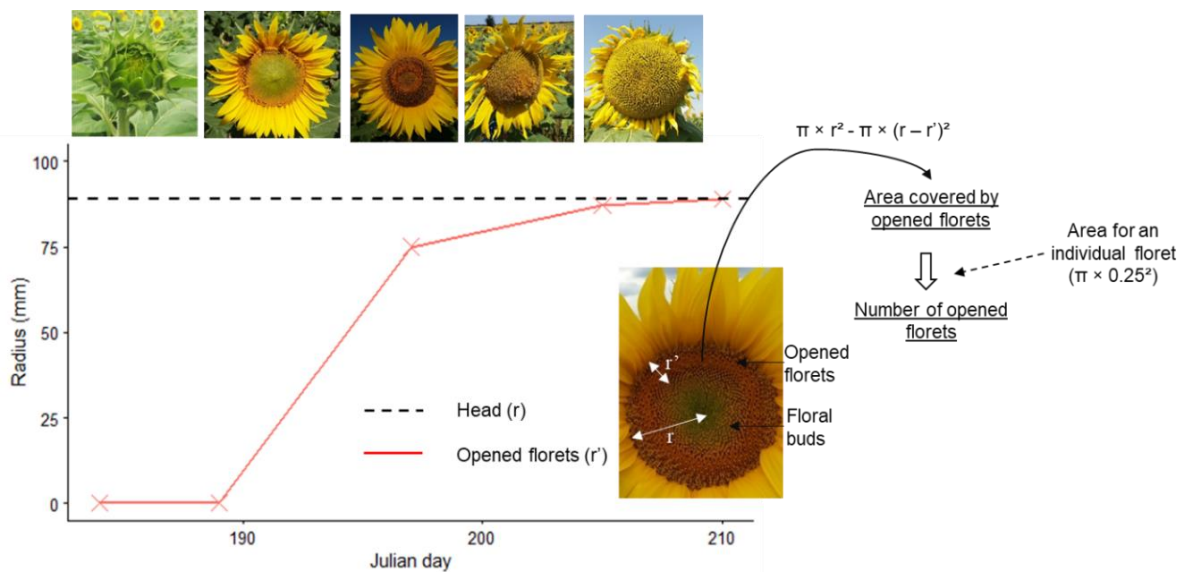


Fig. S1.1: Variation of the radii occupied by the head and by opened florets through the season for a given sunflower individual. On the top are presented pictures representative of the flowering stages. We used the two measures of radius to quantify the area covered by opened florets. We finally determined the number of opened florets with our estimation of the area covered by opened florets and a constant value used for the area covered by an individual floret.

The radius of opened florets, the sum of the radii occupied by staminate and pistillate florets as soon as the radius of the head were used to determine the flower area covered by opened florets. We also used a constant value of 0.25cm as the radius of an individual floret to determine the area covered by an individual floret. We divided the flower area by the floret area to estimate the number of opened florets (Fig. S1.1).

We determined the sunflower head area covered by staminate and pistillate flowers by dividing the respective radii they occupied on the head by the head radius. We observed the highest % pistillate flowers covering the head at the onset and at the peak flowering periods, while % staminate flowers increased through the flowering periods until they totally covered the sunflower head at the end of the flowering (Fig. S1.2).

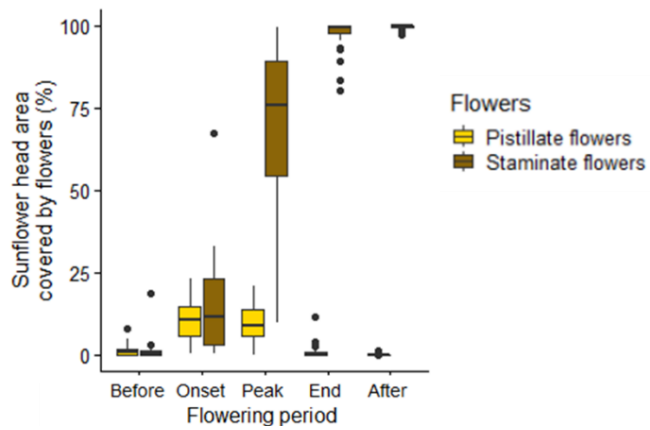


Fig. S1.2: Variation in the sunflower head area covered by pistillate and staminate flowers through the flowering periods.

2. Appendix 1B. Determination of earlier, simultaneous, and later sunflower in the landscape: an example.

We disentangled in our study from sunflower in the landscape from earlier sunflower flowering, simultaneous sunflower flowering, and later sunflower flowering than the focal field to consider heterogeneity between fields in the provision of nectar resources. We presented an example for the determination of the phenological mismatch between the focal field and the fields in the landscape (Fig. S1.3).

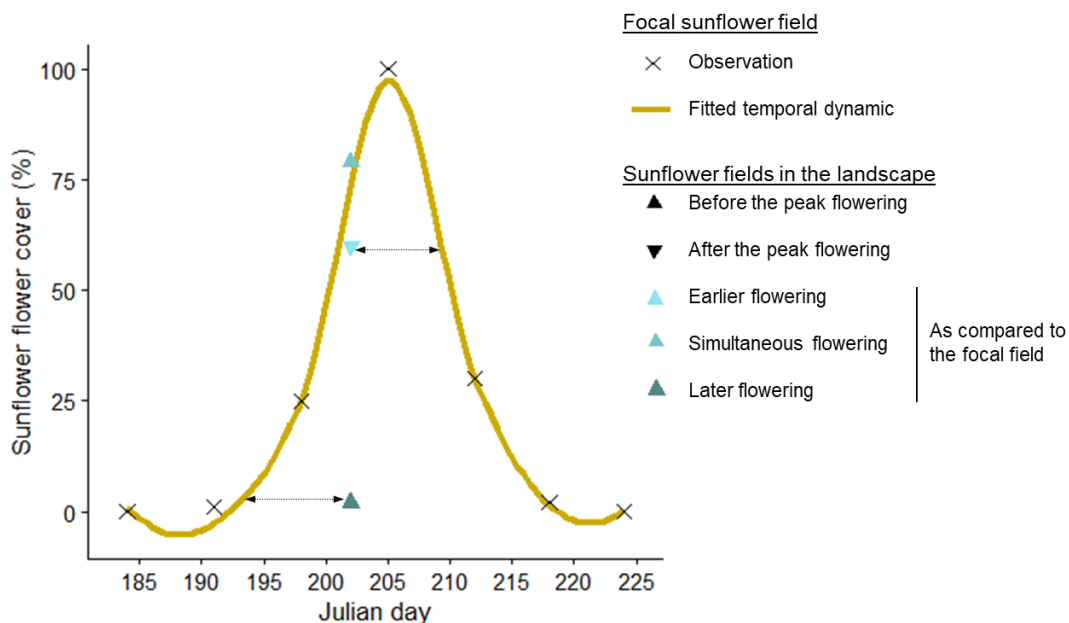


Fig. S1.3: An example to explicit the method used to determine either sunflower in the fields were earlier, simultaneous, or later flowering sunflower than the focal field. As described in the method section, we first determined the temporal dynamic of flowering of the focal field with sunflower flower cover in the field explained by the date. Then, at a date, for each field of the landscape we visually estimated the sunflower flower cover and either the field was before or after the flowering peak. We finally determined the number of days separating the flower cover of the sunflower in the landscape so that the focal field reached the same value of flower cover (indicated by an arrow). Fields in the landscape with > 3 in advance were earlier, those with > 3 days were later, the others were simultaneous sunflower flowering than the focal field.

3. Appendix 1C. Absence of nectar and honeybee before and after the flowering

The surveys of pollinator were performed at five different flowering periods. We detected very low nectar amount and honeybee abundance ‘before’ and ‘after’ the flowering (Fig. S1.4). We excluded these data for our analyses.

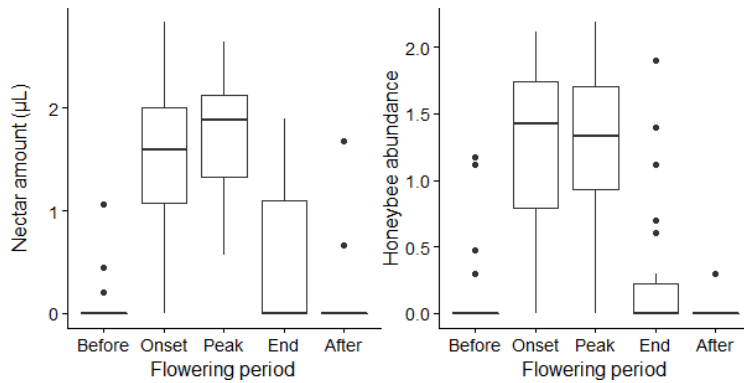


Fig. S1.4: Variation in nectar amount and honeybee abundance ($\log_{10}+1$) through the five flowering periods.

4. Appendix 1D: Variation of nectar amount, sugar rate and honeybee abundance with crop cultivar.

Among the 30 fields, sunflower crop belongs to 13 cultivars. The sunflower fields seem to shelter more or less nectar and to be visited by more or less honeybee during the surveys according to the crop cultivar. Variation in nectar sugar rate seems less important between crop cultivar (Table S1.1). Nectar sugar rate was quantified once in the season in peak flowering period with a light refractometer. We had no statistical power (some cultivars were present once) to test differences in nectar amount or honeybee abundance between cultivars. But cultivars as Holeron, P166HH150 or P64HE118 seem to provide a high amount of nectar. They were however not necessarily the cultivar with the highest, or in the contrary the lowest honeybee abundance. It also appeared to be a strong variation between fields with the same cultivar in nectar amount or honeybee abundance possibly due to the landscape context.

Table S1.1: Variation of nectar amount, nectar sugar rate, and honeybee abundance per cultivar. Nectar amount and honeybee abundance corresponded to the cumulated 54 observations per field (6 sunflower plants surveyed at 3 day and 3 flowering periods). Nectar sugar rate was measured once in the season with a light refractometer, we collected at least 10 μ L of nectar in the field (different from individuals for the survey on interactions). We indicated the number of fields per cultivar (n). When $n > 2$, we presented mean value, then min and max values in square brackets.

Cultivar	n	Nectar amount (μ L)	Nectar sugar rate	Honeybee abundance
CELLESTO	1	102	/	281
ES_NIAGARA	1	27	/	29
HOLERON	1	229	0.39	78
ILICO	1	93	0.26	114
LG_50_525	1	77	0.15	119
MASS_82_OL	1	59	0.36	139
P166HH150	1	201	0.30	47
P63HE133	2	96 [30 ; 161]	/	104 [43 ; 164]
P64HE118	2	603 [521 ; 685]	0.31 [0.27; 0.35]	68 [64 ; 72]
P64HE144	1	172	0.36	60
P64ME1330	2	126 [99 ; 153]	0.29 [0.27; 0.30]	78 [61 ; 95]
PE64HE118	2	77 [64 ; 90]	0.35 [0.35; 0.36]	74 [42 ; 105]
SY_RIALTO	5	301 [94 ; 764]	0.34 [0.25; 0.50]	43 [3 ; 93]

5. Appendix 1E. No effect of the number of hives and %Sunflower at the onset flowering period.

We found no effect of the landscape context on nectar amount and honeybee abundance at the onset flowering period contrary. The summary of statistics is presented in Table S1.2.

Table S1.2: summary statistics of models testing the effects of the distance to field border, number of hives, %earlier, simultaneous, and later flowering sunflower in the landscape than the focal field, and field size on nectar amount (a) and honeybee abundance (b). Are indicated degree of freedom (df), the results of the type II ANOVA (chi-square and p-value) and the effect size (mean and standard error of the slope).

	df	Onset flowering period									
		Early-morning			Mid-day			Late-afternoon			
		X ²	p	Effect	X ²	p	Effect	X ²	p	Effect	
a. Nectar amount	Distance to field border	1	0.01	0.90	0.010 ± 0.073	0.33	0.57	0.026 ± 0.047	1.63	0.20	0.059 ± 0.048
	Number of hives	1	0.16	0.69	0.004 ± 0.010	1.08	0.30	-0.007 ± 0.007	0.07	0.80	-0.002 ± 0.008
	%Later sunflower	1	0.23	0.63	0.006 ± 0.014	0.16	0.69	0.004 ± 0.010	0.73	0.39	-0.008 ± 0.010
	%Simultaneous sunflower	1	0.74	0.39	0.017 ± 0.021	1.08	0.30	-0.013 ± 0.014	0.17	0.68	-0.005 ± 0.015
	%Earlier sunflower	1	0.16	0.69	-0.008 ± 0.020	1.28	0.26	0.015 ± 0.015	0.07	0.79	0.004 ± 0.017
	Field size	1	0.36	0.55	0.015 ± 0.027	0.03	0.87	-0.003 ± 0.019	0.05	0.83	0.004 ± 0.021
	Distance × Number of hives	1	0.00	0.97	0,000 ± 0.006	0.67	0.41	0,003 ± 0.004	0.51	0.47	0,003 ± 0.004
	Distance × %Later sunflower	1	0.04	0.84	-0,002 ± 0.009	0.58	0.45	-0,004 ± 0.006	1.65	0.20	0,007 ± 0.006
	Distance × %Simultaneous sunflower	1	1.30	0.26	0,015 ± 0.013	0.02	0.89	-0,001 ± 0.008	2.06	0.15	0,012 ± 0.008
	Distance × %Earlier sunflower	1	0.00	0.95	-0,001 ± 0.012	0.00	0.96	0,000 ± 0.008	0.08	0.78	0,002 ± 0.008
b. Honeybee abundance	Distance to field border	1	2.09	0.15	-0.080 ± 0.056	0.13	0.72	-0.016 ± 0.052	1.01	0.32	0.040 ± 0.040
	Number of hives	1	2.13	0.14	0.008 ± 0.006	1.99	0.16	0.008 ± 0.006	0.69	0.41	0.005 ± 0.007
	%Later sunflower	1	0.00	0.98	0.000 ± 0.009	0.02	0.89	0.001 ± 0.008	1.51	0.22	-0.010 ± 0.009
	%Simultaneous sunflower	1	0.05	0.82	0.003 ± 0.013	0.00	0.96	0.001 ± 0.012	0.54	0.46	-0.008 ± 0.012
	%Earlier sunflower	1	0.25	0.62	-0.006 ± 0.013	0.26	0.61	-0.005 ± 0.013	0.06	0.80	0.003 ± 0.014
	Field size	1	0.02	0.89	-0.002 ± 0.017	0.06	0.80	-0.004 ± 0.016	0.64	0.42	-0.012 ± 0.017
	Distance × Number of hives	1	0.68	0.41	0,004 ± 0.005	2.27	0.13	0,007 ± 0.005	0.02	0.88	-0,001 ± 0.004
	Distance × %Later sunflower	1	0.10	0.76	-0,002 ± 0.007	2.26	0.13	-0,010 ± 0.006	0.02	0.90	-0,001 ± 0.005
	Distance × %Simultaneous sunflower	1	0.10	0.75	0,003 ± 0.010	0.64	0.42	0,007 ± 0.009	0.00	0.99	0,000 ± 0.007
	Distance × %Earlier sunflower	1	0.34	0.56	-0,006 ± 0.010	1.87	0.17	-0,012 ± 0.009	0.00	0.99	0,000 ± 0.007

II. Informations supplémentaires du chapitre 2

1. Appendix 2A. Presentation of the experimental design

The experimental design was slightly modified throughout the duration of the study because of experimental or field constraints. A summary is given in Table S2.1.

Table S2.1: Experimental design performed during the five study years.

	2015	2016	2017	2018	2019
OSR phytometers					
OSR phytometer cultivar	DK Ekstrom		Astronom	DK Ekstrom	
Pot			3L		
Position of phytometers in fields	One pot in field core & one pot at field edge				
Number of treatments	Four (control, large mesh, small mesh, Osmolux)				
Total number of phytometers (fields)	200 (99)	194 (98)	94 (38)	58 (20)	70 (35)
Number of phytometers (OSR)	64 (31)	60 (30)	80 (21)	58 (20)	44 (22)
Number of phytometers (cereal)	98 (49)	94 (47)	14 (7)	0	14 (7)
Number of phytometers (grassland)	38 (19)	42 (21)	0	0	12 (6)
Phytometers in OSR (min/max dates)	04-16/05-15	04-01/04-29	04-06/05-05	04-10/05-10	04-05/05-04
Phytometers in cereals (min/max dates)	04-24/05-19	04-07/05-05	04-20/05-05	/	05-05/05-05
Phytometers in grasslands (min/max dates)	04-24/05-19	04-07/05-05	/	/	05-05/05-05
Measures on OSR phytometers					
Number of flowers	Number of flowers that produced pods				
Number of pods	Number of pods containing seeds				

In 2017 and 2018, OSR phytometers were placed twice in respectively 33% and 24% of OSR fields. We studied the influence of repeated measures by comparing the estimations of the models that include only the first observation or both (see ‘Methods’ for details on models). No differences were observed (Table S.ii-2) between the two models, we thus conserved the repeated observations in the analyses.

Table S2.2: Summary statistic of linear models testing the effects of field (‘Field size and ‘Focal Field–Regional Flowering Temporal Matching’), landscape (%SNH, OF and OSR) and temporal (‘Phytometer–Regional Flowering Temporal Matching’) variation in flower availability on fruiting success in OSR fields with the repeated observations (a.) or without the repeated observations (b.). Significant values are in bold.

	df	a. With repetitions			b. Without repetitions		
		%Var	F	p	%Var	F	p
Year	4	15.2	7.13	<0.001	14.4	5.97	<0.001
Field size	1	0.0	0.07	0.79	0.0	0.03	0.87
Phytometer–Regional Flowering Temporal Matching	1	14.0	26.36	<0.001	18.1	30.02	<0.001
Focal Field–Regional Flowering Temporal Matching	2	1.1	1.00	0.37	1.0	0.83	0.44
%OSR (Landscape Flower Quantity)	1	2.9	5.45	0.02	3.3	5.43	0.02
%SNH (Landscape Flower Quantity)	1	3.0	5.65	0.02	3.1	5.08	0.03
%OF (Landscape Flower Quantity)	1	2.8	5.32	0.02	3.0	5.07	0.03
Field size x Phytometer–Regional Flowering Temporal Matching	1	2.3	4.32	0.04	2.4	3.98	0.05
Focal Field–Reg. Flow. Temp. Matching x Phytometer–Regional Flow. Temp. Matching	2	1.5	1.41	0.25	1.8	1.53	0.22
Field size x Focal Field–Reg. Flow. Temp. Matching	2	0.8	0.71	0.50	0.2	0.18	0.84
%OSR x Phytometer–Reg. Flow. Temp. Matching	1	0.1	0.26	0.61	0.2	0.38	0.54
%SNH x Phytometer–Reg. Flow. Temp. Matching	1	0.7	1.23	0.27	0.4	0.68	0.41
%OF x Phytometer–Reg. Flow. Temp. Matching	1	0.0	0.02	0.89	0.0	0.03	0.86

2. Appendix 2B. Estimation of the ‘Phytometer–Regional Flowering Temporal Matching’ and ‘Focal Field–Regional Flowering Temporal Matching’.

‘Phytometer–Regional Flowering Temporal Matching’ was defined to describe the period of OSR flowering during which phytometers were deposited in OSR fields, cereal fields, and grasslands. Based

on visual estimations of OSR flower cover in OSR fields in the ZA-PVS (0% means no OSR flower in the OSR fields, 100% means that OSR flowers covered the total area of the field), we estimated each year the temporal dynamic of OSR flowering in the site using generalized additive models (GAMs). From the fitted GAMs, we identified the period of OSR peak flowering, i.e. the day range between the maximal estimated OSR flower cover and a relative 20% reduction of OSR flower cover (Fig. S2.1 a-e). Phytometers were therefore placed in the OSR fields during or after the OSR peak flowering (i.e. before or after the 20% threshold date). The 20%-threshold was determined in order to balance the data between the two categories with a representation of each year of study in both categories (Fig. S2.1 f-j). As phytometers were placed later in cereals and grasslands (i.e. OSR phytometers were placed on average 12 days later in cereals/grasslands than in OSR fields), we determined a different threshold following the same method and thus considered a 60% reduction of OSR flower cover as the end of flowering. Thus, the phytometers in cereals and grasslands were placed during OSR flowering, i.e. before the 60% threshold date or after its flowering, i.e. after the 60% threshold date.

‘Focal field–Regional Flowering Temporal Matching’ described the temporal matching in OSR flowering between the focal OSR fields in which phytometer plants were placed and the overall flowering of OSR fields in the study site. This metric was thus only defined for OSR fields. For each estimation of OSR flower cover, we estimated the gap between OSR flower cover from a focal field and the OSR flower cover estimated on the corresponding day in the study site (based on the GAMs previously built). We applied quantile regressions (33% and 66%) on the estimated gaps with days as the explanatory variable. This allowed the classification of the OSR fields into three categories of Focal Field–Regional Flowering Temporal Matching: OSR fields were either relatively late (i.e. less deflowered than 66% of the OSR fields), relatively early (i.e. more deflowered than 66% of the OSR fields) or relatively normal compared to the OSR flowering estimated in the study site (Fig. S2.1 a-e).

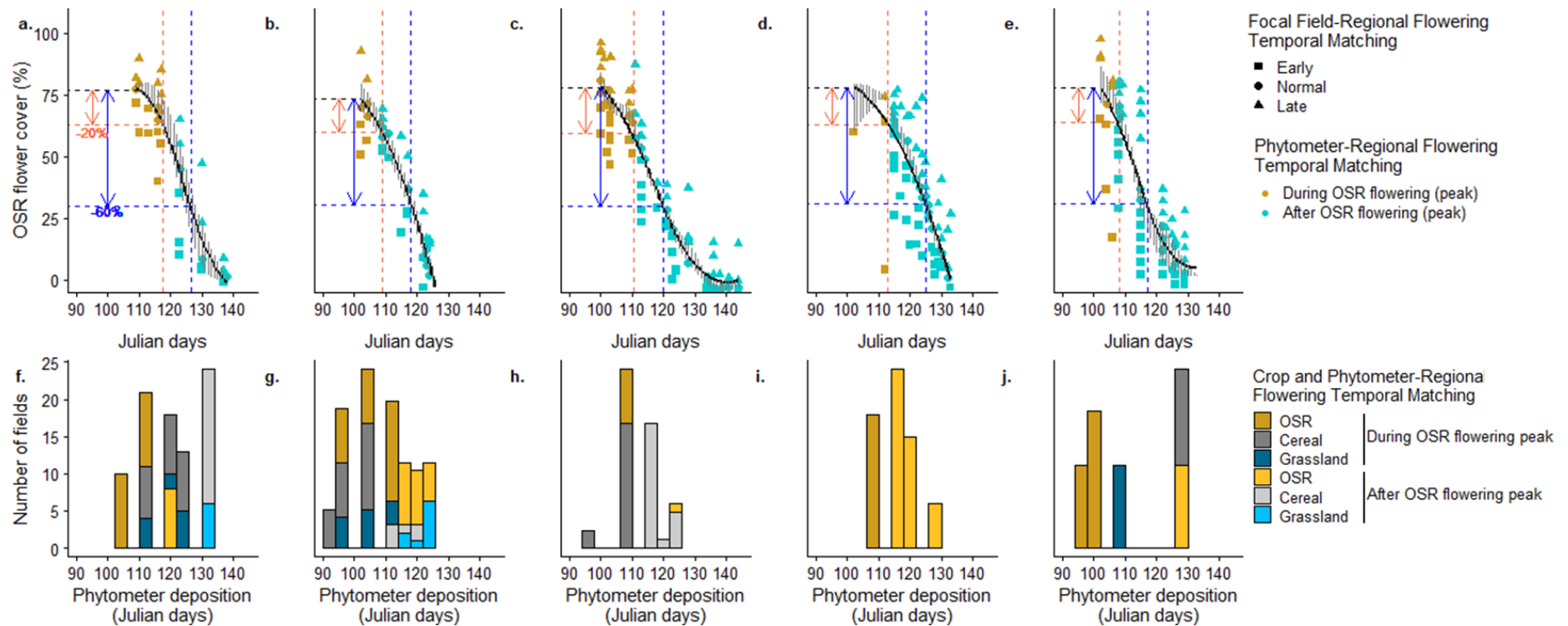


Fig. S2.1: Relationships between the OSR flower cover (%) in OSR fields and Julian days in 2015 (a), 2016 (b), 2017 (c), 2018 (d) and 2019 (e). A point corresponds to the OSR flower cover in an OSR field (on average 29 ± 6 sd OSR fields per year, of which $83\% \pm 18\%$ sd contained phytometers) corrected by the observer effect (on average 5 ± 2 sd observers per year). The descriptions of temporal dynamics of OSR flowering were performed with GAMs (black lines), OSR flower cover and Julian day were the explanatory variables (the observer was a covariable). The maximum estimated OSR flower cover (flowering peaks) are represented by horizontal black dashed lines, the threshold days at which the predicted OSR flower cover was reduced by 20% (for phytometers in OSR fields) and 60% (for phytometers in cereals and grasslands) compared to the peaks are presented by vertical orange and blue lines. The barplots give information about the sample sizes for each crop and for each ‘Phytometer–Regional Flowering Temporal Matching’ category for 2015 (f), 2016 (g), 2017 (h), 2018 (i) and 2019 (j). Quantile regressions (33% and 66%) were applied to estimate the mismatch between the flowering stage (i.e. observed flower cover) in the OSR focal field and the flowering stage in the study site (i.e. estimated flower cover) the same day. The Julian day was also included in the regressions as an explanatory variable. Based on the quantile regressions, we defined the 33% and 66% threshold quantiles (grey vertical segments were the predicted GAMs + 33% and 66% thresholds quantiles) used to assign a level of the variable ‘Focal field-Regional Flowering Temporal Mismatch’ for OSR fields. Note that flower cover estimation was repeated over time in 78% of the OSR fields, to attribute a level of ‘Focal field-Regional Flowering Temporal Mismatch’ for these fields, we used the averaged deviations from the 33% and 66% quantiles. A relatively early OSR field had flower coverage on average below the 33% threshold quantile, a late OSR field had flower coverage on average above the 66% threshold quantile and a ‘relatively normal’ field was between the 33% and 66% threshold quantiles.

3. Appendix 2C. Effect on pollination efficiency of the position of phytometers in the field

Phytometers were placed at the field edge or core as pollinator communities are known to differ between these two field compartments (Ahrenfeldt et al., 2015; Ricketts et al., 2008). We compared the pollination efficiency between these field positions. Paired T-tests revealed an absence of significant difference of fruiting success between field core and edge in OSR fields ($t_{df=115} = -1.19$; $p = 0.24$); cereal fields ($t_{df=87} = 0.59$; $p = 0.56$) and grasslands ($t_{df=35} = 0.56$; $p = 0.58$; Fig. S2.2).

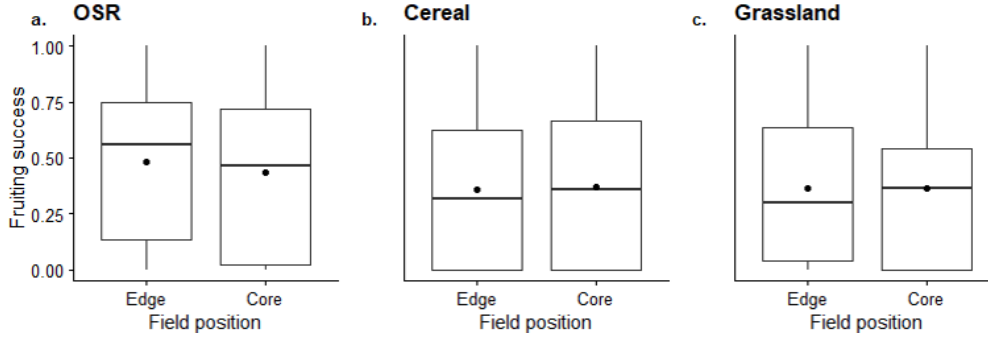


Fig. S2.2: Variations in fruiting success between field edge and core in OSR (a), cereal (b) and grassland (c). Quantiles and mean (black point) are represented.

4. Appendix 2D. Description of the model of fruiting success

We used the approach proposed by Carpentier & Martin, (2021) to simultaneously infer the effects of local, temporal and landscape variables, as well as the scale of effect of landscape variables. The effects of landscape variables were assumed constant over a buffer area defined from the edge of the focal field. We described the fruiting success of the control treatment, Y_{ijk} (i stands for the year, j for the Phytometer Temporal Lag and k the observation).

$$Y_{ijk} \sim N(\mu_{ijk}, \sigma^2) \text{ (independent identically distributed)}$$

For the OSR model,

$$\begin{aligned} \mu_{yjk} = & \mu + \alpha_y + \beta_i^{P.FTM} + \beta_j^{F.FTM} + (\eta + \eta_i^{P.FTM} + \eta_j^{F.FTM}) FFQ_{yijk} + \\ & + \alpha^{OSR} P_{OSR}(x_{yijk}, r_{OSR}) + \alpha^{SNH} P_{SNH}(x_{yijk}, r_{SNH}) + \alpha^{OF} P_{OF}(x_{yijk}, r_{OF}) \\ & + \gamma_i^{P.FTM:OSR} P_{OSR}(x_{yijk}, r_{OSR}) + \gamma_j^{P.FTM:SNH} P_{SNH}(x_{yijk}, r_{SNH}) \\ & + \gamma_j^{P.FTM:OF} P_{OF}(x_{yijk}, r_{OF}) \end{aligned}$$

Where y is the year, $\beta_i^{P.FTM}$, the effect of ‘Phytometer–Regional Flowering Temporal Matching’ (FTM) i , $\beta_j^{F.FTM}$, the effect of Focal Field–Regional FTM j , η the effect of ‘Field size’ (FFQ), $\eta_i^{P.FTM}$ and $\eta_j^{F.FTM}$ the interaction effect between FFQ with Phytometer–Regional FTM i and Focal Field–Regional FTM j , respectively, $P_{OSR}(x, r_{OSR})$, stands for the percentage of oilseed rape fields (OSR) in a buffer around the focal field x of radius r_{OSR} , $P_{SNH}(x, r_{SNH})$ and $P_{OF}(x, r_{OF})$ stands for the proportion of semi-natural habitat and organic fields, respectively.

The cereal model is the OSR model excluding the effect of the variable: Focal Field–Regional FTM (i.e. without parameters $\beta_j^{F.FTM}$ and $\eta_j^{F.FTM}$). The grassland model is identical to the cereal model excluding the interaction terms (i.e. without parameters $\eta_i^{P.FTM}$, $\gamma_i^{P.FTM:OSR}$, $\gamma_i^{P.FTM:SNH}$ and $\gamma_i^{P.FTM:OF}$).

The estimation is obtained by a sequential Maximum Likelihood Estimation procedure implemented in the R package ‘siland’ (Carpentier & Martin, 2020). Therefore, all the model parameters are estimated simultaneously, including the r parameters and the buffer radii.

5. Appendix 2E. Landscape scales of influence and correlations between landscape variables.

We simultaneously estimated effects and scales of effects of landscape with the ‘siland’ method (Carpentier and Martin 2021) and checked for good estimation of scales of influence of each landscape variable for all models (six models in each of the three crops) with profile likelihoods (Fig. S2.3).

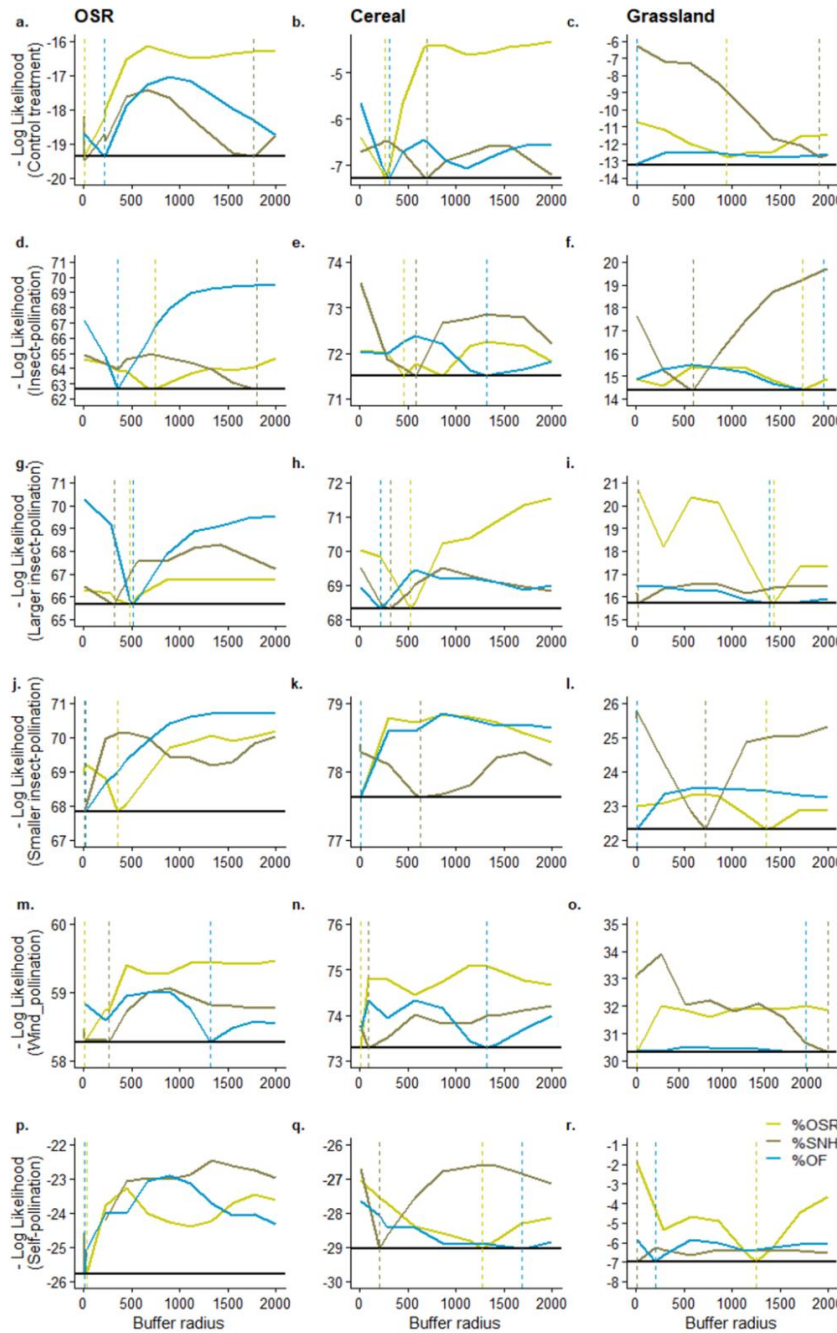


Fig. S2.3: Profile likelihoods of the models (see Table 1 and Table 2), testing for amount of floral resources in the field and in the landscape and ‘Phytometer–Regional Flowering Temporal Matching’, varying the buffer radii outside the fields at which %OSR, %SNH and %OF were simultaneously estimated on fruiting success (a, b, c), insect pollination (d, e, f), large insect pollination (g, h, i), small insect pollination (j, k, l), wind pollination (m, n, o) and self-pollination (p, q, r) in OSR fields (a, d, g, j, m, p), cereal fields (b, e, h, k, n, q) and grasslands (c, f, i, l, o, r). Horizontal black lines are minimum – log likelihoods, and vertical-coloured dashed lines indicate the estimated scales of influence.

We also studied the correlations between landscape features at the estimated scales of effect by multiple correlation tests in each crop. Landscape features were generally little correlated (Table. S2.3).

Table S2.3: Correlations between landscape variables in OSR fields (a.), cereal fields (b.) and grasslands (c.) for models studying fruiting success of the control treatments (correlation between landscape variables were similar with models on pollination processes even if at different spatial scales). Mean and 95 confidence intervals (in brackets) of the Spearman correlation coefficient are noted between pairs of landscape features. Significant values are in bold.

	a. OSR fields		b. Cereal fields		c. Grasslands	
	% OF	% OSR	% OF	% OSR	% OF	% OSR
% SNH	-0.13 [-0.29; 0.04]	-0.14 [-0.30; 0.03]	-0.10 [-0.29; 0.10]	-0.22 [-0.40; -0.03]	-0.01 [-0.31; 0.29]	-0.18 [-0.45; 0.13]
% OF	/	-0.03 [-0.20; 0.14]	/	-0.20 [-0.38; -0.00]	/	-0.18 [-0.46; 0.13]

6. Appendix 2F. Effect of landscape on fruiting success is not affected by its interaction with ‘Phytometer–Regional Flowering Temporal Matching’

Models explaining the variation of fruiting success of OSR phytometers in OSR and cereal fields included interactions between ‘Landscape Flower Quantity’ and ‘Phytometer–Regional Flowering Temporal Matching’, contrary to models for grasslands. We built models with and without these interactions and performed analyses with the ‘siland’ method to ensure that these interactions did not change the effects and the scales of effects of landscape variables in OSR (Table S2.4a) and cereals (Table S2.4b)

Table S2.4: Summary statistics of linear models testing the response of fruiting success in OSR (a) and cereals (b) to floral resource availability in the field (‘Field size’ and ‘Focal Field–Regional Flowering Temporal Matching’ for OSR field), in the landscape (%SNH, OF and OSR) and ‘Phytometer–Regional Flowering Temporal Matching’ with or without interactions between landscape variables ‘Phytometer–Regional Flowering Temporal Matching’. Landscape scales of influence estimated with ‘siland’ were similar with or without interactions in OSR: %OSR (11 m vs 12 m), %SNH (1775 m vs 1819 m) and %OF (209 m vs 209 m) and in cereal: %OSR (260 m vs 257 m), %SNH (699 m vs 706 m) and %OF (303 m vs 311 m). Significant values are in bold.

	df	With interactions			Without interactions		
		%Var	F	p	%Var	F	p
a. OSR							
Year	4	15.2	7.13	<0.001	14.8	7.06	<0.001
Field size	1	0.0	0.07	0.79	0.0	0.12	0.73
Phytometer–Regional Flowering Temporal Matching	1	14.0	26.36	<0.001	13.9	26.65	<0.001
Focal Field–Regional Flowering Temporal Matching	2	1.1	1.00	0.37	1.0	0.94	0.39
%OSR (Landscape Flower Quantity)	1	2.9	5.45	0.02	3.0	5.83	0.02
%SNH (Landscape Flower Quantity)	1	3.0	5.65	0.02	2.9	5.55	0.02
%OF (Landscape Flower Quantity)	1	2.8	5.32	0.02	2.8	5.38	0.02
Field size x Phytometer–Regional Flowering Temporal Matching	1	2.3	4.32	0.04	2.8	5.42	0.02
Focal Field-Reg. Flow. Temp. Matching x Phytometer-Regional Flow. Temp. Matching	2	1.5	1.41	0.25	1.5	1.39	0.25
Field size x Focal Field- Reg. Flow. Temp. Matching	2	0.8	0.71	0.50	0.6	0.65	0.53
%OSR x Phytometer-Reg. Flow. Temp. Matching	1	0.1	0.26	0.61	-	-	-
%SNH x Phytometer-Reg. Flow. Temp. Matching	1	0.7	1.23	0.27	-	-	-
%OF x Phytometer-Reg. Flow. Temp. Matching	1	0.0	0.02	0.89	-	-	-
b. Cereal							
Year	3	18.1	6.34	<0.001	5.4%	6.74	<0.001
Field size	1	0.3	0.27	0.60	0.1	0.27	0.60
Phytometer–Regional Flowering Temporal Matching	1	7.9	8.34	<0.01	2.2	8.38	<0.01
%OSR (Landscape Flower Quantity)	1	4.6	4.82	0.03	1.3	4.73	0.03
%SNH (Landscape Flower Quantity)	1	0.4	0.46	0.50	0.1	0.30	0.59
%OF (Landscape Flower Quantity)	1	2.4	2.51	0.12	0.7	2.45	0.12
Field size x Phytometer–Regional Flowering Temporal Matching	1	0.2	0.20	0.65	0.0	0.05	0.82
%OSR x Phytometer–Regional Flowering Temporal Matching	1	0.5	0.48	0.49	-	-	-
%SNH x Phytometer–Regional Flowering Temporal Matching	1	1.0	1.07	0.30	-	-	-
%OF x Phytometer–Regional Flowering Temporal Matching	1	0.4	0.39	0.53	-	-	-

7. Appendix 2G. Variation in fruiting success and insect pollination with local amount of OSR

‘Phytometer–Regional Flowering Temporal Matching’ affected fruiting success (Table 1a) and insect pollination (Table 2a) strongly, as they were higher during the OSR peak flowering than after (Fig. 2a, Fig. 4f).

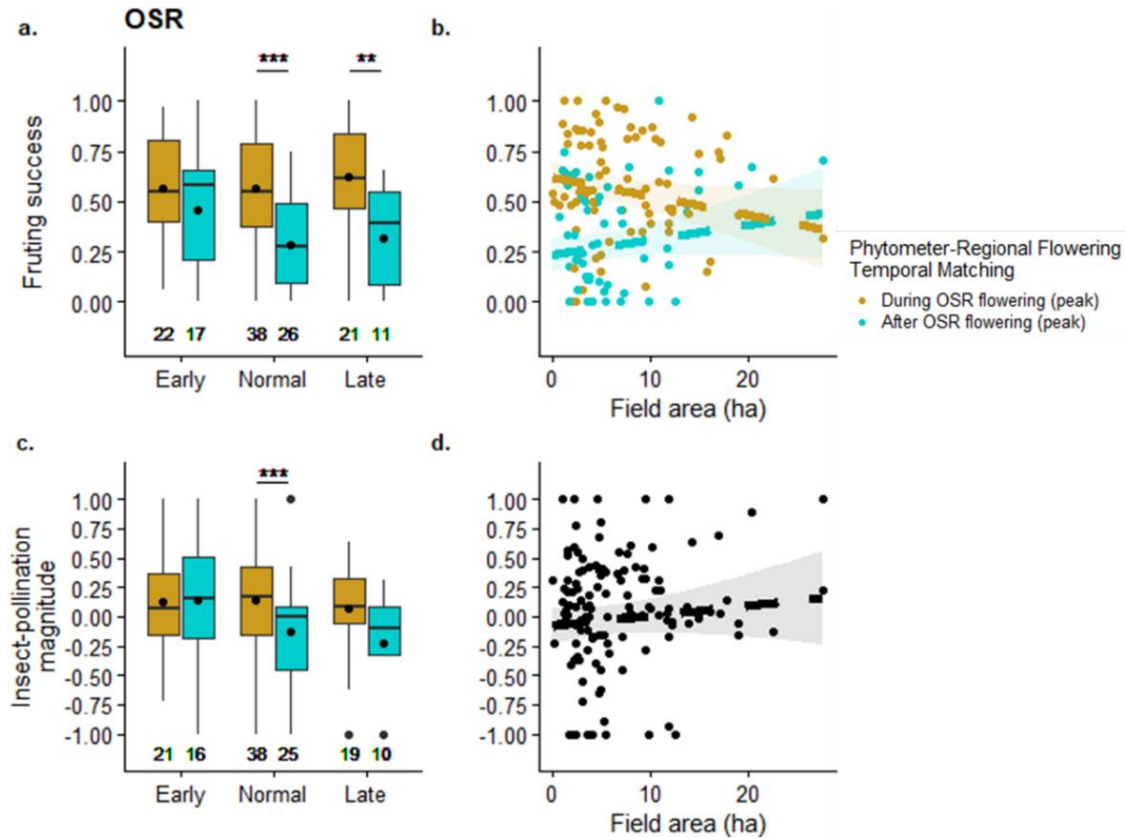


Fig. S2.4: Variation in fruiting success and insect pollination with ‘Phytometer–Regional Flowering Temporal Matching’ and ‘Focal Field–Regional Flowering Temporal Matching’ (a, c). Stars (***) < 0.001; ** < 0.01 and * < 0.05) indicated significant differences between levels of ‘Phytometer–Regional Flowering Temporal Matching’ for each category of ‘Focal Field–Regional Flowering Temporal Matching’. OSR field size (area), used as a proxy of the amount of OSR flowers in the fields (b, d) influenced fruiting success by interacting with ‘Phytometer–Regional Flowering Temporal Matching’ (colours indicate the levels of ‘Phytometer–Regional Flowering Temporal Matching’) and insect pollination (non-significantly). Raw data for each year is represented by dots with different shapes. The lines show the predicted relationships (from models presented in Table 1a and Table 2a) and the shaded area their standard errors. Bold lines show significant effects and dashed lines non-significant effects.

Fruiting success was higher during the OSR peak flowering than after in relatively early (mean \pm se estimated from model presented in Table 1a: 0.11 ± 0.08), normal (0.27 ± 0.07) and late (0.25 ± 0.09) OSR fields. Insect pollination magnitude was higher during than after the OSR peak flowering in OSR fields with relatively normal flowering (mean \pm se estimated from model presented in Table 2a: 0.49 ± 0.13), relatively late flowering (0.31 ± 0.20), and was almost similar between the two levels of ‘Phytometer–Regional Flowering Temporal Matching’ for fields with relatively early flowering (-0.01 ± 0.16). These effects were independent of ‘Focal Field–Regional Flowering Temporal Matching’ for fruiting success in OSR fields (Fig. S2.4a), although the differences in magnitude of insect pollination among the levels of ‘Phytometer–Regional Flowering Temporal Matching’ differed between the modalities of ‘Focal Field–Regional Flowering Temporal Matching’ (Table 2a). Differences between levels of ‘Phytometer–Regional Flowering Temporal Matching’ were greater in OSR fields with

relatively ‘normal’ or late flowering compared to OSR fields with relatively early flowering (Fig. S2.4c). We observed a significant effect of OSR field size (used as a proxy of the local amount of OSR flowers) in interaction with ‘Phytometer–Regional Flowering Temporal Matching’ on fruiting success (Table 1a). Fruiting success tended to decrease with field area during the OSR peak flowering, while it tended to increase after the peak (Fig. S.24b). Insect pollination tended to increase with OSR field size (Fig. S2.4d).

8. Appendix 2H. Self-pollination magnitude and its variation between local, temporal and landscape contexts

In all crops, significantly in OSR and cereals, self-pollination was lower in periods with a low amount of OSR flowers (Fig. 4b). To better highlight the mechanisms, we explored the relationships between the number of flowers on an Osmolux treatment of a plant phytometer, day and magnitude of self-pollination.

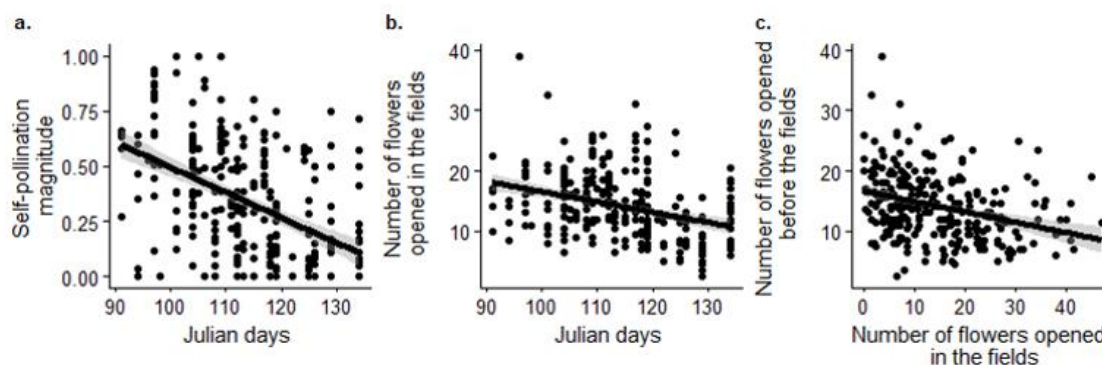


Fig. S2.5: Influence of Julian days on the effect of self-pollination on fruiting success (a) and on the number of flowers opened in the fields (b). Influence of the number of flowers opened before phytometers were placed in the fields on the number of flowers opened in the fields (c). We represented raw data (dots shaped in function of the studied year), the predicted relationships (from Table S.6) and their standard errors (shaded area).

A first model (Table S2.5a) revealed an effect of Julian day on the magnitude of self-pollination. Self-pollination decreased with the Julian day (Fig. S2.5a). Studying the effect of the Julian day on the number of flowers opened in the fields in the Osmolux treatment, we highlighted that the number decreased significantly with the Julian day (Fig. S2.5b; Table S2.5b). A third linear model indicated that the number of flowers opened in the fields was influenced negatively (Fig. S2.5c; Table S2.5c) by the number of flowers opened before phytometers were placed in the fields. The studied position of the branch was apical at the end of the season. In apical position, the number of flowers is reduced compared to basal position, thus the availability of pollen may be lower, and the magnitude of self-pollination decreased.

Table S2.5: Summary statistics of models testing for the effects of self-pollination with Julian day (a.) Number of flowers opened in the fields (during the four days of the experiment for the Osmolux treatment) with Julian days (b.) Branch position estimated by the number of flowers opened in the greenhouse before placement in the field (c.). Year and crop were used as covariables in all models. Degree of freedom, F-value (F) and p-value (p) are indicated. Significant values are in bold.

a. Self-pollination			b. Number of flowers			c. Number of flowers					
	df	F	p		df	F	p		df	F	p
Year	4	12.83	<0.001	Year	4	12.05	<0.001	Year	4	24.19	<0.001
Day	1	38.45	<0.001	Day	1	9.73	<0.01	Branch position	1	52.47	<0.001
Crop	2	1.86	0.16	Crop	2	2.64	0.07	Crop	2	4.03	0.02

The results showed that self-pollination was modified by local, temporal and landscape variables (Table 2). In OSR fields, self-pollination was influenced by %SNH and %OF at very small scales (< 10 m outside fields) and by ‘Field size’ in interaction with ‘Phytometer–Regional Flowering Temporal Matching’ and ‘Focal Field–Regional Flowering Temporal Matching’. In cereal fields, self-pollination responded to the amount of OSR in the landscape by interacting with ‘Phytometer–Regional Flowering Temporal Matching’, %OSR also influenced self-pollination in grasslands at a similar spatial scale to cereal (Fig. S2.6). We expected constant self-pollination of OSR plant phytometers in local, temporal and landscape conditions, presuming that self-pollination is influenced by processes acting at the branch scale. More studies on this are needed, especially regarding the mechanical bias induced by bags on OSR branches and on the ability of OSR to compensate for lack of pollen.

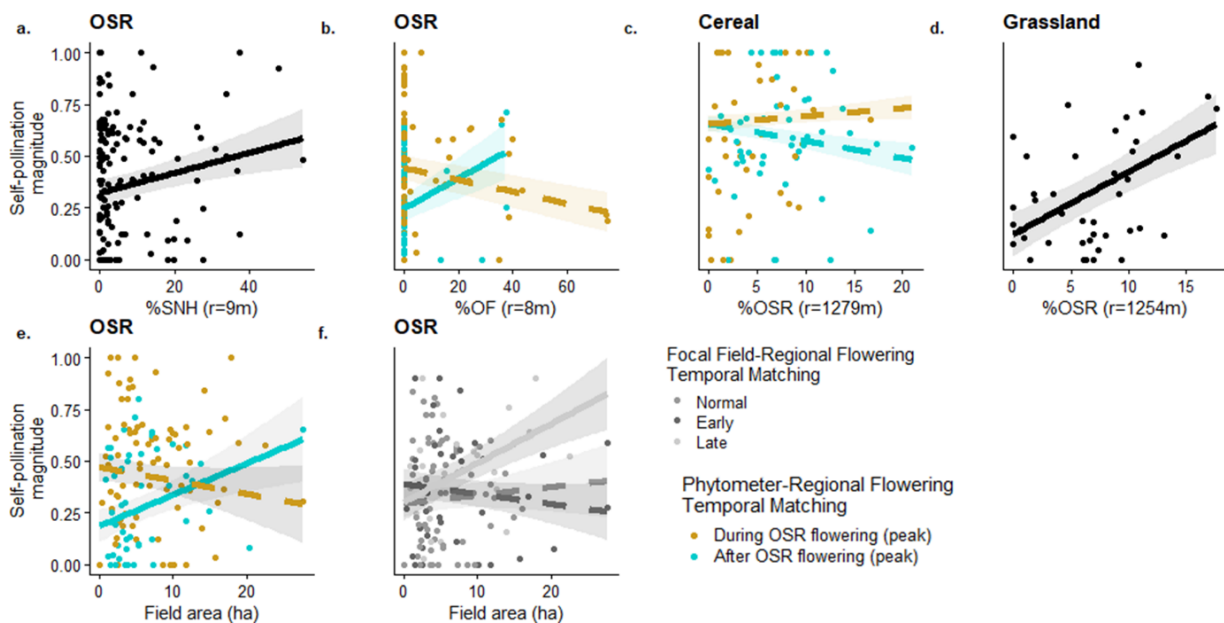


Fig. S2.6: Variation in the magnitude of self-pollination in OSR (a, b, e, f), cereals (c) and grasslands (d) with landscape (a, b, c, d) and local variables (e, f). Based on models presented in Table 2, predicted relationships were represented (significant relationships indicated by bold lines, non-significant by dashed lines).

9. Appendix 2I. Variation in pollination processes in OSR fields with amount of OSR in the landscape

Fruiting success increased in OSR with %OSR in the surrounding landscape (Fig 4a). All pollination processes (insect, wind- and self-pollination) increased, though non-significantly, with %OSR (Fig S2.7), insect pollination at a larger spatial scale (747 m outside OSR fields) than wind (3 m) and self-pollination (34 m). This may suggest an increase in pollination efficiency with increasing OSR pollen availability. The dilution hypothesis was not supported in our study on OSR pollination efficiency, perhaps because the increasing amount of OSR pollen may have compensated for a dilution of pollinators.

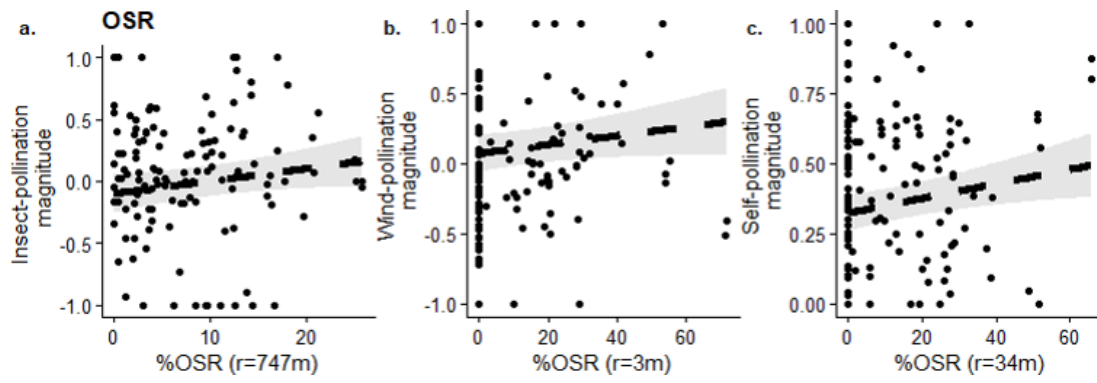


Fig. S2.7: Effect of the amount of OSR in the surrounding landscape on pollination processes in OSR crops. Insect (a.), wind (b.) and self-pollination (c.) tended to increase with %OSR (dashed lines). Buffer radii were estimated using the ‘siland’ method.

III. Informations supplémentaires du chapitre 3

1. Appendix 3A. Details about weed, wild pollinator and honeybee samplings.

Weed, wild pollinator and honeybee were sampled in 569 fields of the ZA-PVS during five years. The sampling strategy in each field is presented in Fig. S3.1.

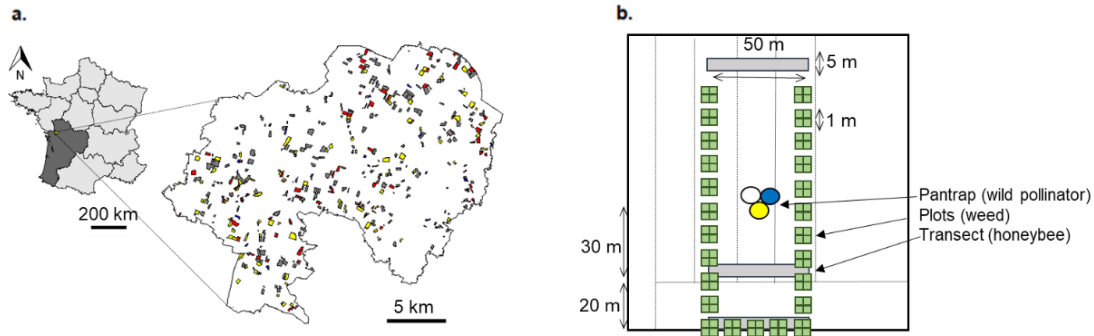


Fig. S3.1. Locations of the LTSER “Zone Atelier Plaine & Val de Sèvre” (46°14’N 0°28’W) in France (a.). Monitoring was performed in farmers’ fields in cereal (gray), OSR (yellow), grassland (blue) and sunflower (red) (b.). Weed species were sampling in 1 m² plots (five placed in field margin and 20 in field core) spaced from 10m and divided in four subplots of 0.25 m²; wild pollinators were sampled using pantraps; and the honeybee was monitoring along three 50m transects.

Wild pollinators were surveyed from the beginning of April to the beginning of August, first in OSR and cereals to overlap the flowering of OSR then in sunflower and grasslands to overlap the period of sunflower flowering (Fig. S3.2; Table S1).

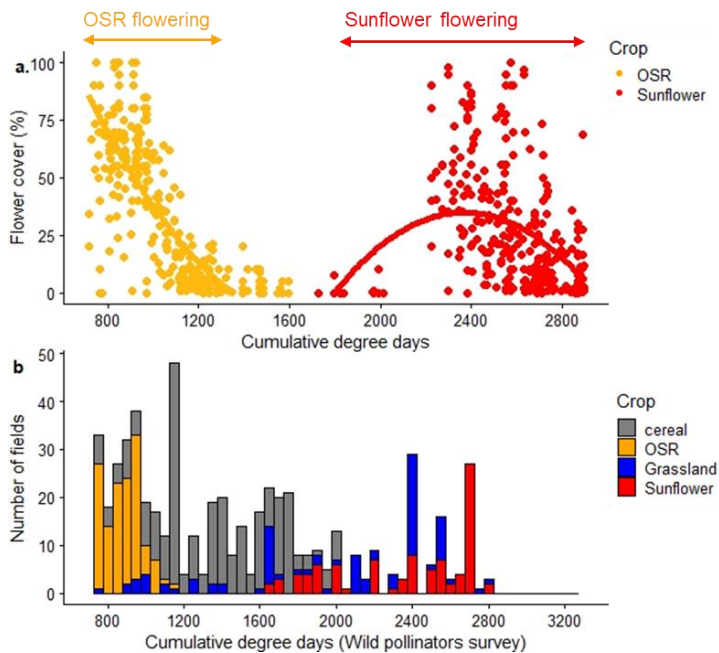


Fig. S3.2: Variation of the flower cover in OSR and sunflower fields with cumulative degree days (a.). Data of visual estimation of flower cover (from 0% when absence of flowers to 100% when the fields was totally covered by flowers) over cumulative degree days from the 1st of January (Niort weather station, Météo France) in fields of the study site was used (351 observations for 155 fields in OSR and 361 observations for 181 fields in sunflowers). Lines are the fitted quadratic relationships of flower cover explained by cumulative degree days. Histogram of the number of fields surveyed for wild pollinator catching with cumulative degree days in each crop (b.).

There is a high variability in the number of sampling fields between years (Table S1). We tested for well repartition of years among crops to ensure repartition of sampling effort was similar across crops among years. The test revealed a heterogeneity of sampled between crops and years ($X^2 = 59.73$, $df = 12$, $p < 0.001$).

Table S. 3.1: A. First and last dates of wild pollinators, weed and honeybee surveys for each year and crops. Sample sizes are indicated (n).

		OSR n = 30	Cereal n = 66	Grassland n = 0	Sunflower n = 32
2015	Wild pollinators	04-16 to 05-14	05-14 to 06-19	/	06-25 to 08-03
	Weed	04-10 to 04-23	04-23 to 07-18	/	06-16 to 07-22
	Honeybee	04-23 to 05-18 n = 32	05-27 to 08-05 n = 60	/ n = 46	06-29 to 08-12 n = 11
2016	Wild pollinators	04-07 to 04-28	04-15 to 07-01	04-07 to 08-11	07-21 to 08-04
	Weed	03-24 to 05-20	04-15 to 06-23	04-08 to 08-15	06-30 to 08-02
	Honeybee	04-04 to 05-12 n = 22	05-17 to 08-25 n = 48	05-25 to 07-07 n = 15	07-18 to 07-29 n = 13
2017	Wild pollinators	04-06 to 04-24	04-13 to 06-23	04-28 to 07-20	06-08 to 07-27
	Weed	04-06 to 04-25	04-20 to 05-29	04-28 to 07-27	06-13 to 07-25
	Honeybee	04-10 to 04-29 n = 25	04-29 to 07-06 n = 48	05-04 to 08-11 n = 17	07-06 to 08-01 n = 18
2018	Wild pollinators	04-12 to 04-26	04-12 to 06-14	04-26 to 07-05	06-15 to 07-26
	Weed	04-09 to 04-24	05-07 to 07-23	05-25 to 07-31	06-28 to 07-30
	Honeybee	04-26 to 05-06 n = 21	05-09 to 06-30 n = 35	06-02 to 08-22 n = 12	07-09 to 08-06 n = 18
2019	Wild pollinators	04-05 to 05-03	04-12 to 06-14	04-19 to 07-30	06-14 to 08-01
	Weed	04-04 to 04-23	04-25 to 06-18	05-28 to 08-13	07-03 to 08-08
	Honeybee	04-01 to 05-13	05-06 to 06-26	05-03 to 08-13	07-17 to 08-13

A year may thus have strong contribution on the “weed-wild pollinator relationship”, e.g., a positive relative relationship between weed and wild pollinator diversity is expected if weed and wild pollinator diversity and abundance covaried with the studied year. We thus checked for variation of wild pollinators and weed community indexes among years (Fig. S3.2). We observed some years with higher wild pollinator community indexes (e.g. wild pollinator species richness in OSR was more important in 2019), it revealed the need to add the studied year (factor) in the models testing the effect of weeds on wild pollinators. But, year during which wild pollinator community indexes were the highest/lowest were not those during which weed community indexes were the highest/lowest. It was not necessary to add year as a random effect factor on the slope between weeds and wild pollinators.

Table S. 3.2: Summary statistics of models testing the effect of weeds (abundance in cereals, the inverse of Simpson diversity in OSR and sunflower and specific richness in grasslands), temporal covariables (cumulative degree days and years) on wild pollinators (the inverse of Simpson diversity in cereals and OSR, the exponential of Shannon diversity in Sunflower and abundance in grasslands). The models included honeybee abundance and its interaction with weeds in OSR and sunflowers. We included in the models the temporal gap (in cumulative degree days) between wild pollinator and weed surveys (Δ wild pollinator – weed) and between wild pollinator and honeybee surveys (Δ wild pollinator – honeybee). We presented degree of freedoms (df), F-value (F) and p-value (p) obtained by type II Anova performed with the “car” package of the R software.

	a. Cereals			b. Grasslands		
	df	F	p	df	F	p
Weed	1	9.14	<0.01	1	3.13	0.08
Year	4	5.05	<0.001	3	4.94	<0.01
°day	1	19.56	<0.001	1	4.90	0.03
°day ²	1	20.43	<0.001	1	4.28	0.04
Δ wild pollinator - weed	1	2.27	0.13	1	0.23	0.63
	c. OSR			d. Sunflower		
	df	F	p	df	F	p
Weed	1	2.52	0.11	1	13.09	<0.001
Honeybee abundance	1	0.34	0.56	1	2.57	0.11
Weed \times Honeybee abundance	1	7.83	<0.01	1	0.54	0.47
Year	4	1.17	0.32	4	3.38	0.01
°day	1	12.81	<0.001	1	1.37	0.24
°day ²	1	12.32	<0.001	1	1.48	0.23
Δ wild pollinator - weed	1	0.04	0.83	1	0.24	0.63
Δ wild pollinator - honeybee	1	<0.01	0.99	1	1.48	0.23

Wild pollinators, honeybee and weeds were surveyed at different dates (Table S1). The absolute value of number of days between wild pollinators and weed surveys was on average 14.78 ± 15.01 sd days, those for difference of days between wild pollinators and honeybee surveys in OSR and sunflowers was on average 11.43 ± 9.80 sd days. Wild pollinators and weed communities show high temporal dynamics (Balfour et al., 2018) as well as honeybee abundance. We added differences of sampling dates among wild pollinators versus honeybee and weed samplings in the models to consider for differences in sampling dates. The influences of difference in sampling dates between wild pollinators and weeds as well as the difference in the sampling days between wild pollinators and honeybee were weak (Table S. 2). The effects of the other factors did not change by adding these variables.

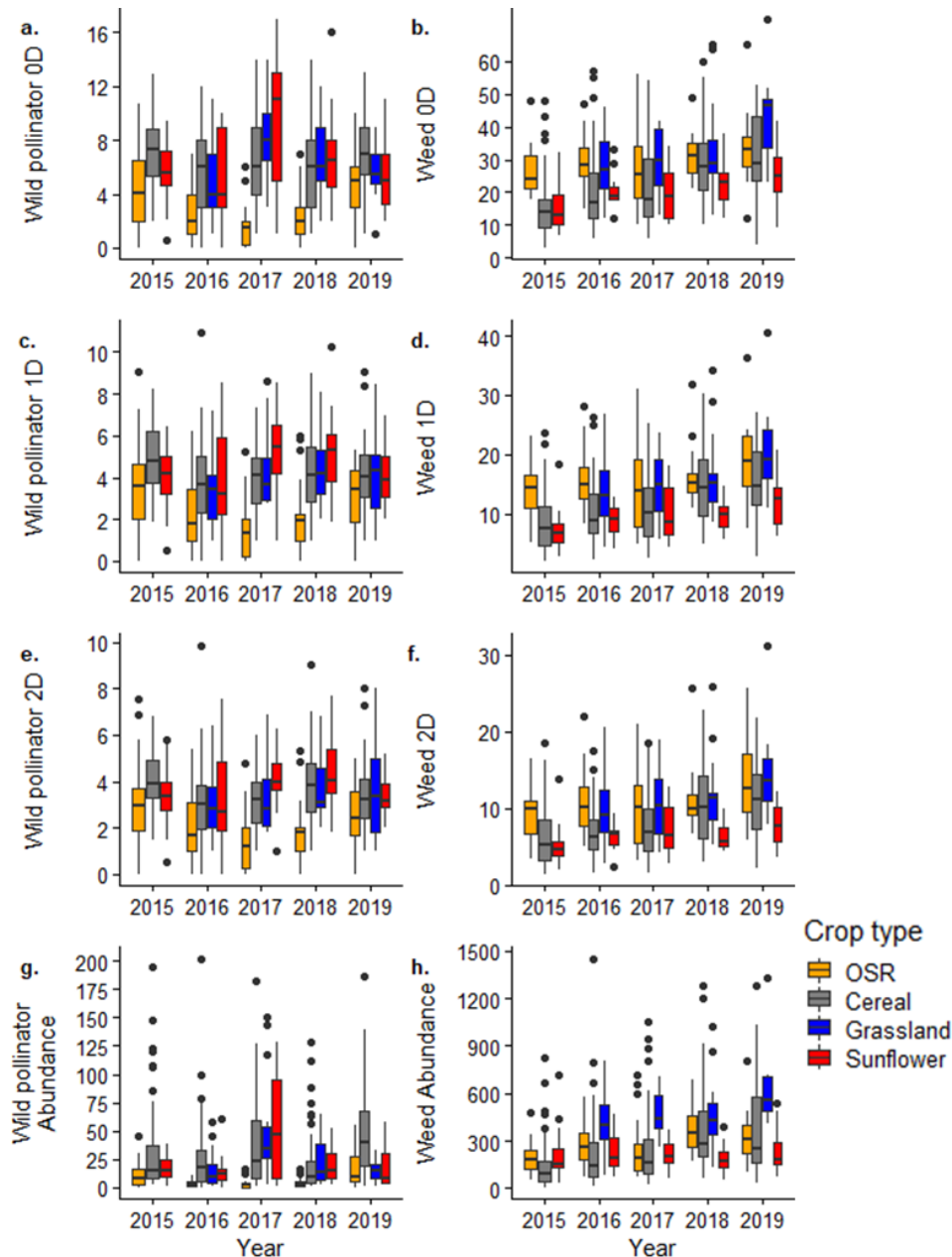


Fig. S3.3: Variation of wild pollinator (a, c, e, g) and weed (b, d, f, h) community indexes among year and crops.

2. Appendix 3B. Estimation of the threshold values for honeybee abundance and Temporal Matching with Mass Flowering crop.

We translated two quantitative variables namely honeybee abundance in OSR and sunflower, and Temporal Matching with Mass Flowering Crop (i.e. the temporal lag between the flowering period of OSR or sunflower and the sampling date of wild pollinators in OSR, cereal, grassland, and sunflower) into two qualitative variables with two levels (high and low). We had no *a priori* on the threshold that best separates fields with the levels low or high for each variable. We thus ran the models 2 and 3 with different levels. From 20 to 100 models (Fig. S3.4) were ran and for each variable (honeybee and temporal matching with mass flowering crop) in each crop type we selected the threshold values that minimized the AIC of the models 2 and 3 respectively (Fig. S3.4).

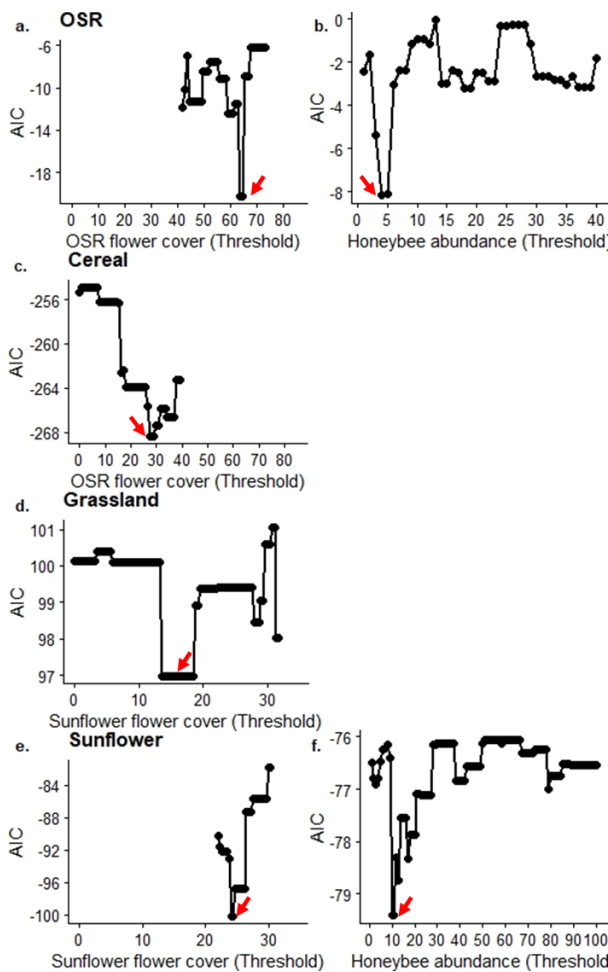


Fig. S3.4: Variation of the AIC varying the threshold of Temporal Matching with Mass Flowering crop (a, c, d, e) (see models 3 in section “statistical analyses”) and honeybee abundance (b, f) (see models 2 in “statistical analyses”) in OSR (a, b), cereal (c), grassland (d) and sunflower (e, f). The selected threshold (a value of OSR or sunflower flower cover estimated at the site scale or a value of honeybee abundance), those that minimized the AIC of the models (models 2 or models 3), is indicated by a red arrow. We tested thresholds conserving ≥ 30 observations by levels of the variables.

3. Appendix 3C. Estimation of honeybee abundance in field core

In 2015, only one 50m transect was performed in field core to estimate honeybee abundance, while two were performed from 2016 to 2019. With data from these four years, we run a linear model with honeybee abundance in the second transect explained by honeybee abundance in the first transect in field core. We found 63% of variation of honeybee abundance in the second transect to be explain by honeybee abundance in the first transect ($df = 1$; $F = 893.4$; $p < 0.001$; Fig. S3.5). From the relationships we predicted the honeybee abundance in the second transect in 2015 by those in the first transect in field core.

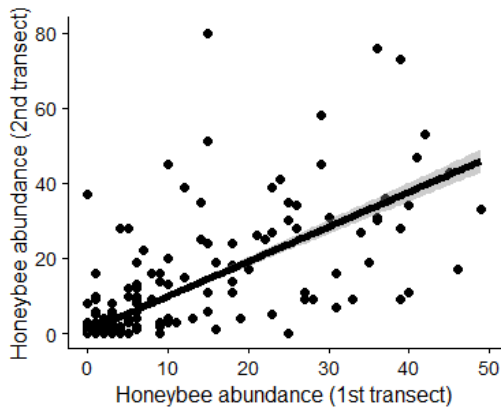


Fig. S3.5: Variation of honeybee abundance in the 2nd transect by the number of honeybees counted along the first transect in field core. Dots are observations data from 2016 to 2019, lines and shade area are the predicted relationship and the standard error.

4. Appendix 3D. Effects of weed abundance on wild pollinators varied between OF and CF cereal fields

17% of cereal fields were organically farmed (hereafter OF), while 83% were conventionally farmed (CF). Weed abundance was higher in OF (mean number of total weed species occurrence in the fields \pm sd: 651.30 ± 346.13) than in CF (186.90 ± 157.21). We explored if the effects of weeds on wild pollinators and its variation with the local, temporal, and spatial contexts was similar in OF and CF cereal fields. We added, at each step of the sequential analysis (see method) as an explanatory variable “farming system” with two levels (field in OF vs field in CF) and its interaction with all explaining variables of the models except covariables (cumulative degree days, and year).

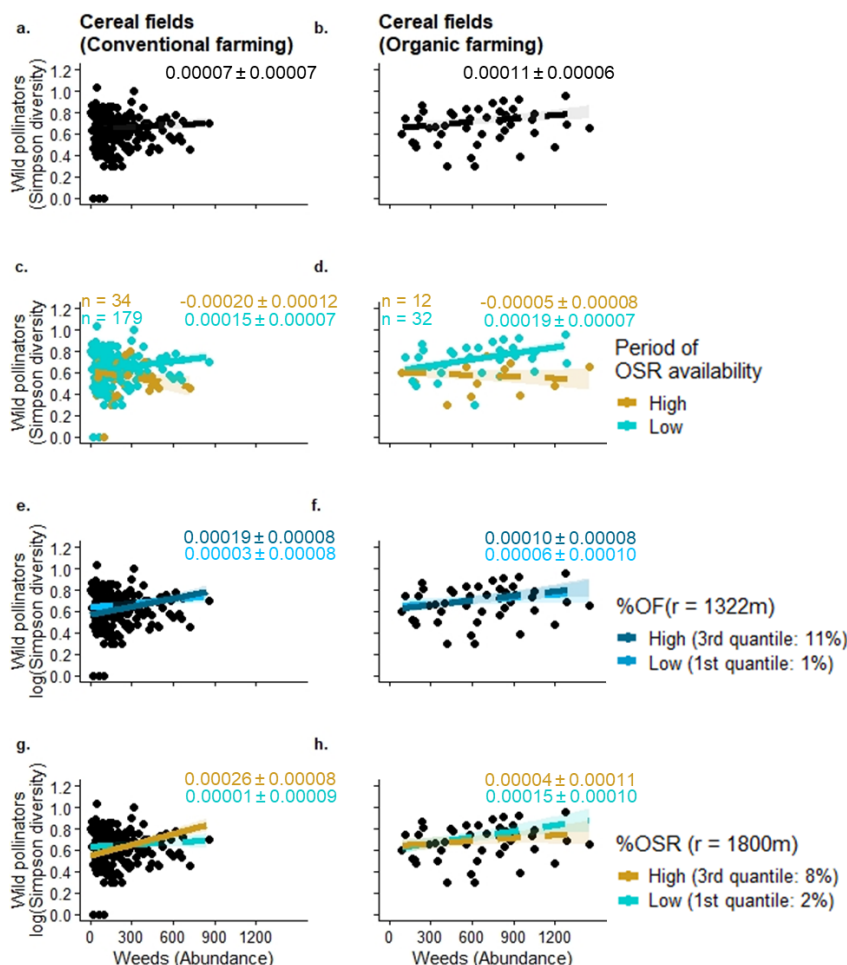


Fig. S3.6: Variation of the effects of weed abundance on wild pollinator diversity with farming system (conventional vs organic farming), Temporal matching with OSR flowering and with Landscape floral resource availability (%OF and %OSR). Slope \pm standard errors were estimated from models performed in step (i) (a and b), step iii (c and d) and step (iv) (e, f, g and h) by adding the variable Farming system in the model.

The first analysis (corresponding to model 1 in the statistical analysis in the main text) first revealed that farming system had no effect on wild pollinator diversity ($F = 0.53$; $p = 0.47$) and that the effect of weed abundance on wild pollinator diversity was similar in OF and CF (weed abundance \times farming system interaction: $F = 0.15$; $p = 0.71$; Fig. S3.6a, b). Similarly, the variation of the effect of weed abundance on wild pollinators with Temporal matching with OSR flowering was similar between CF and OF (model 3: weed abundance \times temporal matching with OSR flowering \times farming system: $F = 0.67$; $p = 0.51$; Fig. S3.6c, d). Finally (see step 4), we observed a significant effect of farming system on the effect of the interaction between “Landscape floral resource availability and weed abundance” on wild pollinator diversity. The effect of %OSR on “weed abundance – wild pollinator diversity” differed significantly between OF and CF cereal fields (Weed abundance \times %OSR \times farming system: $F = 4.57$; $p = 0.03$; Fig. S3.6g, h). Weed abundance had a positive effect on wild pollinator diversity when %OSR outside fields was high, but only in CF fields. Including farming system in the model also modified the results: the effect of weed abundance on wild pollinator diversity became non-significant possibly because the gradient of weed abundance was more restricted. However, our principal conclusion is unchanged: weed abundance maintained wild pollinator diversity in cereal fields in periods of lower availability of OSR, and when surrounded by a high amount of OF.

5. Appendix 3E. Effects of Landscape floral resource availability in OSR and cereals.

We detected a significant effect of Landscape floral resource availability in OSR and cereals directly in wild pollinator diversity. %SNH had significant effects on wild pollinator diversity in OSR ($F = 11.66$; $p < 0.001$) and n cereal ($F = 7.78$; $p < 0.01$), similarly the effects of %OSR were significant in OSR ($F = 5.32$; $p = 0.02$) and cereal ($F = 5.20$; $p = 0.02$). All effects were negative (Fig. S3.7).

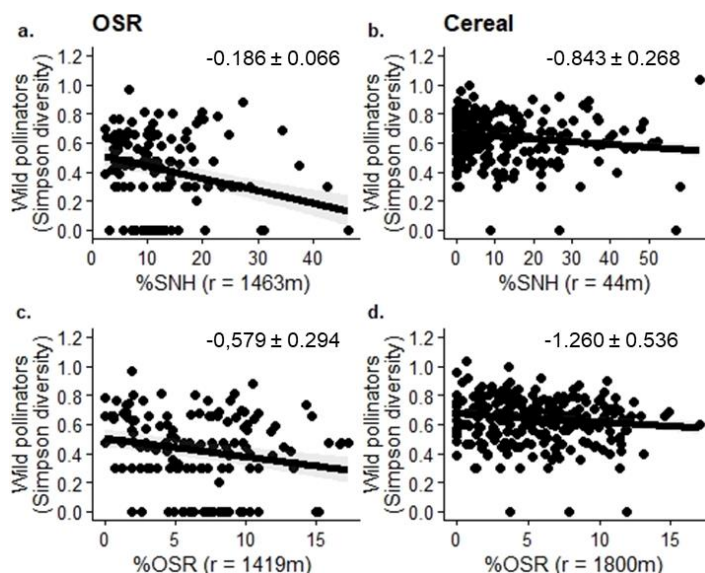


Fig. S3.7: Relationship between wild pollinator diversity and %SNH (a, b) and %OSR (c, d) in OSR (a, c) and cereal (b, d). The effect sizes (slopes \pm se) are estimated from models 4 (see section statistical analyses). Lines show significant relationship and r indicated the estimated scales of influence of landscape features.

6. Appendix 3F. Weeds diversity and abundance are highly correlated to dicotyledonous weeds diversity and abundance.

Weed community are composed of a diversity of species, more or less attractive to pollinators. We studied how the most entomophilous weeds (approximate through dicotyledonous weeds) were

correlated with all weeds (including non-entomophilous weeds) with correlations tests of Pearson by crop type and weed community index (Specific richness, Shannon diversity, Simpson diversity, and abundance). All indexes were highly correlated in all crop types (>0.90 ; Fig. S3.8). It highlighted that weed diversity and abundance was a good approximation of diversity and abundance of floral resource in the fields. However, more information is needed on the effects of weed diversity and abundance on the availability of floral resource in times (weed phenology).

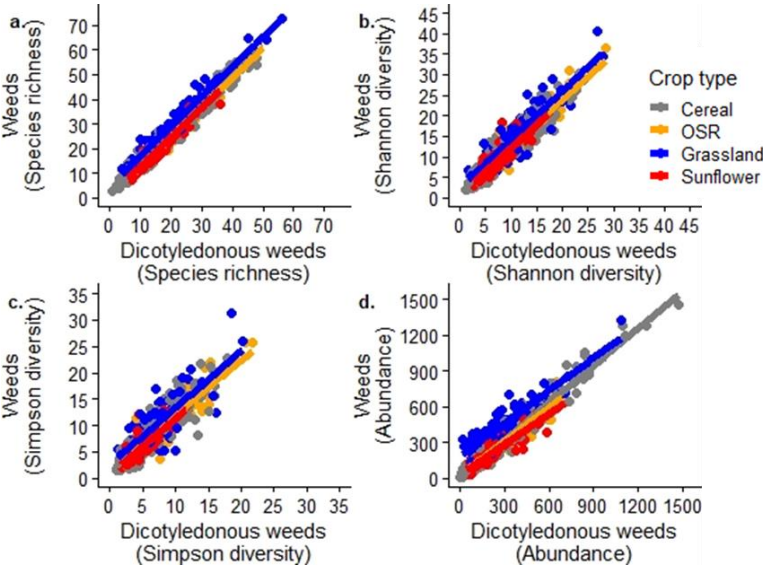


Fig. S. 3.8: Correlation between specific richness (a.), Shannon diversity (b.), Simpson diversity (c.) and abundance (d.) of weeds (comprising dicotyledonous and monocotyledonous weeds) and dicotyledonous weeds in cereal, OSR, grassland and sunflower.

IV. Communications orales pendant la thèse

1. *How do landscape and local factors affect insect-pollination efficiency in oilseed rape phytometers?*
International conference on ecological sciences - SFE (25 octobre 2018 - Rennes).

Maxime Ragué, Vincent Bretagnolle, Olivier Martin, Thomas Perrot, Jean-Luc Gautier, Florence Carpentier, Sabrina Gaba

2. *Spatial & temporal dynamics of pollination success in the LTSER “Zone Atelier Plaine & Val de Sevre”: the case of oilseed rape.*

Journées des doctorants - Département Santé des plantes et environnement INRAE (21 mai 2019, Rennes).

Maxime Ragué, Vincent Bretagnolle, Olivier Martin, Thomas Perrot, Jean-Luc Gautier, Florence Carpentier, Sabrina Gaba

3. *Influence of honeybee and flowering crops on the dependence of wild pollinators to weeds.*

Ecology and Agriculture Summit for Young Scientists (26 novembre 2019, Nice).

Maxime Ragué, Florence Carpentier, Olivier Martin, Sabrina Gaba

4. *Les plantes adventices participent au maintien des pollinisateurs sauvages dans les paysages agricoles.*

5ème édition du colloque des Zones Ateliers (4 novembre 2020, visioconférence).

Maxime Ragué, Florence Carpentier, Olivier Martin, Sabrina Gaba

5. *Le maintien des insectes pollinisateurs par les plantes sauvages dans les paysages agricoles.*

Colloque des doctorants de 2ème et 3ème année (24 septembre 2021, La Rochelle).

Maxime Ragué, Florence Carpentier, Olivier Martin, Sabrina Gaba

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RESUME

Dynamiques spatiale et temporelle des paysages agricoles : conséquences sur les interactions plantes-pollinisateurs et la pollinisation

Résumé :

Le maintien des insectes pollinisateurs en milieu agricole est essentiel car ils pollinisent les plantes sauvages et cultivées, il peut reposer sur l'augmentation de la disponibilité des ressources florales. Les cultures à floraison massive (CFM) fournissent des ressources abondantes et de façon discontinue dans le temps, au contraire des prairies et des plantes adventices présentes dans les cultures. Cet aspect temporel a été peu étudié alors que les paysages agricoles sont caractérisés par une dynamique temporelle importante du fait des successions culturales. L'objectif de la thèse est de comprendre l'effet de la distribution spatiale et temporelle des ressources florales dans les paysages agricoles sur les interactions plantes-pollinisateurs et la pollinisation.

Nous montrons que les CFM au pic de floraison attirent les pollinisateurs sauvages des prairies et l'abeille domestique et supportent ainsi la fonction de pollinisation à cette période. Au sein des CFM, l'abeille domestique consomme les ressources fournies par les cultures préférentiellement en bordure de parcelle, et semble exclure les pollinisateurs sauvages des fleurs cultivées ceux-ci sont alors maintenus par les plantes adventices. A la fin de la floraison des CFM, les pollinisateurs dispersent vers les prairies et les céréales qui supportent ainsi la pollinisation. A cette période, les plantes adventices à travers leur abondance dans les céréales, et leur diversité dans les prairies supportent les pollinisateurs sauvages.

La persistance des pollinisateurs et de la pollinisation dans les paysages agricoles, repose sur (i) le maintien des prairies et des plantes adventices qui assurent la continuité spatio-temporelle de la disponibilité en ressources florales, (ii) les CFM qui supplémentent les paysages en ressources florales, et (iii) la réduction de la taille des parcelles qui facilite l'accès aux ressources florales. Ces mesures sont compatibles avec la production agricole.

Mots clés : Abeille domestique | Continuité des ressources | Composition du paysage | Cultures à floraison massive | Habitats semi-naturels | Pollinisateurs sauvages | Plantes adventices

Spatial and temporal dynamics of agricultural landscapes: consequences on plant-pollinator interactions and pollination

Summary:

Maintaining insect pollinators in farmland is essential for ensuring the pollination of crops and wild plants. This partly relies on the increase of floral resource availability. Mass flowering crops (MFC) provide a high amount of resources, but on a short period of time contrary to grasslands or weeds sheltered in fields. This temporal aspect is rarely studied, although it might be crucial in the maintenance of pollinators and insect pollination over the season. The aim of the thesis is to understand how the spatial and temporal distribution of the floral resources in farmland influence plant-pollinator interactions and pollination.

Our results indicate that MFC at their peak flowering period, attract wild pollinators from grasslands and the honeybee; thus, supporting the pollination function. Within MFC, the honeybee preferentially consumes floral resources provided by crops, and may exclude wild pollinators from crop flowers which therefore foraged on weeds. After MFC flowering, pollinator insects spillover to grasslands and cereals which support pollination. Weeds, through their diversity in grasslands, and through their abundance in cereals support wild pollinators at this time period.

The persistence of pollinators and pollination in farmland landscapes is based on (i) the maintenance of grasslands and weeds that ensure the spatio-temporal continuity of floral resources, (ii) MFC that supplement the landscapes in floral resources, and (iii) the reduction of field size that facilitates the access to the floral resources. Such measures appear to be compatible with crop production.

Keywords: Honeybee | Landscape composition | Mass flowering crop | Resource continuity | Semi natural habitats | Weeds | Wild pollinators

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