



HAL
open science

Du suivi des pollinisateurs et de leurs interactions au service de pollinisation en milieu agricole : influence des champs cultivés

Ludovic Crochard

► To cite this version:

Ludovic Crochard. Du suivi des pollinisateurs et de leurs interactions au service de pollinisation en milieu agricole : influence des champs cultivés. Sciences de l'environnement. Museum national d'Histoire naturelle, 2023. Français. NNT: . tel-04694516

HAL Id: tel-04694516

<https://hal.science/tel-04694516v1>

Submitted on 11 Sep 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NoDerivatives 4.0 International License



MUSEUM NATIONAL D'HISTOIRE NATURELLE
Ecole Doctorale Sciences de la nature et de l'Homme – ED 227

Année 2023

N°attribué par la bibliothèque

□□□□□□□□□□

THESE

Pour obtenir le grade de

DOCTEUR DU MUSEUM NATIONAL D'HISTOIRE NATURELLE

Spécialité : Sciences écologiques et agronomiques

Présentée et soutenue publiquement par

Ludovic Crochard

Le 20 janvier 2023

**Du suivi des pollinisateurs et de leurs interactions au service de
pollinisation en milieu agricole : influence des champs cultivés**

Sous la direction de : **Romain Julliard, Mathilde Baude et Colin Fontaine**

JURY :

Mme. Emmanuelle Baudry	Professeure, Université Paris-Saclay, UMR 8079 Ecologie, Systématique et Evolution, Gif sur Yvette	Rapportrice
M. Mickaël Henry	Chargé de Recherche, Institut national de recherche pour l'agriculture, l'alimentation et l'environnement, UR 406 Abeilles et Environnement, Avignon	Rapporteur
Mme. Audrey Alignier	Chargée de Recherche, Institut national de recherche pour l'agriculture, l'alimentation et l'environnement, UMR Biodiversité, Agroécologie et Aménagement du Paysage	Examinatrice
Mme. Isabelle Dajoz	Professeure, Université de Paris, UMR 7618 Institut d'Ecologie et des Sciences de l'Environnement, Paris	Présidente du jury
M. Bertrand Schatz	Directeur de Recherche, Centre National de la Recherche Scientifique, UMR 5175 Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier	Examinateur
M. Romain Julliard	Professeur, Muséum national d'Histoire naturelle, UMR 7204 Centre d'Ecologie et des Sciences de la Conservation, Paris	Directeur de thèse
Mme. Mathilde Baude	Maître de Conférences, Université d'Orléans, UMR 7618 Institut d'Ecologie et des Sciences de l'Environnement, Paris	Directrice de thèse
M. Colin Fontaine	Chargé de Recherche, Centre National de la Recherche Scientifique, UMR 7204 Centre d'Ecologie et des Sciences de la Conservation, Paris	Directeur de thèse

A ma famille, mes amis,

Remerciements

Tout d'abord merci à **Audrey Alignier, Emmanuelle Baudry, Isabelle Dajoz, Mickaël Henry** et **Bertrand Schatz** d'avoir accepté de faire partie de mon jury de thèse et d'évaluer mes travaux.

Romain je te remercie d'avoir suivi mon travail. Merci pour tes conseils et pour tes réflexions qui ont permis de faire avancer ma thèse.

Colin et **Mathilde** je vous remercie infiniment de m'avoir encadré avec patience et bienveillance. Merci de m'avoir fait confiance pour réaliser ce travail de thèse mais aussi de M2. Votre complémentarité était très agréable pour travailler. Merci pour votre disponibilité, y compris quand j'étais sur le terrain, l'ensemble de vos conseils qui m'ont permis de progresser tout au long de ces trois années. Merci d'avoir pris le temps de répondre à toutes mes questions. **Colin** merci de m'avoir poussé lors de certaines réunions ça m'aura bien fait progresser. **Mathilde** merci de m'avoir fait découvrir le monde de l'écologie lors de ce premier cours lors de ma première année de licence à l'université d'Orléans, c'est grâce à toi que je suis parti dans cette voie.

Yves merci pour ton aide pour la mise au point de la méthode acoustique et d'avoir pris le temps de m'expliquer comment fonctionne les logiciels.

Merci à **Sabrina Gaba, Nathalie Machon, Oriane Rollin** et **Elisa Thébault** d'avoir fait partie de mon comité de suivis de thèse. Merci pour l'ensemble des conseils que vous m'avez apporté.

Merci à l'ensemble des personnes que j'ai rencontré à Chizé durant mes sessions de terrain. On en aura tous bien bavé mais on se sera bien marré quand même. Merci **Jean-Luc** pour toute ton aide sur le terrain et au labo, il paraît qu'on formait la paire de grognons. Merci **Claire G., Alexis** et **Claire L.** d'être venu m'aider sur le terrain notamment avec notre chère amie, la barre à mine. Merci **Adrien, Claire G., Claire L., Lucas** (alias « Chatoune ») **Corneille** et **Bernie** (faites gaffe la prochaine fois que vous roulez dans les chemins), **Alexis, Thomas, Alicia** et **Hugo** pour les superbes journées

passées au camping pendant les week-ends.

Merci au **CESCO et à tous ses membres** pour ces presque quatre années. Merci pour les moments tous les bons moments passés.

Merci à l'ensemble de mes co-bureau qui se sont succédés au cours de ces trois années **Zheng, Loubna, Irene, Fatma, Martin, Marie.**

Merci à l'ensemble des habitants du 135, **Alice, Robin, Adrienne, Clémentine, Milena, Charles, Anne-Christine, Camille, Clément, Jeannot, Perrine, Romain, Simon, Greg, Marine, Jérôme, Vincent, Diane, Baptiste, Nora, Suzanne, Anne, Benoit, Lise** et **Nelly** (nos deux expatriées du 61) pour tous ces moments à la cantine et pendant les pauses café.

Merci aux doctorants de Concarneau **Fabien, Camille** et **Léa**, pour ces supers moments passés quand vous veniez à Paris. J'ai hâte de vous revoir. Merci aux autres doctorants du Museum, **Inessa, Alicia, Charly, Gaspard, Nicolas** pour les soirées et les apéros.

Mathilde, Martin, Charles, Marie, Marine, merci de m'avoir prêté main forte ces derniers jours pour les dernières relectures.

Clément et **Jeannot** merci pour votre bonne humeur et vos conseils stats. Clément merci pour ce séjour à Grenoble c'était bien sympa. Jeannot (alias « FufuFau ») merci pour nos parties de MarioKart le midi, il va falloir qu'on s'y remette.

Lise et **Mathilde** un grand merci pour votre sourire et votre bonne humeur. Merci pour les séances ciné. Lise merci pour ta recette de mousse au chocolat, au final elle est vraiment bonne. Mathilde un grand merci pour ton soutien moral au cours de ces derniers mois et surtout ces dernières semaines qui m'aura été d'une grande aide. Merci aussi pour tes conseils stats.

Merci à tous mes amis du tir à l'arc : **Vincent, Sandra, Ludo, Sophie, Aurore, Jean-Phi, Jean-Claude, JP, Camille, Jordan, Franck, José, Lucas, Marie** pour tous les

moments conviviaux qui m'ont permis de me resourcer. Merci à **Thomas** et **Pascalou** pour nos repas du samedi midi à discuter tir à l'arc. **Ferdinand** merci d'avoir toujours été là pour faire des sorties et discuter de tout et de rien, heureusement qu'on a fait la fac de bio plutôt que de médecine finalement.

Maxou merci d'avoir été mon binôme sur le terrain et ce même si cette période n'a pas été simple, entre les galères, nos humeurs massacrant certains jours. Merci de m'avoir hébergé lorsque les logements de Chizé étaient fermés. Je me souviendrais toujours de notre rencontre, une journée hors norme de mars 2020 alors que l'incertitude planait sur la possibilité de faire le terrain à cause de la pandémie, on se faisait une soirée console chez toi en attendant les annonces. Juste après les annonces, la visio la plus mémorable de ma thèse avec **Mathilde** et **Colin** pour décider de la suite. Au final, un abandon de la manip mais heureusement, ce n'était que partie remise. Encore un grand merci pour tous ces moments. J'ai hâte de passer te voir lorsque tu te seras installé dans ton nouveau projet.

Enfin, je remercie **toute ma famille** pour leur soutien et leur intérêt pour mon travail. **Maman, Papa**, merci de m'avoir toujours soutenu dans mes choix et d'avoir veillé à ce que j'aie toujours bien. **Rachou** merci pour ton soutien sans faille pendant ces trois années, nos week-ends d'évasion qui m'ont permis de me changer les idées. Merci d'avoir été présente à chaque instant, notamment d'avoir passé le deuxième confinement dans mon 12m² à Paris. Merci pour tout ce que tu m'as apporté.

Résumé

La pollinisation par les animaux est essentielle pour la production de 70% des cultures mondiales. Cette contribution aux rendements des cultures est souvent associée à la diversité et à l'abondance des pollinisateurs au sein des cultures. Diversité et abondance des pollinisateurs sont souvent impactées par le paysage qui, en fonction de sa composition, fournit des quantités de ressources florales qui varient spatialement et temporellement. Malgré la prédominance des champs cultivés dans les systèmes agricoles, l'impact des facteurs paysagers liés aux champs cultivés reste assez peu documenté contrairement aux habitats semi-naturels. De plus, le cycle de vie des pollinisateurs suggère que les effets du paysage peuvent se répercuter d'une année sur l'autre. L'objectif général de cette thèse est d'étudier les liens entre effets des champs cultivés, suivi des pollinisateurs et service de pollinisation des cultures. Ce travail repose sur l'analyse de réseaux d'interactions plantes-pollinisateurs et le développement d'une méthode de suivi acoustique des pollinisateurs pour étudier le service de pollinisation et les mécanismes sous-jacents.

Dans un premier temps, nous avons quantifié la contribution de différentes ressources florales des champs cultivés de l'année précédente au service de pollinisation du colza. Nous montrons que le colza dépend en majorité des autres ressources florales plutôt que de lui-même pour le maintien des espèces de pollinisateurs délivrant le service de pollinisation. La contribution de la flore adventice des cultures est au moins aussi importante que celle provenant des cultures à floraison massive. La majeure partie de cette contribution provient des adventices présentes au sein des parcelles des céréales, habituellement négligées dans les études sur le service de pollinisation. Dans un deuxième temps, nous avons cherché à déterminer si le suivi acoustique des pollinisateurs pouvait être une méthode permettant d'étudier le service de pollinisation du tournesol. Nous montrons que l'apprentissage profond semble être la méthode d'apprentissage machine la plus efficace pour reconnaître le son émis par les pollinisateurs et que la méthode de suivi acoustique des pollinisateurs donne des informations en adéquation avec la littérature sur la biologie des pollinisateurs. Nous

démontrons également que cette méthode de suivi des pollinisateurs, de par sa continuité temporelle, permet de s'affranchir de certains biais inhérents aux méthodes classiques et permet ainsi de mettre en évidence des effets paysagers subtils.

En conclusion, notre travail permet de souligner l'importance des champs cultivés dans le cadre des études sur le service de pollinisation. Nous démontrons que des modifications de l'assolement et de pratiques au sein des champs cultivés, y compris dans les champs dont les cultures ne dépendent pas des pollinisateurs, peuvent avoir un impact important sur le service de pollinisation des cultures. Bien que de nombreux développements techniques et méthodologiques restent à mettre au point, nous montrons que le suivi acoustique est une méthode prometteuse pour le suivi des pollinisateurs dans le cadre des études sur le service de pollinisation. Enfin, nous discutons des liens entre les proxys de pollinisation issus des suivis de pollinisateurs et le service de pollinisation.

Mots clés : Service de pollinisation, Champs cultivés, Ressources florales, Adventices des cultures, Suivi acoustique passif, Apprentissage profond

Abstract

Animal pollination is essential for the production of 70% of the world's crops. This contribution to crop yields is often associated with the diversity and abundance of pollinators within crops. Pollinator diversity and abundance are often impacted by the landscape, which, depending on its composition, provides spatially and temporally varying amounts of floral resources. Despite the predominance of cultivated fields in agricultural systems, the impact of landscape factors related to cultivated fields remains relatively undocumented, unlike semi-natural habitats. In addition, the life cycle of pollinators suggests that landscape effects can be carried over from year to year. The overall objective of this thesis is to investigate the links between cultivated field effects, pollinator monitoring and crop pollination services. This work is based on the analysis of plant-pollinator interaction networks and the development of an acoustic pollinator monitoring method to study the pollination service and the underlying mechanisms.

First, we quantified the contribution of different floral resources from the previous year's cultivated fields to the pollination services of oilseed rape. We show that oilseed rape depends mostly on other floral resources rather than on itself for the maintenance of pollinator species delivering the pollination services. The contribution of crop weeds is at least as important as that from mass-flowering crops. Most of this contribution comes from weeds within cereal fields, which are usually neglected in pollination services studies. In a second step, we investigated whether acoustic pollinator monitoring could be a method to study the pollination services of sunflower. We show that deep learning appears to be the most effective machine learning method for recognizing the sound emitted by pollinators and that the acoustic pollinator monitoring method provides information consistent with the literature on pollinator biology. We also demonstrate that this method of monitoring pollinators, because of its temporal continuity, allows to get rid of some biases inherent to classical methods and thus allows to highlight subtle landscape effects.

In conclusion, our work highlights the importance of cultivated fields in

pollination services studies. We demonstrate that changes in cropping patterns and practices within cultivated fields, including fields where crops are not pollinator-dependent, can have a significant impact on the pollination services of crops. Although many technical and methodological developments remain to be developed, we show that acoustic monitoring is a promising method for monitoring pollinators in pollination services studies. Finally, we discuss the links between pollination proxies from pollinator monitoring and pollination services.

Keywords: Pollination services, Cultivated fields, Floral resources, Crop weeds, Passive acoustic monitoring, Deep learning

Sommaire

Remerciements	4
Résumé	8
Abstract.....	10
Introduction générale	1
La fonction écologique de pollinisation	5
1. La pollinisation	5
2. La pollinisation en tant que service écosystémique	7
a) Le service de pollinisation dans les milieux agricoles	7
b) Les insectes pollinisateurs des milieux agricoles	10
3. Le déclin des pollinisateurs et les facteurs associés au milieu agricole.....	11
a) L'importance des cultures à floraison massive	13
b) La destruction des habitats.....	14
c) Les pesticides	14
4. Le suivi des pollinisateurs en milieu agricole	16
a) Les méthodes classiques	16
b) Les nouvelles méthodes disponibles	18
Problématique et objectifs	21
Chapitre 1 : Les adventices des cultures non fleuries comme contributeurs potentiels à la pollinisation du colza	25
Abstract.....	27
Introduction	28
Material and methods	31
Site description and fields selection	31
Sampling method.....	32
Visitation frequencies per square meter of crop fields.....	33
Potential for inter-annual indirect effect from floral resources to oilseed rape pollination	33
Statistical analyses	36
Results.....	37
Pollinators are shared among crops and weeds.....	37
The support of oilseed rape pollinators is mainly provided by floral resources other than oilseed rape	37
The support of oilseed rape pollinators provided by weeds and flowering crops is equivalent	38

The dominance of cereal fields makes cereal weeds a key resource for oilseed rape pollinating fauna	39
Discussion.....	41
Conclusion.....	43
Acknowledgments.....	44
Supplementary.....	45
Appendix A.....	53
References	54
Chapitre 2 : Quantification de l'activité des abeilles dans les champs de tournesol à l'aide du suivi acoustique et de l'apprentissage profond.....	63
Buzzy bees, quantifying bee activity within sunflower fields using acoustic monitoring and deep learning	65
Abstract.....	65
Introduction	66
Material & Methods.....	69
a) Site description	69
b) Acoustic records.....	69
c) Relationship between pollinator activity estimated by audio recording and visual observations .	73
d) Daily activity of pollinators estimated by audio recording	74
Results.....	75
1. Comparison of convolutional neural networks and random forest classifiers for pollinator acoustic monitoring	75
2. Relationship between pollinator activity estimated by audio recording and visual observations	77
3. Daily activity of the honeybee estimated by audio recording.....	78
Discussion.....	79
Acknowledgments.....	83
Author contributions	83
Supplementary.....	83
Appendix A - Setting up the audiomoths.....	83
References	86
Chapitre 3 : L'acoustique pour améliorer le suivi des pollinisateurs et la détection de l'influence du paysage sur leur activité	95
Abstract.....	97
Introduction	98

Material and Methods	101
a) Site description and sunflower fields selection	101
B. Monitoring pollinator activity	102
C. Estimating pollinator contribution to sunflower yield.....	103
D. Statistical analyses.....	104
Results.....	106
Discussion.....	111
Conclusion.....	113
Acknowledgments.....	114
Author contributions	114
Supplementary.....	115
References	117
Discussion générale	127
Effet de l'assolement des espaces cultivés sur le service de pollinisation	127
Le suivi acoustique passif : une méthode efficace pour suivre l'activité des pollinisateurs au sein des cultures	129
Le service de pollinisation : quelles méthodes pour l'évaluer ?	133
Perspectives	135
Références	137

Introduction générale

Actuellement, le monde est confronté à la sixième extinction de masse de la biodiversité (Barnosky et al., 2011; Ceballos et al., 2015; Pimm et al., 2014). L'Union Internationale pour la Conservation de la Nature a montré qu'au moins 680 espèces de vertébrés se sont éteintes depuis 1500. Aujourd'hui, ce sont près de 41 000 espèces de plantes et d'animaux qui sont menacées d'extinction, soit 28% des espèces évaluées à l'échelle mondiale (UICN 2022, version 2022.1). L'ensemble des groupes taxonomiques sont donc concernés par ce déclin, et même si le niveau de menace varie selon les groupes, on observe une détérioration progressive de leur état de conservation sur les dernières décennies (UICN 2022 et Fig.1a). En observant la tendance globale des abondances relatives des populations d'espèces sauvages, ce déclin apparaît encore plus alarmant. Entre 1970 et 2018, l'Indice Planète Vivante mondial, qui vise à mesurer les changements temporels d'état de la biodiversité par rapport à 1970, montre un déclin moyen de 69% des populations de vertébrés sauvages (WWF 2022, Fig.1b).

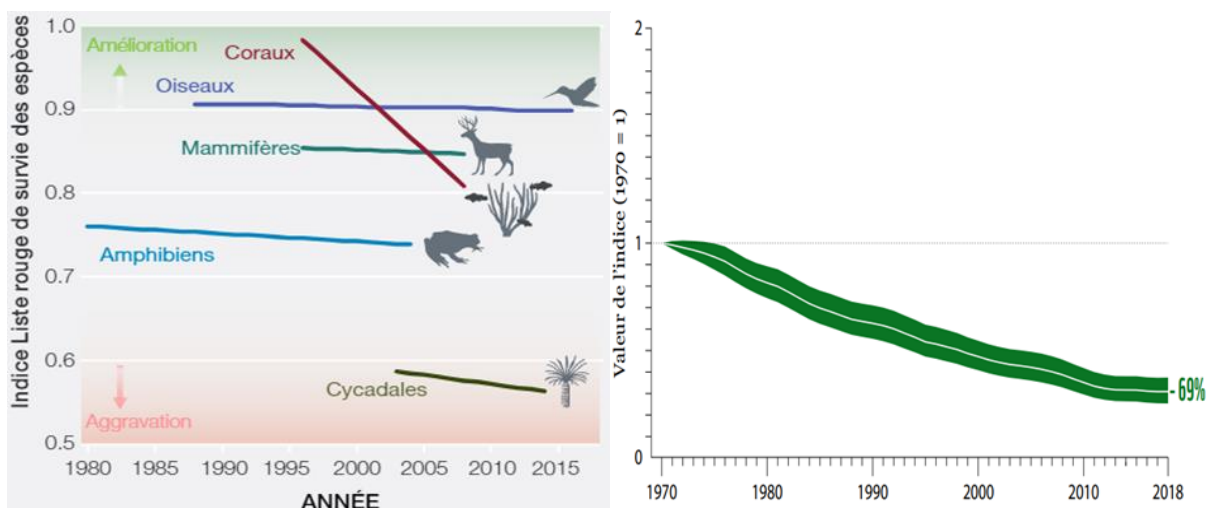


Figure 1 - a) Indice Liste rouge pour les groupes taxonomiques qui ont été évalués. Une valeur de 1 signifie que toutes les espèces du groupe taxonomique sont classées dans la catégorie "Préoccupation mineure". Une valeur de 0 signifie que l'ensemble des espèces est classé dans la catégorie "Eteint". b) Evolution de l'Indice Planète Vivante mondial de 1970 à 2018. Sources : a) Union Internationale pour la Conservation de la Nature ; b) WWF/ZSL (2022)

Face au constat de l'érosion massive de la biodiversité, la Plateforme Intergouvernementale scientifique et politique sur la Biodiversité et les Services Écosystémiques (IPBES) a produit en 2019 une évaluation mondiale permettant de mieux comprendre les tendances de biodiversité, leur impact sur les sociétés et les causes de ce déclin. La synthèse des travaux scientifiques démontre bien que ce déclin a pour origine les activités humaines. Le facteur ayant le plus d'impact varie en fonction du type de milieu, mais pour le milieu terrestre, le premier facteur responsable de ce déclin est le changement d'usage des sols et la fragmentation des habitats (IPBES, 2019). En cause notamment l'expansion des terres agricoles qui occupent environ 40% du territoire européen, 50% du territoire français (Chatellier and Delame, 2007; Néron, 2018). Parmi les causes de ce déclin, on trouve également la surexploitation, les pollutions, l'introduction d'espèces envahissantes et le changement climatique (Maxwell et al., 2016).

Au sein des écosystèmes, les espèces sont en interaction constante avec le biotope et les organismes vivants constituant la biocénose. Ces multiples interactions sont à l'origine de nombreuses fonctions écologiques qui bénéficient à la qualité de vie de l'espèce humaine. Or, par ses activités, l'espèce humaine provoque la disparition des espèces sauvages et de leurs interactions, entraînant une détérioration du fonctionnement des écosystèmes et donc la perte des services rendus par la nature dont les sociétés humaines dépendent. En 2005, l'Évaluation des Écosystèmes pour le Millénaire (MEA 2005) a classé ces services écosystémiques en différentes catégories selon les bénéfices qu'ils apportent aux sociétés humaines : les services de "support ou de soutien" assurent le bon fonctionnement de la biosphère et intègrent par exemple le cycle de la matière ou de l'eau ; les services "d'approvisionnement ou de production" sont les produits issus des écosystèmes comme les aliments, les combustibles et les médicaments ; les services de "régulation" permettent de moduler les phénomènes naturels comme l'érosion ou la pollinisation ; les services "culturels" permettant l'enrichissement éducatif et spirituel (Fig.2).

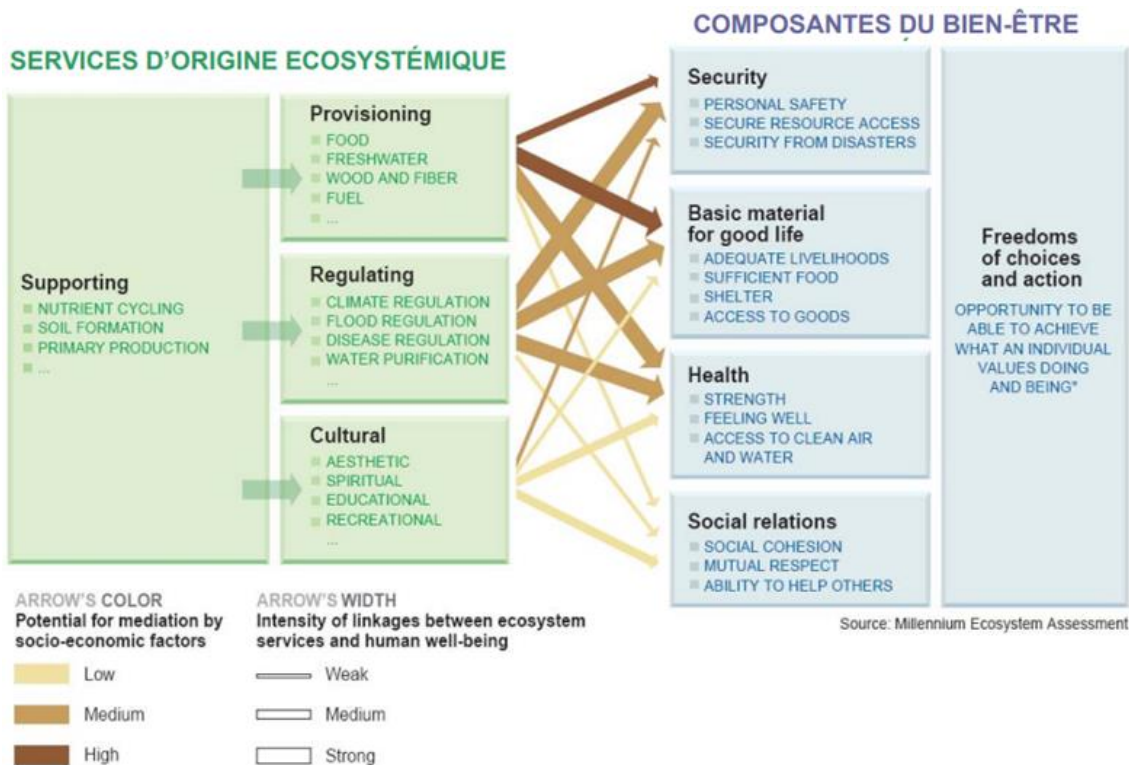


Figure 2 - Liens entre services écosystémiques et bien-être humain. Les flèches représentent les liens courant entre les services écosystémiques et les composantes du bien-être humain. Leur épaisseur représente l'intensité du lien et leur couleur le degré d'intervention possible de facteurs sociaux-économiques. Source : Evaluation des Ecosystèmes pour le Millénaire (MEA 2005)

L'approche développée par l'IPBES intègre cette notion de services écosystémiques dans le contexte plus englobant des contributions de la nature aux populations (Díaz et al., 2018). Des travaux de synthèse ont montré que ces contributions de la nature à la qualité de vie humaine sont aujourd'hui directement menacées par le déclin de la biodiversité (Díaz et al., 2019). Bien que certains ouvrages techniques humains tentent de remplacer certaines de ces contributions, ils sont bien souvent imparfaits et coûteux (IPBES, 2019) et pour certaines contributions, comme la production d'oxygène par les plantes, aucun substitut n'existe.

Ainsi, en raison des services que fournit la nature aux sociétés humaines grâce aux fonctions écologiques générées par les interactions au sein des communautés d'être-vivants, il apparaît essentiel de protéger la biodiversité (Mace, 2014). Néanmoins, cette vision reste très anthropocentrée. Or, ces services sont pour certains assurés par un petit nombre d'espèces qui ne sont pas menacées (Kleijn et al., 2015).

Ainsi, l'un des arguments essentiels qui devrait être pris en considération pour la conservation de la biodiversité est la valeur intrinsèque de chaque espèce. Afin de mettre en place des processus efficaces visant à protéger la biodiversité, il est nécessaire de comprendre le fonctionnement des écosystèmes et donc d'étudier les fonctions écologiques qui s'y déroulent. Dans la suite de ce travail, nous nous intéresserons au service et à la fonction écologique de pollinisation.

La fonction écologique de pollinisation

1. La pollinisation

La pollinisation correspond au transfert des grains de pollen des pièces reproductrices mâles (les étamines, composées de filets et d'anthers) d'une fleur jusqu'aux pièces reproductrices femelles (le pistil, composé de l'ovaire, du style et des stigmates) d'une même fleur ou d'une autre fleur compatible. Une fois déposé sur le stigmate, le pollen entre en germination et donne un tube pollinique qui s'allonge le long du style et qui permet aux deux gamètes mâles de rejoindre le sac embryonnaire. L'un des gamètes mâles féconde alors l'oosphère (gamète femelle) pour donner l'embryon et l'autre fusionne avec les noyaux polaires pour donner l'albumen qui servira de tissu de réserve à l'embryon. Après le développement de l'embryon, il en résulte une graine qui dans certains cas sera protégée par un fruit (Fig.3).

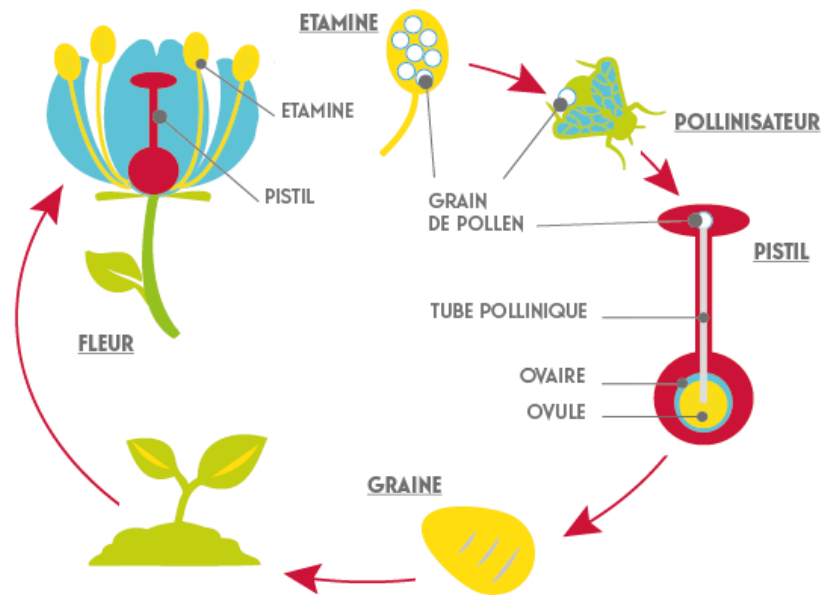


Figure 3 - Cycle de vie d'une plante à fleur entomogame. Source: <https://www.insectes.org/content/37-ils-pollinisent>, consulté le 09/11/2022.

Chez les Angiospermes, 75% des espèces sont hermaphrodites (Chapman and

Reiss, 1992), c'est-à-dire que leurs fleurs possèdent à la fois les pièces reproductrices mâles et femelles. Pour ces espèces, le transfert de pollen peut ainsi se faire au sein d'une même fleur, on parle alors d'autopollinisation. Toutefois, il est nécessaire que ces espèces soient auto-compatibles. En effet, pour certaines espèces, il existe des mécanismes et des adaptations morphologiques ou temporelles pouvant empêcher l'adhésion du grain de pollen ou encore la formation du tube pollinique ce qui entraîne une auto-incompatibilité de ces espèces (Bateman, 1952). Parmi les 25% d'Angiospermes restants, on pourra trouver des plantes possédant à la fois des fleurs femelles et des fleurs mâles sur le même individu (espèce monoïque) ou bien des espèces pour lesquelles les individus seront composés uniquement de fleurs femelles ou uniquement de fleurs mâles (espèce dioïque).

L'autopollinisation n'étant pas obligatoire, voire impossible pour de nombreuses espèces de plantes, il existe une autre forme de pollinisation nécessitant le transfert du pollen entre individus via un vecteur biotique ou abiotique, l'allopollinisation ou pollinisation croisée. Ce type de pollinisation, favorisant le brassage génétique, peut faire intervenir une grande diversité de vecteurs. Le pollen pourra, ainsi, être transporté par le vent (pollinisation anémophile), l'eau (pollinisation hydrophile) ou encore par des animaux (pollinisation zoophile). Il a été estimé qu'environ 87,5% des Angiospermes, soit 310 000 espèces, ont recours à la pollinisation zoophile (Ollerton et al., 2011). L'animal vient généralement se nourrir des ressources mises à disposition par les fleurs (nectar et/ou pollen) (Willmer, 2011) transportant alors le pollen avec lui lors de ses déplacements de fleurs en fleurs. Le nombre d'espèces visitant les fleurs et étant de potentiels pollinisateurs est estimé entre 130 000 et 300 000 (Buchmann and Nabhan, 1996; Kearns et al., 1998). Parmi ces espèces on trouve essentiellement des insectes mais aussi des oiseaux, des mammifères tels que des chauves-souris ou encore quelques espèces de reptiles. En Europe, la pollinisation zoophile est quasi exclusivement réalisée par les insectes pollinisateurs.

Certains auteurs considèrent que les interactions plantes-pollinisateurs tendent vers un système spécialiste. En effet, les plantes possèdent des traits pouvant être plus

ou moins attractifs pour les insectes pollinisateurs (Dafni, 1992; Kearns and Inouye, 1993). Ces traits sont le fruit d'une coévolution plus ou moins étroite entre les plantes et les pollinisateurs qui à mesure de leur apparition réduisent l'accès à une grande diversité de pollinisateurs pour s'y nourrir. Le cas le plus extrême est celui où une seule espèce de pollinisateur ne peut butiner qu'une seule espèce de plante. L'exemple le plus célèbre de ce niveau de spécialisation est celui prôné par Darwin (1862) entre l'orchidée *Angraecum sesquipedale* et son sphinx *Xanthopan morgani praedicta*. Néanmoins, cette vision d'une spécialisation des interactions plantes-pollinisateurs a été remise en cause par différents auteurs (Ollerton et al., 2009; Waser et al., 1996). Waser et al., (1996) ont notamment démontré un généralisme important des interactions plantes-pollinisateurs qui se structurent alors en réseau. Ces réseaux d'interactions plantes-pollinisateurs sont bipartites (deux compartiments de niveaux trophiques différents) et constitués de nœuds représentant les plantes et les pollinisateurs reliés par des liens. Le degré de généralisme d'une espèce de pollinisateur peut ainsi être évalué par le nombre de liens entre elle et les plantes du réseau (Bascompte and Jordano, 2007).

2. La pollinisation en tant que service écosystémique

La pollinisation est souvent assimilée à un service de "régulation" (FAO, 2022) puisqu'en permettant la reproduction des végétaux, elle permet à la fois le maintien de la diversité végétale et animale, via l'apport de ressources consommées par des niveaux trophiques supérieurs, mais aussi la structuration des sols et la captation du CO₂. De plus, ces plantes produisent des fruits, des graines ou de la matière organique qui peuvent servir à la confection de médicaments, de matériaux de construction, d'alimentation pour l'espèce humaine, ce qui fait que la pollinisation participe au service "d'approvisionnement".

a) Le service de pollinisation dans les milieux agricoles

Dans les milieux agricoles, la pollinisation de 70% des plantes cultivées dépend des pollinisateurs et représente 35% de la production agricole mondiale annuelle

(Klein et al., 2007). Cette dépendance aux pollinisateurs varie en fonction de l'espèce cultivée, notamment en fonction de leur tolérance à l'auto-fécondation (Klein et al., 2007, Fig.4). Il a été estimé que 5 à 8% de la production agricole serait perdue sans le service de pollinisation (Potts et al., 2016). De plus, l'augmentation croissante des surfaces cultivées de cultures dépendantes des pollinisateurs depuis le début des années 1960 (Aizen et al., 2008) a rendu la production agricole mondiale de plus en plus dépendante des pollinisateurs. Enfin, bien que cette vision soit une vision de monétarisation de la nature qui divise la communauté scientifique, on estime entre 235 et 577 milliards de dollars la valeur de la production des plantes cultivées dépendantes des pollinisateurs (Lautenbach et al., 2012).

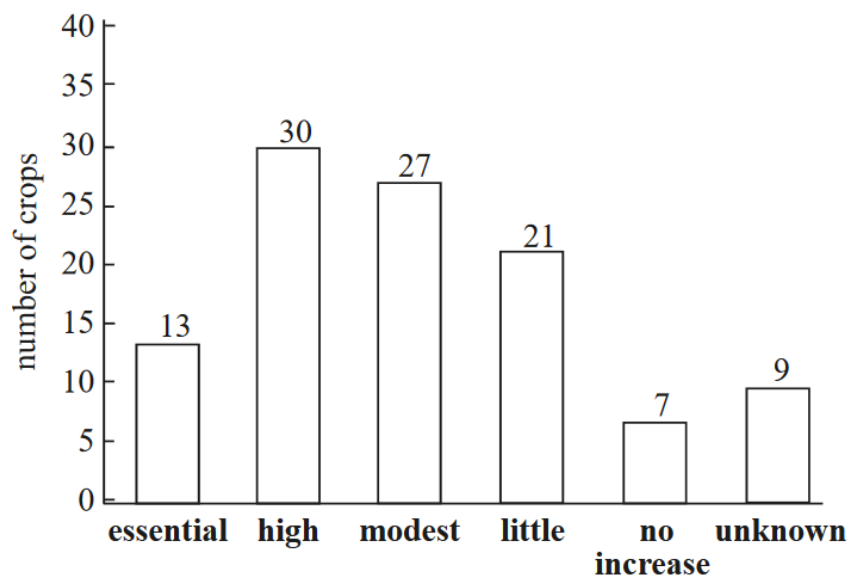


Figure 4 - Niveau de dépendance à la zoogamie de 70 cultures (issue de Klein et al., 2007)

Cette importance du service de pollinisation s'explique par le fait que la pollinisation permet d'augmenter de manière importante la production des cultures. En effet, à l'échelle de la plante, la pollinisation permet l'augmentation des rendements et de la qualité de la production (Bartomeus et al., 2014). Cela peut se traduire par l'augmentation du nombre de fruits par plante comme pour les cucurbitacées (Knapp and Osborne, 2019; Wijesinghe et al., 2020), l'augmentation du nombre de graines comme pour le colza et le tournesol (encadré 1) ou l'augmentation du poids des graines ou des fruits (Garratt et al., 2014; Wietzke et al., 2018). La qualité de la

production peut également être impactée par la pollinisation entomophile. Par exemple, la pollinisation permet la diminution du nombre de graines vides pour le sarrasin ou encore l'augmentation de la qualité commerciale des fraises (Bartomeus et al., 2014; Wietzke et al., 2018). Les facteurs liés à la pollinisation permettant d'expliquer cette amélioration de la production sont en général l'abondance des pollinisateurs et la diversité des communautés de pollinisateurs (e.g Garibaldi et al., 2013; Klein et al., 2003; Lindström et al., 2016; Mallinger and Gratton, 2015; Perrot et al., 2019, 2018; Zou et al., 2017).

Encadré 1

Le colza (*Brassica napus* L.) et le tournesol (*Helianthus annuus* L.) sont deux cultures très présentes dans les systèmes agricoles européens. En effet, le colza, cultivé essentiellement pour la production d'huile alimentaire et plus récemment pour la production de biocarburants, est la 5e culture en termes de surface cultivée à l'échelle européenne et la 4e en France. Le tournesol quant à lui occupe le 3e rang au niveau européen et le 5e rang au niveau français (FAOSTAT, 2020). Ces deux cultures sont hermaphrodites. Leur taux d'autopollinisation est très différent, il se situe entre 53 et 83% pour le colza (Becker et al., 1992; Perrot et al., 2018) et 35 et 53,5% pour le tournesol (Javed and Mehdi, 1992; Perrot et al., 2019; Roumet et al., 2012). Elles sont également pollinisées par le vent, qui représente entre 3 et 12% des rendements pour le colza (Hudewenz et al., 2014; Mesquida and Renard, 1982; Perrot et al., 2018) et un peu plus de 20% pour le tournesol (Perrot et al., 2019). Ces cultures bénéficient également de la pollinisation par les insectes. Ce mode de pollinisation permet une augmentation du rendement du colza entre 10 et 50% (Araneda Durán et al., 2010; Bartomeus et al., 2014; Bommarco et al., 2012; Lindström et al., 2016; Perrot et al., 2018; Stanley et al., 2013; Zou et al., 2017) et du tournesol entre 18 et 100% (Carvalho et al., 2011; Degrandi-Hoffman and Chambers, 2006; Garibaldi et al., 2016; Greenleaf and Kremen, 2006; Perrot et al., 2019). Ces deux cultures sont dites à floraison massive puisqu'elles fleurissent sur un temps court, quelques semaines entre mars et mai pour le

colza et quelques semaines en juillet et août pour le tournesol, et fournissent durant cette période une quantité très importante de ressources alimentaires pour les insectes pollinisateurs (Requier et al., 2015; Rollin et al., 2015; Todd et al., 2016; Westphal et al., 2003). Néanmoins, malgré le réservoir en ressources important que représente chacune de ces cultures, les communautés d'insectes pollinisateurs les visitant sont très différentes. En effet, même si pour ces deux cultures l'abeille domestique (*Apis mellifera* L.) est l'espèce de pollinisateur la plus abondante dans la communauté, elle ne représente que 70 à 80% des visites dans le colza (Bartomeus et al., 2014; Bommarco et al., 2012; Perrot et al., 2018; Zou et al., 2017) contre 72 à 97,8% dans le tournesol (Bartual et al., 2018; Carvalho et al., 2011; Greenleaf and Kremen, 2006). Pour le colza, les syrphes représentent 10 à 20% des visites et les abeilles sauvages 5 à 10%. Pour le tournesol, le reste de la communauté est composé essentiellement d'abeilles sauvages, de syrphes ou encore de Lépidoptères. La plupart des études ont montré que l'effet des insectes pollinisateurs sur le rendement du tournesol et du colza provenait essentiellement de l'abondance de ces derniers, qu'ils soient gérés ou sauvages (Bartomeus et al., 2014; Greenleaf and Kremen, 2006; Jauker et al., 2012; Lindström et al., 2016; Perrot et al., 2019, 2018; Zou et al., 2017). Pour chacune de ces cultures, une seule étude a montré un effet de la richesse spécifique des pollinisateurs sur leur rendement (Carvalho et al., 2011; Zou et al., 2017).

b) Les insectes pollinisateurs des milieux agricoles

Bien que de nombreux groupes taxonomiques permettent la pollinisation des plantes, les principaux pollinisateurs sont les insectes. Dans les milieux agricoles, les insectes pollinisateurs les plus étudiés sont les Hyménoptères et les Diptères. Parmi les Hyménoptères, ce sont les abeilles qui sont les plus fréquentes (Greenleaf et al., 2007; Khalifa et al., 2021), la plus connue étant l'abeille domestique ou abeille mellifère (*Apis mellifera* L.). Le fait que cette espèce forme de grandes colonies (plusieurs dizaines de milliers d'individus) et soit généraliste (butine une grande diversité de plantes) fait de celle-ci un soutien majeur au service de pollinisation (Cunningham et al., 2016; Gallai et al., 2009; Lindström et al., 2016; Perrot et al., 2019). Néanmoins, la présence de cette espèce est fortement liée à l'apiculture, puisque c'est une espèce gérée. De nombreuses abeilles sauvages sont également connues pour être des pollinisateurs efficaces des cultures comme les bourdons ou les *Megachilidae* (Garibaldi et al., 2013; Klein et al., 2007). Contrairement à l'abeille domestique, la présence de ces pollinisateurs est dépendante essentiellement du contexte paysager et de la disponibilité en habitats semi-naturels (Benjamin et al., 2014; Garibaldi et al., 2011; Nooten and Rehan, 2022). Le deuxième groupe le plus commun dans le milieu agricole est celui des Diptères ("mouches"). La famille la plus étudiée dans les milieux agricoles est celle des *Syrphidae*, mais les Diptères non *Syrphidae* sont généralement plus abondants et divers que les Diptères *Syrphidae* et transporteraient plus de 80% du pollen transporté par l'ensemble des Diptères (Orford et al., 2015). Bien qu'elles semblent être de moins bonnes vectrices pour le transport du pollen que les abeilles, les mouches compenseraient par un grand nombre de visites (Rader et al., 2016) et seraient ainsi au moins aussi efficaces que les abeilles (Howlett et al., 2017). Néanmoins, les Diptères sont encore peu considérés dans les études sur la pollinisation des cultures et leur importance dans le soutien qu'ils apportent au service de pollinisation pourrait être sous-estimée.

Dans les milieux agricoles, toutes ces espèces sont soumises à de nombreuses contraintes pouvant avoir des conséquences négatives sur leurs populations, sur les

communautés et par conséquent sur le service de pollinisation. La structure des réseaux d'interactions plantes-pollinisateurs conditionne leur stabilité et leur robustesse à la perte d'espèces et joue ainsi un rôle majeur dans la capacité de résilience des réseaux aux perturbations environnementales. Dans les réseaux mutualistes comme les réseaux plantes-pollinisateurs, la diversité spécifique et le nombre de liens sont un indicateur important de la stabilité. Une autre caractéristique importante de ces réseaux est l'emboîtement (nestedness en anglais). Si les espèces interagissant avec les spécialistes sont une partie des espèces interagissant avec les généralistes alors le réseau est dit emboîté (Mariani et al., 2019). Ainsi, si les espèces spécialistes sont perdues, les espèces généralistes interagissent toujours avec l'autre niveau trophique. Les réseaux les plus connectés, ayant un grand nombre de liens entre espèces par rapport au nombre maximum de liens potentiels, sont donc attendus comme étant ceux ayant une plus forte résilience face aux perturbations (Thébault and Fontaine, 2010). En revanche, les réseaux faiblement connectés et non emboîtés sont fragiles face aux perturbations (Thébault and Fontaine, 2010). Ainsi, les réseaux d'interactions peuvent être utilisés comme indicateur des variations environnementales.

3. Le déclin des pollinisateurs et les facteurs associés au milieu agricole

Depuis plusieurs dizaines d'années, des études montrent un déclin des pollinisateurs (Biesmeijer et al., 2006; Kearns et al., 1998; Potts et al., 2010). Ce déclin n'a pas lieu uniquement dans les zones anthropisées puisque Hallmann et al., (2017) ont montré une perte de 75% de la biomasse d'insectes dans les zones protégées allemandes entre 1989 et 2016. Concernant les pollinisateurs, Zattara and Aizen (2021) ont montré, à partir des données disponibles sur la plateforme GBIF, un fort déclin des espèces d'abeilles au cours du dernier siècle et plus précisément au cours des 30 dernières années.

Comme pour l'ensemble de la biodiversité, ce déclin a pour origine les activités

des sociétés humaines. Les facteurs sont multiples et ils ont pu être mis en évidence par différents auteurs ces dernières années. On retrouve la perte d'habitat liée à la l'intensification de l'agriculture et à l'urbanisation, les pollutions notamment liées aux pesticides, les agents pathogènes et les espèces introduites ainsi que le changement climatique (Potts et al., 2010, 2016; Sánchez-Bayo and Wyckhuys, 2019; Wagner, 2020; Fig.5). Dans la suite, nous décrivons uniquement les facteurs propres aux milieux agricoles.

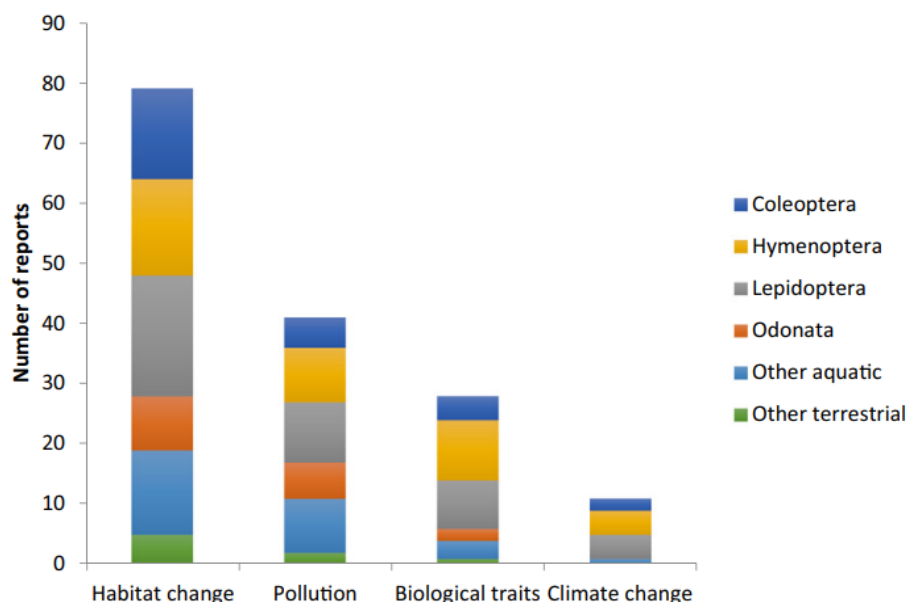


Figure 5 - Les quatre grandes causes du déclin des taxons majeurs d'insectes relevés par Sánchez-Bayo and Wychkuys (2019) : les modifications des habitats incluant la perte d'habitat et de ressources (habitat change), les pollutions incluant les pesticides (pollution), l'effet des parasites et des pathogènes, ou des espèces exotiques envahissantes (biological traits), et le changement climatique global (climate change).

Pour leur survie et leur reproduction, les pollinisateurs ont besoin de deux ressources essentielles, à savoir des ressources florales (nectar et/ou pollen) ainsi que des sites de nidification. Cependant chaque espèce de pollinisateur n'a pas les mêmes besoins, en termes de diète alimentaire certaines sont spécialistes (butinage d'une seule espèce de plante) tandis que d'autres sont généralistes et peuvent se nourrir sur une plus grande diversité de plantes, en termes de sites de nidification certaines nichent directement au sol, d'autres dans des bois morts ou encore dans des tiges

creuses. De plus, les besoins peuvent être différents au sein d'une même espèce, mais entre stades de développement différents avec des besoins qui peuvent varier entre les larves et l'imago. Or, au cours de ces dernières décennies, l'agriculture s'est intensifiée homogénéisant les paysages agricoles avec de grandes parcelles en monoculture, réduisant les espaces semi-naturels, tels que les prairies ou encore les haies et induisant l'utilisation d'herbicides et d'insecticides (Potts et al., 2010, 2016a; Vanbergen et al., 2013). Tous ces facteurs pèsent sur la diversité et l'abondance des pollinisateurs dans ces milieux en réduisant l'accès aux ressources qui sont vitales pour les pollinisateurs (Baude et al., 2016; Biesmeijer et al., 2006). En 2019, Timberlake et al., ont montré que dans les milieux agricoles la phénologie de production de ressources florales et la phénologie des besoins en ressources de la part des pollinisateurs pouvaient être asynchrones, créant ainsi des disettes alimentaires à certains moments de la saison. Ces moments correspondent aux périodes où les cultures à floraison massive ne sont plus en fleur et où les seules ressources florales pour les pollinisateurs se trouvent au niveau des éléments semi-naturels ou des adventices des cultures (Requier, 2013).

a) L'importance des cultures à floraison massive

Comme nous l'avons présenté précédemment avec le colza et le tournesol, les cultures à floraison massive sont des composantes essentielles des milieux agricoles. Elles fournissent une quantité de ressources florales très importante pendant un court laps de temps (Westphal et al., 2003). Ces ressources pourraient alors être complémentaires des autres ressources florales comme celles disponibles dans les habitats semi-naturels qui ont des phénologies de floraison qui peuvent varier. Il a d'ailleurs été démontré qu'une couverture élevée du paysage en culture à floraison massive pouvait améliorer les densités d'abeilles sauvages de l'année suivante (Beyer et al., 2021; Riedinger et al., 2015). Néanmoins, d'autres études ont montré que ces cultures pourraient jouer un rôle de dilution des densités d'insectes du paysage (Holzschuh et al., 2016; Montero-Castaño et al., 2016; Stanley and Stout, 2014). De plus, bien que les ressources fournies soient abondantes, ces dernières peuvent ne

pas permettre un approvisionnement suffisamment diversifié en termes de composés métaboliques constituant les nectars et pollens et certaines espèces spécialistes pourraient ne pas pouvoir profiter de ces dernières. Enfin, étant donné leur densité, ces cultures pourraient entrer en compétition avec la flore adventice pourtant indispensable au maintien des populations de pollinisateurs sauvages (Geslin et al., 2017).

b) La destruction des habitats

En raison des ressources florales (Baude et al., 2016; Langlois et al., 2020; Timberlake et al., 2019) et des sites de nidification (Lye et al., 2009) qu'ils offrent, les habitats semi-naturels sont connus pour avoir des effets positifs sur la diversité et l'abondance des pollinisateurs sauvages (Carvalho et al., 2010; Garibaldi et al., 2011; Klein et al., 2012; Ricketts et al., 2008). Cependant, au cours du dernier siècle, à des fins d'optimisation du travail agricole, la tendance a été d'augmenter la taille des parcelles cultivées au détriment des milieux semi-naturels (Potts et al., 2016b, 2010; Vanbergen et al., 2013). Ainsi, les pollinisateurs ont perdu des ressources essentielles à leur survie que ce soit en termes d'habitat ou de ressources alimentaires. Par exemple, entre 1975 et 1987, l'inventaire forestier national a noté une perte annuelle de 45 000 km de haies et actuellement ce sont 8500 km qui sont perdues chaque année, pourtant ces milieux sont connus pour fournir des ressources florales importantes aux pollinisateurs et pour être utiles à leur dispersion (Garratt et al., 2017; Hannon and Sisk, 2009; Morandin and Kremen, 2013; Sardiñas and Kremen, 2015). Ces habitats se sont également retrouvés plus fragmentés et isolés causant ainsi des perturbations dans les déplacements des individus ayant des capacités de vol limitées.

c) Les pesticides

L'utilisation d'insecticides ayant pour cibles les insectes ravageurs des cultures peut avoir un impact sur les pollinisateurs. En effet, bien qu'ils n'en soient pas la cible et bien qu'il existe des lois limitant l'épandage de ces produits, et donc leur impact sur les pollinisateurs, l'exposition à des produits tels que les néonicotinoïdes (Godfray et

al., 2014; Wood and Goulson, 2017) peut avoir des effets létaux (Johnson et al., 2010; Tsvetkov et al., 2017) et sublétaux sur les pollinisateurs (Desneux et al., 2007; Henry et al., 2012; Wood and Goulson, 2017; Woodcock et al., 2017). Néanmoins, le rôle de ces produits dans le déclin généralisé des pollinisateurs est difficile à mesurer par rapport aux autres facteurs impliqués. Outre l'utilisation d'insecticides, l'utilisation d'herbicides, visant à éliminer la flore adventice des cultures, considérée comme indésirable en raison de l'éventuelle compétition qu'elle peut avoir avec la plante cultivée (Milberg and Hallgren, 2004), peut nuire aux pollinisateurs sauvages des cultures qui perdent ainsi une ressource florale essentielle (Bretagnolle and Gaba, 2015; Willmer, 2011).

Au vu des effets des activités humaines sur la disponibilité en ressources florales dans les milieux agricoles, il est nécessaire de connaître l'importance des différents types floraux pour le maintien des communautés de pollinisateurs des cultures et donc pour le maintien du service de pollinisation des cultures. L'importance des habitats semi-naturels et des cultures à floraison massive est relativement bien connue, mais celle de la flore adventice des cultures reste encore assez méconnue. De plus, les études s'étant intéressées à l'impact de ces facteurs paysagers se déroulent souvent sur une même année. Or, le cycle de vie des pollinisateurs suggère que les effets peuvent se répercuter d'une année sur l'autre, comme cela a pu être montré dans quelques études (Beyer et al., 2021; Riedinger et al., 2015; Timberlake et al., 2020). Il serait donc intéressant d'étudier l'impact de ces facteurs paysagers d'une année sur l'autre en intégrant la flore adventice des champs cultivés. Pour cela, on peut utiliser les réseaux d'interactions plantes-pollinisateurs qui peuvent révéler des interactions indirectes relativement insoupçonnées entre des espèces d'un même niveau trophique via le partage de partenaires communs (Müller et al., 1999). Pour les réseaux plantes-pollinisateurs, ce genre d'interactions peut correspondre aux interactions indirectes entre les plantes via le partage de pollinisateurs communs.

4. Le suivi des pollinisateurs en milieu agricole

Pour étudier la fonction de pollinisation, les mécanismes permettant son maintien ou pour évaluer le service qu'elle rend, il est nécessaire d'acquérir une quantité importante de données. En fonction des questions posées, ces données doivent être de différentes natures et impliquent par conséquent la mise en place de protocoles particuliers.

a) Les méthodes classiques

Dans les milieux agricoles, les études portent le plus souvent sur l'impact de facteurs paysagers et locaux sur la présence, l'activité de butinage et la diversité des pollinisateurs dans les cultures (e.g. Carvalho et al., 2011; Kennedy et al., 2013; Perrot et al., 2018; Ricketts et al., 2008) ou encore sur l'évaluation du service de pollinisation (e.g. Bartomeus et al., 2014; Garibaldi et al., 2013; Perrot et al., 2018).

Pour l'étude du service de pollinisation, différentes méthodes existent. L'une d'elles est expérimentale et consiste à bloquer l'accès à tout ou partie de la plante aux pollinisateurs et à comparer la production de fruits et/ou de graines de cette partie de la plante n'ayant pas accès à la pollinisation entomophile avec la production d'une plante dite "contrôle" qui était en situation de pollinisation ouverte permettant l'accès à l'ensemble des pollinisateurs. Une autre méthode consiste à observer directement les variations de traits propres au rendement (production de graines et/ou de fruits) de la culture en fonction d'un gradient de pollinisation. Le gradient de pollinisation peut être naturel ou être modifié artificiellement en faisant varier la densité de ruches autour de certaines parcelles (Lindström et al., 2016). La contribution des pollinisateurs est alors évaluée en comparant la valeur de traits du rendement de parcelles avec une forte activité de pollinisation avec celles de parcelles ayant une faible activité de pollinisation. Néanmoins, cette méthode nécessite d'avoir accès à un paysage varié pour avoir des différences d'activité de pollinisation ou bien à investir dans l'achat et dans l'entretien de ruches.

La méthode la plus courante consiste à recourir à des proxys de pollinisation.

Ces études s'intéressent alors aux données d'abondance, de diversité des communautés ou encore au nombre de visites dans les cultures. Ces méthodes sont également celles utilisées pour l'étude de l'impact des facteurs paysagers et locaux sur les communautés de pollinisateurs ainsi que pour les études portant sur les réseaux d'interactions plantes-pollinisateurs. L'obtention de ces proxys nécessite toutefois la mise en place de protocoles de suivi des insectes pollinisateurs dans les parcelles cultivées. Les méthodes classiques consistent généralement à piéger ou capturer les insectes. Le protocole des pots pièges (pan traps) consiste à poser des bols colorés (blanc, bleu et jaune) remplis d'eau savonneuse à hauteur de la culture. Ainsi les insectes tombent dans l'eau savonneuse et se noient. Ils peuvent ensuite être récoltés et identifiés en laboratoire. La technique du filet fauchoir consiste à se déplacer le long d'un transect et à capturer l'ensemble des insectes butinant les fleurs le long de ce transect. Après leur mort, les individus capturés peuvent eux aussi être identifiés en laboratoire. Ces méthodes permettent par conséquent d'obtenir des données de diversité des communautés de pollinisateurs et d'abondance de chaque espèce. Les captures au filet permettent de construire les réseaux d'interactions plantes-pollinisateurs qui peuvent par exemple être utilisés dans le cadre d'études sur les ressources florales consommées par les pollinisateurs.

Néanmoins, ces méthodes classiques nécessitent très souvent le sacrifice des individus afin de pouvoir les déterminer. Il a été estimé qu'en l'espace d'une trentaine d'années plus de 820 000 abeilles sauvages ont été sacrifiées par les scientifiques (Montero-Castaño et al., 2022) et que 63% des individus capturés par les pots pièges appartiennent à des espèces non étudiées dans le cadre de la pollinisation (Gonzalez et al., 2020). Or, dans un contexte de forte médiatisation du déclin des insectes, l'utilisation de méthodes létales est difficile à défendre auprès du grand public (Drinkwater et al., 2019). Ces méthodes sont destructives pour la biodiversité, mais elles sont également très chronophages (Montgomery et al., 2021). En effet, l'identification des insectes en laboratoire prend un temps considérable et le nombre de taxonomistes capables de faire ces déterminations est très restreint. De plus, le temps d'identification, mais également celui passé au sein des cultures limitent

considérablement l'effort d'échantillonnage spatialement et temporellement (van Klink et al., 2022). Cependant, pour comprendre les effets agissant sur le service de pollinisation, il est nécessaire de disposer de données avec de fines résolutions spatiales et temporelles et notamment de données continues couvrant l'ensemble de la période de floraison des cultures.

Les développements technologiques récents ont permis la mise au point de nouvelles méthodes de suivi des pollinisateurs (van Klink et al., 2022) qui pour certaines sont moins destructives et moins chronophages.

b) Les nouvelles méthodes disponibles

Depuis quelques années, de nouvelles méthodes de suivi de la biodiversité ont été développées. Ces méthodes peuvent faire intervenir des avancées dans le domaine de la génétique ou encore de l'intelligence artificielle.

Concernant les insectes, ces nouvelles méthodes font l'objet de nouveaux projets de recherche dont les objectifs sont d'améliorer le suivi et de mieux connaître les communautés d'insectes (Lehmann et al., 2021; Wägele et al., 2022).

Parmi ces méthodes on trouve des méthodes moléculaires reposant sur l'information génétique (Fig.6D). Elles peuvent être utilisées à différentes fins comme la découverte de nouvelles espèces (Srivathsan et al., 2021), la détection dans les milieux d'espèces rares (Doi et al., 2017), envahissantes et nuisibles (Batovska et al., 2021), ou encore d'évaluer la diversité taxonomique et génétique de communautés entières d'insectes (Elbrecht et al., 2018; Thomsen and Sigsgaard, 2019). Elles peuvent également permettre de mieux caractériser les interactions plantes-pollinisateurs (Tiusanen et al., 2019) en détectant des interactions qui n'avaient pas pu être caractérisées avec les méthodes traditionnelles de suivi. Toutefois, ces méthodes nécessitent encore aujourd'hui le sacrifice ou la récupération d'une patte des insectes afin de récolter des séquences ADN ce qui reste un inconvénient majeur. Seules les méthodes ayant recours à l'ADN environnemental ne nuisent pas à l'intégrité des individus puisqu'il est récupéré sur les fleurs.

Parmi les nouvelles méthodes disponibles, on trouve également la surveillance

radar (Fig.6C). Cette méthode peut permettre de détecter la présence d'insectes et d'étudier les déplacements des espèces sur de grandes fenêtres spatiales. La méthode conventionnelle consiste à utiliser les ondes radio pour détecter les insectes volants dans l'espace aérien. La puissance des nouveaux radars permet de détecter les individus volants entre 150 m et 1,2 km du sol (Chapman et al., 2011) et de déterminer des paramètres comme la taille, la vitesse ou encore la trajectoire des individus (Rhodes et al., 2022). Cette méthode a pour principaux avantages d'avoir un grand rayon d'action spatial (Bauer et al., 2017), mais également temporel et d'être non invasive. De nouvelles évolutions permettent aujourd'hui d'améliorer la détection des insectes volant à proximité du sol (Rydhmer et al., 2022) ainsi que d'identifier les espèces d'insectes (Brydegaard et al., 2020; Brydegaard and Jansson, 2019; Kirkeby et al., 2021).

Les deux dernières méthodes, la vision par ordinateur et le suivi acoustique, reposent sur la même évolution technologique à savoir, l'apprentissage machine. La vision par ordinateur (Fig.6A) consiste à extraire de l'information d'images ou de vidéos afin de pouvoir collecter automatiquement une identification de l'espèce sur l'image et donc une donnée de présence. Cette méthode peut ainsi permettre de mesurer l'activité, l'abondance des insectes, dont les pollinisateurs (Bruijning et al., 2018; Schneider et al., 2022) ou encore d'étudier leurs interactions avec les plantes (Bjerge et al., 2022). Cette méthode nécessite l'utilisation d'algorithmes d'apprentissage comme les réseaux de neurones convolutifs qui sont entraînés sur une base de données d'images pré-classées et peuvent être très performants avec des taux de précision d'identification au niveau de l'espèce supérieure à 90% pour certains taxons (Knyshov et al., 2021; Martineau et al., 2017; Spiesman et al., 2021; Valan et al., 2019). Cette méthode est non létale et peut permettre de réduire les difficultés liées au manque de taxonomistes. Néanmoins, cette méthode nécessite une très grande quantité de données d'apprentissage pour pouvoir être performante. En effet, les réseaux de neurones convolutifs sont peu performants lorsque la base de données de référence d'une espèce est restreinte (comme les espèces rares ou non décrites) et ont tendance à surestimer la présence des espèces pour lesquelles la base de données de

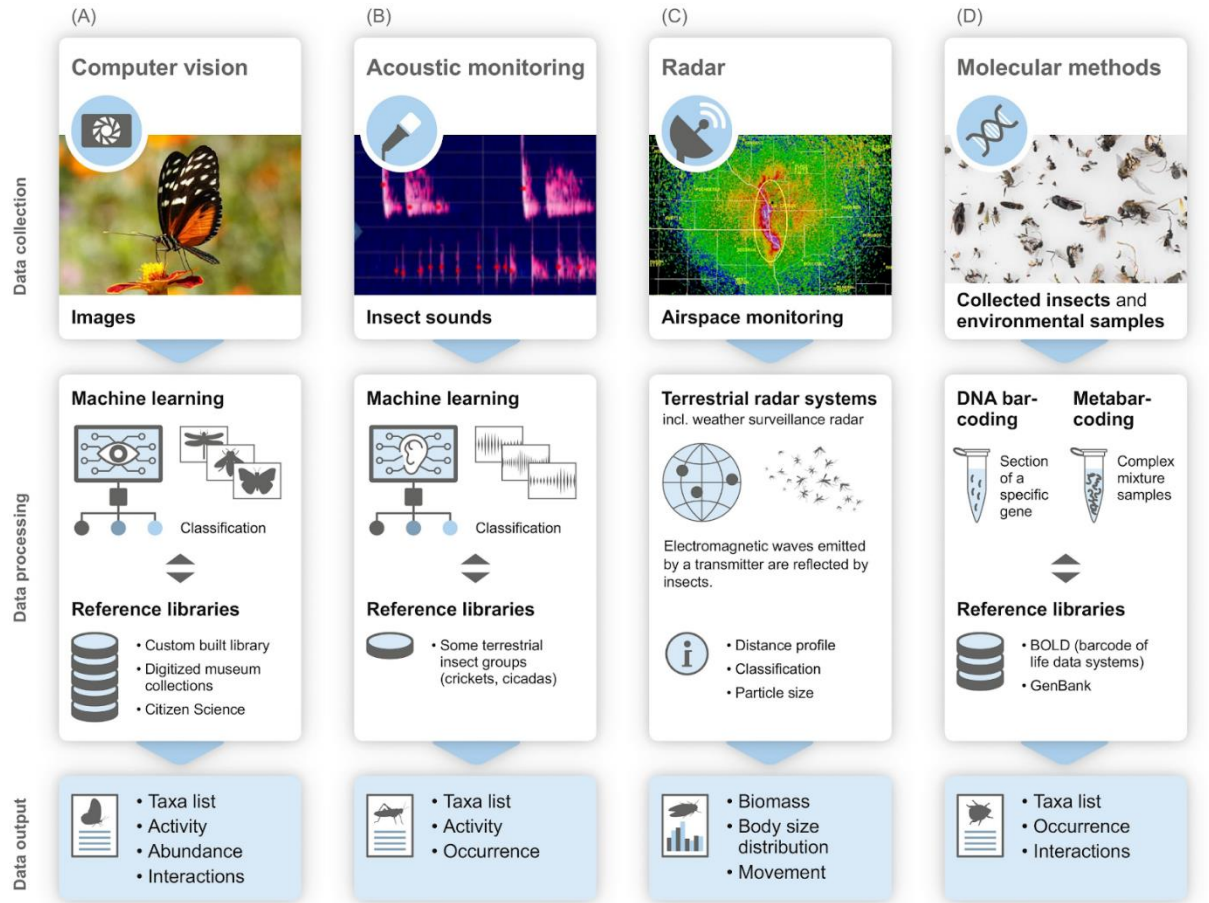
référence est très fournie. L'autre inconvénient de cette méthode est la consommation d'énergie de la caméra et le stockage des images/vidéos qui peuvent nécessiter la mise en place d'une logistique particulière.

Le suivi acoustique des pollinisateurs (Fig.6B) repose sur le même principe que la vision par ordinateur, c'est-à-dire extraire de l'information à partir d'enregistrements sonores à l'aide d'algorithmes d'apprentissage automatique. Cette méthode a été d'abord utilisée sur les insectes vocalisant comme les Orthoptères et les cigales (Jeliazkov et al., 2016; Penone et al., 2013) puis sur les insectes d'eau douce (Desjonquères et al., 2020; Gottesman et al., 2020). Depuis quelques années, elle a été testée sur des insectes volants comme les moustiques (Kiskin et al., 2021) et les pollinisateurs (voir encadré 2) en utilisant le son émis par leur battement d'ailes pour les détecter. Comme pour la vision par ordinateur, l'identification spécifique reste extrêmement dépendante de la taille des bases de sons de référence pour les espèces. Néanmoins, cette méthode pourrait permettre de mesurer l'activité des pollinisateurs. Cette méthode présente plusieurs avantages dont son faible coût, et son caractère non invasif.

Encadré 2 : Les pollinisateurs et l'acoustique : tour d'horizon des premières applications

Les insectes pollinisateurs ne vocalisant pas, leur détection acoustique passe par le son émis par leurs battements d'ailes (Kawakita and Ichikawa, 2019). Les études de Kawakita et Ichikawa (2019) et de (Gradišek et al., 2017) se sont respectivement intéressées à l'identification de trois espèces d'abeilles ainsi que d'une espèce de frelon et à celle de 12 espèces de bourdons. Pour cela, ils ont mis au point des classificateurs permettant, grâce à des algorithmes d'apprentissage machine, de classer automatiquement les sons émis par les différentes espèces. Toutefois, à ce jour, ces études sont les seules portant sur l'identification des espèces de pollinisateurs à partir de leur signal acoustique. En effet, les autres études se sont essentiellement intéressées au dynamique

d'activité des pollinisateurs sans passer par la détermination des espèces. Miller-Struttmann et al., (2017) ont mis en évidence la possibilité d'utiliser le suivi acoustique des pollinisateurs dans le cadre de l'étude du service de pollinisation. A partir de l'activité des bourdons mesurée, ils ont mis en évidence que cette activité a un impact sur la production de graines de deux espèces de plantes alpines. Galen et al., (2019) se sont quant à eux intéressés à l'impact de facteurs environnementaux comme la luminosité et la température sur l'activité des pollinisateurs. Enfin, Heise et al., (2019) ont mis en évidence qu'il y a des différences entre les sons émis par les bourdons au départ et à l'arrivée du nid permettant ainsi d'étudier la dynamique de colonies (Heise et al., 2020).



Trends in Ecology & Evolution

Figure 6 - Flux de travail, de la collecte des données au produit final, pour chacune des quatre technologies présentées (issue de van Klink et al., 2022).

Problématique et objectifs

Dans ce contexte, mes travaux de thèse consistent à étudier le service de pollinisation dans les milieux agricoles et les méthodes pour le mesurer. Plus précisément, je me suis intéressé à l'impact de l'assolement des milieux agricoles sur le service de pollinisation, ainsi qu'aux capacités du suivi acoustique des pollinisateurs à constituer une méthode efficace pour estimer le service de pollinisation et étudier les mécanismes dont il découle. Ces travaux s'appuient sur des données de réseaux d'interactions et sur des données de suivis acoustique et visuel récoltées au sein de la Zone Atelier Plaine et Val de Sèvre (encadré 3).

Encadré 3 : Présentation du site d'étude : La Zone Atelier Plaine et Val de Sèvre

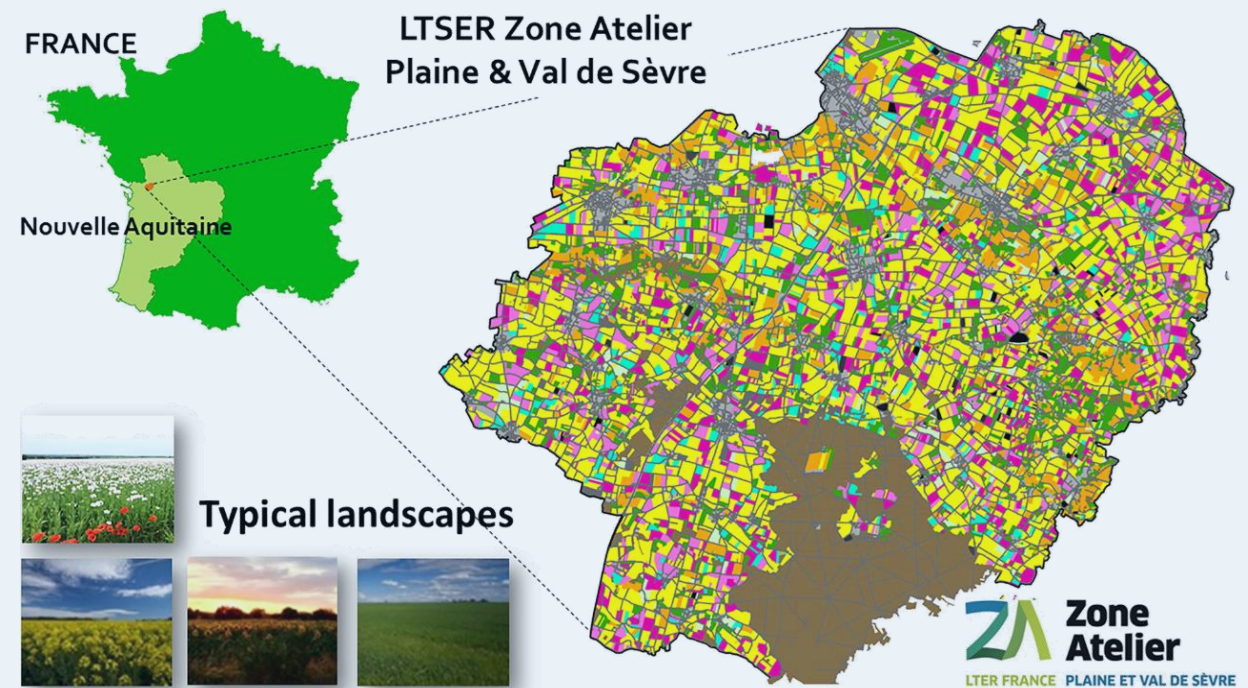


Figure 7 - Carte de la Zone Atelier Plaine et Val de Sèvre. L'utilisation des sols dans la zone est représentée par différentes couleurs, par exemple les céréales d'hiver en jaune, les bois en brun et les zones urbaines en gris. Quatre paysages typiques de ces zones sont représentés en bas à gauche de la figure (issue de Bretagnolle et al., 2018a).

La Zone Atelier "Plaine et Val de Sèvre" est une zone atelier du Centre National de la Recherche Scientifique depuis 2008 mais la collecte de données y a commencé en 1994. Ce site est dédié à l'analyse des trajectoires de la biodiversité en lien avec les pratiques agricoles. Elle se situe à l'Ouest de la France au Sud de la ville de Niort. Sa surface est d'environ 435 km², fragmentée en 13 000 parcelles, ayant une surface moyenne de 4 à 5 hectares, partagée entre 450 exploitants. La surface cultivée s'étend sur environ 87%

de la zone. L'agriculture est principalement céréalière et intensive. Le paysage y est tout de même relativement varié avec de grandes zones céréalières (grandes parcelles et peu d'éléments semi-naturels), mais aussi des zones plus bocageuses (petites parcelles et une proportion importante d'éléments semi-naturels). Une partie importante est classée Natura 2000 ce qui permet de promouvoir l'agriculture extensive (Bretagnolle et al., 2018a, 2018b).

En raison du manque d'information concernant l'importance des ressources florales passées sur le maintien des communautés de pollinisateurs dans les espaces cultivés, nous nous sommes tout d'abord demandé **(i) Quelle est la contribution des différentes ressources florales de l'année précédente présentes au sein des espaces cultivés au maintien de la pollinisation du colza ? (Chapitre 1)**. Cette étude s'appuie sur l'analyse des effets indirects des ressources florales de l'année passée sur le colza via les pollinisateurs partagés. Ces effets ont été mesurés à l'aide des réseaux d'interactions plantes-pollinisateurs entre les ressources florales des espaces cultivés de l'année précédente, les pollinisateurs et le colza de l'année suivante construits à partir de données de captures au filet réalisées entre 2015 et 2019. Ce premier chapitre nous a permis de déterminer quelles étaient les ressources florales passées des espaces cultivés essentielles au maintien du service de pollinisation du colza.

Par la suite, nous avons cherché à déterminer **(ii) Quel est l'algorithme d'apprentissage machine le plus efficace pour le suivi acoustique de l'activité de vol des pollinisateurs? (Chapitre 2)**. Dans les études portant sur le suivi acoustique des pollinisateurs (Gradišek et al., 2017; Kawakita and Ichikawa, 2019; Miller-Struttmann et al., 2017), les algorithmes d'apprentissage utilisés sont généralement d'ancienne génération à part pour une de ces études qui utilise les réseaux de neurones convolutifs (Folliot et al., 2022) connus pour être très performants en écoacoustique (Stowell, 2022). Néanmoins, aucune étude jusqu'ici n'a cherché à comparer l'efficacité de ces algorithmes pour la détection des pollinisateurs et n'a cherché à démontrer que les données d'activité de butinage des pollinisateurs obtenues étaient cohérentes avec la littérature existante sur la biologie des pollinisateurs. A partir de données acoustiques récoltées en 2020 au cours de la saison de floraison du tournesol, et à des logiciels d'apprentissage machine existants (Tadarida (Bas et al., 2017) et TadariDeep (<https://github.com/YvesBas/TadariDeep>)), nous avons comparé l'efficacité des réseaux de neurones convolutifs et de l'algorithme des forêts aléatoires pour la détection des sons émis par les pollinisateurs au cours de leur vol. Une fois

l'algorithme le plus efficace déterminé, nous nous sommes demandé si le suivi acoustique des pollinisateurs pouvait refléter les connaissances sur la phénologie d'activité d'*Apis mellifera* L..

Enfin, nous nous sommes demandé **(iii) Quelle méthode de suivi des pollinisateurs fournit le meilleur proxy de l'activité des pollinisateurs pour répondre à des questions écologiques ? (Chapitre 3)**. A partir de données de comptage d'abeilles domestiques le long de transects de manière ponctuelle et du suivi acoustique continu réalisé en 2020 dans des parcelles de tournesol, nous avons la relation entre les proxys d'activité des pollinisateurs obtenus grâce à ces deux méthodes. Puis nous avons cherché à déterminer si ces proxys étaient impactés par des effets paysagers. Enfin, nous avons testé les relations entre les deux proxys de l'activité des pollinisateurs et le service de pollinisation du tournesol.

Chapitre 1 : Les adventices des cultures non fleuries comme contributeurs potentiels à la pollinisation du colza

Alors que la pollinisation zoophile est essentielle pour la production agricole mondiale puisque 70% des cultures dépendent des pollinisateurs pour leur rendement, les changements d'usage des sols dans les milieux agricoles ont considérablement modifié la disponibilité des ressources florales pour l'alimentation des pollinisateurs. L'augmentation des surfaces des parcelles a homogénéisé les types de ressources disponibles en raison des monocultures et de la réduction des habitats semi-naturels alors que l'utilisation d'herbicides a drastiquement diminué la présence de la flore adventice au sein des cultures. Des études ont montré que les ressources florales passées, notamment les cultures à floraison massive, pouvaient avoir un impact important sur les densités de pollinisateurs sauvages. Néanmoins, l'importance des ressources issues de la flore adventice de l'année précédente sur le maintien des pollinisateurs sauvages et leur effet sur la pollinisation des cultures n'ont jamais été étudiés.

Dans cette étude nous avons quantifié la contribution des différentes ressources florales présentes dans les espaces cultivés à la pollinisation du colza l'année suivante. Grâce à des captures au filet entre 2015 et 2019, nous avons pu construire des réseaux d'interactions plantes-pollinisateurs tripartites, composés des différentes ressources florales passées (année n), du colza (année $n+1$) et des espèces de pollinisateurs sauvages ayant visité à la fois les ressources florales passées et le colza. En modifiant l'indice de Müller (Müller et al., 1999) pour qu'il s'adapte au contexte inter-annuel de notre étude, nous avons pu calculer la contribution de chaque type de ressource florale passée aux effets indirects inter-annuels potentiels reçus par le colza par le biais des pollinisateurs sauvages partagés (Fig.8). Ainsi, nous avons déterminé que le soutien de la faune pollinisatrice du colza provenait essentiellement des autres ressources florales que de lui-même. Nous avons également constaté que les adventices des cultures

participaient au moins autant au soutien de la faune pollinisatrice du colza que les cultures à floraison massive. Enfin, nous avons démontré que la ressource florale passée participant le plus au soutien de pollinisateurs sauvages du colza était les adventices des parcelles cultivées en céréales.

Par conséquent, nous constatons que la pollinisation dans les milieux agricoles peut dépendre fortement d'espaces qui eux ne dépendent pas de la pollinisation, comme les champs de céréales. Cette étude souligne le fait que les pratiques agricoles, comme l'épandage des herbicides, dans les espaces cultivés ne dépendant pas de la pollinisation animale, peuvent avoir un impact majeur sur la pollinisation des cultures dépendantes des pollinisateurs.

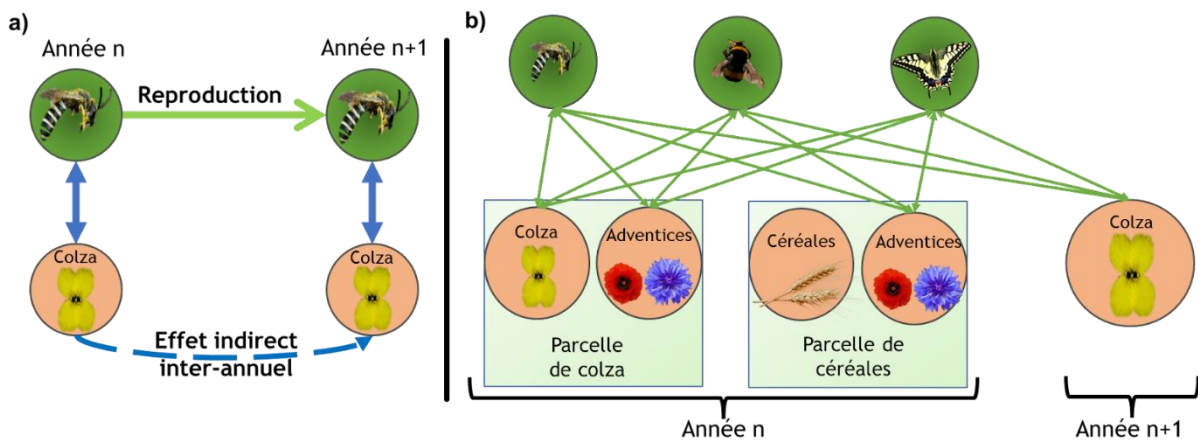


Figure 8 - a) Représentation de l'effet indirect du colza de l'année n sur le colza de l'année n+1 via une espèce de pollinisateur sauvage partagée entre ces deux cultures. b) Représentation des effets indirects reçus par le colza de l'année n+1 des différentes ressources florales passées (année n) par le biais d'une communauté de pollinisateurs sauvages partagés.

Weeds from non-flowering crops as potential contributors to oilseed rape pollination

Published in Agriculture, Ecosystems & Environment

<https://doi.org/10.1016/j.agee.2022.108026>

Ludovic Crochard ^{a,1}, Romain Julliard ^a, Sabrina Gaba ^{b,d}, Vincent Bretagnolle ^{c,d}, Mathilde Baude ^{e,f,2}, Colin Fontaine ^{a,2}

^a Centre d'Ecologie et des Sciences de la Conservation, UMR 7204 MNHN-CNRS-Sorbonne Université, Museum national d'Histoire naturelle, F-75005 Paris, France

^b INRAE, USC 1339, Centre d'Etudes Biologiques de Chizé, F-79360 Villiers-en-Bois, France

^c CNRS, Université de La Rochelle, UMR 7372, Centre d'Etudes Biologiques de Chizé, F-79360 Beauvoir-sur-Niort, France

^d LTSER "Zone Atelier Plaine & Val de Sèvre", CNRS, Beauvoir-sur-Niort, France

^e Université d'Orléans, EA 1207 LBLGC, F-45067 Orléans, France

^f Institute of Ecology and Environmental Sciences-Paris (iEES-Paris), Sorbonne Université, CNRS, IRD, INRAE, Université Paris Cité, UPEC, Paris, France

Abstract

Pollination is essential for many crops since 70% of the world's cultivated plants depend on pollinators for their production. Floral resources within cultivated areas, especially those produced by flowering crops such as oilseed rape, are known to have a positive effect on wild pollinators. Nevertheless, little is known about the contribution of other floral resources, such as weeds within cultivated areas, in supporting wild pollinator communities and subsequent pollination services. Here, we investigate the extent to which oilseed rape pollination benefits from floral

resources produced within cultivated areas, either crops or associated weeds. Based on the Müller index, we analyzed, during four pairs of consecutive years, the potential for inter-annual indirect effects received by oilseed rape through shared wild pollinators from major crops, and their associated weeds, in a typical French intensive agricultural landscape. Our results show that most of the support for oilseed rape pollinating fauna came from alternative types of floral resources than itself. We also find that weeds support oilseed rape pollination as much as flowering crops. Finally, we show that weeds growing within cereal fields have a major contribution to the support of oilseed rape pollination, exceeding the contribution of other floral resources, except oilseed rape. Our results underline that oilseed rape pollination benefits from floral resources present within cultivated fields, whatever the type of crops, including those that do not depend on pollinators for their pollination. Management practices like herbicide reduction in non-pollinator-dependent crops such as cereals are thus likely to impact the pollination of pollinator-dependent crops.

Keywords: Agricultural landscape; Floral resources; Indirect interactions; Müller index; Plant-pollinator networks; Wild pollinators

Introduction

Animal pollination is essential for human food production. 70% of major global food crops are affected by pollinators and these crops represent approximately 35% of annual global food production (Klein et al., 2007). Growing human demand for pollinator-dependent crops, reflected in a disproportionate increase in the area of cultivated pollinator-dependent crops since the 1960's (Aizen et al., 2008), has led to global agricultural production becoming increasingly dependent on pollinators and vulnerable to their decline. This decline, caused by several local and global drivers (Biesmeijer et al., 2006; Potts et al., 2010), impairs the ecosystem service of pollination (Garibaldi et al., 2013; Hoehn et al., 2008; Steffan-Dewenter et al., 2005).

The diet of pollinators mainly consists of pollen and nectar. In agricultural

landscapes, these resources come from different sources, including hedgerows and woodlands (Timberlake et al., 2019), arable weeds (Bretagnolle and Gaba, 2015) and mass flowering crops (e.g., oilseed rape, sunflower, or alfalfa), the latter providing pulses of resource in large quantities for a short period (Westphal et al., 2003). Since the amount of collected resources is likely to affect the reproduction success of pollinators (Beyer et al., 2021; Riedinger et al., 2015; Timberlake et al., 2020; Van der Meersch et al., 2021), the availability of appropriate floral resources during their flight periods can influence their presence and abundance the following year. The pollination services delivered to a crop can therefore be influenced by the floral resources collected in the previous year by the crop's pollinator species. Such indirect facilitation of crop pollination services by other floral resources, flowering in the same year as crops, has been shown with the pollinating fauna of sunflowers benefiting from weeds (Carvalheiro et al., 2011), with apple orchards supporting the pollination services of strawberries (Grab et al., 2017) and might partly explain the positive effect of semi-natural habitats within farmlands on crop pollination services (Bommarco et al., 2012; Shaw et al., 2020; Woodcock et al., 2013; Andersson et al., 2014; Garibaldi et al., 2011; Holzschuh et al., 2012; Kennedy et al., 2013). However, the relative contribution of the various floral resources present in agricultural landscapes to support the pollinating fauna of pollinator-dependent crops remains unknown. Here, the various floral resources could be assimilated into the different crops or the weeds communities associated with each crop.

The Müller index (Müller et al., 1999) aims to quantify the potential for indirect effects from one species to another via shared interacting species. Originally developed for host-parasitoid interactions, this index has previously been used in the pollinator context to assess the potential for indirect effects among flowering plants via shared pollinators (Bergamo et al., 2017; Carvalheiro et al., 2014). For two plants and a shared pollinator, this index quantifies the potential for indirect interaction of one plant to the other and is calculated as the contribution of the first plant to the pollinator's diet multiplied by the contribution of the pollinator to the

pollination of the second plant. In the context of pollination services in agricultural landscapes, summing this index over all pollinator species of a crop allow the relative contribution of the different floral resources needed to deliver pollination services to the crop to be quantified. While this index is usually calculated between co-flowering species, here we propose to address inter-annual indirect interactions from floral resources in a given year to the pollination of a crop the following year. Indeed, most insect pollinators have annual life cycles, with the floral resources available during a year influencing the abundance and composition of the pollinator community the following year. For instance, Timberlake et al. (2020) observed that farmland nectar supply during September is a strong predictor of *Bombus terrestris* colony density in the following year. Similarly, it was demonstrated that high coverage of mass flowering crops in past years could enhance wild bee densities (Beyer et al., 2021; Riedinger et al., 2015).

We aimed to quantify the contribution of the different floral resources present in an agricultural landscape to the potential for inter-annual indirect effects received by oilseed rape. For this, we used plant-pollinator interaction data collected between 2015 and 2019 in 494 fields from the Zone Atelier Plaine & Val de Sèvre, an area located in central-western France where agricultural practices and biodiversity is monitored (Bretagnolle et al., 2018a). Oilseed rape (*Brassica napus* L.) is a flowering crop cultivated for oil that is used for human consumption and biofuel production. Despite being mainly self-pollinated, Perrot et al., (2018) showed that in our study area, insect pollination improved oilseed rape yield by about 37% at the field scale. Nevertheless, there is considerable uncertainty in the estimates of this contribution with values ranging from 10% to 50%, depending on the cultivar studied or the yield parameter used (Araneda Durán et al., 2010; Bartomeus et al., 2014; Bommarco et al., 2012; Lindström et al., 2016; Stanley et al., 2013; Zou et al., 2017). In oilseed rape fields, honeybees (*Apis mellifera*) are usually found to be the most abundant flower-visiting insects (70-80%) followed by hoverflies (10-20%) and wild bees (5-10%) (Bartomeus et al., 2014; Bommarco et al., 2012; Zou et al., 2017; Perrot et al., 2018).

Using the Müller index, we compared the respective contributions of oilseed rape and the sum of the contribution of other floral resources to the potential inter-annual indirect effects received by oilseed rape, to find out whether most of the support comes from oilseed rape itself or from other resources. We then compared the contributions of weeds and crops to the effects received by oilseed rape. To know in more detail the identity of the floral resources producing the most potential for inter-annual indirect effects on oilseed rape, we further investigated the contribution of each floral resource to the potential inter-annual indirect effects received by oilseed rape. Finally, we discuss the respective contributions of cultivated areas, including crops and weeds, and semi-natural habitats to the potential inter-annual indirect effects received by oilseed rape.

Material and methods

Site description and fields selection

This study took place in the Long-Term Social-Ecological Research site “Zone Atelier Plaine & Val de Sèvre” located in South-West France. The study site was an area of 435 km², 87% of which was cultivated and split into 13,000 fields (Bretagnolle et al., 2018a). Oilseed rape represented on average 6.9% (from a minimum of 1.6% in 2019 to a maximum of 9.1% in 2016) of the cultivated area in the study site.

Each year, different fields were selected for pollinator sampling according to the method described by Bretagnolle et al. (2018a,b). Within the study area, we selected each year, 40–60 landscape windows of 1 km², spaced at least 200 m apart, and distributed along gradients of semi-natural habitats, meadows, and organically farmed fields. We further follow the procedure described by Fahrig et al. (2011) to minimize inter-gradient correlations. These gradients were chosen because they are known to influence pollinators (Kennedy et al., 2013). Within each window, 3–4 fields growing different crops were selected for pollinator sampling, depending on

the number of crops grown in the window. Here, we focused on the five main crops grown in the study site, namely: alfalfa, cereals (wheat and barley), meadows, oilseed rape and sunflower. These crops represented together approximately 70% of the area cultivated on the study site each year (Table S.A).

Sampling method

Pollinator sampling was performed annually, from 2015 to 2019. For each selected field, flower-visiting insects were sampled using sweep nets along three 50 m long and 5 m wide transects. The three transects were positioned at the edge, 20 m from the edge and the center of the field. In 2015 however, only transects at the edge and the center of the field were carried out. The sampling effort for each transect was standardized, lasting 10 min, not counting the time needed to process captured insects. Individuals that could not be identified directly during sampling were identified in the laboratory and each captured flower-visiting insect was assigned to the plant species on which it was collected.

As we were interested in the respective roles of crops and their associated weeds, we grouped the pollinator visits into eight different types of floral resources: oilseed rape, weeds located within oilseed rape fields, sunflower, weeds within sunflower fields, alfalfa, weeds within alfalfa fields, weeds within cereal fields, and weeds within meadows (see Table S.B for details about the weed species list associated with each crop). As no pollinators were collected on cereal crops or grasses from meadows during the sampling period, these plants were not considered as floral resources for pollinators in our study. Each year, the sampling period extended from April to August. For each crop and associated weeds, pollinators were captured during the flowering period of the crop. This sampling period extended from April to the end of May for oilseed rape, from mid-April to mid-August for alfalfa, from the end of June to mid-August for sunflower, from the end of April to the end of August for cereal, and from mid-May to mid-August for meadows.

Visitation frequencies per square meter of crop fields

The number of fields sampled per crop per year (Table S.C) was not representative of cultivated areas per crop and per year in our study site. This may result in an over- or underestimation of the effects of a floral resource relative to the area it covers in our study site. To account for that, for each crop and associated weeds, and each year, we first calculated the number of visits of each pollinator species relative to the total area of transects performed (number of the pollinator species visits per square meter). Second, variations in the sampling effort among crops and associated weeds for a given year affect the detection of the least abundant pollinator species, with an over-representation of these pollinator species in the most sampled crop fields. To avoid this bias, we defined a detectability threshold per year, which was equal to: one divided by the area sampled for the crop with the lower sampled area this year. For a given year, all pollinator species with a number of visits per square meter below this threshold were discarded from the analysis. This resulted in the exclusion of approximately 13% of individuals caught over the 5 years of our sampling (740 individuals out of 5815) corresponding to 61% of pollinator species (100 species out of 165).

Potential for inter-annual indirect effect from floral resources to oilseed rape pollination

We calculated the potential for inter-annual indirect effect from each floral resource to oilseed rape via shared pollinators, from one year to the next (Fig.1, Fig. S.A), based on the Müller index (Müller et al., 1999) that we adapted for the inter-annual case. This index is defined as the relative contribution of a floral resource in the diet of a pollinator, multiplied by the relative contribution of the pollinator in the pollination of a focal plant species (the following year, in our case). The contribution to the diet and the pollination is quantified by the number of flower visits. Summing this index over all pollinators shared between a floral resource and the focal plant gives the potential for indirect effect from the floral resource to the focal plant species.

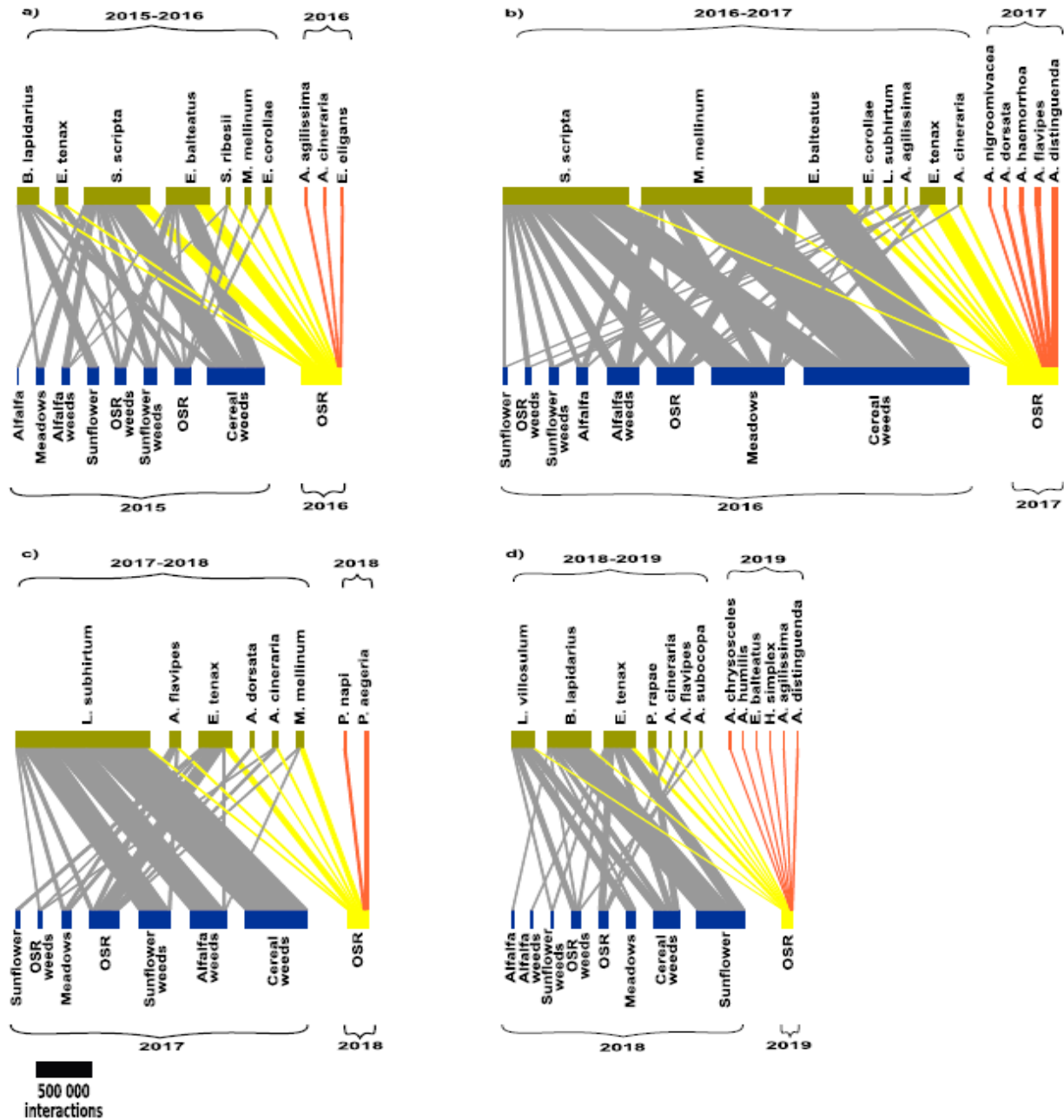


Figure 1. Flower-visitor interaction networks restricted to the pollinator species that were captured during the year $n + 1$ on oilseed rape flowers accounting for the areas covered by each floral resource. The width of the links is proportional to the number of visits which corresponds to the intensity of the interactions between floral resources and pollinators, taking into account the areas covered by the different floral resources each year. The blue boxes correspond to the floral resource present in year n , while the green boxes correspond to the pollinators present in both year n and year $n+1$. The orange boxes correspond to pollinator species only present in year $n+1$ and the yellow box corresponds to the oilseed rape of year $n+1$. The grey links correspond to interactions between floral resources of year n and pollinator species of year n . The yellow links correspond to interactions of pollinators of year $n+1$ (already present the year n) on oilseed rape $n+1$. The orange links correspond to interactions between pollinator species only present in year $n+1$ and oilseed rape of year $n+1$.

The formula is as follows:

$$d_{i_n,osr_{n+1}} = \sum_{k=1}^l \left(\frac{\alpha_{i_n,k} area_{i_n}}{\sum_{j=1}^m \alpha_{j_n,k} area_{j_n}} \times \frac{\alpha_{osr_{n+1},k} area_{osr_{n+1}}}{\sum_{k=1}^l \alpha_{osr_{n+1},k} area_{osr_{n+1}}} \right)$$

Where $d_{i_n,osr_{n+1}}$ is the value of the potential for the indirect effect of the floral resource i of the year n on oilseed rape (osr) of the year $n + 1$ via shared pollinators. $\alpha_{i_n,k}$ is the number of visits of pollinators of the species k on floral resource i the year n per unit of area of the floral resource i . $area_{i_n}$ corresponds to the cultivated area of the floral resource i the year n . m and l correspond to all floral resource types and all pollinator species respectively. The first part of the equation corresponds to the proportion of floral resource i in the diet of the pollinator species k in year n . The second part of the equation corresponds to the proportion of pollinator visits performed by pollinator species k on oilseed rape crop in the year $n + 1$. The potential for inter-annual indirect effect of each floral resource on oilseed rape was calculated by taking into account the area of each floral resource within the study site but also per unit area, i.e. with $area_{i_n} = 1$.

Honeybees (*Apis mellifera*) were excluded from the analysis because they should not propagate inter-annual indirect effects in the same way as wild pollinators. Indeed, changes in honeybee abundance from one year to the next might be more affected by beekeeping practices (e.g. winter feeding, colony displacement) than by the availability of floral resources. However, we also performed the analysis including honeybees as efficient pollinators of oilseed rape. In this case, the visits made by honeybees were taken into account in the second part of the equation, depicting their contribution to the pollination of oilseed rape, but not in the first part of the equation thereby not propagating inter-annual indirect effects. This did not change the results we present next. Only the strength of the indirect effects was modified by taking into account honeybees (Fig. S.B).

Statistical analyses

As sampling was carried out for five consecutive years, we were able to calculate the potential for inter-annual indirect effects received by oilseed rape from each floral resource for four couples of consecutive years. For each of these couple of consecutive years, we regrouped floral resources into different sets, summing their potential for inter-annual indirect effects, to ask three questions. First, do inter-annual indirect effects received by oilseed rape mainly come from oilseed rape from the previous year or from other floral resources? To answer this question, we compared the indirect effect from oilseed rape to oilseed rape to the sum of indirect effects from all other floral resources to oilseed rape, this using a two-tailed Student test. Second, we asked do weeds produce more, or less, potential for inter-annual indirect effects on oilseed rape pollination than flowering crops? For that, we compared the sum of potential for inter-annual indirect effects produced by flowering crops, (i.e. oilseed rape, alfalfa and sunflower), to the sum of potential for inter-annual indirect effects produced by the weeds present in all crop fields, this using a two-tailed Student test. Third, we asked does the potential for inter-annual indirect effect provided to oilseed rape pollination differ among the height type of floral resources? To do so, we performed a linear model using generalized least squares with the potential for inter-annual indirect effects as dependent variable and the identity of the floral resource as explanatory factor comprising height modalities corresponding to the eight types of floral resources described before. We used the `gls` function from the `nlme` package (Pinheiro et al., 2020). As the homoscedasticity assumption was not met, we modeled heteroscedasticity as the power of the fitted values using the “weight” argument of the `gls` function. The significance of the identity of the type of floral resource was tested with an ANOVA (Chisq test).

These three tests were performed for both the value of potential for inter-annual indirect effects calculated accounting for the area covered by each resource as well as the value per unit area. These two modes of calculation allowed us to better understand whether particular floral resources were key in producing the potential for

inter-annual indirect effect on oilseed rape pollination because of the large area cultivated or because they were intrinsically more attractive to oilseed rape pollinators. All statistical analyses were performed using R (R Core Team, 2019).

Results

Pollinators are shared among crops and weeds

During the five years of our study, and after applying the detectability threshold, 5075 wild pollinators from 65 species collected from floral resources were considered in subsequent analyses. Among them, 48.9% were Diptera, 44.9% were Hymenoptera and 6.2% were Lepidoptera. Meadows were the floral resource in which the most pollinator species were caught with 31 species (Table 1). Conversely, weeds growing in oilseed rape fields were the floral resource in which the fewest pollinator species were caught with 15 species. On oilseed rape flowers, 515 insects from 25 species were sampled, of which 9 (36%) were exclusively sampled on these flowers. Weeds growing in oilseed rape fields were the floral resource that shared the most pollinator species with oilseed rape flowers, with 13 species, while alfalfa and sunflower were the floral resources sharing the least pollinator species with oilseed rape, with only 6 species. The sharing of pollinators, that we observed, between oilseed rape and other floral resources indicates that there is a potential for indirect effects from these different floral resources on oilseed rape pollination.

The support of oilseed rape pollinators is mainly provided by floral resources other than oilseed rape

We found a significant difference when comparing the potential for inter-annual indirect effect produced by oilseed rape to the one produced by all other floral resources taken together (Table 2). We found the same result when accounting for the areas covered by each floral resource and considering the potential for indirect interactions per unit area. Oilseed rape produced significantly less potential for inter-annual indirect effects (0.53 ± 0.15 , mean \pm standard deviation) than the other floral resources taken together (0.26 ± 0.13 ; Fig. 2a, Fig. S.C.a). This indicated that most of

the support provided by floral resources within cultivated areas to the pollinating fauna of oilseed rape the following year came from alternative floral resources to oilseed rape.

Floral resource	Abundance per unit area	Species richness	Number of shared species with oilseed rape
Alfalfa	670	16	6
Weeds within alfalfa fields	1979	25	10
Weeds within cereal fields	867	19	10
Meadows	1626	31	10
Oilseed rape	707	25	
Weeds within oilseed rape fields	253	15	13
Sunflower	839	19	6
Weeds within sunflower fields	702	28	9

Table 1 - Pollinator abundance per unit area (ha), species richness, and number of shared species with oilseed rape recorded over the 5 years of sampling for each floral resource.

Test	Scale	Df	T	P-value
Oilseed rape vs other floral resources	Accounting for the relative areas covered by each floral resource	6	2.78	0.032
Crop vs Weeds		6	-1.40	0.210
Oilseed rape vs other floral resources	Unit area	6	3.60	0.011
Crop vs Weeds		6	-1.75	0.132

Table 2 - Results of Student tests performed to study the difference of the potential for inter-annual indirect effects produced by oilseed rape and all other floral resources accounting for the relative areas covered by each floral resource and per unit area; and the difference of the potential for inter-annual indirect effects produced by crops and weeds accounting for the relative areas covered by each floral resource and per unit area.

The support of oilseed rape pollinators provided by weeds and flowering crops is equivalent

We did not detect a significant difference between the potential for inter-annual indirect effects produced by flowering crops (0.33 ± 0.12) and the one produced by the flowering weeds growing within crop fields (0.46 ± 0.15), although there was a

tendency for a higher contribution of weeds. The same results were found when considering the potential for indirect interactions per unit of area and accounting for the areas covered by each floral resource (Table 2, Fig. 2b, Fig. S.C.b). This indicated that the contribution of weeds and flowering crops to feed oilseed rape pollinating fauna was not statistically different.

The dominance of cereal fields makes cereal weeds a key resource for oilseed rape pollinating fauna

We found a significant effect of the type of floral resource on the potential for inter-annual indirect effect received by oilseed rape whatever the type of calculation: per unit area (Chisq = 26.64, df = 7, $p = 3.87e-4$) and accounting for the areas covered by each floral resource (Chisq = 36.514, df = 7, $p < 0.0001$). Accounting for the areas of each floral resource, weeds growing in cereal fields (0.20 ± 0.17) and oilseed rape (0.26 ± 0.13) seemed to be the floral resource producing the strongest potential for inter-annual indirect effect compared to other floral resources (Fig. 2c). The other floral resources contributed approximately 3.5 times less to the pollination support of oilseed rape, except alfalfa with almost no potential for inter-annual indirect effect. Looking at the potential for inter-annual indirect effect per unit area, the pattern was different: only oilseed rape seemed to produce a higher potential for inter-annual indirect effect (0.26 ± 0.09) than the other floral resources (Fig. S.C.c). This suggests that when accounting for the areas of each floral resource, oilseed rape pollination mainly benefits from weeds growing within cereal fields and oilseed rape flowers.

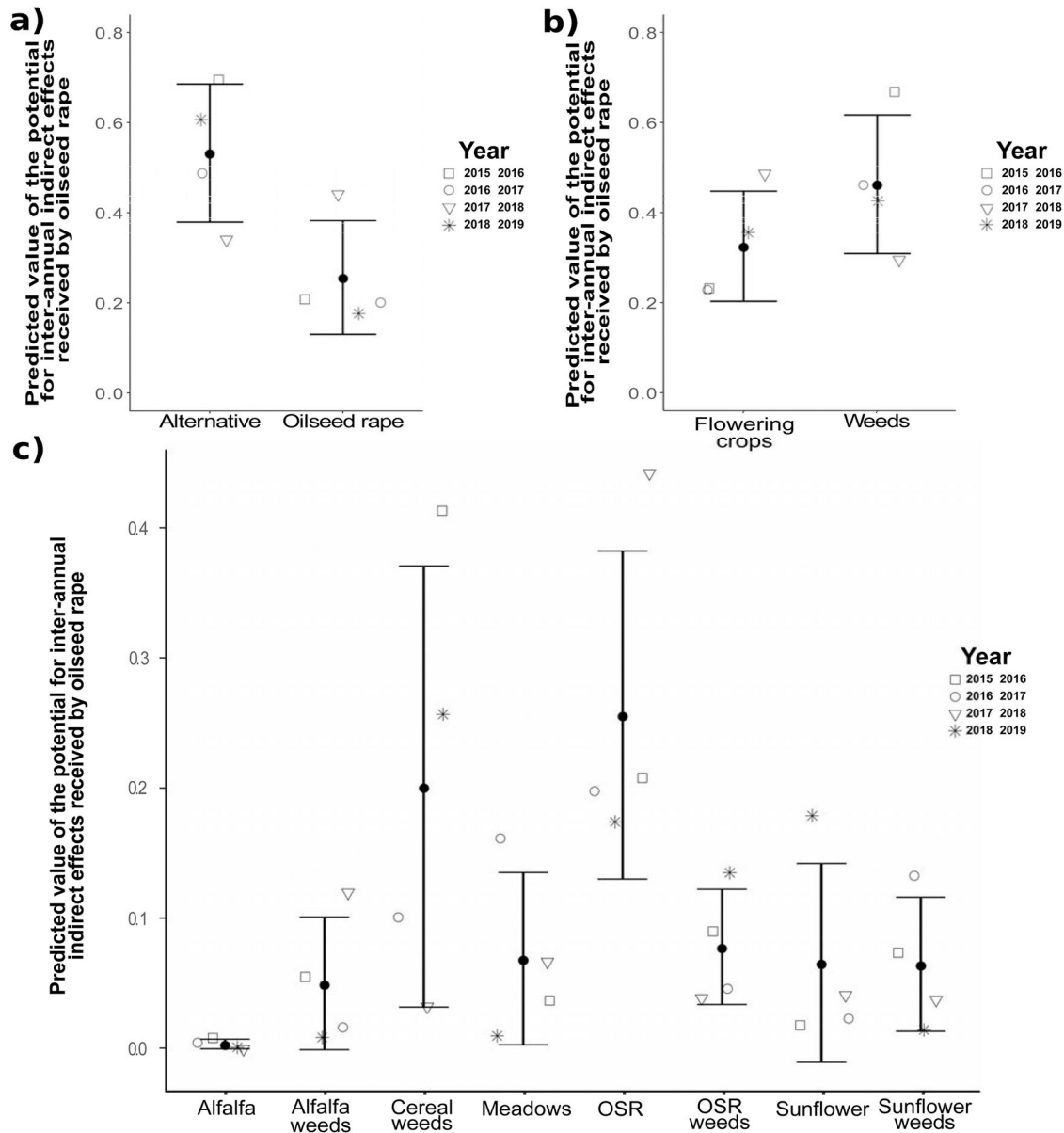


Figure 2. Predicted values (mean \pm 1 standard deviation) of the potential for inter-annual indirect effects received by oilseed rape flowers accounting for the relative areas covered by each floral resource: (a) oilseed rape alone vs the alternative types of floral resources together, (b) weeds vs crops and (c) each floral resource. The type « Alternative » corresponds to the sum of values of the potential for inter-annual indirect effects produced each year by all floral resources excepted oilseed rape. In each panel, points correspond to the predicted potential for inter-annual indirect effects calculated for each successive pair of years and the error bars to the estimated standard deviations. The different symbols correspond to the potential for inter-annual indirect effects calculated for each successive pair of years.

Discussion

Our analysis brings evidence that pollinators are shared among flowering crops and also among flowering crops and associated weeds. By quantifying the potential for inter-annual indirect interactions on the pollination of oilseed rape in a typical French agricultural landscape, our results further indicate that the insect-pollination of oilseed rape is mainly supported by alternative floral resources. This reflects that the main part of the diet of oilseed rape pollinators was made of floral resources other than oilseed rape in the previous year (Fig. 1). Our results thereby suggest that the pollination services of oilseed rape is affected by other flowering crops as well as arable weeds, making crop fields, flowering or not, and associated weeds potential levers for enhancing pollination services in an agricultural landscape. This is further supported by recent results showing that crop diversity may have a positive effect on the densities of some wild pollinator species (Raderschall et al., 2021).

The contribution of arable weeds that we reported is equivalent to that of flowering crops, which is in line with other studies highlighting arable weeds as important resources for wild pollinators (Bretagnolle and Gaba, 2015; Carvalheiro et al., 2011; Holzschuh et al., 2007; Rollin et al., 2013). This result is even more striking as among the considered crops here, sunflower and oilseed rape, are mass flowering crops known to provide large amounts of food resources to pollinators and to favor wild pollinators in rapeseed fields (Holzschuh et al., 2013; Westphal et al., 2003). Further, the relative contribution of weeds and flowering crops we found might underestimate weeds' contribution as we only sampled pollinator visits during the crop flowering period, and we know that weed resources are particularly needed between crop flowering peaks (Timberlake et al., 2019).

Detailing the contribution among weeds, we found that weeds growing in cereal fields made a strong contribution to the inter-annual indirect effects on oilseed rape pollination, but this pattern vanished when considering the contribution per unit area. This indicated that their contribution was mainly due to the large area cereal fields represent in our study site, though such dominance of cereal fields is representative of

cultivated areas at the scale of France or Europe (FAOSTAT, 2020). This contrasts with the view that cereals fields are irrelevant to pollinators because cereals are poor resources for pollinators (Roulston et al., 2000). Our study suggests that cereal weeds can substantially contribute to the floral resources supporting the pollination fauna of oilseed rape, and thereby its pollination services. This has consequences for both our understanding of the functioning of pollination services in agricultural landscapes and also of the agricultural practices related to pollination services. For instance, practices favoring flowering weeds, by limiting herbicides, whose positive effect on yields has not been clearly demonstrated unlike their negative effect on weed flora (Gaba et al., 2016), and limiting insecticides in cereal fields might benefit pollinators (Holzschuh et al., 2007) and pollination services of other crops. Cereal organic farming could have a positive impact on the pollination services of surrounding pollinator-dependent crops, since it promotes weed diversity in cultivated fields as well as in the margins of neighboring fields, even those grown conventionally (Henckel et al., 2015). Weeds may also compete for resources with crops, potentially lowering yield (Milberg and Hallgren, 2004). If so, innovative crop management such as reduced sowing density (Sidemo-Holm et al., 2021) or sowing competitive cultivars (Gaba et al., 2018) might be promoted. In flowering crops, we found that oilseed rape was the crop that generated the most inter-annual indirect interactions on itself, both per unit area and taking into account the areas of each floral resource. This is in accordance with previous results showing that the potential influence of one plant on another via shared pollinators increases when plants are phylogenetically close (Carvalheiro et al., 2014).

One key limitation of our study is that we did not sample pollinator visits in semi-natural habitats, preventing us from quantifying their contribution. There is strong evidence that the visitation frequency of flowering crops by wild pollinators and their diversity are positively linked to the proximity to semi-natural habitats (Carvalheiro et al., 2010; Garibaldi et al., 2011; Klein et al., 2012; Ricketts et al., 2008). In addition to nesting sites, semi-natural areas provide floral resources to wild pollinators in agricultural landscapes (Rollin et al., 2013; Woodcock et al., 2013). Therefore the strength of the potential for inter-annual indirect effects received by oilseed rape from

cultivated areas could be weaker than the one we estimated here if we included the floral resources provided by these habitats in the analysis. Although nectar production from semi-natural habitats is likely to be higher than from cultivated areas (Baude et al., 2016), the area of semi-natural habitats in our study site relative to one of the crop fields suggests that the contribution of cultivated areas should remain higher than the one of semi-natural habitat (Appendix A). However, some more work is needed to compare the contribution of cultivated areas to one of semi-natural areas, for example accounting for the contribution of semi-natural habitats to other key resources, such as nesting sites (Lye et al., 2009; Nayak et al., 2015). Another simplifying assumption of our approach is that all visits are considered equivalent in terms of resources for pollinators and pollination efficiency. Yet it is well known that flowers from different species differ in quantity and quality of resources they provide to pollinators (Baude et al., 2016; Pamminger et al., 2019). Even within crop species, cultivars are not equivalent in the resources they provided (Ouvrard and Jacquemart, 2019). Similarly, the pollination efficiency of one oilseed rape visit depends on the identity of the visiting species (Garibaldi et al., 2011; Jauker et al., 2012; Kremen et al., 2002; Rader et al., 2016). Accounting for such differences in our framework is possible by weighting visits by the benefit they provide but would require more data on pollination efficiency (but see: Woodcock et al., 2013) and nectar production than currently available.

Conclusion

Our results suggest that cultivated areas support oilseed rape pollination by wild pollinators. To promote the pollination of a given crop, it is therefore necessary to consider the whole cultivated area and not only the one where the crop of interest is grown. Our results indicate that it is also essential to promote associated weeds of crops located in the vicinity of the crop of interest. This could be an interesting lever to improve pollination services. Finally, our analysis also suggests that agricultural practices favoring the presence of weed flora, even in pollinator independent crops like cereals, are beneficial for pollination services.

Acknowledgments

We would like to express our thanks to Alexis Saintilan and Marylin Roncoroni for their help to fields sampling and for insect identification. This research was funded through the ANR IMAGHO (ANR-18- CE32-0002) and the Projet 'Pollinisateurs' from Ministry of Ecological Transition.

Supplementary

Table S.A The cultivated area of each crop in the site 'Zone Atelier Plaine & Val de Sèvre' for each year and the corresponding percentage of the total cultivated area of the study site.

Crop field	Year	Area in ha	Percentage of the cultivated areas
Alfalfa	2015	951	2.7
	2016	1109	3.1
	2017	1312	3.7
	2018	1524	4.3
	2019	1547	4.4
Cereals	2015	16185	45.3
	2016	16439	46
	2017	15685	44.1
	2018	15090	42.3
	2019	15715	44.3
Meadows	2015	2865	8
	2016	2701	7.6
	2017	2620	7.4
	2018	2674	7.5
	2019	2616	7.4
Oilseed rape	2015	2945	8.2
	2016	3256	9.1
	2017	2827	7.9
	2018	2606	7.3
	2019	582	1.6
Sunflower	2015	4157	11.6
	2016	3479	9.7
	2017	3516	9.9
	2018	4258	12
	2019	4280	12.1

Table S.B Lists of weed species found in fields of each crop type. A total of 131 weed species were recorded overall.

Weed species name	Alfalfa	Cereals	Meadows	Oilseed rape	Sunflower
<i>Achillea millefolium</i>			X		X
<i>Agrimonia eupatoria</i>		X	X		
<i>Althaea cannabina</i>					X
<i>Althaea officinalis</i>			X		
<i>Ammi majus</i>	X		X		X
<i>Anthemis arvensis</i>		X			
<i>Anthemis cotula</i>		X			X
<i>Anthriscus caucalis</i>	X	X	X	X	
<i>Anthriscus sylvestris</i>		X	X		
<i>Arctium lappa</i>					X
<i>Bellis perennis</i>	X	X	X	X	
<i>Borago officinalis</i>				X	
<i>Bryonia dioica</i>					X
<i>Bupleurum subovatum</i>		X			
<i>Carduus crispus</i>	X				
<i>Carduus nutans</i>				X	
<i>Carduus pycnocephalus</i>		X	X	X	
<i>Carduus sp</i>		X		X	X
<i>Carduus tenuiflorus</i>	X	X	X	X	
<i>Centaurea jacea</i>	X	X	X	X	X
<i>Centaurea scabiosa</i>					X
<i>Chaerophyllum temulum</i>		X	X		
<i>Cichorium intybus</i>	X	X	X		X
<i>Cirsium arvense</i>		X	X	X	X
<i>Cirsium vulgare</i>			X		
<i>Clematis vitalba</i>					X
<i>Convolvulus arvensis</i>	X	X	X		X
<i>Convolvulus sepium</i>	X				X
<i>Cornus sanguinea</i>	X	X			
<i>Coronilla varia</i>			X		
<i>Crataegus monogyna</i>			X		
<i>Crepis biennis</i>			X		
<i>Crepis capillaris</i>	X				
<i>Crepis foetida</i>				X	
<i>Crepis sancta</i>	X	X	X	X	X
<i>Crepis setosa</i>	X	X			X
<i>Cuscuta epithimum</i>	X				
<i>Cyanus segetum</i>					X

Dactylis glomerata				X	
Daucus carota	X	X	X		X
Erodium cicutarium		X		X	
Eryngium campestre			X		X
Falcaria vulgaris					X
Fallopia convolvulus	X				
Galium aparine		X	X	X	
Galium mollugo	X	X	X		X
Galium verum		X	X		
Geranium columbinum			X		
Geranium dissectum		X	X	X	
Geranium molle	X	X	X	X	
Geranium pusillum		X		X	
Geranium robertianum		X	X	X	
Geranium rotundifolium				X	
Geum urbanum			X		
Helminthotheca echioides	X	X	X		X
Hippocrepis comosa			X		
Humulus lupulus		X			
Hypericum perforatum	X	X	X		X
Hypochaeris radicata			X		X
Jacobaea vulgaris			X		
Knautia arvensis	X	X	X		
Lamium purpureum				X	X
Lapsana communis		X	X		
Lathyrus pratensis			X		
Lathyrus sylvestris			X		
Legousia speculum		X			
Lepidium campestre			X		
Leucanthemum vulgare	X	X	X		X
Ligustrum vulgare		X			
Linaria vulgaris					X
Loncomelos pyrenaicus		X			
Lysimachia arvensis			X		
Malva sylvestris	X	X	X		X
Matricaria chamomilla					X
Medicago arabica		X	X	X	
Medicago lupulina		X	X		
Medicago sativa		X	X		X
Mentha suaveolens	X				

Mercurialis annua		X			
Myosotis arvensis	X	X	X	X	
Origanum vulgare	X		X		X
Papaver rhoeas	X	X		X	
Persicaria maculosa					X
Phacelia tanacetifolia				X	
Picris hieracioides	X	X	X	X	X
Pisum sativum			X		
Plantago lanceolata	X	X	X		X
Poa trivialis		X			
Potentilla reptans		X	X		
Ranunculus acris			X		
Ranunculus arvensis			X	X	
Ranunculus bulbosus			X	X	
Ranunculus parviflorus			X		
Ranunculus repens			X		
Reseda lutea		X		X	X
Rosa canina	X	X		X	X
Rubus fruticosus	X	X	X		X
Rubus idaeus			X		
Salvia pratensis			X		
Sambucus ebulus		X			
Sambucus nigra	X				
Scandix pecten				X	
Senecio vulgaris		X			
Sherardia arvensis		X			
Silene latifolia	X	X		X	
Silybum marianum		X	X		
Sinapis alba		X		X	
Sinapis arvensis		X	X	X	
Sisymbrium officinale		X		X	
Solanum nigrum	X				
Sonchus asper	X	X			
Sonchus oleraceus	X		X	X	
Stachys annua	X				
Taraxacum ruderales				X	X
Thymus serpyllum			X		
Torilis arvensis	X	X	X		
Tragopogon pratensis			X		
Trifolium campestre			X		
Trifolium dubium			X		

<i>Trifolium pratense</i>	x		x	
<i>Trifolium repens</i>			x	x
<i>Tripleurospermum inodorum</i>		x		
<i>Verbena officinalis</i>			x	x
<i>Veronica arvensis</i>		x		
<i>Veronica hederifolia</i>				x
<i>Veronica persica</i>		x		x
<i>Viburnum lantana</i>		x		
<i>Vicia cracca</i>			x	
<i>Vicia faba</i>				x
<i>Viola arvensis</i>				x
<i>Zea mays</i>	x			

Table S.C Number of fields sampled in each type of floral resource type for each year of our study

Year	Alfalfa (crop & weeds)	Cereal (weeds)	Meadows (weeds)	Oilseed rape (crop & weeds)	Sunflower (crop & weeds)
2015	15	72	11	31	33
2016	12	58	47	41	29
2017	10	57	17	26	69
2018	13	53	18	25	24
2019	12	32	12	25	19

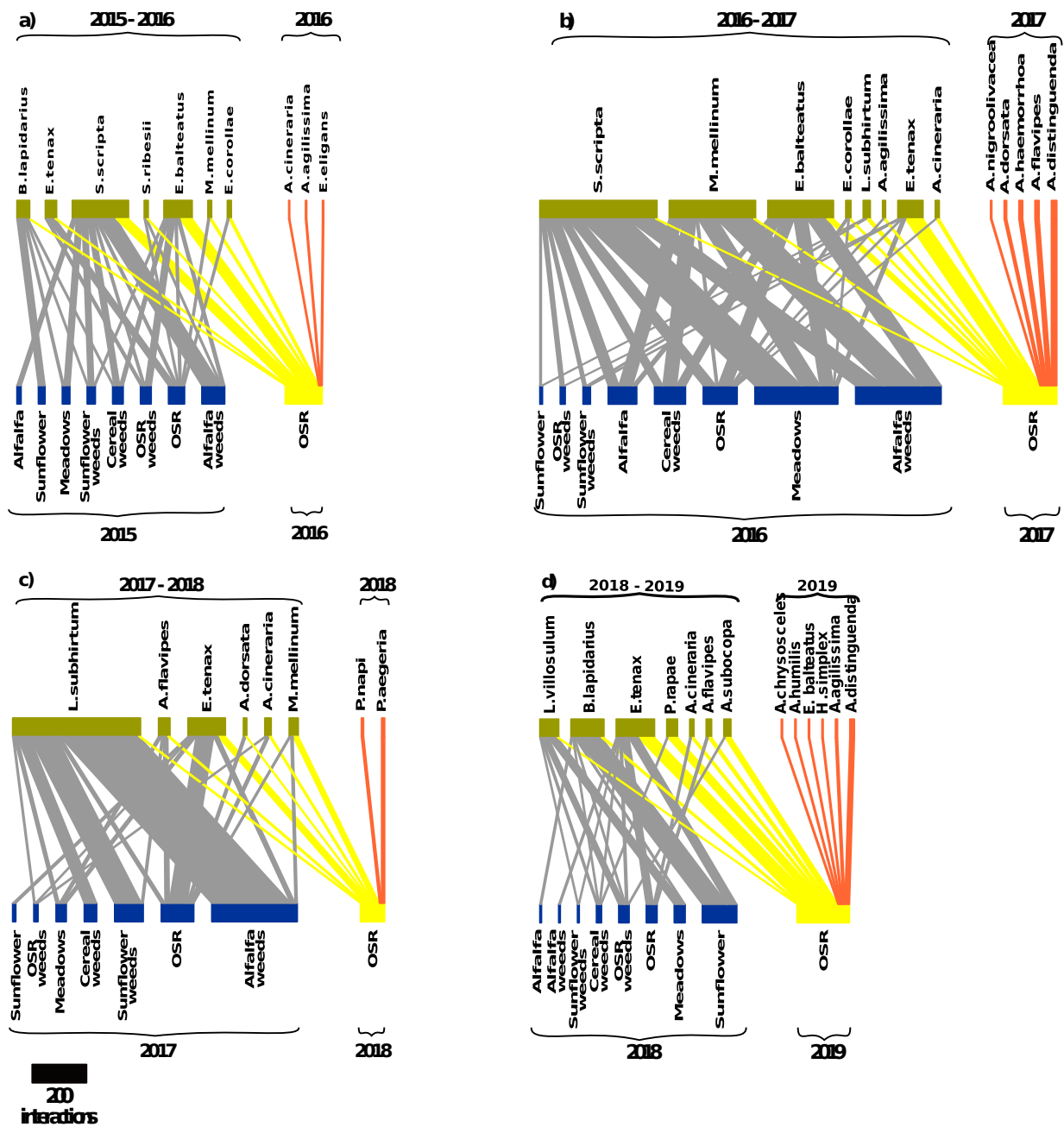


Figure S.A Flower-visitor interaction network restricted to the pollinator species that were captured during the year $n + 1$ on oilseed rape flowers per unit area (ha) of each floral resource. The width of the links is proportional to the number of visits which corresponds to the intensity of the interactions between floral resources and pollinators, taking into account the mean intensity per unit area of interactions. The blue boxes correspond to the floral resource present in year n , while the green boxes correspond to the pollinators present in both year n and year $n + 1$. The orange boxes correspond to pollinator species only present in year $n + 1$ and the yellow box corresponds to the oilseed rape of year $n + 1$. The grey links correspond to interactions between floral resources of year n and pollinator species of year n . The yellow links correspond to interactions of pollinators of year $n + 1$ (already present the year n) on oilseed rape $n + 1$. The orange links correspond to interactions between pollinator species only present in year $n + 1$ and oilseed rape of year $n + 1$.

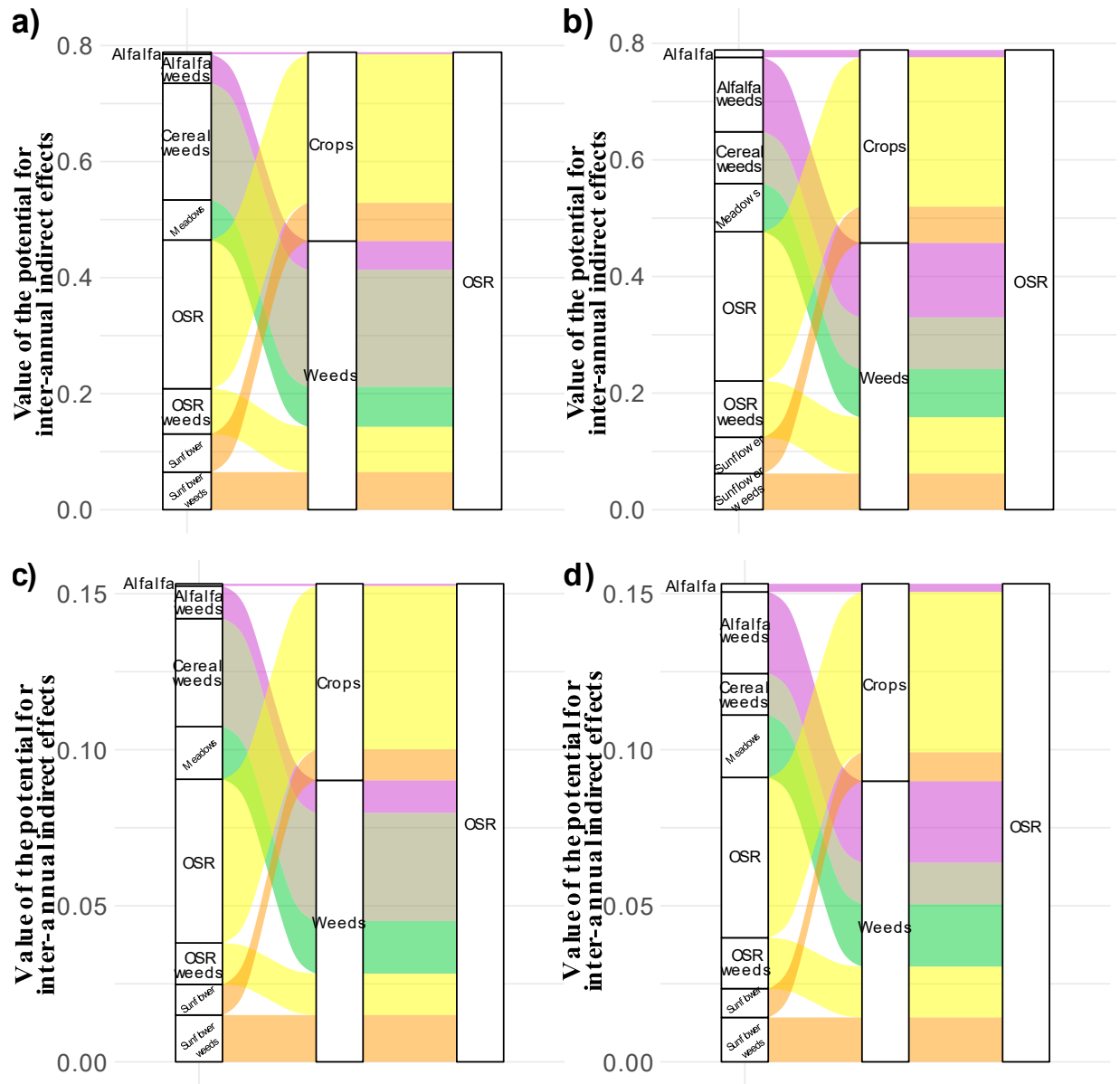


Figure S.B Alluvial plots describing the distribution of the average of the potential for inter-annual indirect effects received by oilseed rape (column 3) according to floral resource type (column 1) and the flora type (column 2): a) accounting for the relative areas covered by each resource type and without taking into account *Apis mellifera* as a pollinator of oilseed rape. b) per unit area of each floral resource type without taking into account *Apis mellifera* as a pollinator of oilseed rape. c) accounting for the relative areas covered by each resource type and by accounting for *Apis mellifera* as a pollinator of oilseed rape. d) per unit area of each floral resource type by accounting for *Apis mellifera* as a pollinator of oilseed rape.

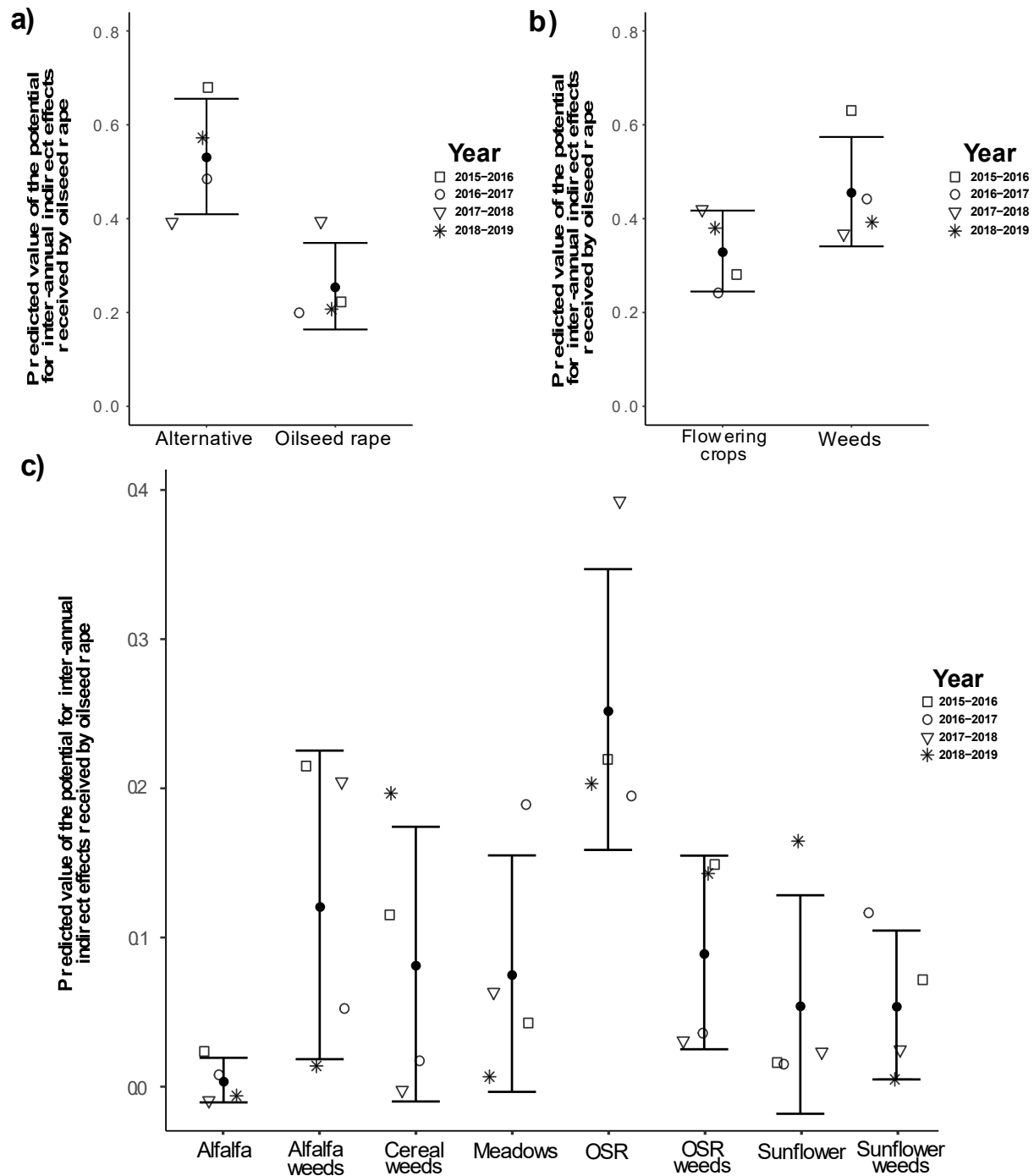


Figure S.C Predicted values (mean +/- 1 standard deviation) of the potential for inter-annual indirect effects received by oilseed rape per unit area of each resource type that are produced (a) by oilseed rape alone vs the other types of floral resources together, (b) type by weeds vs crops and (c) by each floral resource. The type « Alternative » corresponds to the sum of values of the potential for inter-annual indirect effects produced each year by all floral resource types excepted oilseed rape. In each panel, points correspond to the predicted potential for inter-annual indirect effects calculated for each successive pair of years and the error bars to the estimated standard deviations. The different symbols correspond to the potential for inter-annual indirect effects calculated for each successive pair of years.

Appendix A

As pollinator visits were not recorded in semi natural habitats, we cannot quantify their contribution to oilseed rape pollination through the calculation of potential for indirect effects. We nonetheless indirectly assessed the contribution of cultivated areas and semi-natural areas to the support of oilseed rape pollination by comparing nectar production between cultivated areas and semi-natural habitats. To do this, we estimated average nectar production of crop fields and semi-natural habitats from the literature and multiplied it by the areas of each land use in our study site.

Estimates of nectar production came from Baude et al. (2016) which provides an assessment of nectar production for different floral habitats in Great Britain. They indicate that cultivated areas produce on average 6.9 kg of sugars per hectare and per year. However, this estimate is based on the distribution of crops in Great Britain in 2007, which may be different from that observed at our study site. Turning to semi-natural habitats, we averaged the nectar productions of the following floral habitat: acid grass, bog, bracken, broadleaf, calcareous grass, conifer, fen, improved grass, neutral grass and shrub heath. This leads to 52.6 kg of sugars per hectare per year, hence 7.6 times higher than cultivated areas.

To estimate the area of semi-natural habitats in our study site, we used the 2017 OSO database (Inglada et al., 2017). We summed areas of deciduous forest, coniferous forest, grassland, woody heath, and meadows that were not included in the "Registre Parcellaire Graphique" of 2017 (Institut National de l'Information Géographique et Forestière, 2017) as they are part of the cultivated areas. We found that the area of semi-natural habitats in 2017 was 2030 hectares (4.7% of the study site). The cultivated area, estimated from the "Registre Parcellaire Graphique" of 2017 was 35500 hectares (81.6% of the study site).

Based on these estimates, cultivated areas produce more than twice the amount of nectar produced by semi-natural habitats suggesting that the contribution of cultivated areas to the support of oilseed rape pollinator should remain higher than the one of semi natural habitat.

References

- Aizen, M.A., Garibaldi, L.A., Cunningham, S.A., Klein, A.M., 2008. Long-Term Global Trends in Crop Yield and Production Reveal No Current Pollination Shortage but Increasing Pollinator Dependency. *Curr. Biol.* 18, 1572-1575. <https://doi.org/10.1016/j.cub.2008.08.066>
- Andersson, G.K.S., Ekroos, J., Stjernman, M., Rundlöf, M., Smith, H.G., 2014. Effects of farming intensity, crop rotation and landscape heterogeneity on field bean pollination. *Agric. Ecosyst. Environ.* 184, 145-148. <https://doi.org/10.1016/j.agee.2013.12.002>
- Araneda Durán, X., Breve Ulloa, R., Aguilera Carrillo, J., Lavín Contreras, J., Toneatti Bastidas, M., 2010. Evaluation of Yield Component Traits of Honeybee-Pollinated (*Apis mellifera* L.) Rapeseed Canola (*Brassica napus* L.). *Chil. J. Agric. Res.* 70, 309-314. <https://doi.org/10.4067/S0718-58392010000200014>
- 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>
- 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, 85-88. <https://doi.org/10.1038/nature16532>
- Bergamo, P.J., Wolowski, M., Maruyama, P.K., Vizenin-Bugoni, J., Carvalheiro, L.G., Sazima, M., 2017. The potential indirect effects among plants via shared hummingbird pollinators are structured by phenotypic similarity. *Ecology* 98, 1849-1858. <https://doi.org/10.1002/ecy.1859>
- 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. *Agric. Ecosyst. Environ.* 319, 107537.

<https://doi.org/10.1016/j.agee.2021.107537>

- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science* 313, 351–354. <https://doi.org/10.1126/science.1127863>
- Bommarco, R., Marini, L., Vaissière, B.E., 2012. Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia* 169, 1025–1032. <https://doi.org/10.1007/s00442-012-2271-6>
- Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhausser, I., Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018a. Towards sustainable and multifunctional agriculture in farmland landscapes: Lessons from the integrative approach of a French LTSER platform. *Sci. Total Environ.* 627, 822–834. <https://doi.org/10.1016/j.scitotenv.2018.01.142>
- Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhausser, I., Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018b. Description of long-term monitoring of farmland biodiversity in a LTSER. *Data Brief* 19, 1310–1313. <https://doi.org/10.1016/j.dib.2018.05.028>
- Bretagnolle, V., Gaba, S., 2015. Weeds for bees? A review. *Agron. Sustain. Dev.* 35, 891–909. <https://doi.org/10.1007/s13593-015-0302-5>
- Carvalheiro, L.G., Biesmeijer, J.C., Benadi, G., Fründ, J., Stang, M., Bartomeus, I., Kaiser-Bunbury, C.N., Baude, M., Gomes, S.I.F., Merckx, V., Baldock, K.C.R., Bennett, A.T.D., Boada, R., Bommarco, R., Cartar, R., Chacoff, N., Dänhardt, J., Dicks, L.V., Dormann, C.F., Ekroos, J., Henson, K.S.E., Holzschuh, A., Junker, R.R., Lopezaraiza-Mikel, M., Memmott, J., Montero-Castaño, A., Nelson, I.L., Petanidou, T., Power, E.F., Rundlöf, M., Smith, H.G., Stout, J.C., Temeitope, K., Tscharrntke, T., Tscheulin, T., Vilà, M., Kunin, W.E., 2014. The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. *Ecol. Lett.* 17, 1389–1399. <https://doi.org/10.1111/ele.12342>
- Carvalheiro, L.G., Seymour, C.L., Veldtman, R., Nicolson, S.W., 2010. Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *J.*

- Appl. Ecol. 47, 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. *Ecol. Lett.* 14, 251-259. <https://doi.org/10.1111/j.1461-0248.2010.01579.x>
- 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. *Ecol. Lett.* 14, 101-112. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>
- FAOSTAT [WWW Document], 2020. . Food Agric. Organ. U. S. WWW Doc. URL <http://www.fao.org/faostat/en/#data/QC> (accessed 7.15.21).
- 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, e02413. <https://doi.org/10.1002/ecs2.2413>
- Gaba, S., Gabriel, E., Chadœuf, J., Bonneu, F., Bretagnolle, V., 2016. Herbicides do not ensure for higher wheat yield, but eliminate rare plant species. *Sci. Rep.* 6, 30112. <https://doi.org/10.1038/srep30112>
- Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalho, 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., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 14, 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., Carvalho, 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., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts,

- S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. *Science* 339, 1608-1611. <https://doi.org/10.1126/science.1230200>
- 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. *Sci. Rep.* 7, 45296. <https://doi.org/10.1038/srep45296>
- Henckel, L., Börger, L., Meiss, H., Gaba, S., Bretagnolle, V., 2015. Organic fields sustain weed metacommunity dynamics in farmland landscapes. *Proc. R. Soc. B Biol. Sci.* 282, 20150002. <https://doi.org/10.1098/rspb.2015.0002>
- Hoehn, P., Tscharntke, T., Tylianakis, J.M., Steffan-Dewenter, I., 2008. Functional group diversity of bee pollinators increases crop yield. *Proc. R. Soc. B Biol. Sci.* 275, 2283-2291. <https://doi.org/10.1098/rspb.2008.0405>
- Holzschuh, A., Dormann, C.F., Tscharntke, T., Steffan-Dewenter, I., 2013. Mass-flowering crops enhance wild bee abundance. *Oecologia* 172, 477-484. <https://doi.org/10.1007/s00442-012-2515-5>
- Holzschuh, A., Dudenhöffer, J.-H., Tscharntke, T., 2012. Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biol. Conserv.* 153, 101-107. <https://doi.org/10.1016/j.biocon.2012.04.032>
- Holzschuh, A., Steffan-Dewenter, I., Kleijn, D., Tscharntke, T., 2007. Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *J. Appl. Ecol.* 44, 41-49. <https://doi.org/10.1111/j.1365-2664.2006.01259.x>
- Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. *Agric. For. Entomol.* 14, 81-87. <https://doi.org/10.1111/j.1461-9563.2011.00541.x>
- 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., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* 16, 584-599. <https://doi.org/10.1111/ele.12082>
- Klein, A.-M., Brittain, C., Hendrix, S.D., Thorp, R., Williams, N., Kremen, C., 2012. Wild pollination services to California almond rely on semi-natural habitat. *J. Appl. Ecol.* 49, 723-732. <https://doi.org/10.1111/j.1365-2664.2012.02144.x>
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* 274, 303-313. <https://doi.org/10.1098/rspb.2006.3721>
- Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci.* 99, 16812-16816. <https://doi.org/10.1073/pnas.262413599>
- Lindström, S.A.M., Herbertsson, L., Rundlöf, M., Smith, H.G., Bommarco, R., 2016. Large-scale pollination experiment demonstrates the importance of insect pollination in winter oilseed rape. *Oecologia* 180, 759-769. <https://doi.org/10.1007/s00442-015-3517-x>
- Lye, G., Park, K., Osborne, J., Holland, J., Goulson, D., 2009. Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). *Biol. Conserv.* 142, 2023-2032. <https://doi.org/10.1016/j.biocon.2009.03.032>
- Milberg, P., Hallgren, E., 2004. Yield loss due to weeds in cereals and its large-scale variability in Sweden. *Field Crops Res.* 86, 199-209. <https://doi.org/10.1016/j.fcr.2003.08.006>
- Müller, C.B., Adriaanse, I.C.T., Belshaw, R., Godfray, H.C.J., 1999. The structure of an aphid-parasitoid community. *J. Anim. Ecol.* 68, 346-370. <https://doi.org/10.1046/j.1365-2656.1999.00288.x>

- 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*). *Agric. Ecosyst. Environ.* 199, 58–66. <https://doi.org/10.1016/j.agee.2014.08.016>
- Ouvrard, P., Jacquemart, A.-L., 2019. Review of methods to investigate pollinator dependency in oilseed rape (*Brassica napus*). *Field Crops Res.* 231, 18–29. <https://doi.org/10.1016/j.fcr.2018.11.006>
- 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>
- Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.-L., Bretagnolle, V., 2018. Bees increase oilseed rape yield under real field conditions. *Agric. Ecosyst. Environ.* 266, 39–48. <https://doi.org/10.1016/j.agee.2018.07.020>
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carvalheiro, L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J., Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipólito, J., Jaggar, S., Jauker, F., Klein, A.-M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattemore, D.E., Pereira, N. de O., Pisanty, G., Potts, S.G., Reemer, M., Rundlöf, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. *Proc. Natl. Acad. Sci.* 113, 146–151. <https://doi.org/10.1073/pnas.1517092112>
- 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. *Agric. Ecosyst. Environ.* 306, 107189.
<https://doi.org/10.1016/j.agee.2020.107189>
- 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? *Ecol. Lett.* 11, 499-515.
<https://doi.org/10.1111/j.1461-0248.2008.01157.x>
- Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I., Holzschuh, A., 2015. Annual dynamics of wild bee densities: attractiveness and productivity effects of oilseed rape. *Ecology* 96, 1351-1360. <https://doi.org/10.1890/14-1124.1>
- 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. *Agric. Ecosyst. Environ.* 179, 78-86.
<https://doi.org/10.1016/j.agee.2013.07.007>
- Roulston, T.H., Cane, J.H., Buchmann, S.L., 2000. What Governs Protein Content of Pollen: Pollinator Preferences, Pollen-Pistil Interactions, or Phylogeny? *Ecol. Monogr.* 70, 617-643. [https://doi.org/10.1890/0012-9615\(2000\)070\[0617:WGPCOP\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2000)070[0617:WGPCOP]2.0.CO;2)
- 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. *Landsc. Ecol.*
<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. *J. Appl. Ecol.* 58, 1421-1430.
<https://doi.org/10.1111/1365-2664.13887>
- 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. *J. Insect Conserv.* 17, 1181-1189.
<https://doi.org/10.1007/s10841-013-9599-z>

- Steffan-Dewenter, I., Potts, S.G., Packer, L., 2005. Pollinator diversity and crop pollination services are at risk. *Trends Ecol. Evol.* 20, 651-652. <https://doi.org/10.1016/j.tree.2005.09.004>
- Timberlake, T.P., Vaughan, I.P., Baude, M., Memmott, J., 2020. Bumblebee colony density on farmland is influenced by late-summer nectar supply and garden cover. *J. Appl. Ecol.* n/a. <https://doi.org/10.1111/1365-2664.13826>
- Timberlake, T.P., Vaughan, I.P., Memmott, J., 2019. Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *J. Appl. Ecol.* 56, 1585-1596. <https://doi.org/10.1111/1365-2664.13403>
- Van der Meersch, V., Billaud, O., San Cristobal, M., Vialatte, A., Porcher, E., 2021. Landscape floral resources provided by rapeseed correlate with next-year reproduction of cavity-nesting pollinators in a national participatory monitoring program. *Landsc. Ecol.* <https://doi.org/10.1007/s10980-021-01353-0>
- Westphal, C., Steffan-Dewenter, I., Tschardtke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol. Lett.* 6, 961-965. <https://doi.org/10.1046/j.1461-0248.2003.00523.x>
- Woodcock, B., Edwards, M.S.B., Redhead, J., Meek, W., Nuttall, P., Falk, S., Nowakowski, M., Pywell, R., 2013. Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape. <https://doi.org/10.1016/J.AGEE.2013.03.005>
- 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 Ecol.* 17, 6. <https://doi.org/10.1186/s12898-017-0116-1>

Chapitre 2 : Quantification de l'activité des abeilles dans les champs de tournesol à l'aide du suivi acoustique et de l'apprentissage profond

Dans le contexte du déclin des pollinisateurs que nous connaissons, la nécessité de connaître les impacts des facteurs locaux et paysagers sur la présence des pollinisateurs dans les espaces cultivés, mais également l'estimation du service de pollinisation rendu par les pollinisateurs est essentielle. Pour cela, les scientifiques ont recours à des méthodes de capture et de piégeage des pollinisateurs afin d'obtenir des proxys de la pollinisation tels que l'abondance ou la diversité des communautés d'insectes pollinisateurs. Néanmoins, ces méthodes sont destructives pour les pollinisateurs (Gonzalez et al., 2020; Montero-Castaño et al., 2022; Montgomery et al., 2021) et chronophages, ce qui limite les échelles spatiales et temporelles des études. Toutefois, les développements technologiques récents ont permis l'émergence de nouvelles méthodes de suivi des pollinisateurs, notamment le suivi acoustique. La plupart des études sur le suivi acoustique des pollinisateurs font intervenir des algorithmes d'apprentissage machine relativement ancien et aucune étude n'a cherché à déterminer si les méthodes récentes d'apprentissage profond étaient plus performantes pour détecter les pollinisateurs que les méthodes plus anciennes. De même, il n'a pas été démontré que le suivi acoustique des pollinisateurs *in natura* permettait d'obtenir une vision réaliste de l'activité des pollinisateurs.

Grâce à des enregistrements acoustiques réalisés au cours de la saison de floraison du tournesol en 2020 (Fig.8a), nous avons déterminé que l'apprentissage profond, à travers les réseaux de neurones convolutifs, était plus performant que l'algorithme des forêts aléatoires pour détecter le son émis par les pollinisateurs via leur battement d'ailes au cours de leur vol (Fig.8b). De plus, nous avons montré que les données de phénologies d'activité des pollinisateurs étaient similaires aux connaissances présentes dans la littérature.

Cette étude montre que le suivi acoustique de pollinisateurs pourrait être une méthode efficace pour surveiller les services de pollinisation à de grandes échelles

spatio-temporelles même si de nombreux développements restent encore nécessaires à mettre au point pour gagner en précision.

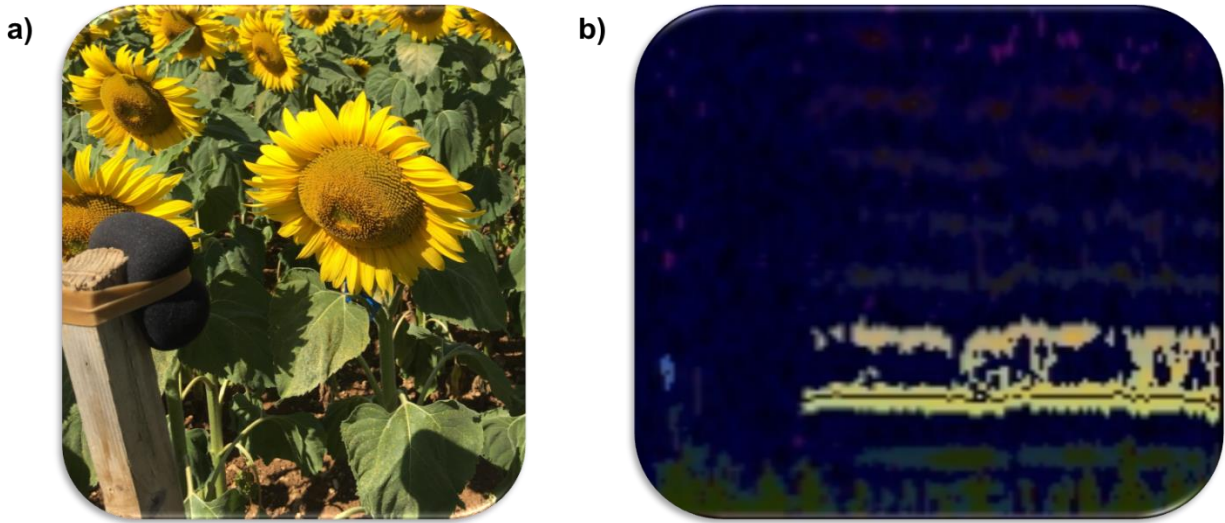


Figure 9 - a) Dispositif expérimental ayant permis d'enregistrer le son émis par les pollinisateurs. Le micro, recouvert d'une bonnette de protection pour réduire l'effet du vent, est placé à une vingtaine de centimètres d'un capitule de tournesol. b) Spectrogramme du son émis par un pollinisateur au cours du vol via le bruit de ses battements d'ailes.

Buzzy bees, quantifying bee activity within sunflower fields using acoustic monitoring and deep learning

In preparation

L. Crochard^a, C. Fontaine^a, M. Baude^{b,c}, M. Ragué^{d,e}, D. Bas^f, S. Gaba^{d,e}, V. Bretagnolle^{g,e}, R. Julliard^a, Y. Bas^{a,h}

^a Centre d'Ecologie et des Sciences de la Conservation, UMR 7204 MNHN-CNRS-Sorbonne Université, Muséum national d'Histoire naturelle, F-75005, Paris, France

^b Université d'Orléans, Orléans, France

^c Sorbonne Université, UPEC, Université Paris Cité, CNRS, IRD, INRAE, Institut d'Ecologie et des Sciences de l'Environnement (iEES-Paris), Paris, France

^d INRAE, USC 1339, Centre d'Etudes Biologiques de Chizé, F-79360 Villiers-en-Bois, France

^e LTSER "Zone Atelier Plaine & Val de Sèvre", CNRS, Beauvoir-sur-Niort, France

^f none (volunteer), FR

^g CNRS, Université de La Rochelle, UMR 7372, Centre d'Etudes Biologiques de Chizé, F-79360 Beauvoir-sur-Niort, France

^h CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

Abstract

Since 70% of the world's crops depend on pollinators for production and concerns are growing regarding their decline, it is essential to implement robust and efficient monitoring of pollinator activity. However, traditional methods of pollinator monitoring are generally time-consuming and destructive. With the rise of technology, passive and non-destructive methods are being developed using computer vision or acoustic recording coupled with machine learning, offering the possibility to increase the temporal and spatial coverage of biodiversity and ecosystem functioning monitoring. Passive acoustic monitoring is a promising method for tracking pollinators. However,

it has been seldom implemented, most often using fairly old machine learning methods. Deep learning methods initially used for image analysis start to be used for acoustic monitoring of various taxa, including flying insects. Here we proposed a method for quantifying pollinator activity based on the automatic identification of the sounds produced by their beating wings. We tested a random forest to a deep learning algorithm on acoustic recordings performed within sunflower fields and using a new open access software dedicated to acoustic biodiversity monitoring named TadariDeep. First, we showed better performance of deep learning compared to random forest algorithm for the classification of pollinator flight sounds. Second, we argued that our deep learning method provides a realistic view of pollinator activity by comparing acoustic and visual data, as well as by analyzing the daily phenology of pollinator activity and the impact of temperature on such activity that we found consistent with the literature. Acoustic monitoring of pollinators using deep learning therefore appears as a reliable method to quantify and monitor pollinator activity and might be used to monitor pollination services over large spatial and temporal scales. Further improvements are however still needed for the species identification of pollinators.

Keywords: Pollination services, passive acoustic monitoring, convolutional neural networks, data augmentation

Introduction

Animal pollination is an essential ecological function involved in the reproduction of 90% of flowering plants, often involving insects (Ollerton et al., 2011). In agricultural landscapes, 70% of major global food crops benefit from insect pollination, representing approximately 35% of the annual global food production (Klein et al., 2007). This makes insect pollination a major ecosystem service that is, however, impaired by pollinator decline (Biesmeijer et al., 2006; Potts et al., 2010; Steffan-Dewenter et al., 2005). Because pollinator communities exhibit significant spatial and temporal variability (Grab et al., 2017; Reverté et al., 2019), pollinator monitoring is important to quantify pollinator activity over time and indirectly assess

pollination services. Monitoring pollinators is therefore important to quantify pollinator activity over time and indirectly assess pollination services.

Several methods are used to monitor insect pollinators. The most common ones consist in capturing insects using pan traps or sweep nets along transects (O'Connor et al., 2019; Westphal et al., 2008), which are often used to describe the taxonomic composition of pollinator communities and to identify the interactions they established with flowering plants. These methods usually involve the killing of caught individuals and are extremely time-consuming since they require a significant amount of time in the field and in the laboratory (Montgomery et al., 2021). This high time cost necessarily leads to monitoring pollinators with limited spatial and temporal resolutions.

Thanks to technological developments, passive and non-destructive methods of biodiversity monitoring are being developed (van Klink et al., 2022). In particular, bioacoustic methods based on automatic sound classification thanks to machine learning algorithms (Gibb et al., 2019), are already used to study several taxa such as birds (e.g Kahl et al., 2021; Metcalf et al., 2022), bats (e.g Kerbiriou et al., 2019; Roemer et al., 2021), and marine mammals (e.g Shiu et al., 2020; Van Uffelen et al., 2017). Regarding insects, acoustic monitoring has already been developed to study the impact of anthropogenic pressures on Orthopteran communities (Jeliazkov et al., 2016; Penone et al., 2013) but also for aquatic insects (Desjonquères et al., 2020; Gottesman et al., 2020). Concerning flying insects like pollinators, they can be detected through the sound emitted by beating their wings while flying (Kawakita and Ichikawa, 2019). Early studies on pollinator acoustics focused mainly on bumblebees, through the study of colony dynamics (Heise et al., 2020), sounds emitted by bumblebees, and their morphological characteristics involved in pollination (Miller-Struttman et al., 2017). On the other hand, studies on the specific identification of pollinators are rare, notably, Gradišek et al., (2017) have implemented an application to identify bumblebee species. Nevertheless, these studies rely on rather “traditional” machine learning methods, such as support-vector machine or random forest, to identify and classify the sounds emitted by pollinators. Since 2016, a new machine learning method relying on convolutional neural networks has spread in bioacoustic (Stowell, 2022). This method

achieved breakthroughs in automatic image classification (Hicks et al., 2021; Mohanty et al., 2016; Weinstein, 2018) and can analyze the spectrograms of recorded sounds in an analogous way. This emerging method is becoming widespread since it has been demonstrated that it is more efficient than classical machine learning methods, making fewer errors in sound classification, and is used for the monitoring of various taxa, such as birds, marine mammals, bats, fish (Stowell, 2022) and most recently flying insects (Folliot et al., 2022).

In this context, we aimed at developing a convolutional neural network (CNN) for the automatic recognition and classification of sounds emitted by pollinators during their flight to quantify pollinator activity in field conditions. AudioMoth recorders which are low-cost, small, and low-energy (Hill et al., 2018) were used to perform audio recording within 30 sunflower fields in France. Sunflower is the most important oil crop in terms of cultivated area in Europe (FAOSTAT, 2020) and the contribution of insect pollination to its yield is estimated between 18% and 100% (i.e. doubling the yield) (Carvalho et al., 2011; Degrandi-Hoffman and Chambers, 2006; Garibaldi et al., 2016; Greenleaf and Kremen, 2006; Perrot et al., 2019). Sunflower is mostly visited and pollinated by a single species: the honeybee, which represents between 72 to 97.8% of pollinator visits (Bartual et al., 2018; Carvalho et al., 2011; Greenleaf and Kremen, 2006). This makes it a good candidate to monitor the dynamics of pollinator activity, without necessarily knowing their identity (Rader et al., 2016). We compared the performance of a deep learning method based on convolutional neural networks trained on spectrograms using the newly developed TadariDeep software (<https://github.com/YvesBas/TadariDeep>) with a method based on random forest, trained on sound events features using the Tadarida software. Finally, to test the ecological validity of acoustic monitoring, we investigated whether the estimate of pollinator activity from continuous acoustic monitoring reflects punctual visual observations of pollinator activity and what is known from the daily activity and the sensitivity to the temperature of honeybees.

Material & Methods

a) Site description

In 2020, we selected 30 sunflower fields from the Long-Term Social-Ecological Research site “Zone Atelier Plaine et Val de Sèvre” in South-West France. This research site is 435 km² large, and composed of 87% of cultivated areas (Bretagnolle et al., 2018a,b), dominated by cereals and sunflowers, representing roughly 55% and 13% of the cultivated area, respectively. To promote heterogeneity in pollinator activity between sunflower fields, they were selected from landscapes with varying densities of semi-natural habitats, sunflowers and organic fields. Sunflower fields had an average area of 6 ha. The flowering of these fields was spread out between the beginning of July and the middle of August and lasted between 2 and 3 weeks for a field.

b) Acoustic records

Experimental device and records pretreatment

In each field, we placed an audiomoth, which is a sound recorder (see Appendix A For the description and parameters), at 10 to 20 cm, facing a randomly selected sunflower flower located at approximately 20m from the field edge. The audiomoth was covered by a windscreen to reduce the wind sound. To cover the period between sunrise and sunset at our study site over the period July - August, we made continuous audio recordings between 6 am to 10 pm.

To analyze our records we used the Tadarida toolbox (Bas et al., 2017), composed of Tadarida-L which allows to detect and label sound events, and Tadarida-C which allows building classifiers of sound events. To optimize the use of this toolbox, it was necessary to pre-process our records. We cut them into sub-records of 10 sec thanks to Kaleidoscope (<https://www.wildlifeacoustics.com/products/kaleidoscope-pro>) software and increased 10 times the sampling rate to get a longer Fast Fourier Transformation size (FFT is fixed in Tadarida-L). Then, Tadarida-L was used to detect sound events within the 3 705 554 records (Table S1). To train Tadarida-C classifiers to recognize flying pollinators from other sound events, we built several training datasets.

For this, we proceeded in several steps:

Step 1: Building the training dataset

Machine learning classifying methods need a training dataset on which the algorithm learns to classify sound events into predefined categories. Such training datasets are made of labeled sound events, the labels corresponding to the classes into which sounds should be classified. To ensure that our training dataset includes pollinator sound events, we randomly selected the records from 12 out of 291 5-minutes long observation sessions for which we knew that pollinators were present (see section C of the material and methods below). Sound events that Tadarida-L detected within these 375 10-second long records were listened to and labeled using 8 classes still using Tadarida-L. Three of the classes corresponded to pollinators "*Apis mellifera*", "*Bombus* sp.", and "Unidentified pollinator", which we could differentiate thanks to the visual observations made (see B of the material and methods). Table S2 presents the full list of classes and the number of sound events labeled correspondingly that constitute the training dataset A. Then from this training dataset, we used Tadarida-C to build a first classifier based on a random forest algorithm, hereafter named "random forest-0" (see the "Step4: Classifier training" section for details).

Step 2: Training dataset enhancement

In order to ensure that all possible sound conditions were represented in our training dataset, 10% of all records not coupled to the visual observations were randomly selected. We classified all sound events detected in these records based on our classifier "random forest-0" and obtained for each record a confidence score for the "pollinator" class, which corresponds to the sum of confidence scores of "*Apis mellifera*", "*Bombus* sp." and "Unidentified pollinator" classes. Higher is this score, higher the "probability" that the record contains a sound emitted by a pollinator. We defined six groups for the confidence score for the "pollinator" class (1: 0-0.5; 2: >0.5-0.6; 3: >0.6-0.7; 4: >0.7-0.8; 5: >0.8-0.9; 6: >0.9). To improve the training dataset, we

wanted to increase the number of sound events in the “pollinator” class and correct the main errors made by the classifier “random forest-0” (not a pollinator but a high confidence score of the “pollinator” class). For this, we conducted a stratified sampling of the records by sunflower field and “pollinator” confidence score group, with the number of records sampled increasing with confidence score groups. All of these records were listened to and all sound events were labeled with Tadarida-L. We obtained a training dataset B with 17 classes of sounds (see Table S3 to see the list of classes and the number of sound events we had labeled per class).

Step 3: Data augmentation

Data augmentation consists of artificially increasing the size of the training dataset thanks to data samples to which a small modification is applied (Stowell, 2022). Here, our preliminary tests seemed to show that the human voice could be the source of many classification errors. In order to improve the performance of our classifier in differentiating between pollinator sounds and human voice, we increased the class of sounds corresponding to the human voice. To do so, we collected human voice events from the Common voice Corpus 9.0 database (<https://commonvoice.mozilla.org/fr/datasets>) and mixed these events with the events from the training dataset B. A training dataset C was then created by adding to the training dataset B, 1700 of these events mixing human voice and sound events from our recordings in sunflower fields. In the same way, we created training dataset D by adding 3300 sound events mixing human voice mixing events and sound events from our recordings to the training dataset C. In the following, we only use the training datasets B, C, and D (see Fig.1).

Step 4: Classifier training

We compared two different methods of machine learning, i.e. random forest and convolutional neural networks to classify sound events as either pollinator flying sound or other sounds emitted in the same frequency band. To do so we used two softwares: Tadarida-C which allowed us to extract 269 acoustic features for each

labeled sound event and to train a classifier using a random forest classification and to train a classifier based on convolutional neural networks we used TadariDeep (<https://github.com/YvesBas/TadariDeep>) which is based on computer vision, using Tensorflow 2.0.0 framework and transfer learning (MobileNet architecture). For this last method, we optimized batchsize and the number of iterations (nbepochs). For both methods, we used the three training datasets previously described leading to a total of 15 classifiers (see Fig.1 and Table S4 for the characteristics of each classifier).

It is also important to note that between the two softwares, the detection process is the same. Nevertheless, with TadariDeep used for the convolutional neural networks, a filter is applied to limit short sound events with a small amount of information. Thus, only sound events with a frequency between 50 to 2000 Hz and a duration greater or equal to 90 ms were taken into account for this method.

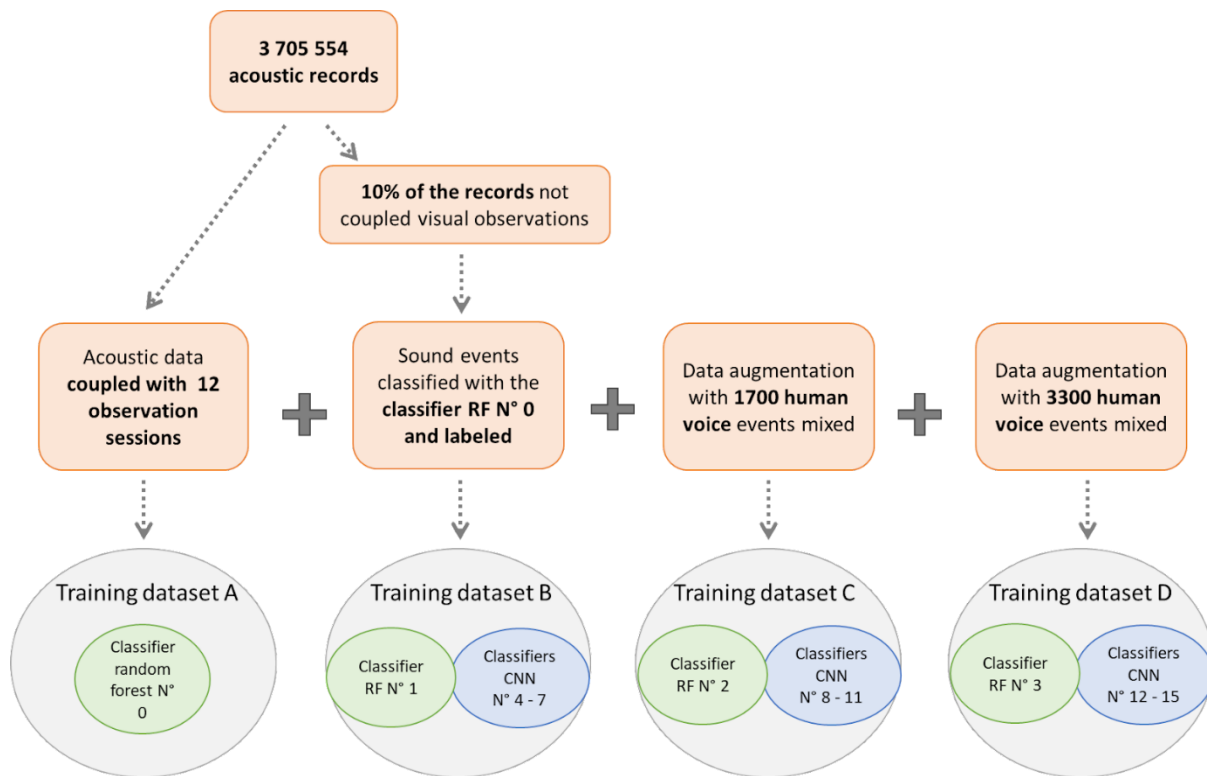


Figure 1: Overview of the datasets and the classifiers. The orange boxes represent the different components of the training datasets. The green circles represent the random forest classifiers built with Taradida-C. The blue circles represent the convolutional neural networks classifiers built with TadariDeep.

Step 5: Classifiers testing

We tested the effectiveness of the random forest classifiers and convolutional neural networks on the 8709 unlabeled 10-second recordings for which we also had a visual observation of the pollinator run. (see section C of the material and methods below). To be able to make comparable tests between classifiers, all sound events of these records were classified with the random forest classifier 1 (see Table S4) and we randomly selected 100 records of 10-seconds per pollinator score group described above to build a test dataset. Each score group is picked in order to evaluate the effectiveness of the method at all possible score thresholds. The test dataset then consisted of 600 records of 10-seconds. We listened to all records of this test dataset and determined if they contained at least one sound made by a pollinator.

Thanks to the test dataset, we assessed the efficiency of our 15 classifiers to identify pollinators against other sounds with receiver operator characteristics (ROC) curves. These curves are generated based on the probability (confidence score) that the classifier classifies a pollinator sound event as a “pollinator” accounting for the specificity (inverse of false positive rate) and sensitivity (inverse of false negative rate). We made a ROC curve for each classifier we created. We calculated the area under the curve (AUC) which provides a summary of the classifier's performance.

c) Relationship between pollinator activity estimated by audio recording and visual observations

To test the ecological validity of acoustic monitoring using the convolutional neural networks method, the following analyses were performed by considering all sounds with a pollinator confidence score greater or equal to 78.1 as being pollinator sounds. This confidence score is maximizing both sensitivity and specificity (see red point on Fig. 2). With this confidence threshold, the average number of pollinator buzzes per field throughout the season was 4880 ± 472 and the average number of pollinator buzzes per day was 197 ± 10 .

To estimate visually pollinator activity in fields with a sound recorder, each of week three visual observation sessions were organized, taking care to distribute each

observation at different times of the day. We had a total of 291 observation sessions coupled with acoustic monitoring. For the observation sessions, the observer was placed about 50 centimeters from the plant in front of which the sound recorder was located. For five minutes, every 15 seconds, each insect close (<15 cm) to the sunflower capitulum was noted. For each pollinator, its guild (honeybee, *Bombus*, other wild bees, hoverfly, other Diptera, Coleoptera, other insects) and its position (on the capitulum or around the capitulum) were noted. Each capitulum was visually surveyed before, during, and after the flowering period, representing between four and five weeks of monitoring depending on the field.

To determine if the acoustic method provides results consistent with the ground truth, we studied the relationship between the pollinator activity measured with acoustic monitoring and the pollinator activity visually measured. To test the relationship between these two measures of pollinator activity, we used a generalized linear model with a negative binomial distribution adapted for count data. We used the 279 observation sessions of 5 minutes that were not used for the training datasets (see section “Step 1: Building the training dataset”).

d) Daily activity of pollinators estimated by audio recording

Then we wanted to determine whether the passive acoustic monitoring reflects what is known about the daily phenology of the honeybee (*Apis mellifera*) (Eban-Rothschild and Bloch, 2008; Joshi and Joshi, 2010; Nderitu et al., 2008) and about the sensitivity to temperature of this species (Blažytė-Čereškienė et al., 2010; Woyke et al., 2003). For these analyses, we built generalized linear mixed models with a negative binomial distribution explaining the number of buzzes detected during one hour (we only used the hours for which we had at least 55 minutes of recording time out of 60), which reflect pollinator activity, which is considered to be the activity of *Apis mellifera* since it is the most abundant pollinator in sunflower. Field identity was considered as a random effect. To study the daily pollinator’s phenology, the “hour” was included in the model as an explanatory polynomial variable of the fourth degree. To study the response of pollinator activity to temperature, a second model was built with

“temperature” as a fourth-order polynomial explanatory variable. For these two models, the best model was selected on AIC criteria. For temperature data, we used meteorological data from the “Niort Souché-Aérodrome” (<https://www.infoclimat.fr/observations-meteo/archives/1er/juillet/2020/niort-souche/07330.html>, visited on 27/07/2022), which is a Météo France station located North from our study site, giving the average temperature per hour, taken undercover at about 1.5m from the ground.

All statistical analyses were performed using R (R Core Team, 2022). The residuals of all models were controlled thanks to the package DHarma (Hartig and Lohse, 2022).

Results

1. Comparison of convolutional neural networks and random forest classifiers for pollinator acoustic monitoring

Tadarida-L detected sound events in 99.3% (596) of the files while TadariDeep detected them in 95% (570) of the files. This difference between the two softwares is explained by the short event filter applied with TadariDeep (minimum duration 90 ms and frequency between 50 to 2000 Hz). To compare the classification accuracy between the two methods, we considered only the records for which both methods detected sound events.

In the test dataset, we counted 94 records out of 600 that contained at least one pollinator sound. Tadarida-L detected sound events for each of them but for the same reasons as above, TadarariDeep detected sound events corresponding to pollinator sound for 91 of these records.

ROC curves and their AUC show that, for the random forest method, the best classifier performance was obtained by the classifier based on the training dataset D, composed of the labeled sound events (training data set B) and 5000 mixed human voice sound events (AUC=0.878). For the convolutional neural networks method, the best performance was also obtained by the classifier based on the training dataset D

with a batchsize of 16 and 160 iterations (AUC=0.957). The best classifiers based on the training dataset B, without data augmentation, obtained an AUC of 0.856 and 0.953 for the random forest method and for the convolutional neural networks method respectively. So for both methods, data augmentation improved the performance of classifiers very slightly, approximately 2.6% for the random forest method and 0.4% for the convolutional neural networks method (Fig.2). Comparing the best classifier of each method, based on their ROC curves and AUCs, we see that the convolutional neural networks method outperforms the random forest method (Fig.1). Calculating the average error rate according to the different selection thresholds (1-AUC), we were able to determine that the error rate of the convolutional neural networks method is three times lower than that of the random forest method for the classification of pollinator flight sounds.

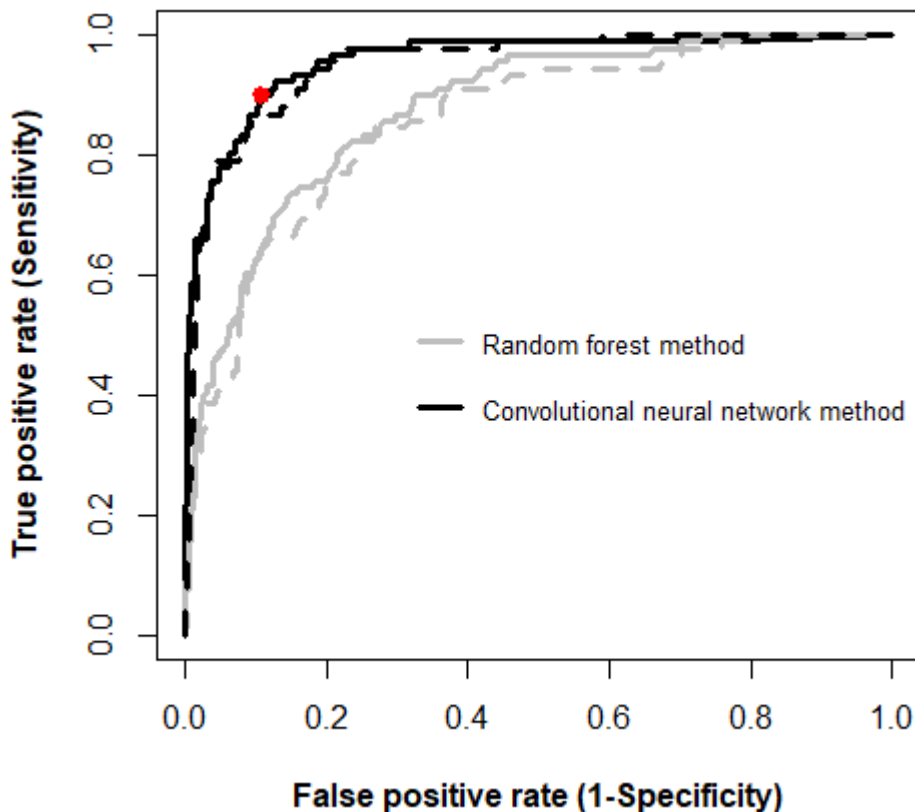


Figure 2: Receiver operating characteristic (ROC) curves between the confidence score of the false-positive rate (FPR) and the true-positive rate (TPR) for the best classifiers of the random forest method (grey curves) and the best classifiers of the convolutional neural network method (black curves). Continuous lines correspond to the best classifiers trained with data augmentation and dashed lines without data augmentation. The red point corresponds to the threshold selected for the rest of the study concerning the “pollinator” confidence score (see section C of the material and methods).

2. Relationship between pollinator activity estimated by audio recording and visual observations

We found a significant positive non-linear relationship (LR chisq= 16.022, p-value <0.0001) between the number of buzzes detected by TadariDeep and the number of honeybees and bumblebees visually observed, during observation sessions (Fig.3). We see that the number of buzzes is lower than the number of individuals observed during the five minute sessions, except for some rare cases. The check of raw data indicates that the two points with more than 15 buzzes detected and 0 individuals visually observed correspond all to classification errors related to the human voice.

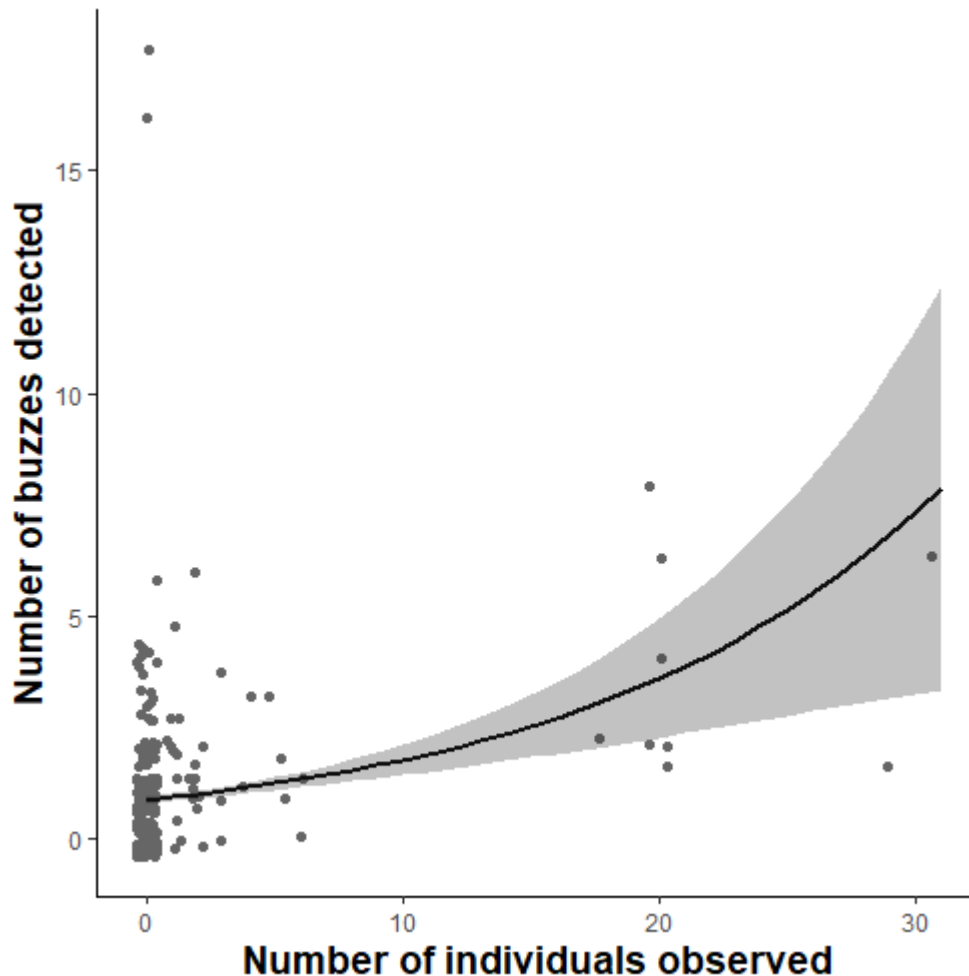


Figure 3: Relationship between the number of buzzes detected by TadariDeep and the number of individuals of honeybees and bumblebees visually observed during an observation session. Dots correspond to field data and to improve the visibility, we have represented them with the `geom_jitter` function from the `ggplot2` package (Wickham et al., 2022). The line corresponds to the predicted values of the generalized linear model and the grey ribbon to the standard error.

3. Daily activity of the honeybee estimated by audio recording

Pollinator activity (probably honeybees activity) varies significantly during day time (Tab.1). We found a fourth order relationship with the hour of the day, indicating that pollination activity increases sharply from the sun rising up to 11 am with approximately 19 pollinator-attributed sound events per hour, then more slowly reaches its maximum around 04 pm with 26 pollinators per hour, to then decreases until sunset (Fig.4a). Pollinator activity also depends significantly on the temperature (Tab.1). As before, we found a fourth order relationship with the temperature. Below 10°C, there is no pollinator. Pollinator activity increases slowly until about 15°C, then progresses to about 29°C, with about 24 pollinator-attributed sound events per hour. But, there is no sign of a decline in activity above 30°, but we have a few points (Fig. 4b).

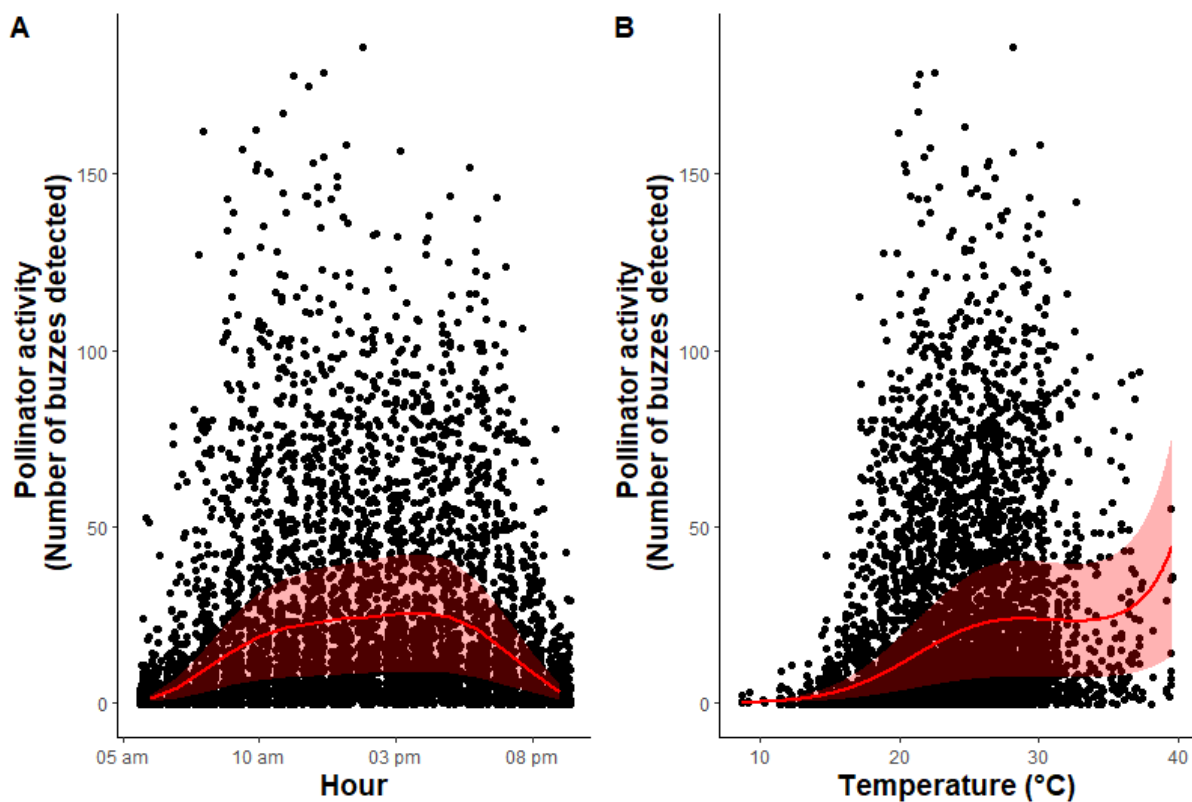


Figure 4: Relationship between the pollinator activity (number of buzzes detected in one hour by TadariDeep) and a) the hour of the day and b) the temperature. Lines correspond to the predicted values of the generalized linear mixed models and the red ribbon to the standard error. Dots correspond to the field data, i.e. the number of buzzes detected per hour, and to improve the visibility, we represented them with the `geom_jitter` function of the `ggplot2` package.

Test	Variable	Chisq	Df	P-value
Relationship between the hour of the day and the pollinator activity	Hour	273.15	1	<0.0001
	Hour ²	222.53	1	<0.0001
	Hour ³	201.89	1	<0.0001
	Hour ⁴	199.74	1	<0.0001
Relationship between the temperature and the pollinator activity	Temperature	0.0869	1	0.77
	Temperature ²	1.1852	1	0.28
	Temperature ³	3.4749	1	0.06
	Temperature ⁴	5.2577	1	0.02

Table 1 - Summary statistics of generalized linear mixed models investigating the relationship between pollinator activity and the hour of the day and between pollinator activity and the temperature. Field identity is used as a random variable.

Discussion

Convolutional neural networks outperforms random forest classifiers in acoustic pollinator monitoring

Our study shows that monitoring pollinator activity in sunflower fields through acoustic records is feasible, reliable, and promising. We tested different models to automatically identify and quantify sound events emitted by flying pollinators from other environmental sounds. We demonstrated that convolutional neural networks is a more powerful machine learning method than random forests for such a task, with convolutional neural networks three times more reliable than the random forest method to classify the sounds emitted by pollinators against other sounds. Although the superiority of convolutional neural networks in terms of performance over other machine learning algorithms is not always obvious (Garcia et al., 2020), for several taxa such as birds their superiority is not in doubt (Knight et al., 2017; Marchal et al., 2022). Here, our results suggest that the convolutional neural networks method would be the most reliable method for passive acoustic monitoring of pollinator flying activity so far.

Nevertheless, regarding buzz detection, the random forest based method was able to detect 3.2% more buzz, because of the minimum duration and frequency interval we imposed for analyzing sound events with the deep learning method. Further, during the training of our different classifiers, we noticed that the human voice was often misclassified, reaching high confidence scores for pollinator sound classes,

and this was despite the data augmentation we carried out. This kind of problem with the human voice has already been noted for the detection of birds in particular (Stowell et al., 2019). Here, the human voice errors are only due to the voices of the experimenters who were close to the sound recorders during the observation sessions. But outside of these times, it is unlikely that anyone would be 20 meters inside a sunflower field, so it is likely that there are fewer errors due to human voice outside of these observation sessions. The human voice data that we used for data augmentation are records of people in front of their computers near a sound recorder and without background noise. They are therefore quite different from the human voice recordings in our data, which were related to conversations of the experimenters during the observation sessions. This may explain the fact that data augmentation did not lead to a higher improvement in the performance of the classifiers. It might therefore be interesting to test the effects of data augmentation with human voice sounds manually labeled from field records and with a lower Signal Noise Ratio (SNR).

The positive relationship between the number of buzzes and the number of individuals visually observed suggests that the number of buzzes could be used as a proxy for pollinator activity. However, the relationship we presented was quite far from a 1:1 relationship, with fewer buzzes than visually observed individuals, except for a few outliers presenting much more buzzes than observed individuals. As previously acknowledged, the outliers appeared to be related to classification errors related to the human voice. Regarding the fact that we, on average, found fewer buzzes than observed individuals, the difference in protocols between the two monitoring methods, continuous for acoustic and punctual for visual, may explain the differences in activity quantification. If we assume that pollinators land on the flower head at the beginning of the observation session and remain there throughout the session, there will be an underestimate of pollinator activity measured with the acoustic method compared to that measured visually.

Usage and perspectives

Using the acoustic method, we were able to reconstruct the daily phenology of the foraging activity of sunflower pollinators, which should be mainly honeybees (Bartual et al., 2018; Carvalheiro et al., 2011; Greenleaf and Kremen, 2006). We found that such honeybees activity varied throughout the day and was notably close to 0 at sunrise and sunset. This is in agreement with Joshi and Joshi, (2010) who determined that *Apis mellifera* activity is at its peak in the middle of the day and with the fact that honeybees sleep at night (Eban-Rothschild and Bloch, 2008). The fact that observe high pollination activity between 11 am and 04 pm may be explained by the fact that sunflower nectar production tends to increase during the day between 07 am and 05 pm (Chabert et al., 2020) since honeybees have the ability to remember the time of the day of the maximum production of nectar and adapt their foraging phenology to that time (Klein and Seeley, 2011; Silva et al., 2013). Nevertheless, other patterns of daily phenology of honeybees activity were observed, e.g Yücel and Duman (2005) and Reyes-Carrillo et al., (2007), and the authors related peaks in bee activity with peaks in production of floral resources of the species studied. We were also able to demonstrate that ambient temperature has an impact on honeybees activity. As demonstrated by Blažytė-Čereškienė et al. (2010) and Woyke et al. (2003), honeybees are only active from a temperature of about 10°C but unlike them, pollination activity does not decrease above 30°C but stagnates then increases. This increase is quite surprising and it is probably necessary to treat it with caution since the number of data available for temperatures above 30°C is much lower than for temperatures below 30°C. The fact that the honeybees activity stagnates probably comes from a compromise between the expenditure of energy for the food search and that for the thermoregulation of its body.

Passive acoustic monitoring of pollinators method could also be used to estimate the pollination services (van Klink et al., 2022). For this, it could be interesting first to quantify the link between the number of buzzes and seed production of the crop. For crops such as sunflowers, where the effect of pollinators on yields depends primarily on honeybee abundance (Altayeb and Nagi, 2015; Aslan and Yavuksuz, 2010;

Perrot et al., 2019), a simple measure of pollinator activity could quantify the pollination services received. Nevertheless, for other crops, such as oilseed rape, the effect of the pollinator diversity on the yields is known (Bartomeus et al., 2014; Perrot et al., 2018; Zou et al., 2017), each with its own pollination efficiency (Garibaldi et al., 2011; Jauker et al., 2012; Kremen et al., 2002; Rader et al., 2016). Therefore, it would be interesting to think of a way to effectively detect small pollinators that emit lower sound levels than honeybees or bumblebees, it would probably be necessary to find settings for the sound recorder or to position it closer to the flower. It could also be interesting to develop an acoustic identification of pollinator species. This type of identification has already been performed by Kawakita and Ichikawa (2019) for three bee species and one hornet species, by Gradišek et al. (2017) for bumblebees, and involved "traditional" machine learning methods. Considering convolutional neural networks method performance compared to other machine learning methods, we can think that it could efficiently identify pollinator species from the sound of their wing beats. Nevertheless, considering the diversity of pollinators, it will require a lot of work to obtain a large number of reference sounds per species.

To accurately estimate the pollination service in a field, it would also be necessary to determine the detection radius of the pollinators around the sound recorder. Compared to other methods such as transects, which are conducted over a large area, our method measures pollinator activity at a fixed point in the plot. Yet, the activity of some pollinator species is known to decrease as the distance from the edge increases (Hevia et al., 2016). Therefore, it may be interesting to place multiple sound recorders along a transect from the edge to the centroid at the field to more accurately estimate pollinator activity within the field.

Although further developments are needed to fully relate passive acoustic monitoring of wing beats to the diversity and abundance of pollinators within fields as well as to the pollination services they deliver, such methodology appears very promising to monitor pollinators and the pollination services in a non-lethal way over large spatial and temporal scales.

Acknowledgments

We would like to express our thanks to CCAIN2P3 for allowing us to perform our deep learning analysis on their platform. This research was funded through the ANR IMAGHO (ANR-18-CE32-0002).

Author contributions

Y. Bas, C. Fontaine, L. Crochard, M. Baude conceived the ideas and designed methodology; L. Crochard and M. Ragué collected the data; L. Crochard analysed the data; D. Bas and Y. Bas designed the data analysis software; L. Crochard, Y. Bas, C. Fontaine, M. Baude led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Supplementary

Appendix A - Setting up the audiomoths

Sample rate: 16 kHz

Gain: Low-Medium

Sleep duration: 5 s

Recording duration: 900 s

Start recording: 6 am

End recording: 10pm

Field	Theoretical number of records of 10s	Number of 10s records we have	Number of hours recorded	Percentage of loss
12	152 460	147 220	409	3.5
116	151 740	125 194	348	17.5
376	132 840	131 966	367	0.7
1823	151 110	110 758	308	26.7
2187	131 310	130 279	362	0.8
2230	143 190	141 997	394	0.8
2939	180 450	179 194	498	0.7
3107	207 180	157 846	438	23.8
3253	148 860	147 657	410	0.8
3271	159 840	118 384	329	25.9
4566	141 840	140 346	390	1.1
5572	171 630	135 085	375	21.3
5595	148 680	147 448	410	0.9
5867	192 690	191 389	532	0.7
6223	169 470	145 255	403	14.3
7029	139 860	105 708	293	24.4
7413	156 870	127 159	353	18.9
7507	162 450	144 321	401	11.2
8690	133 380	90 503	251	32.1
9523	99 450	69 789	194	29.8
10106	183 510	92 117	256	49.8
10486	175 950	105 273	292	40.2
10626	95 310	86 702	263	9
12446	145 620	143 887	400	1.2
12473	121 770	69 586	193	42.9
13138	138 240	114 444	318	17.2
13253	159 480	158 204	439	0.8
14499	108 360	82 404	229	24
15339	106 650	71 567	199	32.9
17019	126 180	93 872	261	25.6

Table S1 - Overview of records. The percentage of loss is due to a hard drive problem and sound recorders that fell to the ground

Sound event class	Number of events labeled
<i>Apis mellifera</i>	198
<i>Bombus sp.</i>	20
Unidentified pollinator	7
Bird	9
Human voice	201
Car	216
Noise (i.e, mechanical or experimenter noise)	1077
Wind	124

Table S2 - Number of sound events labeled per class of the first training dataset

Sound event class	Number of events labeled
<i>Apis mellifera</i>	198
<i>Bombus sp.</i>	20
Unidentified pollinator	12651
Bird	734
Turtledove and pigeon	625
Cock	225
Corvidae	32
Dog	85
Sheep	4
Human voice	378
Car	1343
Motorcycle	562
Truck	171
Plane	980
Bell	50
Noise (i.e, mechanical or experimenter noise)	4567
Wind	1436

Table S3 - Number of sound events labeled per class of the second training dataset

N° classifier	Method used	Training set	Batchsize
1	Random forest	2 nd	
2	Random forest	3 rd	
3	Random forest	4 th	
4	Convolutional neural networks	2 nd	4
5	Convolutional neural networks	2 nd	8
6	Convolutional neural networks	2 nd	16
7	Convolutional neural networks	2 nd	32
8	Convolutional neural networks	3 rd	4
9	Convolutional neural networks	3 rd	8
10	Convolutional neural networks	3 rd	16
11	Convolutional neural networks	3 rd	32
12	Convolutional neural networks	4 th	4
13	Convolutional neural networks	4 th	8
14	Convolutional neural networks	4 th	16
15	Convolutional neural networks	4 th	32

Table S4 - Description of each classifier tested

References

- Altayeb, O. a. E., Nagi, S.K.A., 2015. Efficacy of honeybees (*Apis mellifera*) on the production of sunflower (*Helianthus annuus* L.) seeds in the Sudan. *J. Exp. Biol. Agric. Sci.* 3, 191-195.
- Aslan, M.M., Yavuksuz, C., 2010. Effect of honey bee (*Apis mellifera* L.) and bumblebee (*Bombus terrestris* L.) pollinators on yield and yield factors in sunflower (*Helianthus annuus* L.) production areas. *J. Anim. Vet. Adv.* 9, 332-335.
- 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.M., Bocci, G., Marini, S., Moonen, A.C., 2018. Local and landscape factors affect sunflower pollination in a Mediterranean agroecosystem. *PLOS ONE* 13, e0203990. <https://doi.org/10.1371/journal.pone.0203990>
- Bas, Y., Bas, D., Julien, J.-F., 2017. Tadarida: A Toolbox for Animal Detection on Acoustic Recordings. *J. Open Res. Softw.* 5, 6. <https://doi.org/10.5334/jors.154>
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T.,

- Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science* 313, 351–354. <https://doi.org/10.1126/science.1127863>
- Blažytė-Čereškienė, L., Vaitkevičienė, G., Venskutonytė, S., Būda, V., 2010. Honey bee foraging in spring oilseed rape crops under high ambient temperature conditions. *Žemdirb. Agric.* 97, 61–70.
- Bommarco, R., Marini, L., Vaissière, B.E., 2012. Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia* 169, 1025–1032. <https://doi.org/10.1007/s00442-012-2271-6>
- Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhäusser, I., Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018a. Description of long-term monitoring of farmland biodiversity in a LTSER. *Data Brief* 19, 1310–1313. <https://doi.org/10.1016/j.dib.2018.05.028>
- Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhäusser, I., Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018b. Towards sustainable and multifunctional agriculture in farmland landscapes: Lessons from the integrative approach of a French LTSER platform. *Sci. Total Environ.* 627, 822–834. <https://doi.org/10.1016/j.scitotenv.2018.01.142>
- 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. *Ecol. Lett.* 14, 251–259. <https://doi.org/10.1111/j.1461-0248.2010.01579.x>
- Chabert, S., Sénéchal, C., Fougeroux, 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., 2020. Effect of environmental conditions and genotype on nectar secretion in sunflower (*Helianthus annuus* L.). *OCL Oilseeds Fats Crops Lipids* 27, 51. <https://doi.org/10.1051/ocl/2020040>
- Crochard, L., Julliard, R., Gaba, S., Bretagnolle, V., Baude, M., Fontaine, C., 2022. Weeds from non-flowering crops as potential contributors to oilseed rape pollination. *Agric. Ecosyst. Environ.* 336, 108026. <https://doi.org/10.1016/j.agee.2022.108026>
- Degrandi-Hoffman, G., Chambers, M., 2006. Effects of Honey Bee (Hymenoptera: Apidae) Foraging on Seed Set in Self-fertile Sunflowers (*Helianthus annuus* L.). *Environ. Entomol.* 35, 1103–1108. <https://doi.org/10.1603/0046-225X-35.4.1103>

- Desjonquères, C., Rybak, F., Ulloa, J.S., Kempf, A., Bar Hen, A., Sueur, J., 2020. Monitoring the acoustic activity of an aquatic insect population in relation to temperature, vegetation and noise. *Freshw. Biol.* 65, 107–116. <https://doi.org/10.1111/fwb.13171>
- Eban-Rothschild, A.D., Bloch, G., 2008. Differences in the sleep architecture of forager and young honeybees (*Apis mellifera*). *J. Exp. Biol.* 211, 2408–2416. <https://doi.org/10.1242/jeb.016915>
- FAOSTAT, 2020. FAOSTAT [WWW Document]. Food Agric. Organ. U. S. WWW Doc. URL <http://www.fao.org/faostat/en/#data/QC> (accessed 7.15.21).
- Folliot, A., Hauptert, S., Ducrettet, M., Sèbe, F., Sueur, J., 2022. Using acoustics and artificial intelligence to monitor pollination by insects and tree use by woodpeckers. *Sci. Total Environ.* 838, 155883. <https://doi.org/10.1016/j.scitotenv.2022.155883>
- Galen, C., Miller, Z., Lynn, A., Axe, M., Holden, S., Storcks, L., Ramirez, E., Asante, E., Heise, D., Kephart, S., Kephart, J., 2019. Pollination on the Dark Side: Acoustic Monitoring Reveals Impacts of a Total Solar Eclipse on Flight Behavior and Activity Schedule of Foraging Bees. *Ann. Entomol. Soc. Am.* 112, 20–26. <https://doi.org/10.1093/aesa/say035>
- Garcia, H.A., Couture, T., Galor, A., Topple, J.M., Huang, W., Tiwari, D., Ratilal, P., 2020. Comparing Performances of Five Distinct Automatic Classifiers for Fin Whale Vocalizations in Beamformed Spectrograms of Coherent Hydrophone Array. *Remote Sens.* 12, 326. <https://doi.org/10.3390/rs12020326>
- Garibaldi, L.A., Carvalheiro, L.G., Vaissière, B.E., Gemmill-Herren, B., Hipólito, J., Freitas, B.M., Ngo, H.T., Azzu, N., Sáez, A., Åström, J., An, J., Blochtein, B., Buchori, D., García, F.J.C., Oliveira da Silva, F., Devkota, K., Ribeiro, M. de F., Freitas, L., Gaglianone, M.C., Goss, M., Irshad, M., Kasina, M., Filho, A.J.S.P., Kiill, L.H.P., Kwapong, P., Parra, G.N., Pires, C., Pires, V., Rawal, R.S., Rizali, A., Saraiva, A.M., Veldtman, R., Viana, B.F., Witter, S., Zhang, H., 2016. Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science* 351, 388–391. <https://doi.org/10.1126/science.aac7287>
- 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., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 14, 1062–1072. <https://doi.org/10.1111/j.1461-0248.2011.01669.x>

- Gibb, R., Browning, E., Glover-Kapfer, P., Jones, K.E., 2019. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods Ecol. Evol.* 10, 169–185. <https://doi.org/10.1111/2041-210X.13101>
- Gottesman, B.L., Francomano, D., Zhao, Z., Bellisario, K., Ghadiri, M., Broadhead, T., Gasc, A., Pijanowski, B.C., 2020. Acoustic monitoring reveals diversity and surprising dynamics in tropical freshwater soundscapes. *Freshw. Biol.* 65, 117–132. <https://doi.org/10.1111/fwb.13096>
- 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. *Sci. Rep.* 7, 45296. <https://doi.org/10.1038/srep45296>
- Gradišek, A., Slapničar, G., Šorn, J., Luštrek, M., Gams, M., Grad, J., 2017. Predicting species identity of bumblebees through analysis of flight buzzing sounds. *Bioacoustics* 26, 63–76. <https://doi.org/10.1080/09524622.2016.1190946>
- Greenleaf, S.S., Kremen, C., 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proc. Natl. Acad. Sci.* 103, 13890–13895. <https://doi.org/10.1073/pnas.0600929103>
- Hartig, F., Lohse, L., 2022. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.
- Heise, D., Miller, Z., Wallace, M., Galen, C., 2020. Bumble Bee Traffic Monitoring Using Acoustics, in: 2020 IEEE International Instrumentation and Measurement Technology Conference (I2MTC). Presented at the 2020 IEEE International Instrumentation and Measurement Technology Conference (I2MTC), pp. 1–6. <https://doi.org/10.1109/I2MTC43012.2020.9129582>
- Hevia, V., Bosch, J., Azcárate, F.M., Fernández, E., Rodrigo, A., Barril-Graells, H., González, J.A., 2016. Bee diversity and abundance in a livestock drove road and its impact on pollination and seed set in adjacent sunflower fields. *Agric. Ecosyst. Environ.* 232, 336–344. <https://doi.org/10.1016/j.agee.2016.08.021>
- Hicks, D., Baude, M., Kratz, C., Ouvrard, P., Stone, G., 2021. Deep learning object detection to estimate the nectar sugar mass of flowering vegetation. *Ecol. Solut. Evid.* 2, e12099. <https://doi.org/10.1002/2688-8319.12099>
- Hill, A.P., Prince, P., Piña Covarrubias, E., Doncaster, C.P., Snaddon, J.L., Rogers, A., 2018. AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the

- environment. *Methods Ecol. Evol.* 9, 1199-1211. <https://doi.org/10.1111/2041-210X.12955>
- Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. *Agric. For. Entomol.* 14, 81-87. <https://doi.org/10.1111/j.1461-9563.2011.00541.x>
- Jeliazkov, A., Bas, Y., Kerbiriou, C., Julien, J.-F., Penone, C., Le Viol, I., 2016. Large-scale semi-automated acoustic monitoring allows to detect temporal decline of bush-crickets. *Glob. Ecol. Conserv.* 6, 208-218. <https://doi.org/10.1016/j.gecco.2016.02.008>
- Joshi, N., Joshi, P., 2010. Foraging Behaviour of *Apis* Spp. on Apple Flowers in a Subtropical Environment. *N. Y. Sci. J.* 3.
- Kahl, S., Wood, C.M., Eibl, M., Klinck, H., 2021. BirdNET: A deep learning solution for avian diversity monitoring. *Ecol. Inform.* 61, 101236. <https://doi.org/10.1016/j.ecoinf.2021.101236>
- Kawakita, S., Ichikawa, K., 2019. Automated classification of bees and hornet using acoustic analysis of their flight sounds. *Apidologie* 50, 71-79. <https://doi.org/10.1007/s13592-018-0619-6>
- Kerbiriou, C., Bas, Y., Le Viol, I., Lorrilliere, R., Mougnot, J., Julien, J.F., 2019. Potential of bat pass duration measures for studies of bat activity. *Bioacoustics* 28, 177-192. <https://doi.org/10.1080/09524622.2017.1423517>
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* 274, 303-313. <https://doi.org/10.1098/rspb.2006.3721>
- Klein, B., Seeley, T., 2011. Work or sleep? Honeybee foragers opportunistically nap during the day when forage is not available. *Anim. Behav.* 82, 77-83. <https://doi.org/10.1016/j.anbehav.2011.03.026>
- Knight, E., Hannah, K., Foley, G., Scott, C., Brigham, R., Bayne, E., 2017. Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. *Avian Conserv. Ecol.* 12. <https://doi.org/10.5751/ACE-01114-120214>
- Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci.* 99, 16812-16816. <https://doi.org/10.1073/pnas.262413599>
- Marchal, J., Fabianek, F., Aubry, Y., 2022. Software performance for the automated

- identification of bird vocalisations: the case of two closely related species. *Bioacoustics* 31, 397-413. <https://doi.org/10.1080/09524622.2021.1945952>
- Metcalf, O.C., Barlow, J., Bas, Y., Berenguer, E., Devenish, C., França, F., Marsden, S., Smith, C., Lees, A.C., 2022. Detecting and reducing heterogeneity of error in acoustic classification. *Methods Ecol. Evol.* n/a. <https://doi.org/10.1111/2041-210X.13967>
- Miller-Struttman, N.E., Heise, D., Schul, J., Geib, J.C., Galen, C., 2017. Flight of the bumble bee: Buzzes predict pollination services. *PLOS ONE* 12, e0179273. <https://doi.org/10.1371/journal.pone.0179273>
- Mohanty, S.P., Hughes, D.P., Salathé, M., 2016. Using Deep Learning for Image-Based Plant Disease Detection. *Front. Plant Sci.* 7.
- Montgomery, G.A., Belitz, M.W., Guralnick, R.P., Tingley, M.W., 2021. Standards and Best Practices for Monitoring and Benchmarking Insects. *Front. Ecol. Evol.* 8.
- 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. *Span. J. Agric. Res.* 6, 271-278. <https://doi.org/10.5424/sjar/2008062-318>
- O'Connor, R.S., Kunin, W.E., Garratt, M.P.D., Potts, S.G., Roy, H.E., Andrews, C., Jones, C.M., Peyton, J.M., Savage, J., Harvey, M.C., Morris, R.K.A., Roberts, S.P.M., Wright, I., Vanbergen, A.J., Carvell, C., 2019. Monitoring insect pollinators and flower visitation: The effectiveness and feasibility of different survey methods. *Methods Ecol. Evol.* 10, 2129-2140. <https://doi.org/10.1111/2041-210X.13292>
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321-326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Penone, C., Le Viol, I., Pellissier, V., Julien, J.-F., Bas, Y., Kerbiriou, C., 2013. Use of Large-Scale Acoustic Monitoring to Assess Anthropogenic Pressures on Orthoptera Communities. *Conserv. Biol.* 27, 979-987. <https://doi.org/10.1111/cobi.12083>
- Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.-L., Bretagnolle, V., 2018. Bees increase oilseed rape yield under real field conditions. *Agric. Ecosyst. Environ.* 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 Appl. Ecol.* 34, 75-84. <https://doi.org/10.1016/j.baae.2018.09.005>

- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345-353. <https://doi.org/10.1016/j.tree.2010.01.007>
- R Core Team, 2022. R: A Language and Environment for Statistical Computing.
- Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carvalheiro, L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J., Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipólito, J., Jaggard, S., Jauker, F., Klein, A.-M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattermore, D.E., Pereira, N. de O., Pisanty, G., Potts, S.G., Reemer, M., Rundlöf, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Wojciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. *Proc. Natl. Acad. Sci.* 113, 146-151. <https://doi.org/10.1073/pnas.1517092112>
- Reverté, S., Bosch, J., Arnan, X., Roslin, T., Stefanescu, C., Calleja, J.A., Molowny-Horas, R., Hernández-Castellano, C., Rodrigo, A., 2019. Spatial variability in a plant-pollinator community across a continuous habitat: high heterogeneity in the face of apparent uniformity. *Ecography* 42, 1558-1568. <https://doi.org/10.1111/ecog.04498>
- Reyes-Carrillo, J.L., Eischen, F.A., Cano-Rios, P., Rodriguez-Martinez, R., Nava Camberos, U., 2007. Pollen collection and honey bee forager distribution in cantaloupe. *Acta Zool. Mex.* 23, 29-36.
- Roemer, C., Julien, J.-F., Bas, Y., 2021. An automatic classifier of bat sonotypes around the world. *Methods Ecol. Evol.* 12, 2432-2444. <https://doi.org/10.1111/2041-210X.13721>
- Shiu, Y., Palmer, K.J., Roch, M.A., Fleishman, E., Liu, X., Nosal, E.-M., Helble, T., Cholewiak, D., Gillespie, D., Klinck, H., 2020. Deep neural networks for automated detection of marine mammal species. *Sci. Rep.* 10, 607. <https://doi.org/10.1038/s41598-020-57549-y>
- Silva, D.P., Serres, J.M.-D., Souza, D.R., Hilgert-Moreira, S.B., Fernandes, M.Z., Kevan, P.G., Freitas, B.M., 2013. Efficiency in pollen foraging by honey bees: Time, motion and pollen depletion on flowers of *Sisyrinchium palmifolium* Linnaeus (Asparagales: Iridaceae). *J. Pollinat. Ecol.* 11, 27-32. [https://doi.org/10.26786/1920-7603\(2013\)8](https://doi.org/10.26786/1920-7603(2013)8)
- Steffan-Dewenter, I., Potts, S.G., Packer, L., 2005. Pollinator diversity and crop pollination services are at risk. *Trends Ecol. Evol.* 20, 651-652.

<https://doi.org/10.1016/j.tree.2005.09.004>

- Stowell, D., 2022. Computational bioacoustics with deep learning: a review and roadmap. *PeerJ* 10, e13152. <https://doi.org/10.7717/peerj.13152>
- Stowell, D., Wood, M.D., Pamuła, H., Stylianou, Y., Glotin, H., 2019. Automatic acoustic detection of birds through deep learning: The first Bird Audio Detection challenge. *Methods Ecol. Evol.* 10, 368-380. <https://doi.org/10.1111/2041-210X.13103>
- van Klink, R., August, T., Bas, Y., Bodesheim, P., Bonn, A., Fossøy, F., Høye, T.T., Jongejans, E., Menz, M.H.M., Miraldo, A., Roslin, T., Roy, H.E., Ruczyński, I., Schigel, D., Schäffler, L., Sheard, J.K., Svenningsen, C., Tschan, G.F., Wäldchen, J., Zizka, V.M.A., Åström, J., Bowler, D.E., 2022. Emerging technologies revolutionise insect ecology and monitoring. *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2022.06.001>
- Van Uffelen, L.J., Roth, E.H., Howe, B.M., Oleson, E.M., Barkley, Y., 2017. A Seaglider-Integrated Digital Monitor for Bioacoustic Sensing. *IEEE J. Ocean. Eng.* 42, 800-807. <https://doi.org/10.1109/JOE.2016.2637199>
- Weinstein, B.G., 2018. Scene-specific convolutional neural networks for video-based biodiversity detection. *Methods Ecol. Evol.* 9, 1435-1441. <https://doi.org/10.1111/2041-210X.13011>
- 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. *Ecol. Monogr.* 78, 653-671. <https://doi.org/10.1890/07-1292.1>
- Wickham, H., Chang, W., Henry, L., Pedersen, T.L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., Dunnington, D., RStudio, 2022. *ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics.*
- Woyke, J., Wilde, J., Wilde, M., 2003. Flight activity reaction to temperature changes in *Apis dorsata*, *Apis laboriosa* and *Apis mellifera*. *J. Apic. Sci.* 47.
- Yücel, B., Duman, İ., 2005. Effects of Foraging Activity of Honeybees (*Apis mellifera* L.) on Onion (*Allium cepa*) Seed Production and Quality. *Pak. J. Biol. Sci.* <https://doi.org/10.3923/pjbs.2005.123.126>
- 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.

Chapitre 3 : L'acoustique pour améliorer le suivi des pollinisateurs et la détection de l'influence du paysage sur leur activité

Pour étudier le service de pollinisation, les scientifiques ont recours à des proxys. Ces derniers peuvent être obtenus par des méthodes de piégeage, de capture ou bien de comptage visuel. Néanmoins, nous avons constaté dans la partie précédente de ce travail que grâce aux avancées technologiques de nouveaux proxys peuvent être obtenus. Toutefois, il est nécessaire de tester ces méthodes dans la nature pour comparer les différents proxys obtenus par différentes méthodes, étudier leurs réponses aux facteurs paysagers et leur capacité à renseigner sur le service de pollinisation.

Grâce aux enregistrements acoustiques et aux comptages visuels de pollinisateurs le long de transects réalisés au cours de la saison de floraison du tournesol en 2020, nous avons observé que lorsque les périodes de suivi sont concordantes (le même jour) ces deux indicateurs sont significativement et positivement corrélés. A contrario, lorsque les périodes de suivi ne sont plus concordantes (élargies à la saison), ces proxys d'activité de pollinisateurs n'étaient pas corrélés sur l'ensemble de la saison. Cela s'explique sans doute par la forte variabilité spatiale et temporelle de l'activité des pollinisateurs. Nous avons également mis en évidence l'effet attractif de la densité de tournesol sur l'activité des pollinisateurs avec les deux proxys. Un effet de dilution des champs de tournesol environnants a également été détecté grâce à la méthode de suivi acoustique. Enfin, nous avons montré un effet positif des pollinisateurs sur le rendement du tournesol. Toutefois, nous n'avons pas été en mesure de mettre en relation ce service de pollinisation avec nos proxys.

Cette étude montre que le suivi acoustique est une méthode prometteuse pour le suivi des pollinisateurs qui permet d'éviter les problèmes liés à l'échantillonnage discontinu des méthodes classiques. Elle met en évidence des effets importants du paysage qui ne peuvent pas toujours être détectés avec les méthodes classiques.

Acoustic to improve the monitoring of pollinators and the detection of the influence of the landscape on their activity

In preparation

L. Crochard^a, M. Ragué^{b,c}, J-L. Gautier^{b,c}, S. Gaba^{b,c}, V. Bretagnolle^{c,d}, R. Julliard^a, C. Fontaine^a and M. Baude^{e,f}

^a Centre d'Ecologie et des Sciences de la Conservation, UMR 7204 MNHN-CNRS-Sorbonne Université, Muséum national d'Histoire naturelle, F-75005, Paris, France

^b INRAE, USC 1339, Centre d'Etudes Biologiques de Chizé, F-79360 Villiers-en-Bois, France

^c LTSER "Zone Atelier Plaine & Val de Sèvre", CNRS, Beauvoir-sur-Niort, France

^d CNRS, Université de La Rochelle, UMR 7372, Centre d'Etudes Biologiques de Chizé, F-79360 Beauvoir-sur-Niort, France

^e Université d'Orléans, Orléans, France

^f Sorbonne Université, UPEC, Université Paris Cité, CNRS, IRD, INRAE, Institut d'Ecologie et des Sciences de l'Environnement (iEES-Paris), Paris, France

Abstract

Human food production is dependent on entomophilous pollination with the abundance or diversity of pollinators playing a key role in improving the yield of many crops. However, it is known that the presence of pollinators in cultivated areas can be influenced by many factors, including the landscape. In order to understand the factors influencing pollinator activity in cultivated areas and to be able to estimate pollination services, it is necessary to set up monitoring of pollinator activity at a large spatial scale and fine temporal resolution. Acoustic monitoring could be an effective method for

this but it needs to be tested against more traditional monitoring methods. In this study, we compared two proxies of pollinator activity in sunflower fields, namely: the punctual visual proxy which corresponds to the number of honeybees estimated from observation sessions performed within fields several times during the flowering season, and the continuous acoustic proxy which corresponds to the number of pollinator buzzes detected by continuous passive acoustic monitoring within fields. Our results first indicate that these indicators were not correlated when averaging over the entire flowering season. They were however when considering only days during which both proxies were recorded. Second, we showed that the two proxies were positively related to the density of sunflower plants within fields and that the continuous acoustic proxy was further impacted by the number of hives present around the fields, in interaction with the density of sunflower fields in the landscape. This suggested a dilution effect since more buzzes were detected where more hives were present, but this increase was lower within landscapes dominated by sunflower fields. Finally, thanks to a pollinator exclusion experiment, we showed that pollinators increase sunflower yield, but we were not able to relate such pollination services to either the punctual visual proxy nor the continuous visual proxy. Our results suggest that continuous acoustic monitoring within fields is a promising method to monitor pollinator activity, allowing to prevent issues regarding the timing of observation sessions, and thereby highlighting important landscape effects that could not be detected using observation session data. Surprisingly, however, we did not find a relationship between our indicator of pollinator activity and the pollination service received by sunflowers.

Introduction

In agricultural landscapes, 70% of major global food crops, representing 35% of the annual global food production, are dependent on insect pollinators for their yield (Klein et al., 2007). The growing human demand for pollinator-dependent crops has led to a global increase in the area of these crops since the 1960s (Aizen et al., 2008). Pollination has thus become a major ecosystem service in agricultural ecosystems.

Nevertheless, pollinator decline observed for several decades (Biesmeijer et al., 2006; Potts et al., 2010 notably because of intensive agriculture with the destruction and fragmentation of habitats (Potts et al., 2016, 2010; Vanbergen and Initiative, 2013), and the use of pesticides, (Desneux et al., 2007; Henry et al., 2012; Johnson et al., 2010; Tsvetkov et al., 2017; Wood and Goulson, 2017; Woodcock et al., 2017) that could threaten this ecosystem service.

Monitoring pollinators in the agricultural landscape is thus essential to identify the drivers influencing pollinator activities and pollination services. Previous studies showed that semi-natural habitats were good predictors of pollinator diversity and visitation rate but less so of pollination services (Ricketts et al., 2008), although visitation rate was shown to be positively related to pollination services (Bartomeus et al., 2014; Carvalheiro et al., 2011; Garibaldi et al., 2016; Perrot et al., 2019; Woodcock et al., 2019; Zou et al., 2017). Data on the abundance, diversity, or number of visits of pollinators in agricultural fields are most often collected using methods such as pan traps or transects (Westphal et al., 2008). Transects can involve observing and counting pollinators (Feltham et al., 2015) or capturing and sacrificing them for identification (Westphal et al., 2008). These methods are very time-consuming, reducing the temporal and spatial scales of the monitoring, and pan traps and transects involving the capture of insects are destructive for pollinators (Montgomery et al., 2021). Indeed, Montero-Castaño et al., (2022) determined that in 30 years out of 1426 publications on wild bees, 536 had involved their sacrifice, for a total of over 800 000 wild bees sacrificed.

Thanks to technological advancement, new methods of insect monitoring are being developed (van Klink et al., 2022). One of them is passive acoustic monitoring, which records and quantifies the sounds made by insects. This approach has proven to work well for vocalizing insects such as Jeliaskov et al., (2016) and Penone et al., (2013) and has recently been extended to flying insects, such as pollinators, by recording and analyzing the sounds emitted by their wing beats (Kawakita and Ichikawa, 2019). The first studies on pollinator acoustics focused on the dynamics of bumblebee colonies (Heise et al., 2020), on the links between the morphological

characteristics of bumblebees involved in pollination and the sound they emit (Miller-Struttman et al., 2017) or on monitoring pollinator activity (Folliot et al., 2022; Galen et al., 2019; Miller-Struttman et al., 2017). Two studies on the specific identification of pollinators were conducted by Gradišek et al., (2017) who implemented an application to identify bumblebee species and Kawakita and Ichikawa, (2019) who successfully identified 3 bee species and one hornet species. Monitoring pollinator activity by acoustic surveys offers the opportunity to increase sampling effort, by increasing both the number of sampling points and the temporal coverage of the sampling period (Crochard et al. in prep), and this at no cost to the monitored insects. This makes it a good candidate to monitor pollination services within agricultural landscapes compared to more traditional monitoring methods that most often only capture snapshots of pollinator activity and that may have their sampling effort more strongly limited by the human workforce.

Sunflower (*Helianthus annuus L.*) is one of the main worldwide mass flowering crops essentially cultivated for oil production and livestock feed. It is a pollinator-dependent crop whose insect contribution has been estimated between 18% and 100% according to studies (Carvalheiro et al., 2011; Degrandi-Hoffman and Chambers, 2006; Garibaldi et al., 2016; Greenleaf and Kremen, 2006; Perrot et al., 2019). Although the diversity of pollinators can improve yields Carvalheiro et al., (2011), the domestic honeybee (*Apis mellifera L.*) dominates the pollinator communities, with between 72 to 97.8% of pollinator visits (Bartual et al., 2018; Carvalheiro et al., 2011; Greenleaf and Kremen, 2006), and constitutes the main pollinating species of sunflower. Such dominance of honeybees in the pollinating fauna of sunflowers makes it a good candidate to start developing acoustic monitoring of pollinators by simplifying the issue of identifying pollinators.

Here we aimed at comparing passive acoustic monitoring of insect wing beats and insect counting during observation sessions along transects as indicators of pollinator activity within sunflower fields. We first tested for a relationship between the number of insect wing beats detected by acoustic monitoring and the number of honeybees observed during observation sessions, at both day and extended flowering

period scales. Second, we investigated whether pollinator activity quantified by the two methods were affected by landscape factors. Specifically, we tested for effects of the resource offer, expecting more pollinator activity in large and densely sown fields Perrot et al., (2019), and less pollinator activity in landscapes with high sunflower cover due to the dilution effect (Holzschuh et al., 2016). These effects, whether attractive or dilutive, could potentially be modulated by the number of hives in the landscape (Lindström et al., 2016), while we expected semi-natural habitats not to influence pollinator activity as the location of honeybee colonies is primarily determined by human activities. Finally, we tested for relationships between pollinator activity quantified by the two methods and the pollination services delivered to sunflowers by conducting a pollinator exclusion experiment to estimate the insect contribution to sunflower seed production.

Material and Methods

a) Site description and sunflower fields selection

1. Site description

Pollinator activity survey took place in 20 sunflower fields from the Long-Term Social-Ecological Research site “Zone Atelier Plaine et Val de Sèvre” in South-West France in 2020. This site of 435km² is composed of 87% of cultivated areas (Bretagnolle et al., 2018) and this area is dominated by cereals and sunflowers, representing 55% and 13% of this area respectively.

2. Sunflower field characteristics

The 20 sunflower fields were selected from landscapes with varying degrees of semi-natural habitats and sunflower fields so that they exhibit heterogeneity in pollinator activity. We quantified the area of sunflowers, semi-natural habitats, and the number of hives in a buffer of 500m around the edges (Table S1). For sunflower areas, we used the “Registre Parcellaire Graphique” of 2020 based on farmers' declarations to the Common Agriculture Policy (Institut National de l'Information Géographique et

Forestière, 2017), and for areas of semi-natural habitats the OSO land cover maps (Inglada et al., 2017; <https://www.theia-land.fr/ceslist/ces-occupation-des-sols/>). Because the field area on itself could influence pollinator activity, we also measured the area of each of the 20 sunflower fields (Table S1). All of these spatial analyses were performed with the R package "sf" (Pebesma et al., 2018). The flowering of these sunflower fields started at the beginning of July and ended in the middle of August, with the flowering of each field lasting between 2 and 3 weeks (supplementary figure S1).

Within each field, we estimated the density of sunflower plants by measuring the number of sunflower plants in three non-overlapping 1m² quadrats, located a few meters away from the acoustically monitored plant (see section B1).

B. Monitoring pollinator activity

1. Passive acoustic monitoring

We randomly selected a sunflower plant about 20m from the edge of each field and we equipped it with a microphone, an audiomoth (Hill et al., 2018). The microphone was placed about 20 cm in front of the plant's head and was covered with a windscreen. The recordings take place each day continuously from 6 am to 10 pm (see Table S2 for the detail of the number of days of acoustic records per field). We used a machine learning algorithm to detect pollinator buzzes in records and quantify their activity. For this, records of 10 seconds were generated by the Kaleidoscope software (<https://www.wildlifeacoustics.com/products/kaleidoscope-pro>) and analyzed by TadariDeep (<https://github.com/YvesBas/TadariDeep>) with a convolutional neural networks classifier (Crochard et al., in prep) which determines whether or not there was an insect wing beating sound during those 10 seconds. This method provides for each recorded sound event a confidence score that the sound is indeed that emitted by a pollinator. This implies determining a confidence threshold to consider a sound event as a sound emitted by a pollinator. Here, we fixed the threshold to 78.1, which maximizes the sensitivity and specificity of the classifier

(Crochard et al., in prep). Thus, if at least one sound event in the 10-second record has a confidence score greater than or equal to this threshold, it is considered to have been a pollinator sound (insect wings beating) during that period.

2. Visual honeybee counts

In each field, we also counted the number of visits of sunflower plants by honeybees along a 5-meter wide and 20-meter long transect as a second proxy of pollinator activity. For each field, the transect began 10 meters from the edge and ended 30 meters from the edge and it was not timed. The position of the transect was chosen so that it passes within a few meters of the sunflower plant monitored by the acoustic method. For each field, visual honeybee counts have been repeated 4 to 6 times during a period that encompasses the sunflower bloom, with some counts conducted before, during, and after the flowering (supplementary figure S1).

C. Estimating pollinator contribution to sunflower yield

1. Pollinator exclusion experiments

A pollinator exclusion experiment was conducted in each field on three sunflower plants from the same row (the one acoustically monitored plus two other plants also located 20 meters from the edge of the field) to estimate the contribution of pollinators to sunflower yield. Three pollinator exclusion treatments were applied. The plant acoustically monitored was used as a control with flowers accessible to all pollination processes. The second plant was bagged with a large mesh (3 mm mesh size), blocking the pollination by large insects but allowing the pollination by small pollinators, wind, and self-pollination. The third plant was bagged with a more fine mesh bag (0.6 mm mesh size), allowing only wind pollination and self-pollination. Sunflower heads were bagged at the end of the flower bud stage, just before flowering, and removed after the last flowers faded, to avoid the bag affecting seed formation.

2. Measurement of yield components

We collected 60 sunflower plants in September 2020 just a few days before the crop

harvest (20 fields * 3 plants). The diameter (in mm) of each collected head plant was measured. Then each head was stored in an individual bag with the rest of the plant and left in a heat chamber at 60°C for 48 h. Seeds were removed mechanically from the heads, and fertilized seeds were separated from the empty ones (threshold of 9 mg based on expertise) by seed density with a wind machine (Batteuse petites graines, ATID, France). Fertilized seeds were counted with a seed counter (Contador 2, Pfeuffer, Germany).

D. Statistical analyses

Is there a relationship between the punctual visual and continuous acoustic proxy of pollinator activity?

To characterize the relationship between our punctual visual and continuous acoustic proxies of pollinator activity, we used generalized linear models with a negative binomial distribution adapted for count data.

We first analyzed the relationship between the average number of buzzes detected per day during the acoustic recording period (i.e. sum of buzzes divided by the number of days of acoustic recording) and the average number of honeybees counted per visual observation session (i.e. sum of honeybees divided by the number of observation session). For both proxies, the data before, during, and after the flowering period were used. For all parts of the study, only the days with a minimum of 14 hours of recording out of the 16 theoretical hours were retained. Because our two methods differ greatly in their temporal resolution (a continuous period of 12 to 32 days recording for the acoustic method versus 4-6 distinct observation sessions for the visual honeybee count, see supplementary figure S1), we then explored the relationship between our two pollinator activity methods after restricting the time window of the acoustic recordings to match the days of visual observations. We thus analyzed at a more fine temporal scale the relationship between the number of buzzes detected during the day of the visual observation session and the number of honeybees counted during that session. Since previous studies have shown that honeybee activity varies with the

time of day (Crochard et al., in prep; Eban-Rothschild and Bloch, 2008; Joshi and Joshi, 2010; Nderitu et al., 2008), we also added the time of day at which the observation session was conducted as a second-order polynomial explanatory variable. Moreover, we added the field identity as a random effect.

Is pollinator activity affected by landscape factors?

To identify the factors explaining the differences in pollinator activity among fields, we analyzed the response of (1) the average number of honeybees per observation session and (2) the average number of buzzes detected per day to landscape characteristics. For both pollinator activity indicators, we have restricted the data to the flowering period of the acoustically monitored sunflower plant. Generalized linear models with a negative binomial distribution were built to study the response of these two response variables to the landscape factors (the percentage of sunflowers, the percentage of semi-natural habitats, and the number of hives surrounding the field), and more local factors (the field area, the density of sunflower plants within the field). Since the effect of hive number might be modulated by the percentage of surrounding sunflowers, by the plant density, and since the effect of plant density might modulate the effect of the percentage of surrounding sunflowers, we also tested the interactive effects between these factors by including two-by-two interactions of previous variables. Since buzzes were recorded from a specific sunflower plant, we also included the diameter of the sunflower head in the model dedicated to this acoustic proxy of pollinator activity. Since the head diameter can modulate the effect of the previous variables, we tested second order interactions between head diameter and these variables. All variables were centered and scaled.

Do the differences in pollinator activity impact the sunflower yields?

To study the contribution of pollinators to the sunflower yield, we analyzed the response of the total number of fertilized seeds per plant to the pollinator exclusion treatment, the head diameter, the pollinator activity proxy, and the interactions between all of these variables. Field identity was considered as a random effect since

in each field we had three sunflower plants. Two distinct generalized linear mixed models with a negative binomial distribution were built by changing only the pollinator activity proxy (either average buzzes number per day or average honeybee count per session, both restricted to the flowering period). The variable “head diameter” and the pollinator activity proxy were centered and scaled.

All statistical analyses were performed using R (R Core Team, 2022). From the list of models with combination of fixed effects terms and their interactions in the full model, we selected the best model with the dredge function from the package MuMin (Bartoń, 2022) on the basis of the second-order Akaike Information Criterion (differences in AICc < 2). The residuals of all models were controlled thanks to the package DHarma (Hartig and Lohse, 2022).

Results

In the 20 fields, a total of 111 observation sessions were realized. During these sessions, 806 honeybees were counted, with a minimum of 0 and a maximum of 65 honeybees counted per session. Using acoustic recording, a total of 106 415 buzzes of pollinators were detected in 7032 hours of recording. Only 51 observation sessions were performed at the same time as the acoustic recording sessions since many observation sessions were conducted before and after the flowering period.

Is there a relationship between the punctual visual and continuous acoustic proxy of pollinator activity?

When acoustic data and visual honeybee counts were averaged over the full season, we did not find a significant relationship between the average number of buzzes detected per day and the average number of honeybees counting per session of observation, (Chisq=1.1577, p-value=0.2819, Fig. 1a). When acoustic and visual data were retrieved the same days (by restricting acoustic data to the days of visual observation session), we found a significant positive non-linear relationship between the number of buzzes recorded during the day of an observation session and the number of honeybees counted during this observation session (Chisq=14.485, p-

value < 0.001, Fig.1b). However, the time of day the observation session was conducted does not appear to affect this relationship.

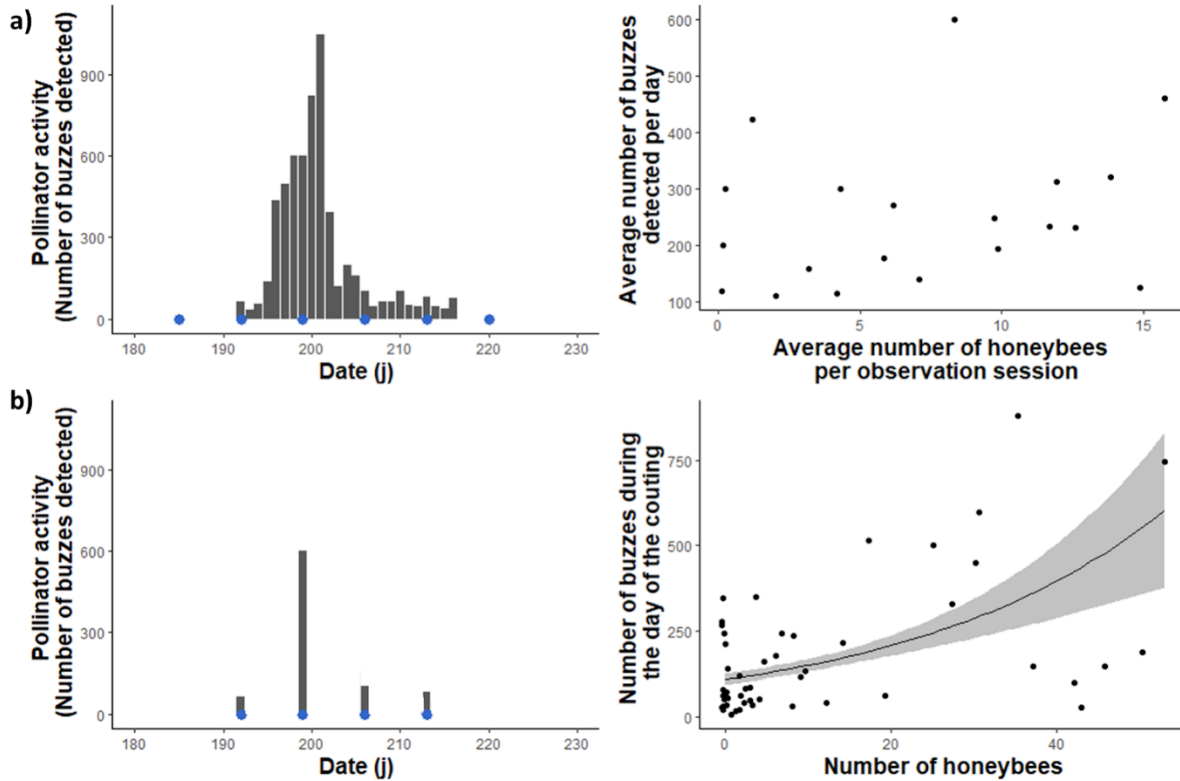


Figure 1 - a) Relationship between the average number of buzzes detected per day before, during, and after the flowering period and the average number of honeybees counted per observation session during the same period. b) Relationship between the number of buzzes detected during the day of the visual observation session and the number of honeybees counted during that session. For a) and b) the graph on the left represents the data taken into account for the analysis and the graph on the right represents the relationships between variables. In the graphs on the left, dots represent the dates on which the observation sessions were carried out. For the right graphs, dots correspond to the acquired field data. The black line corresponds to the predicted values of the generalized linear model and the grey ribbon to the standard error.

Is pollinator activity affected by landscape factors?

In the case of the punctual visual proxy of pollinator activity, we only found a significant effect of sunflower plant density ($\text{Chisq}=7.28$, $p\text{-value}=0.007$) on the average number of honeybees counted per observation session during the flowering period. An increase in sunflower plant density was associated with a non-linear increase in the number of counted honeybees (Fig.2a). However, we did not detect any significant effects of the landscape factors, neither hives number on the visual proxy of pollinator activity.

In the case of the continuous acoustic proxy of pollinator activity, we found, in addition to a significant positive effect of sunflower plant density (Fig 2b), a significant interaction between the number of hives around the field and the percentage of the sunflowers in the landscape on the average number of buzzes detected per day during the flowering period (Tab.1). At low levels of sunflowers in the landscape, the acoustic pollinator activity increases with the number of hives around the field whereas this trend was not found at higher levels of surrounding sunflowers in the landscape (Fig 2c).

In other words, when hives were present around the field, the acoustic pollinator activity decreases as the percentage of the landscape covered by sunflowers increases whereas when hives were absent from the surrounding landscape, the acoustic pollinator activity remains at a very low level regardless of the percentage of sunflowers in the landscape (Fig 2c).

Pollination activity variable used	Variable	Chisq	Df	p-value
Punctual visual proxy Average number of honeybees counted per observation session during the flowering period	Local sunflower plant density	7.28	1	0.007
	Local sunflower plant density	6.15	1	0.013
Continuous acoustic proxy Average number of buzzes per day during the flowering period	Number of hives around the field	5.16	1	0.023
	Percentage of sunflower in the surrounding landscape	0.99	1	0.32
	Number of hives around the field : Percentage of sunflower in the surrounding landscape	11.43	1	<0.001

Table 1 - Summary statistics of the best generalized linear model investigating the effects of landscape and local factors on visual (average number of honeybees counted per observation session during the flowering period) and acoustic proxy (average number of buzzes detected per day during the flowering period) of pollinator activity. All variables have been normalized prior to running models.

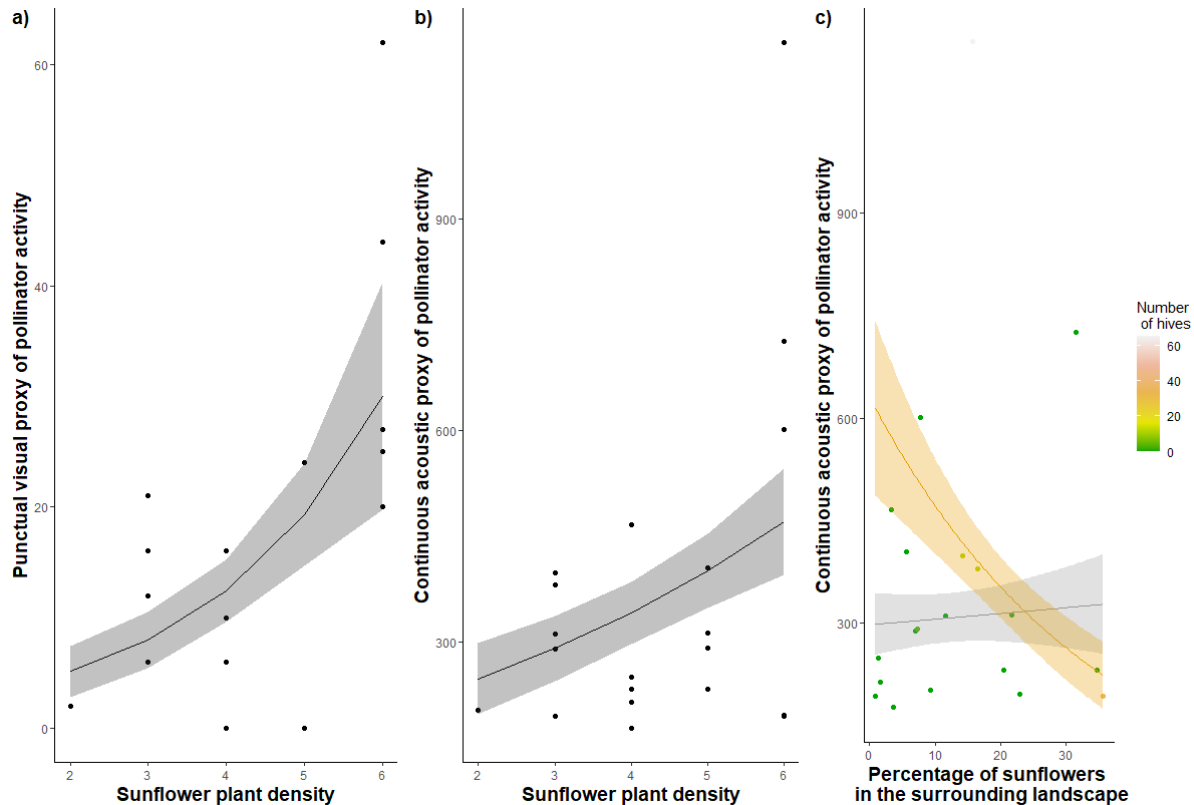


Figure 2 - Relationship between a) the punctual visual proxy of pollinator activity (average number of honeybees counted per observation session during the flowering period) and the local density of sunflower plants, b) the continuous acoustic proxy of pollinator activity (average number of buzzes detected per day during the flowering period) and the local density of sunflower plants, c) the continuous acoustic proxy of pollinator activity (average number of buzzes detected per day during the flowering period) and the percentage of sunflowers in the surrounding landscape according to the number of hives around the field. Dots correspond to field data and lines correspond to the predicted values of the generalized linear models. In c) the grey line corresponds to the predicted values without hives around the field and the orange line corresponds to the predicted values with 15 hives around the field. The dot color depends on the number of hives around the field.

Do the differences in pollinator activity impact the sunflower yields?

Regardless of the proxy used for pollinator activity (visual or acoustic), we found that the number of fertilized seeds is significantly impacted by the interaction between pollinator exclusion treatment and head diameter (Tab.2). This indicates that the effect of the pollinator exclusion treatment varied significantly with the sunflower head diameter (Tab.2). For sunflower heads with the largest diameters, the number of fertilized seeds is higher for the control plants (open pollination) compared to the bagged plants (pollinators excluded) whereas it was not the case for the smallest sunflower heads. Actually, the larger the diameter of the head, the greater the

difference in the number of seeds between the control and the bagged plants (Fig. 3).

Regardless of the proxy used for pollinator activity (visual or acoustic), the simplified model does not include the interaction between treatment and pollination activity. This indicates that there is no effect of the number of visits on pollinator contribution to sunflower yield.

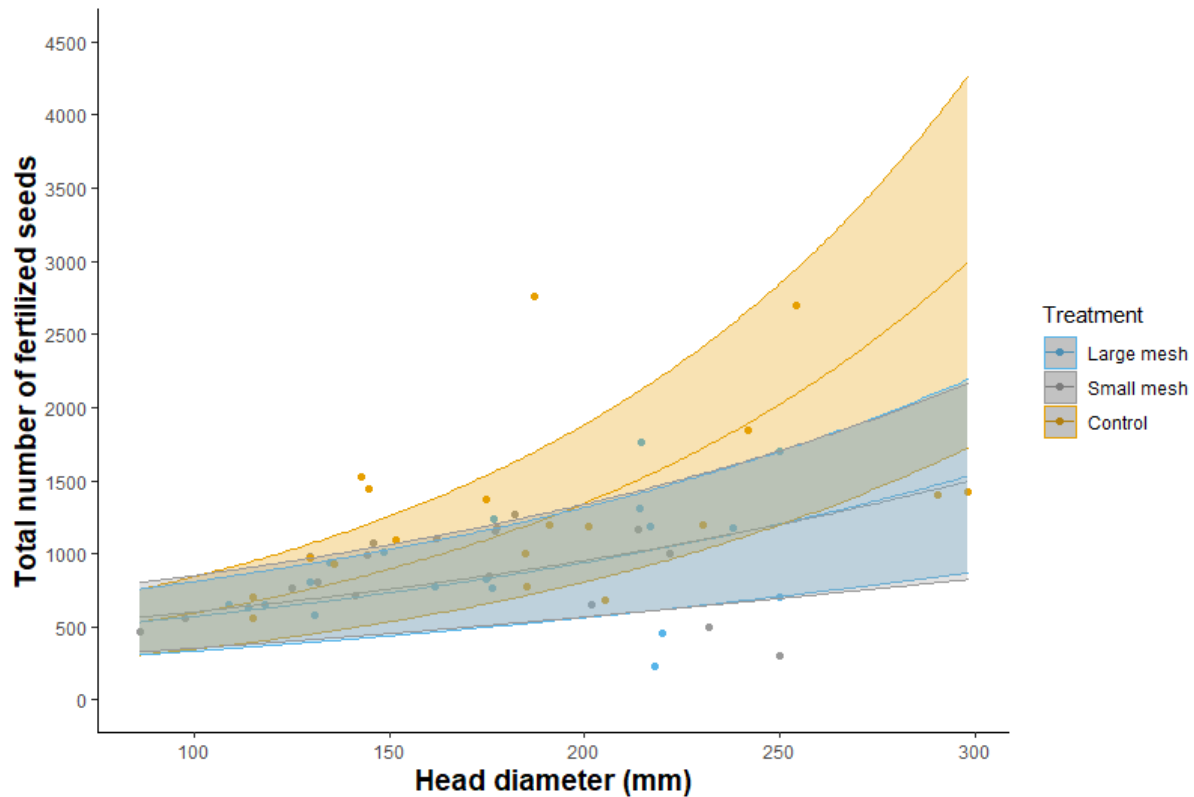


Figure 3 - Relationship between the total number of fertilized seeds per sunflower plant and the head diameter according to the pollinator exclusion treatment applied to the sunflower plant. Lines correspond to the predicted values of the generalized linear models. The grey line corresponds to the predicted values for sunflower plants bagged with small mesh (large and small pollinators excluded), the blue line is for sunflower plants bagged with large mesh (only large pollinators excluded) and the orange is for the control plant (open pollination).

Response variable	Proxy used as the pollinator activity variable	Variable	Chisq	Df	P-value
Total number of fertilized seeds per plant	Visual proxy Average number of honeybees counted per observation session during the flowering period	Head Diameter	31.98	1	<0.0001
		Treatment	24.39	2	<0.0001
		Head Diameter : Treatment	8.18	2	0.017
	Acoustic proxy Average number of buzzes per day during the flowering period	Head Diameter	32.59	1	<0.0001
		Treatment	23.84	2	<0.0001
		Head Diameter : Treatment	9.34	2	0.009

Table 2 - Summary statistics of the best generalized linear model investigating the effect of pollinators on the number of fertilized seeds per sunflower plant. The variable Head Diameter has been normalized prior to running models.

Discussion

In this study, we compared two pollinator activity proxies, a punctual visual proxy, and a continuous acoustic proxy. We tested their sensitivity to landscape effects and their relationships with sunflower yields. We determined that the proxy obtained from acoustic pollinator monitoring is more sensitive to the landscape than that obtained from visual observations. This is probably due to a better coverage of the flowering season with the acoustic monitoring which is continuous. Surprisingly, none of the proxies were related to sunflower yield.

First, we found a positive and significant relationship between the visual and acoustic proxies when data retrieved from the same day indicating that these two methods provide concordant information on pollinator activity. Nevertheless, when averaged for the extended flowering period, the relationship between the two proxies of pollinator activity vanished. This could be due to the fact that counting sessions are not representative of the entire phenology of pollinator activity during the season, unlike acoustic monitoring which is continuous and takes place over longer periods of time. Indeed, pollinator activity can vary from day to day, for example, due to weather

or due to the phenology of nectar production in the landscape that varies throughout the flowering season (Grab et al., 2017). However, these observation sessions are not necessarily conducted during peak plant flowering, which is often associated with peak pollinator activity. Indeed, it may be difficult to conduct sessions at peak flowering when several fields are in flower at the same time. To explore this hypothesis it could be interesting to develop indices to know if the counting sessions and the passive acoustic monitoring allowed to cover each period of the sunflower season, the beginning, the peak, and the end of the flowering period.

As expected, we did not find an effect of the percentage of landscape cover of semi-natural habitats on pollinator activity whatever the proxy used. This could be because sunflowers are pollinated almost exclusively by honeybees, which are managed pollinators whose density depends on the location of hives and not semi-natural habitats (Bartual et al., 2018; Carvalheiro et al., 2011; Greenleaf and Kremen, 2006; Perrot et al., 2019). Indeed, semi-natural habitats are acknowledged to especially affect wild pollinators thanks to the floral and nesting resources they provide to them (Baude et al., 2016; Langlois et al., 2020; Lye et al., 2009; Timberlake et al., 2019). In contrast, whatever the method used, we determined that the sunflower plant density positively affects pollinator activity, which is in line with Perrot et al., (2019). A high density of sunflowers is likely to be highly attractive to pollinators due to a greater amount of floral resources, as has been found for other plants (Delmas et al., 2016). Only the passive acoustic monitoring reveals an effect of the number of hives around the cultivated field in interaction with the percentage of the landscape covered by sunflowers. This result suggests that when the environment is saturated with honeybees, they disperse to other sunflower fields. This spillover phenomenon has already been observed for many mass-flowering crops (Holzschuh et al., 2016; Rollin et al., 2013; Tschardt et al., 2012).

We found a difference in seed production between the control (open pollination) and bagged plants (pollinators excluded) and this difference varied with sunflower head diameter. This reflects the overall contribution of insects to sunflower pollination and indicates that the larger the head diameter, the stronger the effect of

pollinators on seed production. However, this trend is similar whether all pollinators are excluded (large mesh treatment) or only large pollinators (small mesh treatment), revealing the main contribution of large pollinators to sunflower pollination. This is in agreement with other studies that determined that honeybees, which are large pollinators excluded by the large mesh treatment, are the most efficient pollinators of sunflowers (Nderitu et al., 2008). Several studies using pollinator exclusion, with exclusion cages and flower head bagging, or using a pollinator gradient have shown the positive effect of honeybee abundance on sunflower yields (Altayeb and Nagi, 2015; Aslan and Yavuksuz, 2010; Greenleaf and Kremen, 2006; Perrot et al., 2019). Therefore, we expected to find a positive effect of pollinator activity on seed production. Nevertheless, as Hevia et al., (2016), we did not find any effect of pollinator activity on sunflower seed production, regardless of the method used to calculate the proxy. This may be explained by non-linear relationships between the number of pollinator visits and seed production, or by the fact that a low number of visits is sufficient to generate seed formation and thus additional visits have no effect on production.

Conclusion

Our results suggest that passive acoustic monitoring is at least as effective as traditional methods in monitoring pollinator activity if the diversity of pollinators is not addressed. Continuous monitoring avoids the biases inherent in other methods and therefore better takes into account the phenology of the crops. Nevertheless, like the traditional method we used, acoustic monitoring did not show an effect of pollinator activity on yield. In order to apply this method to other crops, it could be interesting to develop specific identification of pollinators in order to study the impact of pollinator diversity on crop yield.

Acknowledgments

We would like to express our thanks to CCAIN2P3 for allowing us to perform our deep learning analysis on their platform. This research was funded through the ANR IMAGHO (ANR-18- CE32-0002).

Author contributions

L. Crochard, C. Fontaine, M. Baude conceived the ideas; L. Crochard and M. Ragué collected the data; L. Crochard analyzed the data; L. Crochard, C. Fontaine, M. Baude led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Supplementary

Field	Area of the sunflower field (ha)	Number of hives around the field	Percentage of semi-natural habitats in the surrounding landscape	Percentage of sunflower in the surrounding landscape	Head diameter of the sunflower plant acoustically monitored (mm)	Local sunflower plant density
10626	10,8	0	13,9	11,5	187	3
116	6,7	0	19,3	31,5	185	6
12	13,8	12	9,3	16,5	230	3
12446	2,0	0	24,6	22,9	115	6
13138	2,1	0	8,6	7,0	115	3
13253	14,9	0	19,0	1,3	136	4
14499	2,0	0	24,0	3,6	205	4
17019	2,2	0	4,6	7,7	130	6
2187	5,6	0	26,6	20,4	254	5
2230	3,4	0	7,8	34,8	185	4
2939	13,8	12	30,5	14,1	298	3
3253	11,1	0	33,1	9,2	152	2
3271	5,3	65	15,9	15,8	145	6
376	9,2	32	5,0	35,7	143	6
4566	15,5	0	8,9	5,7	148	5
5572	3,2	0	38,3	3,3	242	4
5595	3,6	0	5,5	0,9	201	3
5867	8,6	0	43,1	1,5	175	4
7507	9,7	3	13,2	7,2	290	5
9523	2,9	0	10,0	21,6	191	5

Table S1 - Landscape and local characteristics of the 20 selected sunflower fields

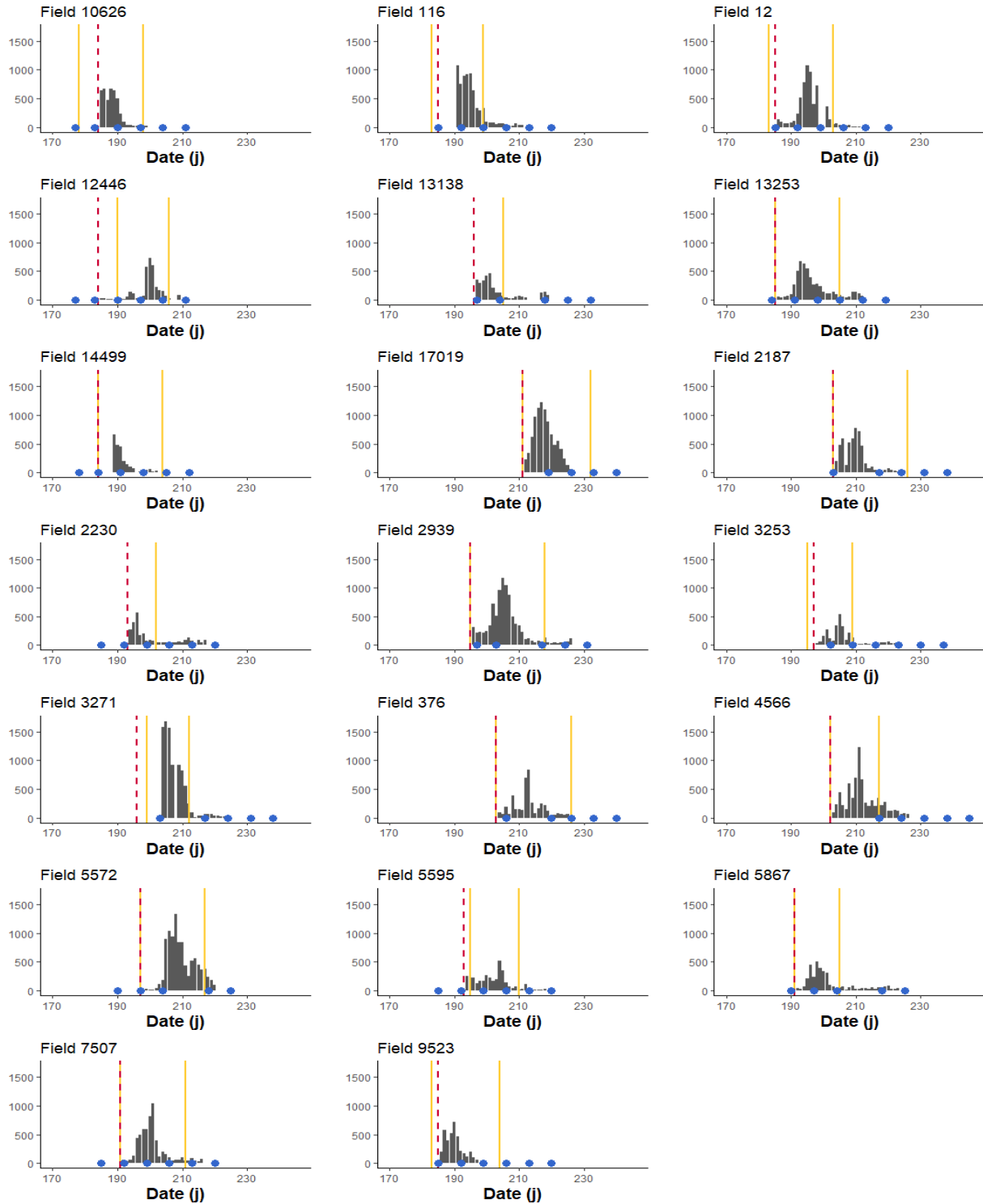


Figure S1 - Number of buzzes detected per day in each field. Only days with a minimum of 14 hours of recordings were taken into account. The red dashed line corresponds to the day the microphone was set up in the field. Orange lines correspond to the last day for which we were sure that the acoustically monitored sunflower plant was not yet in bloom and to the first day for which we were sure that it was deflowered. Blue dots correspond to the days during which visual monitoring of pollinators was carried out in the field.

Field	Total number of days of acoustic recording	Number of days of acoustic recording during the flowering period of the acoustically monitored plant
10626	15	13
116	21	8
12	24	15
12446	25	15
13138	19	8
13253	27	19
14499	13	13
17019	15	15
2187	22	22
2230	24	8
2939	31	22
3253	25	11
3271	19	7
376	22	22
4566	24	14
5572	23	19
5595	25	14
5867	32	13
7507	25	19
9523	12	12

Table S2 - Detail of number of days acoustic recording for each field

References

- Aizen, M.A., Garibaldi, L.A., Cunningham, S.A., Klein, A.M., 2008. Long-Term Global Trends in Crop Yield and Production Reveal No Current Pollination Shortage but Increasing Pollinator Dependency. *Curr. Biol.* 18, 1572-1575. <https://doi.org/10.1016/j.cub.2008.08.066>
- Altayeb, O. a. E., Nagi, S.K.A., 2015. Efficacy of honeybees (*Apis mellifera*) on the production of sunflower (*Helianthus annuus* L.) seeds in the Sudan. *J. Exp. Biol. Agric. Sci.* 3, 191-195.
- Aslan, M.M., Yavuksuz, C., 2010. Effect of honey bee (*Apis mellifera* L.) and bumblebee

- (*Bombus terrestris* L.) pollinators on yield and yield factors in sunflower (*Helianthus annuus* L.) production areas. *J. Anim. Vet. Adv.* 9, 332–335.
- 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>
- Bartoń, K., 2022. MuMIn: Multi-Model Inference.
- Bartual, A.M., Bocci, G., Marini, S., Moonen, A.C., 2018. Local and landscape factors affect sunflower pollination in a Mediterranean agroecosystem. *PLOS ONE* 13, e0203990. <https://doi.org/10.1371/journal.pone.0203990>
- 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, 85–88. <https://doi.org/10.1038/nature16532>
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science* 313, 351–354. <https://doi.org/10.1126/science.1127863>
- Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhausser, 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. *Sci. Total Environ.* 627, 822–834. <https://doi.org/10.1016/j.scitotenv.2018.01.142>
- 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. *Ecol. Lett.* 14, 251–259. <https://doi.org/10.1111/j.1461-0248.2010.01579.x>
- Crochard, L., Fontaine, C., Baude, M., Ragué, M., Bas, D., Gaba, S., Bretagnolle, V., Julliard, R., Bas, Y., in prep. Buzzy bees, quantifying bee activity within sunflower

fields using acoustic monitoring and deep learning

- Degrandi-Hoffman, G., Chambers, M., 2006. Effects of Honey Bee (Hymenoptera: Apidae) Foraging on Seed Set in Self-fertile Sunflowers (*Helianthus annuus* L.). *Environ. Entomol.* 35, 1103-1108. <https://doi.org/10.1603/0046-225X-35.4.1103>
- Delmas, C.E.L., Fort, T.L.C., Escaravage, N., Pornon, A., 2016. Pollen transfer in fragmented plant populations: insight from the pollen loads of pollinators and stigmas in a mass-flowering species. *Ecol. Evol.* 6, 5663-5673. <https://doi.org/10.1002/ece3.2280>
- Desneux, N., Decourtye, A., Delpuech, J.-M., 2007. The Sublethal Effects of Pesticides on Beneficial Arthropods. *Annu. Rev. Entomol.* 52, 81-106. <https://doi.org/10.1146/annurev.ento.52.110405.091440>
- Eban-Rothschild, A.D., Bloch, G., 2008. Differences in the sleep architecture of forager and young honeybees (*Apis mellifera*). *J. Exp. Biol.* 211, 2408-2416. <https://doi.org/10.1242/jeb.016915>
- Feltham, H., Park, K., Minderman, J., Goulson, D., 2015. Experimental evidence that wildflower strips increase pollinator visits to crops. *Ecol. Evol.* 5, 3523-3530. <https://doi.org/10.1002/ece3.1444>
- Folliot, A., Hauptert, S., Ducrettet, M., Sèbe, F., Sueur, J., 2022. Using acoustics and artificial intelligence to monitor pollination by insects and tree use by woodpeckers. *Sci. Total Environ.* 838, 155883. <https://doi.org/10.1016/j.scitotenv.2022.155883>
- Galen, C., Miller, Z., Lynn, A., Axe, M., Holden, S., Storcks, L., Ramirez, E., Asante, E., Heise, D., Kephart, S., Kephart, J., 2019. Pollination on the Dark Side: Acoustic Monitoring Reveals Impacts of a Total Solar Eclipse on Flight Behavior and Activity Schedule of Foraging Bees. *Ann. Entomol. Soc. Am.* 112, 20-26. <https://doi.org/10.1093/aesa/say035>
- Garibaldi, L.A., Carvalheiro, L.G., Vaissière, B.E., Gemmill-Herren, B., Hipólito, J., Freitas, B.M., Ngo, H.T., Azzu, N., Sáez, A., Åström, J., An, J., Blochtein, B., Buchori, D., García, F.J.C., Oliveira da Silva, F., Devkota, K., Ribeiro, M. de F., Freitas, L., Gaglianone, M.C., Goss, M., Irshad, M., Kasina, M., Filho, A.J.S.P., Kiill, L.H.P., Kwapong, P., Parra, G.N., Pires, C., Pires, V., Rawal, R.S., Rizali, A., Saraiva, A.M.,

- Veldtman, R., Viana, B.F., Witter, S., Zhang, H., 2016. Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science* 351, 388–391. <https://doi.org/10.1126/science.aac7287>
- 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. *Sci. Rep.* 7, 45296. <https://doi.org/10.1038/srep45296>
- Gradišek, A., Slapničar, G., Šorn, J., Luštrek, M., Gams, M., Grad, J., 2017. Predicting species identity of bumblebees through analysis of flight buzzing sounds. *Bioacoustics* 26, 63–76. <https://doi.org/10.1080/09524622.2016.1190946>
- Greenleaf, S.S., Kremen, C., 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proc. Natl. Acad. Sci.* 103, 13890–13895. <https://doi.org/10.1073/pnas.0600929103>
- Hartig, F., Lohse, L., 2022. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.
- Heise, D., Miller, Z., Wallace, M., Galen, C., 2020. Bumble Bee Traffic Monitoring Using Acoustics, in: 2020 IEEE International Instrumentation and Measurement Technology Conference (I2MTC). Presented at the 2020 IEEE International Instrumentation and Measurement Technology Conference (I2MTC), pp. 1–6. <https://doi.org/10.1109/I2MTC43012.2020.9129582>
- Henry, M., Béguin, M., Requier, F., Rollin, O., Odoux, J.-F., Aupinel, P., Aptel, J., Tchamitchian, S., Decourtye, A., 2012. A Common Pesticide Decreases Foraging Success and Survival in Honey Bees. *Science* 336, 348–350. <https://doi.org/10.1126/science.1215039>
- Hevia, V., Bosch, J., Azcárate, F.M., Fernández, E., Rodrigo, A., Barril-Graells, H., González, J.A., 2016. Bee diversity and abundance in a livestock drove road and its impact on pollination and seed set in adjacent sunflower fields. *Agric. Ecosyst. Environ.* 232, 336–344. <https://doi.org/10.1016/j.agee.2016.08.021>
- Hill, A.P., Prince, P., Piña Covarrubias, E., Doncaster, C.P., Snaddon, J.L., Rogers, A., 2018. AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods Ecol. Evol.* 9, 1199–1211.

<https://doi.org/10.1111/2041-210X.12955>

- 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. *Ecol. Lett.* 19, 1228-1236. <https://doi.org/10.1111/ele.12657>
- Inglada, J., Vincent, A., Arias, M., Tardy, B., Morin, D., Rodes, I., 2017. Operational High Resolution Land Cover Map Production at the Country Scale Using Satellite Image Time Series. *Remote Sens.* 9, 95. <https://doi.org/10.3390/rs9010095>
- Institut National de l'Information Géographique et Forestière, n.d. Registre parcellaire graphique (RPG) : contours des parcelles et îlots cultureux et leur groupe de cultures majoritaire - data.gouv.fr [WWW Document]. URL /fr/datasets/registre-parcellaire-graphique-rpg-contours-des-parcelles-et-ilots-cultureux-et-leur-groupe-de-cultures-majoritaire/ (accessed 2.10.21).
- Jeliazkov, A., Bas, Y., Kerbiriou, C., Julien, J.-F., Penone, C., Le Viol, I., 2016. Large-scale semi-automated acoustic monitoring allows to detect temporal decline of bush-cricket. *Glob. Ecol. Conserv.* 6, 208-218. <https://doi.org/10.1016/j.gecco.2016.02.008>
- Johnson, R.M., Ellis, M.D., Mullin, C.A., Frazier, M., 2010. Pesticides and honey bee toxicity - USA. *Apidologie* 41, 312-331. <https://doi.org/10.1051/apido/2010018>
- Joshi, N., Joshi, P., 2010. Foraging Behaviour of Apis Spp. on Apple Flowers in a Subtropical Environment. *N. Y. Sci. J.* 3.
- Kawakita, S., Ichikawa, K., 2019. Automated classification of bees and hornet using acoustic analysis of their flight sounds. *Apidologie* 50, 71-79. <https://doi.org/10.1007/s13592-018-0619-6>
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* 274, 303-313. <https://doi.org/10.1098/rspb.2006.3721>
- Langlois, A., Jacquemart, A.-L., Piqueray, J., 2020. Contribution of Extensive Farming

- Practices to the Supply of Floral Resources for Pollinators. *Insects* 11, 818. <https://doi.org/10.3390/insects11110818>
- Lindström, S.A.M., Herbertsson, L., Rundlöf, M., Smith, H.G., Bommarco, R., 2016. Large-scale pollination experiment demonstrates the importance of insect pollination in winter oilseed rape. *Oecologia* 180, 759-769. <https://doi.org/10.1007/s00442-015-3517-x>
- Lye, G., Park, K., Osborne, J., Holland, J., Goulson, D., 2009. Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). *Biol. Conserv.* 142, 2023-2032. <https://doi.org/10.1016/j.biocon.2009.03.032>
- Miller-Struttman, N.E., Heise, D., Schul, J., Geib, J.C., Galen, C., 2017. Flight of the bumble bee: Buzzes predict pollination services. *PLOS ONE* 12, e0179273. <https://doi.org/10.1371/journal.pone.0179273>
- Montero-Castaño, A., Koch, J.B.U., Lindsay, T.-T.T., Love, B., Mola, J.M., Newman, K., Sharkey, J.K., 2022. Pursuing best practices for minimizing wild bee captures to support biological research. *Conserv. Sci. Pract.* 4, e12734. <https://doi.org/10.1111/csp2.12734>
- Montgomery, G.A., Belitz, M.W., Guralnick, R.P., Tingley, M.W., 2021. Standards and Best Practices for Monitoring and Benchmarking Insects. *Front. Ecol. Evol.* 8.
- 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. *Span. J. Agric. Res.* 6, 271-278. <https://doi.org/10.5424/sjar/2008062-318>
- Pebesma, E., Bivand, R., Racine, E., Sumner, M., Cook, I., Keitt, T., Lovelace, R., Wickham, H., Ooms, J., Müller, K., Pedersen, T.L., Baston, D., Dunnington, D., 2018. sf: Simple Features for R.
- Penone, C., Le Viol, I., Pellissier, V., Julien, J.-F., Bas, Y., Kerbiriou, C., 2013. Use of Large-Scale Acoustic Monitoring to Assess Anthropogenic Pressures on Orthoptera Communities. *Conserv. Biol.* 27, 979-987. <https://doi.org/10.1111/cobi.12083>
- 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 Appl. Ecol.* 34, 75-84.
<https://doi.org/10.1016/j.baae.2018.09.005>
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345-353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. *Nature* 540, 220-229. <https://doi.org/10.1038/nature20588>
- R Core Team, 2022. R: A Language and Environment for Statistical Computing.
- 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? *Ecol. Lett.* 11, 499-515. <https://doi.org/10.1111/j.1461-0248.2008.01157.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. *Agric. Ecosyst. Environ.* 179, 78-86. <https://doi.org/10.1016/j.agee.2013.07.007>
- Timberlake, T.P., Vaughan, I.P., Memmott, J., 2019. Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *J. Appl. Ecol.* 56, 1585-1596. <https://doi.org/10.1111/1365-2664.13403>
- 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., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.* 87, 661-685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Tsvetkov, N., Samson-Robert, O., Sood, K., Patel, H.S., Malena, D.A., Gajiwala, P.H.,

- Maciukiewicz, P., Fournier, V., Zayed, A., 2017. Chronic exposure to neonicotinoids reduces honey bee health near corn crops. *Science* 356, 1395–1397. <https://doi.org/10.1126/science.aam7470>
- van Klink, R., August, T., Bas, Y., Bodesheim, P., Bonn, A., Fossøy, F., Høye, T.T., Jongejans, E., Menz, M.H.M., Miraldo, A., Roslin, T., Roy, H.E., Ruczyński, I., Schigel, D., Schäffler, L., Sheard, J.K., Svenningsen, C., Tschan, G.F., Wäldchen, J., Zizka, V.M.A., Åström, J., Bowler, D.E., 2022. Emerging technologies revolutionise insect ecology and monitoring. *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2022.06.001>
- Vanbergen, A.J., Initiative, the I.P., 2013. Threats to an ecosystem service: pressures on pollinators. *Front. Ecol. Environ.* 11, 251–259. <https://doi.org/10.1890/120126>
- 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., Wojciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J., Steffan-Dewenter, I., 2008. Measuring Bee Diversity in Different European Habitats and Biogeographical Regions. *Ecol. Monogr.* 78, 653–671. <https://doi.org/10.1890/07-1292.1>
- Wood, T.J., Goulson, D., 2017. The environmental risks of neonicotinoid pesticides: a review of the evidence post 2013. *Environ. Sci. Pollut. Res. Int.* 24, 17285–17325. <https://doi.org/10.1007/s11356-017-9240-x>
- Woodcock, B.A., Bullock, J.M., Shore, R.F., Heard, M.S., Pereira, M.G., Redhead, J., Ridding, L., Dean, H., Sleep, D., Henrys, P., Peyton, J., Hulmes, S., Hulmes, L., Sárospataki, M., Saure, C., Edwards, M., Genersch, E., Knäbe, S., Pywell, R.F., 2017. Country-specific effects of neonicotinoid pesticides on honey bees and wild bees. *Science* 356, 1393–1395. <https://doi.org/10.1126/science.aaa1190>
- 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., van der Werf, W., Stout, J.C., Steffan-Dewenter, I., Morandin, L., Bullock, J.M., Pywell, R.F., 2019. Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. *Nat. Commun.* 10,

1481. <https://doi.org/10.1038/s41467-019-09393-6>

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 Ecol.* 17, 6. <https://doi.org/10.1186/s12898-017-0116-1>

Discussion générale

Effet de l'assolement des espaces cultivés sur le service de pollinisation

Les études s'intéressant à l'impact du paysage sur le service de pollinisation se concentrent en général sur l'effet des milieux se trouvant hors des espaces cultivés, en particulier les habitats semi-naturels (e.g Andersson et al., 2014; Carvalheiro et al., 2011; Földesi et al., 2016; Garratt et al., 2017; Klein et al., 2012; Ricketts et al., 2008). En revanche, les espaces cultivés sont rarement pris en compte dans ces études (mais Gaba et al., 2017; Holzschuh et al., 2013). L'un des objectifs de cette thèse était donc d'étudier l'impact que peut avoir l'assolement des espaces cultivés sur le service de pollinisation. Pour cela, nous avons tout d'abord utilisé les réseaux d'interactions plantes-pollinisateurs (chapitre 1). Classiquement, les réseaux d'interactions sont utilisés pour étudier les interactions entre les ressources florales et les pollinisateurs au sein d'une même année (Carvalheiro et al., 2011). L'originalité de notre travail a donc été de modifier ces réseaux afin de prendre en compte les dynamiques temporelles de l'assolement d'une année sur l'autre. Cela nous a permis d'étudier la contribution des ressources florales passées au service de la pollinisation du colza de l'année suivante. Nous avons constaté qu'à l'échelle de notre site d'étude, le service de pollinisation dépendait essentiellement des ressources florales autres que du colza lui-même. Cela indique que pour maintenir la pollinisation d'une culture, la conservation de la diversité des ressources florales est essentielle (Raderschall et al., 2021). De plus, le fait que la flore adventice des cultures contribue au moins autant au service de pollinisation du colza que les cultures à floraison massive montre que ces ressources sont essentielles pour le maintien des pollinisateurs dans les milieux agricoles. On peut d'ailleurs supposer que leur importance dans le maintien des communautés de pollinisateurs est d'autant plus grande pour pallier au manque de ressources florales (Timberlake et al., 2019) lorsque les habitats semi-naturels sont absents du paysage. La forte contribution de la flore adventice des céréales était liée à la surface importante

qu'ils occupent au sein de notre site d'étude. Ce résultat plutôt surprenant souligne l'importance de prendre en considération l'ensemble du paysage agricole pour étudier le service de pollinisation des cultures, même si les espèces cultivées, comme les céréales, sont connues pour ne pas fournir de ressources aux pollinisateurs (Roulston et al., 2000). A surface identique, nous avons déterminé que le colza était le plus important contributeur au maintien de son propre service de pollinisation. Toutefois, les effets indirects que nous avons mesuré sont en réalité des potentiels d'effets indirects, car de nombreuses simplifications ont été réalisées en négligeant par exemple les différences de ressources en nectar et pollen générées par les différentes espèces de plantes ou encore les différences d'efficacité de pollinisation entre les espèces de pollinisateurs. De plus, comme nous n'avons pas mesuré les rendements du colza, les effets que nous avons calculé peuvent être assimilés à des proxys de l'effet des ressources florales sur le service de pollinisation du colza. L'étude que nous avons menée sur le suivi acoustique des pollinisateurs du tournesol (chapitre 3), nous a permis de mettre en évidence l'effet attractif d'une forte densité de tournesol provenant sans doute d'une forte disponibilité en ressources florales dans les zones denses (Delmas et al., 2016). Nous avons également pu mettre en évidence un effet de dilution du tournesol sur l'activité des pollinisateurs lorsque le paysage environnant la parcelle avait une densité de tournesol élevée.

L'ensemble de ces résultats montre l'importance d'étudier les effets des espaces cultivés sur le service de pollinisation. En effet, à l'instar de notre site d'étude, ces espaces occupent une grande proportion des paysages agricoles et peuvent donc jouer un rôle essentiel sur le service de pollinisation. Il pourrait être d'autant plus important de s'intéresser à ces surfaces qu'elles sont sans doute plus faciles à modifier que les milieux non cultivés. Les recommandations actuelles visant à favoriser la pollinisation dans les milieux agricoles consistent souvent à augmenter les surfaces d'habitats semi-naturels. Or, agir également sur les espaces cultivés pourrait conduire à des bénéfices importants. En effet, afin d'augmenter l'abondance totale et la diversité des pollinisateurs à l'échelle du paysage, il pourrait être intéressant de modifier l'assolement des cultures de façon à limiter les périodes de disette alimentaire en

jouant sur la succession des cultures. Un changement de pratique au sein de ces espaces pourrait également jouer un rôle important en faveur de la pollinisation. Outre la diminution de pesticides dans les parcelles de céréales, des réflexions autour du travail du sol pourraient être menées puisque le labourage peut détruire à la fois les sites de nidification des insectes terricoles, mais aussi la flore adventice dont les ressources florales sont essentielles au maintien des communautés de pollinisateurs entre les floraisons des cultures à floraison massive. Concernant les effets indirects inter-annuels des ressources florales sur le service de pollinisation du colza (chapitre 1), on peut supposer que cultiver du colza dans une zone où la culture était très présente l'année passée pourrait être bénéfique pour sa pollinisation. Toutefois, il serait nécessaire de spatialiser cette étude afin de connaître les effets réels du paysage proche des parcelles de colza. De plus, dans l'ensemble des espaces cultivés, limiter l'utilisation des herbicides pourrait être bénéfique pour le service de pollinisation, notamment dans les céréales, car l'élimination des adventices dans ces espaces entraîne la disparition de ressources florales pour les pollinisateurs sur une grande part des paysages agricoles et ne permet pas forcément une amélioration des rendements (Gaba et al., 2016). Pour éviter les débats sur la compétition de la flore adventice avec les espèces cultivées, notamment les céréales (Milberg and Hallgren, 2004), la limitation des herbicides pourrait s'accompagner de nouvelles mesures visant à réduire cette compétition, comme réduire la densité des semis ou le semis de cultivars compétitifs (Gaba et al., 2018; Sidemo-Holm et al., 2021). Néanmoins, afin de comprendre au mieux l'importance de ces espaces par rapport aux zones non cultivées, il serait intéressant de réaliser des études en prenant en compte à la fois les espaces cultivés et les espaces non cultivés.

Le suivi acoustique passif : une méthode efficace pour suivre l'activité des pollinisateurs au sein des cultures

Le deuxième objectif de ces travaux consistait à évaluer les capacités du suivi acoustique passif (chapitres 2 et 3) qui présente l'avantage d'être non létal et moins chronophage que les méthodes de suivi des pollinisateurs classiques pour étudier le

service de pollinisation et les mécanismes sous-jacents. En effet, avec la forte médiatisation du déclin des pollinisateurs, des insectes et de la biodiversité en général, la question de l'utilisation de méthodes létales pour étudier les communautés de pollinisateurs pose des questions d'ordre éthique (Drinkwater et al., 2019). On peut se demander si le sacrifice de plusieurs centaines de milliers d'insectes au cours des 30 dernières années (Montero-Castaño et al., 2022) dans le cadre d'études scientifiques est justifié. De plus, comme nous l'avons décrit précédemment, les méthodes classiques d'échantillonnage des pollinisateurs sont lourdes à mettre en place et chronophages que ce soit lors des sessions de récolte des pollinisateurs ou lors de leur identification par les taxonomistes (Montgomery et al., 2021). Cela limite donc les échelles spatiales et temporelles des études, alors même que la compréhension des mécanismes autour du service de pollinisation nécessite de travailler à de larges échelles spatiales et à une fine échelle temporelle afin de ne manquer aucune phase de la phénologie d'activité des pollinisateurs qui varie fortement au cours de la saison. Les taxonomistes sont peu nombreux et ne sont pas forcément experts de l'ensemble des taxons capturés au cours des récoltes ce qui signifie qu'une part importante des individus capturés (avec les pots pièges) est souvent sacrifiée inutilement (Gonzalez et al., 2020). Il semble donc que l'utilisation de méthodes non létales et moins chronophages puisse être une solution pour continuer à étudier la pollinisation entomophile tout en évitant des débats éthiques et en améliorant l'effort d'échantillonnage des études. Toutefois, ces méthodes nécessitent des développements importants et une évaluation de leur capacité à être utilisées dans le cadre d'études sur la fonction et le service de pollinisation. Pour le suivi acoustique passif des pollinisateurs, l'une des parties importantes du développement consiste à utiliser un algorithme d'apprentissage machine qui soit efficace pour la reconnaissance et la classification des sons émis par les pollinisateurs via le battement de leurs ailes. Or, aucune comparaison n'avait encore été faite sur les performances des différents algorithmes. Nos résultats ont montré que l'utilisation des réseaux de neurones convolutifs, se basant sur la reconnaissance des spectrogrammes, permet de réduire de trois fois le taux d'erreur comparé à la méthode des forêts aléatoires (chapitre 2),

classiquement utilisée dans les études de suivi acoustique des pollinisateurs (Gradišek et al., 2017). Ce résultat indique également que les pollinisateurs ne font pas exception et que comme de nombreux autres taxons pour lesquels l'utilisation des réseaux de neurones convolutifs est devenue la norme (Stowell, 2022), il s'agit de la méthode permettant de réduire au maximum le risque d'erreur de reconnaissance des sons. Toutefois, il est important de noter que notre système d'étude est relativement simple puisque nous travaillons dans des milieux où les communautés de pollinisateurs sont dominées par *Apis mellifera*, et avons ainsi considéré que chaque son de pollinisateur détecté correspondait à cette espèce. De plus, nous avons démontré que le suivi acoustique passif des pollinisateurs permet d'obtenir des informations sur la phénologie de butinage des pollinisateurs qui semblent cohérentes avec la littérature existante, notamment au niveau horaire avec une activité élevée entre 11 et 16 heure, qui correspond globalement à la période de production maximale de nectar par le tournesol (Chabert et al., 2020). Cela laisse penser que cette méthode permet d'obtenir un proxy de l'activité des pollinisateurs reflétant relativement bien la réalité.

Pour promouvoir le recours à cette méthode de suivi des pollinisateurs, il est nécessaire d'étudier les apports qu'elle peut avoir au niveau scientifique et d'évaluer si elle peut effectivement être utilisée comme proxy du service de pollinisation. Ainsi, nous avons montré que sur une large période de temps, les proxys d'activité des pollinisateurs fournis par le suivi acoustique, et le comptage visuel, n'étaient pas corrélés. Cela s'explique par le fait que les deux méthodes de suivi se sont déroulées sur différentes périodes. En effet, lorsque les périodes d'échantillonnage sont concordantes, nous avons trouvé une relation positive entre ces deux proxys (chapitre 3). Cela suppose que ces deux méthodes fournissent des informations sur l'activité des pollinisateurs similaires, mais qu'il existe un biais en raison des différences d'effort d'échantillonnage. En effet, le comptage visuel ne pouvant pas être réalisé chaque jour, cette méthode implique la perte d'information lors de phases importantes de la phénologie de butinage des pollinisateurs, notamment si le comptage n'est pas réalisé au moment du pic de floraison de la culture qui est sans doute relié au pic d'activité des pollinisateurs. Puisqu'il est impossible de suivre plusieurs parcelles en même

temps lorsque des observateurs sont impliqués, la météo peut également générer du bruit dans les données de suivi ponctuel. En revanche, ces problèmes ne se posent pas avec le suivi acoustique qui peut être continu et simultané entre les parcelles. Cela nous a permis de mettre en évidence des effets du paysage sur l'activité de pollinisateurs impossible à mettre en évidence avec les données de comptage des pollinisateurs le long de transects (chapitre 3). Ces résultats suggèrent que le suivi acoustique passif et continu des pollinisateurs est une méthode prometteuse pour le suivi de l'activité des pollinisateurs et pour étudier les facteurs pouvant la faire varier. L'abondance des pollinisateurs étant souvent décrite comme le facteur explicatif de l'action positive des pollinisateurs sur le rendement des cultures comme le tournesol (Altayeb and Nagi, 2015; Aslan and Yavuksuz, 2010; Greenleaf and Kremen, 2006; Perrot et al., 2019), nous nous attendions à ce que le proxy de l'activité des pollinisateurs fourni par la méthode de suivi acoustique explique les différences de rendement entre les parcelles de tournesol suivies. Cela peut être expliqué par des relations non linéaires entre le nombre de visites de pollinisateurs et la production de graines ou par le fait qu'un faible nombre de visites suffit à engendrer la formation de graines et donc que les visites supplémentaires n'ont pas d'effet sur la production.

L'activité des pollinisateurs n'étant pas homogène au sein d'une parcelle (Hevia et al., 2016), il serait intéressant de déterminer avec précision le rayon de captation des sons pour améliorer cette méthode de suivi et obtenir des données reflétant l'activité des pollinisateurs au sein des parcelles de la façon la plus réaliste possible. Pour promouvoir l'utilisation de cette méthode auprès des scientifiques, l'amélioration essentielle à mettre en œuvre reste l'identification taxonomique des individus à partir de leurs sons. Cela a déjà été réalisé sur quelques espèces d'abeilles gérées et sauvages et sur une espèce de frelon (Gradišek et al., 2017; Kawakita and Ichikawa, 2019) avec des méthodes d'apprentissage machine anciennes. Nous pouvons donc penser que les réseaux de neurones convolutifs seront également efficaces pour cela, d'autant qu'il ont déjà permis l'identification d'autres insectes volants, comme les moustiques (Kiskin et al., 2021). Néanmoins, au vu du nombre d'espèces de pollinisateurs existant, il est peu probable de réussir à obtenir un jeu de données de

référence exhaustif. De plus, certaines espèces émettent des sons de moindre intensité qu'*Apis mellifera*, probablement les espèces de petite taille, et seront donc plus difficiles à détecter et nécessiteront la mise en place de protocoles de suivi adaptés. Il est donc sans doute plus raisonnable de penser qu'il sera possible de différencier de grands groupes taxonomiques et fonctionnels. Le frein majeur au développement de cette capacité d'identification restant la disponibilité de données de référence, il est nécessaire que les scientifiques travaillent en collaboration afin de constituer un jeu de données de référence important pour une grande diversité de pollinisateurs. Cette collaboration est également essentielle pour éviter de futurs biais méthodologiques. Enfin, il sera nécessaire d'assurer la reproductibilité des études en travaillant notamment sur le stockage des données et des métadonnées associées aux études (van Klink et al., 2022).

Le service de pollinisation : quelles méthodes pour l'évaluer ?

La non détection d'un effet de l'activité des pollinisateurs sur le rendement du tournesol nous a amenés à nous interroger sur les méthodes mises en place pour étudier le service de pollinisation. En effet, pour démontrer un effet des pollinisateurs sur le rendement des cultures, deux méthodes expérimentales existent : l'exclusion des pollinisateurs et les gradients des pollinisateurs. L'exclusion des pollinisateurs permet, par la mise en place d'un protocole expérimental, de mesurer de façon précise la contribution des pollinisateurs au rendement des cultures. Les gradients de pollinisateurs permettent quant à eux d'étudier les variations de traits associés au rendement le long de ces gradients. Ces méthodes peuvent toutefois être lourdes à mettre en place avec par exemple la mise en place de cages d'exclusion des pollinisateurs ou encore la manutention de ruches pour créer des gradients de pollinisateurs. Elles peuvent également générer des biais qu'il est nécessaire de prendre en compte, comme la création d'un microclimat pouvant impacter négativement le rendement sous les filets d'exclusion des pollinisateurs ou le blocage par les filets du pollen transféré par le vent (Jacobs et al., 2009; Kunjwal et al., 2014;

Wragg and Johnson, 2011). Néanmoins, la plupart des études sur le service de pollinisation ne cherchent pas à le quantifier de manière directe ou expérimentale. Noriega et al. (2018) ont déterminé qu'entre 1989 et 2016, moins de 30% des études sur le service de pollinisation l'ont quantifié directement ou de manière expérimentale. En revanche, ils ont déterminé qu'environ 50% des études utilisaient des proxys de pollinisation, comme l'abondance ou la diversité des pollinisateurs pour quantifier ce service. On peut donc s'interroger sur ces différences de métriques utilisées en fonction des différentes études.

Liss et al., (2013) ont déterminé que les différences de métriques utilisées entre les études sur le service de pollinisation pourraient provenir de la définition de "service de pollinisation" utilisée par chaque chercheur, aussi influencé par leur discipline de recherche. Néanmoins, en écologie il me semble que les différences de métriques utilisées sont dues principalement aux objectifs des études et moins à la définition du service de pollinisation. En effet, l'utilisation des proxys peut permettre de comprendre les mécanismes et les espèces impliqués dans le service de pollinisation. Toutefois, pour comprendre correctement les mécanismes du service de pollinisation, il semble indispensable de coupler l'utilisation des proxys basés sur les insectes pollinisateurs avec des mesures quantitatives de l'effet de la pollinisation sur la production agricole. En effet, l'utilisation seule des proxys de pollinisation pour quantifier le service de pollinisation pourrait conduire à des erreurs dans l'interprétation des résultats. Par exemple, bien que de nombreuses études ont montré que la diversité ou l'abondance des pollinisateurs sont positivement corrélées avec le rendement des cultures (e.g Garibaldi et al., 2013; Klein et al., 2003; Lindström et al., 2016; Mallinger and Gratton, 2015; Perrot et al., 2019, 2018; Zou et al., 2017), et que ces deux proxys sont liés au paysage, il n'est pas évident qu'il y ait un lien entre paysage et rendement des cultures (Ricketts et al., 2008). Cela peut sans doute s'expliquer par le fait que, dans de nombreux cas, ce n'est pas la communauté de pollinisateurs de la culture qui est identifiée avec les proxys, mais celle des visiteurs de la culture. Or, l'ensemble des visiteurs de la culture ne sont pas forcément des pollinisateurs de celle-ci (Chifflet et al., 2011).

Perspectives

Notre étude sur les effets indirects des ressources florales passées sur la pollinisation du colza ne prenait pas en compte les effets indirects potentiels des habitats semi-naturels. Il pourrait donc être intéressant de les prendre en compte en même temps que les espaces cultivés afin de connaître plus précisément les ressources florales les plus impliquées dans le maintien du service de pollinisation du colza d'une année sur l'autre. De plus, notre étude ne disposant pas de mesure quantitative des rendements du colza, nous pouvons assimiler les effets indirects des ressources florales sur le colza comme des proxys de l'effet de ces ressources florales sur le service de pollinisation du colza. Spatialiser cette étude en se concentrant sur le paysage environnant des parcelles de colza et en mesurant le rendement du colza pourrait ainsi permettre de connaître le véritable effet des ressources florales passées sur le service de pollinisation des cultures.

Pour ce qui est du développement de l'identification des pollinisateurs à partir de leur son, l'utilisation de la vision par ordinateur couplée à l'utilisation de capteurs sonores devrait permettre de constituer des bases de référence de façon non létale. La dernière réunion du Groupement De Recherche POLLINÉCO (Pollinisation, réseaux d'interaction et fonctionnalité des écosystèmes) a permis de mettre en relation les chercheurs francophones souhaitant travailler sur cette thématique ce qui devrait permettre une évolution plus rapide de la méthode. L'une des solutions pour augmenter l'acquisition de données pourrait également permettre de mettre en place un protocole de sciences participatives qui couplerait à la fois la prise de photos des pollinisateurs, à l'image du SPIPOLL, et l'enregistrement acoustique des pollinisateurs.

Références

- Aizen, M.A., Garibaldi, L.A., Cunningham, S.A., Klein, A.M., 2008. Long-Term Global Trends in Crop Yield and Production Reveal No Current Pollination Shortage but Increasing Pollinator Dependency. *Curr. Biol.* 18, 1572-1575. <https://doi.org/10.1016/j.cub.2008.08.066>
- Altayeb, O. a. E., Nagi, S.K.A., 2015. Efficacy of honeybees (*Apis mellifera*) on the production of sunflower (*Helianthus annuus* L.) seeds in the Sudan. *J. Exp. Biol. Agric. Sci.* 3, 191-195.
- Andersson, G.K.S., Ekroos, J., Stjernman, M., Rundlöf, M., Smith, H.G., 2014. Effects of farming intensity, crop rotation and landscape heterogeneity on field bean pollination. *Agric. Ecosyst. Environ.* 184, 145-148. <https://doi.org/10.1016/j.agee.2013.12.002>
- Araneda Durán, X., Breve Ulloa, R., Aguilera Carrillo, J., Lavín Contreras, J., Toneatti Bastidas, M., 2010. Evaluation of Yield Component Traits of Honeybee-Pollinated (*Apis mellifera* L.) Rapeseed Canola (*Brassica napus* L.). *Chil. J. Agric. Res.* 70, 309-314. <https://doi.org/10.4067/S0718-58392010000200014>
- Aslan, M.M., Yavuksuz, C., 2010. Effect of honey bee (*Apis mellifera* L.) and bumblebee (*Bombus terrestris* L.) pollinators on yield and yield factors in sunflower (*Helianthus annuus* L.) production areas. *J. Anim. Vet. Adv.* 9, 332-335.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471, 51-57. <https://doi.org/10.1038/nature09678>
- 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.M., Bocci, G., Marini, S., Moonen, A.C., 2018. Local and landscape factors

- affect sunflower pollination in a Mediterranean agroecosystem. *PLOS ONE* 13, e0203990. <https://doi.org/10.1371/journal.pone.0203990>
- Bas, Y., Bas, D., Julien, J.-F., 2017. Tadarida: A Toolbox for Animal Detection on Acoustic Recordings. *J. Open Res. Softw.* 5, 6. <https://doi.org/10.5334/jors.154>
- Bascompte, J., Jordano, P., 2007. Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 38, 567-593.
- Bateman, A.J., 1952. Self-incompatibility systems in angiosperms: I. Theory. *Heredity* 6, 285-310. <https://doi.org/10.1038/hdy.1952.40>
- Batovska, J., Piper, A.M., Valenzuela, I., Cunningham, J.P., Blacket, M.J., 2021. Developing a non-destructive metabarcoding protocol for detection of pest insects in bulk trap catches. *Sci. Rep.* 11, 7946. <https://doi.org/10.1038/s41598-021-85855-6>
- 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, 85-88. <https://doi.org/10.1038/nature16532>
- Bauer, S., Chapman, J.W., Reynolds, D.R., Alves, J.A., Dokter, A.M., Menz, M.M.H., Sapir, N., Ciach, M., Pettersson, L.B., Kelly, J.F., Leijnse, H., Shamoun-Baranes, J., 2017. From Agricultural Benefits to Aviation Safety: Realizing the Potential of Continent-Wide Radar Networks. *BioScience* 67, 912-918. <https://doi.org/10.1093/biosci/bix074>
- Becker, H.C., Damgaard, C., Karlsson, B., 1992. Environmental variation for outcrossing rate in rapeseed (*Brassica napus*). *Theor. Appl. Genet.* 84, 303-306. <https://doi.org/10.1007/BF00229487>
- Benjamin, F., R. Reilly, J., Winfree, R., 2014. Pollinator body size mediates the scale at which land use drives crop pollination services. *J. Appl. Ecol.* 51, 440-449. <https://doi.org/10.1111/1365-2664.12198>
- 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. *Agric. Ecosyst. Environ.* 319, 107537.

<https://doi.org/10.1016/j.agee.2021.107537>

- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science* 313, 351–354. <https://doi.org/10.1126/science.1127863>
- Bjerge, K., Mann, H.M.R., Høye, T.T., 2022. Real-time insect tracking and monitoring with computer vision and deep learning. *Remote Sens. Ecol. Conserv.* 8, 315–327. <https://doi.org/10.1002/rse2.245>
- Bommarco, R., Marini, L., Vaissière, B.E., 2012. Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia* 169, 1025–1032. <https://doi.org/10.1007/s00442-012-2271-6>
- Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhausser, I., Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018a. Towards sustainable and multifunctional agriculture in farmland landscapes: Lessons from the integrative approach of a French LTSER platform. *Sci. Total Environ.* 627, 822–834. <https://doi.org/10.1016/j.scitotenv.2018.01.142>
- Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhausser, I., Monceau, K., Allier, F., Monestiez, P., Gaba, S., 2018b. Description of long-term monitoring of farmland biodiversity in a LTSER. *Data Brief* 19, 1310–1313. <https://doi.org/10.1016/j.dib.2018.05.028>
- Bretagnolle, V., Gaba, S., 2015. Weeds for bees? A review. *Agron. Sustain. Dev.* 35, 891–909. <https://doi.org/10.1007/s13593-015-0302-5>
- Bruijning, M., Visser, M.D., Hallmann, C.A., Jongejans, E., 2018. trackdem: Automated particle tracking to obtain population counts and size distributions from videos in r. *Methods Ecol. Evol.* 9, 965–973. <https://doi.org/10.1111/2041-210X.12975>
- Brydegaard, M., Jansson, S., 2019. Advances in entomological laser radar. *J. Eng.* 2019, 7542–7545. <https://doi.org/10.1049/joe.2019.0598>
- Brydegaard, M., Jansson, S., Malmqvist, E., Mlacha, Y.P., Gebru, A., Okumu, F., Killeen, G.F., Kirkeby, C., 2020. Lidar reveals activity anomaly of malaria vectors during pan-African eclipse. *Sci. Adv.* 6, eaay5487. <https://doi.org/10.1126/sciadv.aay5487>

- Buchmann, S.L., Nabhan, G.P., 1996. The Pollination Crisis. *The Sciences* 36, 22-27. <https://doi.org/10.1002/j.2326-1951.1996.tb03254.x>
- 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. *J. Appl. Ecol.* 47, 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. *Ecol. Lett.* 14, 251-259. <https://doi.org/10.1111/j.1461-0248.2010.01579.x>
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Sci. Adv.* 1, e1400253. <https://doi.org/10.1126/sciadv.1400253>
- Chabert, S., Sénéchal, C., Fougeroux, 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., 2020. Effect of environmental conditions and genotype on nectar secretion in sunflower (*Helianthus annuus* L.). *OCL Oilseeds Fats Crops Lipids* 27, 51. <https://doi.org/10.1051/ocl/2020040>
- Chapman, J.L., Reiss, M.J., 1992. *Ecology: Principles and Applications*. Cambridge University Press.
- Chapman, J.W., Drake, V.A., Reynolds, D.R., 2011. Recent Insights from Radar Studies of Insect Flight. *Annu. Rev. Entomol.* 56, 337-356. <https://doi.org/10.1146/annurev-ento-120709-144820>
- Chatellier, V., Delame, N., 2007. Les exploitations agricoles européennes et françaises, in: *L'agriculture, Nouveaux Défis, Références*. INSEE, p. np.
- Chifflet, R., Klein, E.K., Lavigne, C., Le Féon, V., Ricroch, A.E., Lecomte, J., Vaissière, B.E., 2011. Spatial scale of insect-mediated pollen dispersal in oilseed rape in an open agricultural landscape. *J. Appl. Ecol.* 48, 689-696. <https://doi.org/10.1111/j.1365-2664.2010.01904.x>
- Cunningham, S.A., Fournier, A., Neave, M.J., Le Feuvre, D., 2016. Improving spatial arrangement of honeybee colonies to avoid pollination shortfall and depressed fruit

- set. *J. Appl. Ecol.* 53, 350-359. <https://doi.org/10.1111/1365-2664.12573>
- Dafni, A., 1992. *Pollination ecology: a practical approach*. Pollinat. Ecol. Pract. Approach.
- Darwin, C. R. 1862. *On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing*. London: John Murray.
- Degrandi-Hoffman, G., Chambers, M., 2006. Effects of Honey Bee (Hymenoptera: Apidae) Foraging on Seed Set in Self-fertile Sunflowers (*Helianthus annuus* L.). *Environ. Entomol.* 35, 1103-1108. <https://doi.org/10.1603/0046-225X-35.4.1103>
- Delmas, C.E.L., Fort, T.L.C., Escaravage, N., Pornon, A., 2016. Pollen transfer in fragmented plant populations: insight from the pollen loads of pollinators and stigmas in a mass-flowering species. *Ecol. Evol.* 6, 5663-5673. <https://doi.org/10.1002/ece3.2280>
- Desjonquères, C., Rybak, F., Ulloa, J.S., Kempf, A., Bar Hen, A., Sueur, J., 2020. Monitoring the acoustic activity of an aquatic insect population in relation to temperature, vegetation and noise. *Freshw. Biol.* 65, 107-116. <https://doi.org/10.1111/fwb.13171>
- Desneux, N., Decourtye, A., Delpuech, J.-M., 2007. The Sublethal Effects of Pesticides on Beneficial Arthropods. *Annu. Rev. Entomol.* 52, 81-106. <https://doi.org/10.1146/annurev.ento.52.110405.091440>
- Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M.A., Baste, I.A., Brauman, K.A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P.W., van Oudenhoven, A.P.E., van der Plaats, F., Schröter, M., Lavorel, S., Aumeeruddy-Thomas, Y., Bukvareva, E., Davies, K., Demissew, S., Erpul, G., Failler, P., Guerra, C.A., Hewitt, C.L., Keune, H., Lindley, S., Shirayama, Y., 2018. Assessing nature's contributions to people. *Science* 359, 270-272. <https://doi.org/10.1126/science.aap8826>
- Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A.,

- Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R.R., Shin, Y.-J., Visseren-Hamakers, I., Willis, K.J., Zayas, C.N., 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science* 366, eaax3100. <https://doi.org/10.1126/science.aax3100>
- Doi, H., Katano, I., Sakata, Y., Souma, R., Kosuge, T., Nagano, M., Ikeda, K., Yano, K., Tojo, K., 2017. Detection of an endangered aquatic heteropteran using environmental DNA in a wetland ecosystem. *R. Soc. Open Sci.* 4, 170568. <https://doi.org/10.1098/rsos.170568>
- Drinkwater, E., Robinson, E.J.H., Hart, A.G., 2019. Keeping invertebrate research ethical in a landscape of shifting public opinion. *Methods Ecol. Evol.* 10, 1265-1273. <https://doi.org/10.1111/2041-210X.13208>
- Elbrecht, V., Vamos, E.E., Steinke, D., Leese, F., 2018. Estimating intraspecific genetic diversity from community DNA metabarcoding data. *PeerJ* 6, e4644. <https://doi.org/10.7717/peerj.4644>
- FAO [WWW Document], 2022. . Food Agric. Organ. U. N. URL <http://www.fao.org/ecosystem-services-biodiversity/background/regulating-services/fr/> (accessed 11.18.22).
- FAOSTAT, 2020. FAOSTAT [WWW Document]. Food Agric. Organ. U. S. WWW Doc. URL <http://www.fao.org/faostat/en/#data/QC> (accessed 7.15.21).
- Földesi, R., Kovács-Hostyánszki, A., Kőrösi, Á., Somay, L., Elek, Z., Markó, V., Sárospataki, M., Bakos, R., Varga, Á., Nyisztor, K., Báldi, A., 2016. Relationships between wild bees, hoverflies and pollination success in apple orchards with different landscape contexts. *Agric. For. Entomol.* 18, 68-75. <https://doi.org/10.1111/afe.12135>
- Folliot, A., Hauptert, S., Ducrettet, M., Sèbe, F., Sueur, J., 2022. Using acoustics and artificial intelligence to monitor pollination by insects and tree use by woodpeckers. *Sci. Total Environ.* 838, 155883. <https://doi.org/10.1016/j.scitotenv.2022.155883>
- 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, e02413. <https://doi.org/10.1002/ecs2.2413>

- Gaba, S., Gabriel, E., Chadœuf, J., Bonneu, F., Bretagnolle, V., 2016. Herbicides do not ensure for higher wheat yield, but eliminate rare plant species. *Sci. Rep.* 6, 30112. <https://doi.org/10.1038/srep30112>
- Gaba, S., Perronne, R., Fried, G., Gardarin, A., Bretagnolle, F., Biju-Duval, L., Colbach, N., Cordeau, S., Fernández-Aparicio, M., Gauvrit, C., Gibot-Leclerc, S., Guillemin, J.-P., Moreau, D., Munier-Jolain, N., Strbik, F., Reboud, X., 2017. Response and effect traits of arable weeds in agro-ecosystems: a review of current knowledge. *Weed Res.* 57, 123-147. <https://doi.org/10.1111/wre.12245>
- Galen, C., Miller, Z., Lynn, A., Axe, M., Holden, S., Storcks, L., Ramirez, E., Asante, E., Heise, D., Kephart, S., Kephart, J., 2019. Pollination on the Dark Side: Acoustic Monitoring Reveals Impacts of a Total Solar Eclipse on Flight Behavior and Activity Schedule of Foraging Bees. *Ann. Entomol. Soc. Am.* 112, 20-26. <https://doi.org/10.1093/aesa/say035>
- Gallai, N., Salles, J.-M., Settele, J., Vaissière, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.* 68, 810-821. <https://doi.org/10.1016/j.ecolecon.2008.06.014>
- Garibaldi, L.A., Carvalheiro, L.G., Vaissière, B.E., Gemmill-Herren, B., Hipólito, J., Freitas, B.M., Ngo, H.T., Azzu, N., Sáez, A., Åström, J., An, J., Blochtein, B., Buchori, D., García, F.J.C., Oliveira da Silva, F., Devkota, K., Ribeiro, M. de F., Freitas, L., Gaglianone, M.C., Goss, M., Irshad, M., Kasina, M., Filho, A.J.S.P., Kiill, L.H.P., Kwapong, P., Parra, G.N., Pires, C., Pires, V., Rawal, R.S., Rizali, A., Saraiva, A.M., Veldtman, R., Viana, B.F., Witter, S., Zhang, H., 2016. Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science* 351, 388-391. <https://doi.org/10.1126/science.aac7287>
- 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., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 14, 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., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelík, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharrntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. *Science* 339, 1608-1611. <https://doi.org/10.1126/science.1230200>
- Garratt, M.P.D., Breeze, T.D., Jenner, N., Polce, C., Biesmeijer, J.C., Potts, S.G., 2014. Avoiding a bad apple: Insect pollination enhances fruit quality and economic value. *Agric. Ecosyst. Environ.* 184, 34-40. <https://doi.org/10.1016/j.agee.2013.10.032>
- Garratt, M.P.D., Senapathi, D., Coston, D.J., Mortimer, S.R., Potts, S.G., 2017. The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context. *Agric. Ecosyst. Environ.* 247, 363-370. <https://doi.org/10.1016/j.agee.2017.06.048>
- 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: Bohan, D.A., Dumbrell, A.J., Massol, F. (Eds.), *Advances in Ecological Research, Networks of Invasion: Empirical Evidence and Case Studies*. Academic Press, pp. 147-199. <https://doi.org/10.1016/bs.aecr.2016.10.007>
- Godfray, H.C.J., Blacquière, T., Field, L.M., Hails, R.S., Petrokofsky, G., Potts, S.G., Raine, N.E., Vanbergen, A.J., McLean, A.R., 2014. A restatement of the natural science evidence base concerning neonicotinoid insecticides and insect pollinators. *Proc. Biol. Sci.* 281, 20140558. <https://doi.org/10.1098/rspb.2014.0558>
- Gonzalez, V.H., Osborn, A.L., Brown, E.R., Pavlick, C.R., Enríquez, E., Tscheulin, T.,

- Petanidou, T., Hranitz, J.M., Barthell, J.F., 2020. Effect of pan trap size on the diversity of sampled bees and abundance of bycatch. *J. Insect Conserv.* 24, 409-420. <https://doi.org/10.1007/s10841-020-00224-4>
- Gottesman, B.L., Francomano, D., Zhao, Z., Bellisario, K., Ghadiri, M., Broadhead, T., Gasc, A., Pijanowski, B.C., 2020. Acoustic monitoring reveals diversity and surprising dynamics in tropical freshwater soundscapes. *Freshw. Biol.* 65, 117-132. <https://doi.org/10.1111/fwb.13096>
- Gradišek, A., Slapničar, G., Šorn, J., Luštrek, M., Gams, M., Grad, J., 2017. Predicting species identity of bumblebees through analysis of flight buzzing sounds. *Bioacoustics* 26, 63-76. <https://doi.org/10.1080/09524622.2016.1190946>
- Greenleaf, S.S., Kremen, C., 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proc. Natl. Acad. Sci.* 103, 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, 589-596. <https://doi.org/10.1007/s00442-007-0752-9>
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hürren, T., Goulson, D., Kroon, H. de, 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE* 12, e0185809. <https://doi.org/10.1371/journal.pone.0185809>
- Hannon, L.E., Sisk, T.D., 2009. Hedgerows in an agri-natural landscape: Potential habitat value for native bees. *Biol. Conserv.* 142, 2140-2154. <https://doi.org/10.1016/j.biocon.2009.04.014>
- Heise, D., Miller, Z., Harrison, E., Gradišek, A., Grad, J., Galen, C., 2019. Acoustically Tracking the Comings and Goings of Bumblebees, in: 2019 IEEE Sensors Applications Symposium (SAS). Presented at the 2019 IEEE Sensors Applications Symposium (SAS), pp. 1-6. <https://doi.org/10.1109/SAS.2019.8705973>
- Heise, D., Miller, Z., Wallace, M., Galen, C., 2020. Bumble Bee Traffic Monitoring Using Acoustics, in: 2020 IEEE International Instrumentation and Measurement Technology Conference (I2MTC). Presented at the 2020 IEEE International

- Instrumentation and Measurement Technology Conference (I2MTC), pp. 1-6.
<https://doi.org/10.1109/I2MTC43012.2020.9129582>
- Henry, M., Béguin, M., Requier, F., Rollin, O., Odoux, J.-F., Aupinel, P., Aptel, J., Tchamitchian, S., Decourtye, A., 2012. A Common Pesticide Decreases Foraging Success and Survival in Honey Bees. *Science* 336, 348-350.
<https://doi.org/10.1126/science.1215039>
- Hevia, V., Bosch, J., Azcárate, F.M., Fernández, E., Rodrigo, A., Barril-Graells, H., González, J.A., 2016. Bee diversity and abundance in a livestock drove road and its impact on pollination and seed set in adjacent sunflower fields. *Agric. Ecosyst. Environ.* 232, 336-344. <https://doi.org/10.1016/j.agee.2016.08.021>
- 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. *Ecol. Lett.* 19, 1228-1236. <https://doi.org/10.1111/ele.12657>
- Holzschuh, A., Dormann, C.F., Tschardtke, T., Steffan-Dewenter, I., 2013. Mass-flowering crops enhance wild bee abundance. *Oecologia* 172, 477-484.
<https://doi.org/10.1007/s00442-012-2515-5>
- Howlett, B.G., Evans, L.J., Pattemore, D.E., Nelson, W.R., 2017. Stigmatic pollen delivery by flies and bees: Methods comparing multiple species within a pollinator community. *Basic Appl. Ecol.* 19, 19-25.
<https://doi.org/10.1016/j.baae.2016.12.002>
- Hudewenz, A., Pufal, G., Bögeholz, A.-L., Klein, A.-M., 2014. Cross-pollination benefits differ among oilseed rape varieties. *J. Agric. Sci.* 152, 770-778.
<https://doi.org/10.1017/S0021859613000440>
- IPBES, 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. E. S. Brondizio, J. Settele, S. Díaz, and H. T. Ngo (editors). IPBES secretariat, Bonn, Germany. 1148 pages. <https://doi.org/10.5281/zenodo.3831673>
- Jacobs, J.H., Clark, S.J., Denholm, I., Goulson, D., Stoate, C., Osborne, J.L., 2009.

- Pollination biology of fruit-bearing hedgerow plants and the role of flower-visiting insects in fruit-set. *Ann. Bot.* 104, 1397–1404. <https://doi.org/10.1093/aob/mcp236>
- Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. *Agric. For. Entomol.* 14, 81–87. <https://doi.org/10.1111/j.1461-9563.2011.00541.x>
- Javed, N., Mehdi, S., 1992. Self-incompatibility and autogamy of sunflower (*Helianthus annuus* L.) cultivars. *Helia* 15, 17–24.
- Jeliazkov, A., Bas, Y., Kerbiriou, C., Julien, J.-F., Penone, C., Le Viol, I., 2016. Large-scale semi-automated acoustic monitoring allows to detect temporal decline of bush-crickets. *Glob. Ecol. Conserv.* 6, 208–218. <https://doi.org/10.1016/j.gecco.2016.02.008>
- Johnson, R.M., Ellis, M.D., Mullin, C.A., Frazier, M., 2010. Pesticides and honey bee toxicity - USA. *Apidologie* 41, 312–331. <https://doi.org/10.1051/apido/2010018>
- Kawakita, S., Ichikawa, K., 2019. Automated classification of bees and hornet using acoustic analysis of their flight sounds. *Apidologie* 50, 71–79. <https://doi.org/10.1007/s13592-018-0619-6>
- Kearns, C.A., Inouye, D.W., 1993. Techniques for pollination biologists. *Tech. Pollinat. Biol.*
- Kearns, C.A., Inouye, D.W., Waser, N.M., 1998. ENDANGERED MUTUALISMS: The Conservation of Plant-Pollinator Interactions. *Annu. Rev. Ecol. Syst.* 29, 83–112. <https://doi.org/10.1146/annurev.ecolsys.29.1.83>
- 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., Carvalho, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* 16, 584–599. <https://doi.org/10.1111/ele.12082>

- Khalifa, S.A.M., Elshafiey, E.H., Shetaia, A.A., El-Wahed, A.A.A., Algethami, A.F., Musharraf, S.G., AlAjmi, M.F., Zhao, C., Masry, S.H.D., Abdel-Daim, M.M., Halabi, M.F., Kai, G., Al Naggat, Y., Bishr, M., Diab, M.A.M., El-Seedi, H.R., 2021. Overview of Bee Pollination and Its Economic Value for Crop Production. *Insects* 12, 688. <https://doi.org/10.3390/insects12080688>
- Kirkeby, C., Rydhmer, K., Cook, S.M., Strand, A., Torrance, M.T., Swain, J.L., Prangma, J., Johnen, A., Jensen, M., Brydegaard, M., Græsbøll, K., 2021. Advances in automatic identification of flying insects using optical sensors and machine learning. *Sci. Rep.* 11, 1555. <https://doi.org/10.1038/s41598-021-81005-0>
- Kiskin, I., Sinka, M., Cobb, A.D., Rafique, W., Wang, L., Zilli, D., Gutteridge, B., Dam, R., Marinos, T., Li, Y., Msaky, D., Kaindoa, E., Killeen, G., Herreros-Moya, E., Willis, K.J., Roberts, S.J., 2021. HumBugDB: A Large-scale Acoustic Mosquito Dataset. <https://doi.org/10.48550/arXiv.2110.07607>
- 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., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tscharntke, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldtman, R., Ward, K.L., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* 6, 7414. <https://doi.org/10.1038/ncomms8414>
- Klein, A.-M., Brittain, C., Hendrix, S.D., Thorp, R., Williams, N., Kremen, C., 2012. Wild pollination services to California almond rely on semi-natural habitat. *J. Appl. Ecol.* 49, 723-732. <https://doi.org/10.1111/j.1365-2664.2012.02144.x>
- Klein, A.-M., Steffan-Dewenter, I., Tscharntke, T., 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. B Biol. Sci.* 270, 955-

961. <https://doi.org/10.1098/rspb.2002.2306>
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* 274, 303-313. <https://doi.org/10.1098/rspb.2006.3721>
- Knapp, J.L., Osborne, J.L., 2019. Cucurbits as a model system for crop pollination management. *J. Pollinat. Ecol.* 25. [https://doi.org/10.26786/1920-7603\(2019\)535](https://doi.org/10.26786/1920-7603(2019)535)
- Knyshov, A., Hoang, S., Weirauch, C., 2021. Pretrained Convolutional Neural Networks Perform Well in a Challenging Test Case: Identification of Plant Bugs (Hemiptera: Miridae) Using a Small Number of Training Images. *Insect Syst. Divers.* 5, 3. <https://doi.org/10.1093/isd/ixab004>
- Kunjwal, N., Kumar, Y., Khan, M.S., 2014. Flower-visiting insect pollinators of Brown Mustard, *Brassica juncea* (L.) Czern and Coss and their foraging behaviour under caged and open pollination 9.
- Langlois, A., Jacquemart, A.-L., Piqueray, J., 2020. Contribution of Extensive Farming Practices to the Supply of Floral Resources for Pollinators. *Insects* 11, 818. <https://doi.org/10.3390/insects11110818>
- Lautenbach, S., Seppelt, R., Liebscher, J., Dormann, C.F., 2012. Spatial and Temporal Trends of Global Pollination Benefit. *PLOS ONE* 7, e35954. <https://doi.org/10.1371/journal.pone.0035954>
- Lehmann, G.U.C., Bakanov, N., Behnisch, M., Bourlat, S.J., Brühl, C.A., Eichler, L., Fickel, T., Geiger, M.F., Gemeinholzer, B., Hörren, T., Köthe, S., Lux, A., Meinel, G., Mühlethaler, R., Poglitsch, H., Schäffler, L., Schlechtriemen, U., Schneider, F.D., Schulte, R., Sorg, M., Sprenger, M., Swenson, S.J., Terlau, W., Turck, A., Zizka, V.M.A., 2021. Diversity of Insects in Nature protected Areas (DINA): an interdisciplinary German research project. *Biodivers. Conserv.* 30, 2605-2614. <https://doi.org/10.1007/s10531-021-02209-4>
- Lindström, S.A.M., Herbertsson, L., Rundlöf, M., Smith, H.G., Bommarco, R., 2016. Large-scale pollination experiment demonstrates the importance of insect pollination in winter oilseed rape. *Oecologia* 180, 759-769.

<https://doi.org/10.1007/s00442-015-3517-x>

- Liss, K.N., Mitchell, M.G., MacDonald, G.K., Mahajan, S.L., Méthot, J., Jacob, A.L., Maguire, D.Y., Metson, G.S., Ziter, C., Dancose, K., Martins, K., Terrado, M., Bennett, E.M., 2013. Variability in ecosystem service measurement: a pollination service case study. *Front. Ecol. Environ.* 11, 414–422. <https://doi.org/10.1890/120189>
- Lye, G., Park, K., Osborne, J., Holland, J., Goulson, D., 2009. Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). *Biol. Conserv.* 142, 2023–2032. <https://doi.org/10.1016/j.biocon.2009.03.032>
- Mace, G.M., 2014. Whose conservation? *Science* 345, 1558–1560. <https://doi.org/10.1126/science.1254704>
- Mallinger, R.E., Gratton, C., 2015. Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop. *J. Appl. Ecol.* 52, 323–330. <https://doi.org/10.1111/1365-2664.12377>
- Mariani, M.S., Ren, Z.-M., Bascompte, J., Tessone, C.J., 2019. Nestedness in complex networks: Observation, emergence, and implications. *Phys. Rep., Nestedness in complex networks: Observation, emergence, and implications* 813, 1–90. <https://doi.org/10.1016/j.physrep.2019.04.001>
- Martineau, M., Conte, D., Raveaux, R., Arnault, I., Munier, D., Venturini, G., 2017. A survey on image-based insect classification. *Pattern Recognit.* 65, 273–284. <https://doi.org/10.1016/j.patcog.2016.12.020>
- Maxwell, S.L., Fuller, R.A., Brooks, T.M., Watson, J.E.M., 2016. Biodiversity: The ravages of guns, nets and bulldozers. *Nature* 536, 143–145. <https://doi.org/10.1038/536143a>
- MEA, 2005. Millennium Ecosystem Assessment. Ecosystems and Human Well-being: Synthesis. Island Press, Washington, DC.
- Mesquida, J., Renard, M., 1982. ÉTUDE DE LA DISPERSION DU POLLEN PAR LE VENT ET DE L'IMPORTANCE DE LA POLLINISATION ANÉMOPHILE CHEZ LE COLZA (BRASSICA NAPUS L., VAR. OLEIFERA METZGER). *Apidologie* 13, 353–366. <https://doi.org/10.1051/apido:19820403>

- Milberg, P., Hallgren, E., 2004. Yield loss due to weeds in cereals and its large-scale variability in Sweden. *Field Crops Res.* 86, 199-209. <https://doi.org/10.1016/j.fcr.2003.08.006>
- Miller-Struttman, N.E., Heise, D., Schul, J., Geib, J.C., Galen, C., 2017. Flight of the bumble bee: Buzzes predict pollination services. *PLOS ONE* 12, e0179273. <https://doi.org/10.1371/journal.pone.0179273>
- Montero-Castaño, A., Koch, J.B.U., Lindsay, T.-T.T., Love, B., Mola, J.M., Newman, K., Sharkey, J.K., 2022. Pursuing best practices for minimizing wild bee captures to support biological research. *Conserv. Sci. Pract.* 4, e12734. <https://doi.org/10.1111/csp2.12734>
- Montero-Castaño, A., Ortiz-Sánchez, F.J., Vilà, M., 2016. Mass flowering crops in a patchy agricultural landscape can reduce bee abundance in adjacent shrublands. *Agric. Ecosyst. Environ.* 223, 22-30. <https://doi.org/10.1016/j.agee.2016.02.019>
- Montgomery, G.A., Belitz, M.W., Guralnick, R.P., Tingley, M.W., 2021. Standards and Best Practices for Monitoring and Benchmarking Insects. *Front. Ecol. Evol.* 8.
- Morandin, L.A., Kremen, C., 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecol. Appl.* 23, 829-839. <https://doi.org/10.1890/12-1051.1>
- Müller, C.B., Adriaanse, I.C.T., Belshaw, R., Godfray, H.C.J., 1999. The structure of an aphid-parasitoid community. *J. Anim. Ecol.* 68, 346-370. <https://doi.org/10.1046/j.1365-2656.1999.00288.x>
- Néron, F., 2018. *Petit précis d'agriculture*. Éditions France Agricole.
- Nooten, S.S., Rehan, S.M., 2022. Effects of land use type and seasonal climate on ground nesting wild bees. *Agric. For. Entomol.* 24, 229-236. <https://doi.org/10.1111/afe.12486>
- Noriega, J.A., Hortal, J., Azcárate, F.M., Berg, M.P., Bonada, N., Briones, M.J.I., Del Toro, I., Goulson, D., Ibanez, S., Landis, D.A., Moretti, M., Potts, S.G., Slade, E.M., Stout, J.C., Ulyshen, M.D., Wackers, F.L., Woodcock, B.A., Santos, A.M.C., 2018. Research trends in ecosystem services provided by insects. *Basic Appl. Ecol., Insect Effects on Ecosystem services* 26, 8-23. <https://doi.org/10.1016/j.baae.2017.09.006>

- 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. *Ann. Bot.* 103, 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, 321-326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Orford, K.A., Vaughan, I.P., Memmott, J., 2015. The forgotten flies: the importance of non-syrphid Diptera as pollinators. *Proc. R. Soc. B Biol. Sci.* 282, 20142934. <https://doi.org/10.1098/rspb.2014.2934>
- Penone, C., Le Viol, I., Pellissier, V., Julien, J.-F., Bas, Y., Kerbiriou, C., 2013. Use of Large-Scale Acoustic Monitoring to Assess Anthropogenic Pressures on Orthoptera Communities. *Conserv. Biol.* 27, 979-987. <https://doi.org/10.1111/cobi.12083>
- Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.-L., Bretagnolle, V., 2018. Bees increase oilseed rape yield under real field conditions. *Agric. Ecosyst. Environ.* 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 Appl. Ecol.* 34, 75-84. <https://doi.org/10.1016/j.baae.2018.09.005>
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344, 1246752. <https://doi.org/10.1126/science.1246752>
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345-353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016a. Safeguarding pollinators and their values to human well-being. *Nature* 540, 220-229. <https://doi.org/10.1038/nature20588>
- Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D.,

- Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016b. Safeguarding pollinators and their values to human well-being. *Nature* 540, 220-229. <https://doi.org/10.1038/nature20588>
- Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carvalheiro, L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J., Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipólito, J., Jaggar, S., Jauker, F., Klein, A.-M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattemore, D.E., Pereira, N. de O., Pisanty, G., Potts, S.G., Reemer, M., Rundlöf, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. *Proc. Natl. Acad. Sci.* 113, 146-151. <https://doi.org/10.1073/pnas.1517092112>
- 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. *Agric. Ecosyst. Environ.* 306, 107189. <https://doi.org/10.1016/j.agee.2020.107189>
- Requier, F., 2013. Dynamique spatio-temporelle des ressources florales et écologie de l'abeille domestique en paysage agricole intensif (phdthesis). Université de Poitiers.
- 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. *Ecol. Appl.* 25, 881-890. <https://doi.org/10.1890/14-1011.1>
- Rhodes, M.W., Bennie, J.J., Spalding, A., Ffrench-Constant, R.H., Maclean, I.M.D., 2022. Recent advances in the remote sensing of insects. *Biol. Rev. Camb. Philos. Soc.* 97, 343-360. <https://doi.org/10.1111/brv.12802>
- 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? *Ecol. Lett.* 11, 499-515.
<https://doi.org/10.1111/j.1461-0248.2008.01157.x>
- Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I., Holzschuh, A., 2015. Annual dynamics of wild bee densities: attractiveness and productivity effects of oilseed rape. *Ecology* 96, 1351-1360. <https://doi.org/10.1890/14-1124.1>
- Rollin, O., Bretagnolle, V., Fortel, L., Guilbaud, L., Henry, M., 2015. Habitat, spatial and temporal drivers of diversity patterns in a wild bee assemblage. *Biodivers. Conserv.* 24, 1195-1214. <https://doi.org/10.1007/s10531-014-0852-x>
- Roulston, T.H., Cane, J.H., Buchmann, S.L., 2000. What Governs Protein Content of Pollen: Pollinator Preferences, Pollen-Pistil Interactions, or Phylogeny? *Ecol. Monogr.* 70, 617-643. [https://doi.org/10.1890/0012-9615\(2000\)070\[0617:WGPCOP\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2000)070[0617:WGPCOP]2.0.CO;2)
- Roumet, M., Ostrowski, M.-F., David, J., Tollon, C., Muller, M.-H., 2012. Estimation of mating system parameters in an evolving gynodioecous population of cultivated sunflower (*Helianthus annuus* L.). *Heredity* 108, 366-374. <https://doi.org/10.1038/hdy.2011.79>
- Rydhmer, K., Bick, E., Still, L., Strand, A., Luciano, R., Helmreich, S., Beck, B.D., Grønne, C., Malmros, L., Poulsen, K., Elbæk, F., Brydegaard, M., Lemmich, J., Nikolajsen, T., 2022. Automating insect monitoring using unsupervised near-infrared sensors. *Sci. Rep.* 12, 2603. <https://doi.org/10.1038/s41598-022-06439-6>
- Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.* 232, 8-27. <https://doi.org/10.1016/j.biocon.2019.01.020>
- Sardiñas, H.S., Kremen, C., 2015. Pollination services from field-scale agricultural diversification may be context-dependent. *Agric. Ecosyst. Environ.* 207, 17-25. <https://doi.org/10.1016/j.agee.2015.03.020>
- Schneider, S., Taylor, G.W., Kremer, S.C., Burgess, P., McGroarty, J., Mitsui, K., Zhuang, A., deWaard, J.R., Fryxell, J.M., 2022. Bulk arthropod abundance, biomass and diversity estimation using deep learning for computer vision. *Methods Ecol. Evol.* 13, 346-357. <https://doi.org/10.1111/2041-210X.13769>

- 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. *J. Appl. Ecol.* 58, 1421-1430. <https://doi.org/10.1111/1365-2664.13887>
- Spiesman, B.J., Gratton, C., Hatfield, R.G., Hsu, W.H., Jepsen, S., McCornack, B., Patel, K., Wang, G., 2021. Assessing the potential for deep learning and computer vision to identify bumble bee species from images. *Sci. Rep.* 11, 7580. <https://doi.org/10.1038/s41598-021-87210-1>
- Srivathsan, A., Lee, L., Katoh, K., Hartop, E., Kutty, S.N., Wong, J., Yeo, D., Meier, R., 2021. ONTbarcoder and MinION barcodes aid biodiversity discovery and identification by everyone, for everyone. *BMC Biol.* 19, 217. <https://doi.org/10.1186/s12915-021-01141-x>
- 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. *J. Insect Conserv.* 17, 1181-1189. <https://doi.org/10.1007/s10841-013-9599-z>
- Stanley, D.A., Stout, J.C., 2014. Pollinator sharing between mass-flowering oilseed rape and co-flowering wild plants: implications for wild plant pollination. *Plant Ecol.* 215, 315-325. <https://doi.org/10.1007/s11258-014-0301-7>
- Stowell, D., 2022. Computational bioacoustics with deep learning: a review and roadmap. *PeerJ* 10, e13152. <https://doi.org/10.7717/peerj.13152>
- Thébault, E., Fontaine, C., 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329, 853-856. <https://doi.org/10.1126/science.1188321>
- Thomsen, P.F., Sigsgaard, E.E., 2019. Environmental DNA metabarcoding of wild flowers reveals diverse communities of terrestrial arthropods. *Ecol. Evol.* 9, 1665-1679. <https://doi.org/10.1002/ece3.4809>
- Timberlake, T.P., Vaughan, I.P., Baude, M., Memmott, J., 2020. Bumblebee colony density on farmland is influenced by late-summer nectar supply and garden cover. *J. Appl. Ecol.* n/a. <https://doi.org/10.1111/1365-2664.13826>

- Timberlake, T.P., Vaughan, I.P., Memmott, J., 2019. Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *J. Appl. Ecol.* 56, 1585–1596. <https://doi.org/10.1111/1365-2664.13403>
- Tiusanen, M., Huotari, T., Hebert, P.D.N., Andersson, T., Asmus, A., Bêty, J., Davis, E., Gale, J., Hardwick, B., Hik, D., Körner, C., Lanctot, R.B., Loonen, M.J.J.E., Partanen, R., Reischke, K., Saalfeld, S.T., Senez-Gagnon, F., Smith, P.A., Šulavík, J., Syvänperä, I., Urbanowicz, C., Williams, S., Woodard, P., Zaika, Y., Roslin, T., 2019. Flower-visitor communities of an arcto-alpine plant–Global patterns in species richness, phylogenetic diversity and ecological functioning. *Mol. Ecol.* 28, 318–335. <https://doi.org/10.1111/mec.14932>
- Todd, K.J., Gardiner, M.M., Lindquist, E.D., 2016. Mass Flowering Crops as a Conservation Resource for Wild Pollinators (Hymenoptera: Apoidea). *J. Kans. Entomol. Soc.* 89, 158–167. <https://doi.org/10.2317/0022-8567-89.2.158>
- Tsvetkov, N., Samson-Robert, O., Sood, K., Patel, H.S., Malena, D.A., Gajiwala, P.H., Maciukiewicz, P., Fournier, V., Zayed, A., 2017. Chronic exposure to neonicotinoids reduces honey bee health near corn crops. *Science* 356, 1395–1397. <https://doi.org/10.1126/science.aam7470>
- IUCN, 2022. The IUCN Red List of Threatened Species. Version 2022-1. <https://www.iucnredlist.org>. Accessed on [24 11 2022].
- Valan, M., Makonyi, K., Maki, A., Vondráček, D., Ronquist, F., 2019. Automated Taxonomic Identification of Insects with Expert-Level Accuracy Using Effective Feature Transfer from Convolutional Networks. *Syst. Biol.* 68, 876–895. <https://doi.org/10.1093/sysbio/syz014>
- van Klink, R., August, T., Bas, Y., Bodesheim, P., Bonn, A., Fossøy, F., Høye, T.T., Jongejans, E., Menz, M.H.M., Miraldo, A., Roslin, T., Roy, H.E., Ruczyński, I., Schigel, D., Schäffler, L., Sheard, J.K., Svenningsen, C., Tschan, G.F., Wäldchen, J., Zizka, V.M.A., Åström, J., Bowler, D.E., 2022. Emerging technologies revolutionise insect ecology and monitoring. *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2022.06.001>
- Vanbergen, A.J., Baude, M., Biesmeijer, J.C., Britton, N.F., Brown, M.J.F., Bryden, J.,

- Budge, G.E., Bull, J.C., Carvell, C., Challinor, A.J., Connolly, C.N., Evans, D.J., Feil, E.J., Garratt, M.P., Greco, M.K., Heard, M.S., Jansen, V.A.A., Keeling, M.J., Kunin, W.E., Marris, G.C., Memmott, J., Murray, J.T., Nicolson, S.W., Osborne, J.L., Paxton, R.J., Pirk, C.W.W., Polce, C., Potts, S.G., Priest, N.K., Raine, N.E., Roberts, S., Ryabov, E.V., Shafir, S., Shirley, M.D.F., Simpson, S.J., Stevenson, P.C., Stone, G.N., Termansen, M., Wright, G.A., 2013. Threats to an ecosystem service: Pressures on pollinators. *Front. Ecol. Environ.* 11, 251-259. <https://doi.org/10.1890/120126>
- Wägele, J.W., Bodesheim, P., Bourlat, S.J., Denzler, J., Diepenbroek, M., Fonseca, V., Frommolt, K.-H., Geiger, M.F., Gemeinholzer, B., Glöckner, F.O., Haucke, T., Kirse, A., Kölpin, A., Kostadinov, I., Köhl, H.S., Kurth, F., Lasseck, M., Liedke, S., Losch, F., Müller, S., Petrovskaya, N., Piotrowski, K., Radig, B., Scherber, C., Schoppmann, L., Schulz, J., Steinhage, V., Tschan, G.F., Vautz, W., Velotto, D., Weigend, M., Wildermann, S., 2022. Towards a multisensor station for automated biodiversity monitoring. *Basic Appl. Ecol.* 59, 105-138. <https://doi.org/10.1016/j.baae.2022.01.003>
- Wagner, D.L., 2020. Insect Declines in the Anthropocene. *Annu. Rev. Entomol.* 65, 457-480. <https://doi.org/10.1146/annurev-ento-011019-025151>
- Waser, N.M., Chittka, L., Price, M.V., Williams, N.M., Ollerton, J., 1996. Generalization in Pollination Systems, and Why it Matters. *Ecology* 77, 1043-1060. <https://doi.org/10.2307/2265575>
- Westphal, C., Steffan-Dewenter, I., Tschardt, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol. Lett.* 6, 961-965. <https://doi.org/10.1046/j.1461-0248.2003.00523.x>
- Wietzke, A., Westphal, C., Gras, P., Kraft, M., Pfohl, K., Karlovsky, P., Pawelzik, E., Tschardt, T., Smit, I., 2018. Insect pollination as a key factor for strawberry physiology and marketable fruit quality. *Agric. Ecosyst. Environ.* 258, 197-204. <https://doi.org/10.1016/j.agee.2018.01.036>
- Wijesinghe, E., Evans, L., Kirkland, L., Rader, R., 2020. A global review of watermelon pollination biology and ecology: The increasing importance of seedless cultivars. *Sci. Hortic.* 271, 109493. <https://doi.org/10.1016/j.scienta.2020.109493>

- Willmer, P., 2011. Pollination and floral ecology. Princeton University Press, Princeton, N.J.
- Wood, T.J., Goulson, D., 2017. The environmental risks of neonicotinoid pesticides: a review of the evidence post 2013. *Environ. Sci. Pollut. Res. Int.* 24, 17285–17325. <https://doi.org/10.1007/s11356-017-9240-x>
- Woodcock, B.A., Bullock, J.M., Shore, R.F., Heard, M.S., Pereira, M.G., Redhead, J., Ridding, L., Dean, H., Sleep, D., Henrys, P., Peyton, J., Hulmes, S., Hulmes, L., Sároszpataki, M., Saure, C., Edwards, M., Genersch, E., Knäbe, S., Pywell, R.F., 2017. Country-specific effects of neonicotinoid pesticides on honey bees and wild bees. *Science* 356, 1393–1395. <https://doi.org/10.1126/science.aaa1190>
- Wragg, P.D., Johnson, S.D., 2011. Transition from wind pollination to insect pollination in sedges: experimental evidence and functional traits. *New Phytol.* 191, 1128–1140. <https://doi.org/10.1111/j.1469-8137.2011.03762.x>
- WWF, 2022. Living Planet Report 2022 – Building a nature-positive society. Almond, R.E.A., Grooten, M., Juffe Bignoli, D. & Petersen, T. (Eds). WWF, Gland, Switzerland.
- Zattara, E.E., Aizen, M.A., 2021. Worldwide occurrence records suggest a global decline in bee species richness. *One Earth* 4, 114–123. <https://doi.org/10.1016/j.oneear.2020.12.005>
- 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 Ecol.* 17, 6. <https://doi.org/10.1186/s12898-017-0116-1>

