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Clémentine Leroy

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Clémentine Leroy. Sensibilité des abeilles sauvages face aux transformations du paysage dans les agroécosystèmes : Utilisation d'une approche écophysiological pour évaluer l'influence des ressources florales sur la condition corporelle des abeilles sauvages. Biologie animale. Université d'Avignon, 2023. Français. NNT : 2023AVIG0616 . tel-04563390

**HAL Id: tel-04563390**

**<https://theses.hal.science/tel-04563390v1>**

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# THÈSE DE DOCTORAT D'AVIGNON UNIVERSITÉ

École Doctorale N° 536

**Sciences & Agrosciences**

**Spécialité / Discipline de doctorat :**

Biologie des populations et écologie

UR 406 Abeilles et environnement – INRAE

Présentée par

**Clémentine Leroy**

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## **Sensibilité des abeilles sauvages face aux transformations du paysage dans les agroécosystèmes**

**Utilisation d'une approche écophysiological pour évaluer l'effet des ressources florales  
sur la condition corporelle des abeilles sauvages**

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Soutenue publiquement le 18/12/2023 devant le jury composé de :

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# Résumé

Le contexte actuel du déclin de diverses espèces d'abeilles sauvages soulève la nécessité de trouver et de réfléchir à des mesures de conservation et de restauration plus proactives et plus pertinentes. Dans ce cadre, l'utilisation de mesures de la vitalité et condition corporelle des organismes pourrait représenter une opportunité intéressante pour évaluer comment ces derniers répondent aux changements environnementaux. Nous avons ainsi émis l'hypothèse que des modifications physiologiques pourraient informer sur la sensibilité individuelle des abeilles aux changements environnementaux et agir comme des indicateurs de la qualité des habitats. Ces mesures physiologiques sont très prometteuses et présentent déjà des exemples de réussite pour de nombreuses espèces soumises à diverses perturbations environnementales, à savoir la pollution environnementale, le changement climatique et les ressources du paysage. Dans cette optique, nous avons appliqué cette approche éco-physiologique pour mesurer les effets de la disponibilité et de la richesse des ressources florales sur la condition corporelle de diverses espèces d'abeilles sauvages. La condition corporelle des abeilles est, dans nos travaux, une compilation de la masse corporelle et des indicateurs du statut nutritionnel (concentrations en protéines, triglycérides et glycogène). Nous avons tout d'abord examiné l'influence d'éléments semi-naturels (prairies temporaires et permanentes, jachères et landes boisées) et des haies sur le succès reproducteur et la condition corporelle de l'abeille maçonne (*Osmia cornuta*) dans des vergers de pommiers. Les habitats semi-naturels et les haies dans les vergers n'ont pas affecté la reproduction des osmies, mais ont eu des effets bénéfiques sur le poids et la teneur en protéine de la descendance, probablement en raison d'une meilleure diversité des pollens récoltés. Parallèlement, nous avons testé l'effet en zone de prairies, d'un indice d'utilisation des terres (compilation des pratiques des agriculteur·ices incluant la fauche, le pâturage et la fertilisation) et de la diversité florale sur les communautés d'abeilles sauvages en se focalisant sur les bourdons. Le poids des bourdons a particulièrement diminué avec l'intensité de gestion des prairies chez une espèce formant des colonies de petites tailles (*Bombus sylvarum*), alors que les autres espèces n'ont pas été affectées. Les concentrations en protéines (en particulier chez *Bombus terrestris*) et glycogène ont également varié selon les pratiques de gestion des prairies, ces variations étant conditionnées par la longueur du proboscis des espèces. Ces travaux montrent que des mesures de la condition corporelle peuvent être utiles pour améliorer notre compréhension des réponses des abeilles sauvages à la qualité des habitats. En particulier, les mesures de la masse corporelle et de la teneur en protéines semblent être d'un intérêt particulier pour attester de la sensibilité individuelle. L'acquisition de ces connaissances et leur mise en pratique, de concert avec d'autres champs disciplinaires (écologie comportementale, sciences sociales, épidémiologie...) ainsi qu'avec les acteur·ices engagé·es dans la protection des pollinisateurs, pourraient permettre d'affiner et co-construire des stratégies de conservation des populations d'abeilles sauvages pour lutter contre le déclin des abeilles.

Mots clés : écologie de la nutrition, changements environnementaux, communautés d'abeilles, physiologie de la conservation

# Abstract

The actual context of bee species decline raises the actual needs of finding and thinking about more proactive and relevant conservation and restoration measures. In this initiative, the use of new biological metrics that can link individual bee responses to environmental alteration with population-level responses could represent an interesting opportunity. We hypothesized that physiological indicators could communicate the actual individual bee sensitivity to environmental changes and act as early warning signals of bee population decline or sustainability. Physiological markers can for example, provide helpful information on the interface between bee populations and their resources. Those indicators are indeed very promising and already show benefits and success for numerous organisms and numerous environmental perturbations they have to cope with, namely chemicals, climate change and landscape resources. In that extent, we used such ecophysiological approach to measure the effects of floral resources abundance, availability and richness on female's bee body condition. We approximate bee body condition as a compilation of body mass, and nutritional health indicators (proteins, triglycerides and proteins) contents. Firstly, we examined the effect of semi-natural elements (temporary and permanent grasslands, fallows and woody moorlands) on the reproductive success and the body condition of a mason bee in apple orchards from south of France. Parallely, we tested the effect of a land-use index (compilation of farmers practices including mowing, grazing and fertilizing) and floral diversity from agroecosystems habitats on the health state of wild bee communities in Belgium and Germany thanks to the multilevel approach of the European NutriB<sup>2</sup> project.

This thesis work shows that metrics of body condition can be useful to improve our understanding of pollinator responses to habitat quality with a focus on nutrition. In particular, the measure of body mass and proteins content seem to be of particular interest to attest for individual sensitivity. Additional physiological health parameters including stoichiometry and pathogen loads also provide valuable information on the health state of wild bees and are also the focus of working groups within the european project. We can optimistically assume that the acquisition of this knowledge and its application in practice, in conjunction with these other disciplinary fields and with players involved in pollinator conservation, could enable us to refine and co-construct wild bee conservation or restoration strategies to combat bee decline.

Keywords: ecological nutrition, environmental changes, bee communities health, conservation  
physiology

# Remerciements

## Au pôle abeilles et collègues extérieurs

A Cédric, tu introduis cette section de remerciements et pour cause. Ta disponibilité et ton soutien tout au long de ce parcours de thèse m'ont permis d'avancer avec confiance. Je te suis reconnaissante de m'avoir accordée cette chance de démarrer (et terminer) cette thèse. On dirait que c'est à toi qu'il faut dire « bon courage » maintenant. Thèse en direction c'est pas tous les jours facile...

A Mickaël, j'ai été heureuse de te compter parmi mes superviseurs et d'avoir pu côtoyer à la fois l'encadrant et le directeur. Malgré tes fonctions administratives tu n'as pas failli dans celles d'encadrement et pour preuve.

A Jean-Luc merci de m'avoir accompagnée dans ce domaine de la biochimie dont j'ignorais presque tout. Les apports en nutriments glucidiques via les sucreries que tu apportais étaient de chouettes remontants.

Merci à Fabrice Requier et Benoit Geslin d'avoir généreusement et de façon toujours très juste et avisée, accepté de prendre part au suivi de mon travail lors des comités de suivi de thèse.

Merci à Alice Michelot-Antalik et David Giron d'avoir accepté de plonger dans le cœur de mon travail en endossant les rôles de rapporteur-es de mon travail.

Merci à Maryse Vanderplanck et à Isabelle Dajoz de prendre également part à ce travail de thèse en tant qu'examinatrices de mon travail.

A Guy, probablement un de mes êtres-humains préférés sur cette planète. Tu as irradié chacune de mes journées par tes éclats de vie, de rire, par ton écoute et tout simplement par ta gentillesse brute et véritable dont je vais avoir du mal à me passer.

A Nicolas et Laurent, merci à vous pour votre soutien et compagnie lors des sessions *Côte Bleue*. Je n'aurai pas pu débiter ma thèse d'une plus belle façon qu'en arpentant ces terres magnifiques au rythme de vos pas, blagues et anecdotes. Merci d'avoir été des compagnons de travail (et même de laboratoire !) et de CS si agréables, je retiendrai que « c'était du velours ».

A Hanine, ta compagnie m'a manquée dès les premiers instants suivant ton départ. Tu m'as permise de me sentir à l'aise dans nos locaux et notre petit cocon de bureau dès mon arrivée. Les jours n'auraient pas été si doux et paisibles sans ta présence.

A Déborah, ta générosité mêlée à ta rigueur et ton professionnalisme façonnent une personne que j'ai été heureuse de côtoyer et avec laquelle j'ai pu passer de très chouettes moments.

Aux *belettes*, Mathilde, Léna et Amélie ; merci pour l'accueil que vous m'avez réservé et pour les moments très chouettes passés ensemble.

A Alix, merci d'avoir toujours été présente, d'une façon ou d'une autre, durant cette expérience de presque quatre ans. M'avoir intégrée dès mes toutes premières heures dans l'unité a fait de toi ma référence sociale, mais pas que ! Tu es une personne très inspirante et qui m'a réservée des moments mémorables. Pour preuve, nos chemins continuent de se croiser et je ferai en sorte que cela perdure.

A Luca, Elsa, Zoé, Pierre-Alban, Léo, Ugoline, Dina, Mahira, Marion merci d'avoir été des compagnons (compères) de galère (ou moins galère) incroyables et infaillibles. Beaucoup de rires, pas de bil, c'était notre light motive. A nos pauses, nos soirées, nos jeux, nos missions, nos discussions, nos réunions j'ai voué un attachement tout particulier et je continuerai d'y penser très longtemps. Je vous considère comme mes amies véritables et je me sens chanceuse de vous avoir près de moi. Comptez sur moi pour ne pas vous lâcher de sitôt.

A Pierre-Jules, merci pour ton implication, ton dévouement, ta volonté. Ton travail m'aura été d'une aide précieuse et je t'en suis reconnaissante. Que le futur te soit favorable et rempli de réussite.

A Alexandre, Q de Quoicoubehhhh et P de pâté, tu as été un co-bureau et ami de haut vol qui m'aura délectée de ses crises tantôt de nerfs, tantôt de rires, des crises de vie en somme ! Malgré mes pratiques statistiques déviantes, tu m'as accueillie et choyée. Bon en même temps faut dire que j'étais la caution sucreries de ce bureau. Oh tchi régales le sang.

A Fantine, ma coccinelle pref, créatrice de surnoms qui marquent et qui restent. Ta gentillesse, ta détermination et ta solidarité elles aussi, marquent et restent. Merci d'avoir incarné avec le reste de *The Office*, les personnages du début du reste de ma vie au labo. Merci pour ta compagnie lors de nos pauses quasi-quotidiennes, lors de ces nombreuses manif et pour tous les moments de vie qu'on aura eu la chance de partager. Est-ce que comme tant d'autres avant moi, j'ai déjà hâte de te retrouver ? Oui, ~~peut-être~~ sans aucun doute.

A Ugoline (all friendships demonstrations performed with the heart (v 2023.10.infini)), pour qui se restreindre à quelques lignes sera bien difficile. Tu as chargé tes packages de *solidarité*, d'*étonnement*, de *forces de proposition*, de *compassion*, de *colère*, d'*amusement*, d'*aide précieuse*, autant de fois que nécessaire lors de ces trois années. Trois années, ce n'est pas rien, c'est une thèse en amitié, en partages d'émotions, en solidarité de luttes en tous genres. J'aimerais pouvoir crier au monde entier à quel point tu as de quoi être fière de toi, maintenant et pour toujours. Merci pour ton attention et ton aide précieuses en permanence et en particulier sur cette dernière année.

A Léo, je crois que les fonctionnalités (parfait pour l'até) qu'on a pu déverrouiller ensemble sont à la fois nombreuses et inestimables. J'ai été fière de marcher de concert (MusilAAAAAAAc) avec toi (tranquille ou quoi), dans la rue ou dans les couloirs pour tantôt s'insurger, tantôt s'encourager, sans jamais se lâcher. Quoi(coubeh) qu'on puisse en dire, ces prémices de promesses se sont incarnés en réel engagement qu'on a brillamment tenu et qui a de quoi (avec tout le reste), nous rendre fièr·es. Merci infiniment le L, d'avoir été aux fourneaux pour alimenter ma machinerie, d'avoir été au clavier pour améliorer et créer mes figures en suspens, d'avoir été dans l'humanité que l'on te connaît pour m'accompagner dans les moments rudes. Pour mon plus grand plaisir. Reste plus qu'à dead ça d'ici quelques semaines (et maint'nant c'est à nous ?).

### **Aux écologues et biologistes qui ont beaucoup compté.e.s**

A Yannick, tu continues d'occuper la place symbolique de mentor dans mon parcours de recherche. C'est sans conteste grâce à ton encadrement dévoué, ton accompagnement infailible et ta pédagogie aux petits oignons que j'ai cultivé cet appétit pour la recherche. Pour l'opportunité que toi et Julien m'avez offerte : un énorme merci.

A Monica et Silène qui ont également ponctué cette première expérience de recherche de délicatesse, de joie et de solidarité. C'était délicieux d'évoluer scientifiquement et amicalement à vos côtés.

A Marion V., ton accompagnement et ta présence m'ont relevée puis portée au moment où j'en avais sûrement le plus besoin. C'est une chance que j'ai eu d'avoir pu te côtoyer et d'avoir pu bénéficier de tes paroles avisées et inspirantes.

A Antonio, pour nos escapades sur ces terres camarguaises, nos discussions entre le laboratoire et la cantine m'ont tantôt enrichie, tantôt consolée, tantôt les deux. Une chose est sûre, tu as fait de cette expérience un eldorado où rien ne m'a manqué.

A Pili et Ania ; pour votre chaleureux soutien, vos encouragements précieux, je suis très reconnaissante. A nos premiers escape game mémorables et en espérant avoir l'occasion de vous revoir.

A ma team *péyi*, Gabz, Blan, Adija, Guillaume, Ottavia, Maxime, Myriam, Mathieu, Simon, Cindy, Yanouk. Sans hésiter, les protagonistes les plus fidèles et exceptionnels dans la plus belle aventure de ma vie. Vous m'avez comblée par votre amour et votre soutien à chaque fois que j'en ai eu besoin et j'espère en avoir fait autant. Vous m'avez permis de chasser la seule ombre au tableau grâce à votre compagnie. Votre pied, mon pied, on se sait.

Un grand merci également à Sam, Elodie, Marine et Mel, vous avez été notre dose de joie, d'éclats de rire, de talent en chant et en danse et j'en passe. Merci pour cette initiation au carnaval créolo-brésilien dont les airs et les couleurs résonnent encore dans ma tête

To Alejandra, Susie, Fabi and Sara, thanks for your support along those journey. What a pleasure it was to meet you both in the city and in the country, during these two fieldwork sessions! It is so valuable and precious to have you in my professional and social environment. Special thanks to Fabi and Sara for hosting me up for several days between each study region switch.

## A ma famille

A mes parents, venus à ma rescousse un certain nombre de fois. Merci pour l'accompagnement, le soin, l'empathie et la tendresse avec lesquels vous m'accompagnez depuis toujours. J'espère que vous êtes fièr-es de vous.

A mon frère Simon, venu un certain nombre de fois en terre provençale tantôt pour se délecter devant des pièces de théâtre, tantôt pour remettre les pieds sur terre après ses escapades internationales. Me laissant toujours requinquée et apaisée, avec plein de points de vie regagnés. J'ai déjà si hâte de planifier nos prochains périple mon *khey*.

A mon grand-père Papy Mougeot, merci d'avoir pris le temps de fouler avec moi le sol avignonnais. Merci pour les douceurs que tu me ramenaes et pour les chouettes colis que tu m'as adressés. Merci pour cet accueil précieux, au mois d'août, pour cette retraite d'écriture, c'était délicieux.

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# Chapitre 1

## Introduction générale

### Préambule

L'objectif de ce travail de thèse est d'explorer la contribution de la physiologie de la conservation pour informer sur l'influence des ressources florales sur la condition corporelle des abeilles sauvages. La Physiologie de la Conservation (PC) est une approche récente qui consiste à établir des liens mécanistiques de causes-à-effets entre, d'une part les changements internes (intrinsèques) des organismes et de l'autre les perturbations environnementales (extrinsèques). Il s'agit donc d'une approche pluridisciplinaire, à l'interface entre les disciplines de la physiologie, de l'écologie du paysage et de la conservation. Après avoir revu les enjeux et menaces pesant sur la biodiversité dans le contexte actuel de modification des paysages, ce chapitre introductif (chapitre 1) propose une synthèse des apports potentiels de la physiologie pour établir des liens entre fonctionnement des organismes et perturbations environnementales. L'accent est ensuite mis sur la façon dont la physiologie peut s'appliquer aux enjeux de conservation des abeilles sauvages. Cette thèse est ensuite organisée en trois parties principales ; une analyse de la bibliographie récente au travers d'un article d'opinion, traitant des applications existantes et théoriquement utiles de la PC sur les abeilles sauvages (chapitre 2). Ensuite, une évaluation empirique du concept à l'échelle de l'espèce (chapitre 3) où nous avons étudié l'apport d'éléments paysagers particuliers sur la reproduction et la condition corporelle d'une espèce d'abeille maçonne. Nous avons également appliqué les outils physiologiques à l'échelle de la communauté où nous avons étudié l'effet de pratiques d'utilisation du paysage sur la condition corporelle de plusieurs espèces de bourdons (chapitre 4). Enfin, nous discuterons de la pertinence et des apports de l'utilisation de la physiologie soulevés par nos travaux tout en proposant l'intégration de concepts et disciplines complémentaires dans l'idée de pratiques de conservation adaptées.

### **I. Paysages agricoles : menaces et enjeux de conservation**

#### **1. Contexte historique et besoin des sciences de conservation**

Les changements environnementaux sont davantage de l'ordre de la règle que de l'exception dans l'évolution des organismes vivants. Qu'ils concernent les variations de gaz dans l'atmosphère, la salinité et le pH des océans, les températures ambiantes et les teneurs en humidité, ces changements ont oscillé entre des périodes de relative stabilité et des périodes de fluctuations rapides et parfois abruptes (Alley et al., 1997; Severinghaus and Brook, 1999).

Les extinctions d'espèces ont contribué de façon importante à l'évolution de la vie (Myers and Knoll, 2001) et bien que ces extinctions soient survenues de façon récurrente dans l'histoire de l'évolution, de nombreux changements historiques et préhistoriques dans l'environnement, notamment des

changements climatiques dramatiques et rapides, ont été associés à des extinctions de masse de nombreuses espèces (Miller and Foote, 2003). Bien sûr, les extinctions dites « de fond » d'une ou de quelques espèces sont considérées comme des procédés normaux dans l'économie de la nature. Par exemple des extinctions importantes peuvent concerner de nombreuses espèces simultanément, comme les extinctions de masse définies par des hécatombes globales sous lesquelles des classes entières de biodiversité s'effondrent (Bambach, 2006).

La biodiversité ou diversité biologique est par essence une notion ancienne puisqu'elle traduit l'évolution du monde vivant depuis près de cinq milliards d'années. En revanche, l'emploi du mot lui-même est récent puisqu'il date des années 1980. La biodiversité représente la variété des formes de vie ou la variation au sein et entre ces formes de vie, à toutes les échelles, des gènes aux écosystèmes. Une définition internationale a été proposée lors de la Convention sur la Diversité Biologique (ou Convention on Biological Diversity en anglais) et acceptée dans les termes suivants : « la variabilité au sein des organismes vivants de toutes les origines, y compris, entre autres, les écosystèmes terrestres, marins et autres écosystèmes aquatiques ainsi que les complexes écologiques dont ils font partie ; cela comprend la diversité au sein des espèces, entre espèces et entre écosystèmes » (United Nations Conference on Environment and Development, 1992).

Etant donné que les plantes et animaux existant sont des descendants de celles et ceux qui ont survécu à une plusieurs changements environnementaux antérieurs, nous pouvons supposer que la plupart des organismes vivants possèdent des mécanismes physiologiques et comportementaux leur permettant de faire face au moins à un certain degré de variation environnementale (Carey, 2005) Un rapport récent révèle qu'en dépit de certains succès locaux et d'efforts considérables pour ralentir les déclin, le taux de perte de biodiversité ne diminue pas (Butchart et al., 2010). Le déclin de la biodiversité est généralisé et important (Diaz et al., 2019; Hallmann et al., 2017; Pimm et al., 2014) et les taux d'espèces menacées enregistrées à ce jour sont particulièrement élevés et vont de 13% pour les oiseaux à 41% pour les amphibiens et gymnospermes (Figure 1. 1). Chez les espèces d'insectes, les taux sont incertains mais la proportion menacée d'extinction est estimée à 10% et on considère que parmi le million d'espèces faisant face à l'extinction dans les décennies à venir, la moitié est représentée par les insectes (Diaz et al., 2019). A noter toutefois que malgré la réalité déplorable de ces constats, la détérioration des statuts des espèces aurait été bien plus importante en l'absence d'efforts de conservation (Hoffmann et al., 2010).

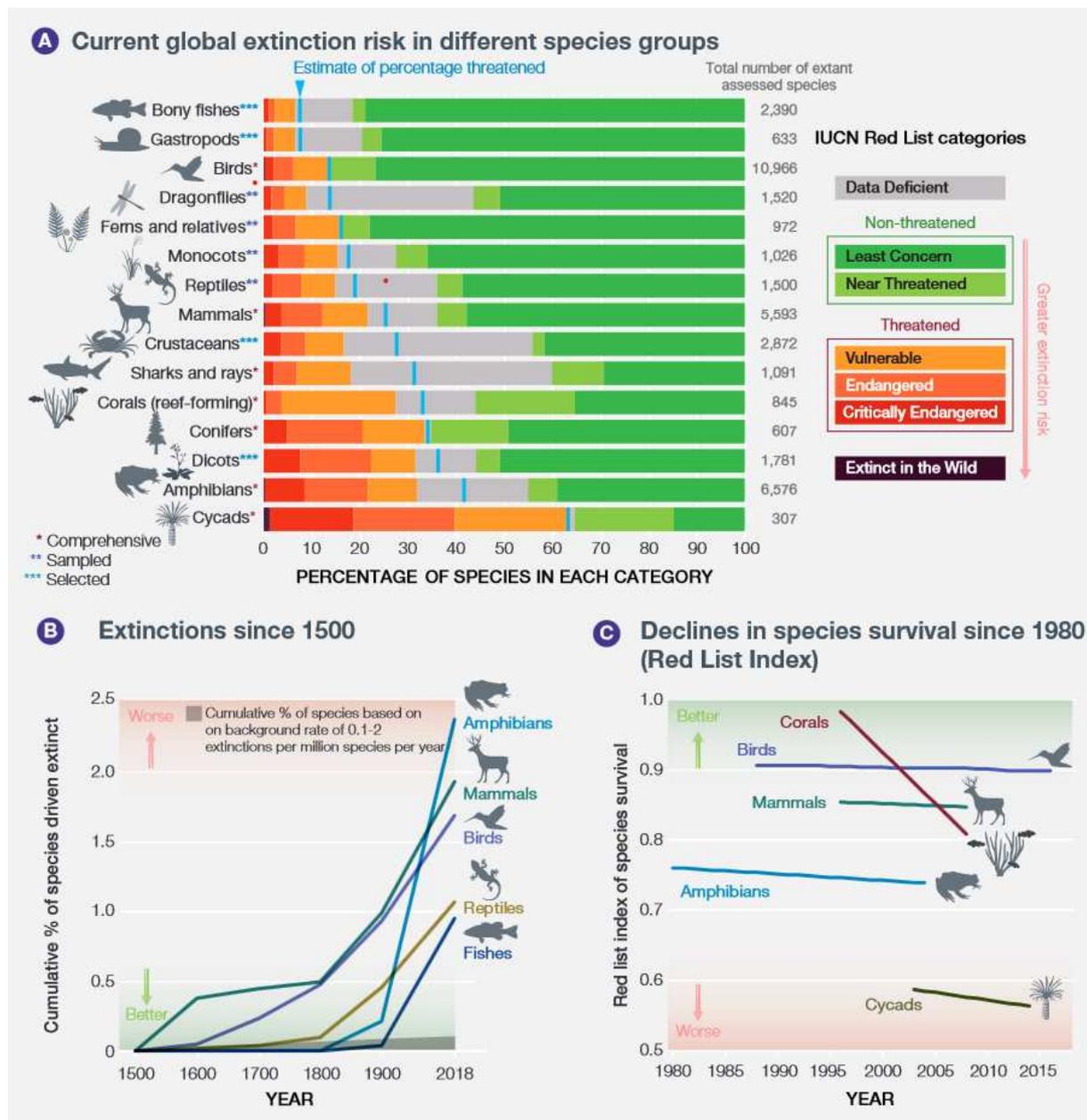


Figure 1. 1: A- Proportion des espèces menacées d'extinction (statut allant de non-menacé "non-threatened" à éteint l'état naturel "extinct in the wild" et B- les tendances générales se détériorent avec des taux d'extinction augmentant de manière abrupte durant le siècle dernier (exemple des amphibiens, des mammifères, des oiseaux, des reptiles et des poissons), C- Déclins observés dans la survie des espèces depuis 1980. Figure extraite du rapport IPBES (Plateforme Intergouvernementale scientifique et politique pour la Biodiversité et les Services Ecosystémiques) 2019 (Diaz et al., 2019).

## 2. Dominance des agroécosystèmes

L'agriculture coexiste et supporte une grande diversité végétale et animale. Selon l'Agence européenne pour l'environnement (AEE), "50 % de toutes les espèces de l'Union Européenne dépendraient des habitats agricoles".

Les agroécosystèmes sont des écosystèmes cultivés, composés par les éléments abiotiques et biotiques qui interagissent entre eux et l'environnement d'un espace agricole (Neyton et al., 2018).

L'intensification agricole n'est pas un phénomène récent puisqu'elle est d'actualité depuis les années 50 et a pour vocation principale l'augmentation de la productivité (Tilman, 1999). Les systèmes de cultures intensives et de production de ruminants sont devenus les fondements des industries agricoles durant le 20<sup>ème</sup> siècle (Eriksson et al., 2021; van den Pol-van Dasselaar et al., 2019). Aujourd'hui, la production agricole couvre plus de 35% de la surface terrestre et dans la plupart des régions du globe, l'agriculture continue à s'étendre et s'intensifier pour répondre à la demande grandissante de nourritures, de biocarburants, et de fibres (Cumming et al., 2014). Il a d'ailleurs été estimé que d'ici 2050, la surface des terres cultivables devraient augmenter de l'ordre de 26% à l'échelle mondiale, entraînant alors la perte d'habitats pour 17 409 espèces (Williams et al., 2020). En Europe, ce ne sont pas moins de 157 millions d'hectares de terres qui sont exploitées pour la production agricole en 2020, soit 38% de la superficie totale (Eurostat, 2018). On y retrouve une dominance des cultures annuelles de blé, d'orge, de colza, de betterave sucrière, de pommes de terre, de seigle etc, ("Agricultural production - crops," 2023) qui sont, pour la plupart, de monocultures ou cultures monoflorales économiquement intéressantes lorsque cultivées en quantité importante. Étant donné que les terres cultivables des zones agricoles occupent plus de la moitié de la surface du globe, il est difficile de mettre de côté ces zones dans les enjeux de conservation ; protéger la biodiversité dans ces zones est donc crucial (Tallis et al., 2009).

### **3. Facteurs anthropiques du déclin de la biodiversité**

En parallèle et de façon combinée, les pratiques menées au sein des agroécosystèmes sont accompagnées d'autres types de changements anthropiques, ainsi, dans les paysages contemporains, les organismes doivent continuellement faire face à des défis environnementaux nouveaux et persistants (Butchart et al., 2010). Les organismes évoluent dans un contexte de paysages évolutifs, fragmentés, perturbés qui ponctuent la façon dont ils s'adaptent et répondent et affectent leur fitness et leur survie (Figure 1. 2).

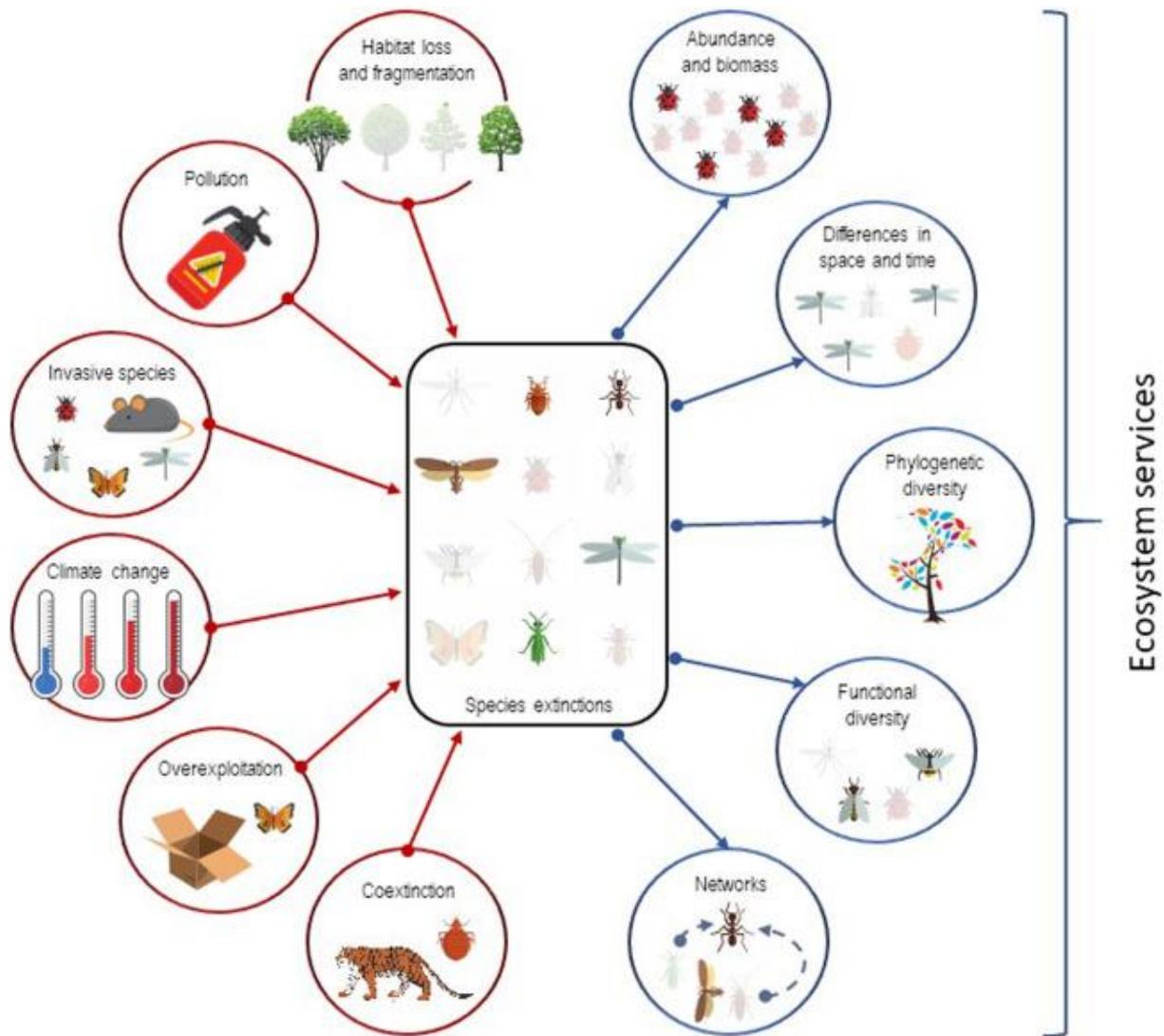


Figure 1. 2: Figure tirée de l'article de Cardoso et al., 2020 représentant les facteurs (en rouge) et les conséquences (en bleu) des extinctions des insectes. A noter que ces facteurs agissent souvent de façon synergique ou à travers des effets indirects, par exemple le changement climatique qui favoriserait la présence d'espèces invasives et exacerberait les effets de fragmentation d'habitats

Les paysages non-agricoles se sont métamorphosés à la suite de défis liés à l'alimentation humaine. Pas moins de 61% des terres ont déjà subies des transformations à des fins humaines (De Palma et al., 2018). Cette intensification agricole se caractérise par la conversion d'écosystèmes naturels complexes en écosystèmes gérés et simplifiés qui ont conduit aux changements globaux et à des pertes de la biodiversité (Tilman et al., 2001).

Ce phénomène d'intensification agricole s'accompagne également de la destruction et la fragmentation des habitats, qui sont parmi les facteurs majeurs dans le déclin global des populations et espèces (Bennett and Saunders, 2010). La fragmentation correspond à une destruction de la surface d'habitat qui réduit un habitat initialement continu en fragments d'habitats isolés les uns des autres et avec moins de capacité de support et/ou moins de connectivité pour permettre aux organismes d'évoluer dans l'espace et aux populations de se maintenir (Lindenmayer and Fischer, 2013). La fragmentation des habitats est une caractéristique dominante de beaucoup de paysages qui peut

résulter en la perte d'habitats due entre autres à la construction de routes, de villes et peut affecter les dynamiques et probabilité d'extinction d'une population (Fahrig, 2002; Hanski et al., 2013; Reed, 2004). La fragmentation revêt de multiples effets menant notamment à (i) la perte d'une zone habitable totale, (ii) la réduction de la taille d'un patch habitable, (iii) l'augmentation des distances séparant les patches.

L'intensification des pratiques agricoles a été accompagnée d'une augmentation générale de l'utilisation de fertilisants et pesticides chimiques (Tilman et al., 2001), et on décompte aujourd'hui 85000 produits chimiques de synthèse (US EPA, 2015). Ces usages ont été démontrés comme affectant sévèrement le comportement et la fitness de nombreux taxons (Rawat et al., 2015). Les impacts surviennent de façon directe, via les effets létaux et sub-létaux des pesticides (principalement les insecticides) et de façon indirecte via l'altération de la composition et de la qualité des habitats (herbicides).

Au-delà des pesticides, la panoplie des polluants est large et contribue, elle aussi, à une perte de biodiversité. Elle va des types de pollution plus connues comme les pollutions de l'air et l'eau via l'utilisation de combustibles fossiles et l'écoulement de produits chimiques respectivement aux pollutions moins connues comme les pollutions sonores, lumineuses et pollution aux microplastiques. Le climat change plus rapidement ces dernières décennies qu'il ne l'a jamais fait ces 2000 dernières années (IPCC, 2021). Les événements liés au changement climatique vont devenir de plus en plus nombreux, fréquents et extrêmes avec l'incidence des crues, sécheresses, tempêtes, vagues de froid et de chaleur qui s'est multipliée par dix ces 50 dernières années (Beniston and Stephenson, 2004; Easterling et al., 2000).

Pour n'en citer que quelques exemples, les changements dans la phénologie dus aux changements climatiques affectent la fitness, la mortalité, la reproduction et le succès de reproduction au sein de plusieurs taxa. Puisque les variations de températures et de précipitations influencent des traits d'histoire de vie clés ainsi que les dynamiques de population, il peut avoir pour conséquence une augmentation de la consommation d'énergie par les organismes qui chercheraient à se maintenir dans des conditions viables. La sécheresse et l'augmentation de CO<sub>2</sub> peuvent altérer des relations entre les animaux et leur environnement (ex. plantes pollinisateurs) et la physiologie des plantes dont les événements de floraison pourraient être avancés. Les fleurs vont par exemple développer moins de couleur de pétales et produire de grandes quantités de composés volatiles lorsqu'elles croissent sous des conditions de sécheresse. Elles peuvent également réduire leur production de graines en réponses à une inadéquation de pollinisation (Kudo and Ida, 2013; Thomson, 2010).

Même si les pratiques d'usage des sols varient grandement de par le monde, leur issue ultime est généralement la même : l'acquisition de ressources naturelles pour les besoins humains immédiats au prix de la dégradation des conditions environnementales (Foley et al., 2005).

Au-delà des trois facteurs anthropiques que sont l'intensification des pratiques agricoles, les polluants et le changement climatique, le Millenium Ecosystem Assessment (2005) et Edward Wilson en 2010,

ont également identifié les espèces invasives et la surexploitation comme responsables majeurs du déclin de la biodiversité. Ces facteurs sont rassemblés sous le modèle HIPPO (H pour « Habitat fragmentation », I pour « Invasive species », P pour « population growth », P pour « pollution » et O pour « overexploitation »), proposé par Edward Wilson en 2010 pour décrire la convergence de ces cinq facteurs interconnectés vers la perte de biodiversité (Wilson, 2010).

Puisque l'ensemble des facteurs entraînant des changements environnementaux sont désormais correctement identifiés, comprendre comment ils interagissent sur la biodiversité et peuvent être atténués, apparaît comme l'un des défis biologiques les plus importants (Chown and Gaston, 2008). Cela dit, même si les politiques menées et les moyens existaient pour endiguer tout impact humain, cela serait logistiquement inatteignable (Seebacher and Franklin, 2012). C'est pour cela que des scientifiques ont statué sur le fait que la conservation se doit d'être sélective et pragmatique. Les décisions doivent être basées sur la compréhension d'impacts que certaines activités humaines auraient sur les écosystèmes et qu'alors les bénéfices des mesures correctives puissent être maximisés tandis que les coûts pour la société seraient minimisés. En d'autres termes, nous sommes face à un besoin urgent de comprendre le lien entre la cause (activités humaines) et ses effets sur la fonction biologique des individus jusqu'aux écosystèmes (Seebacher and Franklin, 2012).

#### **4. Des organismes qui font face aux perturbations environnementales**

Les espèces menacées ne sont pas un sous-ensemble aléatoire de toutes les espèces mais elles partagent des traits biologiques qui influencent leurs risques d'extinction (Chichorro et al., 2019). Il est connu que des espèces affichant des mœurs plutôt spécialistes, soit dans leur type d'habitat soit dans leur régime alimentaires et avec des tailles très petites ou très grandes, sont davantage à risque comparé aux généralistes (Habel et al., 2019). Un individu expérimente son habitat de façon unique et parfois de façon très différente de son voisin, situé à quelques mètres seulement. Cela peut s'expliquer par des différences internes comme la charge parasitaire ou des blessures, le statut social ou des différences environnementales comme le micro-habitat, la présence de prédateurs ou compétiteurs etc...

Les changements environnementaux existants et nouveaux amènent les organismes à devoir s'adapter, depuis des réponses biochimiques jusqu'à des adaptations évolutives (Figure 1. 3). Dès lors, on peut s'interroger sur les choix que font les organismes ; allant des adaptations morphologiques, physiologiques ou comportementales des espèces à une migration pour trouver de meilleurs habitats, des ressources plus abondantes, diverses et adaptées etc. Prédire quelles espèces sont susceptibles de souffrir, ou à l'inverse de bénéficier, du changement climatique et des interactions spécifiques, est nécessaire pour obtenir des estimations précises à propos de la composition future d'une communauté et de la fonction de l'écosystème.

Pour persister, les organismes doivent être capables de convertir les variations biotiques et abiotiques imposées par les variations de paysages qu'ils subissent, incluant celles imposées par la fragmentation, en stratégie d'allocation énergétique adaptative pour les traits d'histoire de vie (THV). Ces THV

permettent en retour aux organismes d'éviter les risques d'extinction (Ziv and Davidowitz, 2019). Les approches basées sur les traits fonctionnels ont connu des succès variables dans l'identification de traits « gagnants » ou « perdants » selon des changements environnementaux (McGill et al., 2006). Identifier les traits qui font que des espèces sont plus susceptibles aux modifications environnementales est essentiel dans la biologie de la conservation et pour assurer des mesures propres à la protection des espèces (Chichorro et al., 2019). Le focus sur des traits morphologiques facilement mesurables peut présenter trois problèmes potentiels ; le premier étant que la sélection restreinte de traits risque de ne pas tenir compte de dimensions fonctionnelles importantes. La deuxième est que les traits sont encore souvent mesurés sous des conditions environnementales fixes. Enfin, la plupart de ces traits sont des traits basés sur des estimations subjectives de quelques expert·es (ex. régimes alimentaires, préférences en matière de microhabitats chez une espèce de coléoptère saproxylique Köhler, 2000; Schmidl and Bußler, 2004). Bien qu'importants, ils ne sont ni reproductibles ni applicables à d'autres espèces pour des études ultérieures ou en dehors de la région d'intérêt dans laquelle ils ont été compilés et ne devraient pas être considérés comme des traits au sens strict (Violle et al., 2007). En clair, dans cette étude de Violle et collaborateur·ices, les "traits fonctionnels" sont définis comme des traits morpho-physio-phénologiques qui influencent indirectement la condition physique par leurs effets sur la croissance, la reproduction et la survie, les trois composantes de la performance individuelle.

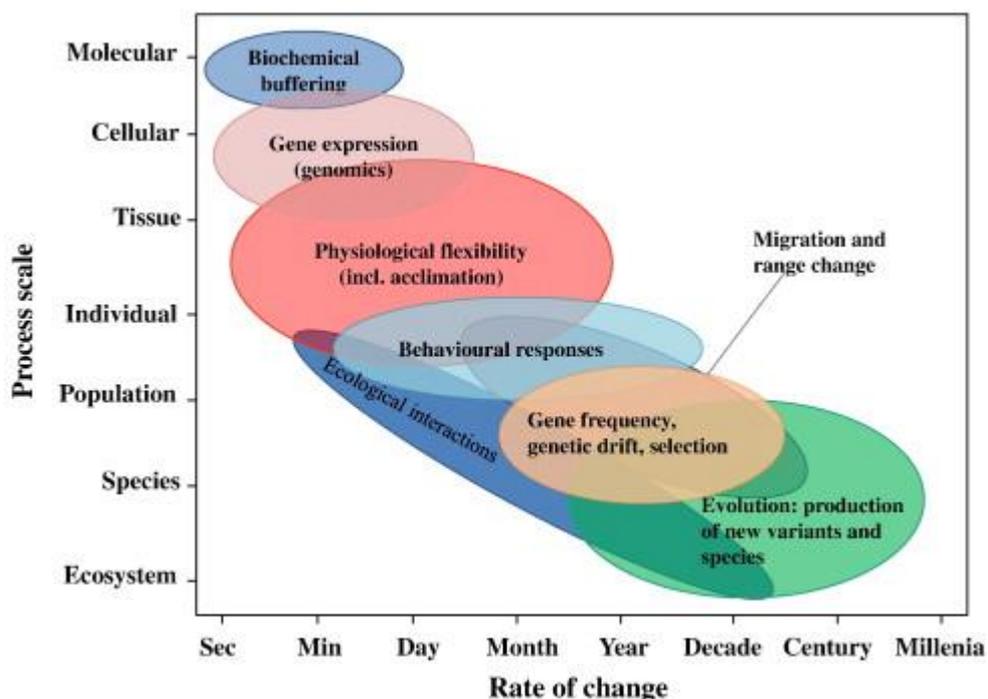


Figure 1. 3: Figure tirée de l'article de Peck 2011 et qui illustre les réponses biologiques (de la molécule à l'écosystème) potentielles en relation à un changement environnemental. Cela peut se traduire par une cascade de processus, depuis les processus biochimiques, en passant par l'adaptation physiologique et les réponses comportementales jusqu'à un changement évolutif.

C'est de ces approches et constatations que découlent les différentes problématiques de ma thèse qui allient enjeux de conservation et outils mécanistiques fonctionnels.

En effet, nous manquons encore à la fois de recul et d'outils pour pouvoir évaluer avec certitude les raisons expliquant la présence des individus et a fortiori des espèces. L'usage des données d'abondance, de distribution, d'occurrence, de richesse est fréquent et les retombées, informatives, (Matthews and Whittaker, 2015) mais affichent des limites bien établies. Les études en question ne permettent pas d'évaluer exhaustivement et précisément ni même d'estimer avec fiabilité (1) si les individus se portent « bien » au regard de ce qu'on peut qualifier d'état de santé (définition proposée dans l'axe III de cette introduction) ni (2) si leur présence témoigne de conditions environnementales favorables et stables. Pour pouvoir établir une compréhension honnête de ce qui régit le bon maintien des communautés, il est primordial de porter le regard sur les liens qu'entretiennent les individus (et leurs fonctionnements) avec leur environnement.

Dans l'importance de prévenir les risques d'affaiblissement de populations ou favoriser leur conservation, il est essentiel de développer une meilleure connaissance des réponses des organismes aux modifications environnementales et aux stress environnementaux, comme proposé par la discipline de la physiologie de la conservation (PC). Cela semble d'autant plus important dans un contexte de paysages évolutifs, fragmentés, perturbés et pour comprendre au mieux la façon dont ces modifications - dites extrinsèques - peuvent venir révéler les voies physiologiques - dites intrinsèques - mobilisées ou bien modifiées.

## **II. Physiologie de la conservation**

### **1. Définitions et évolution des définitions**

La conservation est une discipline appliquée qui se concentre sur l'usage des ressources naturelles, leur allocation et leur protection (McCormick, 1991; Soulé, 1985) tout en développant et en affinant des stratégies pour reconstituer les populations, restaurer les écosystèmes, informer les politiques de conservation et générer des outils de support de décision (Hobbs and Harris, 2001). En 2002, lors de la Convention sur la Diversité Biologique, les décideur·euses se sont accordé·es à une réduction significative de la dynamique actuelle de perte de biodiversité d'ici 2010 (CBD, 2002). Cette Convention a conçu un cadre conceptuel d'indicateurs de mesure de la perte de biodiversité aux niveaux génétique, populationnel, espèces et des écosystèmes. La discipline de la physiologie ne semblait pas encore être une discipline d'intérêt face aux enjeux soulevés. Et pourtant, les physiologistes ont deux rôles capitaux dans la conservation de la biodiversité. Le premier, assez trivial est l'utilisation d'approches physiologiques pour apporter des réponses aux enjeux de conservation. Par exemple chez la tortue du désert *Gopherus agassizi*, classée comme menacée depuis 1989 en raison d'anomalies respiratoires, l'étude physiologique des besoins nutritionnels a permis de déterminer des décisions de gestion concernant la qualité de son habitat (Tracy et al., 2006). Cela fait partie des mécanismes courants et de plus en plus adoptés en physiologie de la conservation (Franklin, 2009;

Wikelski and Cooke, 2006). Le second plus obscur, concerne la quantification de la diversité physiologique (l'un des aspects de la diversité des organismes, selon Spicer and Gaston, 1999) pour identifier les génomes et physiologies uniques ou exceptionnels qui nécessiteraient des actions de conservation. Chez l'araignée fouetteuse, *Damon annulatipes*, le taux métabolique moyen a considérablement diminué, passant de 30,2 à 21,8  $\mu\text{L CO}_2 \text{ h}^{-1}$ , bien que la masse corporelle moyenne n'ait pas changé, après deux semaines passées en laboratoire (Terblanche et al., 2004). Démonstration est faite que les individus d'une même espèce peuvent faire varier leur état physiologique en fonction des conditions de stress ou d'activités (propres au laboratoire dans ce cas) auxquelles ils sont confrontés.

La physiologie est axée sur l'étude des mécanismes impliqués dans la façon dont fonctionne et répond un organisme à son environnement, considérant entre autres son anatomie et sa structure ainsi que celles de ses organes, les flux d'énergie et le métabolisme, l'acquisition de ressources, et les phénomènes d'homéostasie et de régulation (Randall et al., 2002; Spicer and Gaston, 1999).

La combinaison de ces deux disciplines, ou physiologie de la conservation (PC), émerge en 2006 pour la première fois et est définie comme « l'étude des réponses physiologiques des organismes aux altérations humaines de l'environnement et qui pourraient causer ou contribuer aux déclin des populations » (Wikelski and Cooke, 2006). Au cours des années, la définition de la discipline a connu des évolutions et, se saisissant des concepts des spécialistes des domaines concernés, a vu sa définition être complétée et se préciser. En 2012, une définition révisée est proposée en tenant compte des éléments soulevés par les publications de Carey en 2005 et de Tracy en 2006, et la PC devient "*the application of physiological theory, approaches and tools to elucidate and address conservation problems with the aim to provide a mechanistic understanding of how environmental disturbances and threatening processes impact physiological responses and thereby ecological function, population persistence, and species survival*" (Seebacher and Franklin, 2012). En 2013 la définition est quelque peu remaniée par Cooke et collaborateurs, comme « *An integrative scientific discipline applying physiological concepts, tools, and knowledge to characterizing biological diversity and its ecological implications; understanding and predicting how organisms, populations, and ecosystems respond to environmental change and stressors; and solving conservation problems across the broad range of taxa* » (Cooke et al., 2013).

Bien que la définition la plus exhaustive date des années 2010, l'application d'approches physiologiques pour étudier la réponse des organismes à leur environnement ne date pas d'hier. Déjà dans les années 1920/1930 soit près d'un siècle avant, les exemples ne manquent pas avec les travaux de Cook en 1924 sur la distribution de plusieurs espèces de vers gris occidentaux en fonction de l'humidité des sols ou encore ceux de Payne en 1926 sur l'effet de la température sur le point de congélation des perçes-bois. L'un des premiers exemples phares dans le domaine de la PC vient du regard et de la plume avisés de Rachel Carson en 1962 avec la parution de son incontournable ouvrage *Silent Spring* qui relate et compile de très nombreuses données d'études physiologiques qui ont permis d'identifier les relations de causes-à-effets entre des pesticides et la défaillance reproductive des

rapaces (Carson, 1962). Certain-es estiment même qu'elle est à l'origine de l'avènement de l'écologie et des disciplines qui s'en rattachent et que les prises de consciences sociétales et politiques ont commencé autour de cette période.

### **Encadré 1 : Physiologie de la conservation (PC)**

Il s'agit d'une discipline scientifique intégrative appliquant des concepts, des outils et des connaissances physiologiques pour à la fois caractériser la diversité biologique et ses implications écologiques ; comprendre et prévoir comment les organismes, les populations et les écosystèmes réagissent aux changements environnementaux et aux facteurs de stress ; et également résoudre les problèmes de conservation à travers un large éventail de taxons.

### **Encadré 2 : Biomarqueurs/Marqueurs du statut nutritionnel**

Modifications physiologiques (ex. métabolisme énergétique) observables ou mesurables chez un individu en réponse à un changement dans le régime alimentaire. Idéalement, ces marqueurs seraient suffisamment sensibles pour révéler la qualité et l'abondance des ressources environnementales.

## **2. Macrophysiologie et physiologie contemporaine**

La compréhension des relations entre organismes et leur environnement a été identifiée comme l'un des cinq grands challenges en Biologie des Organismes (Schwenk et al., 2009). Cette dernière étant généralement étudiée à travers l'analyse de la distribution des espèces (ex. présence/absence, abondance, richesse spécifique). Estimer la distribution géographique des espèces, conditionnées à leur niche écologique est en effet une étape primordiale pour évaluer le risque d'affaiblissement des espèces.

La plupart des études visant à caractériser l'état de santé des populations se sont concentrées sur l'abondance comme un proxy de la taille de population et de la santé des organismes. L'état de santé, dont la définition sera enrichie dans l'axe suivant, fait référence à la vitalité d'un organisme, liée à sa capacité de survie et reproduction. Mais, face à des enjeux de conservation vis-à-vis d'une biodiversité de plus en plus déclinante (en septembre 2023, 28% des 150388 espèces recensées par l'UICN -Union Internationale pour la Conservation de la Nature- étaient considérées comme menacées, c'est-à-dire avec le statut vulnérable, en danger ou en danger critique d'extinction, UICN, 2023), ces niveaux d'analyses ne suffisent plus.

Dans l'idée de concilier distribution géographique et physiologie, la macrophysiologie est définie en 2004 par l'étude de variations au sein des traits physiologiques sur de larges échelles temporelles et géographiques ainsi que les implications écologiques de cette variation (Chown et al., 2004). La macrophysiologie est une approche qui permet d'identifier de grandes tendances au sein des populations mais ne permet malheureusement pas, en raison de la large échelle d'analyses, d'obtenir

des informations précoces sur la vitalité d'une espèce. En effet, elle ne permet qu'une réalisation tardive du déclin avec des mesures d'effets délétères en décalage par rapport aux enjeux (Ellis et al., 2012).

Les perturbations environnementales induisent des stress au sein des organismes comme c'est le cas de la perte d'habitat (perte actuelle de l'habitat), de la fragmentation (morcellement de l'habitat) et de la dégradation (chute des conditions d'habitat) (Fahrig, 2003). L'analyse de ces perturbations au niveau physiologique (ex. endocrinologie, immunologie, neurophysiologie, bioénergétique, physiologie de la reproduction) apporte alors des éléments de réponses sur les chaînes de causes-à-effets reliant les changements dans l'environnement aux réponses des populations (Ellis et al., 2012). Ces liens de causes-à-effets sont également important car ils permettent d'évaluer de manière précoce la qualité de l'habitat pour l'organisme en question, c'est-à-dire avant que la dynamique populationnelle ne change. En effet, les modifications physiologiques ont généralement lieu bien en amont des modifications démographiques.

En 2005 déjà, Carey suggère que les études peuvent être attribuées à la PC lorsque les physiologistes contribuent à la connaissance, aux concepts et aux perspectives dans la prise de décision de conservation, proposant alors une dynamique d'inclusivité et d'intégration de disciplines entre elles (Cooke et al., 2020; Hof, 2021). Hof exprime d'ailleurs que « l'intégration inter-disciplinaire est vraiment gratifiante et permet de lever nombre de leviers ». Malgré cela, en 2014 était publiée une étude indiquant que l'intégration des champs disciplinaires de la biologie de la conservation au sein des articles de physiologie était de l'ordre d'1% (Lennox and Cooke, 2014), attestant que des efforts sont encore nécessaires pour établir une routine et des travaux intégratifs.

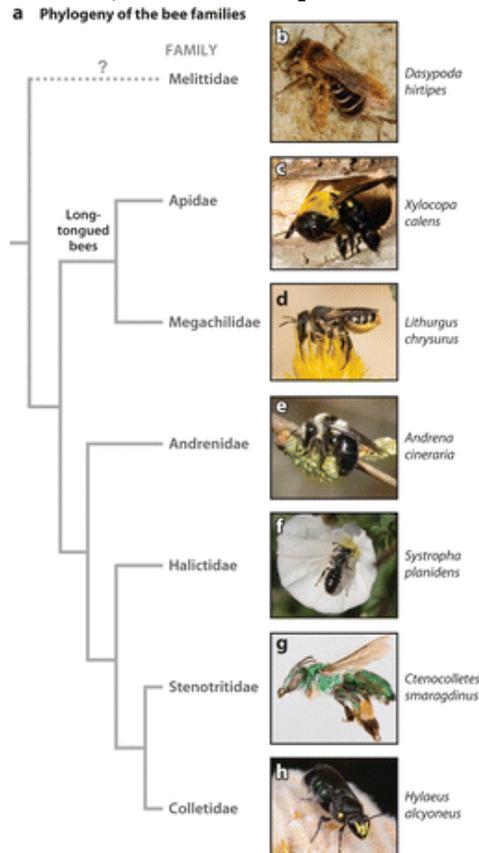
### **3. La physiologie de la conservation intégrée à l'écologie du paysage**

Classiquement, l'écologie du paysage repose sur les corrélations entre paysage et paramètres de la population ou de la communauté, en « ignorant » les mécanismes au niveau individuel. La physiologie, au contraire, est une discipline mécanistique qui se concentre sur le microhabitat et ignore souvent les processus au niveau paysager. Ainsi l'intégration des deux peut générer des hypothèses explicites et testables sur la façon dont un organisme est affecté par les caractéristiques d'un habitat. Déjà suggérée dans les études de (Chown et al., 2004; Chown and Gaston, 2008; Ellis et al., 2012), mais malgré ça, très rare en pratique (Ellis et al., 2012), l'intégration de la physiologie de la conservation à l'écologie du paysage peut en effet s'appliquer à des enjeux de protection et de restauration des habitats. Elle peut permettre d'identifier les traits du paysage « stressant » ou au contraire favorable aux organismes. Dans leur étude, Gibbs and Van Dyck, 2010 ont montré que les papillons provenant de paysages agricoles ouverts et fortement fragmentés et qui étaient forcés de voler, ne souffraient pas d'une longévité réduite par rapport aux papillons provenant de paysages non fragmentés, ce qui suggère que les papillons provenant de paysages fragmentés étaient physiologiquement mieux à même de faire face aux exigences accrues en matière de dispersion par rapport à ceux provenant de paysages non fragmentés.

### III. La Conservation des abeilles sauvages

#### 1. Diversité, spécificité des abeilles sauvages

Les abeilles (Hymenoptera : Apoidea) représentent le groupe le plus important de pollinisateurs de plantes. Et d'ailleurs, il y a davantage d'espèces d'abeilles que d'espèces d'oiseaux et de mammifères réunies (déclaration du professeur John Ascher). On décompte 20000 espèces d'abeilles sauvages dans



le monde, dont 10% de cette diversité, soit 2000 espèces, sont hébergées en Europe et 1000 en France (Nieto et al., 2014a; Potts et al., 2016) où on y retrouve six des (Andrenidae, Colletidae, Halictidae, Apidae, Megachilidae, Melittidae) des sept familles (avec les Stenotritidae en plus) identifiés dans le monde (Error! Reference source not found.).

Figure 1. 4: Phylogénie des sept familles d'abeilles avec (b) femelle de *Dasygaster hirtipes*, (c) *Xylocopa calens*, (d) *Lithurgus chrysurus*, femelle (crédit: Nicolas Vereecken). (e) *Andrena cineraria*, femelle (crédit: James K. Lindsey). (f) *Systropha planidens*, mâle (crédit: Alain Cipièrre). (g) *Ctenocolletes smaragdinus*, femelle (crédit: Laurence Packer, York University: Bee Tribes of the World photographic project). (h) *Hylaeus alcyoneus*, femelle (crédit and copyright: Bernhard Jacobi).

 Danforth BN, et al. 2013.  
Annu. Rev. Entomol. 58:57–78

Une abeille solitaire a une période d'activité très restreinte en comparaison à ses homologues sociales, et ne vit que quelques semaines durant lesquelles elle nidifie et collecte sur les fleurs les ressources (pollen et nectar) nécessaires à sa survie, sa reproduction et à la croissance des larves. Elle est en règle générale univoltine, ce qui signifie qu'elle ne sera active qu'une fois dans l'année et ne constituera qu'une seule génération.

Chez les espèces strictement solitaires, comme les osmies, après une brève interaction avec un congénère mâle pour la reproduction, chaque femelle va constituer elle-même un nid pour une larve en devenir, qu'elle approvisionnera de pollens et nectar qu'elle collecte elle-même puis mourra sans apporter de soin à sa progéniture. Les espèces solitaires représente plus de 77% du total des espèces avec 15 000 espèces. Chez les espèces semi-sociale ou primitivement sociales comme certaines espèces d'Halictidae (ou abeilles de la sueur), il n'existe ni organisation hiérarchique du travail, ni castes morphologiques distinctes mais les individus vont exercer une cohabitation plus ou moins étroite avec

une nidification commune (sur le même site), accompagnée d'une défense collective du territoire et par conséquent, d'une longévité plus importante. En résumé, chaque femelle se comporte de façon solitaire et individuelle mais partage une entrée commune de leur nid. Chez les Cératines par exemple, les soins maternels se prolongent jusqu'à l'éclosion et la femelle va même interagir avec les jeunes adultes. Enfin, les espèces cleptoparasites, comme celles de la famille des Nomadinae représentent autour de 12% des espèces et dans certaines familles comme celles des Apidae, elles peuvent compter pour plus de 25% des espèces (Danforth et al., 2013). Ces abeilles vont occuper et pondre leur progéniture sur des ressources qu'elles n'auront pas collectées et dans un nid qu'elles n'auront pas constitué.

En plus du mode de nidification parasitique des abeilles coucou, on distingue deux grands groupes fonctionnels d'abeilles, basés sur le mode de nidification (Potts et al., 2005). D'un côté, on retrouve les espèces terricoles fouisseuses, qui comptent pour plus de la moitié des espèces au niveau mondial (Michener, 2007). Pour ces espèces, la texture du sol (granulométrie), l'humidité, l'exposition au soleil et le degré de la pente sont autant de facteurs importants dans le choix et la disponibilité de sites de nidification et qui affichent un rôle important dans les variations d'abondance des abeilles (Carré, 2008; Julier and Roulston, 2009; Potts et al., 2005). De l'autre, on retrouve les espèces non fouisseuses qui vont, pour certaines s'établir dans des cavités déjà existantes comme des tiges de plantes (les maçonnes), de la roche, alors que d'autres vont creuser elles-mêmes leur galerie dans du bois (les charpentières).

Les abeilles peuvent également se distinguer en fonction de la morphologie de leur langue. Les familles Apidae et Megachilidae forment le groupe des abeilles à « langues longues » tandis que les quatre autres familles forment le groupe des abeilles à « langues courtes ». La distinction se fait via la morphologie des palpes labiaux, qui sont de courts segments similaires à ceux qu'on peut retrouver chez les guêpes chasseuses ou chez les abeilles à « langues courtes », alors que chez les abeilles à « langues longues » ils sont composés de deux segments élancés, minces et plats, en forme de lame tandis que les deux autres segments apicaux sont extrêmement réduits en taille. Le terme de langue, utilisé dans ce manuscrit, se réfère plus précisément à un élément particulier des pièces buccales des abeilles. Il s'agit du proboscis, une trompe, qui est souvent allongée pour accéder au nectar des fleurs à longue épine. Cette trompe se compose elle-même (i) des galéas allongés des maxillaires et (ii) des palpes labiaux allongés, qui forment ensemble le tube alimentaire qui englobe (iii) la glosse.

Le régime alimentaire herbivore des abeilles sauvages se décline également le long d'un continuum de stratégies, plus ou moins spécifiques allant d'une extrême spécialisation à une extrême généralisation. On retrouve ainsi le monolectisme assimilé à la consommation des ressources d'une seule espèce de plante, l'oligolectisme avec la consommation des ressources d'une seule famille de plantes et enfin le polylectisme avec la consommation des ressources de plusieurs familles de plantes (Cane and Sipes, 2006; Müller and Kuhlmann, 2008). Parmi les familles affichant les taux d'affaiblissement de population les plus importants, on retrouve, notamment les Colletinae, les

Dasypodainae et les Melittinae avec respectivement 32.1, 25 et 14.3% d'espèces menacées. L'une des explications pourrait être rattachée à la spécialisation de leurs comportements alimentaires, qui les rend possiblement plus susceptibles à des changements dans leur environnement (Scheper et al., 2014).

Comme beaucoup d'animaux, qui le sont pour toute ou partie de leur vie, les abeilles sont des *central place foragers*. Cela signifie qu'elles se déplacent depuis un emplacement défini (le nid) pour des vols d'approvisionnements et retournent à cet emplacement entre chaque recherche de nourriture (Olsson et al., 2008). Cet emplacement représente également un refuge dans lequel les individus peuvent se retirer pour s'abriter. Les abeilles entreprennent ces déplacements avec des distances de vols d'approvisionnement très variables. Bien que l'on retrouve des exceptions avec notamment une espèce butinant à 6km de son emplacement de nidification, le rayon d'approvisionnement est assez restreint chez les abeilles solitaires et est souvent inférieur à 500m (Zurbuchen et al., 2010).

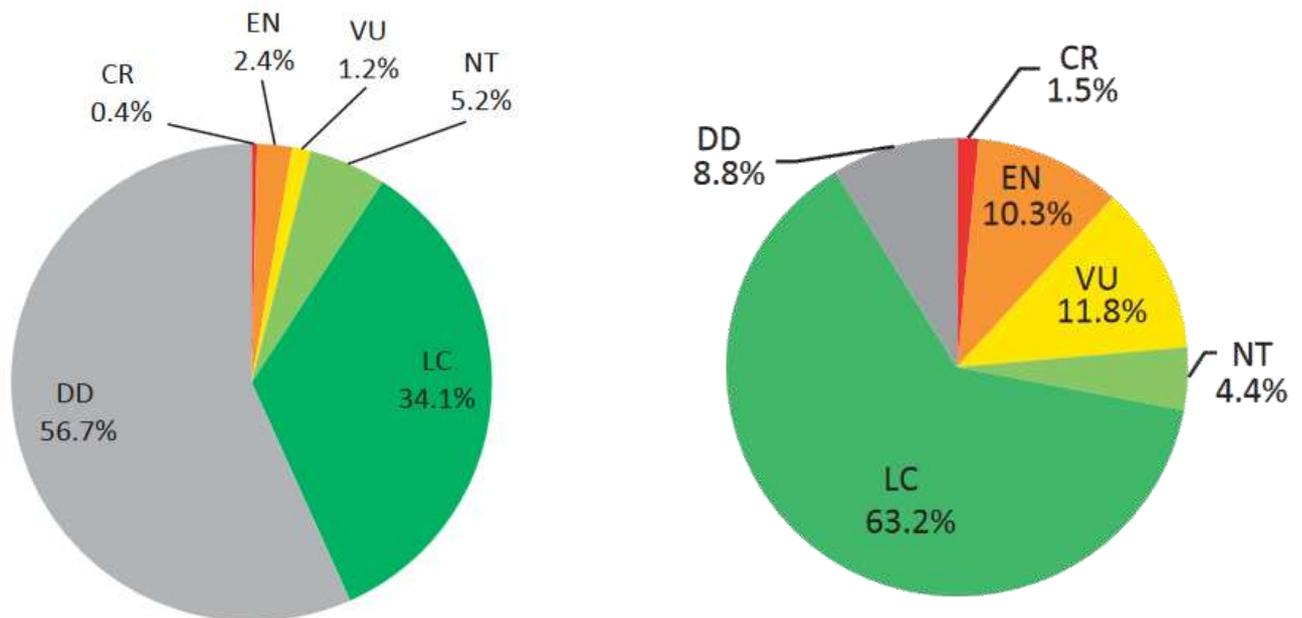
L'approvisionnement des cellules larvaires implique une série de vols de butinage durant lesquels la femelle rassemble pollen et nectar à destination de la croissance de ses larves. La durée de ces voyages est extrêmement variable et peut durer de quelques minutes chez une espèce de *Lasioglossum* à une heure chez plusieurs espèces d'Andrènes voire quasiment deux heures chez une abeille orchidée (Euglossini) (Bohart and Youssef, 1976; Cameron and Ramírez, 2001).

## **2. Statut et menaces sur les populations d'abeilles**

Dans le contexte de déclin de la biodiversité, les abeilles ne sont pas épargnées. Le déclin des abeilles est évidemment mondial (Cameron et al., 2011; Goulson et al., 2015; Potts et al., 2016) et a ainsi également été identifié en Europe (Biesmeijer, 2006; Scheper et al., 2014).

Les populations de pollinisateurs ont décliné depuis les deux dernières décennies (Potts et al., 2010), avec notamment un déclin estimé de 77% de la biomasse d'insectes volants de 1989 à 2016 observé dans 63 aires naturelles protégées en Allemagne (Hallmann et al., 2017). Ce qui contraste avec le fait que chaque espèce d'arthropode reçoit environ 1000 fois moins de financement pour sa conservation que chaque espèce de mammifère (Cardoso et al., 2011) et le statut de conservation de moins d'1% des espèces d'insectes décrites a été évaluée (Warren et al., 2007).

Par exemple, au sein des bourdons, 23.6% des espèces européennes sont menacées d'extinction tandis que 4.4% sont considérés comme quasi-menacée (Nieto et al., 2014a). Considérant que les 56.7% d'espèces européennes ont un statut de conservation qualifié de *data deficient* par l'UICN Union Internationale pour la Conservation de la Nature (Figure 1. 4), il est possible que le pourcentage d'espèces menacées, soit supérieur aux 9% estimé (à partir des espèces avec suffisamment de données).



*Figure 1. 4: Statuts de la liste rouge UICN (Union Internationale pour la Conservation de la Nature) des espèces d'abeilles sauvages, tout confondu (à gauche) et des espèces de bourdons (à droite) en Europe, tirée du rapport de Nieto 2014. DD pour Data Deficient, CR pour "Critically Endangered", EN pour "Endangered", VU pour "Vulnerable", NT pour "Non-Threatened", LC pour "Least Concern".*

L'une des menaces majeures d'un déploiement efficace de mesures de conservation des abeilles d'Europe vient de l'incapacité à comprendre et identifier les espèces présentes et d'en évaluer correctement l'état des populations sur le territoire.

Une étude rassemblant les travaux d'une vingtaine d'expert-es a permis d'évaluer et de classer les importances relatives de huit facteurs majeurs du déclin des abeilles (Dicks et al., 2021). Parmi les plus prégnantes, on retrouve la couverture et configuration du paysage ainsi que la gestion du territoire classée comme « la plus importante » au niveau européen et comme « très importante » dans toutes les autres régions, exceptée l'Afrique (Figure 1. 5).

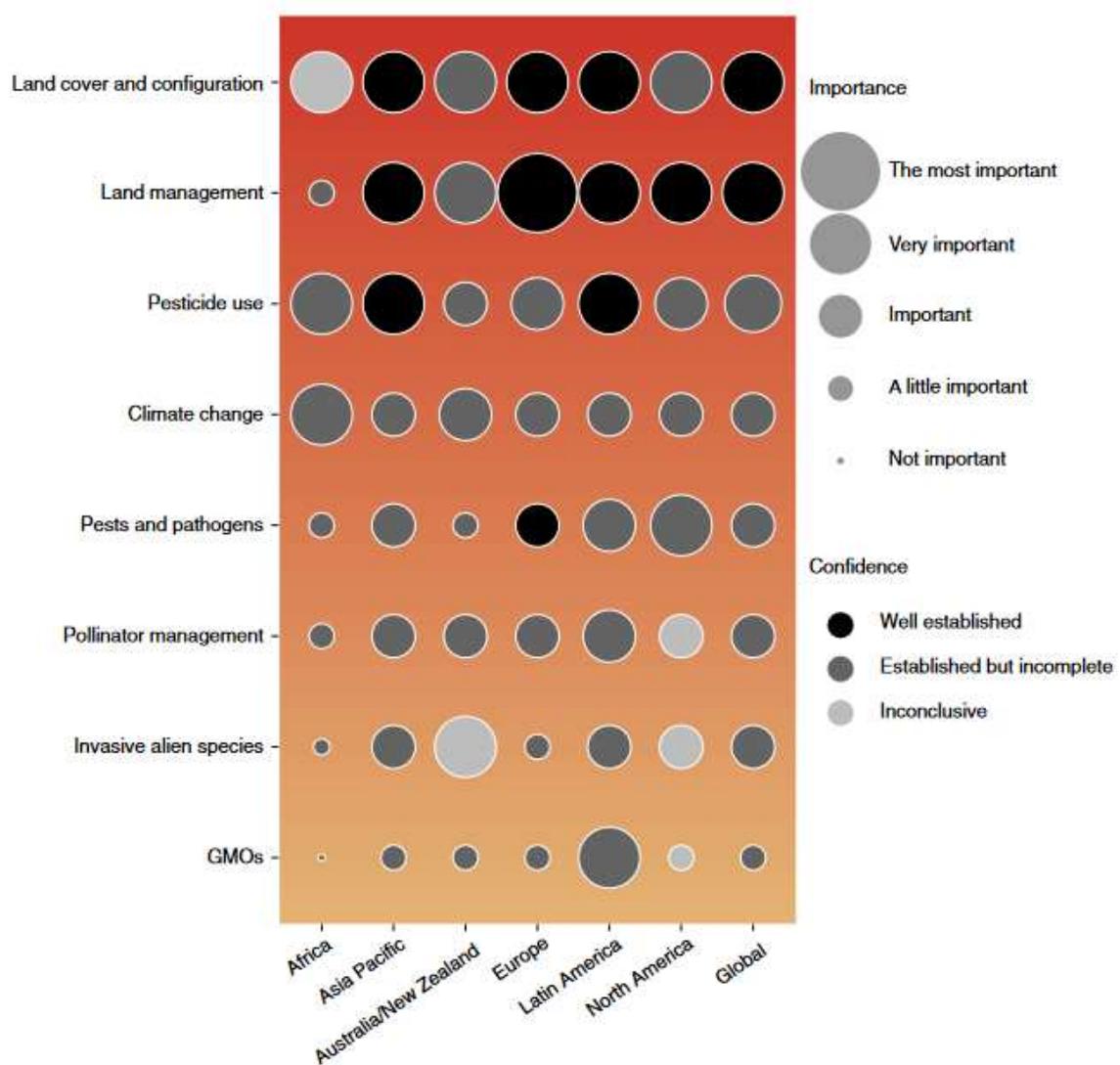


Figure 1. 5: Évaluation de l'importance de huit facteurs majeurs du déclin des pollinisateurs (Configuration et utilisation du sol, gestion du sol, utilisation des pesticides, changement climatique, parasites et pathogènes, gestion des pollinisateurs, espèces invasives et OGM (Organismes Génétiquement Modifiés) dans six régions (Afrique, Asie Pacifique, Australie/Nouvelle Zélande, Europe, Amérique Latine, Amérique du Nord), tirée de Dicks et al., 2021

L'application de pesticides incluant les insecticides, acaricides, fongicides, et herbicides ont également des effets négatifs importants sur la fitness et la survie des pollinisateurs, comme en attestent les études de Rundlöf et collaborateur·ices, et celle de Whitehorn qui démontrent une diminution du succès reproducteur chez les osmies et bourdons (Rundlöf et al., 2015; Whitehorn et al., 2012). D'autre part, les effets peuvent être indirects avec notamment l'usage des herbicides, qui réduit l'abondance et la diversité des plantes à fleurs et par conséquent du pollen et nectar qu'elles pourraient fournir (Gabriel and Tschamtkke, 2007).

## 2.1 Pathogènes et espèces invasives

Les parasites et les pathogène sont considérées comme l'une des causes majeures de mortalité chez

les abeilles mellifères et également chez les abeilles gérées commercialement (bourdons, abeilles maçonnes...). Parallèlement, l'introduction de nouvelles espèces en dehors de leur aire de répartition est connue pour bouleverser la structure des réseaux d'interactions entre organismes dont font partis les abeilles sauvages. Cela peut se traduire par l'émergence de nouvelles prédatations (exemple de la guêpe et du lézard qui ont prédaté les espèces d'abeilles sauvages autochtones, laissant une pollinisation reposant exclusivement sur les abeilles mellifères introduites) et compétitions, ainsi que par la propagation de maladies.

L'introduction de pollinisateurs n'est pas à exclure dans les perturbations de la composition des communautés de pollinisateurs indigènes. A titre d'exemple, en Europe, deux espèces d'abeilles solitaires de la famille des Mégachile, venues d'Asie ont par exemple été accidentellement introduites en France et menacent d'autres espèces d'abeilles sauvages à travers la compétition pour les sites de nidification en outre (Le Féon et al., 2018).

## 2.2 Les changements climatiques

Les effets du changement climatique sur les pollinisateurs n'ont peut-être pas été apparents pendant plusieurs décennies (Intergovernmental Panel on Climate Change (IPCC), 2014), mais depuis de récentes méta-analyses ont identifié un lien entre changement climatique et changements dans les aires de distributions de certaines espèces d'abeilles. En Europe et aux Etats-Unis par exemple, les modifications climatiques n'ont pas entraîné une migration des populations vers le nord mais une diminution des aires de répartition (Ghisbain et al., 2023; Kerr et al., 2015). D'ailleurs, on considère que 136 espèces d'abeilles semblent menacées par ces changements (Nieto et al., 2014a).

## 2.3 Changements d'usage des sols et pollutions

Les changements d'usage des sols, via l'intensification agricole et l'utilisation d'intrants, ont entraîné une homogénéisation des cultures ainsi qu'une réduction des ressources florales et de nidification, disponibles pour les abeilles (Biesmeijer, 2006; Scheper et al., 2014). Les abeilles étant des *central-place foragers*, elles subissent particulièrement la séparation spatiale entre leur environnement de nutrition et de nidification causée par la simplification du paysage (Kremen et al., 2002).

La présence de cultures de floraison massive, bien que présentant un pic de ressources abondantes, reste limitée dans le temps et est associée à une diminution de l'abondance et de la diversité des pollinisateurs (Campbell et al., 2017; Joshi et al., 2016; Ratto et al., 2021). Ainsi un déficit alimentaire (ou stress nutritionnel) à un stade précoce de développement (larvaire) peut se traduire par des répercussions dramatiques sur les stades ultérieurs de l'organisme (Stoks and Córdoba-Aguilar, 2012). Ces effets ont pu être observés sur les éléments paysagers affectant l'abondance et la richesse spécifique des abeilles solitaires l'année suivante (Le Féon et al., 2013).

Selon la liste rouge européenne, 366 espèces d'abeilles sauvages seraient affectées par les changements dans les pratiques agricoles notamment dans les régions tempérées (Nieto et al., 2014a). Les bourdons,

par exemple, sont particulièrement sensibles à la diminution dans le temps de la disponibilité des ressources florales, comme c'est le cas dans les régions intensément cultivées (Carvell et al., 2007; Rundlöf et al., 2008).

### 3. Santé des abeilles : définition et échelle

Alors que chez les humains, la définition de la santé s'est départie de la notion « d'absence de maladies » pour intégrer des notions d'adaptation et devenir dans les années 1990 la « capacité à s'adapter et répondre ou contrôler les défis de la vie et les changements » (Frankish et al., 2001), la définition de santé chez la faune est restée centralisée sur l'aspect de maladie (Stephen, 2014). Les manques de définitions de la santé représentent plus qu'un enjeu académique. L'absence de standards et de termes clairs s'opposent comme un frein à l'évaluation adéquate des risques posés aux organismes.

#### **Encadré 3 : État de santé/vitalité nutritionnel·le**

Il peut être défini comme le lien entre divers traits physiologiques des individus et leur environnement nutritionnel. L'état de santé d'une population devrait ainsi être une conséquence directe de l'état de santé moyen des individus et la taille de la population devrait être positivement corrélée à la santé moyenne individuelle.

Le terme de santé de l'abeille est originellement apparu dans la littérature dans un contexte de maladie et d'études toxicologiques des abeilles mellifères. Par la suite, les termes de santé de l'abeille ou santé des pollinisateurs se sont étendus taxonomiquement et sont désormais utilisés pour les autres espèces de pollinisateurs autre que l'abeille mellifère (Pollinator Health Task Force, 2014; Williams, 2003). L'expansion ne s'est pas faite à tous les niveaux puisque les études dans ce domaine se sont largement concentrées sur la détection de parasites et de pathogènes. Dans une revue, Lopez-Urbe suggèrent une approche à plusieurs niveaux ainsi que l'utilisation de différents paramètres pour mesurer la santé de l'abeille au niveau de l'individu, de la colonie (pour les abeilles mellifères) et de la population (López-Urbe et al., 2020). L'état de santé d'une population devrait ainsi être une conséquence directe de l'état de santé moyen des individus où la taille de la population est positivement corrélée à la santé moyenne individuelle. Dans une revue de Parreno à laquelle j'ai collaboré en tant que co-auteurice (voir Annexes), la santé de l'abeille est proposée comme un concept multidimensionnel où l'état de santé de chaque individu résulte de son interaction avec son environnement local (Parreño et al., 2022a), en particulier son environnement floral car une nutrition incomplète est l'un des facteurs de stress majeurs sur la santé des abeilles domestiques et sauvages (Goulson et al., 2015). En effet, le cycle de vie des abeilles est intimement lié à la disponibilité des ressources florales.

#### 4. Relations plantes-abeilles

Bien que les Hyménoptères apparaissent comme étant le groupe de pollinisateurs le plus important, d'autres groupes tels que les Lépidoptères ou les Coléoptères ne sont pas en reste avec 140000 espèces visitant les fleurs chez les Lépidoptères (Rader et al., 2016). Les diptères, le groupe actuellement le moins diversifié de ces quatre grands groupes, comporte toutefois 71 familles visitant des fleurs (issues de 555 espèces de plantes) (Larson et al., 2001).

Les abeilles visitent plus de 90% des variétés cultivables (Potts et al., 2016) et permettraient la reproduction de 78% des cultures les plus importantes, contribuant ainsi à 35% des rendements agricoles globaux (Ollerton et al., 2011). Les abeilles mellifères sont des pollinisateurs hautement polyvalents avec la pollinisation d'un spectre incomparable de plantes. Cependant, elles ne sont spécialistes d'aucunes plantes et présentent donc des limites d'efficacité et de succès de pollinisation comme c'est le cas pour les myrtilles ou les Solénacées (tomates et pommes de terre) en raison de leur incapacité à *buzz-pollinate* (ou pollinisation par bourdonnement). Les espèces non domestiquées (autres qu'*Apis mellifera*, *Bombus terrestris* et quelques espèces d'osmies) sont également des pollinisateurs clés puisque beaucoup d'entre elles sont genre-spécifiques de plantes, liant alors la diversité des plantes sauvages à la diversité des abeilles sauvages (Ollerton, 2017).

Le paysage floral (fleurs disponibles dans l'environnement des abeilles) varie en termes de quantité et de qualité de ressources (Burkle and Irwin, 2009; Zimmerman, 1981). Ceci peut ainsi influencer directement l'activité nutritionnelle des abeilles qui sont capables de détecter certaines des variations qualitatives des nectars et pollen (Howell and Alarcón, 2007; Nuttman et al., 2006) pour en optimiser leurs besoins nutritionnels.

#### 5. Besoins nutritionnels des abeilles

Une des principales récompenses de la pollinisation des fleurs par les abeilles est le nectar. La composition de ce nectar peut considérablement varier au sein des espèces d'angiospermes et une part de cette variation est associée à l'attraction des espèces de pollinisateurs en particulier. Les composés majeurs du nectar foral sont l'eau, les glucides, les ions, des acides aminés ainsi que des protéines à faible poids moléculaire (Nicolson and Thornburg, 2007). Ces composants permettent de répondre aux demandes énergivores que sont les fonctions de vol et de thermorégulation (Haydak, 1970). La portion de glucides du nectar floral se décline en saccharose et ses « dérivés » monosaccharides : le glucose et le fructose. La concentration en sucre du nectar peut varier de 7 à 70% même si la plupart des nectars sont compris dans la fourchette 25-55%. A titre de comparaison, il faut savoir que la fameuse boisson pétillante foncée contient approximativement 10% de sucre.

Le pollen est la ressource florale la plus collectée par les abeilles solitaires et de loin. Le pollen est la source principale de macronutriments tels que les protéines nécessaires à la fois au développement larvaire ainsi qu'à la production des œufs par les femelles, et les graisses (triglycérides, phospholipides)

(Cane et al., 2017; Vaudo et al., 2015). Les œufs sont en effet coûteux à produire en termes de protéine et les femelles doivent être capables de reconstituer leurs stocks protéiniques de façon régulière afin de produire des œufs continuellement. On sait d'ailleurs que le volume de pollen consacré à la consommation propre d'une femelle quotidiennement atteint 10% du pollen collecté pour une cellule larvaire (Cane et al., 2017). Le contenu en protéines est considéré comme le premier déterminant de la valeur nutritionnelle du pollen (Roulston et al., 2000; Roulston and Cane, 2000) auquel il ne faut pas oublier d'ajouter les contenus en stérols et acides aminés (Klein et al., 2007; Vanderplanck et al., 2017). Le contenu protéinique du pollen varie entre 12 et 61% pour les pollens communément collectés par les espèces spécialistes et généralistes (Roulston et al., 2000). Le pollen est une ressource multidimensionnelle qui fournit également d'autres macronutriments tels que les lipides. Les voies de production des triglycérides (principale forme de stockage des lipides) viennent soit directement de la nourriture, soit résultent de la transformation des carbohydrates (Hahn and Denlinger, 2007). Les lipides sont cruciaux pour une variété de procédés physiologiques chez les abeilles (production des œufs et source d'énergie secondaire, développement larvaire) et contribuent également à la survie pendant la diapause (Canavoso et al., 2001; Fliszkiewicz and Wilkaniec, 2007).

Le glycogène, apporté par le nectar est un polysaccharide qui représente la principale réserve de glucides pour les insectes effectuant la diapause ou non. Le tréhalose est le glucide circulant majeur. Le glycogène connaît des procédés de conversion et reconversion plusieurs fois au cours de la vie d'un organisme et notamment durant la période de diapause pour la production de cryoprotectants.

Le profil nutritionnel des pollens et nectars varie ainsi grandement entre les différentes espèces de plantes (Belsky and Joshi, 2019; Vaudo et al., 2020) et parfois même au sein de deux individus d'une même espèce selon les conditions pédoclimatiques (Venjakob et al., 2020). Les abeilles peuvent donc manifester de fortes préférences pour certains types de pollens. Chez les abeilles mellifères, les ouvrières sont d'ailleurs capables de distinguer les différences nutritionnelles des pollens et vont ainsi collecter les pollens complémentaires pour répondre aux besoins nutritionnels (Hendriksma and Shafir, 2016). La discrimination peut se faire aussi au niveau de petites différences dans des concentrations en sucre des nectars où les individus préfèrent les concentrations importantes (Afik et al., 2006; Nicolson, 2007; Roubik and Buchmann, 1984).

#### **IV. Mesures de conservation**

Nous savons que les insectes sont capables d'évaluer leur propre statut nutritionnel, ainsi lors de la navigation dans son paysage nutritionnel, l'individu décide quelle ressource semble satisfaire ses exigences nutritionnelles, chimiques et structurelles innées, pour lui-même et sa descendance. Pour ce faire, il faut que les individus puissent avoir accès à ces paysages et idéalement, à une diversité de paysages. Par ailleurs, de nombreuses études ont démontré que la diversité des abeilles est associée avec une diversité d'habitats et de ressources dans le paysage (Bendel et al., 2019; Billeter et al., 2008; Kremen et al., 2018; Rivers-Moore et al., 2020).

## 1. Hétérogénéité spatiale

Les mesures de l'hétérogénéité ont souvent été pratiquées de façon binaire car basées sur la *théorie biogéographique des îles* qui fait le postulat que les paysages peuvent être vus comme des îlots d'habitat répartis au milieu d'une mer hostile (MacArthur and Wilson, 1967). Ainsi on retrouverait d'un côté les habitats semi-naturels considérés comme complexes et favorables à la biodiversité et de l'autre la matrice agricole considérée comme simple et peu favorable à la biodiversité (Batáry et al., 2010; Fahrig et al., 2011). Les paysages avec de hautes proportions d'éléments semi-naturels, de forêts, de haies, de franges forestières ou de zones humides (au-delà de 20% d'éléments semi-naturels) seraient qualifiés de complexes tandis que la matrice qualifierait les abords non-adéquats de ces habitats favorables (Wiens, 1995).

Il est d'ailleurs établi désormais que du point de vue de l'organisme, la représentation des paysages est bien plus complexe. En effet plutôt que d'être vus comme un contraste dichotomique entre « habitats » *versus* « non-habitat », les paysages sont davantage perçus comme une mosaïque d'habitats de qualités diverses (Kupfer et al., 2006; Murphy and Lovett-Doust, 2004; Storkey et al., 2011). Ces habitats spatialement hétérogènes, sont également temporellement dynamiques en raison de la variabilité dans l'étendu, la distribution et la qualité des habitats au cours du temps (Fahrig, 1992).

L'hétérogénéité des habitats se décline en (a) hétérogénéité de composition qui est le nombre d'habitats et la proportion des différents types de surfaces et (b) l'hétérogénéité de configuration qui réfère à la complexité du paysage (Fahrig and Nettle, 2005). On peut y ajouter l'hétérogénéité fonctionnelle du paysage référant à la présence de ressources jouant un rôle fonctionnel dans chaque habitat (nourriture, sites de nidification, voie de dispersion...) pour soutenir une espèce ou un groupe d'espèces.

L'hétérogénéité des paysages ainsi basée sur l'ensemble des types d'habitats qu'ils soient semi-naturels ou cultivés n'est pas aisée à prendre en compte dans les études. Cela dit, des études chez les insectes floricoles ont permis de démontrer que des facteurs structurels comme l'orientation des lisières forestières ou la pente moyenne des prairies en bord de culture affectent l'abondance et la distribution des syrphes et des abeilles sauvages (Carrié et al., 2018; Sarthou et al., 2005). La prise en compte de ces facteurs dans la conception ou la restauration des éléments paysagers importants pour les abeilles est capitale. En effet, ils jouent un rôle parfois plus important que la seule proportion des éléments paysagers sur la structure des communautés d'abeilles sauvages.

## 2. Complémentation des habitats

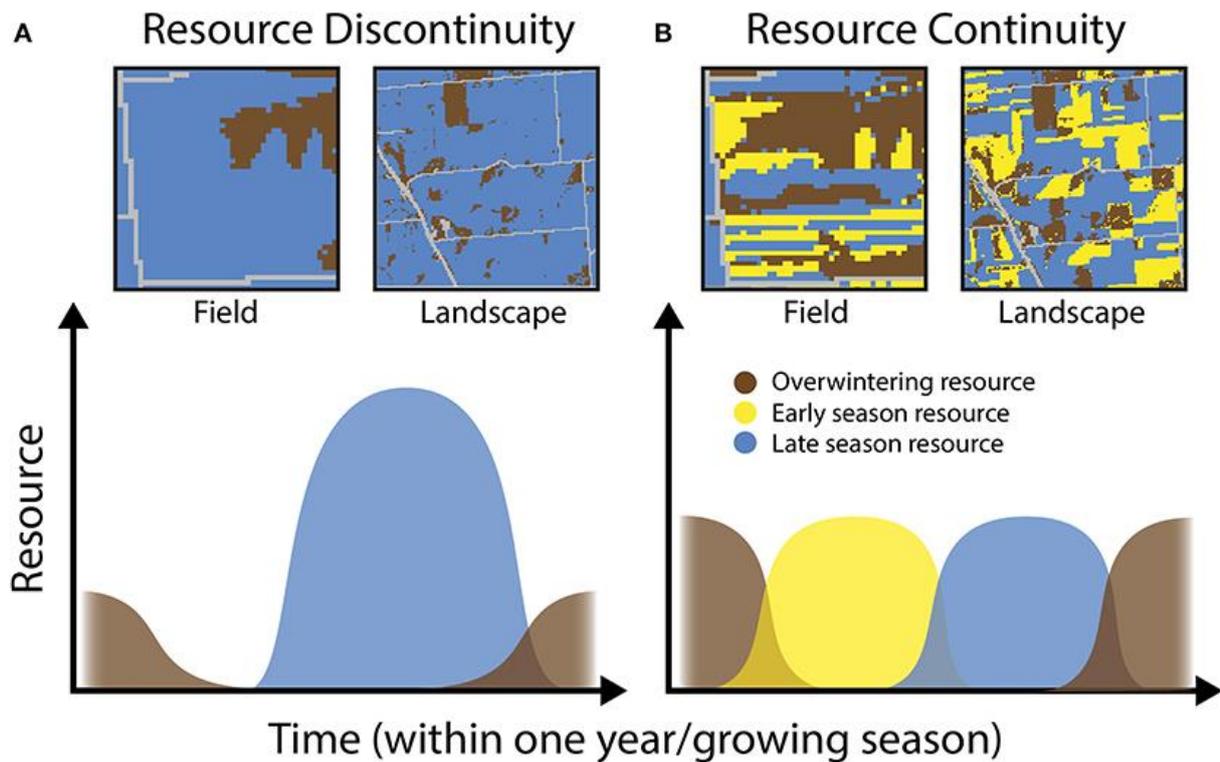
### Encadré 4 : Complémentarité du paysage

En 1992, Dunning et collaborateur·ices ont introduit le concept de **complémentarité du paysage** pour décrire les situations dans lesquelles les séries de ressources critiques nécessaires à un organisme pour compléter son cycle de vie seraient contenus non pas dans un seul type d'habitat mais au sein

d'habitats divers, spatialement séparés les uns des autres. En clair, une espèce peut avoir besoin de ressources distinctes provenant de différents habitats pour subvenir à ses besoins nutritifs, reproductifs, et de nidification au cours de la saison (Figure 1. 6). Cela sous-entend des interactions positives entre habitats ou, plutôt que de s'exclure et d'être considérés de façon binaire « favorables » versus « hostiles », comme dans la *théorie biogéographique des îles* de 1967, les habitats seraient considérés comme complémentaires et hétérogènes (en composition ou en configuration) pour permettre le maintien des populations. La supplémentation du paysage, elle, décrit la disponibilité de ressources dans différents habitats adjacents et la capacité des organismes à en faire l'acquisition si ces ressources se trouvent à manquer dans l'habitat de l'organisme (Dunning et al., 1992).

La continuité des ressources est définie comme la disponibilité continue de ressources dans le temps dans des paysages agricoles et requis par une population d'organismes pour sa survie et sa reproduction au cours d'une année. Les notions de complémentarité et supplémentation sont donc essentielles dans des contextes d'agroécosystèmes simplifiés, ne contenant qu'une ou quelques variétés annuelles cultivables, où la pénurie des ressources est fréquente au cours de l'année. En effet, malgré des périodes de ressources abondantes, présentant des opportunités alimentaires considérables lors des pics de floraison des monocultures pour les insectes floricoles, la diversité nutritionnelle est faible.

Afin de restaurer un continuum phénologique et une dynamique temporelle des ressources, il peut être préférable de cultiver des cultures entomophiles phénologiquement complémentaires plutôt que de se contenter de restaurer des habitats-semi-naturels. Estimer la saisonnalité et la durabilité des ressources permettrait notamment d'évaluer à quel point la disponibilité des ressources coïncide avec le cycle de vie des organismes ainsi que le développement de la population d'une espèce au cours d'une année (Schellhorn et al., 2015). Au sein des communautés d'abeilles d'ailleurs, la phénologie des plantes joue le rôle de filtre écologique en influençant l'occurrence, le succès reproducteur et les décisions nutritionnelles des abeilles sauvages (Ogilvie and Forrest, 2017).



*Figure 1. 6: Représentation schématique du concept de continuité des ressources tirée de l'étude de Iuliano & Gratton (Iuliano and Gratton, 2020). Les ressources peuvent varier au cours du temps dans des agroécosystèmes hétérogènes. La figure A schématise un scénario de faible continuité, dans le champ isolé d'une exploitation. On peut imaginer ici que certaines populations seraient limitées par la présence d'habitat d'hivernation et subiraient un déficit de ressources tôt dans la saison. La figure B représente un scénario de haute continuité où les populations auraient suffisamment de ressources disponibles en tout temps.*

En plus de la dimension temporelle de l'abondance et de la disponibilité des ressources au temps T, la dimension passée peut également être considérée. Lorsque la composition du paysage de l'année précédente continue d'exercer une influence à travers des effets durables et interannuels sur l'abondance des organismes, on parle de répercussions ou de reports des effets ou *carry-over effects*.

Ils ont été précédemment définis comme « tout événement survenant au cours d'une saison et influençant de manière non létale les performances d'un individu au cours d'une saison ultérieure » (Norris, 2005). Ces effets peuvent s'illustrer par un déficit alimentaire précoce au cours du cycle de vie, expliqué notamment par le fait que le continuum floristique n'est que peu ou plus représenté, et qui exercent des effets néfastes à des stades tardifs, affectant par conséquent la fitness et le succès reproducteur des individus (Harrison et al., 2011). Chez les abeilles, la prise en compte des *carry-over effects* est importante puisque la disponibilité en ressources détermine les dynamiques et la santé des populations (Requier et al., 2017). Dès lors, il serait raisonnable de centrer une partie des études sur les réponses comportementales et reproductives des abeilles sauvages face aux fluctuations dans la disponibilité des ressources au cours du temps.

### 3. Apports des éléments semi-naturels

#### Encadré 5 : Habitat semi-naturel

Selon l'encyclopédie d'agroécologie, un **habitat semi-naturel (HSN)** correspond à tout habitat d'un agroécosystème dans ou autour duquel se développe une végétation spontanée essentiellement composée d'espèces bisannuelles, pluri-annuelles ou pérennes, ou un couvert semé dit « de service » et intentionnellement non récolté. Cet habitat est un lieu de vie permanent ou intermittent permettant reproduction, alimentation, refuge, estivation ou hibernation de groupes biologiques appartenant aux six règnes du vivant (archées, bactéries, protistes, fonge, flore, faune) (Sarhou and Chabert, 2016). Plus simplement, les HSN sont également définis comme « n'importe quel habitat au sein ou en dehors d'une culture, contenant une communauté d'espèces végétales non-cultivées » (Holland et al., 2017).

Fréquemment utilisée comme un substitut de la complexité ou de l'hétérogénéité du paysage, la superficie de la couverture en éléments semi-naturels dans les paysages agricoles a été démontrée comme présentant un effet positif à la fois sur les insectes, les oiseaux ainsi que de petits mammifères (Benton et al., 2003a; Billeter et al., 2008; Hendrickx et al., 2007). Les HSN en tant que tels ou associés à des paysages plus anthropisés, sont connus pour supporter des taux plus élevés de biodiversité (Habel et al., 2013). Ces couverts semi-naturels jouent un rôle capital dans le maintien de la biodiversité des zones cultivées en subvenant aux besoins de nidification, d'hibernation, de nutrition, de dissimulation et peuvent même être source de recolonisation pour les populations des habitats perturbés (Chaplin-Kramer et al., 2011; Tschardt et al., 2005).

Les prairies temporaires et permanentes forment l'un des écosystèmes les plus importants du monde, occupant près d'1/3 de surface terrestre du globe (Suttie et al., 2005), proportion similaire retrouvée en Europe (Bengtsson et al., 2019). Au sein de l'Union Européenne, les prairies permanentes couvrent près de 60 millions d'hectares soit un tiers de sa surface agricole utile (Eurostat, 2017). En France, les prairies permanentes occupent neuf millions d'hectares tandis que les prairies temporaires occupent trois millions d'hectares (Agreste, 2019). Il est également de plus en plus souligné dans la littérature l'importance des bords entre les couverts semi-naturels et entre les cultures. En effet des études ont pu démontrer qu'ils augmentaient les mouvements et les débordements (*spillover*) d'espèces de plantes et d'animaux locaux entre des patches adjacents (Blitzer et al., 2012; Brudvig et al., 2009; Tschardt et al., 2007). Chez les abeilles, les HSN sont des éléments clés dans la notion de complémentarité et de continuité temporelle des ressources (Rivers-Moore, 2022). Au-delà des aspects quantitatifs, il est nécessaire de considérer des aspects de diversité des HSN dans le paysage dont les différents types (lisières, prairies...) peuvent se faire relai des autres au cours de la saison (Neumüller et al., 2020).

A noter que les habitats semi-naturels ne sont pas seulement importants pour les communautés locales

qu'ils abritent mais contribuent également à maintenir les communautés des terres cultivées (ex. 'beetle bank', MacLeod et al., 2004). Ce sont des espaces qui permettent un effet un peu tampon, transitoire face à des surfaces gérées intensivement. En dehors de leur valeur conservatrice, les HSN sont de plus en plus reconnus pour d'autres bénéfices publics comme des valeurs esthétiques paysagères, l'héritage culturel, la séquestration en carbone, la rétention en eau et en tant que réservoirs de diversité génétique (Bengtsson et al., 2019; Torralba et al., 2018).

## Objectifs, questions et hypothèses

Afin d'évaluer la disponibilité des ressources florales sur l'état de santé/vitalité des abeilles, nous nous sommes focalisé-es sur leur condition corporelle rassemblant à la fois des mesures morphométriques (poids) et de réserves énergétiques, telle que les concentrations en triglycérides, protéines et glycogène. Ces macronutriments sont essentiels pour un certain nombre de traits d'histoire de vie et étapes du cycle de vie des insectes, et sont principalement acquis par la consommation de pollen et de nectar. Nous faisons donc l'hypothèse qu'une variation dans la disponibilité des ressources florales entraînerait une variation au niveau de la concentration de ces macronutriments mais aussi dans le poids des individus (largement dépendant de leur taille et de la consommation de pollen à l'état larvaire). L'ensemble de ces traits physiologiques pourrait ainsi jouer le rôle de marqueur de l'état nutritionnel des abeilles.

A noter que nous avons mené ces analyses sur les femelles d'abeille sauvage puisqu'il est admis que ce sont elles qui effectuent la part majoritaire des tâches de reproduction fortement dépendante de la disponibilité en ressources alimentaires.

Nous avons ainsi testé l'influence de la disponibilité des ressources florales sur la condition corporelle des abeilles à différentes échelles :

- à l'échelle populationnelle, sur une espèce d'abeille sauvage solitaire, l'osmie cornue *Osmia cornuta* en mesurant à la fois le succès reproducteur de la génération n ainsi que la condition corporelle de la descendance n+1, dans des vergers de pommiers complémentés par diverses ressources florales.
- à l'échelle communautaire, sur un sous-ensemble de 30 espèces et en particulier neuf espèces d'Andrènes, dix espèces de bourdons, cinq espèces d'Halictes et six espèces de *Lasioglossum* pour un total d'environ 1300 femelles dans des prairies européennes caractérisées par un gradient dans la diversité florale ainsi que dans l'utilisation du sol (considérant la compilation de trois notes attribuées aux pratiques de fauchage, pâturage et utilisation d'intrants). Dans cette thèse, ne seront évoqués que les résultats sur les bourdons.

Dans le premier cas nous nous sommes interrogé-es sur les effets potentiellement bénéfiques de la présence d'éléments paysagers complémentaires aux vergers, tels que les haies, les éléments semi-naturels et les surfaces de cultures sur le succès reproducteur des osmies cornues et la condition corporelle de la descendance. Sous l'hypothèse de la complémentation de l'habitat, nous nous

attentions à ce que la présence d'éléments semi-naturels, à proximité de vergers (de pommiers et/ou de poiriers) à floraison massive, influence positivement le succès reproductif des *Osmia cornuta* et l'état corporel de leur progéniture. Nous avons également exploré la contribution possible de ces différents éléments du paysage sur la qualité du régime alimentaire (pollen récolté) des abeilles en analysant les taxons végétaux et les valeurs nutritionnelles des pollens butinés. Notre hypothèse ici est que des éléments paysagers complémentaires aux vergers procurent une plus grande diversité et disponibilité de ressources dans le temps, favorable au succès reproducteur des femelles d'osmies et à la condition corporelle de la descendance.

Dans le deuxième cas, en nous plaçant cette fois à l'échelle de la communauté d'abeilles, nous nous sommes demandé.es dans un premier temps si, en zones de prairies, une diversité plus importante des ressources florales (approximée via des calculs d'indice de diversité) ainsi qu'un indice d'utilisation du paysage (LUI en anglais) pouvaient influencer les nutriments stockés et ainsi la condition corporelle de plusieurs espèces d'abeilles sauvages. Puis, nous nous sommes interrogé.es sur l'existence de différences de sensibilité interspécifique à la diversité des ressources florales, et sur un lien potentiel avec des traits fonctionnels des espèces. Notre hypothèse étant que la diversité florale est généralement bénéfique à la communauté d'espèces d'abeilles mais cette sensibilité varie selon les traits fonctionnels des abeilles (ex. chez les bourdons : taille des colonies, longueur du proboscis).

# Chapitre 2



# Using physiology to better support wild bee conservation

Article publié dans Conservation Physiology, doi: <https://doi.org/10.1093/conphys/coac076>

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## Lay summary

Due to growing environmental pressures on wild bee populations, there is an urgent need to better monitor population trends, identify environmental drivers of population changes and develop conservation strategies. In this paper, we discussed how physiological metrics could contribute to solving those conservation issues for wild bees.

## Préambule

Cet article d'opinion est le point de départ de la réflexion autour de l'utilisation de la physiologie pour répondre aux enjeux de conservation qui concernent les abeilles sauvages.

Nous partons du postulat qu'une compilation de mesures morphométriques et marqueurs physiologiques serait pertinente pour attester/informer de l'état de santé des abeilles sauvages, avec déjà quelques exemples (rares) à l'appui.

Nous sommes en effet confronté·es à un manque de connaissance du statut physiologique chez les abeilles sauvages en fonction de la qualité environnementale. Certains exemples d'application de la physiologie à des questions de conservation existent d'ores et déjà, y compris chez les insectes mais ne sont pas légion chez les abeilles sauvages.

## Abstract

There is accumulating evidence that wild bees are experiencing a decline in terms of species diversity, abundance or distribution, which leads to major concerns about the sustainability of both pollination services and intrinsic biodiversity. There is therefore an urgent need to better understand the drivers of their decline, as well as design conservation strategies. In this context, the current approach consists of linking observed occurrence and distribution data of species to environmental features. While useful, a highly complementary approach would be the use of new biological metrics that can link individual bee responses to environmental alteration with population-level responses, which could communicate the actual bee sensitivity to environmental changes and act as early warning signals of bee population decline or sustainability. We discuss here through several examples how the measurement of bee physiological traits or performance can play this role in better assessing the impact of anthropogenic pressures on bees, but also in guiding conservation practices with the help of the documentation of species' physiological needs. Last but not least, because physiological changes generally occur well in advance of demographic changes, we argue that physiological traits can help in predicting and anticipating future population trends, which would represent a more proactive approach to conservation. In conclusion, we believe that future efforts to combine physiological, ecological and population-level knowledge will provide meaningful contributions to wild bee conservation-based research.

## Introduction

Like many organisms on earth, wild bees are facing growing anthropogenic pressures, including agricultural intensification (e.g. habitat loss, lack of food resources, and pesticide use), climate change, and the spread of invasive species and diseases (Potts et al., 2010). Consequently, in recent decades, a decline in bee species richness has been observed on all continents except Oceania (Biesmeijer, 2006; Cameron *et al.*, 2011; Ollerton *et al.*, 2014; Zattara and Aizen 2021). In fact, according to the International Union for Conservation of Nature and Natural Resources, for which geographic range and population size are two of the criteria used for assessing conservation status, around 9% of the

wild bee species in Europe could be declared as threatened, a percentage potentially underestimated given the high data deficiency for over half of the European bee species (Nieto et al., 2014b; Potts et al., 2016). This is especially worrisome given that wild bees, through pollination, play a critical role in the maintenance and functioning of both natural and agricultural ecosystems (Garibaldi et al., 2014; Klein et al., 2007; Ollerton et al., 2011). This crucial role in maintaining pollination services therefore provides strong arguments for promoting their conservation (Winfree et al., 2018) in addition to the argument of their intrinsic value of biodiversity.

As a result, there is an urgent need to *i*) better identify population trends at local or national scales, as well as their environmental drivers and *ii*) develop agricultural practices that are as supportive as possible for bee populations. The evaluation of wild bee population status and trends generally relies on species records, giving an estimate of species abundance, distribution and richness (Winfree *et al.*, 2009; Zattara and Aizen 2021). Combined with statistical modeling, such data can help in identifying drivers of bee decline. However, standardized (i.e. not opportunistic recordings by volunteers) and long-term surveys of pollinator occurrence are needed to reliably identify pollinator trends and therefore determine the impact of environmental changes (Breeze et al., 2020; Garibaldi et al., 2020). Interestingly, a 10-year monitoring scheme was identified as the most suitable by bee experts for detecting long-term trends in bee populations, with longer periods for assessing the influence of climate change (30 years) or landscape complexity (15 years) (Breeze et al., 2020). Nevertheless, from an ecological point of view, conservation action should start before a species is endangered, i.e. before its population size declines to critical levels (Soulé, 1987). Such proactive conservation approaches, besides being more successful, are also more cost effective than reactive strategies (Drechsler et al., 2011). Therefore, alternative methods that are more time- and cost-effective would highly benefit the conservation of wild bee populations.

In this context, conservation biologists need biological metrics that are sensitive to environmental changes and/or suitable as early warning signals of bee population declines (i.e. before they become local or regional extinctions). For that purpose, physiology offers a promising framework to link bee responses to environmental alteration with population-level responses. First, physiology is highly sensitive and often changes quickly to allow the organism to respond to environmental disturbance. Second, physiological changes can be linked to life-history traits tightly associated with population dynamics and sustainability, such as reproductive performance and survival (Chown *et al.*, 2002; Cooke *et al.*, 2014). Accordingly, physiological changes generally occur well in advance of demographic changes and before a potential population decline (Ellis et al., 2012), and therefore, can help in characterizing population dynamics and its environmental constraints (Chown, 2012).

Physiological knowledge and tools, spanning a broad range of disciplines, such as endocrinology, immunology, neurophysiology, toxicology, bioenergetics, and reproductive physiology, have been used for many years in solving conservation issues (Cooke et al., 2013). This approach integrating physiology into the challenges of conservation has contributed to several successful stories, especially

in vertebrates (Madliger et al., 2016), attesting to its high potential and interest for delivering practical guidelines in conservation (K Birnie-Gauvin et al., 2017). Due to its potential for identifying drivers of population decline, monitoring population status, and assessing the efficiency of remedial actions, we believe this approach could also benefit the field of wild bee conservation. We outline several examples of the power of physiological metrics for better understanding the influence of anthropogenic stressors and developing conservation strategies. We then highlight the key challenges that will need to be addressed for monitoring and predicting population-level changes using physiological measurements in wild bees.

## **1. Physiology provides a better understanding of the impact and consequences of anthropogenic pressures on bees**

All bees (social and solitary) have the particularity to be central-place foragers. Once adult, bees establish a nest and forage for pollen and nectar around that nest for their entire life. Contrary to animals that move from place to place for collecting resources, the foraging distance of bees is limited to a specific range around the nest, which is generally related to their body size (Greenleaf et al., 2007). This has strong implications for their populations, since bee survival and fitness will be determined by the habitat quality in a specific range around their nest (e.g. floral resource availability, pollution...), which makes them particularly sensitive to changes in these habitats. It is therefore crucial to better understand how anthropogenic pressures leading to changes in habitat quality affect bees, before developing management strategies to minimize or reverse current population trends of species of concern. In this regard, physiological markers measured in response to environmental stressors or habitat quality can reveal mechanisms that contribute to population decline and thereby provide a cause-and-effect relationship between environmental characteristics and bee survival (Tracy et al., 2006). Here we offer examples of the importance of physiology for better evaluating the risks posed by anthropogenic pressures in bees. We focus on the main threats that may act at large scales and affect most of bee taxa, such as environmental chemicals, decline of floral resources and climate change.

### **a) Environmental chemicals**

Landscapes have been largely transformed by agronomic practices and one of the most striking consequences is the widespread use of agrochemicals, which have permeated the biosphere causing exposure to many non-target organisms. To investigate the potential effects of such exposure on non-target organisms, ecotoxicology has emerged as a leading discipline and is perhaps the oldest discipline linking physiology to questions of conservation (Stevenson et al., 2005). The most popular

and precursory example is undoubtedly the discovery of the inhibition, by the chemical dichlorodiphenyltrichloroethane (DDT), of calcium carbonate deposition in eggshells of birds of prey, leading to their reproductive failure (Grier, 1982). Bees are also exposed to pesticides as multiple residues can be found in pollen and nectar of crops and wild flowers (Botías et al., 2015; Rundlöf et al., 2015). To analyse the consequences of bee exposure to pesticides, ecotoxicological studies have traditionally assessed the lethal effects. However, more recently, a large body of evidence has shown that this approach underestimates the risks related to low environmental doses and current research methods generally integrate sublethal effects into toxicological studies (Brandt et al., 2020; Lehmann and Camp, 2021; Sandrock et al., 2014; Sgolastra et al., 2018; Strobl et al., 2021).

Sublethal exposure to environmental chemicals can be investigated by the use of biomarkers of effects, which are defined as any measurable biochemical, physiological or genetic variation that provides evidence of exposure to and/or effects of one or more environmental pollutants (Mouneyrac and Amiard-Triquet, 2013). Such biomarkers enable one to determine whether and what type of exposure took place, and have proven to be promising tools for evaluating ecotoxicological health status and monitoring environmental quality of honeybees (*Apis mellifera*) (Badiou-Bénéteau et al., 2012; Caliani et al., 2021). Applying this biomarker approach to *Osmia* and *Bombus*, which have been recently proposed as additional test surrogates to honeybees (European Food Safety Authority, 2013), but also to other bee genera, would greatly improve the evaluation of past and present exposure to anthropic contamination and determine habitat quality for wild bee populations. This was confirmed by a study, which found an increase in acetylcholinesterase expression in bumblebees (*Bombus impatiens*) foraging in agricultural areas using neonicotinoid crop protection (Samson-Robert et al., 2015). More recently, another study identified genes differentially expressed between *Bombus terreicola* worker bees sampled in agricultural and non-agricultural sites (Tsvetkov et al., 2021). These differentially expressed genes significantly overlap with those found in honeybees exposed to insecticides, suggesting an exposure of *Bombus terreicola* to insecticides in the studied sites. Changes in the expression of several genes upon exposure to neonicotinoids have also been identified in *Osmia bicornis* (Beadle et al., 2019), which could potentially provide biomarkers of field exposure to pesticides for this solitary bee species. An alternative and more specific approach is the multi-biomarker approach that is widely used in various aquatic and terrestrial organisms to detect and evaluate the effects of exposure to chemical contaminants. By testing and analyzing variations of several biomarkers (often enzymatic activities) upon exposure to a chemical in the laboratory or in the field, it is then possible to calculate a simple “Integrated Biological Response” that is specific to the chemical and its concentration (Beliaeff and Burgeot, 2002). This has notably been developed successfully in honeybees for discriminating exposure to different concentrations of Cadmium and the fungicide Amistar® Xtra (Caliani et al., 2021).

Another key aspect of pesticide risk assessment is to determine whether such exposure leads to irreversible modifications of bee physiology that might translate into damage to bee populations. A

consistent decline in the production of new queens by colonies of *Bombus terrestris* has been reported upon exposure to neonicotinoids (Whitehorn et al., 2012). Whether this lowered reproduction is due to reduced pollen foraging (Feltham et al., 2014), to direct pesticide effects on queen physiological development or to both is not known, but, in any case, it could have severe consequences for bumblebee populations. Physiological impairments, such as immunosuppression and reduced thoracic temperatures in *Osmia bicornis* and alteration of mitochondrial functions in *Bombus terrestris*, have also been identified in response to pesticide exposure (Azpiazu et al., 2019; Brandt et al., 2020; Colgan et al., 2019). However, perhaps the most striking effects are the decrease in ovary development, male fertility, and total offspring production, as well as a male-biased sex ratio, and higher mortality of eggs and larvae (Franke et al., 2020; Minnameyer et al., 2021; Sandrock et al., 2014; Sgolastra et al., 2018; Strobl et al., 2021). These latter effects clearly suggest mechanisms that explain the observed decline of solitary bee populations in conventional agroecosystems (using pesticides) (Rundlöf et al., 2015). Finally, it was recently found in bumblebees and fig wasps that high ozone concentrations can decrease the antennal sensitivity, and consequently, the attraction to floral volatile organic compounds (Vanderplanck et al., 2021a). This physiological impairment might directly affect plant-pollinator chemical communication, and consequently bee survival. All of these examples clearly illustrate the interest of studying physiologically related endpoints for the risk assessment of environmental chemicals in wild bees.

#### b) Landscape resources

All bees have in common a reliance on floral pollen and nectar for their growth and survival. Nectar contains carbohydrates fuelling their energetic demands, and pollen provides all of the proteins, amino acids, lipids, sterols and vitamins required for their ovary development and larval diets (Leach and Drummond, 2018; Roulston and Cane, 2000). However, a decrease in the diversity and abundance of floral resources in agricultural landscapes may generate a nutritional stress for bees (Goulson et al., 2015; Vaudo et al., 2015), especially for wild bees, who are generally more selective for pollen nutrition than honeybees, who collect pollen from a wide spectrum of plant species (polylecty) (Danner et al., 2017; Galimberti et al., 2014). For instance, bumblebees seem to favour pollen quality over quantity (Leonhardt and Blüthgen, 2012), while some solitary bees have a rather specialised pollen diet by collecting pollen from a limited number of plant species (oligolecty) (Cane and Sipes, 2006; Müller, 1996; Müller and Kuhlmann, 2008).

By investigating the influence of pollen diet abundance, quality and diversity on bee physiology, several experimental studies have attempted to identify what might represent a nutritional stress for bees. It is now well-established that the protein and lipid contents of pollens have a significant impact on bumblebee immunity, development and survival (Roger et al., 2017; Vanderplanck et al., 2014). If pollen diversity might not provide an added value *per se* (as compared to higher quality monofloral pollens), it might help to mitigate the negative effect of unfavourable pollens (Carnell et al., 2020;

Moerman et al., 2017). The benefits of pollen mixing was notably demonstrated by Eckhardt et al. in the pollen-generalist solitary bee *Osmia cornuta* (Eckhardt et al., 2014). Pure *Ranunculus* pollen had a negative effect on larval development and survival and adult body mass of both males and females, but when not predominant (less than 50% of the pollen diet), bees remained unaffected. In addition, decreased access to resources has been shown to reduce reproductive performance of solitary bees and bumblebees (Cane, 2016; Centrella et al., 2020; Peterson and Roitberg, 2006; Requier et al., 2020). Such data might explain the lower bee abundance and diversity observed in agricultural systems embedded in simple landscapes or with low levels of semi-natural habitats (Kennedy et al., 2013; Lichtenberg et al., 2017).

Finally, bee body traits (e.g. body mass and size) and nutritional health indicators (e.g. lipid content) may be useful for predicting the vulnerability of species, or at least an actual response, to changes in landscape-level floral resources. For instance, by measuring the mass, size and lipid content of several bumblebee and sweat bee species sampled in the field, Smith *et al.* (2016) and Stein *et al.* (2020) could identify which species were affected by which grassland management practices in agricultural landscapes. Body size, which is strongly affected by pollen nutrition during larval development, has also been used as a proxy for assessing the response or sensitivity of wild bees to resource availability along landscape gradients. Results vary across bee species, diet breadth and landscape types, making it difficult to draw general conclusions on a local scale (Banaszak-Cibicka et al., 2018; Reeth et al., 2018; Renauld et al., 2016). However, two meta-analyses, performed on museum samples from the northeastern United States and the Netherlands, found that a large body size is among the traits that are negatively related to population trends (Bartomeus et al., 2013; Scheper et al., 2014), which is probably due to the greater pollen needs of larger bee species combined with food limitation. Altogether these experimental and survey data highlight nutritional stress as a driver of bee decline, and identify, for some species, which specific diets might be unfavorable.

### c) Climate Change

Since bees, as insects, have limited ability to regulate their body temperature, their physiology, behaviour and survival are largely constrained by environmental temperatures. Determining and predicting the consequences of climate change on bees therefore has become a growing research topic. To quantify the sensitivity of bees to temperature, several studies have measured the consequences of artificial or environmental variations in temperature on physiological traits. For instance, changes in the queen body size of different bumblebee species have been linked to an increase in the mean annual minimum temperature (Gérard et al., 2020a). However, a large body of literature has focused on the effect of temperature on completion of the winter diapause, likely because insects generally rely on low temperatures to reduce their metabolism and preserve their energy storage until the next spring (Brown et al., 2004; C. M. Williams et al., 2015). Climate change is therefore expected to increase energy expenditure during the diapause, which can lead to vulnerable bees in the spring. Although

bee species differ in their responses (Fründ et al., 2013), this hypothesis has been verified many times, with natural or artificial pre-winter and winter conditions causing a shorter diapause duration and a decrease in fat body, body weight and consequently winter survival (Bosch and Kemp, 2004; CaraDonna et al., 2018; Sgolastra et al., 2011). Characterizing the baseline of overwintering gene expression, as it was done for the small carpenter bee *Ceratina calcarata*, could also help to better understand adaptations to overwintering and molecular responses to climate change (Durant et al., 2016).

Variations in summer temperatures have been investigated as well and have been shown to affect voltinism in a solitary bee (*Osmia iridis*) (Forrest et al., 2019). Under controlled conditions, increased temperatures were found to decrease prepupal weight and the duration of all development phases in *Osmia bicornis* (Radmacher and Strohm, 2011), and reduce wing size in *Bombus terrestris* (Gerard et al., 2018). Heat shock stress also has a negative impact on bumblebee reproduction by impairing sperm viability, sperm DNA integrity and the production of pheromones involved in male attractiveness, but interestingly, this was observed only in the tested declining species (not in the widespread and warm-adapted species) (Martinet et al., 2021b). Similarly, a study showed that two invasive bee species in Fiji tend to be more resistant to thermal and desiccation stress than an endemic species, which might contribute to a higher resilience to climate change (da Silva et al., 2021). Warming summers can also lead to changes in bee morphology as evidenced by the decrease in tongue length of two alpine bumblebee species within 40 years (Miller-Struttman et al., 2015). Interestingly, a decrease in the abundance of long-tongued bumblebees and an immigration of short-tongued species from lower altitudes have been reported during the same period (Miller-Struttman et al., 2015). While the underlying mechanisms are not clear, it shows some phenotypic plasticity in response to climate (De Keyzer et al., 2016). Last but not least, data on the thermal physiology can be extremely useful for understanding and/or predicting how different species might respond to climate stress. This was the case with the identification of bumblebee critical thermal limits, which correspond to the temperatures at which an organism may encounter failure or loss of essential functions (e.g. motor and respiratory). Measurements of thermal tolerance helped to explain population declines and range shifts in relation to climate change (Martinet et al., 2021b; Oyen et al., 2016; Zambra et al., 2020), as well as local adaptation in bumblebees (Pimsler et al., 2020). In sum, documenting variations of physiological and body traits in response to temperature changes proves to be extremely valuable for better understanding the temporal and spatial shifts in bee distribution.

## **2. Physiology can help in designing conservation practices**

To mitigate or combat habitat loss and therefore the decline of wild bee populations, conservation efforts have been focusing on the provision of consistent foraging and nesting resources in human-dominated areas. Large-scale actions have been developed for that purpose. In Europe, the European Agri-Environmental Schemes promote environmentally friendly practices in farmlands (e.g.

implementation of flower strips and hedgerows in field margins, restoration of pastures and meadows, or organic farming) (Scheper et al., 2013). In the United States, the Conservation Reserve Program supports the conversion of croplands into long-term conservation habitats with a recent priority given to the promotion of forage for pollinators (Osteen et al., 2012).

To further improve such conservation practices, high-resolution data are needed on the nutritional needs of bee species. Studies first attempted to identify the minimum ‘pollen budget’ for maintaining a self-reproducing population (Larsson and Franzén, 2007; Müller et al., 2006). However, most of the research efforts are now focusing on the determination of foraging preferences and diets that are most appropriate for bees. Among others, preferred pollen protein:lipid macronutrient ratios have been identified in *Bombus impatiens* and linked to bumblebee colony health and fitness (Vaudo et al., 2016). Some of the minimum nutrient requirements for bee development have been described as well for several species (Barraud et al., 2022; Moerman et al., 2016; Vanderplanck et al., 2014) and nutritional physiology has shed light on stage-specific nutritional limitations in the bee life cycle (S. Hollis Woodard et al., 2019). Physiological markers can also provide helpful information on the interface between bee populations and their resources. For instance, by characterizing the elemental composition of bees (female, male, adult, larva) and their resources, ecological stoichiometry allows one to determine whether there is a mismatch between the elemental demands of bees and floral resources, potentially leading to an imbalanced diet (Filipiak, 2018). By using this approach, Filipiak et al. reported some stoichiometric mismatches between larvae of *Osmia bicornis* and particular pollen species and identified specific elements related to bee fitness (Filipiak, 2019; Filipiak et al., 2021; Filipiak and Filipiak, 2020). Assessing bee nutritional requirements is therefore also a promising field of research for tailoring conservation measures to bee communities. In summary, by studying the bee–nutrient–floral networks, we can identify the preferred floral species as well as the nutrients or nutrient ratios important for specific bees and the plant species providing them. Such information can then be used to adjust floral enhancement schemes or support the conservation of key plant species for bees (*i.e.* preferred floral species or with high nutritive values for bees) (Parreño et al., 2022b; Woodard, 2017).

Besides the identification of nutritional needs, assessing the efficiency of habitats designed for promoting the sustainability of bee populations is also essential. Most of the research has focused on the attractiveness of these habitats by quantifying the potential positive effects on bee abundance and species richness (Scheper et al., 2013). However, the creation of floral hot spots highly attractive to a broad range of bee species might have negative side effects on bee health. Indeed, in landscapes with low amounts of semi-natural habitats, wildflower fields seeded to boost bee populations in field margins might create hot spots for parasite transmission (Piot et al., 2019). In addition, such wildflowers can get contaminated with pesticides (under non-organic farming practices) and thus prolong exposure to pesticides beyond the treated crop flowering (Botías et al., 2015). Therefore, in addition to attractiveness data, physiological metrics of bee health may be used as complementary

criteria to evaluate the efficiency of habitats designed to be pollinator-friendly and develop Habitat Suitability Indices (HSI) to be used as operational decision support by conservationists and land-managers. HSIs are widely used tools in applied conservation (Larson et al., 2004). However, physiological factors are seldom implemented into HSI algorithms, which yet is critical regarding physiological constraints faced by central place foragers (Chudzinska et al., 2021). As a prerequisite, one should objectivate the links between environment and physiology in the taxonomic group of interest. In this context, physiological measures have been successfully used in honeybees to demonstrate the beneficial effects of floral landscape enrichments and uncultivated forage (e.g. pasture, grasslands, woody areas and hedgerows...) on bee health (Alaux et al., 2017; Dolezal et al., 2019; Smart et al., 2016). A few studies have shown that several markers of nutritional state in bumblebees could be promising for monitoring bee health and assessing habitat quality (Smith et al., 2016; Wang et al., 2019). However, further field studies with wild bees are required to provide a proof-of-concept of this ecophysiological approach for evaluating how well remedial actions are working.

### **3. Physiology for predicting population-level changes**

The measure of physiological traits is highly valuable in the identification of the sources and consequences of stressors on bees, which inform conservation actions. However, field monitoring, which consists of tracking the population status of species of concern, also plays a key role in conservation strategies (Nichols and Williams, 2006). The quantitative information that originates from monitoring programs can guide decision-making for environmental management and rehabilitation, and then help to evaluate the success of management actions. The only concern is that conventional monitoring (e.g. estimating population size) “is by its very nature *post hoc* — that is, it can only tell us what has already happened” (Keddy, 1991). Predicting and anticipating future population changes or sustainability would represent a more powerful approach to conservation. In this context, early indicators of individual fitness, such as physiological traits, have the potential to predict organismal responses to environmental changes, and therefore anticipate changes or stability in wild bee populations. However, several challenges first need to be addressed for incorporating physiological biomarkers into conservation monitoring actions.

### **4. Linking variations in physiology to changes in population dynamics**

Biomarkers or signatures of stress might not always be indicative of declining populations, in particular when physiological changes have little effects on the organism (e.g. sublethal effects), or compensatory mechanisms allow the organism to ultimately survive and reproduce or tolerate changing environments (Van Dievel et al., 2016). Furthermore, upon exposure to high levels of stress, the population may be able to persist by relying on the most physically fit or healthiest individuals (Fefferman and Romero, 2013). Therefore, to determine whether a physiological biomarker can be used as a monitoring tool for the management of wild bee populations, the most suitable approach

would be to confirm that such a biomarker can be linked to proxies of individual fitness or demographic changes (Bergman et al., 2019).

First, studies that simultaneously connect environmental, physiological and population metrics should be carried out. Several biomarkers, such as bee body conditions based on morphometric variables (e.g. weight, body size, body parts size), could be used since they are affected by both genetic and environmental factors that have operated through physiological mechanisms during larval development (Nijhout, 2003). These body variables are easy to acquire and potentially non-lethal and have been found to be related to population trends (Bartomeus et al., 2013; Scheper et al., 2014). However, in several cases they might be less informative about the type of stressor (Gerard et al., 2018). Alternatively, the assessment of biochemical and genomic markers require sacrificing several specimens but are expected to provide more specific information on the stressor and its severity (Badiou-Bénéteau et al., 2013; Kent et al., 2018; Wang et al., 2019; Woodard et al., 2015). However, the lack of multidisciplinary expertise in longitudinal surveys of wild bee populations might have prevented so far the realization of studies linking eco-physiological data with population-level metrics for wild bees, as seen for honeybees (Alaux et al., 2017; Smart et al., 2016). Nonetheless, this could be overcome by sampling bees in monitoring surveys and integrating candidate biomarkers (e.g. bee size, weight or nutritional health indicators) into datasets of bee population demography (e.g. abundance, growth rate). Identifying individual physiological biomarkers that correlate to population trends may then help to evaluate species resilience and responses to environmental changes.

Secondly, studies could also determine whether physiological biomarkers that were already found to be affected by environmental variables are also related to some component of individual fitness (survival, reproductive performances). For instance, body size in bees, which is highly correlated to the amount of food ingested (during larval stage) and therefore to the abundance of floral resources, has been found to be positively related to female fecundity in different bee species (Bosch and Vicens, 2006a; O'Neill et al., 2014; Slominski and Burkle, 2021). These relationships highlight body size as a promising biomarker for monitoring population trends. However, further research is needed given that the relationship between body size and female fecundity is not consistent across studies and may depend on species and/or local environmental contexts (Bosch and Vicens, 2006a).

Thirdly, comparing baseline levels of physiological biomarkers in both a decreasing and an increasing or stable population could help in determining whether a biomarker could be used to measure demographic changes (Bergman et al., 2019). For instance, data about heat stress sensitivity have been especially convincing for explaining population trends and restricted habitat types in bumblebees. By measuring the physiological thermal limit of individual bees, a direct link between the thermotolerance of bumblebee species and their distribution area was found (Martinet et al., 2021a, 2015; Oyen et al., 2016) and widespread species proved to be less sensitive to heat stress than declining species (Martinet et al., 2021b; Zambra et al., 2020). Similarly, physiological thermal limits were found to be a strong predictor of bee population response to heat in urban areas, with those bees

having the lowest critical thermal maximum showing the most population decline with warming (Hamblin *et al.*, 2017). Altogether, these studies showed that species' physiology could shape community composition, and therefore help in predicting their future trends under changing environmental conditions.

### **5. Including physiological performances into ecological niche modelling**

Ecological niche modeling has become an important tool for inferring species distribution and habitat suitability. By linking the observed distribution of a species to environmental data, the correlative ecological niche models have the advantage of requiring little information on the mechanistic links between the organism and its environment, and are therefore especially useful for species that are poorly studied. For instance, ecological niche modeling allowed for the prediction of overall range losses under climate change for 30 North American bumblebee species, even for species with high dispersal abilities (Sirois-Delisle and Kerr, 2018). However, such models are constrained by the availability of detailed data on species distribution, and when extrapolating species distribution to future environmental conditions (not yet experienced by species), mechanistic ecological niche models that are parametrized with physiological data are expected to be more robust (Evans *et al.*, 2015; Kearney and Porter, 2009). Notably, the inclusion of information on physiological limits of major life history characteristics (e.g. survival, growth, and reproduction) can help to make inferences on species' range limits and to understand the environmental characteristics defining the species range. This mechanistic modelling was elegantly used as a tool for the ecosystem restoration of four insect pollinators at a local scale in Australia (Tomlinson *et al.*, 2018a). By projecting data of metabolic rates and thermotolerance of these pollinator species onto high-resolution topoclimatic models, the authors showed the importance of mechanistic models fitted with physiological data in providing evidence-based guidance for ecological management programs. Finally, individual- or agent-based models, by simulating the fate of individuals with respect to their behavioral and/or physiological traits, might represent an alternative to better predict population and community changes. They can incorporate any number of individual-level mechanisms and take into account their changes through time (DeAngelis and Grimm, 2014; Grimm and Railsback, 2005). Agent-based models have notably been used for exploring potential benefits of bee-friendly farming measures on the population dynamics of six bumblebee species (Becher *et al.*, 2018). However, using such these modeling approaches to predict the resilience and trends of bee populations in changing habitats implies that physiological limits of species of concern are readily available. Therefore, these knowledge gaps need to be addressed in the future to strengthen the implementation of mechanistic models. For instance, data on thermal limits and energy balance would be particularly helpful to better anticipate the persistence of population under climate and resource changes.

## 6. Surrogate species for community-based monitoring

With over 20,000 known bee species in the world, it appears virtually impossible to develop a species-by-species monitoring approach for the prediction of population trends. This is also the case for the monitoring of bee communities in specific habitats, in particular within the goal here to use early indicators (physiological markers) of population dynamics. Measuring physiological traits of all species within a community can quickly become expensive and time consuming, and it might not always be possible to sample all species or a sufficient number of specimens per species for assessing population trends. In addition, the ecology and biology of most of wild bee species are still poorly understood. Therefore, one solution to fill these gaps would be to focus on some species that can be easily monitored and for which we could standardize relevant physiological traits measurement in order to inform on the community's status and thus apply them in conservation contexts.

For that purpose, conservation biologists have showed a growing interest in the identification of surrogate species indicative of the state of species communities or ecosystems (Fleishman et al., 2005, 2000). Surrogate species notably include indicator and umbrella species (Caro and Girling, 2010); the latter focusing on species that have large area requirements and for which conservation offers protection to species that co-occur in the same habitat (Wilcox, 1984). However, empirical tests of umbrella species validity have provided equivocal results, in part due to the focus on a large home range, which might hinder their applicability (Branton and Richardson, 2011; Ozaki et al., 2006a). Consequently, the concept of local umbrella species, that occupy a more spatially limited area, has been introduced by (Caro and Girling, 2010). In addition, the efficacy of putative umbrella species may depend on the co-occurring taxonomic diversity that is targeted, since umbrella species are likely more indicative of elevated biodiversity within their own taxonomic groups than across taxa (Sattler et al., 2014). Because here, the goal is to monitor and predict community changes of wild bees that inhabit relatively limited areas, efforts should rather be made on the identification of local umbrella species specifically indicative of their own community. A first attempt has been made in urban areas of the Central Swiss Plateau and lowland areas of southern Switzerland by analyzing 139 bee species (Sattler et al., 2014). By using several functional traits, such as dietary specialization (oligolectic and polylectic) and nesting habits (miner-carder, renter, carpenter, mason), they were able to identify 6 umbrella species (*Andrena bicolor*, *Heriades truncorum*, *Hylaeus nigritus*, *Hylaeus sinuatus*, *Lasioglossum calceatum*, *Psithyrus barbutellus*), which were indicative of bee functional biodiversity (i.e., dietary specialization, nesting habits).

An alternative or complementary approach is to target a species or a group of species whose status (abundance, population dynamics) rather reflects the environmental conditions (Carignan and Villard, 2002). The selection of such species, named indicator species, is more focused on their ecology and life history traits, and as such, they can be used as a proxy to determine the health of an ecosystem and provide early warning signals about environmental changes. Interestingly, within the aim of better supporting conservation strategies for bumblebee species in China, a recent study

identified, among the 125 studied species, 26 species as indicator species of the different biogeographic regions: 14, 13, 12 and 12 species were associated with the regions of South China, North China, the Mongolian Plateau and the Tibetan Plateau, respectively (Naeem et al., 2020). Although no empirical test was performed, these first studies suggest that some bee species could potentially be assimilated as surrogate species to monitor bee communities and/or environmental conditions in their respective biogeographic ranges.

Detailed studies of physiological health indicators on surrogate species (see *Linking variations in physiology to changes in population dynamics*) should then provide valuable information on the conditions of the environment where they are found, and consequently, for other co-occurring bee species or larger bee communities. Notably, building standard biomarkers values for these reference populations should help identifying poor or declining environmental conditions (when biomarkers deviate from the baseline or average values), especially if these biomarkers can be linked to proxies of individual fitness or demographic changes. Such species could therefore facilitate monitoring programs (a single or a few species to monitor), especially within the objective to perform proactive conservation with early indicators of species community changes.

## **7. Dealing with time effects**

In some cases, adverse environmental conditions can affect the survival or fitness of the studied organism in a subsequent season (Harrison et al., 2011). If not taken into account, these carry-over effects can lead to erroneous conclusions about the effectiveness of conservation efforts (O'Connor and Cooke, 2015). Such carry-over effects have been described in honeybees, with an increase of winter mortality risks in colonies that have experienced a pollen shortage the previous season (Requier et al., 2017). But they have also been documented in wild bees. By exposing, adult bees of *Osmia lignaria* to the neonicotinoid insecticide imidacloprid, researchers demonstrated a reduction of the offspring fitness (reproduction) the following season due to maternal and/or larval effects (Stuligross and Williams, 2021). Carry-over effects can also be observed at the level of bee communities' since their abundance is typically influenced by the floral resource availability of the previous year's (Le Féon et al., 2013; Potts et al., 2003). This phenomenon is due to the specific life cycle of most wild bees: females generally emerge in the spring, mate, and then provision their nests with pollen to feed their larvae, which develop into adults in the autumn and emerge the next spring. As a result, the number of offsprings, as well as some of their morphological and physiological traits, may be affected by the environmental conditions of the previous year. For instance, their body size should reflect the amount and quality of pollen resources ingested as a larva the previous spring/summer (Chole et al., 2019). Similarly, diet quality may affect resource assimilation and allocation during larval development and consecutively some of the physiological processes essential to bee fitness (Filipiak et al., 2021). The specificity of bee species life cycle needs therefore to be taken into account to deal with such carry-over effects and better interpret the influence of environmental factors on bee health.

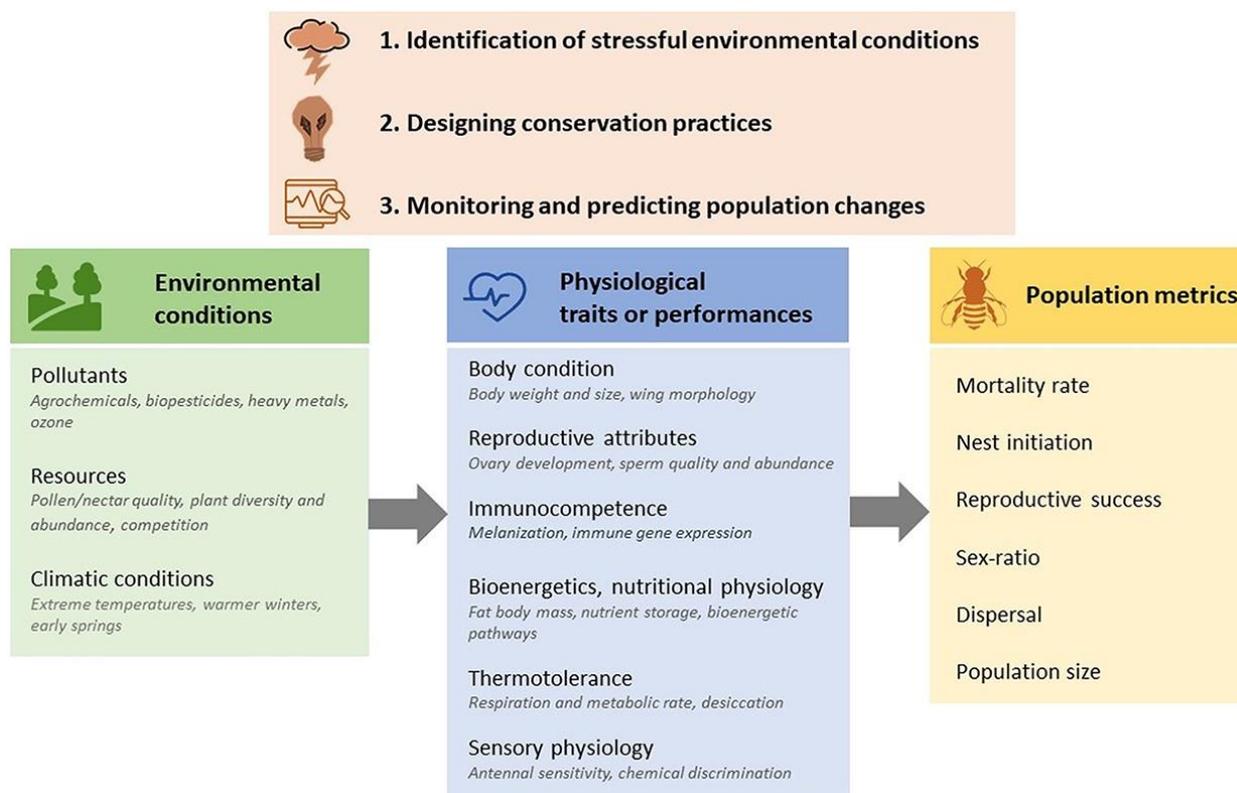
Finally, physiological traits can vary in their response time to environmental changes, with some markers being more sensitive or responsive over shorter timescales than others (within minutes) (Bergman et al., 2019). But also, the level of some physiological traits can naturally vary over time during the organism development or maturation. For instance, ovary development and the level of vitellogenin, the precursor of major yolk proteins in insects, gradually increases after the emergence in the mason bee *Osmia cornifrons* to reach a peak at 6 days and then decline (Lee et al., 2015). Physiological markers could therefore induce some biases in the way they reflect environmental conditions if time changes are not taken into account. For such typical traits, a specific and consistent monitoring should be performed, rather than a single or random sampling over time, so as to acquire thorough time series databases.

## Conclusions

Understanding and undertaking a comprehensive mitigation of the impact of anthropogenic pressures on wild bee populations is currently a demanding research challenge due to the large gaps in evaluating bee sensitivity to environmental changes (López-Urbe et al., 2020), as well as in monitoring the status and trends of populations (Lebuhn et al., 2013). However, we showed here, through several examples, that physiological metrics can help solve several issues related to the conservation of wild bees (Figure 2. 1). Indeed, the measure of physiological traits or performances, by providing a cause-and-effect relationship between environmental characteristics and bee survival, can help in identifying stressful environmental conditions. The documentation of species' physiological needs and limits can also offer valuable information for identifying and testing the efficiency of remedial actions. Equally important are physiological metrics that can be used as early indicators of population decline. Incorporating such physiological metrics into monitoring programs is still uncommon but promising for developing a more proactive approach to conservation (Madliger et al., 2018). Future efforts should however be made in the identification of physiological metrics for assessing bee population status or dynamics. To reach this goal, the identification of generalized stress biomarkers in insects would be extremely useful. For instance, glucocorticoids have been largely used in vertebrates, through noninvasive sampling (e.g. faeces, feathers, saliva), as a general stress indicator to better understand the impact of environmental variables (Fairhurst et al., 2011; Reeder and Kramer, 2005; Romano et al., 2010). If such an analog does not seem to exist in insects, several elements of a general stress response have been studied in honeybees (e.g. biogenic amines, pathways of the energetic metabolism, heat shock proteins, vitellogenin) (Bordier et al., 2017; Even et al., 2012). Whether they could be transposed to other bee species remains to be investigated. However, this should be a reasonable target since moving physiological methodologies from model species (e.g. honeybees, bumblebees) to non-model species, and including physiological markers in monitoring programs, are becoming increasingly feasible (Vanderplanck et al., 2021b).

In sum, the integration of physiological data into species distribution and abundance data has the potential to provide decidedly complementary points of view on how bees deal with environmental

constraints and how their populations change. To achieve this goal, a clear reinforcement of multidisciplinary approaches (e.g. spatial and landscape ecology, physiology, taxonomy), combined with training, sharing of protocols and methods, as well as the development of standardized measures for physiological health of bees would be needed in future bee conservation studies. Therefore, in the short-term, assessing physiology might be more complex, expensive, and time consuming than surveying species in the field. However, such an approach, especially with the identification of surrogate species, should lead to early indicators of bee population sensitivity to (positive or negative) environmental changes. Therefore, in the long-term, we hope the benefits will outweigh the costs, especially given that proactive conservation methods (i.e. acting before population size declines to critical levels) are considered more successful and cost effective than reactive strategies (Drechsler et al., 2011).



*Figure 2. 1: Physiological metrics in the conservation of wild bees. By linking environmental conditions to population responses, the measurement of bee physiological traits or performances can help in identifying stressful environmental conditions, and therefore in predicting population trends. Information on physiological needs can also guide conservation strategies. Main and sublists are inexhaustive examples of parameters that have been investigated in conservation-based research of wild bees.*

## Data availability

No new data were generated or analyzed in support of this article.

## Conflicts of interest

The authors declare that they have no conflicts of interest with this manuscript.

## Funding

This work was supported by the 2018-2019 BiodivERsA joint call for research proposals, under the BiodivERsA3 ERA-Net COFUND programme, and with the funding organisation Agence Nationale de la Recherche in France [ANR-19-EBI3-0003].

Chapitre 3



# Quality rather than quantity: Hedgerows and semi-natural habitats positively impact body condition and emergence rate in a solitary bee (*Osmia cornuta*)

Article en préparation, soumission prévue dans le journal *Journal of Economic Entomology*.

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## Préambule

Dans le chapitre précédent, nous avons exposé les grands principes et exemples d'application d'analyses physiologiques à la conservation d'espèces. Et ce, pour avoir une meilleure évaluation de la vitalité des individus et ainsi que la qualité des habitats dans lesquels ils évoluent. Cette approche, pourtant prometteuse, a rarement été appliquée pour étudier l'importance de la qualité des habitats pour les abeilles sauvages comme par exemple l'influence de la disponibilité en ressources florales sur la vitalité et la santé des abeilles.

C'est ce que nous avons entrepris afin d'évaluer l'influence de ressources complémentaires (habitats semi-naturels et haies) sur la condition corporelle d'une espèce d'abeilles (*Osmia cornuta*) en zone d'arboriculture du sud de la France. L'objectif étant double : (1) tester l'hypothèse de la complémentarité de vergers (pommiers et/ou poiriers) à floraisons massives sur le succès reproducteur des osmies et l'état corporel de leur progéniture et (2) évaluer le potentiel de l'approche de la PC pour évaluer la qualité des habitats (ici de la disponibilité des ressources) sur l'état de santé d'une espèce d'abeille.

Nous avons ainsi établi que la condition corporelle (masse corporelle et concentration en protéines) et le taux d'émergence de la descendance produite par les femelles nicheuses ont été significativement et positivement influencés par l'augmentation de la surface des SNH et la longueur des haies. Si la concentration en protéines de la descendance est une mesure assez sensible aux changements d'habitats, les teneurs en triglycérides et en glycogène sont apparues comme peu ou pas affectées par la composition du paysage.

Ces résultats témoignent du bénéfice de la complémentarité de vergers pour *Osmia cornuta* et la pertinence de l'approche de la PC.

## Abstract

Complementary habitats around mass flowering crops, like orchards, have proven to be effective in promoting bee community's diversity and abundance. However, it may not necessarily reflect an increase in bee populations but rather more attractive habitats. Complementary information on bee fitness-related traits is therefore needed to further evaluate their potential sustainability in such landscapes. To address this issue, we analyzed the influence of semi-natural habitats and hedgerows surrounding apple orchards on both the reproductive success of nesting females (number of cocoons) and the body condition (body weight and energy reserves in the form of protein, triglyceride and glycogen) of female offspring of *Osmia cornuta*, one of the most efficient pollinator of apple trees in Europe. If semi-natural habitats and hedgerows near orchards did not influence the reproductive success of nesting females; the emergence rate, weight and protein content of female offspring were improved along a gradient of these landscape elements. Triglyceride contents were not affected, but the amount of glycogen marginally increased with the area of orchards. Finally, the protein and lipid contents of pollen provisions were not modified by the landscape, but we observed changes in the

palynological composition with greater volumes of pollen from non-apple woody species, at the expense of apple pollen, along a gradient of semi-natural habitats. This caused a moderate increase in the diversity of foraged pollen. This study highlights the critical role of complementary habitats around mass flowering crops and shows that metrics of body condition can be useful to improve our understanding of pollinator responses to habitat quality.

**Keywords:** Mass flowering crops, nutrients, reproductive success, palynology, wild bees

## Introduction

The rapid human population growth has led to the expansion and simplification of agricultural surfaces at an unprecedented scale, and to the expanse of more complex and diversified natural and semi-natural habitats (SNH) (Tscharntke et al., 2005). As a consequence, a decrease in the diversity and abundance of floral resources is generally observed in intensive agricultural landscapes (Benton et al., 2003b), which might generate a nutritional stress for floral visitors, like bees (Goulson et al., 2015; Persson et al., 2015; Vaudo et al., 2015). The expansion and intensification of cropping systems are notably exemplified by the development of mass flowering crops (MFCs), which provide abundant and synchronized bloom events of a few weeks. By generating a pulse of resources (Westphal et al., 2003), MFCs can have positive effects on bee abundance and species richness (Diekötter et al., 2014; Holzschuh et al., 2013; Westphal et al., 2006). However, despite the abundance of resources, MFCs may narrow the nutritional landscape accessible to bees due to a poor floral diversity, and be of limited quality if the provided nectar or pollen do not meet the bee nutritional requirements (Tuerlings et al., 2022). In addition, the blooming period of MFCs might not entirely cover the foraging lifespan of bees. Altogether, the poor diversity and the temporary nature of MFCs indicate that bees need complementary floral resources from other habitats during, and pre- and post-MCF blooming periods (Martins et al., 2018). This can be achieved by the ecological intensification of agricultural systems, which consists in the diversification of crops surroundings and a greater continuity of forage resources for bees through the restoration or conservation of natural or semi-natural landscape elements, and/or the implementation of wildflower strips (Bommarco et al., 2013; Kovács-Hostyánszki et al., 2017). One possibility would be to complement a given habitat with an abundant resource type, like mass-flowering orchards, by the proximity of another type of habitat hosting a different resource spectrum so as to be optimal for an organism life cycle and traits. Such leverage point has sometimes been termed the *habitat complementation* hypothesis in the landscape ecology literature (Dunning et al., 1992). Habitat complementation has been evidenced in insects (Dulaurent et al., 2011; Ouin et al., 2004) considering foraging behaviour or demographic metrics. Habitat complementation appears poorly relevant in highly mobile species whose foraging range is much larger than average habitat patch size in the considered landscape. However, for species with foraging ranges (much) smaller than average field size in agricultural landscapes, the proximity of complementary foraging habitats may become critical for individual health and population sustainability.

There is actually compelling evidence that the conservation or restoration of complementary habitats in agricultural landscapes can be effective in promoting bee community's diversity (Cole et al., 2017; von Königslöw et al., 2022; Waser and Ollerton, 2006) and thus for increasing pollination services and crop yields (Albrecht et al., 2020; Pywell et al., 2015; Ratto et al., 2021). However, the observed increase in bee abundance and diversity may not necessarily reflect an increase in bee populations but rather more attractive habitats. Therefore, to ensure the sustainability and the long-term survival of bee species in agricultural landscapes, we need to gather complementary information on bee fitness-related traits, such as their survival, reproductive output and individual health (Crone et al., 2022; Leroy et al., 2023; Parreño et al., 2022a). This has been investigated in several studies, which showed that wildflower plantings and SNHs adjacent to crops can increase the reproductive performances of different bee species (Bihaly et al., 2021; Boyle et al., 2020; Ganser et al., 2021; Holzschuh et al., 2013; Williams and Kremen, 2007). Nevertheless, knowledge on the influence of complementary floral resources on bee fitness-related traits, notably bee health, in agricultural landscapes is still rather limited (Leach and Drummond, 2018).

To further explore this aspect, we focused on apple orchards and one of its most efficient pollinator in Europe, *Osmia cornuta* (Bosch, 1994; Pardo and Borges, 2020). Apples are the second most important fruit crop globally (FAO, 2009), accounting for almost 40% of the total area under fruit crops in Europe (Eurostat, 2019). Apple is a mass-blooming and pollinator-dependent crop, relying on insect to achieve high production and to ensure fruits quality (Delaplane and Mayer, 2000; Garratt et al., 2014). Although apple orchards may surpass natural habitats in the amount of food they provide (Morandin and Winston, 2005; Steele et al., 2022), they may also harbour a low nutritional diversity and limited foraging opportunities, especially pre- and post-blooming. This could explain why bee abundance or visitation rates are lower in apple orchards that do not have nearby natural habitats (Campbell et al., 2017; Joshi et al., 2016; Ratto et al., 2021). As a matter of fact, providing complementary resources in agricultural landscapes through wild flower strips was found to increase the reproductive success of *Osmia cornuta* (Ganser et al., 2021), which is rather polylectic and forages on a wide spectrum of flowering plants (Westrich, 1989). Similarly, *Osmia lignaria* females choose to mix pollens even when they have to travel longer flight distances to do so (N. M. Williams et al., 2015), and wildflower planting in almond orchards results in improved reproductive performances (Boyle et al., 2020). This strongly indicates that farming practices that favour the protection and/or restoration of complementary landscape elements in apple orchard could also benefit *Osmia cornuta*.

To address this question, we analyzed the influence of landscape elements surrounding apple orchards on both the reproductive success of *Osmia cornuta* and the body condition of female offspring (body mass and composition). The body condition of female offspring was notably used as a surrogate of future fitness-related traits (Stevenson and Woods, 2006; Wilder et al., 2016). For instance, in solitary bees, especially in females, body size is correlated with fitness: larger females tend to have a lower overwintering mortality, are more likely to found a nest, live longer, and exhibit a higher fecundity

(Bosch and Kemp, 2004; Bosch and Vicens, 2006b; Larsson, 1990; Tepedino and Torchio, 1989). For the body composition, we quantified the main categories of nutrients stored within insect bodies, i.e. proteins, glycogen and triglycerides. Such stored nutrients are essential for different life-history traits and life cycle stages of insects, including reproduction and survival (Arrese and Soulages, 2010; Hahn and Denlinger, 2011; Lease and Wolf, 2011). They also provide energy needed over extended period of resource scarcity. Since these nutrients are mainly acquired through consumption of pollen and nectar, variations in the availability floral resources likely affect the bee body composition and subsequently health. Under the hypothesis of habitat complementation, we expected that the proximity of semi-natural elements, close to mass-flowering orchards, would positively influence the reproductive success of nesting *Osmia cornuta* and the body condition of their offspring. We further explored the possible contribution of those different landscape elements on bee diets by analysing the plant taxa and nutritional values of foraged pollens.

## Material and methods

### 1. Study design

The study was conducted in 2021 in the Basse Vallée Durance (southeast of France), which is characterized by agricultural landscapes dominated by fruit orchards along with some vineyards, vegetables and cereal crops. Apple and pear orchards together actually represent 87% of all fruit production in the study area (Bouvier *et al.*, 2005).

We set up 18 pairs of artificial nests for cavity nesting bees (i.e. trap nests for *Osmia cornuta* here) in thirteen independent apple orchards under organic management and with diverse amounts of *SNH* and hedgerow coverages in the vicinity. In five orchards, which were large enough, we installed two pairs of artificial nests. All nesting sites were in field margins and at least 250 m apart from each other to limit the possibility of bee migration among artificial nests; the mean foraging ranges identified for *O. cornuta* being of  $106 \pm 107.5$  m (Hofmann *et al.*, 2020). We could meet the minimal threshold distance of 250 m for all but one trap nest, which was only about 200 m away from its nearest neighbour because of field access constraints. Each trap nest was placed in a wooden box fixed on a wooden pole above the ground (between 1.20 and 1.70 m) and the entrance was oriented southeast.

Cocoons of *O. cornuta* were obtained from a local supplier (L'Abeille Rousse) and originated from a single location in the northeast of France where specimens were collected from organic Mirabelle orchards. Before the start of the experiment, cocoons were placed and stored in the fridge at 4°C to complete their cycle. Ten days before the start of the study, cocoons were placed into an incubator with a dark and light cycle (12/12 h) and the temperature was progressively increased from 4°C to 17°C in order to match the emergence of bees with the estimated onset of apple tree blooming. At the end of March, 30 male and 21 female cocoons of *O. cornuta* were introduced in a cardboard emergence box fixed above each trap nest. This ratio (1:1.5 females:males) was used to optimise the chance of a successful mating for all females. In June, after the end of nesting activity, trap nests were brought to

the lab and stored at room temperature. From each pair of trap nest, one nest was used to measure the reproductive success of foundresses and the body conditions of offspring, and the second one to assess the pollen resources foraged by bees within the site (see below).

## **2. Environmental resources**

### **a) Landscape characteristics**

We characterized the land use composition around the trap nests within a radius of 250 m, which was considered to be the optimal focus scale that would virtually encompass all individual foraging ranges (see foraging range estimates above). We further characterized land use within a 500 m radius, with the underlying hypothesis that broader focus scales might be less relevant to assess effects of landscape patterns on the bee metrics. For that purpose, we used GIS layers extracted from the application BeeGIS developed by the Technical and Scientific Institute of Bees and Pollination – ITSAP, France (<https://appli.itsap.asso.fr/app/01-beegis>). The landcover surrounding trap nests was classified into the following classes of landscape elements and expressed in ha: orchards, SNHs (temporary and permanent grasslands, fallows and woody moorlands) and crops (sunflowers, cereals, corn silage, and vegetables), see Annexe 2. We did not distinguish flowering crops (e.g. sunflower) from other crops because their blooming was not concomitant with the study period. We additionally quantified the length of hedgerow as a linear feature of the landscape, which could provide additional resources to *O. cornuta*. Hedgerows corresponded to hedges with trees or groves extracted from non-agricultural surfaces of the French official parcel register RPG (Registre Parcellaire Graphique, Institut National de l'Information Géographique et Forestière).

### **b) Sampling and analysis of provisioned pollen**

To identify the foraged plants, the pollen provisioned by bees was extracted from a trap nest installed in each experimental site. Pollen provisioned at the end of the foraging activity was sampled from sealed brood cells before its full consumption by larvae (pollen was sampled from different cells and in sufficient amount from 15 nest traps). Pollen samples were thoroughly mixed, weighted and stored at -20 °C until palynological analysis, see Annexe 3. Pollen species identification was performed by following the procedure described in Requier (2015). Briefly, two subsamples of 4 g per pollen mix were analyzed. They were first diluted in water and stained with Fuschin before being examined under a light microscope at 400x magnification. Pollen grains were identified to genus and, when possible, to species. The identification process was duplicated and averaged for improving accuracy. The relative contribution of each pollen taxa (genus or species) to the total volume of pollen in a sample was determined based on pollen grain size. All proportions of pollen taxa above 1 % were considered as foraged by bees and were consequently included in subsequent analysis (<1 % considered as environmental contamination, and not included). We then assigned pollen taxa to one of three categories: herbaceous, woody and apple orchards.

Finally, the protein and lipid contents of pollen mixes were assessed following the protocols detailed in Barraud et al. (2022). Protein and lipid contents were then expressed as  $\mu\text{g}/\text{mg}$  pollen, and subsequent P:L ratios were determined for each pollen mix.

### 3. Response variables

#### a) Reproductive success

Beginning of November 2021, trap nests were placed into an incubator and the temperature was progressively decreased to 4 °C (relative humidity between 60-80 %) to standardize and control diapause conditions for all bees. Early February 2022, cocoons from each trap nest were counted and placed in plastic cages (10.5 x 7.5 x 11.5 cm, see Pain 1966). The temperature was then progressively increased: from 4 to 12 °C the last week of February, from 12 to 16 °C the first week of March, and up to room temperature (~23 °C) on the third week of March. Bees were then sampled on the day of their emergence.

The total of number of constructed brood cells, cocoons and the emergence rate (percentage of emerged adults based on the total of number of cocoons) were determined for each nesting unit.

#### b) Bee body condition

We focused on female offspring since they have a higher investment in reproduction than males. The weight ( $\pm 0.1$  mg) of each offspring female bee was determined immediately after their emergence. They were then stored at -20 °C until enzymatic assays for quantifying their glycogen, triglyceride and protein contents (n=8 to 65 females per studied nest, n=261 females in total).

Bees were individually placed in a 7 mL-tube containing ceramic beads of 2.8 and 5 mm and homogenised at 4°C with a Precellys Evolution® tissue homogenizer (5 x 10 s at 12.7 rcf with 30 s break between) in a lysis buffer [10 mM NaCl pH 7.4, 1% (w/v) Triton X-100, protease inhibitors (2 g/ml antipain, leupeptin and pepstatin A, 25 units/ml aprotinin and 0.1 mg/ml soybean trypsin inhibitor), 40 mM LS-phosphate, pH 7.4] based on the weight of each bee (10 % w/v extract). After 10 min, the homogenization procedure was repeated a second time. The homogenate was then centrifuged at 12.7 rcf rpm for 20 min at 4 °C, and the supernatant was used for quantifying glycogen, triglyceride and protein contents. All samples were assayed in triplicates and contents were expressed in  $\mu\text{g}$  per mg of tissues after considering the dilutions factors used for sample homogenization (10% weight/volume) and enzymatic assays.

*Glycogen* – We used the Glycogen Fluorometric Assay (Cayman Chemical) for determining the glycogen level in female bees following the kit instructions. Samples were previously diluted at 1/30 (4  $\mu\text{L}$  of the fresh supernatant diluted in 116  $\mu\text{L}$  of the assay buffer). In this assay, glycogen is hydrolysed by amyloglucosidase to form  $\beta$ -D-glucose, which is then specifically oxidized by glucose

oxidase to form hydrogen peroxide. Hydrogen peroxide in the presence of horseradish peroxidase reacts with 10-acetyl-3,7-dihydroxyphenoxazine to generate the highly fluorescent product resofurin. The fluorescence of resofurin was measured with an excitation wavelength of 540 nm and an emission wavelength of 590 nm using a BioTek® Synergy HT microplate reader.

*Triglycerides* – The triglycerides content was determined by using the Triglycerides Colorimetric Assay (Cayman Chemical) and following the kit instructions. Sample solutions were used as pure without dilution. This assay uses the enzymatic hydrolysis of triglycerides by lipase to produce glycerol and free fatty acids. The released glycerol is then measured by a coupled enzymatic reaction: phosphorylation of glycerol into glycerol-3-phosphate by the glycerol kinase followed by the oxidation of glycerol-3-phosphate into dihydroxyacetone phosphate and hydrogen peroxide by the glycerol phosphate oxidase. The redox-coupled reaction of hydrogen peroxide with 4-aminoantipyrine and N-Ethyl-N-(3-sulfoethyl)-*m*-anisidine is then catalysed by the peroxidase to form quinoneimine, whose absorbance was measured with a wavelength of 550 nm using a BioTek® Epoch microplate reader.

*Proteins* – We used the colorimetric Lowry DC Protein Assay (Biorad) to quantify the soluble protein content in bees by following the kit instructions and using the bovine serum albumin as a standard. The supernatant was previously diluted at 1/5. The assay is based upon the reaction of proteins with *Folin* reagent and an alkaline copper tartate solution. The outcome of this reaction was measured at a wavelength of 750nm with a BioTek® Epoch microplate reader.

The concentration of each stored nutrient was determined using the equation obtained from the linear regression of a standard curve submitted to the same corresponding conditions.

#### **4. Data analyses**

All analyses and graphs were performed with RStudio (v 2022.12.0). For each response variable, generalized linear mixed models (GLMMs) with Gaussian family were used for testing the influence of landscape variables on the reproductive success of *Osmia* females, body condition of offspring, palynological composition of provisioned pollen, and nutritive content of provisioned pollen at two focus landscape scales (250 and 500 m). Possible spatial autocorrelation biases were controlled by setting trap nests apart from each other with a minimal threshold distance larger than usual flight ranges (see above), so as to keep the risks of dispersal events among traps as low as possible. We further specified in all individual-based GLMMs the nesting box locations as a random grouping factor in order to treat within-group errors independently from errors arising from possible spatial autocorrelation (*F. Dormann et al., 2007*). Simple GLMs were preferred for analyses carried out at the trap nest level (e.g. reproductive success, pollen chemical and species composition). All data were beforehand tested for normality (Shapiro-wilk's test) whereas homogeneity of variances was

confirmed by visually inspecting residual plots.

To identify consistent landscape patterns, i.e. significant effects of a given set of land use characteristics on response variables, we first built complete models by implementing all the candidate landscape variables as fixed effects in the models. We beforehand established that no multicollinearity occurred among landscape variables using the Variance Inflation Factor (VIF) function of the `usdm` package, with a recommended VIF threshold  $< 10$  for moderate and acceptable levels of predictor interdependency (Naimi et al., 2014). We then applied a stepwise backward model simplification so as to reach so-called minimum adequate models regarding a trade-off between model fit and complexity based upon the Akaike information criterion (AIC). Models were built with the `glmmTMB` function and predictions plotted using the function `plot_model` of the `sjplot` package (Lüdtke, 2022). Whenever necessary, the Semi-Natural Habitats (SNH) variable was log-corrected to reduce residual variance and maximize model convergence. We described diversity of pollen composition with species richness, Shannon diversity index  $H'$  and Simpson index using the function `diversity` in R package “vegan” (Oksanen et al., 2008).

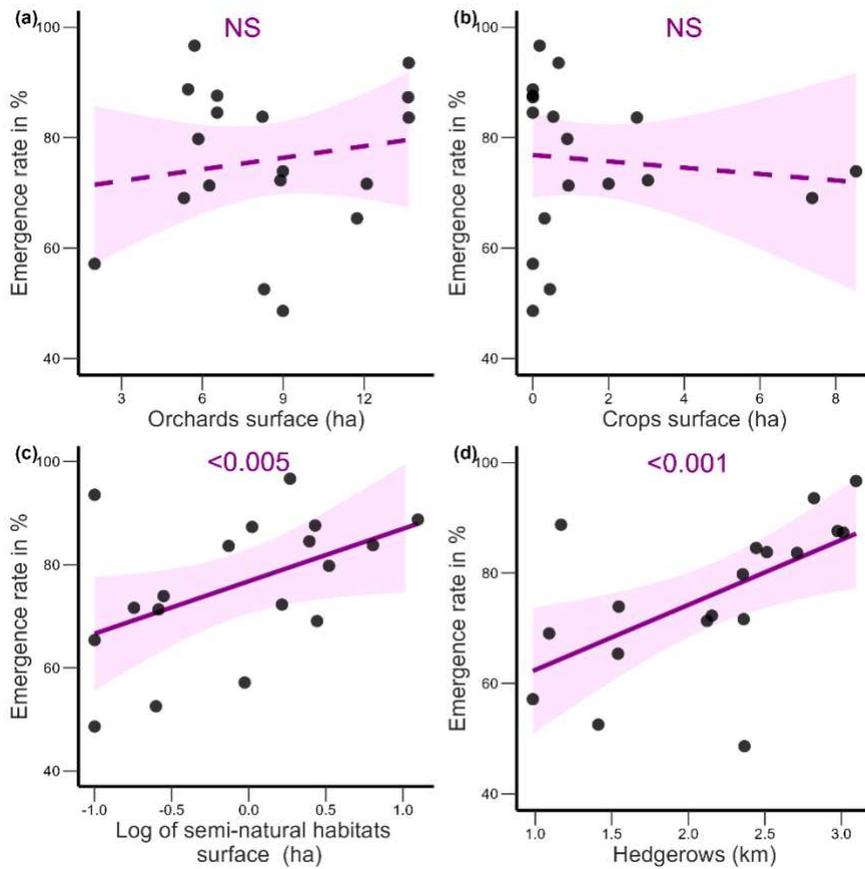
## Results

### 1. Landscape influence on the reproductive success of foundresses

The number of brood cells constructed per nesting unit ranged from 30 to 208 ( $101 \pm 53$ ). Of those 26 to 194 were occupied by cocoons ( $85 \pm 47$ ). Neither the number of brood cells nor the number of cocoons were significantly influenced by landscape variables as the null models were selected as the best models for both focus scales, i.e. 250 and 500 m (Table 3. 1 and Table S3. 1).

### 2. Landscape influence on the emergence rate and body condition of offspring

The emergence rate of *Osmia* progeny ranged from 48.62% to 96.67%. We did not find any effects of the orchards and crop surfaces in the landscape on the bee emergence rate ( $p=0.97$  and  $p=0.12$ , respectively) (Figure 3. 1A and B). However, it significantly increased with both SNH surfaces ( $p<0.005$ ) and hedgerows length ( $p<0.001$ ) (Figure 3. 1C and D). Effects were similar at both focus scales (250 and 500 m, Table 3. 1 and Table S3. 1).

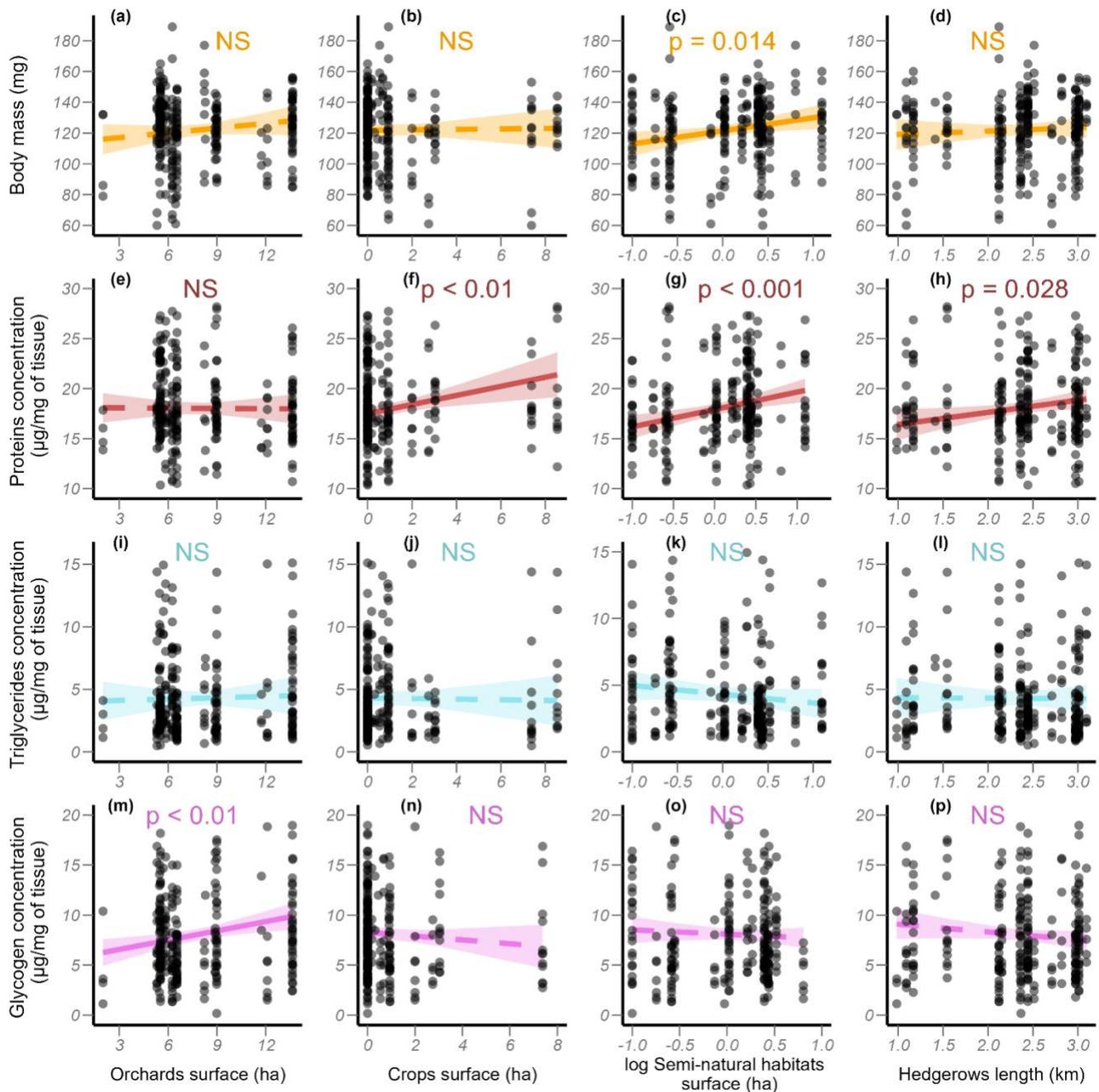


**Figure 3. 1:** Emergence rate in relation to the surface, in hectares (ha) of (a) orchards, (b) crops, (c) SNH, and (d) the length of hedgerows in kilometers. The predicted effects are based on the final model: mean and 95% confidence interval are shown. Solid and dashed lines represent significant and non-significant relationships, respectively.

We then measured the body condition (body mass, protein, triglyceride and glycogen contents) of female bees that were reared in the different nesting sites (n=261 females, 8 to 65 per nesting site). As expected, the shorter focus scale (250 m), adjusted to usual bee flight ranges, appeared more relevant than the largest one (500 m) to assess landscape patterns. For all studied response variables, the 500 m focus scale failed to return models with better statistical support than the 250 m scale, considering a recommended  $\Delta AIC > 2$  (Burnham and Anderson, 2004) (Table 3. 1 and Table S3. 1). The largest 500-m scale returned either clearly less well-supported models (AIC differences = 3.6 to 6.9 in favour of the shortest 250-m scale for protein contents and triglyceride contents), or at best, equally supported models with overall converging conclusions (absolute AIC differences  $< 1.1$  for body mass and glycogen contents). We therefore considered the 500 m scale as less relevant and statistically less parsimonious for our ecophysiological approach. Hereafter, we will focus on the shortest 250 m scale, though detailed statistics for the 500 m scale are provided in Table S3. 1.

We found that if the body mass of females at emergence was not related to the orchard, crop surfaces and hedgerow lengths ( $p=0.19$ ,  $p=0.86$  and  $p=0.55$ , respectively), it was however positively related

to the SNH surface around the nests ( $p=0.014$ , Table 3. 1, **Figure 3. 2a-d**). Likewise, the protein content of female offspring increased with the SNH surface ( $p<0.001$ ) and hedgerows length ( $p=0.028$ ) (Table 3. 1, **Figure 3. 2e-h**). A positive relationship was found with the crop surface as well ( $p<0.01$ ) but not with the orchard surface ( $p= 0.94$ ). The triglyceride content of female offspring was not significantly related to any landscape variables (Table 3. 1, **Figure 3. 2i-l**). Finally, the glycogen content was positively related to the orchard surface ( $p<0.01$ ) but not to the other landscape variables, *i.e.* crop and SNH areas, hedgerow lengths (Table 3. 1 and **Figure 3. 2m-p**).



**Figure 3. 2:** Relationship between the body condition of female offspring (body mass (a-d), protein (e-h), triglycerides (i-l) and glycogen contents (m-p)) and the landscape variables (surface of orchards, crops and SNH in hectares (ha), and the length of hedgerows in kilometers). Solid and dashed lines represent significant and non-significant

relationships, respectively. For glycogen model, the SNH variable was represented as log-transformed even if the adequate model keeps SNH as non-transformed. Dots represent the 261 individuals that were analysed.

### 3. Landscape influence on nutritive and palynological composition of provisioned pollen

A total of 22 plant genera were found in the 15 analysed pollen samples. The four main genera collected by *Osmia* females were crops and woody plant species, belonging to *Malus*, *Prunus*, *Salix* and *Cydonia* with percentages per sample reaching up to 94.2%, 40.8%, 21.6% and 12.9%, respectively. The proportion of undetermined pollen ranged from 0.07 to 1.76%.

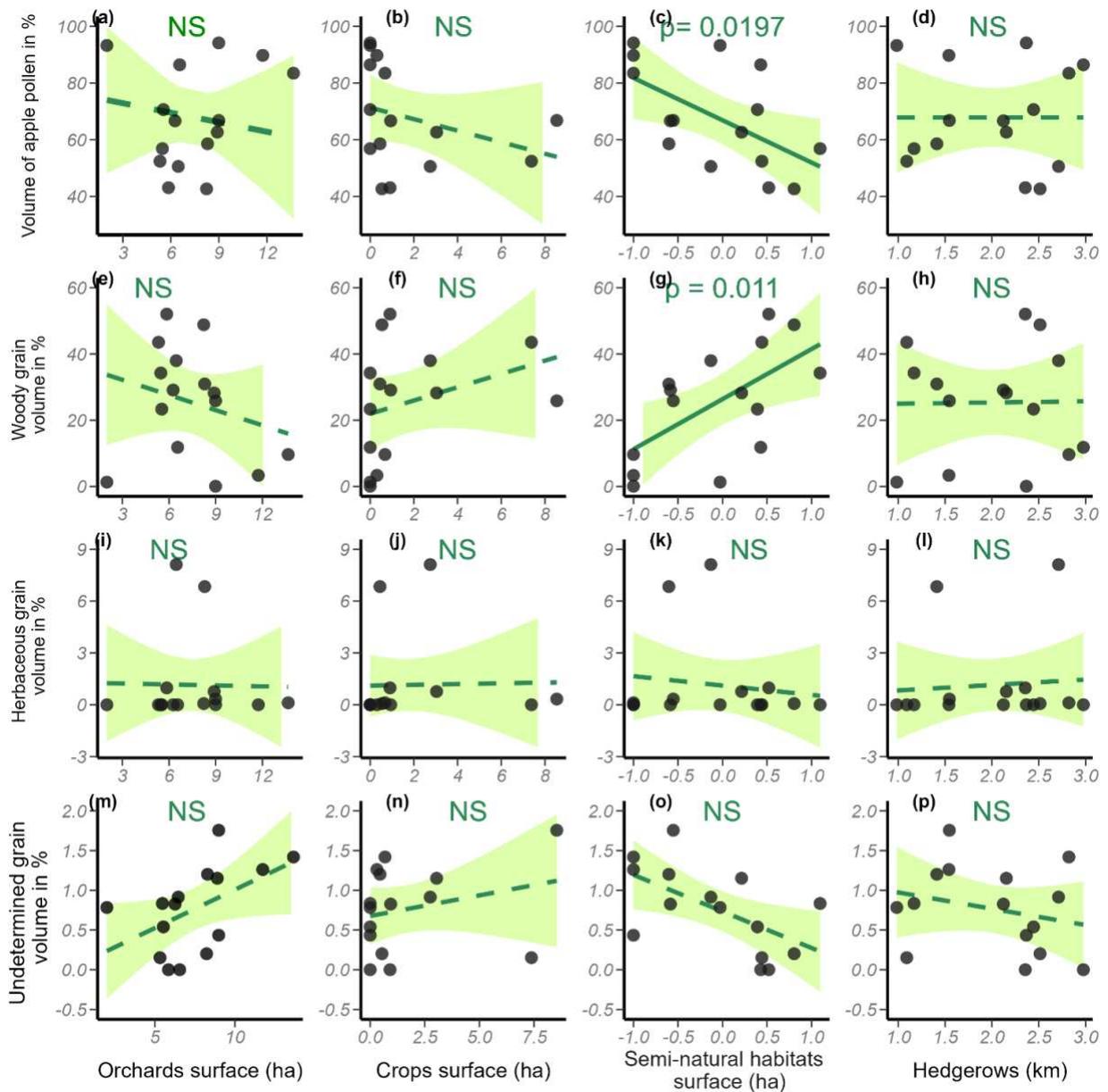
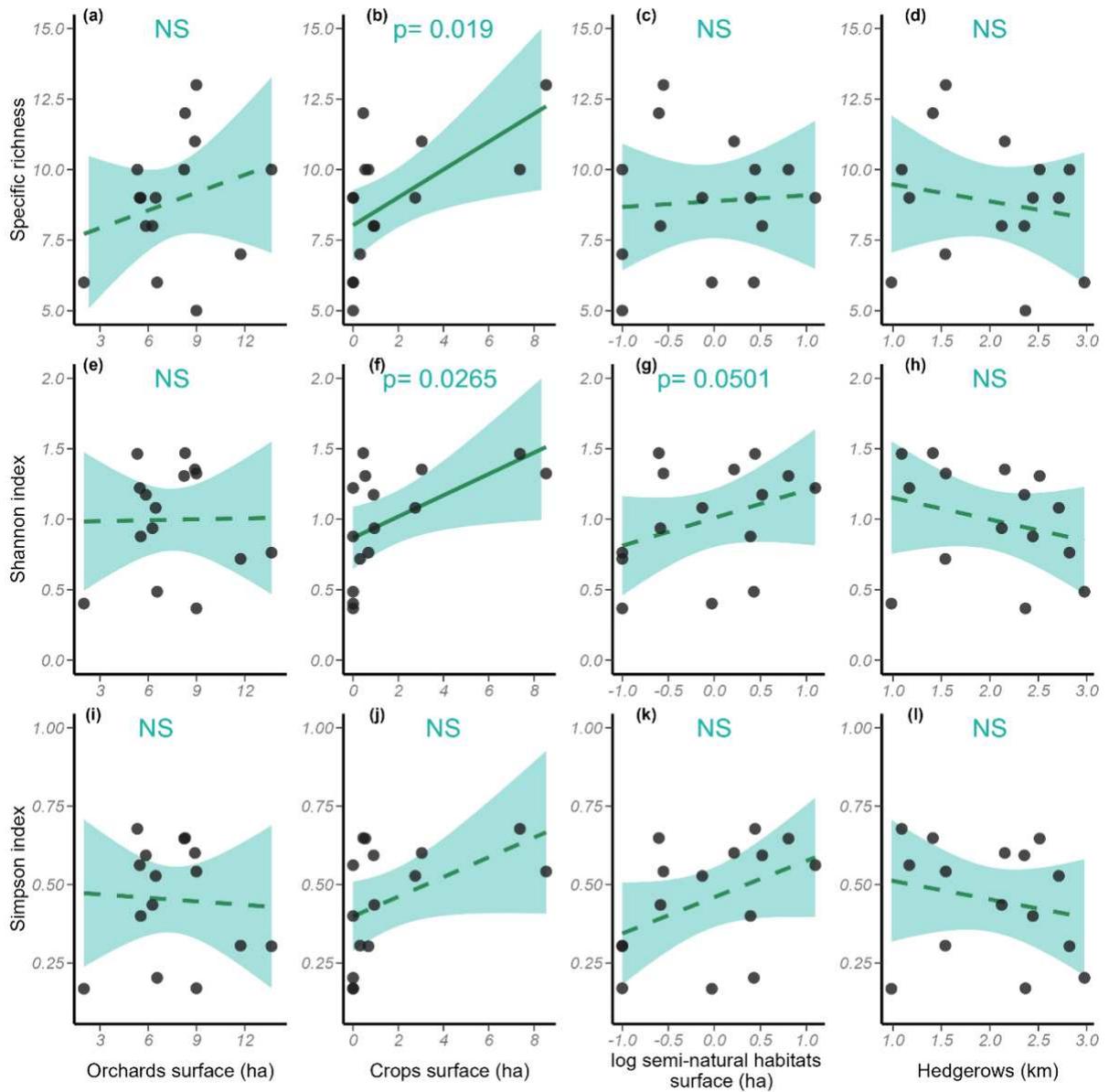


Figure 3. 3: Relationship between the species composition of provisioned pollens (apple (a-d), woody (e-h), herbaceous (i-l) and undetermined pollen (m-p)) and the landscape variables (surface of orchards, crops and SNH in hectares (ha),

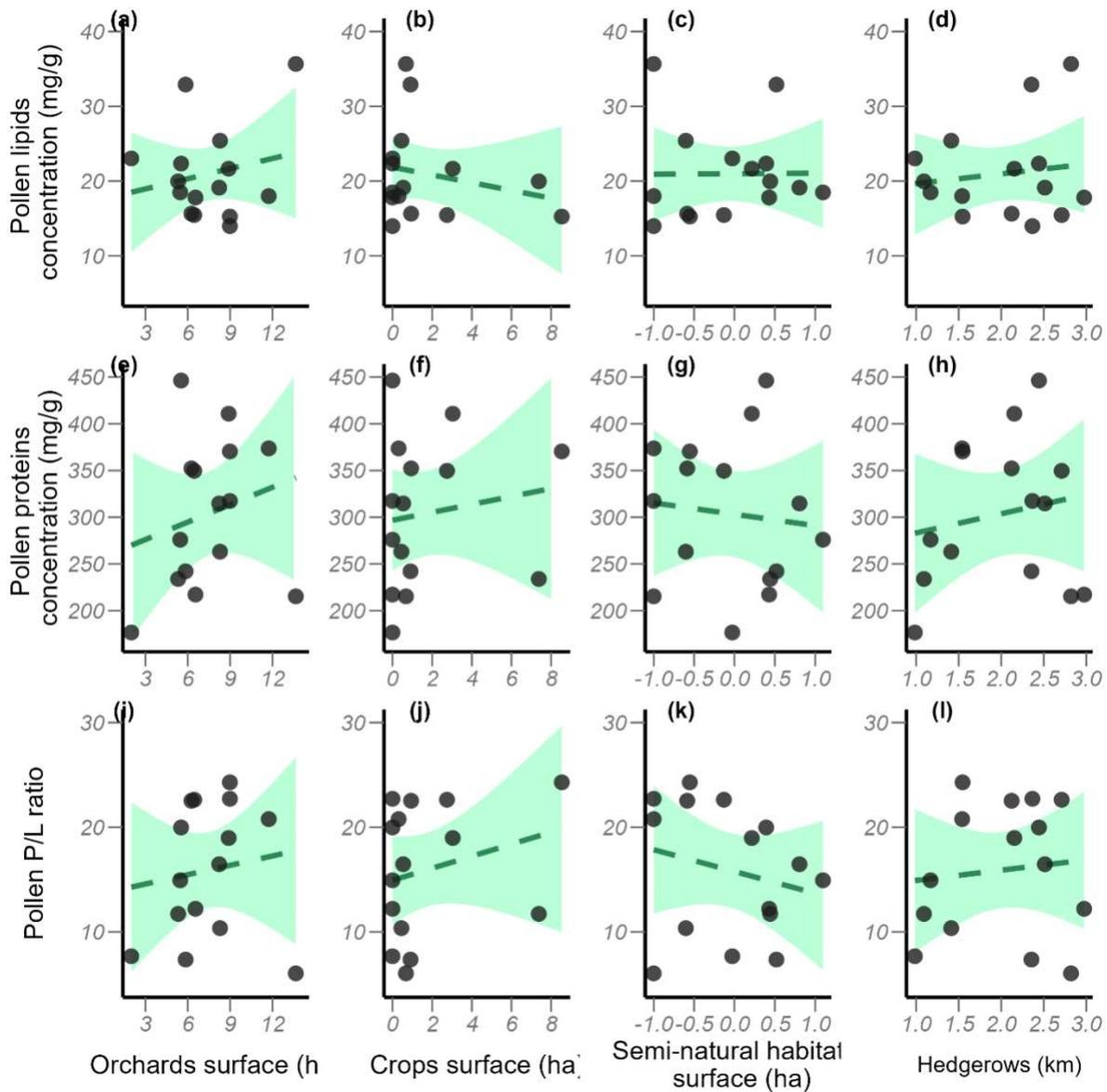
*and the length of hedgerows in kilometers). Solid and dashed lines represent significant and non-significant relationships, respectively. Dots represent the 15 pollen pools that were analysed.*

If variations in the surface of orchards and crops and in the hedgerow length were not associated with changes in the volume of apple, woody, herbaceous and undetermined pollens provisioned by nesting females, the percentage of apple and woody pollens decreased and increased, respectively along a gradient of increasing SNH surface ( $p= 0.02$  and  $p= 0.01$ ; Table 3. 2 **and Figure 3. 3**). The data then revealed, although the species diversity was not impacted ( $p=0.22$ ), moderate evidence for an increase of the Shannon and Simpson indexes of pollen diets with the amount of SNH around the nests ( $p=0.05$  and  $p=0.04$ , respectively; Table 3. 2 **and Figure 3. 4g and k**). There was also moderate evidence for an increase in the diversity of provisioned pollen with the crop surfaces (Table 3. 2 **and Figure 3. 4b, f and j**).

Finally, we did not find any influence of landscape elements on the quality of provisioned pollens (protein and lipid contents, P: L ratio) (Table 3. 2 **and Figure 3. 5**).



*Figure 3.4. Relationship between the species diversity of provisioned pollens (species richness (a-d), Shannon index (e-h), Simpson index (i-l) and the landscape variables (surface of orchards, crops and SNH in hectares, and the length of hedgerows in kilometers). Solid and dashed lines represent significant and non-significant relationships, respectively. Dots represent the 15 pollen pools that were analysed.*



**Figure 3. 5. Relationship between the chemical composition of provisioned pollens (lipid-L (a-d) and protein-P contents (e-h), and P/L ratio (i-l)) and the landscape variables (surface of orchards, crops and SNH in hectares, and the length of hedgerows in kilometers). Dashed lines represent non-significant relationships. Dots represent the 15 pollen pools that were analysed.**

## Discussion

We found evidence in this study that SNH and hedgerows provide a significant habitat complementation for *Osmia cornuta* nesting in mass-flowering orchards. The proximity of greater extents of these landscape elements led to offspring with greater average body mass and higher protein content. Although our study did not detect higher reproductive success at the first generation, the greater body condition of offspring might eventually positively influence reproduction over the subsequent generations.

## 1. Landscape and reproductive success of founding females

Contrary to our expectation, the presence of complementary forage next to mass-flowering orchards did not influence the reproductive success of nesting *O. cornuta*. In previous studies, both landscape (ex. agricultural habitat) and local scale factors (ex. wild flower strips in field margins) have been found to affect the offspring numbers in *Osmia* but results were not always consistent and seemed rather context dependent. For instance, the increasing percentage of agricultural areas was found to have a negative impact on the number of brood cells produced by *O. cornuta* (Kratschmer et al., 2020), while the farming practice (conventional, organic farming, or pasture rich) did not have any significant effects on the production of offspring in *O. bicornis* (Persson et al., 2018). Others studies showed that hedgerows and SNH, as well as landscapes characterized by high floral abundance, significantly improve the reproductive success of *O. bicornis*, in terms of number of brood cells constructed by females (Klaus et al., 2021; Peters et al., 2022; Zaragoza-Trello et al., 2021). Similarly, the availability of floral resources in field margins, such as the amount of field-to-natural borders and wildflower plantings promoted brood cell production in *O. bicornis* (Bednarska et al., 2022) and *O. lignaria* (Boyle et al., 2020), respectively. However, in another study, nest size was not related to the amount of foraging habitats next to the nesting sites (forest, hedgerows, and orchards) in *O. bicornis* (Coudrain et al., 2016). Overall, these studies showed that the production of brood cells rather increase in areas with high floral resources, likely due to more pollen available for brood provisioning and/or the build-up of females reproductive capacities, as evidenced by the higher production of vitellogenin (a precursor of major yolk proteins essential for egg production) in *O. bicornis* provided with sufficient pollen resources (Knauer et al., 2022). This therefore suggests that variation in floral resources across our experimental sites was either not a limiting factor or equally limiting for the reproduction of *O. cornuta*.

## 2. Landscape influence on the emergence rate and body condition of offspring

The body condition (body mass and protein content) and emergence rate of offspring produced by nesting females were however significantly influenced by the amount of hedgerows and SNH. Previous studies in different *Osmia sp* described similar relationships with the mass of cocoons and newly-emerged adults being related to the landscape structure, such as the share of field-to-natural borders, the amount of built-up areas and SNH (Bednarska et al., 2022; Rosas-Ramos et al., 2017). In our study, both the weight of newly-emerged females and emergence rate (males and females) increased with the amount of SNH (and with the length of hedgerows at a focus scale of 500 m), which reinforce earlier observations on the positive link between the bee weight and diapause survival in *O. cornuta* (Bosch and Kemp, 2004). Since, the protein content in insects plays a dual a role as a building block for somatic tissues and an energetic substrate for diapause metabolism and regulation (Hahn and Denlinger, 2007), the positive effects of SNH and hedgerows on diapause survival could also be explained by the higher protein contents quantified in these bees. Overall, the beneficial effects

of SNH and hedgerows on bee body conditions may have consequences at the population level since the number of emergent bees and their size/mass are important for the population sustainability: in solitary bees, large females live longer, have a higher fecundity and are more likely to found a new nest compared to smaller females (Bosch and Kemp, 2004; Bosch and Vicens, 2006b; Larsson, 1990; Tepedino and Torchio, 1989).

If the protein content of emerging females was a rather sensitive metric to changes in habitats, the triglyceride and glycogen contents were poorly or not affected by the landscape composition. Triglycerides, which can represent more than 90% of the lipids stored in the fat body (Canavoso et al., 2001), are synthesized from dietary carbohydrates, fatty acids, or proteins. Pollen contents with these nutrients were either not different across the landscape elements or the triglyceride storage was depleted at the adult emergence. This last hypothesis is maybe the most parsimonious one since *Osmia* species overwinter on a fixed energy budget through their wintering period (Torchio, 1989), and individual bees experienced high energy expenditure in terms of lipids depletion over the winter (Sgolastra et al., 2011). The glycogen concentration in offspring was on the contrary marginally influenced by the surface of orchards around the nest. The fact that glycogen is synthesized from UDP-glucose mainly derived from dietary carbohydrates or amino acids, indicates that pollens originating from apple orchards were rather enriched with these nutrients. However, glycogen is converted to glucose or trehalose during insect diapause to fuel catabolism and is metabolized to produce sugar-based cryoprotectants molecules (Hahn and Denlinger, 2011). As a consequence, glycogen storage may be depleted during the first months of diapause as described in the mosquito *Culex pipiens* (Zhou and Miesfield, 2009), which might explains the poor variations across the different landscapes. In sum, glycogen and triglyceride contents might be sensitive to the nutritional landscape during diapause but fully depleted at the adult emergence and until bees start to feed again, which suggests that protein content would be a better proxy of solitary bee sensitivity to environmental changes, in particular regarding the nutritional landscape.

### **3. Landscape influence on provisioned pollens**

Non-cultivated habitats like field margins or hedgerows play important roles as reservoirs for many wild plants species and represent diverse and available nutritional sources for pollinators (Hass et al., 2018; Kells et al., 2001). Positive effect of SNH has already been proved, notably by increasing wild bee abundance in apple orchards (Joshi et al., 2016; Marini et al., 2012). Such effects are generally attributed to providing pollinators with a better supply of floral resources by SNH, in terms of both temporal availability and abundance, particularly outside of MCF blooming. It was notably found that a minimum of 15% SNH near sweet cherry orchards is needed to optimize pollinator visitation (Eeraerts, 2023). Similarly, hedgerows, which are commonly implemented within agricultural environments of north-western Europe, provide floral resources across bee life cycle and lead to enhanced bee species diversity (Kremen et al., 2019). In our experimental set up, pollen analysis

showed that *Malus* morphogroup, *Prunus*, *Cydonia* and *Salix* were the most foraged plant species, and that the more the foraging buffer in apple orchards contained SNH the higher was the volume of woody pollens collected by nesting females, which was to the expense of apple pollen. This shows that complementary resources, especially from trees, were effectively foraged in apple orchards. This is consistent with the fact that *O. cornuta* prefers pollen floral resources from Rosaceae species (Bosch, 1994) but that other trees like *Salix* and *Quercus* are also foraged (Haider et al., 2014; MacIvor et al., 2014).

Despite some changes in the species composition, the quality of pollen in term of protein and lipid contents did not vary according to the landscape structure. However, more exhaustive analysis of pollen nutrients, including for instance amino acids, fatty acids, carbohydrates, vitamins, would be needed to further conclude on a possible effect of landscape structure on the quality of provisioned pollens and consequently on the body conditions of offspring. For instance, *Salix* pollen, which was one of the most foraged pollen and came from hedgerows and SNH, was found to contain nutrients particularly favourable for bumblebee larva development (Vanderplanck et al., 2014), such as 24-methylenecholesterol and high concentrations of polypeptides/total amino acids. We could assume similar effects on *Osmia* larvae. However, to avoid any perturbation of larvae development during the experiment, pollen and bees used for nutrient and body condition analysis, respectively, were sampled from different nests (although located next to each other's), preventing the establishment of a direct link between the quality of provisioned pollens and bee development. Still, the changes in the composition of provisioned pollens can give some indications on the possible mechanisms underlying the influence of landscape on bee body conditions. For instance, we found moderate evidence for an increase in the pollen diversity with the surface of SNH, which had the most consistent effects on bee metrics; different pollen species tended to be provisioned more evenly. This is somehow in accordance with a recent study, which showed that an increase in the number of plant genera in pollen increases adult emergence, but not oviposition in *O. lignaria* (Westreich et al., 2023). Similar effects were also found with the crop surfaces (notably composed of flowering alfalfa and sunflower) in our study; they marginally increase the diversity of foraged pollen and had a positive effect on bee protein contents. However, a larger sample size would be needed to fully conclude on the positive effects of these landscape elements on the diversity of provisioned pollens, and experimental manipulation of bee diets would be needed to test the influence of pollen diversity on *O. cornuta* body condition.

## Conclusions

We provided empirical evidence for positive effects of hedgerows and SNH on the body condition and emergence rate of offspring in a widely common pollinator in orchards. This further emphasises the critical role of hedgerows and SNH near mass-flowering crops to better support populations of solitary bees. Notably, the development of landscape heterogeneity represents a sustainable practice to enhance and preserve pollinators communities by providing more abundant and more diverse

resources for pollinators (Cole et al., 2017). Equally important, we showed here that some metrics of bee body condition are particularly sensitive to environmental characteristics and may be suitable as early warning signals of habitat quality. Since physiological changes generally occur well in advance of demographic changes, they may help anticipating future population trends. We therefore believe that an integrative approach combining different individual- and population-level metrics (e.g. species richness and abundance, reproductive success, body conditions) will not only improve our understanding of pollinator responses to environmental changes but also reduce the risk that some alteration of bee's environment remains undetected.

## Acknowledgements

This research was funded through a grant from the INRAE SPE department (Macrobee) and the 2018-2019 BiodivERsA joint call for research proposals, under the BiodivERsA3 ERA-Net COFUND programme, and with the funding organisation Agence Nationale de la Recherche in France [ANR-19-EBI3-0003]. We also thank Pierre Franck and Bertrand Gauffre for their valuable help in selecting and facilitating the access to the field sites. Chemical analysis were performed at Mons University by Laetitia Verdy and Dimitri Evrard, under Denis Michez supervision.

## Synthèse

La résolution de notre jeu de données nous a permis de faire le lien entre d'une part les éléments semi-naturels, l'alimentation des osmies cornues au travers des analyses palynologiques et d'autre part la condition corporelle de la descendance au travers des mesures physiologiques.

*Table 3. 1. Summary of the generalized linear mixed effect model analyzing the effect of landscape elements (focus scale of 250 m) on Osmia reproductive success and body condition. Significant p-values (<0.05) are shown in bold.*

Response	Model	Complete model		Minimum	Adequate	Sample size
		parameter	Estimate	Statistics	Estimate	
250m			Pr (>t)			
Brood number	cell	Orchards	-2.378	0.65		18
		Crops	2.88	0.65	Null	
		SNH	- 2.871	0.58	Model	
		Hedgerows	7.831	0.75	conserved	
		AIC		(203.94)	(196.97)	
Cocoon production		Orchards	-3.43	0.45		18
		Crops	0.735	0.90	Null	
		SNH	- 0.093	0.98	Model	
		Hedgerows	18.22	0.41	conserved	
		AIC		(199.25)	(192.6)	
Emergence rate		Orchards	0.03	0.97		18
		Crops	1.50	0.14	1.50	0.12
		SNH	2.71	<0.01	2.70	< 0.005
		Hedgerows	16.15	<0.001	16.20	<0.001
		AIC		(135.93)		(133.93)
Body mass		Orchards	1.03	0.19		261
		Crops	0.15	0.86	Full	
		Log-SNH	8.50	0.01	Model	
		Hedgerows	2.18	0.55	conserved	
		AIC		(2342.12)	(2342.12)	
Protein content		Orchards	-0.009	0.94		261
		Crops	0.46	<0.01	0.45	<0.01
		Log-SNH	1.72	<0.01	1.74	<0.001
		Hedgerows	1.24	0.045	1.22	0.038
		AIC		(1550.3)		(1548.3)
Triglyceride content		Orchards	0.035	0.77	-0.65	0.155
		Crops	-0.025	0.85		
		Log-SNH	-0.58	0.28		
		Hedgerows	-0.035	0.95		
		AIC		(1341.4)		(1335.5)
Glycogen		Orchards	0.32	<0.01	0.31	<0.01

content	Crops	-0.19	0.267		
	SNH	- 0.10	0.399		
	Hedgerows	- 1.37	0.0605	-0.77	0.14
	AIC		(1557.7)		(1555.1)

*Table 3. 2. Summary of the generalized linear mixed effect model analyzing the effect of landscape elements (focus scale of 250 m) on the species composition, diversity and quality of provisioned pollen. Significant p-values (<0.05) are shown in bold.*

Response	Model parameter	Complete model		Minimum	Adequate	Sample size
		Estimate	Statistics	Model	Statistics	
250m			Pr (>t)			
Apple pollen volume	Orchards	-1.12	0.59			15
	Crops	-2.23	0.19	-2.09	0.17	
	Log-SNH	-17.91	0.04	-15.03	0.02	
	Hedgerows	-2.06	0.78			
	AIC		(130.35)		(127.3)	
Woody pollen volume	Orchards	0.70	0.71			15
	Crops	2.28	0.15	2.06	0.14	
	Log-SNH	17.15	0.03	15.24	0.01	
	Hedgerows	3.07	0.64			
	AIC		(127.5)		(124.43)	
Herbaceous pollen volume	Orchards	-0.23	0.56			15
	Crops	0.07	0.82	Null		
	SNH	-1.08	0.48	Model		
	Hedgerows	0.69	0.63	conserved		
	AIC		(81.23)			
Specific richness	Orchards	0.44	0.1	0.37	0.11	15
	Crops	0.44	0.04	0.49	0.02	
	Log-SNH	1.30	0.19	1.15	0.22	
	Hedgerows	-0.63	0.48			
	AIC		(67.05)		(65.84)	
Shannon Index	Orchards	0.06	0.12	0.05	0.20	15
	Crops	0.06	0.06	0.07	0.03	
	Log-SNH	0.36	0.04	0.32		
	Hedgerows	-0.15	0.30		0.05	
	AIC		(12.18)		(11.85)	
Simpson Index	Orchards	0.03	0.20			15
	Crops	0.03	0.11	0.03	0.05	
	Log-SNH	0.18	0.04	0.12	0.07	
	Hedgerows	-0.05	0.46			
	AIC		(-8.27)		(-9.66)	

Pollen content	lipid	Orchards	0.78	0.41		15
		Crops	-0.56	0.46	Null	
		Log-SNH	1.96	0.58	Model	
		Hedgerows	-0.43	0.90	conserved	
		AIC		(106.79)		
Pollen content	protein	Orchards	4.45	0.71		15
		Crops	5.71	0.55	Null	
		Log-SNH	0.26	0.99	Model	
		Hedgerows	21.04	0.62	conserved	
		AIC		(180.02)		
Pollen P/L ratio		Orchards	-0.26	0.77		15
		Crops	0.73	0.33	Null	
		Log-SNH	-2.61	0.46	Model	
		Hedgerows	2.14	0.52	conserved	
		AIC		(106.35)		

*Table S3. 1. Summary of the generalized linear mixed effect model analyzing the effect of landscape elements (focus scale of 500 m) on *Osmia* reproductive success and body condition. Significant *p*-values (<0.05) are shown in bold.*

Response	Model	Complete model		Minimum	Adequate	Sample size	
		parameter	Estimate	Statistics	Estimate		Statistics
Brood cell number	Orchards	- 1.60	0.54			18	
	Crops	- 0.65	0.71	Null			
	SNH	- 1.06	0.45	Model			
	Hedgerows	- 4.13	0.59	conserved			
	AIC		202.66	197.67			
Cocoon production	Orchards	-1.49	0.52			18	
	Crops	-1.26	0.43	Null			
	SNH	- 0.56	0.66	Model			
	Hedgerows	- 1.28	0.85	conserved			
	AIC		199.05	192.64			
Emergence rate	Orchards	0.18	0.69			18	
	Crops	0.19	0.53				
	SNH	0.57	0.039	0.51	0.036		
	Hedgerows	4.01	0.01	4.0	<0.001		
	AIC		140.78		137.55		

Body mass	Orchards	-0.59	0.13			261
	Crops	0.21	0.31	Full		
	SNH	0.36	0.038	Model		
	Hedgerows	2.94	<0.01	conserved		
	AIC		2341.0	2341.0		
Protein content	Orchards	-0.11	0.095			261
	Crops	0.11	<0.01	0.09	0.0115	
	Log-SNH	1.48	0.06	1.44	0.08	
	Hedgerows	0.40	0.035	0.09		
	AIC		1554	1554.1		
Triglyceride content	Orchards	0.046	0.47			
	Crops	-0.020	0.59	Full		
	Log-SNH	0.013	0.99	Model		
	Hedgerows	- 0.061	0.73	conserved		
	AIC		1342.4	1342.4		
Glycogen content	Orchards	0.10	0.13			
	Crops	0.04	0.29			
	Log-SNH	- 1.35	0.09	-1.87	0.051	261
	Hedgerows	- 0.20	0.29			
	AIC		1559.5	1556.0		

# Chapitre 4



# Functional traits and interspecific responses of bumblebee body conditions to grassland managements

Article en préparation avec les partenaires du projet européen NutriB<sup>2</sup>.

## Préambule

Le chapitre précédent démontre que l'application de la Physiologie de la Conservation à l'échelle populationnelle est pertinente mais qu'en est-il de son application à l'échelle de la communauté ? C'est ce à quoi nous avons tenté de répondre dans les travaux de cette section en étudiant l'effet de variables paysagères, liées à la disponibilité de ressources florales, sur la condition corporelle/vitalité de plusieurs espèces d'abeilles sauvages. Notre hypothèse de départ a été que la diversité florale est généralement bénéfique à la communauté d'espèces d'abeilles mais cette sensibilité peut varier selon les traits fonctionnels des abeilles.

Cette étude a été le fruit d'un travail collectif au sein du projet européen Biodiversa (NutriB<sup>2</sup>). Ce projet regroupe cinq partenaires dont font partie l'Université Technique de Munich (TUM), l'Université de Würzburg, l'Université de Ghent et l'Université de Jagiellonian ainsi que notre Unité Abeilles et Environnement (INRAE, Avignon).

Nous nous sommes focalisé-es ici sur diverses espèces de bourdons collectées avec les plus grands effectifs pour les analyses. Nous n'avons pas observé d'influence générale et commune des pratiques de gestion des prairies et de la diversité florale locale sur les bourdons, lorsque les analyses ont été effectuées au niveau du genre. Cependant, nous avons trouvé que les réponses étaient spécifiques aux espèces et aux traits fonctionnels (taille de colonie et longueur du proboscis).

Dans notre étude, certaines mesures de la condition corporelle sont apparues comme sensibles aux changements du paysage comme c'est le cas de la concentration en protéines et de la masse corporelle qui, toutes deux, diminuent avec l'augmentation de l'indice d'utilisation du sol chez certaines espèces. Enfin, nos résultats ont indiqué un lien entre concentration en glycogène et longueur de langue suggérant que les espèces à langue longue ont plus de difficultés à collecter le nectar, qui contient les nutriments nécessaires à la synthèse du glycogène. Cette étude a ainsi démontré que l'approche de la PC est aussi pertinente pour déterminer les différences de sensibilité des espèces d'abeilles à la qualité des habitats.

## Introduction

Despite the growing considerable attention they received, wild bees are experiencing a decline in terms of species diversity on all continents except Oceania (Biesmeijer, 2006; Cameron et al., 2011; Ollerton et al., 2014; Zattara and Aizen 2021). This decline seems to be multi-causal and driven by growing anthropogenic pressures, including agricultural intensification, climate change, and the spread of invasive species and diseases (Nieto et al., 2014a; Potts et al., 2010). Even if the magnitude of such decline is still debated, considering the large part of data deficiency in conservation status (Nieto et al., 2014a), there is actually accumulating evidence for even more pronounced decline in wild bee populations as compared to the overall insect decline (Butchart et al., 2010; Lebuhn et al., 2013). Such higher vulnerability might be explained by the complete dependence of bees on floral resources for development and reproduction, and the need for a diversity of substrates for nesting,

which are both largely declining through the conversion of natural and/or semi-natural habitats into agricultural lands and the intensification of farming practices. Indeed, as central-place foragers, bees rely on the availability and composition of floral cover around their nests, as sources of energy and nutrients for ensuring growth and reproduction (Crone and Williams, 2016; Westphal et al., 2009). Overall local resources are essential for acquiring nectar, rich in carbohydrates, and pollen, which provides proteins, amino acids, lipids, sterols and vitamins, needed for their ovary development and larval diets and their own energy supply (Leach and Drummond, 2018; Roulston and Cane, 2000). As a matter of fact, floral diversity and abundance have been found to be key determinants for bee community composition, and bee species richness often correlates with floral and landscape diversity (Andersson et al., 2013; Gill et al., 2016; Potts et al., 2003; Steffan-Dewenter and Tschardt, 2001). However, bee species are highly diverse in terms of size and life-history traits, suggesting that they might not all respond uniformly in the same way to environmental stressors (Bartomeus et al., 2013; Williams et al., 2010). The diversity and sensitivity of bees in landscapes is modulated by morphological and behavioural traits that determine the types of resources that species require and their functional capacity to access them (Wood et al., 2015). There is therefore a need to better understand the species-specific sensitivity to the changes in floral resource availability for better identifying and protecting vulnerable species.

This is particularly important in grasslands ecosystems, which generally provide both nesting sites and floral resources to a large diversity of wild bee species throughout most of the growing season as long as they are not too intensively managed (Albrecht et al., 2007; Batáry et al., 2010). Permanent grasslands are, with wooded habitats like hedgerows among the most common semi-natural habitats in agricultural landscapes and their favorable role in supporting wild bees is well known (Hatfield and LeBuhn, 2007; Morandin and Kremen, 2013).

However, in Northern Europe, it is estimated that more than 90% of grasslands have been lost at the expense of croplands since the 1930's (Bullock et al., 2011; Eriksson et al., 2002). In addition, natural grasslands have been transformed into highly managed grasslands resulting in the loss of plant biodiversity. For instance, in Germany, grasslands have lost about half of their plant species during the post-Second World war period and are now much poorer in term of plant diversity (only 13 to 14 species per site; Isselstein, 2003), which may have an impact on bee populations. For instance, several studies showed that the frequency of mowing, grazing or fertilizing in grasslands can influence the diversity and abundance of pollinators which decreases as those practices increase (Hudewenz et al., 2012; Lázaro et al., 2016; Sjödin, 2007). This could be explained by the direct effects of early mowing, ungulate grazing and/or nitrogen fertilisation on floral resources diversity and availability (Gaujour et al., 2012; Jacquemyn et al., 2003).

However, evaluation of wild bee population status and trends in relation to environmental changes generally relies on broad scale monitoring of species abundances, distribution and detectability or on long-term local diversity surveys (Winfree et al. 2009; Kerr et al. 2015) on species records, giving an

estimate of species abundance and richness (Winfree *et al.*, 2009; Zattara and Aizen 2021), which are often performed through short-term surveys. It therefore remains difficult to estimate the population sustainability or the long-term survival of bee species in new habitats. In addition, an increase in bee abundance and species richness may not necessarily indicate an increase in bee populations but rather more attractive habitats. In abundance surveys on bumblebees, one problem is that bumble bee workers forage widely for resources, and it is unclear whether the results of these studies reflect differences in true abundance (population size) vs. forager concentration at resource patches (behavioural response) (Carvell *et al.*, 2015; but see Geib *et al.*, 2015 for one example of a correlation between worker and colony abundance). Long-term surveys have therefore been proposed to reliably identify pollinator trends and determine the impact of environmental factors (Breeze *et al.*, 2020; Garibaldi *et al.*, 2020). Notably, a 15-year monitoring scheme was identified as the most suitable by bee experts for detecting long-term trends in bee populations as a function of landscape complexity (Breeze *et al.*, 2020). However, to be more successful and cost-effective, conservation actions should be more proactive and start before its population size declines to critical levels (Drechsler *et al.*, 2011; Soulé, 1987). In this context, conservation biologists can use fitness traits, such as survival and reproduction, to assess the sensitivity of individual bee species responses to environmental changes before being able to transcribe as early warning signals of bee population variations and trends (Cristine *et al.*, 2014). However, while it is feasible for bee model species like some bumblebee and *Osmia* species for which links between fitness and environment have been successfully been demonstrated (Jauker *et al.*, 2012; Krama *et al.*, 2022; S Hollis Woodard *et al.*, 2019; Yourstone *et al.*, 2021), it remains complicated for non-model species to monitor their survival and reproductive output in the field. Alternatively, measurements of fitness-related traits offer a promising framework to assess bee responses to environmental alteration, and to potentially estimate impacts at the population-level. For instance, the body size of bees has often been used as a surrogate of future fitness-related traits (Stevenson and Woods, 2006; Wilder *et al.*, 2016), in particular since in solitary bees the female body size is correlated with fitness: larger females generally exhibit a lower overwintering mortality, are more likely to found a nest, and exhibit a higher fecundity (Bosch and Kemp, 2004; Bosch and Vicens, 2006b; Larsson, 1990; Tepedino and Torchio, 1989).

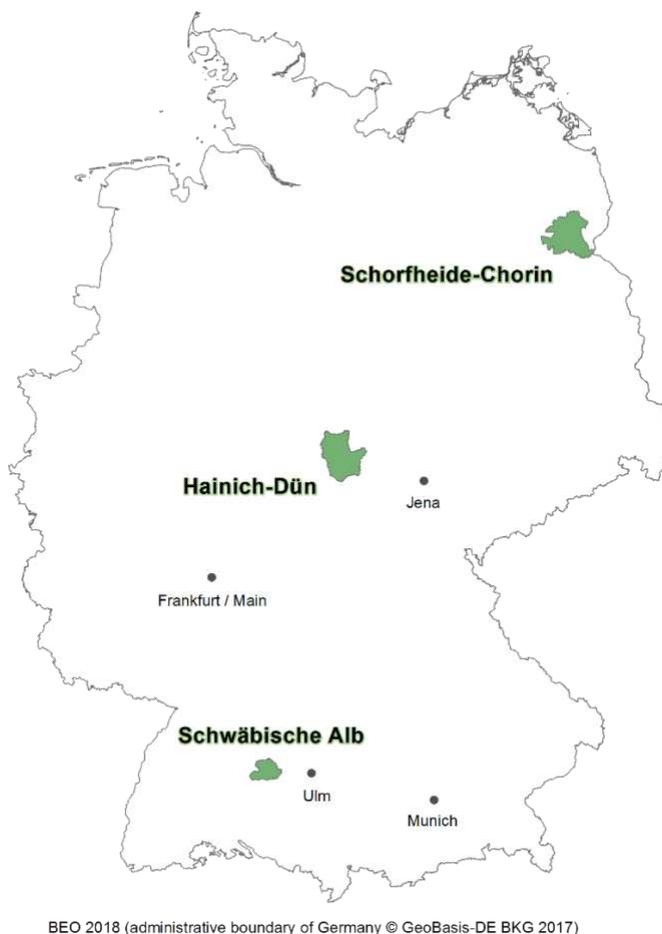
Therefore, to assess the influence of grassland management practices on bee communities and better identify vulnerable species, we monitored bee fitness-related traits along a gradient of land-use intensity in these ecosystems. We specifically determined the influence of environmental variables related to land-use management, such as the land-use intensity index integrating the levels of mowing, grazing and fertilization, and the plant diversity. We used bee body condition parameters (body weight and composition) as fitness-related traits. They were measured on individuals belonging to Apidae (*Bombus*) and by focusing on female bees since they have a higher investment in reproduction than males. Bumblebees (*Bombus spp.*) comprising around 270 species at the global scale and 68 at the European scale are social bees, making their responses to landscape changes completely different to

those of solitary bees (Schweiger et al., 2010). Social bees, which require continuous floral resources might be particularly susceptible to land-use changes compared to their solitary counterparts (Kratschmer et al., 2018; Williams et al., 2010). This has also raised many concerns about their conservation status making them the second most studied bees worldwide after the honeybee *Apis mellifera* (Cameron and Sadd, 2020) and the first wild bee species for declines studies worldwide (Bommarco et al., 2011; Cameron et al., 2011). Most of the specific species traits of European bumble bees are uncertain or unknown, but the existing literature suggests that the species differ markedly in traits such as tongue length, colony size, foraging range, niche breadth, nest position, colony dispersal and length of season (Benton, 2006; Goulson and Darvill, 2004; Walther-Hellwig and Frankl, 2000). For the body composition, we quantified the main categories of compounds stored within insect bodies, i.e. proteins, glycogen and triglycerides. Such stored compounds are essential for insect reproduction and survival (Arrese and Soulages, 2010; Hahn and Denlinger, 2011; Lease and Wolf, 2011). They also provide energy needed over extended period of resource scarcity. Since these compounds are mainly acquired or synthesized from macro- and/or micronutrients found in pollen and nectar, variations in the availability of floral resources was hypothesized to influence the bee body composition. Finally, the sensitivity of bee species to the grassland management practices were related to specific functional traits (colony size and tongue length), which generally determine how organisms interact with their environment. Such functional traits could help to better understand and predict the response of bee species to floral resource availability.

## Material and methods

### 1. Sampling location

Bees were sampled in 2020 and 2021 between April and July at three regions in Germany and one site in Belgium. The three regions in Germany (Schwäbische Alb, Hainich-Dün and Schorfheide-Chorin) are managed within the Biodiversity Exploratories (**Figure 4. 1**), a long-term monitoring program that has carried biodiversity analyses in soil, fauna and flora since its foundation in 2008 (Fischer et al., 2010). A total of 56 plots in grassland ecosystems were visited for bee sampling. The Belgium region consisted of nine plots in accessible grasslands thanks to a collaboration with local farmers. All plots were managed by farmers for cattle (cows/sheep) and/or mowing (cutting of grass regularly for cattle fed). To obtain a gradient of plant diversity in grasslands, we performed a plot selection based on the land-use intensity index (LUI), which is negatively correlated with plant diversity (Dainese et al., 2019; Weiner et al., 2014, 2011). We then selected low, intermediate and high intensity land-use plots in each site. When a selected plot was not accessible for any reason (ongoing mowing or grazing in progress), it was replaced by one with similar land use intensity.



BEO 2018 (administrative boundary of Germany © GeoBasis-DE BKG 2017)

*Figure 4. 1: Geographic location of the three Biodiversity Exploratories (Schorfheide Chorin, Hainich-Dün et Schwäbische Alb) in Germany*

## 2. Sampling procedure

In order to cover the full range of phenology of all species we've collected bees from April to August through four sampling sessions and over two consecutive years; Session 1: April/May 2020, Session 2: June/July 2020, Session 3: April/May 2021, Session 4: June/August 2021.

We performed two types of bee sampling in each plot; transect and targeted. For the transect sampling, we walked through five transects of 50 m x 2 m (length per width) within one hour. For the targeted sampling, we additionally walked in every direction and up to 150 m away from the managed plot (still staying within the same grassland management) during at least one hour. Resting, foraging or flying bees were collected using an entomological net and placed into a 1.5 mL microcentrifuge tube or 15 mL falcon tube according to their size.

## 3. Bee processing

Once collected, all bees (from transect and targeted sampling) were immediately stored in dry ice. They were then sexed and weighted. The identity of a few species, *i.e.* *Andrena haemorrhoa* and *Dasypoda hirtipes*, was determined directly on sites thanks to some characteristic features. Otherwise,

bee's hind legs were carefully removed using clean scissors and forceps and placed in a separate 1.5 ml microcentrifuge tube with a PBS solution for removing pollen from legs. One of the legs (or several in case of small species) was used for DNA barcoding and species identification with the COI marker following Leray protocol. DNA extraction, sequencing, sequence assembly and base calling for DNA barcode markers was performed by two companies: Advanced Identification Methods (AIM) for bees caught in 2020; and by the Canadian Centre for DNA Barcoding (University of Guelph) for bees caught in 2021.

#### 4. Species and individual selection for body condition analysis

Among the 159 wild bee species sampled during the two years campaign of fieldwork, we selected a core set of 30 species based on the following criteria: species should be represented by bees sampled in sufficient numbers along the full gradient and have a minimum weight of 10 mg to correctly perform bee body condition analysis (in particular biochemical assays for nutrient storage analysis). Here, only data for five *Bombus* species *Bombus hortorum*, *B. lapidarius*, *B. pascuorum*, *B. sylvarum* and *B. terrestris* are shown (see Annexe 8). Others bee species belonging to Andrenidae and Halictidae families are currently being analysed.

#### 5. Environmental variables

In order to assess whether the availability and diversity of floral resources had an influence of bee body conditions and whether effects were species and/or trait specific, we recorded and tested the following environmental variables:

##### a) Land-use intensity calculations

The land-use intensity (LUI) index is a continuous variable integrating the frequency of mowing, the frequency and amount of grazing animals and the amount of fertilizer used in the field (nitrogen per hectare) (Blüthgen et al., 2012). Grazing livestock included cattle, sheep and horses which were converted to livestock units as presented by Fischer et al. (2010). Mowing frequency is based on the total of events during the year. Pesticides weren't applied to any plot and therefore not included in the calculation. Fertilization covered organic or inorganic fertilizer applied by farmers and was quantified by kg nitrogen (N) per hectare. The LUI index was calculated following the formula:

$$Li = \frac{Fi}{FR} + \frac{Mi}{MR} + \frac{Gi}{GR}$$

Where  $Fi$  is the fertilization level,  $Mi$  the frequency of mowing per year and  $Gi$  the grazing intensity reflected by the density of livestock on each site  $I$  for a given year and  $FR$ ,  $MR$  and  $GR$  their respective mean within its region  $R$  for that year (the mean across all 56 experimental plots in the Alb, Hainich or Schorfheide, respectively).

##### b) Floral diversity

Plant diversity in each plot was assessed by measuring the percentage of cover from each plant species.

For the plots in Germany, the percentage of cover from each plant species was taken within 16 m<sup>2</sup> per plot from field assessments carried out by one of the Biodiversity Exploratories team and included all plant species (Hinderling et al., 2022). Only plants flowering between April and July were selected in order to picture relevant plants for pollen and nectar collected by bees during the sampling periods. For the plots in Belgium, the number of flowering plants was counted in 10 quadrants of 1 m<sup>2</sup> located in the corners of the transect walks. We then calculated the approximate cover of each plant (based on their size) and extrapolated our measurements to 16 m<sup>2</sup> in order to match the measurements in Germany.

Around 99% of the flowering plant species could be determined using field guides (Spohn and Spohn, 2021) (Eggelte, 2007; Schauer et al., 2020). A total of 253 plants species were identified. We then calculated the floral diversity of plants per plot per season with Shannon index calculations.

## **6. Female body condition**

### **a) Weight and female processing**

The weight ( $\pm 0.1$  mg) of each sampled female bee was determined immediately after their sampling in the field. They were then stored at -20°C until enzymatic assays for quantifying their glycogen, triglyceride and protein concentrations.

Depending on their size, bees were individually placed in a 7 mL-tube containing ceramic beads of 2.8 and 5 mm or a 2 mL-tube containing 2.8 mm polished metal beads and homogenised at 4 °C with a Precellys Evolution® tissue homogenizer (5 x 10 s at 12.7 rcf with 30 s break between) at a 10 % bee weight/volume extract in a lysis buffer (10 mM NaCl pH 7.4, 1% (w/v) Triton X-100, protease inhibitors (2 µg/ml antipain, leupeptin and pepstatin A, 25 units/ml aprotinin and 0.1 mg/ml soybean trypsin inhibitor), 40 mM LS-phosphate, pH 7.4). After 10 min. rest at 4°C, the homogenization procedure was repeated a second time. The homogenate was then centrifuged at 12.7 rcf with a microcentrifuge (5415 for the 2 mL-tubes and 5430 R for the 7 mL-tubes) for 20 min at 4 °C, and the supernatant was used for quantifying glycogen, triglyceride and protein concentrations. All samples were assayed in triplicates.

The concentration of each stored nutrient was determined using the equation obtained from the linear regression of a standard curve submitted to the same corresponding conditions. The glycogen, triglyceride and protein concentrations were expressed in µg per mg of female tissues after considering the dilutions factors (see annexes) used for sample homogenization (10 % weight/volume) and enzymatic assays (see below).

### **b) Proteins**

We used the colorimetric Lowry *DC* (*Detergent Compatible*) Protein Assay (Bio-rad) to quantify the soluble protein concentration in bees by following the kit instructions and the bovine serum albumin

as a standard. Samples were previously diluted according to their species belonging (Annexe 7). The assay is based upon the reaction of proteins with *Folin* reagent and an alkaline copper tartate solution. The outcome of this reaction was measured at a wavelength of 750 nm with a BioTek® Epoch microplate reader.

#### c) Triglycerides

The triglycerides concentration was determined by using the Triglycerides Colorimetric Assay (Cayman Chemical) and following the kit instructions. Samples were previously diluted according to their species belonging (see Annexe 7). This assay uses the enzymatic hydrolysis of triglycerides by lipase to produce glycerol and free fatty acids. The released glycerol is then measured by a coupled enzymatic reaction: phosphorylation of glycerol into glycerol-3-phosphate by the glycerol kinase (1) and the oxidation of glycerol-3-phosphate into dihydroxyacetone phosphate and hydrogen peroxide by the glycerol phosphate oxidase (2). The redox-coupled reaction of hydrogen peroxide with 4-aminoantipyrine and N-Ethyl-N-(3-sulfopropyl)-*m*-anisidine is then catalysed by the peroxidase to form quinoneimine, whose absorbance was measured with a wavelength of 550 nm using a BioTek® Epoch microplate reader.

#### d) Glycogen

We used the Glycogen Fluorometric Assay (Cayman Chemical) for determining the glycogen level in female bees following the kit instructions. Samples were previously diluted according to their species affiliation. In this assay, glycogen is hydrolysed by amyloglucosidase to form  $\beta$ -D-glucose, which is then specifically oxidized by glucose oxidase to form hydrogen peroxide. Hydrogen peroxide in the presence of horseradish peroxidase reacts with 10-acetyl-3,7-dihydroxyphenoxazine to generate the highly fluorescent product resofurin. The fluorescence of resofurin was measured with an excitation wavelength of 540 nm and an emission wavelength of 590 nm using a BioTek® Synergy HT microplate reader.

### 7. Bee functional traits

For each of the five *Bombus* species, we compiled information on the following functional traits, modulate the ecophysiological response of individuals to the environment: colony size and tongue length. For all species, functional traits were gathered from the literature (Amiet et al., 2017; Westrich, 1989).

#### a) Tongue length

Bee proboscis length, hereafter called more simply tongue length, is a proximal determinant of the ability of species to access a wide diversity of floral resources. Empirical evidence show that long-

tongued bumblebee species are more specialised, with a narrower diet breadth, while short-tongued ones tend to be more generalist – with an additional mechanical principle that nectar foraging is more efficient when tongue length and flower depth are matching (Biella et al., 2019; Harder, 1985). Herein, tongue length was coded as a qualitative factorial variable with two levels; short and long. *Bombus lapidarius* and *B. terrestris* are both considered short-tongued species, contrary to *B. hortorum*, *B. pascuorum* and *B. sylvarum*, which fall into the category of long-tongued species.

#### b) Colony size

*Bombus* species colony size is another *a priori* determinant functional trait in influencing physiological responses of individuals. Larger colonies, with greater amounts of pollen and nectar reserves, are likely to be more resilient to periods of floral resource scarcity (Crone and Williams, 2016). Species with larger colonies may therefore benefit from a greater colony buffering effect with regard to individuals' physiology. Herein, colony size was determined either as a numeric variable indicating the maximal known colony size reported from literature for each species (Goulson, 2003), or more simply as an ordinal variable using ranks of colony size from 1 to 5.

Regarding colony size, *B. hortorum*, *B. pascuorum* and *B. sylvarum* are considered as little to medium colony size species whereas *B. lapidarius* and *B. terrestris* are large colony size species.

## 8. Data analyses

### a) Statistical analysis

All analyses were carried out in R version 2023.09.0+463

Correlation matrix and calculation with *cor.test* function from *stats* package showed that LUI calculated in 2020 and the one calculated in 2021 were tightly correlated ( $t=15.7$ ,  $p<0.001$ ,  $cor=0.91$ ). We thus decided to choose LUI 2021 (more exhaustive) to approximate the land use intensity for both years. We conducted the same kind of test to check for the absence of correlation between the two environmental variables (LUI and Plant Shannon Index) and find that no correlation exists between those two ( $t=-0.18$ ,  $p=0.86$ ,  $cor=-0.02$ ).

To investigate the effects of landscape parameters (plant diversity Shannon index, land use intensity LUI) on bee body condition (body mass and proteins, triglycerides and glycogen concentrations), we used generalized linear mixed models (GLMMs – package: *lme4*; Bates et al., 2007), assuming a Gaussian distribution for nutrients data. Plots (60 levels) and sampling sessions (4 levels), were combined as a random grouping variable, while the LUI and diversity index were integrated as fixed effects.

In a first step, we computed a series of models intended to identify general trends among species, with the underlying hypothesis that species would overall display similar patterns with regard to a given environmental variable, either taken alone or as an interactive term of a functional trait (tongue length or colony size). In those models, variations arising from individual species were assumed to be

comparable to a random noise that may be accounted for by specifying the species identity as an additional random grouping variable. Tongue-length category was binary categorical variable indicating species with short or long tongue length. Theoretical colony size was coded either as a numeric variable, indicating the maximal known colony size reported from literature for each species, or more simply as an ordinal variable using ranks of colony size from 1 to 5. For the sake of parsimony, we restricted candidate models to a single environmental variable at a time, either alone or associated in interaction with a single functional trait variable. This led to a total of eight candidate models per response body condition variable, to which we added a null model (no explanatory variable specified) to serve as a reference basis for the null hypothesis of no observed effect. These candidate models were then ranked based on a trade-off between model complexity and fit to data using the Akaike's information Criterion (AIC) following Burnham and Anderson (Burnham and Anderson, 2002). For a more conservative and parsimonious model selection, we favoured the second-order AIC form, i.e. the bias-corrected AICc for small samples. The best model confidence set, i.e. the set of models with a small difference  $\Delta AICc < 2$  compared to the smallest AICc value, were judged as equally well supported by data. Additional models with a  $\Delta AICc < 4$  were judged plausible but less well supported by data. Other models, with a  $\Delta AICc > 4$ , were considered as highly unlikely. We selected the best models and computed the effect estimates of the corresponding explanatory variables for *a posteriori* confirmation of significant body condition variations driven by environmental variables and possible interactions with species' functional traits.

In a second step, we computed species-specific models, with the underlying hypothesis that body condition would respond differently among species, i.e. with no obvious general trend related to the environmental variables and independently from a particular functional trait. This complementary step was deemed necessary whenever no general trend was detected throughout the studied species, in case some species-specific responses would have remained unnoticed at the previous step of general trend analyses. To do so, the species identity was moved back as a fixed variable in body condition models, and environmental variables specified as explanatory variable nested within species. This nested design allowed for testing their respective effects independently for each species.

#### b) Statistical power analysis

To further assess the statistical resolution of our ecophysiological survey, and gauge the tractability of the studied morphological (body mass) and physiological (proteins, triglycerides and glycogen) metrics to serve as indicators of environmental changes, we performed an *a posteriori* power analysis and computed statistical power curves.

Statistical power is the probability that a test of significance will detect a deviation from the null hypothesis, should such a deviation exist. Among others, the power of a test is a function of (i) the magnitude of difference to be detected between two studied modalities, also called effect size, (ii) the sample size and (iii) the natural variability of the studied response variable, i.e. whether values are

more or less dispersed on each side of the mean.

Statistical power will increase as the measured effect size is sharp, sample size is large, and the response metric poorly variable. Conversely, the power of a test can be illustrated by calculating the sample size needed to detect a given effect size with a given confidence. It is usually recommended to target at least à 80% statistical power, i.e. to design the study in order to reach a 80% probability of detecting an expected effect size. Statistical power curves may be computed to help decision making in that respect.

Herein, we built such reference curves for each of the four studied response variables based on their intrinsic variation properties. More specifically, we derived for each variable its mean, standard deviation SD and coefficient of variation CV, which expresses SD as a percent of the mean. The CV can then be used to approximate statistical power as a function of sample size and desired effect size. Alternatively, we assessed the sample size requested to reach a range of effect sizes and a desired power of 80% in an hypothetical control-vs-treatment one-way experimental design (1 degree of freedom, Sokal and Rohlf, 2013).

We performed the analyses separately for each of the commonest *Bombus* species.

## Results

For the body condition analysis, a total of 767 bees sampled in 2020 and 2021 and belonging to five different species were analysed with *Bombus hortorum* (n=34), *B. lapidarius* (n=275), *B. pascuorum* (n=223), *B. sylvarum* (n=102) and *B. terrestris* (n=133) giving a total of 767 female bees: with n=767 for bee weight and protein concentration, n= 757 for triglyceride concentration, and n=665 for glycogen concentration.

### 1. Body mass

The average body mass of foraging bumblebees was as followed: *Bombus hortorum*: 202.3±52.3 mg, *Bombus lapidarius*: 161.6±38.2 mg, *Bombus pascuorum*: 154.3 ±50.1 mg, *Bombus sylvarum*: 144.1±78.4 mg and *Bombus terrestris*: 209.9±47.7 mg.

Comparison of AICc values and model weights showed that none of the candidate models performed satisfactorily to predict the body mass variations of bumblebees, the null model being selected as the most parsimonious one in the candidate model set (AICc= 8091.3, w=0.79, **Table 4. 1**). No general effect of the LUI on bumblebee body mass was therefore detected when considering all five species together. The second model in the list which included the LUI, tongue length and their interaction, was less well supported but still plausible ( $\Delta$ AICc=3.4, w=0.14).

According to the most parsimonious model (set apart the null model), the LUI index did not affect significantly the body mass of either short-tongued (t=0.91, p = 0.36) or long-tongued bumblebee species (t=-0.28, p = 0.78). We similarly tested the influence of colony size on LUI effects and observed no effect in body mass along the LUI index. The relationship between floral diversity index

was neither influenced by the tongue length or colony size.

However, when recomputing models at the species-specific level we found a significant negative effect of LUI on the body mass of *Bombus sylvarum* ( $p < 0.01$ , Figure 4. 2. **A & Table 4. 2**), with females losing 25.5 mg for every LUI index unit increase. No effect of LUI was found in the other four species. When investigating the influence of floral diversity (Shannon diversity index) on bumblebee body mass, we did not find any general nor species-specific effects (**Table 4. 1 & 3**). For bumblebee species body mass, we also saw negative effect of floral diversity index on *Bombus lapidarius* (Figure 4. 2) but only in a marginal way ( $p = 0.09$ , **Table 4. 3**, Figure 4. 2. **B**) with females estimated to lose 12.8 mg for every floral diversity index unit increase.

## 2. Proteins

Comparison of AICc values and model weights showed that the model including the LUI, tongue length and their interaction best predicted the protein concentration of bumblebees (AICc= 7528.2  $w = 0.33$ , **Table 4. 1**). Based on the AICc and the weights of evidence, this model was judged statistically equivalent to the two next best models which included (1) the LUI, colony size (as an ordinal variable) and their interaction ( $\Delta AICc = 0.4$ ,  $w = 0.27$ ) and (2) the null model ( $\Delta AICc = 1.1$ ,  $w = 0.19$ ).

Neither LUI nor floral diversity appear to exert a significant general effect on the protein concentration in bumblebees. The best model returned no significant effect of LUI as a simple term ( $t = -2.36$ ,  $p = 0.25$ ), but a significant interaction term with tongue length ( $t = -5.35$ ,  $p = 0.032$ ), indicating that protein concentration in short-tongued species was more prone to decrease with increasing LUI (Figure 4. 3. **A**), with females losing 5.35  $\mu\text{g}$  of protein/mg of tissue for every LUI index unit increase. We similarly observed a (marginal) decreasing in protein concentration relatively to colony-size (as ordinal variable) along the LUI index ( $t = -1.8$ ,  $p = 0.07$ ) with higher colony size losing 0.92  $\mu\text{g}$  of protein/mg of tissue for every LUI index unit increase (Figure 4. 4.**A**). Neither tongue length nor colony size have influence on the effect of floral diversity on protein concentration.

Models computed at the species level, suggest that the latter general trends are partly accounted for by the short-tongued *B. terrestris*, whose protein concentration sharply decreased with increasing LUI ( $p = 0.04$ , Figure 4. 5. **A**, **Table 4. 2**). Reciprocally, the protein concentration significantly increased with the floral diversity index ( $p = 0.03$ , Figure 4. 5. **B**, **Table 4. 3**), with *B. terrestris* females gaining 13  $\mu\text{g}$  of proteins per mg of tissue for every floral diversity index unit increase. No effect of environmental variables was found in other bumblebee species.

## 3. Triglycerides

Comparison of AICc values and model weights showed that that the null model best predicted the triglyceride concentration of bumblebees (AICc= 629.4,  $w = 0.54$ , **Table 4. 1**). The following two models including (1) the LUI effect, and (2) the LUI, tongue length and their interaction, were

equivalent and considered as well supported by the data ( $\Delta\text{AICc}=2$  and  $w=0.20$  for both, **Table 4. 1**). Neither LUI nor floral diversity appear to exert a significant general effect on the triglycerides concentration in bumblebees. When including tongue length as a factorial variable to determine whether the potential influence of LUI on triglycerides concentration was related to this functional trait, LUI index did not affect the triglycerides concentration of either short-tongued ( $t=-0.75$ ,  $p = 0.45$ ) or long-tongued bumblebee species ( $t=1.14$ ,  $p = 0.26$ ). We similarly tested the influence of colony size (ordinal variable) on LUI effects and observed marginal effect ( $p=0.09$ ) in triglycerides concentration along the LUI index (Figure 4. 4.B) with females from high colony size losing  $0.02 \mu\text{g}$  of triglycerides/mg of tissue.

Altogether, neither the LUI nor the floral diversity significantly affected the bumblebee's triglyceride concentration at the genus and species level (**Table 4. 2 & 3**, Figure 4. 6), and neither tongue length nor colony size exert any influence on the effect of floral diversity or LUI on triglycerides concentration.

#### 4. Glycogen

Comparison of AICc values and model weights showed that the model including the LUI, the tongue length and their interaction best predicted the glycogen concentration of bumblebees (AICc= 4281.4,  $w=0.55$ , **Table 4. 1**). This model was slightly better than the next best model which included the index of floral diversity, the tongue length and their interaction ( $\Delta\text{AICc}= 0.52$ ,  $w=0.42$ ).

Neither the LUI nor the floral diversity significantly exerted a general influence on the bumblebee's glycogen concentration. The LUI and floral diversity did not have any significant influence on the glycogen concentration of the different bumblebee species (**Table 4. 2, Table 4. 3**, Figure 4. 5). However, we found that changes in glycogen concentration along the LUI gradient was moderately influenced by the tongue length ( $t=-2$ ,  $p = 0.05$ ): the glycogen concentration along the LUI gradient increased and decreased in short-tongued and long-tongued bumblebees, respectively (Figure 4. 3.B). Individuals with short tongue are expected to gain  $1.29 \mu\text{g}$  of glycogen per mg of tissue whereas individuals with long tongue lose weight.

The floral diversity index, however, seem to display rather marginal effects on glycogen concentrations for some species, in a different way where *Bombus lapidarius* females are negatively affected whereas *Bombus pascuorum* females are positively affected (Figure 4. 7 B, **Table 4. 3**).

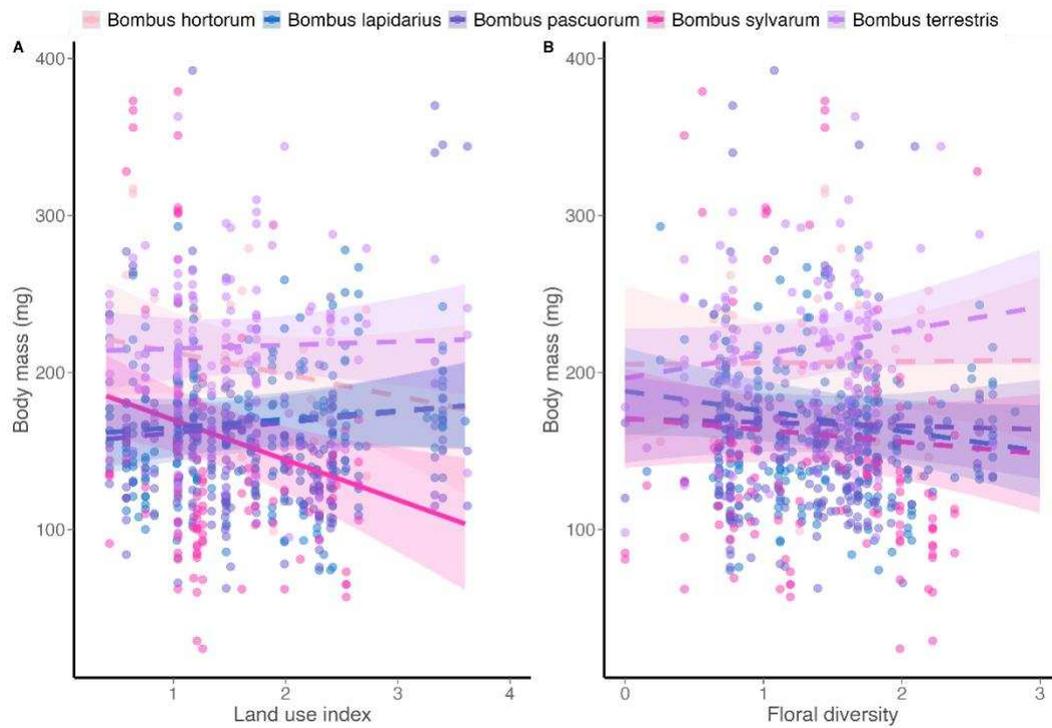
Colony size did not influence the relationship between floral diversity or LUI and glycogen content.

*Table 4. 1: Model selection results for body condition variations (body mass, protein, triglycerides and glycogen concentration) as a function of environmental variables (Land-use intensity LUI and floral diversity as indicated by the Floral diversity index) in Bombus species. Each model stands for a scenario of general effect of an environmental variable, either taken alone or as an interactive term of a functional trait (tongue length category or colony size as ordinal or numeric variable). All models consider possible species-specific responses with the species identity specified as a random grouping variable.*

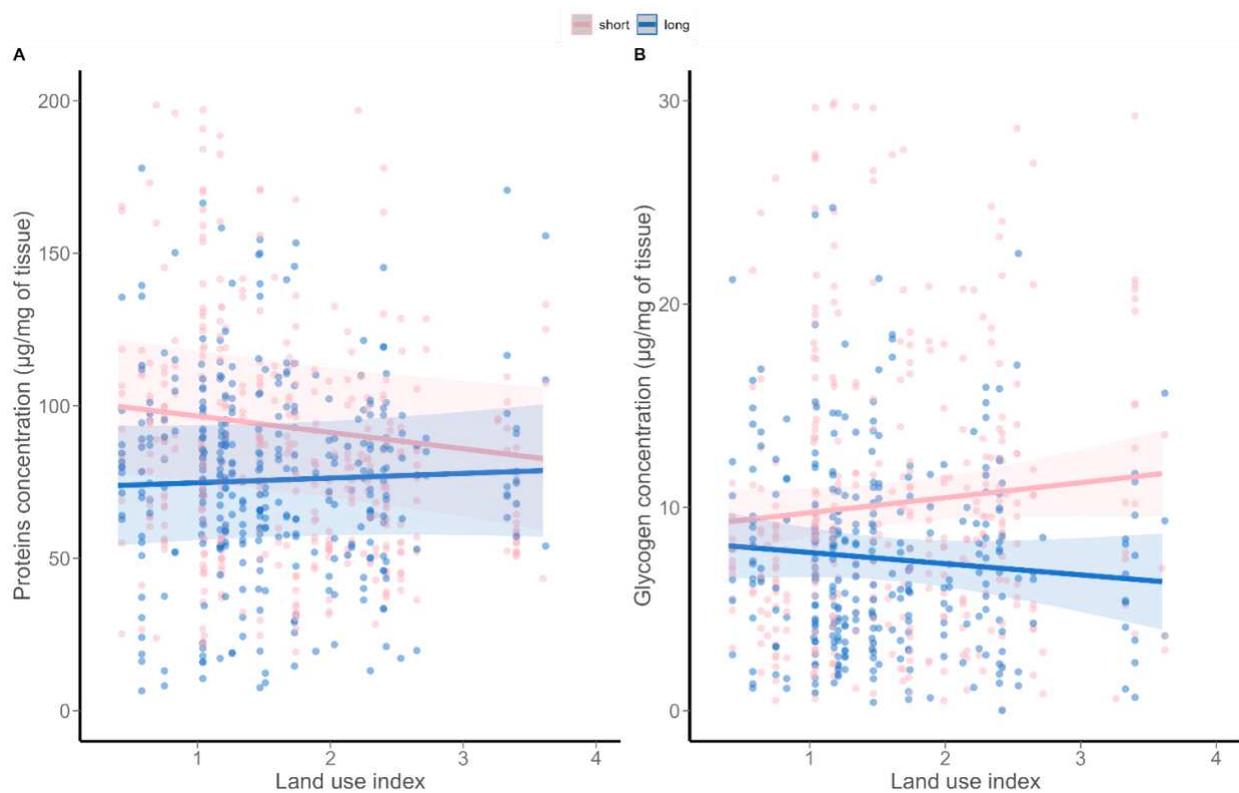
Response	Model Predictor	LL	N2K	AICc	$\Delta$ AICc	AICc Weight
<b>Body mass</b>	<b>Null model</b>	<b>-4040.7</b>	<b>153.4</b>	<b>8091.4</b>	<b>0.0</b>	<b>0.79</b>
	LUI x tongue length	-4039.3	95.9	8094.8	3.4	0.14
	Floral diversity x tongue length	-4040.2	95.9	8096.5	5.1	0.06
	LUI x colony size (numeric)	-4046.5	127.8	8105.2	13.8	0.00
	LUI x colony size (ordinal)	-4047.3	127.8	8106.6	15.2	0.00
	Floral diversity x colony size (ordinal)	-4048.2	127.8	8108.6	17.2	0.00
	Floral diversity x colony size (numeric)	-4048.4	127.8	8108.9	17.5	0.00
	LUI	-4049.6	153.4	8109.4	18.0	0.00
	Floral diversity	-4049.7	153.4	8109.5	18.1	0.00
<b>Proteins concentration</b>	<b>LUI x tongue length</b>	<b>-3756.0</b>	<b>95.4</b>	<b>7528.2</b>	<b>0.0</b>	<b>0.33</b>
	LUI x colony size (ordinal)	-3756.2	95.4	7528.6	0.4	0.27
	Null model	-3759.6	152.6	7529.3	1.1	0.19
	LUI	-3759.0	127.2	7530.0	1.8	0.13
	Floral diversity x tongue length	-3757.8	95.4	7531.7	3.5	0.06
	Floral diversity x colony size (ordinal)	-3761.9	127.2	7535.9	7.7	0.01
	Floral diversity	-3767.1	152.6	7544.3	16.1	0.00
<b>Triglycerides concentration</b>	<b>Null model</b>	<b>-309.7</b>	<b>151.4</b>	<b>629.4</b>	<b>0.0</b>	<b>0.54</b>
	LUI	-309.6	126.2	631.4	2.0	0.20
	LUI x tongue length	-307.6	94.6	631.4	2.0	0.20
	Floral diversity x tongue length	-308.7	94.6	633.7	4.3	0.06
	LUI x colony size (ordinal)	-317.8	108.1	649.7	20.3	0.00
	Floral diversity x colony size (ordinal)	-319.2	126.2	650.6	21.2	0.00
	Floral diversity	-320.7	151.4	651.5	22.1	0.00
	LUI x colony size (numeric)	-320.6	126.2	653.4	24.0	0.00
	Floral diversity x colony size (numeric)	-320.7	108.1	655.6	26.2	0.00
<b>Glycogen concentration</b>	<b>LUI x tongue length</b>	<b>-2132.70</b>	<b>83.1</b>	<b>4281.6</b>	<b>0.00</b>	<b>0.55</b>
	Floral diversity x tongue length	-2132.94	83.1	4282.1	0.52	0.42
	Null model	-2139.10	133.0	4288.3	6.70	0.02
	LUI	-2139.00	110.8	4290.2	8.60	0.01
	Floral diversity x colony size (ordinal)	-2140.99	110.8	4294.1	12.54	0.0
	LUI x colony size (ordinal)	-2140.40	95.0	4295	13.40	0.0
	Floral diversity	-2146.54	133.0	4303.2	21.59	0.0

*Table 4. 2: Summary of the generalized linear mixed effect models analyzing the effect of LUI on the body condition of each bumblebee species. Species-specific effects were investigated through a nested design model, whereby the influence of the LUI was tested as a nested effect within the Species grouping variable.*

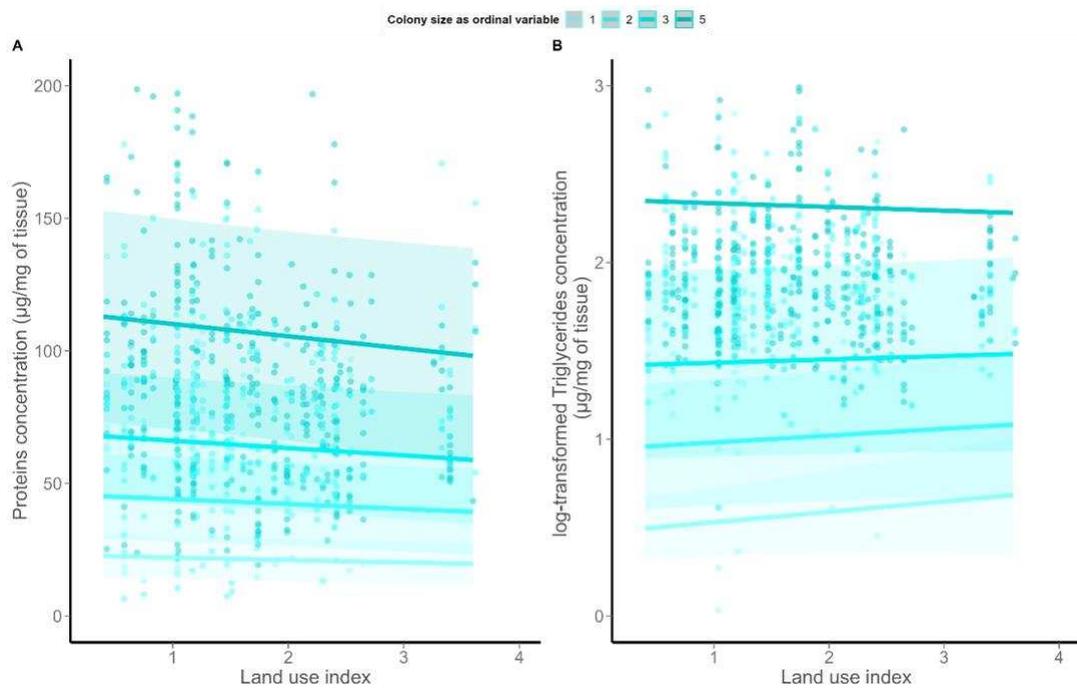
Response	Species	Intercept		Species-specific LUI effect		Sample size
		Estimate	p-value	Estimate	p-value	
<b>Body mass</b>	Bombus_hortorum	226.8	<0.001	- 14	0.26	767
	Bombus_lapidarius	59.5	<0.001	5.3	0.34	
	Bombus_pascuorum	154.8	<0.001	6.7	0.25	
	Bombus_sylvarum	195.3	<0.001	- 25.5	<b>0.004</b>	
	Bombus_terrestris	213.1	<0.001	2.2	0.77	
	AIC			(8072.2)		
<b>Proteins concentration</b>	Bombus_hortorum	72.44	<0.001	6.5	0.45	763
	Bombus_lapidarius	80.39	<0.001	- 3.8	0.18	
	Bombus_pascuorum	73.34	<0.001	2.2	0.49	
	Bombus_sylvarum	71	<0.001	- 2.8	0.62	
	Bombus_terrestris	127.7	<0.001	- 9.6	<b>0.04</b>	
	AIC			(7518.6)		
<b>Triglycerides concentration</b>	Bombus_hortorum	1.81	<0.001	0.03	0.75	757
	Bombus_lapidarius	1.94	<0.001	- 0.03	0.38	
	Bombus_pascuorum	1.86	<0.001	0.03	0.35	
	Bombus_sylvarum	1.62	<0.001	0.03	0.71	
	Bombus_terrestris	1.95	<0.001	- 0.004	0.94	
	AIC			(628.6)		
<b>Glycogen concentration</b>	Bombus_hortorum	0.08	0.99	3.8	0.35	665
	Bombus_lapidarius	9.22	<0.001	0.82	0.13	
	Bombus_pascuorum	9.36	<0.001	-0.9	0.12	
	Bombus_sylvarum	6.88	<0.001	0.06	0.95	
	Bombus_terrestris	9.12	<0.001	0.23	0.80	
	AIC			(4284.2)		



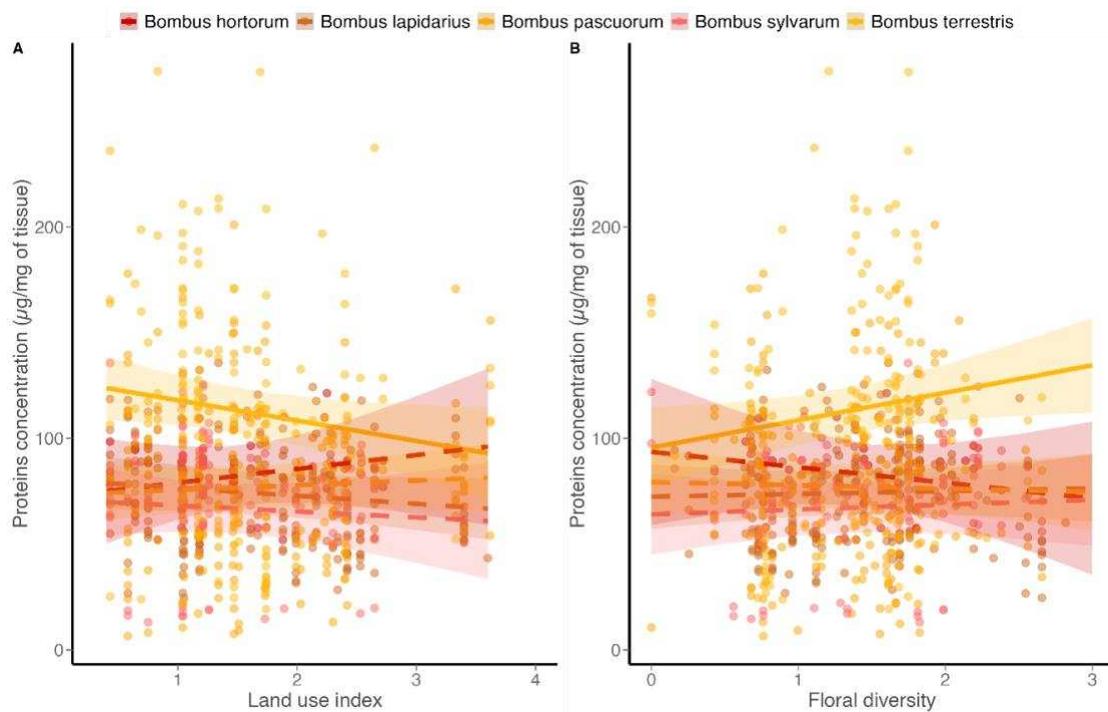
**Figure 4. 2:** Relationship between the body mass (in mg) of five *Bombus* species and A the LUI and B the Shannon Index of floral diversity. Solid and dashed lines represent significant and non-significant relationships, respectively. Dots represent the 767 females that were analysed.



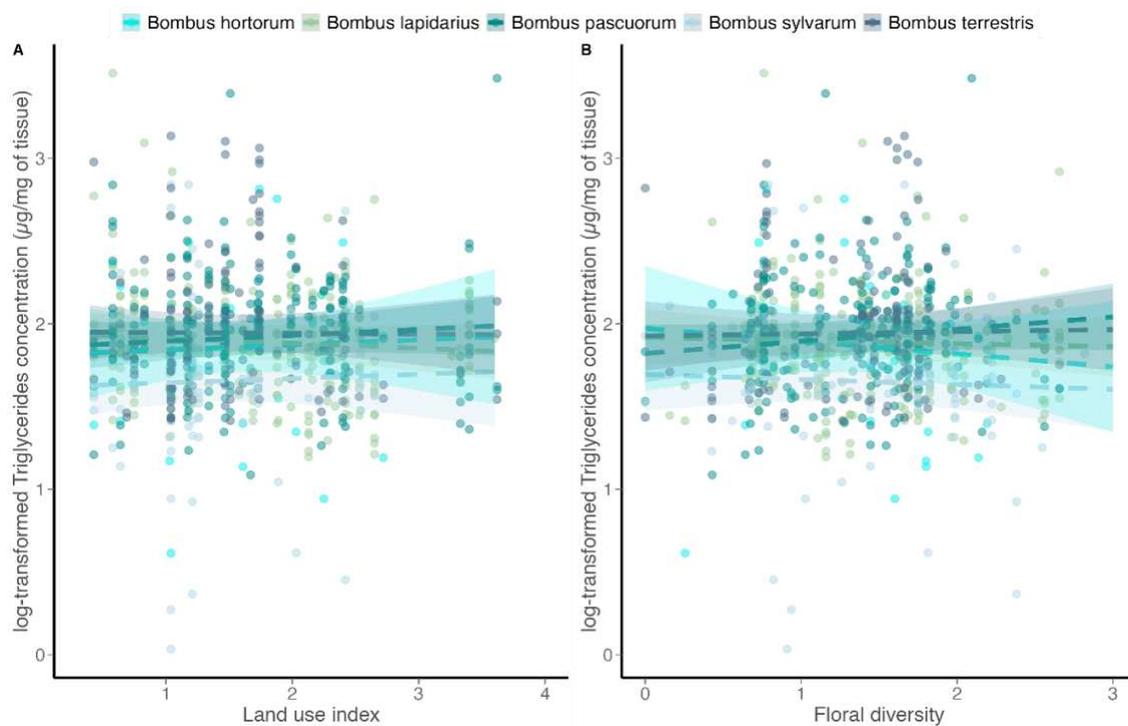
**Figure 4. 3:** Relationship between (A) the protein concentration and (B) the glycogen concentration in bumblebees of different tongue lengths and the LUI index. Few values are hidden for the better representation of trends.



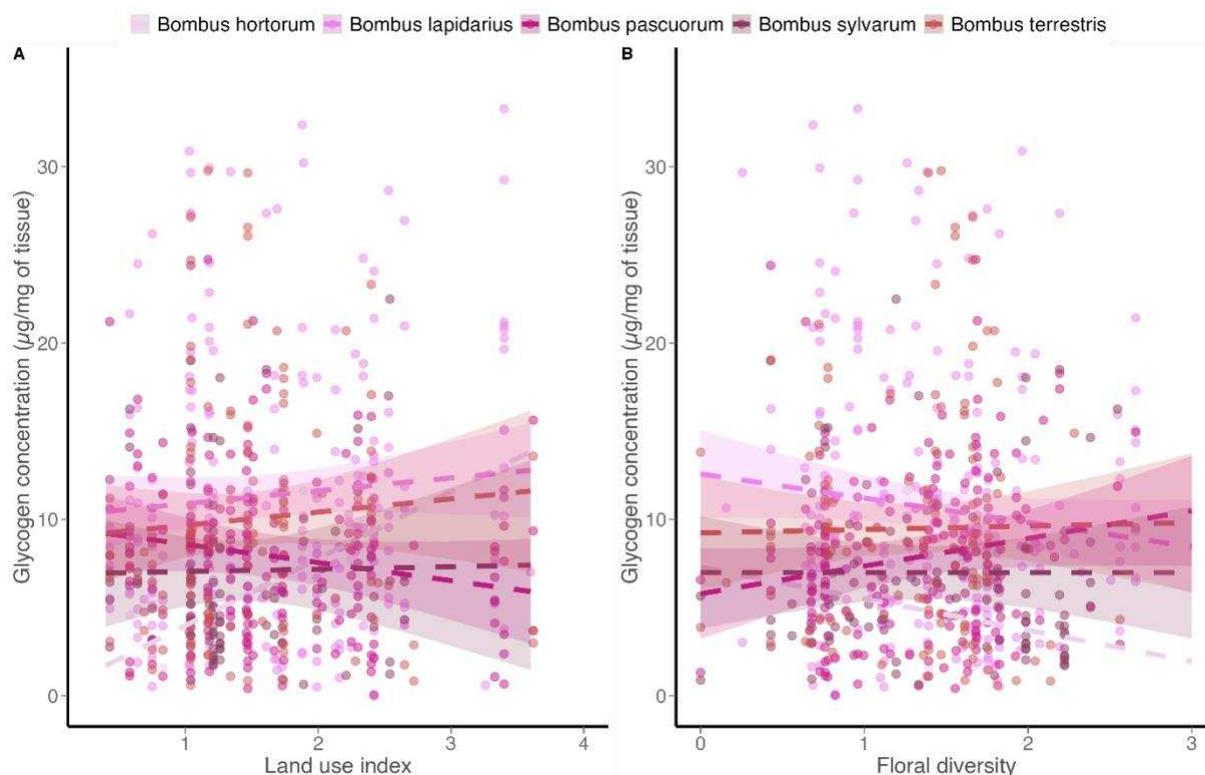
**Figure 4. 4:** Relationship between (A) the protein concentration and (B) the triglycerides concentration in bumblebees of different colony size and the LUI index. Few values are hidden for the better representation of trends.



**Figure 4. 5:** Relationship between the protein concentration in five *Bombus* species and A the LUI and B the Shannon Index of floral diversity. Solid and dashed lines represent significant and non-significant relationships, respectively. Dots represent the 763 females that were analysed.



**Figure 4. 6:** Relationship between the triglycerides concentration in five *Bombus* species and **A** the LUI and **B** the Shannon Index of floral diversity using a Log-transformation. Dashed lines represent non-significant relationships. Dots represent the 757 females that were analysed.



**Figure 4. 7:** Relationship between the glycogen concentration in five *Bombus* species and **A** the LUI and **B** the Shannon Index of floral diversity. Dashed lines represent non-significant relationships. Dots represent the 665 females that were analysed.

*Table 4. 3: Summary of the generalized linear mixed effect models analyzing the effect of the Floral diversity index of floral diversity on the body condition of each bumblebee species. Species-specific effects were investigated through a nested design model, whereby the influence of the Floral diversity index was tested as a nested effect within the Species grouping variable.*

Response	Species	Intercept		Species-specific Floral diversity effect		Sample size
		Estimate	p-value	Estimate	p-value	
<b>Body mass</b>	Bombus_hortorum	205.15	<0.001	0.91	0.95	767
	Bombus_lapidarius	188.17	<0.001	-12.8	<b>0.09</b>	
	Bombus_pascuorum	170.42	<0.001	-2.22	0.78	
	Bombus_sylvarum	170.9	<0.001	-7.53	0.44	
	Bombus_terrestris	196.38	<0.001	15.1	0.12	
	AIC			(8080.1)		
<b>Proteins content</b>	Bombus_hortorum	93.6	<0.001	-7.3	0.51	767
	Bombus_lapidarius	72.4	<0.001	1.3	0.74	
	Bombus_pascuorum	79.3	<0.001	-1.5	0.74	
	Bombus_sylvarum	64.1	<0.001	2.3	0.69	
	Bombus_terrestris	95.6	<0.001	13	<b>0.03</b>	
	AIC			(7520.7)		
<b>Triglycerides content</b>	Bombus_hortorum	1.97	<0.001	-0.08	0.52	757
	Bombus_lapidarius	1.92	<0.001	-0.02	0.7	
	Bombus_pascuorum	1.82	<0.001	0.07	0.17	
	Bombus_sylvarum	1.7	<0.001	-0.03	0.66	
	Bombus_terrestris	1.93	<0.001	0.01	0.85	
	AIC			(628)		
<b>Glycogen content</b>	Bombus_hortorum	7.28	0.52	-1.78	0.83	665
	Bombus_lapidarius	12.6	<0.001	-1.38	<b>0.08</b>	
	Bombus_pascuorum	5.78	<0.001	1.57	<b>0.08</b>	
	Bombus_sylvarum	7	<0.001	0.0	0.997	
	Bombus_terrestris	9.2	<0.001	-0.27	0.81	
	AIC			(4277.2)		

## Discussion

Through studies of bee abundance and richness, it was regularly found that many bee species are sensitive to landscape modifications (Potts et al., 2010; Rollin et al., 2019), which are often related to changes in floral abundance and diversity (Carrié et al., 2017; Kennedy et al., 2013). In particular, a decline in several (not all) bumblebee species has been reported in Europe in terms of local abundance and geographical range; decline that has notably been attributed to land-use changes (losses of floral resources and nesting sites. This may be explained by the fact that bumblebees are able to store nectar and pollen for only a few days and thus, they need habitat exhibiting continuous availability of

resources during their yearly life cycle (Benton, 2006; Goulson, 2003). However, the mechanisms underlying the species sensitivity to changes in land use and resource availability remain unclear. By investigating the influence of grassland management practices and of local plant diversity on bumblebee's body condition, we were able to identify some species traits explaining the bumblebee's responses to the land use.

We did not observe any general influence of the LUI and floral diversity on bumblebees, when analyses were performed at the genus level (all species included). However, we found responses to land use that were species and traits specific.

Body mass is a key functional trait, believed to rapidly change according to changing environmental conditions such as resource availability and climate (Chown and Gaston, 2010) that may relate to flight performance and nutrition in bumblebees. Variations in body mass from several according to grassland management were thus expected. However, among the five studied bumblebee species, only the shrill carder bee *Bombus sylvarum* exhibited a decrease of body mass along the LUI index, with bees being almost twice lighter in the most managed grasslands as compared to bees from the least managed grasslands. This could be attributed to their particularly narrow diet breadth, being rather specialised (Connop et al., 2010), but also to their relatively small-size colonies. Since the size and body mass of bumblebees is determined by the quality and abundance of pollens that are ingested during the larval stage, we could assume that increasing grassland managements might lead to the reduction or disappearance of preferred pollens and therefore pollen storage for larvae (Tasei and Aupinel, 2008).

Returning to our second hypothesis that sites with higher floral diversity will host bees that exhibit positive body condition indicators, we only find partial support. Interestingly, the protein concentration in *Bombus terrestris*, which is a rather generalist species foraging on numerous different plant families (Leonhardt and Blüthgen, 2012; Rasmont et al., 2008), declined with the LUI index but increased with plant diversity on the plots they were collected. This suggests that the LUI influence on protein concentration was related to a decline in plant diversity, and that this later is critical to their protein or amino acid diet. Maybe more surprisingly, this trend was only observed in *Bombus terrestris*, indicating that the protein concentration in bee body was not a sensitive trait in others species. However, the trend for a decline in protein concentration along the LUI appeared to be rather specific to short-tongued species and not to long-tongued species.

Bumblebee's tongue length is known for affecting food access and choice (Harder, 1985), with species with long tongues (like *Bombus pascuorum* or *B. sylvarum*) being able to feed on flowers with long corollas as compared to species with short tongues. It is then believed that short-tongued species, are mostly generalists with better ability to exploit nectar from a large diversity of flowers (Heinrich, 1976), but the opposite assumption was also made (Harder, 1985). Previous studies reported a lack of association between the probability of decline and tongue length in bumblebees (Williams et al., 2009), but our data showed that tongue length may explain to some extent the susceptibility of

bumblebees (in terms of nutritional state) to the availability of food plants. It is therefore possible that the floral resource availability (pollen abundance and diversity) is more critical for short-tongued species for the maintenance of a high level of proteins.

The influence of tongue length on bumblebee's sensitivity to land use was further confirmed with the variations in glycogen concentration. The glycogen concentration increased and decreased along the LUI in short- and long-tongued species, respectively. Glycogen is synthesized from UDP-glucose, mainly derived from dietary carbohydrates or amino acids, suggesting that long-tongued species had more difficulties to collect nectar, which contains the nutrients required for glycogen synthesis. One possible explanation is that the diversity and/or abundance of flowers with long corollas declined with the increasing grassland managements, and inversely the flora composition favorable to short-tongued species increased (e.g. flowers with short corollas). Short-tongued bumblebees are proved to forage more efficiently on short-tubed plant species in the landscape than long-tongued species. They consequently benefit more from such resources like in the oilseed rape mass-flowering crops (Walther-Hellwig and Frankl, 2000; Westphal et al., 2006). In addition to their matching tongue length, the short-tongued bumblebees often have large foraging ranges enabling them to use more distant resources (Greenleaf et al., 2007). They could, therefore may be able to find more nectar with a larger foraging radius. Further analysis including the floral composition along the LUI could help decipher this relationship between tongue length and glycogen concentration on the bee body. However, we cannot exclude that the foraging efforts increase along the LUI gradients in long-tongued species, leading to less energy storage essential to flight activity, such as glycogen.

Interestingly, there was marginal tendency for bees from large colonies to exhibit a decline in protein and triglyceride concentrations. The initial expectation was that medium/large colonies (>150 workers) would be able to better compensate a decline in environmental resources due to higher food storage and foraging capacities. However, it seems that they are more sensitive than small-size colonies, likely due to the large number of bees to feed.

It is also interesting to note that bumblebees were in general more sensitive to the LUI than to the floral diversity. This might come from the scale of these environmental variables. The floral diversity was indeed measured on a local scale (16 m<sup>2</sup> per plot), which very likely did not cover the full foraging range of bumblebees (with studies giving large estimations from several hundred meters up to 2.2 km (Kreyer et al., 2004; Osborne et al., 1999)) contrary to the LUI, although it gave an estimate of the floral diversity in the foraging area.

By conducting an *a posteriori* statistical power analysis, we observed that body mass was generally the less dispersed bee variable, with relatively low coefficients of variations CV for most species (22% to 32%). It was thus possible to detect quite small effect sizes (10% to 20% of the mean) with 100 to 150 individuals per modality in a control vs. treatment experiment. On the contrary, glycogen was a highly variable metric (CV= 57% to 70%), meaning that only moderate effect sizes (e.g. 30% effect) could be detected with a sample size of 100 individuals per modality. Triglycerides and proteins had an

intermediary pattern, with some *Bombus* species being more prone than others to reveal small effect sizes (15-20%) with small sample sizes (50-100 individuals). Conversely, the power analysis, given our sample sizes for the different bumblebee species, suggested that we would have been able to detect rather small physiological variations along the studied LUI or floral diversity gradients, should they have existed. With the exception of *B. hortorum* (n=34 individuals), our survey returned between 100 to nearly 300 individuals per species, which is equivalent to 50 to 150 individuals per tested modality, or per degrees of freedom in a regression analysis. With such sample sizes, we may be confident to affirm that some moderate to large physiological effects occurring along the studied would have been detected with confidence in our study, should they exist. We may however not exclude that smaller effects may actually occur but without being detected with our analysis.

## Conclusion

We clearly showed that bumblebee species respond differently to the changes in land use, as evidenced in previous studies (Bommarco et al., 2011; Dupont et al., 2011).

Most importantly, our results demonstrated that physiological metrics, and specifically indicators of the nutritional state associated with functional traits, may help to better understand the species sensitivity to environmental variables. Within this perspective, studying other wild bee families like Andrenidae or Halictidae and complementary functional traits, related for instance to diet specialization, foraging distance and phenology, may help to better identify the different population responses at the community level. Gathering 'community physiological profiles' in relation to environmental features is indeed particularly relevant for improving conservation measures, since conservation strategies should focus on management practices that support at minima the most vulnerable species. In this context, further studies are needed to decipher the species sensitivity to habitat alteration, and likely anticipating changes in population trends.

## Synthèse

De manière générale, les espèces semblent plus sensibles au changement d'utilisation du sol qu'à la diversité florale. Cette différence pourrait s'expliquer par l'échelle d'analyse : échelle du paysage pour l'utilisation du sol, et une dizaine de mètres carrés pour la diversité florale, résolution possiblement insuffisamment représentative et inadéquate avec le rayon de butinage des bourdons. Ces variables restent tout de même pertinentes à tester pour d'autres espèces d'abeilles solitaires avec un rayon de butinage plus restreint. Les espèces de bourdons étudiées ne semblent pas répondre identiquement à la disponibilité des ressources florales.



# Discussion générale

Les objectifs de cette thèse pluridisciplinaire étaient (1) d'identifier l'importance des éléments paysagers liés à la disponibilité en ressources florales sur l'état de santé des communautés d'abeilles sauvages (conditions corporelles), (2) de tester le potentiel d'indicateurs du statut nutritionnel pour évaluer la sensibilité des abeilles sauvages aux changements dans la disponibilité des ressources florales et (3) de porter la réflexion sur des pistes de conservation adaptées.

## I. Les agroécosystèmes, des zones à fort enjeux de conservation des communautés d'abeilles

Les agroécosystèmes, par la modification des habitats qu'ils engendrent et la superficie qu'ils occupent (près de la moitié de la surface du globe, FAO, 2009), sont au cœur de nombreux enjeux de conservation. La contribution de ces zones à la biodiversité est cruciale pour des aspects de conservation d'où la nécessité d'en étudier les fonctions, les organismes y vivant, les apports et les bénéfices qu'elles fournissent sous la forme de services écosystémiques tels que la pollinisation ou le contrôle biologique, mais également les effets négatifs de ces agroécosystèmes sur la biodiversité (Batáry et al., 2010). En effet, les pratiques agricoles affectent notablement le paysage floral et donc, nutritionnel, à disposition des insectes floricoles et en l'occurrence, des abeilles sauvages. Les terres agricoles sont ainsi connues pour abriter une diversité florale plus faible (Letourneau et al., 2011; Poggio et al., 2013) et abritent par conséquent, une diversité nutritionnelle réduite pour les abeilles (Diekötter et al., 2010; Pasquale et al., 2013).

Les agroécosystèmes que j'ai pu étudier, à savoir les vergers du sud de la France et les zones de prairies en Europe, et plus particulièrement en Belgique et en Allemagne, partagent des points communs. Tous deux présentent des gradients de disponibilité en ressources florales (richesse et abondance des ressources) qui varient en fonction des pratiques de gestion. Ces caractéristiques entraînent donc des changements dans l'abondance et la diversité des ressources florales et par conséquent, de la qualité nutritionnelle à disposition des abeilles. Un stress nutritionnel est donc susceptible d'apparaître (Goulson et al., 2015; Persson et al., 2015; Vaudo et al., 2015). Et malgré l'importance accordée à la recherche sur la nutrition des abeilles, nous n'en sommes qu'aux premiers stades de la compréhension des aspects multidimensionnels de l'écologie nutritionnelle des abeilles, qui peuvent être appliqués pour améliorer la nutrition et la santé générale des abeilles dans un environnement soumis à de nombreux facteurs de stress. Dans ce contexte, nous avons mis en application des nouvelles approches pour mieux évaluer la sensibilité à l'échelle de l'espèce ou à l'échelle de la communauté des abeilles à ces habitats.

Nos travaux ont pu confirmer l'importance des éléments semi-naturels pour les abeilles sauvages au sein des agroécosystèmes (chapitre 3 et voir aussi Carvell et al., 2007; Kremen et al., 2019; Rivers-Moore et al., 2020). Aussi, les travaux du chapitre 4 ont souligné l'importance de la richesse florale à disposition des abeilles et les désavantages que peuvent représenter une utilisation importante du sol

dans des systèmes de prairies sur la condition corporelle des abeilles sauvages. A la suite de nos travaux, il serait important de caractériser et déployer de mesures restauratives au niveau de l'habitat ou du paysage. En effet, la conservation de la biodiversité et des pollinisateurs, ne va pas sans la conservation des habitats et de l'environnement qui l'abrite. Des projets à venir et en préparation (projet européen transdisciplinaire Restpoll porté par l'université de Freiburg) pourraient tenter d'y répondre en intégrant des mesures de préservation ou restauration d'éléments naturels particuliers comme les haies, les milieux boisés etc.

## **II. Apports et complémentarité de la physiologie dans les approches de conservation**

D'un point de vue écologique, les mesures de conservation devraient commencer avant qu'une espèce ne soit en danger, c'est-à-dire avant que la taille de sa population ne décline jusqu'à des niveaux critiques (Soulé, 1987). Ces approches de conservation proactives, en plus d'être plus efficaces, sont également plus rentables que les stratégies réactives (Drechsler et al., 2011). Comme décrit dans notre article d'opinion (chapitre 2, Leroy, 2022), la PC étant une méthode alternative rassemblant ces caractéristiques, nous avons fait l'hypothèse que son utilisation pourrait bénéficier à la conservation des populations d'abeilles sauvages. En se focalisant sur des traits morphologiques comme nous avons pu le faire avec la mesure de la masse corporelle, des études sur les changements morphologiques observés au niveau de collections d'histoire naturelle des insectes ont déjà permis de comprendre les effets du climat et des changements d'utilisation des sols chez des bourdons et des papillons respectivement (Gérard et al., 2020b; MacLean et al., 2018). Dans une autre étude, des mesures de la taille corporelle et du pattern allaire ont permis d'identifier la sensibilité de certaines espèces à l'implantation de bandes herbeuses dans les parcelles de culture (Borchardt et al., 2023).

La physiologie de la conservation est d'ores et déjà appliquée et évaluée de façon approfondie et régulière sur certains taxons sauvages comme les mammifères terrestres avec (Joly et al., 2015; Marín-García et al., 2022) ou marins (Hunt et al., 2013). C'est une discipline qui permet, grâce à son approche mécanistique, d'établir des liens de causes-à-effets entre des phénomènes extrinsèques, liés aux changements environnementaux et des phénomènes intrinsèques de fonctionnements physiologiques. elle constitue en cela un outil précieux qui permet aux gestionnaires la priorisation et la définition des stratégies d'atténuation (Carey, 2005; Wikelski and Cooke, 2006). Certains de ses effets sont déjà visibles dans des programmes de conservation (Madliger et al., 2016). Cette discipline reste toutefois encore peu étudiée et rarement utilisée pour la conservation des abeilles sauvages (Gonzalez et al., 2022; Mogren et al., 2020).

Dans notre travail nous nous sommes intéressé-es plus spécifiquement aux marqueurs du métabolisme reflétant la nutrition en faisant l'hypothèse que les données obtenues par l'intermédiaire

de ces marqueurs seraient informatives sur la sensibilité des abeilles vis-à-vis des modifications dans les ressources du paysage. Dans la mesure où les abeilles sauvages entretiennent des relations très étroites avec les ressources florales pour leur développement, leur reproduction, leur alimentation et leur nidification, des changements survenant dans leur habitat (zone de butinage) pourraient avoir des conséquences directes sur leur état nutritionnel et les fonctions associées (ex. réserves énergétiques, immunité). La compréhension de la nutrition apparaît donc comme un élément essentiel et complémentaire à la compréhension de l'état physiologique des individus. Étant donné que les apports nutritionnels déterminent fortement la santé, la résilience aux pathogènes et la fitness des organismes (Simpson and Raubenheimer, 2012), l'accès à une nutrition diversifiée et équilibrée est un facteur clé de la stabilité d'une population en particulier chez les abeilles (Vaudo et al., 2015). Ainsi, des pressions exercées sur les ressources florales, dont elles dépendent, vont induire des réactions, des réponses physiologiques détectables à l'échelle individuelle comme cela a été démontré dans les travaux de (Mogren et al., 2020; Treanore et al., 2019). De façon expérimentale, Treanore et collaborateur·ices font le lien entre diversité du régime pollinique et physiologie d'une espèce de bourdons tandis que Mogren et collaborateur·ices ont évalué l'effet du paysage et de la composition de la diète sur des concentrations de macronutriments. Ces études, tout comme nos travaux sur le terrain, confirment la pertinence d'utiliser ces traits du métabolisme nutritionnel en relation avec les ressources florales.

Nous avons en effet vu dans le chapitre 2 qu'ils peuvent constituer un levier d'action important, mais que leur étude reste encore à la marge. La physiologie de la nutrition, en particulier chez les mammifères et chez les espèces à fort impact économique, a pourtant été largement étudiée dans le contexte agricole (McDonald, 2011). En effet, l'étude d'indicateurs nutritionnels du métabolisme ont également émergé dans les études portées notamment sur la conservation de la faune sauvage (Kim Birnie-Gauvin et al., 2017). Il existe des marqueurs disponibles et bien établis qui ont déjà fait leur preuve comme la masse corporelle, la largeur du corps, ou des mesures de nutriments comme les compositions en lipides et en vitamines. Les mesures de ces dernières ont d'ailleurs permis de démontrer que les déclinés dramatiques des populations de truites lacustres indigènes sont attribuables à une déficience de vitamine (la thiamine) en raison d'un changement nutritif favorisant la consommation de gaspareau contenant de hauts niveaux de thiaminase (Madliger et al., 2016). Après identification du problème par les gestionnaires des stocks de pêche, les populations de gaspareau ont été réduites dans le but de restaurer les populations de truites lacustres indigènes. Dans ce cas, l'étude de la physiologie de la nutrition a donc permis de mettre en place des mesures adaptées de gestion et de conservation.

On peut en revanche constater que les besoins nutritionnels sont souvent étudiés au regard de la quantité, en accordant pas ou peu d'importance à la qualité (Wright et al., 2018). Cependant, l'usage de biomarqueurs métaboliques a rarement été entrepris chez les abeilles, qu'elles soient domestiques ou sauvages (Castle et al., 2023; Smart et al., 2016; Smith et al., 2016). Nos travaux représentent

donc un apport nécessaire et pluridisciplinaire pour l'application de ces marqueurs au sein des populations d'abeilles sauvages.

### III. La physiologie appliquée à l'échelle monospécifique ou de la communauté

Dans ce travail de thèse, l'approche de physiologie de la conservation a été appliquée aux niveaux d'une espèce (chapitre 3) et de la communauté d'abeilles (chapitre 4). Le premier projet de notre travail, qui fait l'objet du chapitre 3, consistait à appliquer des mesures de marqueurs physiologiques sur les individus d'une seule espèce, l'osmie cornue, dont le cycle de vie est parfaitement connu et maîtrisé et qui fait même l'objet d'élevage pour assurer la pollinisation de cultures (Bosch and Kemp, 2002; Sedivy and Dorn, 2014). Ce projet s'est déroulé dans les vergers d'une zone expérimentale dans le sud de la France et a pu être mené à bien grâce à la collaboration avec une équipe de recherche d'INRAE et à l'accord des arboriculteurs des vergers de la zone de la Durance. Il nous a permis de valider la preuve du concept présentée dans le chapitre 2 sur la pertinence de l'utilisation des marqueurs physiologiques. Nous avons pu mettre en évidence, à travers la physiologie, que certains éléments paysagers ont une influence sur la condition corporelle de la descendance d'osmies implantées dans des vergers.

Les éléments semi-naturels (haies, éléments boisés, bordures fleuries...) sont déjà connus pour présenter des effets bénéfiques sur les abeilles sauvages et sur la famille des mégachilidés en particulier. Comme dans les travaux d'Eckerter et al., 2022, nous avons pu démontrer que les éléments semi-naturels présentent une influence positive sur une espèce d'osmie, *Osmia cornuta* (Latreille). Notre étude sur la condition corporelle des femelles d'osmie cornue a démontré une influence positive du pourcentage d'éléments semi-naturels ainsi que de la longueur des haies (dans un rayon d'étude de 500 m) présents autour des sites de nidifications sur le poids et le contenu protéique des osmies qui ont émergé.

D'autres paramètres de la descendance femelle des osmies sont également positivement influencés ; nous avons notamment détecté un effet positif significatif des éléments semi-naturels et des haies sur le taux d'émergence. C'est en concordance avec les travaux de Bihaly et al., 2021; Boyle et al., 2020 et Ganser et al., 2021, qui ont démontré que la présence ou la proximité d'habitats naturels ou semi-naturels, tels que les haies ou les bordures de champs comportant des ressources variées, entraîne un meilleur succès reproducteur des abeilles sauvages.

Dans le quatrième chapitre, nous avons éprouvé notre concept à l'échelle de la communauté dans le cadre du projet européen NutriB<sup>2</sup> (Nutrition as critical link between Biodiversity and Bee health). Avec plus de 140 espèces échantillonnées à l'échelle du projet, nous avons acquis une multitude de profils physiologiques d'espèce et de traits associés. Les analyses biochimiques sur les marqueurs du métabolisme ont été conduites sur un sous-ensemble de 30 espèces et en particulier neuf espèces d'Andrènes, dix espèces de bourdons, cinq espèces d'Halictes et six espèces de Lasioglossum pour un total d'environ 1300 femelles. En focalisant nos premières analyses sur cinq espèces de bourdons,

nous avons pu démontrer que le poids et les contenus en protéines sont sensibles aux facteurs environnementaux. L'augmentation de l'intensité d'utilisation du sol, estimée à travers l'indice de LUI, impacte significativement et fait diminuer la masse corporelle des femelles de *Bombus sylvarum* et le contenu protéique des femelles de *Bombus terrestris*. Ces dernières sont, en revanche, favorisées par une augmentation de la diversité florale – mesurée avec l'indice de Shannon. Le contenu protéique des femelles de cette espèce augmente significativement avec la diversité florale. Le contenu en glycogène présente des fluctuations marginales et contrastées vis-à-vis de la diversité florale. En effet, le contenu en glycogène diminue marginalement avec la diversité florale chez les femelles de *Bombus lapidarius* et augmente marginalement chez les femelles de *Bombus pascuorum*.

En somme, nos deux études des chapitres trois (échelle monospécifique) et quatre (échelle de la communauté), suggèrent que le poids et la concentration en protéines constituent des marqueurs pertinents pour mesurer la sensibilité des espèces aux effets du paysage.

Tout d'abord ces marqueurs sont liés à l'état nutritionnels des individus. Le poids fortement lié à la taille reflète majoritairement le statut nutritionnel à l'état larvaire, et la concentration en protéines pouvant refléter le statut nutritionnel à la fois au cours du développement ou au stade adulte (selon la période d'échantillonnage : par exemple abeille émergente par opposition à abeille butineuse). D'autre part ces mesures de poids et de de taille corporelle, sont souvent corrélées à des données de survie et succès reproducteur chez les abeilles (Bosch and Vicens, 2006a; O'Neill et al., 2014; Slominski and Burkle, 2021) et sont des indicateurs prometteurs pour le suivi de l'état de santé des populations.

Notre étude a permis de montrer que les mesures de contenus protéiques semblent être suffisamment sensibles pour attester des effets de l'environnement sur les abeilles sauvages. En revanche, des marqueurs métaboliques reflétant l'état nutritionnel comme les contenus en triglycéride et en glycogène, ne semblent pas ou peu affectés, respectivement, par les changements dans la qualité des habitats.

Les protéines sont des macronutriments connus pour être impliqués dans la reproduction, la production d'œufs chez diverses espèces d'abeilles sauvages comme les bourdons (Moerman et al., 2016; Vanderplanck et al., 2014). Les protéines semblent donc faire l'objet de décisions nutritionnelles, notamment chez les bourdons où les ouvrières de certaines espèces sont capables d'orienter leurs choix et ainsi sélectionner des pollens affichant des contenus protéiniques élevés (Ruedenauer et al., 2016; Vaudo et al., 2016). L'absence ou les faibles variations observées pour les autres mesures du statut nutritionnel pourraient s'expliquer par le rôle physiologique exercé par ces nutriments. En effet, en tant que principales réserves énergétiques chez les insectes et autres organismes, les contenus en triglycérides et en glycogène seraient régulièrement mobilisés et reconstitués selon les besoins (par ex. activité de vol). Leur importante fluctuation au cours de la vie d'un individu rend ces marqueurs difficiles à caractériser. D'ailleurs, tout comme dans les travaux de Mogren, l'absence de significativité observée dans les concentrations en triglycérides (lipides) chez

nos espèces étudiées, pourrait être attribuée à un état pré ou post-reproductif (chez les osmies davantage que chez les bourdons dont le statut était celui d'ouvrières). En effet, les abeilles sauvages portent à elles-seules la collecte des ressources à l'attention de leur descendance, ainsi la production d'oeufs entraînerait nécessairement une diminution des stocks de lipides (Lawson et al., 2017). Alors que chez les bourdons, les reines vont être capables d'accumuler des stocks importants de glycogène et de lipides au sein de leurs corps gras, les ouvrières et les mâles n'en sont pas capables (Röseler and Röseler, 1986). Nous savons également que les ouvrières de bourdons privilégient l'apport en glucides au détriment des protéines en cas de mobilisation énergivore (Stabler et al., 2015). De plus, la littérature scientifique nous a appris que des situations de stress, qu'ils soient nutritionnels ou autres, entraînent une augmentation de la consommation de glucides chez les organismes. À l'échelle de nos travaux, nous pourrions suggérer que l'intégration de mesures de triglycérides et de glycogène devrait aller de pair avec la considération d'autres facteurs comme le statut reproducteur, les changements liés à la diapause voire la présence de pathogènes.

Alors, si nos travaux n'ont pas permis de mettre en évidence des liens entre le paysage et ces marqueurs nutritionnels considérés séparément, des ratios ou des rapports entre nutriments pourraient être davantage pertinents. En effet, chaque organisme possède un ratio et des concentrations optimales de nutriments, nommés '*intake targets*'. La géométrie de la nutrition, une approche de modélisation décrit la façon dont les animaux peuvent atteindre et maintenir un état nutritionnel optimal (*the intake target*) en ajustant leur consommation de nourriture à leurs besoins (Simpson and Raubenheimer, 2012). Cette approche a permis de démontrer la pertinence de l'utilisation des ratios de nutriments pour étudier comment les stratégies nutritionnelles peuvent influencer la santé des organismes. Ces stratégies nutritionnelles ont été mises en évidence chez les bourdons (Hendriksma et al., 2019; Leonhardt and Blüthgen, 2012) ou encore chez une espèce d'abeille maçonne (Austin and Gilbert, 2018), avec des différences exprimées dans la priorisation des nutriments et de leurs ratios et qui chez ces deux espèces, donnent la priorité à un régime axé sur les glucides. Une étude de ces ratios en fonction des contextes paysagers à l'aide nos données nous permettrait de potentiellement révéler la sensibilité de certains nutriments jusqu'ici peu réceptifs.

Aussi, il serait intéressant de considérer les fluctuations temporelles pour identifier les concentrations optimales de macronutriments à différents moments de l'année. Chez les bourdons, comme c'est le cas chez les abeilles mellifères, de telles fluctuations pourraient correspondre à des changements dans la physiologie des colonies liés à l'hivernage, au stress dû à la famine, à l'exposition aux pesticides et aux agents pathogènes. Cela entre en cohérence avec l'idée de phénologies des ressources dans le paysage où les apports fluctuent au cours de la saison. Ainsi, les marqueurs métaboliques reflétant la nutrition ne s'illustreraient pas de la même façon chez un individu collecté au printemps ou à l'été.

Ces recherches sur les ratios soulignent la nécessité de recherches approfondies sur les spécificités de chaque espèce pour identifier éventuellement des réponses ou besoins communs entre espèces. Afin

de mieux comprendre ces besoins et les réponses des différentes espèces nous avons cherché à savoir si la sensibilité des espèces aux effets du paysage peut s'expliquer à d'autres niveaux d'influence, par exemple par des traits fonctionnels (chapitre quatre).

#### **IV. Intégration des traits fonctionnels**

Au sein de notre travail de thèse, nous avons voulu mesurer l'effets des traits fonctionnels tels que la longueur du proboscis ainsi que de la taille de colonie sur nos marqueurs nutritionnels d'intérêt.

En intégrant des traits fonctionnels comme variables explicatives des évolutions observées dans la condition corporelle de cinq espèces de bourdons, nous avons pu identifier l'importance de la longueur du proboscis. En effet nous avons montré que la longueur du proboscis module la façon dont les concentrations en nutriments sont significativement impactées par les changements environnementaux. La concentration en protéines était plus susceptible de diminuer chez les individus avec des langues de petite taille avec une intensité de LUI plus élevée. En revanche, la concentration en glycogène était plus susceptible d'augmenter chez les individus possédant des langues courtes avec une intensité de LUI plus élevée. Ces résultats sont cohérents avec les travaux de Diekötter et al., 2010. Dans cette étude, les auteurs ont montré le lien entre la longueur du proboscis chez les bourdons et la surface de zone cultivée avec une diminution de l'abondance des espèces à langue courte avec l'augmentation de la surface de colza dans le paysage.

La taille de la colonie est, elle aussi, un trait fonctionnel intéressant à considérer chez les bourdons et informe sur un grand nombre de paramètres en lien avec la nutrition (temps de prospection, temps et taux de butinage...). Une étude montre que les colonies subissant une diminution de taille (moins d'ouvrières) affichent des potentiels de résilience et d'adaptation permettant de contrer la perte d'individus au sein de la colonie (Gérard et al., 2023). Notre étude a cependant démontré que les individus appartenant à des colonies de grande taille étaient plus susceptibles de subir des diminutions de concentrations en protéines et en triglycérides avec l'augmentation de l'intensité d'utilisation du paysage (LUI). Ainsi, même si les comportements de collecte alimentaire ne sont pas affectés, la qualité des ressources récoltées peut être amoindrie et ainsi, mener à une condition corporelle moins bonne chez les individus.

Bien que représentant une piste très intéressante, il est nécessaire de garder en tête que ces traits sont amenés à évoluer au cours des décennies à venir, comme abordé dans l'étude de Miller-Struttman et al., en 2015 qui souligne la diminution de la longueur de la langue en raison de la diminution dans la densité des ressources florales, favorisant ainsi des espèces aux profils généralistes (à courte langue). D'autres traits fonctionnels comme le degré de socialité, les matériaux nécessaires à la nidification et les mode de nidification, rendus disponibles grâce à des taxonomistes et écologues passionnés (Amiet et al., 2004, 2001; Scheuchl and Willner, 2016; Westrich, 1989) seraient intéressants à considérer. Par exemple, en considérant le degré de socialité, les espèces sociales pourraient exprimer une sensibilité moindre du fait de capacité de stockage des réserves alimentaires, par rapport aux abeilles solitaires

et la phénologie des espèces d'abeilles sauvages pourraient expliquer des différences de sensibilité en cours de saison.

Alors que certaines espèces semblent particulièrement sensibles aux changements environnementaux (ex. *Bombus sylvarum* dans notre étude), d'autres semblent pouvoir faire face à ces pressions (ex. *Bombus lapidarius*). Face à cette diversité de sensibilité, il apparaît intéressant d'explorer des moyens d'optimiser la surveillance de communautés d'abeilles en se focalisant sur un sous-ensemble d'espèces indicatrices.

## V. Les « espèces indicatrices »

Effectuer une gestion et un suivi d'une communauté entière, surtout à de larges échelles spatiotemporelles est un défi de taille dans la restauration écologique (Miller et al., 2017). Il est plus aisé de porter l'attention sur un assemblage restreint d'espèces chez lesquelles les changements de composition présagent d'importants changements écologiques ; on parle d'espèce indicatrices (Siddig et al., 2016). Entre les espèces parapluies, les espèces bioindicatrices, les espèces étendards, les espèces « keystone », le concept d'espèce indicatrice est vaste et diversifié (Siddig et al., 2016). L'idée générale reste de catalyser les actions de conservation. L'une des questions centrales est de savoir si les espèces d'un groupe taxonomique en particulier peuvent être considérées indicatrices de la richesse spécifique d'autres groupes taxonomiques.

Le défi reste d'identifier les critères de sélection et les espèces à surveiller. Parmi les critères utilisés pour déterminer le potentiel d'une espèce à avoir le statut d'espèce indicatrice, un habitat restreint ainsi que des ressources limitées sont des caractéristiques qui peuvent aider à déterminer précisément les zones présentant des valeurs particulières pour la biodiversité (Ozaki et al., 2006b). Les espèces suffisamment sensibles (mais de façon modérée) aux perturbations de l'habitat (proportion, taille et configuration des éléments du paysage) apparaissent comme de bonnes espèces indicatrices. D'autres traits physiologiques peuvent répondre à ces enjeux: par exemple Tomlinson a suggéré dans une étude de 2015 que l'espèce d'abeille *Amegilla chlorocyanea* pourrait être utilisée comme une espèce indicatrice de référence puisque ses besoins énergétiques excèdent de loin celle de toute autre espèce dans la communauté des hyménoptères locaux (Tomlinson et al., 2018b). Dans le contexte de changements environnementaux dans lequel nous nous trouvons, une piste semblant contre-intuitive mais jugée pertinente par d'autres chercheurs seraient de porter l'attention sur les espèces invasives (da Silva et al., 2021). En effet, les facteurs physiologiques mesurés (taux métabolique, résistance à la dessiccation, maximum thermique critique  $CT_{max}$ ) chez des espèces d'abeilles sauvages invasives témoignent de degrés élevés de plasticité et de potentiels adaptatif qui leur permettent de faire face à de nouvelles conditions environnementales (Davidson et al., 2011; Logan et al., 2020) en ajustant leur phénotype à des changements climatiques par exemple (Tepolt and Somero, 2014; Zerebecki and Sorte, 2011). Ces espèces peuvent se montrer plus résilientes à des changements de température et à des réductions d'opportunités alimentaires et plus a-même de se maintenir dans le futur. Dans notre étude, *Bombus terrestris* est une espèce abondante, connue pour être répandue et adaptable dans les

systèmes agricoles comportant moins de fleurs à longue corolles et des fleurs en général moins profondes (Rodríguez-Gironés and Llandres, 2008). Partant de ce constat et des résultats de notre travail, attestant de sa sensibilité aux caractéristiques environnementales, *B. terrestris* est une espèce qui pourrait être candidate en tant qu'indicatrice.

A la façon de Saleeba, nous pourrions, à l'issue de nos travaux, concevoir un modèle informatif, quantitatif et physiologique, considérant les facteurs environnementaux pour établir des prédictions sur l'absence de certaines espèces d'abeilles en fonction de leurs conditions corporelles connues (Saleeba et al., 2020). Dès lors, une posture pourrait être d'affiner l'échelle des approches de conservation à des zones exemptes d'espèces invasives et de mettre l'accent sur la conservation des espèces rares et/ou spécialistes (Russo et al., 2021).

## VI. Bilan et limites

A la question, les mesures physiologiques permettent-elles d'acquérir davantage de résolution que des mesures sur le terrain ? La réponse est évidemment nuancée comme le démontrent mes travaux de thèse qui ont mis en évidence des mesures physiologiques sensibles à la qualité des habitats (concentration en protéines) tandis que d'autres le sont moins ou pas (concentration en triglycérides). La PC présente l'avantage d'utiliser des outils sensibles aux réponses individuelles des organismes, qui en font des signaux d'alarme d'un grand intérêt pour informer sur une perturbation susceptible d'engendrer des effets négatifs à un niveau supérieur d'organisation (population, communauté). Ces signaux peuvent alors être reçus et évalués de façon précoce et permettre ainsi de saisir et établir les stratégies de conservation adaptées. De manière générale, des marqueurs physiologiques (reconnus et établis) de la vitalité des abeilles pourraient nous informer sur la qualité des habitats dans lesquels elles évoluent. Le caractère prédictif affiché par la physiologie est intéressant, et puisque les changements physiologiques surviennent en amont des changements démographiques (Ellis et al., 2012) la mesure de marqueurs physiologiques permettrait également d'anticiper un potentiel déclin des populations. L'utilisation des biomarqueurs physiologiques, de façon complémentaire à l'intégration des traits fonctionnels et à la considération des espèces indicatrices ne fait pas encore légion mais présente le potentiel de révolutionner la conservation (Madliger et al., 2018). En outre, il est raisonnable de voir la physiologie comme une approche complémentaire intéressante avec des aspects mécanistiques qui permettent d'explorer d'autres formes de relations. Par exemple, il pourrait être intéressant de privilégier des études sur les liens entre variations des conditions corporelles et fitness (survie, succès reproducteur).

Ces traits de la condition corporelle sont à même de mettre en évidence la sensibilité intra et interspécifique en tous cas, en partie, par les mesures que nous avons employées. Les mesures, d'abord menées chez des espèces gérées et/ ou commercialisées (une espèce d'osmie et cinq espèces de bourdons) ont vocation à être appliquées chez des espèces non-gérées comme c'est le cas des *Andrènes* par exemple.

Toutefois, ces mesures revêtent en l'état des aspects critiquables et perfectibles. On peut notamment

citer leur caractère invasif car elles requièrent le sacrifice des individus pour pouvoir analyser leurs contenus métaboliques. Pourtant, il est établi que des marqueurs de stress non invasifs existent chez les abeilles mellifères comme c'est le cas de la vitellogénine ou des protéines de choc thermique (Bordier et al., 2017; Even et al., 2012). En revanche, leur transposition aux espèces sauvages reste encore en questionnement. La temporalité est également une notion importante à considérer. Il est intéressant de noter que les spécialistes des abeilles ont estimé qu'un programme de suivi sur dix ans était le plus approprié pour détecter les tendances à long terme des populations d'abeilles, avec des périodes plus longues pour évaluer l'influence du changement climatique (30 ans) ou de la complexité du paysage (15 ans) (Breeze et al., 2020).

Puisque dans les perspectives de conservation, les décisions sont basées sur de la sélectivité et du pragmatisme, il est de mise de concentrer les études et la compréhension de phénomènes sur un cohorte restreint d'espèces plutôt que de miser sur de l'exhaustivité. Cela aurait l'avantage, dans le contexte de la physiologie de la conservation, d'alléger et optimiser les aspects chronophages et coûteux de ces mesures (Drechsler et al., 2011). Ces décisions sont délicates et compliquées, en effet, les questions se multiplient et continueront à se multiplier. Quelles espèces doivent faire l'objet d'une gestion active ? Quelles espèces doivent être conservées ? Où faut-il déployer des efforts pour obtenir le meilleur « rendement » ? Or, ces décisions ne peuvent être prises sans données empiriques sur les espèces, ce qui peut s'avérer difficile pour les espèces cryptiques ou celles qui se rencontrent de manière irrégulière dans l'espace et dans le temps. Compte tenu du nombre croissant d'espèces cryptiques figurant sur les listes d'espèces menacées, des efforts d'enquête plus ciblés sont nécessaires.

## **VII. Concilier conservation et valeur intrinsèque (ou capital nature) de la biodiversité**

Les notions de sélectivité et de pragmatisme, mentionnées précédemment, soulèvent la question cruciale de savoir qui décide et comment communiquer sur les prises de décision ? Cela soulève des enjeux de communication et de compréhension des risques associés à la perte de biodiversité et posés au bien-être « humain ». Le transfert de connaissances sur la biodiversité, au travers de projets interdisciplinaires et de sciences participatives, joue un rôle déterminant dans la sensibilisation à notre dépendance à la nature et pour une transformation sociétale profonde vers la conservation et restauration de la biodiversité dont font partie les abeilles sauvages (Bartomeus and Dicks, 2019; Zattara and Aizen, 2021). En effet, malgré la valeur du capital « nature » dans nos économies et nos sociétés, et les interdépendances de la nature avec d'autres objectifs sociétaux, elles ne sont souvent pas reflétées dans les décisions économiques et politiques, les indicateurs et les systèmes comptables privés et publics de la même manière que le capital économique et humain. Il existe une asymétrie fondamentale où sont favorisées la production et la consommation à court terme de produits commercialisés au détriment de la gestion du capital naturel nécessaire au bien-être de l'homme à long terme (Guerry et al., 2015).

Et même si les aspects économiques entrent en jeu pour orienter telle stratégie de conservation plutôt

qu'une autre, considère-t-on que seules les espèces a-même d'effectuer un service de pollinisation efficacement méritent d'être sauvées (soit 2% des abeilles sauvages seulement (Kleijn et al., 2015)) ? Si l'on se place du point de vue de la valeur intrinsèque de la biodiversité ce n'est pas le cas. La valeur intrinsèque est la valeur qu'une entité a en elle-même pour ce qu'elle est ou en tant que finalité (Chan et al., 2012). Le type de valeur opposé est la valeur instrumentale. La valeur instrumentale est la valeur d'une chose en tant que moyen d'atteindre une fin souhaitée ou appréciée. La valeur instrumentale est toujours dérivée de la valeur d'une autre chose et elle est toujours conditionnelle. La valeur instrumentale d'une chose fluctue en fonction des changements dans la désirabilité de la fin pour laquelle elle est un moyen et de l'existence d'autres moyens plus efficaces. Par exemple, un fil de pêche a une valeur instrumentale au cas où une personne voudrait attraper du poisson ; sa valeur peut diminuer si une personne a accès à un filet de pêche beaucoup plus efficace. Il est incontestable que les écosystèmes et les espèces possèdent une grande variété de valeurs instrumentales (valeur culturelle, valeur récréative, valeur médicinale, valeur spirituelle, valeur transformationnelle, valeur des ressources naturelles et valeur des services écosystémiques). Ce qui est contesté c'est la question de savoir si les écosystèmes et les espèces ont une valeur non instrumentale, une valeur en tant que fin, ou une valeur en soi (c'est-à-dire une valeur intrinsèque) (Norton, 1995; Sarkar, 2005).

En s'inscrivant dans cette dimension, il est facile de considérer que les abeilles sauvages « méritent » d'être conservées, au-delà des services de pollinisation et de la valeur économique auxquels elles renvoient spontanément (Gill et al., 2016). Il serait d'ailleurs intéressant d'évaluer les liens qu'entretient la société vis-à-vis des abeilles en dehors des rapports aux produits de la ruche et à l'apiculture. Certaines études soulignent ainsi les valeurs culturelles et sociales et les bénéfices qu'elles prodiguent à la société (Klein et al., 2018; Matias et al., 2017).

C'est en cela, je crois, qu'il est important de concevoir des programmes de conservation ambitieux mais adaptés, sur le long-terme mais en intégrant un facteur de faisabilité, réalistes tout en étant attrayants pour attiser l'intérêt du grand public notamment. Cela dit, ces manœuvres doivent s'accompagner de communication auprès du grand public pour éviter une mauvaise compréhension ou une vision biaisée en faveur des abeilles mellifères et de la pollinisation uniquement (Colla, 2022). Il est important de pouvoir saisir l'ampleur du phénomène dans son ensemble (par exemple, en considérant l'importance de la combinaison des ressources florales et des sites de nidification, l'existence de différents grands groupes de pollinisateurs aux exigences parfois spécifiques, etc.).

Les abeilles, qu'elles soient domestiques ou sauvages jouissent d'une image et d'une réputation favorables à la curiosité et à l'intérêt portés sur elles et sur leur conservation (Schönfelder and Bogner, 2017). Et pourtant, les manques de connaissances avérés dans certaines études peuvent conduire, sur la base de bonnes intentions, à des actions non pertinentes, mal orientées, voire à des mesures contre-productives pour la protection des espèces de pollinisateurs menacées (Geslin et al., 2022; Wilson et

al., 2017). L'interprétation erronée d'articles scientifiques, parfois amplifiée par les médias, peut même accentuer ces actions inappropriées. Même si la plupart des citoyen·nes n'ont pas été en mesure d'identifier d'autres espèces que les abeilles mellifères et les bourdons (Wilson et al., 2017), il est raisonnable de penser que les abeilles sauvages ont un rôle à jouer dans la prise de conscience du public. Les abeilles sauvages natives représentent un modèle idéal pour sensibiliser l'opinion publique et conscientiser sur de nombreux sujets écologiques et il serait dommage que les scientifiques, les médiateur·ices de la science, les acteur·ices de la connaissance s'en privent car la conservation des abeilles est l'affaire de tous et toutes.

## VIII. Conclusion

La physiologie de la conservation pâtit encore, comme d'autres disciplines avant elle, d'une vision intégrative et inclusive. C'est notamment parce que la conservation a davantage tendance à se focaliser sur des échelles populationnelles ou écosystémiques alors que la physiologie de la conservation se concentre sur les individus (et dimensions inférieures) que les divergences et les déconnexions surviennent (Cooke and O'Connor, 2010). Dans leurs travaux, (Madliger and Love, 2015) soulignent le besoin criant d'une plus grande considération pour les conservationnistes, écologues, manageurs etc. D'autre part, Lennox & Cooke mentionnent l'intérêt d'une vision intégrative pour promouvoir la combinaison de la physiologie de la conservation avec d'autres disciplines comme la conservation (Lennox and Cooke, 2014). Même si le chemin semble encore long, et les effets tardant à se faire ressentir depuis le *Silent Spring* de Rachel Carson, les exemples d'intégration entre conservation et physiologie existent il y a fort à parier qu'ils deviendront légion dans le futur.

Il apparaît donc toujours et encore nécessaire de mettre l'accent sur des façons de communiquer les *success stories* en physiologie de la conservation auprès des acteur·ices concernées (Madliger et al., 2016), comprenant les écologues, les gestionnaires, sans oublier le grand public (Bennett et al., 2017).

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# Annexes

## Annexes du chapitre 3



Photos illustrant l'expérience du chapitre 3. (A) Rang d'un verger de pommiers en fleurs. (B) Installation d'un nichoir sur un poteau d'inter-rang. (C) Reproduction d'osmies lors du lâcher des individus adultes « parents » (fin février 2021). (D) Nichoir, en fin de saison de reproduction (avril 2021). Le nichoir est presque entièrement operculé par les femelles. (E) Au stade oeuf (juin 2021), ouverture d'un nichoir. On distingue les oeufs d'*Osmia cornuta* et les pains de pollen constitués par les femelles. (F) Ouverture d'un nichoir en sortie de diapause avant émergence (février 2022) avec cocons d'*Osmia cornuta* (et *Osmia sp.* sur la troisième rangée en partant du haut).  
Photos : Clémentine Leroy

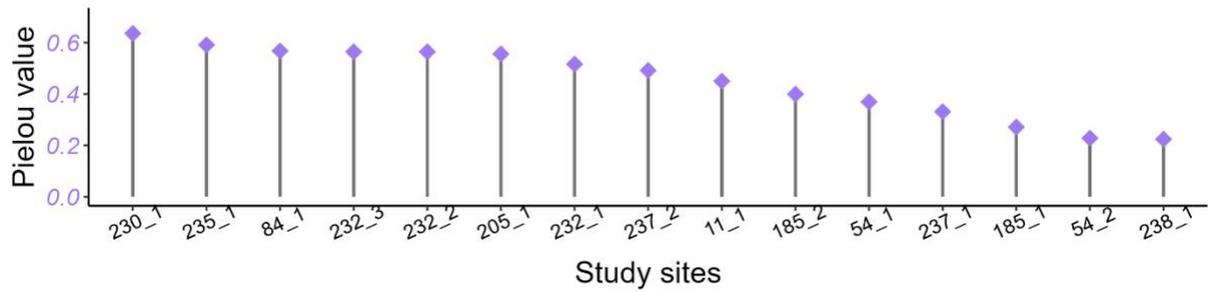
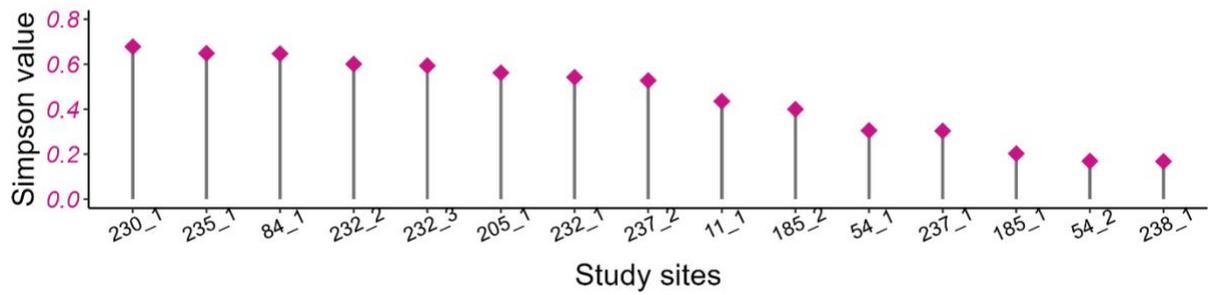
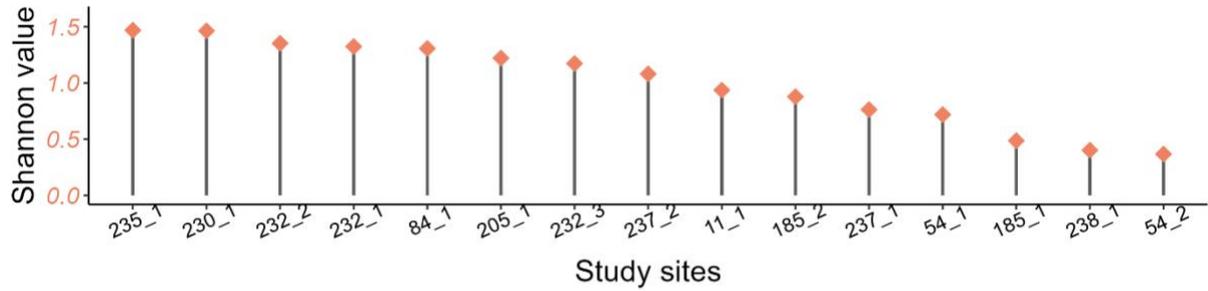
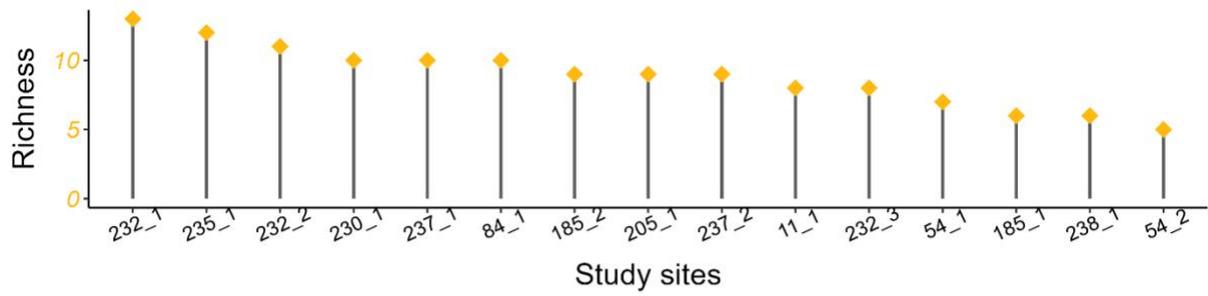
### Annexe 1



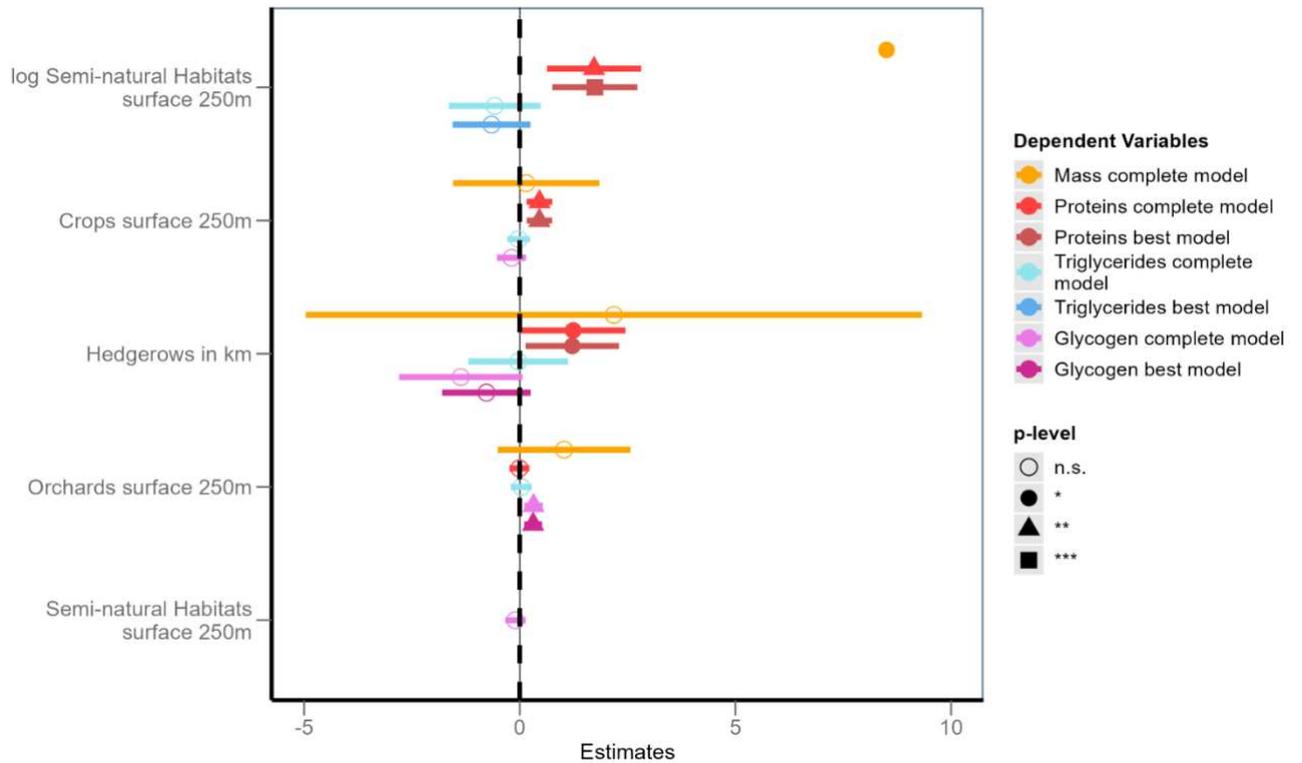
*Annexe 2 : Localisation des plots sur la zone expérimentale Basse Vallée Durance. Focus sur deux plots (vergers de pommiers) et description des types d'occupation du sol (cultures, prairies, jachère) grâce à l'application BeeGIS développée par Alexandre Dangléant (ITSAP)*

<b>Ordre alphabétique</b>	<b>nom d'espèce en latin</b>	<b>nom vernaculaire</b>
1	Allium sp. (40 µm)	Ail (40 µm)
2	Asteraceae (20 µm)	Asteracée (20 µm)
3	Brassicaceae (20 µm)	Brassicacée (20 µm)
4	Brassicaceae (25 µm)	Brassicacée (25 µm)
5	Buxus sempervirens	Buis
6	Cercis sp.	Arbre de Judée
7	Cichorieae type (25 µm)	Cichorieae type (25 µm)
8	Cichorieae type (30 µm)	Cichorieae type (30 µm)
9	Crataegus monogyna group	Aubépine groupe
10	Cupressale	Cupressale
11	Cydonia sp.	Cognassier
12	Fraxinus ornus	Frêne à fleurs
13	Indéterminés (20 µm)	Indéterminés (20 µm)
14	Indéterminés (25 µm)	Indéterminés (25 µm)
15	Indéterminés (30 µm)	Indéterminés (30 µm)
16	Malus type	Pommier type
17	Papaver rhoeas group	Coquelicot groupe
18	Plantago lanceolata group	Plantain groupe
19	Platanus sp.	Platane
20	Prunus sp.	Prunus
21	Quercus robur group	Chêne groupe
22	Rosaceae (25 µm)	Rosacée (25 µm)
23	Rosaceae (30 µm)	Rosacée (30 µm)
24	Rosaceae (35 µm)	Rosacée (35 µm)
25	Salix sp.	Saule
26	Sinapis arvensis type	Moutarde type
27	Syringa sp.	Lilas
28	Tragopogon sp.	Salsifis
29	Veronica sp.	Véronique

*Annexe 3: Liste des 29 taxons identifiés à l'espèce ou au morphogroupe retrouvés dans les analyses palynologiques du chapitre 3 et du diamètre (en microns) des grains de pollen examinés.*

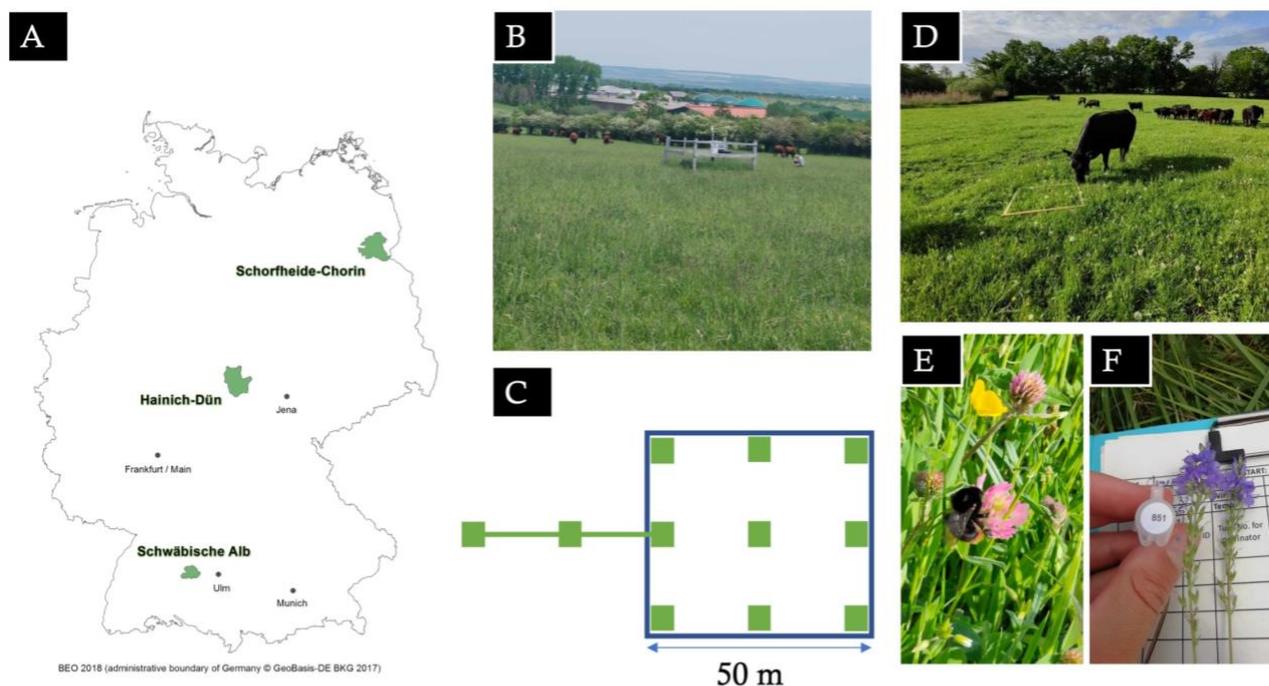


*Annexe 4: Représentation des valeurs de différents indices calculés (richesse spécifique, indices de diversité) des pools de de pollen récoltés dans les nichoirs occupés par les osmies cornues.*



*Annexe 5: Représentation synthétique (aussi appelé forest plot) des valeurs d'estimates issus des modèles montrant l'effet des variables environnementales (surfaces en vergers, cultures, HSN et longueur des haies) sur la condition corporelle (masse corporelle, concentrations en protéines, triglycérides et glycogène) de la descendance des osmies femelles. Les barres d'erreur représentant des intervalles de confiance à 95%. Les symboles pleins caractérisent les intervalles de confiance qui ne croisent pas l'axe des zero (en pointillé) et représentent les effets significatifs des variables explicatives du paysage.*

## Annexes du chapitre 4



Protocole expérimental du chapitre 4 (Projet NutriB<sup>2</sup>). (A) Carte des trois régions échantillonnées en Allemagne. (B) Photo d'un plot d'échantillonnage. Au centre se trouve la station météo. (C) Schéma de la répartition des quadrats de 1m x 1m (carrés verts) au sein d'un plot. (D) Photo d'un plot pendant l'échantillonnage en bonne compagnie. (E) *Bombus lapidarius* butinant une fleur de *Trifolium repens*. (F) Echantillonnage d'une abeille (dans l'eppendorf) et de la fleur sur laquelle elle butinait. Photos : Clémentine Leroy

### Annexe 6

#### Annexe 7: Facteurs de dilution choisis pour les trois marqueurs métaboliques et selon chaque espèce de bourdon étudiée

Espèce	Glycogène	Triglycerides	Protéines
<i>Bombus hortorum</i>	1/50	pure	1/5
<i>Bombus lapidarius</i>	1/100	pure	1/5
<i>Bombus pascuorum</i>	1/50	pure	1/5
<i>Bombus sylvarum</i>	1/50	pure	1/3
<i>Bombus terrestris</i>	1/80	pure	1/5

*Annexe 8: Répartition des effectifs des cinq espèces de bourdons étudiées en fonction des plots et par session (couplage année/saison)*

<b>Plot</b>	<i>Bombus hortorum</i>	<i>Bombus lapidarius</i>	<i>Bombus pascuorum</i>	<i>Bombus sylvarum</i>	<i>Bombus terrestris</i>	<b>Total</b>
AEG01_2020_1	1	5	2	0	1	9
AEG01_2020_2	1	12	4	2	0	19
AEG03_2020_1	0	2	0	0	0	2
AEG03_2020_2	0	1	0	0	0	1
AEG03_2021_4	1	5	2	1	1	10
AEG04_2020_1	0	0	1	0	0	1
AEG04_2021_4	2	1	6	0	0	9
AEG06_2020_1	1	0	1	0	0	2
AEG06_2020_2	2	3	2	3	0	10
AEG07_2020_2	1	4	1	0	0	6
AEG07_2021_4	0	6	0	0	0	6
AEG08_2021_4	0	0	2	14	0	16
AEG09_2020_2	0	9	2	0	1	12
AEG11_2020_2	2	1	6	0	0	9
AEG12_2020_1	0	4	1	0	0	5
AEG14_2021_4	0	7	0	0	1	8
AEG17_2020_2	0	1	1	4	0	6
AEG17_2021_4	0	1	1	12	0	14
AEG21_2020_1	2	0	1	0	2	5
AEG24_2020_1	0	1	0	0	0	1
AEG24_2020_2	0	13	5	2	2	22
AEG32_2020_2	0	2	1	1	0	4
AEG32_2021_4	1	6	15	2	0	24
AEG35_2020_2	0	0	2	0	0	2
AEG35_2021_4	0	3	7	4	0	14
AEG36_2020_2	1	0	6	1	2	10
AEG41_2020_1	1	2	1	0	1	5
AEG46_2020_1	0	0	1	0	0	1
AEG46_2020_2	1	4	11	2	1	19
AEG46_2021_4	0	0	1	0	0	1
BELAS_2020_1	0	0	3	0	0	3
BELAS_2020_2	0	0	2	0	0	2
BELAS_2021_3	0	0	2	0	7	9
BELAS_2021_4	0	0	3	0	4	7
BELDB_2020_1	1	0	2	0	0	3
BELDB_2020_2	0	0	4	0	0	4
BELDB_2021_3	0	0	3	0	6	9
BELDB_2021_4	0	1	5	0	1	7
BELDBE_2020_1	1	0	2	0	1	4
BELDBE_2020_2	0	0	4	0	1	5
BELDBE_2021_3	0	1	1	0	3	5
BELDBE_2021_4	0	1	4	0	5	10
BELHB_2020_1	0	0	0	0	2	2
BELHB_2020_2	0	0	5	0	0	5
BELHB_2021_3	0	0	1	0	0	1
BELHB_2021_4	1	0	3	0	1	5
BELKH_2020_1	0	0	0	0	1	1
BELKH_2020_2	1	0	2	0	8	11
BELKH_2021_3	0	0	0	0	3	3
BELKH_2021_4	0	0	4	0	8	12

BELMJ_2020_1	0	0	4	0	0	4
BELMJ_2020_2	0	0	4	0	0	4
BELMJ_2021_3	0	3	2	0	3	8
BELMJ_2021_4	0	2	2	0	3	7
BELOP_2021_3	0	0	4	0	0	4
BELOP_2021_4	0	0	4	0	0	4
BELRD_2021_3	0	1	0	0	1	2
BELRD_2021_4	1	3	6	0	2	12
BELSG_2020_1	0	0	3	0	0	3
BELSG_2020_2	0	0	2	0	1	3
BELSG_2021_3	0	5	2	0	0	7
BELSG_2021_4	0	3	4	0	1	8
HEG01_2021_4	0	2	0	4	0	6
HEG02_2020_2	0	10	0	0	2	12
HEG02_2021_4	0	1	0	1	0	2
HEG03_2020_2	0	2	0	0	1	3
HEG04_2021_4	0	8	1	1	0	10
HEG05_2021_4	0	0	1	1	1	3
HEG06_2020_2	0	5	0	0	1	6
HEG06_2021_4	1	6	0	0	0	7
HEG07_2020_2	0	14	6	0	0	20
HEG08_2020_2	0	0	1	0	0	1
HEG08_2021_4	0	1	0	0	0	1
HEG09_2020_2	0	10	2	0	6	18
HEG09_2021_4	0	8	3	3	0	14
HEG13_2020_2	0	3	0	0	0	3
HEG13_2021_4	1	2	1	0	0	4
HEG14_2020_2	0	2	4	1	0	7
HEG14_2021_4	1	2	1	2	0	6
HEG17_2020_2	2	5	2	3	0	12
HEG17_2021_4	0	7	1	0	2	10
HEG19_2021_4	0	1	0	0	3	4
HEG32_2020_2	1	3	0	2	0	6
HEG32_2021_4	0	0	0	1	0	1
HEG35_2020_2	0	5	0	1	0	6
HEG35_2021_4	0	6	0	3	1	10
HEG42_2020_2	2	2	2	1	1	8
HEG42_2021_4	0	5	1	5	4	15
HEG47_2020_2	0	0	0	0	2	2
HEG47_2021_4	0	2	0	0	0	2
HEG50_2020_2	1	17	4	0	1	23
HEG50_2021_4	0	1	2	2	0	5
SEG02_2020_1	0	0	0	2	1	3
SEG02_2020_2	0	0	1	0	0	1
SEG02_2021_3	0	0	0	1	0	1
SEG03_2020_2	1	2	0	0	0	3
SEG03_2021_3	0	0	0	2	0	2
SEG03_2021_4	0	0	1	2	1	4
SEG04_2020_2	1	3	2	3	0	9
SEG04_2021_4	1	3	0	1	14	19
SEG05_2020_1	0	0	1	1	4	6
SEG05_2020_2	0	0	0	2	0	2
SEG13_2021_4	0	2	0	0	0	2
SEG15_2021_4	0	2	0	2	2	6

SEG16_2020_1	0	0	1	2	0	3
SEG16_2020_2	0	1	2	2	0	5
SEG16_2021_4	0	0	0	2	3	5
SEG22_2020_2	0	1	1	0	0	2
SEG28_2020_1	0	0	1	0	0	1
SEG28_2021_4	0	0	1	0	1	2
SEG35_2021_4	0	6	0	0	3	9
SEG38_2021_4	0	1	0	1	1	3
SEG42_2020_2	0	1	0	0	0	1
SEG43_2020_2	0	0	1	0	0	1
SEG43_2021_4	0	0	2	0	3	5
SEG44_2020_1	0	0	2	0	1	3
SEG44_2021_4	0	4	5	0	0	9
SEG46_2020_2	0	6	0	0	0	6
<b>Total</b>	<b>34</b>	<b>275</b>	<b>223</b>	<b>102</b>	<b>133</b>	<b>767</b>

Article en collaboration (projet NutriB<sup>2</sup>)

Opinion

# Critical links between biodiversity and health in wild bee conservation

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**Wild bee populations are declining due to human activities, such as land use change, which strongly affect the composition and diversity of available plants and food sources. The chemical composition of food (i.e., nutrition) in turn determines the health, resilience, and fitness of bees. For pollinators, however, the term 'health' is recent and is subject to debate, as is the interaction between nutrition and wild bee health. We define bee health as a multidimensional concept in a novel integrative framework linking bee biological traits (physiology, stoichiometry, and disease) and environmental factors (floral diversity and nutritional landscapes). Linking information on tolerated nutritional niches and health in different bee species will allow us to better predict their distribution and responses to environmental change, and thus support wild pollinator conservation.**

## Bees decline because their food sources disappear

Animals pollinate >85% of flowering plants and 75% of the leading crops worldwide [1] which provide food and medicines for other animals and humankind. They also support natural habitats and play a key role in plant productivity, food webs, and ultimately in human well-being [1–3]. Bees (Apidae) are the most important group of pollinators, and the vast majority are represented by wild species (~20 000 species) [4].

Alarmingly, many wild bee populations are declining due to the impact of different biotic and abiotic stressors caused by human activities that act alone or in combination, such as pesticides, invasive species, pathogens, intensive land-use, and climate change [5–11]. In particular, agricultural intensification appears to negatively impact on wild bee communities [12,13]. In fact, overall biodiversity typically decreases with increasing land-use intensity [14,15], which directly or indirectly leads to loss of floral diversity and nesting sites [10,16], and may alter pathogen prevalence [17–19]. Declining floral diversity in turn decreases the spectrum of flowering plants that are available as food sources, and therefore restricts the nutritional landscape accessible to bees [20–23].

## Nutritional landscapes of bees

As nutritional intake and thus the nutrient composition (henceforth referred to as nutritional quality) of food strongly determine the health, resilience to pathogens, and fitness of animals [24], access to food resources that enable diverse and balanced nutrition is one key driver of population stability [21]. In this context, we consider a nutrient to be any chemical compound (i.e., from chemical elements, phospholipids, and amino acids to 'group components' such as proteins) that are part of the food/nutrition of bees. Bees obtain most nutrients and several potential

## Highlights

The diversity, abundance, and health of wild bees is jeopardized primarily by land-use modifications, among other global change drivers.

Defining and measuring health in wild bees requires an integrative approach across disciplines.

We use elements from chemistry, stoichiometry, ecology, physiology, pathology, and genetics to (i) contribute to a more comprehensive definition of wild bee 'health', and (ii) define a framework linking bee health with floral resource/nutritional landscapes through assessing species-specific nutritional niches.

We suggest a novel and holistic approach for capturing bee health through combining field and laboratory tools.

Knowledge gained by applying this framework will serve as a blueprint for stakeholders engaged in pollinator conservation.

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medically active plant secondary metabolites from flowering plants by consuming mostly nectar and pollen [20,25,26]. Nectar primarily provides carbohydrates for maintaining energy and metabolic processes, whereas pollen is the main source of all other macronutrients (i.e., protein and fat) and micronutrients (e.g., vitamins, sterols) that are required for tissue homeostasis, development (e.g., ovary development), and larval growth [27–29]. Ideally, floral communities provide food resources of both sufficient quality and quantity. The quantity of food resources is determined by the abundance of flowers present in the landscape – namely the number of plants/flowers present per species and the overall amount of flowering species [30]. The quality of food resources depends on the composition of different flowering plant species because each plant species provides pollen and/or nectar with a specific nutrient profile [31]. In fact, the nutritional profiles of pollen and nectar vary greatly among different plant species [32–35] and even between plant individuals of the same species growing in different plant communities [36]. Floral communities, which are characterized by a specific composition and diversity of flowering plant species, consequently determine resource availability and diversity, and thus determine the nutritional landscape in which bees are foraging [21]. More details of variation in nutritional quality in pollen and nectar, the effect of different diets on bee performance and fitness, and differences in foraging preferences among bees are given in Vaudo *et al.* [21].

Although much less well understood, the nutritional needs of bee species are also expected to differ substantially between bee species [21]. The sustainability of bee populations thus depends on flowering plant communities that provide sufficient amounts of the different nutrients required because the quality of food, and in particular of pollen, directly determines offspring survival and development, and can therefore influence the entire population [21,37,38].

Surprisingly, the interaction between flowering plant communities, the available nutritional landscape, and the health status of different wild bee species has hitherto received little attention (*cf* [21,34]). This knowledge is, however, crucial for determining how floral communities and respective conservation measures can support wild bee populations. We therefore propose a conceptual framework for how anthropogenic changes in flowering plant communities can affect bee communities by altering the nutritional landscape and thus niches available to support healthy wild bee populations.

### Measuring wild bee health

Although human health is understood as the physical, mental, and social well-being of an individual or population, the health of wildlife has generally been understood as the absence of disease [39]. For pollinator communities, the term 'health' only recently appeared in the literature and its precise definition is still subject to debate [40]. López-Uribe *et al.* suggested a multilevel approach and the use of various parameters to measure bee health at the individual, colony, and population level [40]. The health status of a population should then be a direct consequence of the average health status of individuals, where population size is likely to correlate positively with average individual health.

We propose to apply a multidimensional concept of bee health to wild bees – defined as the status of well-being of each individual as a result of their interaction with the local environment (Figure 1). We suggest that all or several of the following physiological parameters should be recorded and integrated to comprehensively capture individual bee health – the composition and amount of stored nutrients in bee bodies (such as proteins, lipids, glycogen, chemical elements), body size [41], pathogen load, beneficial microbiota [42], immunocompetence [43], and fertility [44].

Physiological parameters were shown to be important for understanding the sensitivity of species to environmental modifications [45] because the physiology of individuals responds before changes in populations become visible [46]. For instance, diet quality correlates with increased

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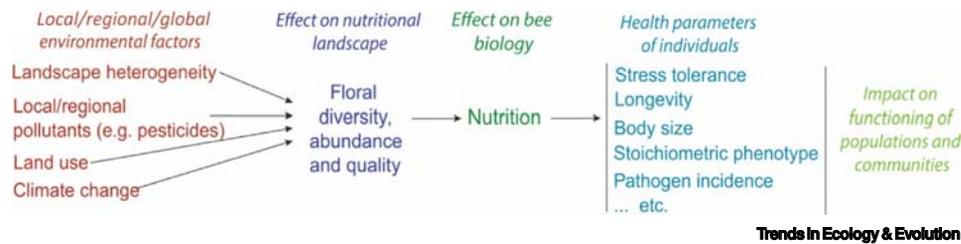
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**Figure 1.** The multifaceted nature of bee health. The main landscape-scale environmental factors, their effects on the floral community and thus on the nutritional landscape and bee diets, and the consequences for bee nutrition and health. These can be observed by recording and integrating different parameters (right column). Bee health based on the physiology of individual bees can then be related to additional parameters, such as population density (i.e., the number of bees caught per plot for a given species and time-period) or variation in population dynamics over time, ideally obtained over multiple seasons to infer changes in population densities across years.

levels of the storage protein and antioxidant vitellogenin in individual honey bees, and this in turn correlates with higher overwintering survival of the entire colony [19,47]. Energy storage is crucial for bee survival. The main categories of macronutrients used for energy storage in insects (glycogen, lipids, and proteins) affect several life-history traits such as dispersal capacity, reproduction, diapause, and survival [48]. Moreover, both macro- and micronutrients are acquired through the consumption of pollen and nectar, and thus are at the interface between bees and floral resources. Variations in floral resource availability will therefore influence the energy budget and ultimately the health of bees.

Additional physiological health parameters *sensu lato* include morphometrics, stoichiometry, microbial communities, and pathogen loads. For example, wing morphometry and fluctuating asymmetry were found to correlate with different stressors [49–51]. In addition, floral composition and diversity are known to shape the bee microbiome composition, particularly in solitary bees, with consequences for nutrient uptake, detoxification, immunity, and health [44,52–54]. By defining stoichiometric phenotypes (i.e., the elemental composition of bee bodies) [55], deviations from optimal phenotypes, as expected in nutritionally impoverished landscapes and for declining populations, can be revealed, which can then also indicate reduced health.

All physiological health parameters mentioned previously are likely affected not only by multiple environmental parameters related to variation in floral resource diversity, abundance, and quality but also by environmental pollutants (e.g., pesticides, antibiotics, heavy metals) and pathogens (Figure 1). Measurement of multiple variables can therefore provide a more complete picture of pollinator health status than focusing on a single parameter.

### Floral diversity as an environmental driver of bee health

Floral diversity, abundance, and community composition correlate with the abundance and diversity of wild bee species [56,57] through food availability [58], nutritional quality or content [21,27,59,60], and resource phenology [23,58,61]. Bees thrive in environments where plant species diversity is high [12,62,63], as is the diversity and quantity of available food resources [23,64,65]. Moreover, resource diversity increases the opportunities for specialist (oligolectic) bee species with restricted pollen host plants to find suitable food resources. In generalist (polylectic) species, access to a diverse spectrum of resources supports immunity, health, performance, and survival (Table 1), presumably through ready access to adequate nutrition and beneficial plant secondary metabolites. By contrast, chronic intake of monotonous, nonsuitable, low quality, or toxic food reduces the immune-competence and vitellogenin levels of bees, thus affecting bee health through 'nutritional stress' [47,66]. Poor nutrition can also lead to higher

Table 1. Effect of floral diet on bee health: key studies on the effects of monofloral and polyfloral diets on the health and performance of different generalist (i.e., polylectic) bee species under both laboratory and field conditions

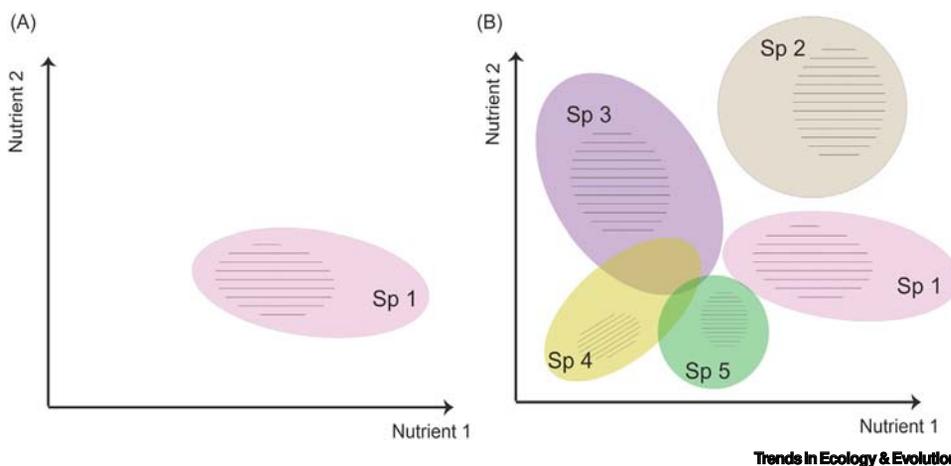
Experiment	Bee species	Effects	Response variable	Refs
Landscapes, enriched or not with melliferous catch crops; effect on colony overwintering	Honeybee ( <i>Apis mellifera</i> )	Access to more diverse floral resources was linked to a higher bee vitality (vitellogenin expression level)	Bee physiology (vitellogenin expression level)	[47]
Monofloral diet combined with pesticides; effects on colony performance	Buff tailed bumblebee ( <i>Bombus terrestris</i> )	Additive negative effects of monofloral diet and pesticides on colony growth, drone size, and reproductive effort	Worker mortality, worker weight, colony weight gain, number of males, food uptake	[73]
Monofloral versus polyfloral pollen diets	Honeybee ( <i>A. mellifera</i> )	When parasitized, bees fed with the polyfloral blend lived longer than bees fed with monofloral pollens	Longevity of adults	[74]
Diets with varying proportions of <i>Ranunculus</i> and <i>Sinapsis</i>	European orchard bee ( <i>Osmia cornuta</i> )	Monofloral diets of <i>Ranunculus</i> are detrimental for larval performance	Larval performance	[75]
Royal jelly supplemented with mono- or polyfloral pollen diets	Honeybee ( <i>A. mellifera</i> )	Larval resistance to disease was enhanced on a diet supplemented with either dandelion or polyfloral pollen	Larval resistance to disease	[76]
Landscapes differing in floral resource diversity; effect on colony performance and reproduction	Sugarbag bee ( <i>Tetragonula carbonaria</i> )	Colony performance and reproduction correlated positively with floral diversity in the landscape	Colony performance and reproduction (brood)	[64]
Wild plant diversity gradient diet (including oilseed rape treated with a neonicotinoid)	Red mason bee ( <i>Osmia bicornis</i> )	Resource diversity offset the effects of insecticides (interactive effects) and increased reproduction parameters	Brood cell production, bee reproduction, larval to adult development	[71]
Monofloral and mixed diets combined with pesticide in nectar; effect on nesting success	Common eastern bumblebee ( <i>Bombus impatiens</i> )	Exposure to pesticides reduces survival and activity and brood size; the effect increased on a monofloral diet	Nesting success, queen mortality and activity levels, queen nectar consumption, colony development (brood)	[77]
Mixture of pollen in diet; effect on lifespan	Common eastern bumblebee ( <i>B. impatiens</i> )	Survival of bees fed a pollen mixture with 50% unfavorable pollen ( <i>Helianthus annuus</i> , Asteraceae) was as good as on a high-quality monofloral diet	Lifespan of bees in captivity	[78]
Mono-, di-, and trifloral diets; effect on colony development	Buff-tailed bumblebee ( <i>B. terrestris</i> )	Colonies developed best on mixed pollen diets or high-quality monofloral pollen diets	Colony development (brood)	[38]
High pollen diversity and protein versus low pollen diversity and protein diets combined with pesticide; effect on the development of hypopharyngeal glands	Honeybee ( <i>A. mellifera</i> )	Size and shape of hypopharyngeal acini was affected by pesticide and diet, whereas protein content in bee head was affected only by pesticide	Physiological development	[79]
Landscape gradient of floral resource abundance and diversity	Honeybee ( <i>A. mellifera</i> )	Decline in pollen availability in summer led to decrease in pollen harvest, colony performance, and overwintering failure	Colony performance (brood, adult population size, honey reserve) and overwintering	[80]
Landscape gradient of semi-natural habitats	Buff-tailed bumblebee ( <i>B. terrestris</i> )	Higher abundance of semi-natural habitats improved reproductive performance	Colony growth and reproductive performance (number of new queens produced)	[35]
Food resource limitation and pesticide exposure	Orchard mason bee or blue orchard bee ( <i>Osmia lignaria</i> )	Pesticides and food limitation had additive effects and reduced reproduction	Survival, nesting, and reproduction	[72]
Diets differing in floral composition; effect on resilience to heat stress	Buff-tailed bumblebee ( <i>B. terrestris</i> )	Colonies were less susceptible to heat stress when fed suitable/high-quality diets	Colony resistance to stress	[81]

susceptibility to disease [67] and pesticides [68]. In fact, nutritional stress as a consequence of restricted access to adequate floral resources is considered to be one of the main drivers of bee pollinator decline [21,69,70]. Although floral diversity may not provide added value *per se* or automatically yield beneficial synergistic effects compared with higher-quality monofloral diets [34,71,72], it can clearly mitigate the negative effects of poor diets and provide overall more choices to various bee species (Table 1).

However, how floral resource diversity and nutritional quality interact and affect bee health remains largely unclear. This is particularly true for wild bees that are considered to be less resilient to environmental changes and are more difficult to study than managed honeybees [72,82]. For example, how different nutrients or nutrient groups contribute to bee health is poorly understood, as is whether bee species differ in their tolerance to deviations from optimal nutritional profiles and thus to the available nutritional landscapes. Understanding these links will shed light on the mechanisms underlying the observed positive effects of, for example, polyfloral diets on bee performance (Table 1). This knowledge will also enable better strategies for conservation or restoration of biodiversity for pollinators, and thus contribute to combating ongoing bee declines (discussed later). We therefore propose to link floral communities, nutritional landscapes, and bee health and diversity through assessing bee species-specific nutritional niches.

### Nutritional niches of bees

The ecological niche of a species describes the range of environmental conditions and resources that are required for its persistence; it positions each species in relation to others in ecosystem space [83], taking into account physical conditions, such as climate, and food resources [84]. The nutritional niche is nested within the ecological niche and describes a specific proportion and ratio of nutrients which enable maximum growth, development, performance, and fitness (Figure 2A) [85–87]. Notably, precise values of the optimal niche can change with the internal state of an animal (e.g., larva versus adult) and with changing environmental conditions [87]. The nutritional niche can consequently be described by a multidimensional geometric space defined by food chemistry where each axis represents a nutrient (e.g., specific amino acids, chemical elements, or group of components) that are functionally relevant to a species (i.e., they are required for their development, survival, and reproduction [37,87,88]) (Figure 2). Within this space, some combinations of nutrients are more important for performance and fitness than others. If they are limited in the environment this can result in a discrepancy between the optimal nutritional niche of a consumer and the niche provided by the environment as suggested by ecological stoichiometry (stoichiometric mismatch) [89]. Such important nutrients are often regulated by animals, as revealed by the Geometric Framework of Nutrition (GFN) [85,90]. For instance, honey bees (*Apis mellifera*), bumble bees (*Bombus* spp.), and mason bees (*Osmia*



**Figure 2. Nutritional niches of bee species in a multidimensional nutritional space.** (A,B) The optimal niche space (shaded) and the tolerated niche space (lighter color) of a species (Sp), and species-specific nutritional niches. Each shaded space represents the combinations and concentration ranges of nutrients that are tolerated, and thus support the growth, development, performance, and fitness of a species. Strong deviations from the nutritional niche over extended time-periods will likely lead to negative impacts on health.

*bicornis*) regulate their protein, lipid, and/or carbohydrate intake depending on their age and the presence of brood [91,92]. For these important nutrients, species likely show little tolerance to deviations from the concentrations that best support their performance/fitness, whereas they are likely more tolerant to deviations from concentrations that are less crucial for performance/fitness (as shown for *Bombus terrestris* [93]).

Such differences in tolerance to deviations are captured by the tolerated nutritional niche – which deviates from the optimal niche – and thus captures the range that is still physiologically manageable by organisms and results in positive growth, development, and fitness [87]. If the actual nutritional niche offered by the available nutritional landscape deviates too far from the tolerated nutritional niche, individuals will fail to achieve successful growth, development, or reproduction [87]. In turn, the degree of variation in the tolerated niche space denotes the tolerance of a specific animal to a suboptimal diet. Different species likely vary not only in the position of their optimal niche (i.e., the specific proportions and ratios required) but also in their tolerance to deviations from the optimum, resulting in species-specific nutritional niche shapes and sizes (Figure 2B). Determining the tolerated nutritional niche of a species can thus provide valuable information to predict the spatial and temporal distribution of that species and its responses to environmental change [87,94].

As a consequence of the complex and diverse chemistry encountered in different plant species, animals must perform nutrient-selective foraging so as to ensure healthy offspring development [95]. In the case of bees, this means that they should choose pollen with a nutritional composition that matches their nutritional needs, as shown for several bumble bee species that thrive on pollen with high protein to lipid (P:L) ratios and low lipid content [21,96], or *O. bicornis* bee larvae that prefer diets with a high carbohydrate content [91]. The chemical profile of pollen jointly collected by individual (female) bees of a population can therefore represent a proxy for their species-specific nutritional niche.

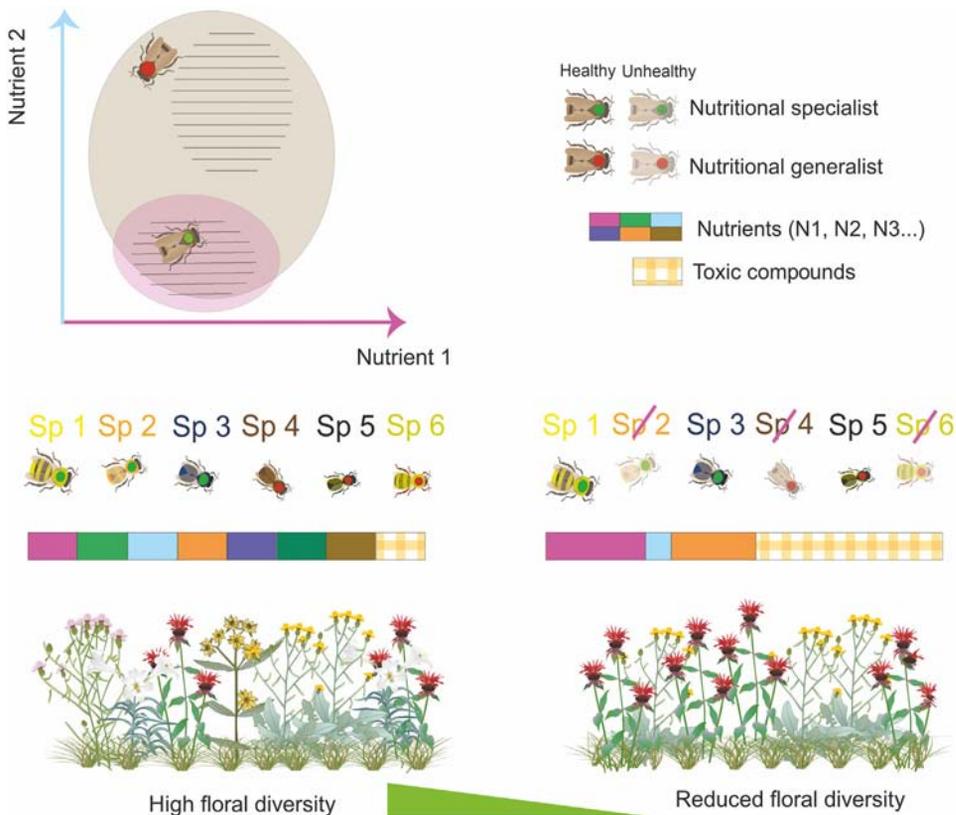
Recent advances in analytical methods facilitate accurate quantitative chemical analysis of pollen, including fatty acids and protein-bound and free amino acids [97], sterols [98–100], plant secondary metabolites [101], and chemical elements [89]. The chemical/nutritional profile of the overall pollen diet of a bee individual can thus be calculated by integrating information on the proportional contributions of the nutritional profiles of pollen of all plant species visited for pollen collection (e.g., obtained through metabarcoding or palynological studies). Notably, this approach does not allow the optimal nutritional niches of species to be determined, which would require cage (semi-field) experiments with manipulated artificial diets. However, through linking measured (actual) nutritional niches and animal health, the nutritional niches measured at sites where populations show generally good health status and high population density can be a good proxy for the tolerated nutritional niches of a species.

### Dietary versus nutritional generalists and specialists in bees

The degree of dietary specialization of a species is determined by its physiological (e.g., ability to break down/tolerate specific plant compounds), sensory (e.g., intrinsic bias towards specific flowers/plants), and morphological (e.g., proboscis length and wing morphology) characteristics. It is typically described by the range of plant taxa used for pollen collection (i.e., pollen hosts) [102,103]. In bees, the full spectrum of flower specialization – sometimes referred to as dietary breadth [53,104] – ranges from species that collect floral pollen from a single plant species or genus only (monolecty, oligolecty) to generalists that do not appear to have distinct flower preferences (polylecty) [20]. However, even generalists, including many social bees, forage pollen from a limited range of flowering species [105–107]. A classification of floral specificity of pollen

collection in bees covering all levels of specialization was suggested by Cane and Sipes [108] and Müller and Kuhlmann [105]. This classification, however, does not consider pollen nutrients, thus is not based on the nutritional niches of a species [105,108].

We propose that bee species differ not only in the specific nutrient amounts and ratios that are required for optimal survival and reproduction (see earlier) but also in the degree of variation in nutrient space that is tolerated, that is, the tolerated nutritional niche, and thus differ in the nutritional landscapes in which they can thrive. Nutritional specialists are thus species with comparatively narrow nutritional niches, whereas generalists are species with a comparatively wide nutritional niche (Figure 3). Nutritional niche breadth and dietary breadth can correlate with each other, but do not necessarily need to be correlated. Although it is likely that dietary specialists also show a narrow nutritional niche, some dietary specialists may have a broader nutritional niche than some generalists. For example, some bees may visit a broad spectrum of plant species with chemically similar pollen profiles, for example, bee species that collect pollen



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Figure 3. Link between floral diversity, nutritional landscapes, and nutritional niches.

For a Figure360 author presentation of Figure 3, see the figure legend at <https://doi.org/10.1016/j.tree.2021.11.013>

Bee species (Sp) with narrow nutritional niches (nutritional specialists, marked with green dots), and thus with little tolerance to changes in the nutritional space (purple area in the nutritional space), are likely to be more susceptible to changes in floral diversity than are bee species with broad nutritional niches (nutritional generalists, marked with red dots) and higher tolerance (brown area in the nutritional space). The nutritional landscape of each environment is reflected by different colors of nutrients (bars in the center). This landscape is more diverse and balanced, and thus provides more nutritional niches, in florally diverse environments (left) compared with environments with reduced floral diversity (right). Florally diverse environments also enable bees to dilute toxic compounds (e.g., harmful plant secondary metabolites or pesticides), thereby exposing them to overall lower levels of harmful compounds compared with environments with reduced floral diversity.

from Asteraceae. These are mostly specialized bees that forage on multiple different Asteraceae species, whereas generalist bee species avoid Asteraceae pollen despite the ubiquitous distribution of this plant family and the substantial amount of pollen provision (known as the Asteraceae paradox [105]). Although the reasons for this paradox remain unresolved, the abundance of specific chemical compounds (e.g.,  $\Delta^7$ -sterols) in the pollen of Asteraceae species may offer an explanation [100].

### Linking bee health, floral diversity, and nutritional niches

Some generalist bees have been shown to mix pollen from different plant sources, either during one or several foraging trips, likely to achieve a nutritional balance and/or to dilute toxic compounds [72,75], indicating that nutritional generalists may even specifically target and clearly benefit from diverse pollen sources in florally diverse environments (Table 1). Nutritional specialists, conversely, depend on the presence of specific plant species which provide pollen with nutrient profiles that are close to their nutritional niches. Access to a nutritionally diverse landscape as typically provided in florally diverse environments would ensure that different species-specific macro- and micronutrient requirements can be met [24,109]. We therefore predict that nutritional specialists with a comparatively small nutritional niche are more common in florally diverse (and thus nutritionally diverse) habitats – where they have access to a broader spectrum of resources and thus of potential nutritional niches, including their own [110] (Figure 3).

Both nutritional generalists and nutritional specialists should therefore thrive in nutritionally diverse landscapes, which are expected to provide more nutritional niches than nutritionally poor landscapes (Figure 3). Bees in nutritionally diverse landscapes will more likely encounter their (potentially even optimal) nutritional niche. As a consequence, they should be better nourished and therefore be healthier than bees in nutritionally poor landscapes.

Notably, bees in more biodiverse environments may also harbor more diverse pathogens and parasites [44,67,111,112]. However, access to (nutritionally) diverse resources may render them more tolerant and resilient to pathogens and parasite virulence factors (through optimal physiology), and/or more resistant to associated infection risks (through optimal immunity) [10,74,81,113]. They may also more easily adjust their diet to combat infection, for example, by increasing the proportion of protein in their diet [114,115] or by collecting resources with antimicrobial plant secondary metabolites [25,33,116]. In fact, the resilience of bees, not only to diseases but also to other stressors (e.g., climatic or weather extremes), varies with floral/nutritional quality [81,117]. We therefore do not expect that more stressors are necessarily linked with decreased health, but instead predict a three-way interaction between nutrition, health, and stressors such as pathogen loads, which may result in different scenarios such as linear and nonlinear shifts in nutritional niches (Figure 4). For example, protein-rich diets improve the immune-competence of bumble bees (*B. terrestris*) exposed to a parasite [66], and lipid-rich diets increase survival in honey bees (*A. mellifera*) exposed to an organophosphate insecticide [117]. These studies indicate that bees can adjust their diets to compensate for different stressors, and this can result in altered nutritional niche spaces (Figure 4). Consequently, floral/nutritional diversity may convey health benefits to generalist and specialist bee species by providing a variety of nutritional niches which can increase the nutritional flexibility and resilience of bees when facing additional stressors.

### Concluding remarks

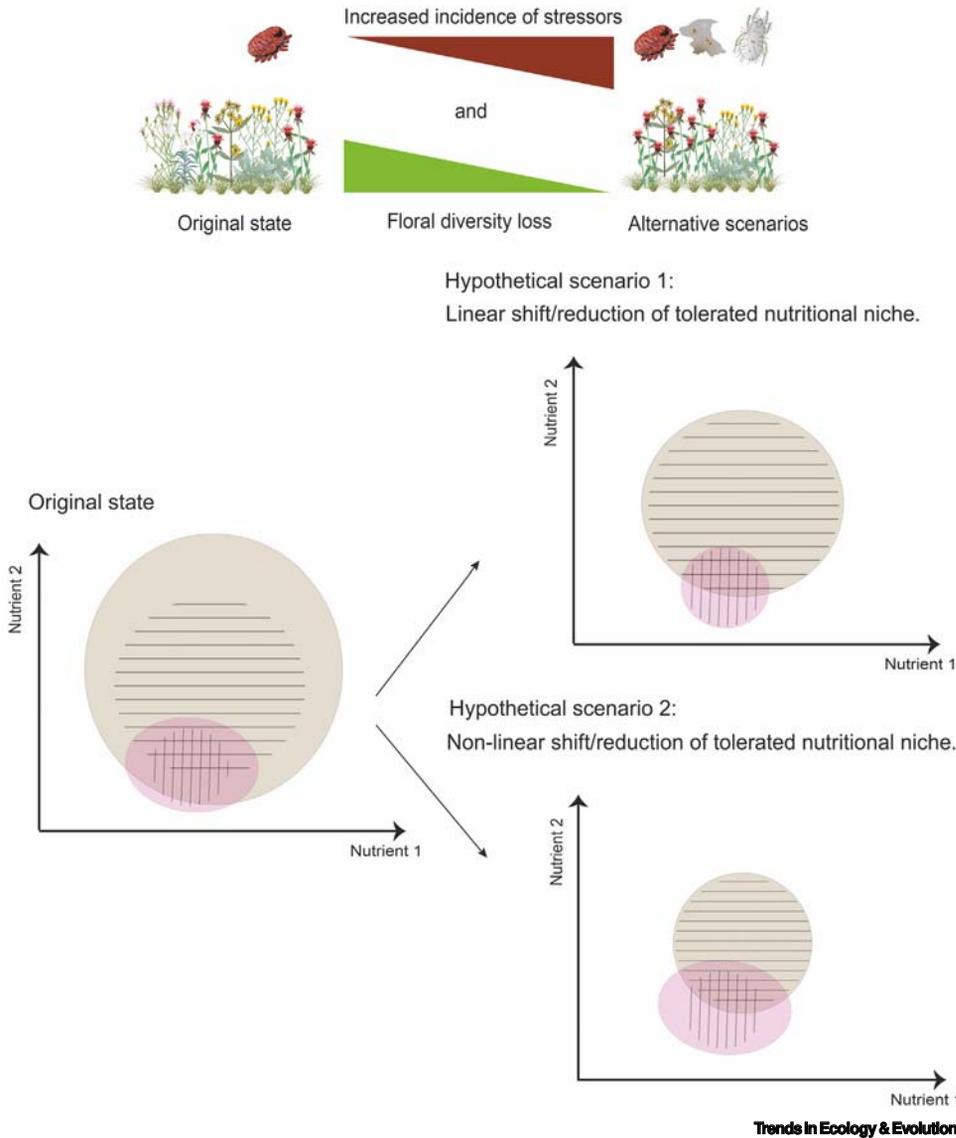
By integrating different physiological health measures and nutritional niches with floral diversity and composition, we can reveal meaningful interactions between nutritional landscapes and bee health (Figures 3 and 4). We can also investigate hitherto unknown interactive effects

### Outstanding questions

How can wild bee health be defined and measured? We propose specific guidelines and parameters to measure health in wild bees and to link it to floral resource/food landscapes by assessing nutritional niches. Applying our conceptual framework will enable better tailored management recommendations for the conservation of wild bees.

How do nutrition, health, and disease interact? Three-way interactions, such as between nutrition, health, and disease loads, are difficult to study for wild bees, in particular in the field. We propose to measure and integrate different elements, namely pathogen loads, physiological parameters, and nutritional niches, based on pollen metabarcoding and analytical chemistry, across environmental gradients that differ in plant diversity so as to disentangle such interactions.

Can knowledge about bee nutritional niches aid in conservation measures and thus support the maintenance of ecosystem services? We suggest that floral/nutritional diversity conveys health benefits to generalist and specialist bee species by providing nutritional landscapes that offer a variety of nutritional niches. Analyzing the nutritional requirements of different species, and of the plant species and communities that support them, will aid in better tailoring conservation measures to specific bee communities.



**Figure 4. Interactions between nutrition, health, and stressors are altered in florally impoverished landscapes.** Hypothetical scenarios depict linear and nonlinear changes in the nutritional niches of nutritional specialists (purple areas) and generalists (brown areas) following loss of floral diversity plus additional stressors (e.g., increased pathogen prevalence). Stressors may shift the tolerated nutritional niche space of a bee species without affecting its optimal nutritional niche (scenario 1). Alternatively, it may result in a nonlinear change in overall nutritional niches (including both the optimal and tolerated niche space). Moreover, the magnitude and direction of ecological niche shifts under stressed scenarios is known to differ among taxonomic groups [118], demonstrating highly species-specific responses. Likewise, the nutritional niche of one species may be strongly decreased, whereas the optimal and tolerated nutritional niche of another species may remain unaffected in the presence of additional stressors (scenario 2). This in turn may result in a species-specific likelihood of becoming (locally) extinct under stressed conditions. To our knowledge no study to date has assessed nutritional niche shifts in different bee species exposed to different stressors.

between different physiological health parameters such as stoichiometry, physiology, and disease loads.

This integrative approach will enable better tailored management recommendations for bee conservation (see [Outstanding questions](#)). Until now most conservation measures have implicitly

assumed that wild bee populations can be enhanced by increasing floral diversity [8]. However, this can lead to shortages in the types, amounts, and proportions of specific nutrients, and thus in a lack of the nutritional niches required by different bees, in particular by nutritional specialists. Such shortages can be elucidated, for example, by comparing bee and pollen stoichiometry to reveal stoichiometric mismatches [89]. Similarly, bee–nutrient networks and ordination analyses could reveal differences in link strength between specific nutrients or nutrient ratios and specific bee species, where strong links indicate important nutrients, nutrient groups, or nutrient ratios and the plant species providing them. This information can then be used to improve flower seed mixes or support the conservation of key plant species and their habitats.

Notably, the quantity and quality of available floral resources can be modulated by environmental conditions, such as water availability [119], rendering nutritional landscapes and bee foraging highly sensitive to global change [120]. For example, global change will likely affect the functional complementarity of bee–plant interactions, for example, through advancing seasonal flowering events. It remains open which bee species are sufficiently plastic in their phenology and/or resource requirements to maintain their floral associations and pollination service [121,122]. It is also poorly understood how such shifts in phenology or resource use induced by global change interact with bee health. Can we use knowledge about links between species-specific nutritional niches (breadth) and health to predict which bees will be able to forage in specific landscapes? Can we adjust floral enhancement schemes to take into consideration factors other than bee nutrition, such as edaphic conditions, climate sensitivity, interactions with other plants within communities, and stakeholder interests? Understanding how global change affects the physiology and adaptability of both bees and plants – and thus (nutritional) niche shifts and health requirements across species – is one of the biggest challenges of ongoing and future research.

### Acknowledgements

This research was funded through the 2018-2019 BiodivERSA joint call for research proposals under the BiodivERSA3 ERA-Net COFUND programme in association with the Agence Nationale de la Recherche in France (ANR-19-EBI3-0003), the Deutsche Forschungsgemeinschaft in Germany (DFG: LE 2750/8-1, KL 1849/19-1 and KE1743/10-1), the National Science Centre (2019/31/Z/NZ8/04030) and Jagiellonian University (Faculty of Biology, N18/DBS/000003) in Poland, and the Research Foundation Flanders (FWO) in Belgium (1SC7120N). P.C.S. was supported by UK Research and Innovation (UKRI) funding from the Biotechnology and Biological Sciences Research Council (BBSRC; BB/T014210/1) and the Natural Environment Research Council (NERC; NE/V012282/1). G.S. also acknowledges the support from the Special Research Fund of Ghent University (BOF). We are very grateful for the constructive comments provided by two anonymous reviewers. The open-access publication of this article was funded by the BioS Priority Research Area under the program “Excellence Initiative – Research University” at the Jagiellonian University in Krakow.

### Declaration of interests

The authors declare no conflicts of interest.

### Author contributions

M.A.P. drafted the manuscript, developed figures and tables, and coordinated co-author contributions until finalization. All co-authors contributed to the original grant application upon which this conceptual paper is based. All co-authors provided comments, proof-checked citations, contributed to text and figures in particular to develop paragraphs specific to their expertise areas (pathogens, stoichiometry, niche theory). S.D.L. initialized the manuscript, invited co-authors, and supervised manuscript development until finalization.

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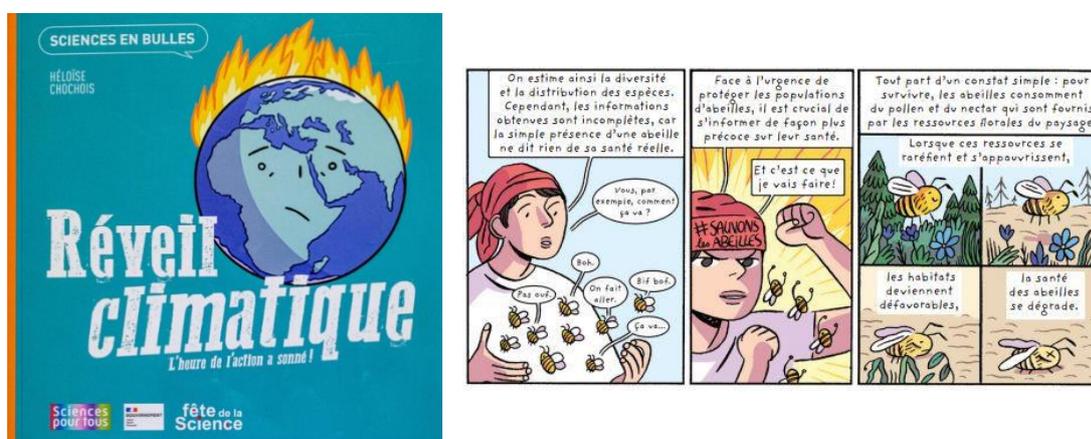
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## Production et diffusion de contenus de vulgarisation scientifique

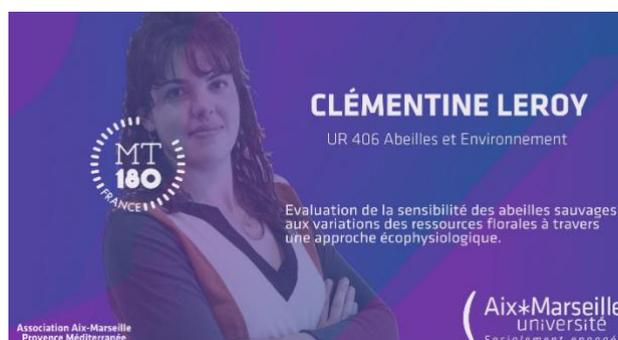
Au-delà des productions types articles scientifiques sur lesquelles j'ai eu l'occasion de travailler et qui sont au cœur de ce manuscrit, j'ai également pu déployer d'autres types de diffusion et notamment dans le domaine de la vulgarisation scientifique.

- **Écriture d'un article** dans *The Conversation* « Quand l'alimentation des abeilles sauvages raconte les modifications de leur environnement. » 2022.
- **Sciences en bulles**, édition 2022 « Réveil Climatique », à l'initiative du Ministère de l'Enseignement et de la Recherche : écriture du scénario d'une BD autour du projet européen NutriB<sup>2</sup> qui a financé ma thèse, en collaboration avec l'illustratrice Héloïse Chochois et en compagnie de 11 autres doctorant·es.



*Annexe 1: Première de couverture de l'édition 2022 de Sciences en Bulles (à gauche) et planches extraites de la BD*

- **Table ronde** à la librairie mémoire des mondes (Avignon) dans le cadre de la sortie de la BD « Réveil climatique »
- **Participation au concours de Ma Thèse en 180s (MT180)** lors de la finale régionale au MUCEM à Marseille (mars 2022) avec le sujet « Évaluation de la sensibilité des abeilles sauvages aux variations des ressources florales à travers une approche écophysio­logique ».



## Rencontre avec Clémentine Leroy, doctorante...



28 ans, prépare sa thèse à l'École doctorale 536 « Agrosociétés & Sciences » d'Avignon Université, au sein de l'unité de recherche Abeilles et environnement (UR406 - INRAE).

Claudie Galnon : Clémentine, parlez-nous de vos recherches sur l'abeille sauvage

Clémentine Leroy : Je n'avais pas une vocation spécialement dévorante pour le modèle « abeille », mais le monde des insectes m'a toujours plus ou moins attiré quand j'avais le choix, en cours, de faire des projets. J'ai commencé mon contrat doctoral en 2020, hébergée par l'INRAE et supervisée par trois chercheurs, au sein de l'unité de recherche Abeilles et environnement. J'étudie exclusivement



↑ Clémentine Leroy, doctorante.

les abeilles sauvages, qui appartiennent à l'ordre des hyménoptères mais qui sont des espèces bien différentes de l'abeille domestique. C'est une diversité à part entière. Elles sont pour la plupart solitaires, c'est-à-dire que l'abeille mâle émerge, souvent le premier, puis attend (im)patiemment la femelle pour la phase de reproduction. Au bout de quelques semaines, le mâle meurt et la femelle va gérer l'intégralité de la construction

- **Réalisation d'un court métrage** *American Wild bees* avec une classe d'élèves de première du Lycée René Char, encadrée par Madame Mélanie Roux (professeur de Sciences Physiques) dans le cadre du Projet Cinésciences, orchestré par Serge Dentin (Directeur de l'association Polly Maggoo) et Barbara Panero (Cinéaste), mars 2023.

*Annexe 3: Affiche du court-métrage American Wild Bees dans le cadre du festival Court c'est court organisé à Cavaillon en novembre 2023 à Cavaillon*

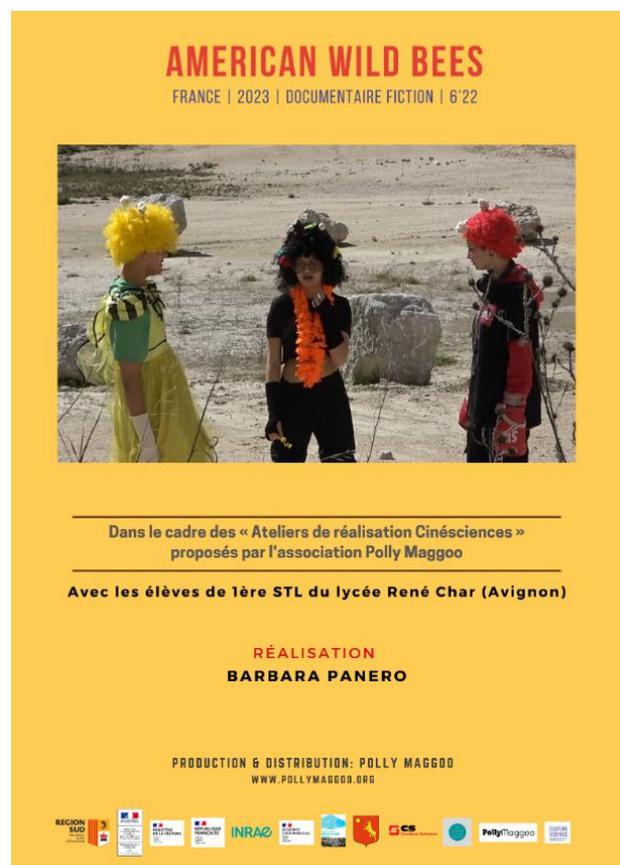
- Participation au stand de l'unité Abeilles et Environnement lors du village des sciences de la **fête des sciences 2022**

J'ai également au cours de mon contrat à l'INRAE, participé aux conseils de service mensuels en tant que représentante des contractuel·les de l'unité Abeilles et Environnement (2021-2023).

- **Interview** donnée auprès de l'association des Petits Débrouillards (juin 2022) pour m'exprimer sur mon sujet de thèse et pour promouvoir l'évènement de la fête de la science.

- **Interview** donnée auprès de Claudie Galnon (septembre 2022), Directrice de la Communication pour le magazine *Carnets* de l'université d'Avignon.

*Annexe 2: extrait du portrait dressé par Claudie Galnon dans l'édition 11 des Carnets de l'Université d'Avignon*



## Équipe d'encadrement

Cédric Alaux, co-directeur, Abeilles et environnement

Mickael Henry, co-directeur, Abeilles et environnement

Jean-Luc Brunet, co-encadrant, Abeilles et environnement

