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Conservation ecology of butterflies and dragonflies in France

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THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Écologie, Evolution, Ressources Génétique, Paléobiologie

École doctorale GAIA

Unité de recherche Centre d'Ecologie
Fonctionnelle et Evolutive (UMR 5175)

Ecologie de la conservation des Papillons de jour et des Libellules en France

Présentée par Gaël DELPON
Le 27 février 2018

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Gaël Delpon
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Liste des abréviations

AU: Administrative Unit

BMS: Butterfly Monitoring Scheme

c.-à-d. : c'est à dire ; *i.e.* dans les articles rédigés en anglais

CNPN: Conseil National pour la Protection de la Nature

DCE : Directive Cadre Eau

DD: Data Deficient (IUCN Red List category)

DDTM: Direction Départementale des Territoires et de la Mer

DHFF: Directive Habitats, Faune, Flore

DREAL : Direction Régionale de l'Environnement, de l'Aménagement et du Logement

EIA: Environmental Impact Assessment

EN: Endangered (IUCN Red List category)

ERC: Eviter, Réduire, Compenser

EX: Extinct (IUCN Red List category)

GOft: Goodness Of Fit test

Ha: Hectares

INPN: Inventaire National du Patrimoine Naturel

LC: Least-Concern (IUCN Red List category)

LPO: Ligue pour la Protection des Oiseaux

MNHN: Muséum National d'Histoire Naturelle

MSOM: Multi-Species Occupancy Model

MTD: Matrix of Taxonomic Distance

NA: Not Applicable (IUCN Red List category)

NT: Near Threatened (IUCN Red List category)

par ex. : par exemple ; *e.g.* dans les articles rédigés en anglais

PNA: Plan National d'Action

SES: Standardized Effect Size

SINP: Système d'Information sur la Nature et les Paysages

SSOM: Single-Species Occupancy Model

STELI: Suivi Temporel des Libellules

STERF: Suivi Temporel des Papillons de France

VU: Vulnerable (IUCN Red List category)

UICN: Union Internationale pour la Conservation de la Nature

Introduction générale

« Le savoir humain sera rayé des archives du monde avant que nous ayons le dernier mot d'un moucheron. »

Jean-Henri Fabre, *Souvenirs Entomologiques*, 1870-1889.

1. Conservation de l'entomofaune : enjeux et lacunes

1.1. La majorité négligée

Une perte de biomasse de plus de 75% au sein des communautés d'insectes au cours des 27 dernières années, c'est le résultat largement diffusé d'une étude menée récemment en Allemagne sur un réseau d'aires protégées (Hallmann *et al.*, 2017). Cette conclusion est venue rappeler le déclin alarmant qu'enregistre cette diversité souvent méconnue, malgré son implication dans de nombreux processus écosystémiques (Yang & Gratton, 2014). Loin de concerner exclusivement l'entomofaune, ce déclin s'intègre dans un patron global de régression de la biodiversité, en lien avec une pression croissante des activités humaines (Dirzo *et al.*, 2003). Issue de divers processus, tels que la dégradation et la fragmentation des habitats naturels, la pollution des milieux, l'urbanisation et la modification globale du climat, cette pression conduit notamment à un taux d'extinction d'espèces particulièrement élevé (Barnosky *et al.*, 2011). Les estimations les plus récentes révèlent un taux 100 à 1000 fois plus rapide que celui caractérisant les crises de la fin du Permien et du Crétacé (De Vos *et al.*, 2015), amenant ainsi certains auteurs à définir la période actuelle comme celle de la sixième crise d'extinction (Ceballos *et al.*, 2015 ; McCallum, 2015). À ces extinctions complètes d'espèces viennent s'ajouter des dynamiques de contraction de l'aire de répartition de nombreuses espèces, à travers la destruction de certaines de leurs populations et la réduction d'abondance des individus (Ceballos *et al.*, 2017), ainsi que des modifications dans la structure des communautés biologiques dont les conséquences en termes de fonctionnement des écosystèmes restent encore peu prévisibles (Butchart *et al.*, 2010 ; Barnosky *et al.*, 2012).

En réponse à la mise en évidence de plus en plus précise de la réalité de l'érosion de la biodiversité, plusieurs réglementations internationales (par ex. la signature de la Convention de Berne en 1979) et nationales (par ex. la loi de 1976 sur la protection de la nature en France) ont vu le jour avec une ambition de protection de la nature. Cette volonté s'est concrétisée lors du sommet de 1992 à Rio de Janeiro, se concluant par la ratification de la première Convention sur la Diversité Biologique par 182 pays. La nécessité de conservation de la biodiversité devient alors un des enjeux sociétaux majeurs à l'échelle globale (Cardinale *et al.*, 2012) et cette convention conduit à l'émergence de nombreuses politiques de protection, de gestion et de restauration de la nature. Leurs mises en place s'est appuyée sur le développement d'un corpus scientifique qui pose les bases de la biologie de la conservation

(Soulé, 1985), qui s'est structurée à l'interface entre recherche fondamentale et gestion opérationnelle des actions de conservation. Bénéficiant aujourd'hui de plus de 30 ans de recul, cette « science de la crise » a comme objectif principal d'assurer la gestion durable de la biodiversité (des gènes aux écosystèmes via les espèces) et à préserver les processus écologiques et évolutifs qui soutiennent cette diversité, dont les interactions entre ces différents éléments (Braby & Williams, 2016). Elle a évolué vers une vision pluridisciplinaire qui intègre progressivement la dimension humaine, à l'interface entre sciences sociales et sciences naturelles (Kareiva & Marvier, 2012). Initialement centrées sur la protection des espèces les plus rares ou menacées, les problématiques ont ainsi progressivement évolué vers une prise en compte croissante de la diversité fonctionnelle (Cadotte *et al.*, 2011) et la description de processus écosystémiques considérés comme des services essentiels au développement humain (Millenium Ecosystem Assessment, 2005 ; Pearson, 2016). Ces évolutions ont mis en évidence le besoin de stratégies plus systémiques, permettant d'intégrer les enjeux spécifiques au sein des réseaux d'interactions biotiques qui soutiennent les communautés et d'avoir une vision plus large de la connectivité de leurs habitats au sein des matrices paysagères (Margules & Pressey, 2000 ; Harvey *et al.*, 2017).

D'un point de vue opérationnel, des cadres législatifs internationaux (par ex. la Directive Habitat/Faune/Flore en 1992) et nationaux (par ex. la récente loi pour la reconquête de la biodiversité) se sont progressivement développés pour encadrer les stratégies de protection de l'environnement et offrir des leviers financiers pour la mise en place de réseaux d'aires protégées (par ex. Natura 2000) ou de plans de conservation (par ex. programmes européens LIFE, plans nationaux d'actions, ...) (Jongman *et al.*, 2004 ; Blandin, 2009). La majorité des politiques publiques ainsi mises en place se sont principalement développées sur la base de programmes visant à maintenir et favoriser des espèces considérées comme des enjeux de conservations importants (par ex. à travers la publication de listes d'espèces protégées) et à travers la protection d'espaces particulièrement riches, à l'image des grands parcs américains ou des parcs nationaux français (Larrère *et al.*, 2009). Dans un second temps, ces politiques publiques se sont révélées coûteuses dans leur mise en application (Laycock *et al.*, 2009) avec parfois des antagonismes susceptibles d'apparaître entre certains objectifs. Il est ainsi devenu important de hiérarchiser les enjeux de conservation afin de réaliser une allocation efficace des ressources disponibles (Weitzman, 1998). Malheureusement, ces procédures de hiérarchisation, de même que la recherche en biologie de la conservation, ont longtemps été marquées par un biais taxonomique important en faveur

des vertébrés (Donaldson *et al.*, 2016 ; Troudet *et al.*, 2017). Les mammifères et les oiseaux ont notamment constitué les principaux modèles biologiques à partir desquels l'impact des activités humaines sur la biodiversité a initialement été mesuré (Ceballos *et al.*, 2015). Les invertébrés ont été peu pris en compte dans les premiers développements de cette dynamique et sont demeurés durant longtemps négligés, et ce malgré le fait qu'ils représentent l'essentiel de la diversité biologique terrestre à l'échelle du globe (Wilson, 1987 ; Dunn, 2005).

Ce biais taxonomique en faveur des vertébrés se retrouve dans tous les niveaux de connaissances qui sont à la base de la biologie de la conservation. Proportionnellement au nombre d'espèces potentiellement présentes à l'échelle du globe, le nombre d'insectes décrits demeure faible et la connaissance de leur répartition est souvent limitée (Troudet *et al.* 2017). Ils font l'objet d'une attention moins importante du monde de la recherche, comme en témoigne la proportion plus faible de publications scientifiques (Marco *et al.*, 2017), en particulier dans le domaine de la conservation de la biodiversité (Donaldson *et al.*, 2016). L'évaluation de leur risque d'extinction à travers le cadre des listes rouges établies par l'UICN demeure largement incomplète, avec seulement 0,5% des espèces décrites évaluées, contre quasiment 100% pour les oiseaux et les mammifères (Rodrigues *et al.*, 2006 ; World Conservation Union, 2014). De plus, au moins un tiers de ces insectes évalués (parfois plus selon les groupes taxonomiques) ont été affiliés à la catégorie Data Deficient (DD), signe d'un manque de données empêchant toute évaluation fiable de leur risque d'extinction (Hochkirch, 2016). Enfin, une large part des financements alloués à aux programmes de conservation européens est dirigée vers les vertébrés, les insectes recevant en moyenne 1000 fois moins de fonds financiers que chaque espèce de mammifère (Cardoso *et al.*, 2011a).

Les insectes constituent pourtant un compartiment majeur dans le fonctionnement des écosystèmes (Weisser & Siemann, 2004), et sont ainsi impliqués dans de nombreuses fonctions écosystémiques, dont la plupart sont considérées comme des services écologiques essentiels (Prather *et al.*, 2013 ; Yang & Graton, 2014). Parmi les plus étudiés peuvent notamment être citées la pollinisation des angiospermes, dont 80% dépendent au moins partiellement des insectes pour leur reproduction (Ollerton *et al.*, 2011 ; Vanbergen *et al.*, 2013), ou encore la décomposition de la matière organique (Barton & Evans, 2017). Environ la moitié des insectes sont des herbivores et sont ainsi impliqués dans la majorité des flux d'énergie qui soutiennent les niveaux trophiques supérieurs (Metcalf *et al.*, 2014). Situés à la base de ces réseaux trophiques, ils constituent une ressource essentielle pour les vertébrés

(Fox *et al.*, 2006 ; Moir *et al.*, 2014), avec par exemple 60% des oiseaux qui dépendent de cette source de nourriture (Morse, 1971), et certaines espèces sont directement exploitées pour la production humaine (par ex. agroalimentaire, pharmaceutique, ... ; Yen, 2015). Les services écosystémiques fournis par les insectes ont été estimés à environ 57 billions de dollars par an aux Etats-Unis (Losey & Vaughan, 2006), et la seule pollinisation représente une valeur économique de 153 milliards d'euros à l'échelle globale (Gallai *et al.*, 2009). Des études récentes menées sur des groupes d'insectes impliqués dans certaines de ces fonctions ou considérés comme représentatifs de leur diversité ont permis de mettre en évidence un déclin important de leur diversité et une homogénéisation de leurs communautés. C'est notamment le cas chez les abeilles et des syrphes (Biesmeijer *et al.*, 2006 ; Potts *et al.*, 2010 ; Carvalheiro *et al.*, 2013), chez les libellules (Rosset *et al.*, 2014) et chez les papillons (Conrad *et al.*, 2006 ; Ekroos *et al.*, 2010 ; Börschig *et al.*, 2013 ; Eskildsen *et al.*, 2015). Environ 7% des invertébrés pourrait avoir disparu depuis les années 1980 (Régnier *et al.*, 2015) et environ un cinquième des espèces serait menacé d'extinction (Collen *et al.*, 2012). Sujets aux mêmes processus d'extinction que les vertébrés, les insectes sont en plus particulièrement touchés par des phénomènes d'extinction d'espèces spécialistes liées à des habitats très restreints et de co-extinction à la suite de la disparition d'un hôte obligatoire (Dunn, 2005 ; Dunne & Williams, 2009).

1.2. Difficultés de mises en œuvre

Ces patrons généraux mettent en avant la nécessité d'améliorer la prise en compte des insectes en vue de mieux couvrir les enjeux réels que représente la conservation de la biodiversité (Leather, 2009). Toutefois, du fait de la grande richesse de ce large taxon et du manque d'attention qui lui a été porté, le développement de stratégies opérationnelles se heurte à plusieurs difficultés principalement liées à un manque de connaissances et de données biologiques (New, 2009 ; Collen *et al.*, 2012). Ces limites ont été formalisées à travers quatre composantes recouvrant le déficit actuel de données (Samways, 2015) :

- le **déficit linnéen**, qui reflète les lacunes encore importantes dans la description des espèces d'insectes. En effet, les synthèses récentes estiment qu'entre 900 000 à 1 million d'espèces d'insectes sont décrites à l'heure actuelle (Footit & Adler, 2009 ; Resh & Cardé, 2009 ; Zhang, 2013), pour un total, tout organisme confondu, considéré comme compris entre 1,5 et 1,7 millions d'espèces décrites actuellement dans le monde (Costello *et al.*, 2012 ;

World Conservation Union, 2014). De nombreuses estimations de la diversité totale d'insectes sur le globe ont été avancées, variant de 1 à 30 millions (Erwin, 1991 ; Ødegaard, 2000). Les estimations récentes les plus conservatives se stabilisent autour de 5,5 millions d'espèces (comprises entre 2,6 et 7,8 million) (Stork *et al.*, 2015). Le nombre total d'espèces animales est quant à lui évalué à 8,7 millions d'espèces (Mora *et al.*, 2011). Les insectes constituent donc une large part de la diversité globale (63%) avec plus de 80% au moins de cette diversité qui restent encore à découvrir et à décrire. Bien que l'effort d'inventaire a été largement amélioré au cours des dernières décennies, permettant de maintenir un taux annuel de description d'espèces particulièrement élevé, le taux d'extinction actuel amène à supposer que plusieurs milliers d'insectes pourraient avoir disparu avant même d'avoir été décrits (Fonseca, 2009 ; Tedesco *et al.*, 2014).

- le **déficit wallacéen**, révélant le manque de connaissances de la distribution spatiale de nombreuses espèces d'insectes (Lomolino, 2004). La compilation de données sur la distribution et l'occurrence des espèces constitue une des étapes fondamentales de la définition d'un plan de conservation (Margules & Pressey, 2000). Cette connaissance est essentielle pour l'estimation de leur vulnérabilité et de leur réponse aux modifications de l'environnement. Bien qu'un nombre croissant de groupes d'insectes soit évalué à travers la procédure standardisée mise en place par l'UICN, une proportion importante d'espèces n'a pas bénéficié d'un effort de prospection assez important pour être reliée à une catégorie de menace (hors de la catégorie DD). Ce déficit limite également l'identification des secteurs les plus originaux et rares ou les plus menacés, qui devraient bénéficier de ressources plus importantes allouées à leur conservation. Outre la faiblesse de l'effort alloué pour l'inventaire de nombreux groupes (Collen *et al.*, 2012), ce manque de données est également sous-tendu par la difficulté que représente la réalisation d'un dénombrement complet des espèces d'insectes sur un site, en particulier dans les écosystèmes les plus riches (Lovell *et al.*, 2010 ; Foggo *et al.*, 2013). De nombreuses espèces sont peu détectables (petite taille, mœurs cryptiques, faible densité ...), ou ne le sont que dans des conditions très particulières. L'imperfection et l'hétérogénéité de la détectabilité des espèces constituent ainsi des paramètres clés devant être pris en compte pour une description ou une prédiction fiable de la répartition des espèces (Iknayan *et al.*, 2014 ; Guillerá-Arroita, 2017).

- le **déficit prestonien**, correspondant au fait que l'abondance de la majorité des espèces et sa variation dans le temps et dans l'espace restent encore inconnus. L'abondance absolue

des populations est généralement trop variable et impossible à mesurer. Elle est approchée, par l'estimation d'abondances relatives à travers des protocoles standardisés souvent coûteux permettant la comparaison de certains sites entre eux ou dans le temps (Cardoso, 2009). Ces initiatives sont généralement limitées à certains taxons ou secteurs mieux connus, pour lesquels des suivis à large échelle sont parfois engagés (Van Swaay *et al.*, 2008). Ces données d'abondance constituent une des sources principales pour l'application de certains critères d'évaluation de l'UICN, qui ne sont de ce fait presque jamais applicables aux insectes (Cardoso *et al.*, 2011b).

- le **déficit hutchinsonien**, lié au besoin d'une meilleure collecte de données sur la biologie, le cycle de vie ou l'écologie des différentes espèces, afin notamment de les replacer dans le contexte actuel d'altération des habitats naturels à large échelle (Mokany & Ferrier, 2011). Les insectes présentent généralement des exigences écologiques très fines, liées à la cooccurrence de plusieurs ressources essentielles, pouvant varier selon le stade considéré, et dans de nombreux cas à des interactions biotiques plus ou moins spécifiques (New, 2009). Le degré de spécialisation à ces différentes ressources pourra être très variable selon l'espèce considérée et aura une influence sur leur capacité de réponse aux changements environnementaux (Öckinger *et al.*, 2010). Malheureusement, même pour les taxa les plus étudiés, la compréhension des paramètres qui conditionnent la favorabilité des habitats et de la position des espèces le long du continuum généraliste-spécialiste reste incomplète (Bartonova *et al.*, 2014 ; Dennis *et al.*, 2014). De plus, il existe un besoin de perfectionnement des méthodologies statistiques pour analyser et interpréter les variations récentes de présence des espèces tout en prenant en compte les différences de détection entre espèces (MacKenzie *et al.*, 2006 ; Guillerá-Arroita *et al.*, 2014 ; Schatz *et al.*, 2016).

Ces différentes lacunes dans la connaissance des insectes constituent encore une limite pour une évaluation et une hiérarchisation cohérente des enjeux de conservation de nombreux taxa (Samways, 2015). De plus, ces problématiques s'entrecroisent avec des enjeux sociétaux, au sein desquels la majorité des insectes ne représente qu'une très faible valeur (Lewis *et al.*, 2007). La perception des insectes dans la société occidentale reste globalement négative (risque de piqûre plus ou moins dangereuse, vecteurs de pathogènes...) et la nécessité de conserver cette part de la biodiversité est parfois difficile à justifier auprès du grand public (Kellert 1993 ; Marin-Lopez *et al.*, 2007). L'importance des menaces qui pèsent sur certaines espèces est souvent ignorée et la prise de conscience de leur implication au sein de

nombreuses fonctions écosystémiques reste relativement récente en Europe (Gadoum & Roux-Fouillet, 2016). La mobilisation du grand public aura souvent une grande influence sur le succès d'un plan de conservation, comme le démontrent les cas du Monarque (*Danaus plexippus*, Linnaeus, 1758) ou du Mélissa bleu (*Lycaeides melissa samuelis*, Nabokov, 1944) aux Etats-Unis (Hess & Hess, 2015 ; Hellmann *et al.*, 2016 ; Stenoien *et al.*, 2016). De la même manière, l'attention des décideurs politiques s'est plus aisément portée vers la protection des vertébrés ; c'est pourquoi les législations permettant une conservation effective des insectes en Europe ne couvrent encore qu'une faible proportion des enjeux réels (Cardoso, 2012 ; Leandro *et al.*, 2017). En effet, depuis la publication de la Directive Habitats, Faune, Flore (DHFF), seules 123 espèces sont protégées, soit seulement 0,12% de la diversité entomologique décrite en Europe (soit plus de 105 000 espèces).

Initialement développés sur le modèle des oiseaux et des mammifères, ces outils législatifs sont largement établis sur la base de listes de protection d'espèces (DHFF à l'échelle de l'Europe, arrêté du 23 avril 2007 en France). Bien qu'elles représentent un cadre relativement facile à appliquer (Mace *et al.*, 2007), ces stratégies « espèces-centrées » montrent progressivement leur manque de pertinence face à la diversité des insectes (New, 2011). Du fait de la faible disponibilité de financement, leur réussite est fortement dépendante du choix des espèces ciblées. Un équilibre doit être trouvé, entre la représentativité de la diversité totale (ou au moins de la portion qui est concernée par une dynamique de déclin) et l'opérabilité de leur conservation (une liste d'espèces trop exhaustive constituerait un outil difficilement applicable). Dans le cadre des politiques européennes et françaises, l'attention s'est principalement portée sur quelques groupes emblématiques, mieux connus et bénéficiant d'une image plus positive auprès du grand public (par ex. papillons de jours, libellules, coléoptères, ...). Cependant, les espèces sélectionnées semblent peu représentatives de la diversité et des enjeux de conservation liées à ces groupes et à l'entomofaune en général. Plusieurs auteurs plaident pour leur révision fréquente, en incluant des critères de sélection objectifs basés sur la rareté, l'endémisme et la vulnérabilité des espèces (Cardoso, 2012 ; Leandro *et al.*, 2017), à l'image de ce qui est proposé pour d'autres groupes taxonomiques telles que les plantes (Gauthier *et al.*, 2010 ; Bacchetta *et al.*, 2012 ; Schatz *et al.*, 2014).

Ce travail de thèse présente des objectifs qui s'intègrent dans les problématiques wallacéennes et hutchisoniennes, tentant de contribuer à une meilleure compréhension des patrons de distribution de deux groupes d'insectes à l'écologie contrastée et à une évaluation

de la représentativité des données d'inventaires utilisées comme base de leur conservation. Les résultats de ces investigations pourront également apporter des éléments utiles pour une meilleure évaluation des enjeux de conservation portés par ces taxa.

2. Deux modèles d'études complémentaires : les Rhopalocères et les Odonates

2.1. Des modèles pertinents

Les Rhopalocères (papillons de jours) et les Odonates (libellules) font partie des groupes d'insectes les mieux connus (distribution, biologie, écologie, ...), en particulier à l'échelle de l'Europe de l'ouest. Chacun de ces groupes montre une variation importante en termes d'exigences écologiques qui conditionnent leur présence et sont impliqués dans plusieurs fonctions écosystémiques essentielles telles que la pollinisation ou la prédation (Kühn *et al.*, 2005 ; Kaunisto *et al.*, 2017). De fait, ils constituent des modèles majeurs pour la recherche sur l'écologie et l'évolution des insectes (Martin *et al.*, 2013 ; Bybee *et al.*, 2016). Considérés comme de bons intégrateurs des changements environnementaux (Thomas, 2005 ; Gerlach *et al.*, 2013) et bénéficiant d'une certaine popularité auprès du grand public (Guiney & Oberhauser, 2008 ; Schlegel *et al.*, 2015), ils ont été particulièrement pris en compte lors de la mise en place des politiques de conservation des insectes en Europe et en France (Warren & Bourn, 2011 ; Bried & Samways, 2015).

Les Rhopalocères et les Odonates ont rapidement été identifiés comme des groupes pertinents pour le développement d'indicateurs de la qualité des milieux ouverts et aquatiques, respectivement (McGoeth, 2007 ; Gerlach *et al.*, 2013). Dans la majorité des cas, ils sont considérés comme des bioindicateurs écologiques, sensibles à l'impact de certains stress environnementaux (par ex. l'altération des habitats naturels, leur fragmentation, le changement climatique, ...) (Braby & Williams, 2016). La mise en place d'un protocole de suivi standardisé de ce type de bioindicateurs peut permettre de détecter ces stress et d'en déduire l'impact sur l'ensemble des organismes présentant une écologie proche de celles-ci. Les Rhopalocères et les Odonates ont ainsi été régulièrement utilisés comme proxy de la richesse ou de l'abondance des communautés d'invertébrés (Thomas, 2005), afin d'évaluer les conséquences de mesures de gestion ou de restauration sur ces communautés (Catling, 2005)

ou encore afin de développer des indices d'évaluation de la qualité des milieux naturels (Feest *et al.*, 2013 ; Berquier *et al.*, 2016).

Couverts par plusieurs programmes d'inventaires ou de suivis nationaux à internationaux, ils sont régulièrement définis comme des organismes parapluies (Fleishman *et al.*, 2000 ; Pe'er & Settele, 2008 ; Barua *et al.*, 2012), dont la conservation pourra bénéficier aux communautés d'insectes liées aux milieux ouverts agropastoraux et aux milieux aquatiques au sein desquels ils se développent respectivement (New, 1997 ; Settele *et al.*, 2005 ; Settele *et al.*, 2009). Etant donné leurs caractéristiques écologiques (préférences d'habitats et/ou de plantes-hôtes, sensibilité aux modifications environnementales, ...), ces deux groupes constituent une bonne entrée pour l'étude de la réponse des communautés d'insectes aux changements globaux et pour le développement de stratégies de conservation opérationnelles venant s'appuyer sur un socle de connaissances scientifiques solides.

2.2. Diversité et répartition

Les Lépidoptères constituent l'un des ordres d'insectes les plus diversifiés de la planète (après les Coléoptères, les Hyménoptères et les Diptères), avec à l'heure actuelle environ 170 000 espèces décrites (Regier *et al.*, 2013 ; Vila, 2014). Parmi ceux-ci, la super-famille des Papilionoidea, qui regroupe les différentes familles de Rhopalocères ciblés dans cette thèse, compte environ 20 000 espèces connues (Kristensen *et al.*, 2007). La richesse spécifique la plus grande se concentre au niveau des régions néotropicales et indoaustralienne, avec cinq fois plus d'espèces par unité spatiale que dans le paléarctique (Merckx *et al.*, 2013). Le nombre d'espèces de papillons de jour présentes en Europe n'est pas encore clairement établi, notamment du fait du statut contesté de certaines espèces cryptiques (Dinca *et al.*, 2015). La majorité des évaluations récentes s'accordent sur une richesse comprenant entre 440 et 489 espèces (Van Swaay *et al.*, 2010 ; Karsholt & Nieuwerkerken, 2013 ; Kudrna *et al.*, 2015). La diversité la plus élevée se répartit dans les régions soumises à un climat méditerranéen ainsi qu'au niveau des secteurs montagneux du sud de l'Europe (Fig.1a) (Van Swaay *et al.*, 2010). C'est au niveau de ces mêmes secteurs que se concentrent la majorité des espèces endémiques du continent (Fig.1b) (Van Swaay *et al.*, 2010).

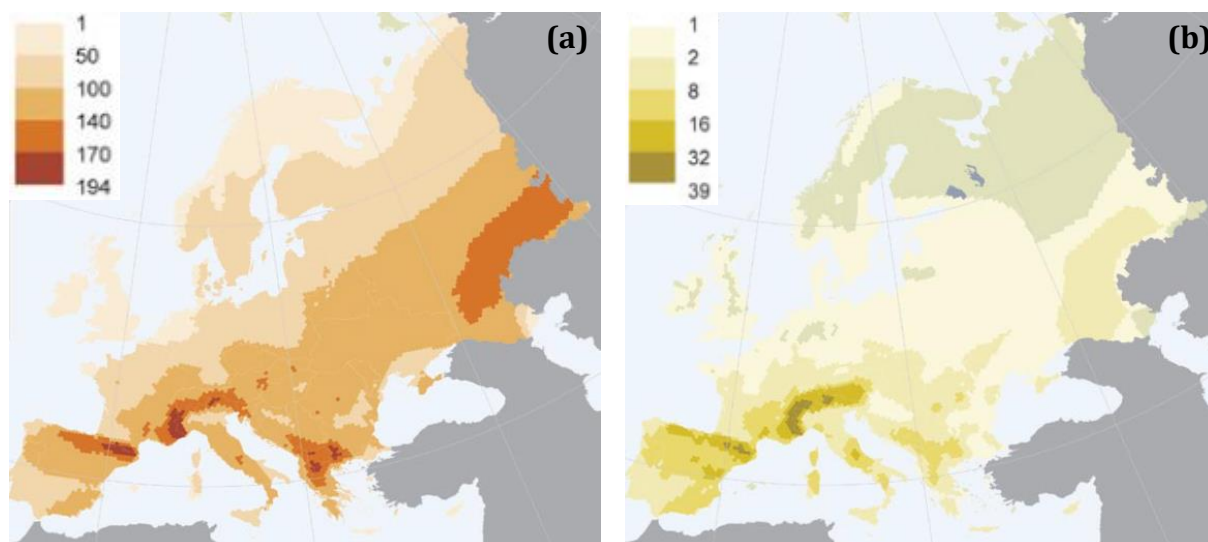


Figure 1 : Cartes de répartition **(a)** de la richesse spécifique et **(b)** des espèces endémiques des Rhopalocères en Europe, d'après la liste rouge UICN des papillons européens (Van Swaay *et al.*, 2010). Les légendes de chaque carte représentent un nombre d'espèces par hexagone de 864 km².

Les Odonates constituent une lignée évolutive plus ancienne (Grimaldi & Engels, 2005) mais un ordre actuellement moins diversifié. Environ 5950 espèces sont actuellement recensées sur le globe (Dijkstra *et al.*, 2013). Du fait de ce nombre relativement faible comparativement aux autres taxons, leur diversité est considérée comme bien connue. Toutefois le taux de découverte et de description d'espèces reste élevé, en particulier au sein de forêts humides néotropicales, qui abritent la richesse la plus élevée pour ce groupe (Paulson, 2004). Récemment encore, 60 espèces ont été décrites en Afrique (Dijkstra *et al.*, 2015), une région jusqu'alors admise comme bien décrite pour ce groupe (Kalkman *et al.*, 2008). Le nombre réel d'espèces d'Odonates est estimé entre 7000 et 7500 (Kalkman *et al.*, 2008). La diversité sur le continent européen est plus réduite et beaucoup plus stable. L'Europe constitue en effet l'un des berceaux de l'étude des libellules et l'odonatofaune y est inventoriée de longue date (par ex. une première synthèse continentale est publiée par Charpentier, 1840). Elle compte actuellement 143 espèces décrites (Dijkstra & Kalkman, 2012 ; Boudot & Kalkman, 2015). Cette richesse se répartit de manière plus homogène que celle des Rhopalocères, avec une diversité importante établie sur plusieurs pays d'Europe de l'ouest et d'Europe centrale (France, Suisse, Allemagne, Pologne, ...) et un gradient négatif en remontant vers les hautes latitudes (Fig.2a) (Kalkman *et al.*, 2010). Les espèces endémiques sont principalement présentes dans le sud ouest de l'Europe, c'est-à-dire dans le sud de la France, au sud-ouest de l'Espagne et au Portugal (Fig.2b) (Kalkman *et al.*, 2010).

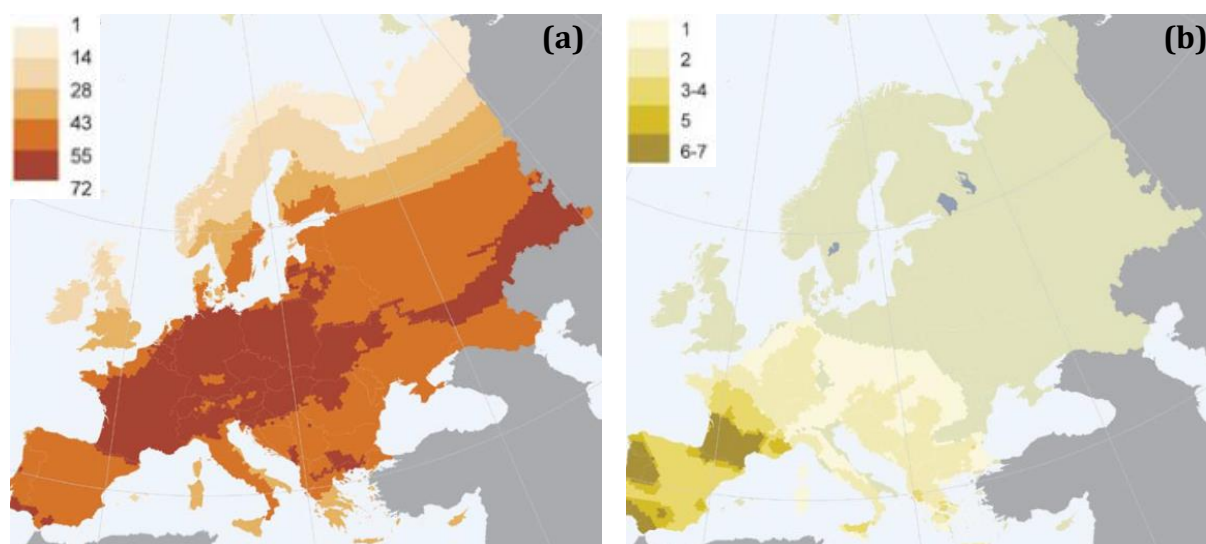


Figure 2 : Cartes de répartition **(a)** de la richesse spécifique et **(b)** des espèces endémiques d'Odonates en Europe, d'après la liste rouge UICN des libellules européennes (Kalkman *et al.*, 2010). Les légendes de chaque carte représentent un nombre d'espèces par hexagones de 864 km².

Sur les 42 000 espèces d'insectes connues en France, sont dénombrés environ 5000 espèces de Lépidoptères, dont seulement 262 sont des Rhopalocères, et 89 espèces d'Odonates (Jong *et al.*, 2014 ; Lafranchis *et al.*, 2015 ; Boudot *et al.*, 2017). La France constitue ainsi l'un des pays abritant la plus large diversité pour les deux groupes considérés. Ce territoire recouvre en effet de larges contrastes de reliefs et de climats, résultant notamment du croisement de plusieurs grandes aires biogéographiques (continentale, alpine, atlantique et méditerranéenne), favorables à l'expression d'une grande diversité de biotopes et de cortèges associés (Joly *et al.*, 2010 ; EEA, 2012). Il englobe ainsi plusieurs « hotspots » de biodiversité, en particulier au niveau des secteurs montagneux des Alpes et des Pyrénées, et un nombre important d'espèces endémiques du sud de l'Europe s'établit sur sa façade méditerranéenne (Figs.1 & 2). La France porte ainsi une forte responsabilité pour la conservation de la diversité de ces deux taxa et notamment des cortèges les plus originaux (Keil *et al.*, 2008)

2.3. Exigences écologiques et habitats de reproduction en Europe

Les Rhopalocères et les Odonates sont caractérisés par des cycles de vie courts et complexes, impliquant des exigences différentes en fonction du stade de développement, souvent liés à des propriétés très particulières du micro-habitat, ainsi que des capacités de déplacement relativement importante à l'état imaginal. De ce fait, ils présentent généralement une réponse

particulièrement rapide aux changements environnementaux, même à des échelles réduites (Warren *et al.*, 2001 ; Córdoba-Aguilar, 2008). Ces réponses sont ainsi contrastées entre ces deux groupes du fait de leurs spécificités biologiques, chacun incorporant également une grande diversité écologique et phénotypique.

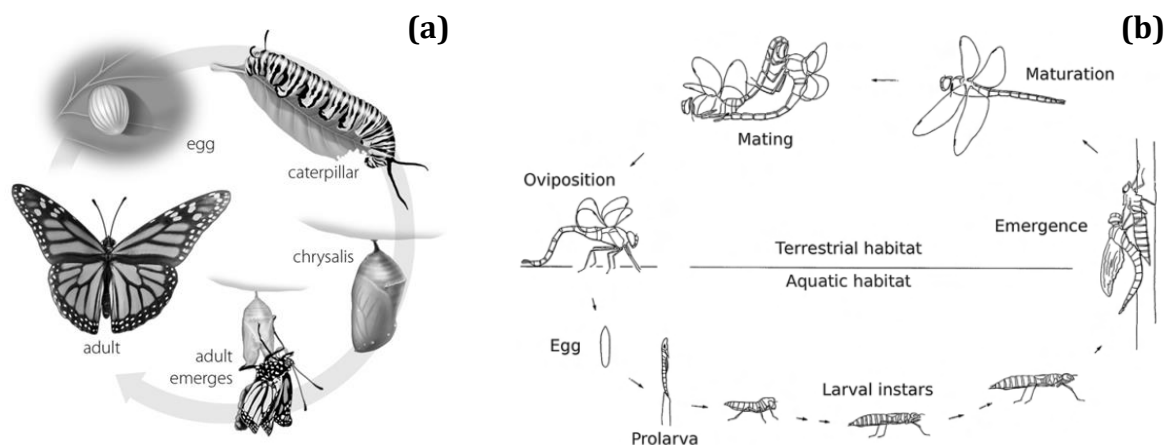


Figure 3 : Schéma du cycle de vie typique **(a)** des Rhopalocères (d'après www.thinglink.com) et **(b)** des Odonates (d'après Suhling *et al.*, 2015).

Les Rhopalocères sont des organismes holométaboles, présentant une métamorphose complète faisant suite à une phase larvaire spécialisée dans l'accumulation de ressources énergétiques (Fig.3a). Les chenilles de la majorité des espèces européennes sont phytophages et consomment les tissus de divers angiospermes (Munguira *et al.*, 2009). La relation avec ces ressources trophiques est généralement très étroite, impliquant une spécificité des processus de sélection des supports de ponte par la femelle et une adaptation de la chenille aux défenses de la plante (Menken *et al.*, 2010 ; Friberg *et al.*, 2015). Les adultes sont également dépendants de la présence d'angiospermes dont le nectar constitue la principale ressource nutritive. Certaines espèces présentent alors un régime très spécialisé au stade imaginal, se nourrissant spécifiquement de quelques espèces qui diffèrent généralement de celles consommées par la larve (Hardy *et al.*, 2007 ; Altermatt & Pearse, 2011). Les Rhopalocères européens sont principalement des organismes thermophiles se développant au sein de paysages prairiaux, souvent liés à des pratiques agro-pastorales et structurés par des réseaux de haies ou de bosquets représentant des secteurs potentiels de reproduction et de repos (Van Swaay *et al.*, 2006). Les pelouses sèches calcaires et les pelouses de moyenne altitude font également partie des paysages les plus riches en espèces (Van Swaay, 2002 ; Stefanescu *et al.*,

2011). Les paramètres du micro-climat local ont une influence sur la capacité d'accueil du milieu, en particulier la température et l'humidité du sol (Schweiger *et al.*, 2014).



Figure 4 : Imagos de Leucorrhine douteuse (*Leucorrhinia dubia*), de Sympétrum déprimé (*Sympetrum depressiusculum*) et d'Azuré du Serpolet (*Maculinea arion*) (de gauche à droite ; clichés : G.Delpon).

Les Odonates sont des organismes hémimétaboles, présentant un cycle biphasique avec une phase larvaire aquatique et une phase imaginaire aérienne (Corbet, 1999) (Fig.3b). Les larves se développent principalement dans des eaux douces. Selon les espèces, elles pourront être courantes ou stagnantes, certaines présentant des adaptations particulières à l'assèchement estival (Strachan *et al.*, 2015) ou à des biotopes acides et pauvres en ressources nutritives, à l'image des tourbières par exemple (Suhling *et al.*, 2015). La durée du développement est fortement conditionnée par la température du milieu et la disponibilité de proies (Hassal & Thompson, 2008). Les larves d'Odonates sont en effet d'importants prédateurs intermédiaires dans les réseaux trophiques aquatiques, se nourrissant d'un large éventail de petits arthropodes (Kaunisto *et al.*, 2017), y compris d'autres Odonates, et constituent eux-mêmes les proies de nombreux organismes tels que les poissons. Étant donné la pression qu'ils peuvent exercer sur les populations de certaines espèces, la composition des communautés de poissons aura une grande influence sur la richesse odonatologique des milieux (Wittwer *et al.*, 2010), excluant les espèces les moins tolérantes telles que par exemple la Leucorrhine douteuse (*Leucorrhinia dubia*, Vander Linden, 1825) (Mikolajewski *et al.*, 2010) (Fig.4). La capacité d'accueil des micro-habitats larvaires dépend des exigences écologiques des espèces, et elle sera principalement conditionnée par la structure de la végétation aquatique, par la nature du substrat ou par les caractéristiques physico-chimiques des milieux aquatiques (charge en nutriments, conductivité, pH, présence de polluants) (Schindler *et al.*, 2003 ; Rouquette & Thompson, 2005). Ces micro-habitats s'insèrent alors dans des entités paysagères plus larges au sein desquelles la structure des milieux terrestres

aura une grande importance lors de la phase imaginaire (maturation des ténéraux (*cf glossaire*), chasse, reproduction, abri face aux intempéries, zones de repos ...) (Hykel *et al.*, 2017).

Les différents stades qui composent ces cycles de vie complexes présentent donc des exigences différentes, avec des besoins en ressources et des capacités de déplacement très variables, qui conditionnent de manière conjointe la valeur sélective des individus (Stoks & Cordoba-Aguilar, 2012). Pour les deux taxa étudiés, l'habitat propre à chaque espèce sera alors représenté par le croisement de l'ensemble des ressources nécessaires à chacun des stades de développement au sein d'un espace donné (Dennis, 2010 ; Dennis *et al.*, 2014). Ces ressources pourront être réparties de manière hétérogènes et discontinues au sein d'un paysage (Taylor & Merriam, 1995 ; Vanreusel & Van Dyck, 2007), obligeant les adultes à des déplacements réguliers entre les différentes unités d'habitats (Baguette & Mennechez, 2004). La qualité de ces différentes unités d'habitats et leur degré d'isolement pourront ainsi avoir une influence importante sur la dynamique et la persistance de certaines populations (Dennis & Sparks, 2006). Certaines espèces seront ainsi dépendantes de la présence d'un riche réseau d'habitats favorables bien connectés pour se maintenir, à l'image du *Sympetrum* déprimé (*Sympetrum depressiusculum*, Selys, 1841) (Fig.4) ou de certains Nymphalidae présentant des dynamiques métapopulationnelles (Baguette *et al.*, 2011 ; Dolny *et al.*, 2014 ; Pyke *et al.*, 2015). Le degré de mobilité des espèces entre ces micro-habitats et leur capacité de dispersion à longue distance constituent des traits essentiels pour la compréhension de la dynamique de leurs populations et de l'impact des changements environnementaux (Stevens *et al.*, 2010 ; McCauley *et al.*, 2014).

2.4. Les interactions biotiques : composantes essentielles de la niche écologique des espèces

Les interactions biotiques représentent une composante essentielle de la niche biologique des espèces et ont une grande influence sur leur distribution, sur leur abondance ou sur la dynamique de leur population. Comme présenté dans la partie précédente, les Rhopalocères sont entièrement dépendants d'interactions avec les plantes à différentes étapes de leur cycle de vie. Le lien trophique entre les chenilles et leurs plantes-hôtes est notamment considéré comme un point central de l'écologie des espèces et a fait l'objet de nombreuses études, notamment en région tropicale (Munguira *et al.*, 2009). Le degré de spécialisation du régime alimentaire des larves montre une grande variabilité entre les espèces, faisant des

Rhopalocères un bon modèle d'étude de la significativité des phénomènes de coextinction chez les insectes (Pearse & Altermatt, 2013). Trois groupes d'espèces peuvent être distingués (Bidart-Bouzat & Kliebenstein, 2011) (Fig.5) :

- Des espèces strictement monophages, qui ne consomment qu'une seule espèce de plante qui conditionne entièrement leur présence. C'est par exemple le cas du Cuivré de la Bistorte (*Lycaena helle*, Dennis & Schiffermüller, 1775) et du Nacré de la Bistorte (*Boloria eunomia*, Esper, 1800), dont les larves sont spécialistes de la même plante (*Bistorta officinalis*, Delarbre 1800).
- Des espèces oligophages, associées à un nombre limité de plantes-hôtes (le nombre est variable selon les études), appartenant généralement à la même famille, voire au même genre. C'est par exemple le cas de la Diane (*Zerynthia polyxena*, Dennis & Schiffermüller, 1775) et de la Proserpine (*Zerynthia rumina*, Linnaeus, 1758) dont les chenilles se développent sur quelques espèces du genre *Aristolochia*.
- Des espèces polyphages, qui consomment une large variété de plantes, à l'image du Flambé (*Iphiclides podalirius*, Linnaeus, 1758) ou du Thècle de la Ronce (*Callophrys rubi*, Linnaeus, 1758) qui sont liées à plus de 20 plantes nourricières.

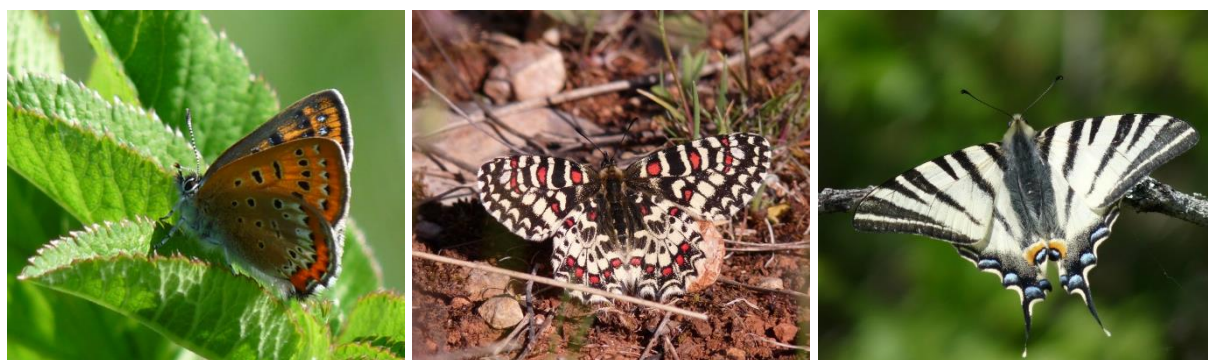


Figure 5 : Imagos de trois espèces de Rhopalocères représentatives de la variabilité du degré de spécialisation trophique : le Cuivré de la Bistorte (*Lycaena helle*) monophage, la Proserpine (*Zerynthia rumina*) oligophage et le Flambé (*Iphiclides podalirius*) polyphage (de gauche à droite ; clichés : G.Delpon).

Un lien important a été mis en évidence entre ce degré de spécialisation et la vulnérabilité des espèces face aux altérations de leurs habitats ou aux changements climatiques, les monophages étant généralement caractérisés par des capacités de réponse plus

limitées à ces variations (Komonen *et al.*, 2004; Stefanescu *et al.*, 2011). La stratégie de développement, les modes de défense ou encore la phénologie des plantes nourricières ont également une influence sur la réaction des espèces face à ce type de perturbations (Dennis *et al.*, 2004 ; Cizek *et al.*, 2006 ; Kemp *et al.*, 2008 ; Altermatt, 2010). À ces caractéristiques s'ajoutent l'abondance des plantes-nourricières, leur distribution dans l'espace et le temps ou encore leur exposition, comme autant de facteur ayant un rôle dans le maintien des populations de papillons (Dennis, 2010). La gestion ou l'exploitation d'un milieu a ainsi des conséquences importantes sur les communautés de papillons de jour via des modifications de richesse ou de structure des assemblages de plantes (Welti *et al.*, 2017). Ce type d'effets indirects est susceptible de mener à des extinctions locales de Rhopalocères avant même tout changement dans la composition des communautés floristiques (Pearse & Altermatt, 2013).

En plus de ce lien avec les plantes, certains Rhopalocères de la famille des Lycaenidae montrent également une forte dépendance avec des espèces de fourmis pour l'aboutissement de leur phase larvaire (Fiedler, 2006). C'est notamment le cas chez les espèces du genre *Maculinea* (Fig.4), qui exploitent ainsi des fourmilières à travers une prédation directe ou un parasitisme, impliquant divers phénomènes de mimétisme chimique et acoustique (Hayes, 2015). La spécificité de ces relations est également variable en fonction des espèces considérées (Lafranchis & Kan, 2012) et leur prise en compte a permis une large amélioration des programmes de conservation ciblés sur les Lycaenidae les plus menacés au cours des dernières années (Mouquet *et al.*, 2005 ; Kaufmann *et al.*, 2014).

La prise en compte des interactions biotiques apparaît donc comme un prérequis indispensable à la mise en place de programmes de conservations des espèces qui entretiennent des liens trophiques aussi spécifiques et obligatoires. Elles permettent une connaissance plus complète des caractéristiques des micro-habitats nécessaires au maintien de l'espèce (Dennis, 2010), ainsi qu'une meilleure prédiction de leurs aires de répartition et de leur réponse et modifications de l'environnement (De Araújo & Luoto, 2007 ; Staniczenko *et al.*, 2017). C'est pourquoi le développement récent de méthodes d'analyses basées sur la construction de réseaux écologiques, mettant en lien les espèces à travers certaines de leurs interactions (Bascompte & Jordano, 2007), offre des opportunités pour un changement de perspectives en biologie de la conservation, en améliorant notre capacité à maintenir l'intégrité des écosystèmes et en augmentant les interactions entre recherche théorique et mise en œuvre opérationnelle (Kaiser-Bunbury & Blüthgen, 2015). Un nombre croissant d'études

tente de définir les métriques les plus pertinentes de description de ces réseaux afin d'aboutir à une vision plus intégrative de la conservation, ciblant des assemblages complets d'espèces, avec une hiérarchisation plus pertinente des enjeux sur la base de l'importance des espèces dans le maintien de la structure du réseau (Harvey *et al.*, 2017). Pour les Rhopalocères, ces nouvelles approches ont permis de questionner les patrons d'associations à l'échelle mondiale (Ferrer-Parris *et al.*, 2013), la significativité de la médiation chimique lié à la spécificité de la défense des plantes (Muto-Fujita *et al.*, 2017), l'influence de la compétition interspécifique sur la structuration des communautés (Nakadai *et al.*, 2017), la résilience des communautés le long des successions secondaires (Villa-Galavitz *et al.*, 2012) ou encore le recouvrement des régimes alimentaires chenilles-imagos (Astegiano *et al.*, 2017). Toutefois, peu de travaux européens ont permis de mettre en perspective le positionnement de ces espèces dans le réseau avec leurs enjeux de conservation ou leur statut de protection.

2.5. Des groupes indicateurs ciblés par des programmes de suivis

Plusieurs programmes d'inventaires ou de suivis de ces deux groupes ont été développés au cours des dernières années dans différents pays d'Europe afin d'avoir une meilleure image de la richesse et de l'abondance des assemblages en fonction des caractéristiques des milieux et de leur évolution (Van Swaay *et al.*, 2008). Initialement centrés sur les Rhopalocères, des protocoles standardisés ont été construits afin de mesurer annuellement l'abondance des espèces sur certains sites (par ex. le Butterfly Monitoring Scheme (BMS) développé au Royaume-Uni), ou d'améliorer la connaissance de la répartition des espèces. Une proportion importante de ces protocoles est basée sur la définition de transects (c.-à-d. des itinéraires-échantillons) fixes le long desquels les Rhopalocères observés sont dénombrés (Pollard & Yates, 1993). Bien que ce type de plan d'échantillonnage montre des limites pour la détection de certaines espèces (Kéry & Plattner, 2007), ces programmes ont amené au développement d'indicateurs de la qualité des milieux ouverts et de leur évolution à l'échelle européenne (par ex. l'European grassland butterfly indicator ; Van Swaay *et al.*, 2012). À travers l'initiative du BMS, cette méthodologie a été mise en place dans 18 pays d'Europe (Fig.6a), permettant d'obtenir une indication de l'évolution des effectifs relatifs de Rhopalocères depuis les années 1990. Six nouveaux pays sont susceptibles de contribuer à cette initiative dans les prochaines années (Van Swaay, 2014) et des lignes directrices ont été développées afin d'assurer une comparabilité des données, auxquelles les différents protocoles nationaux déjà en place se sont adaptés.

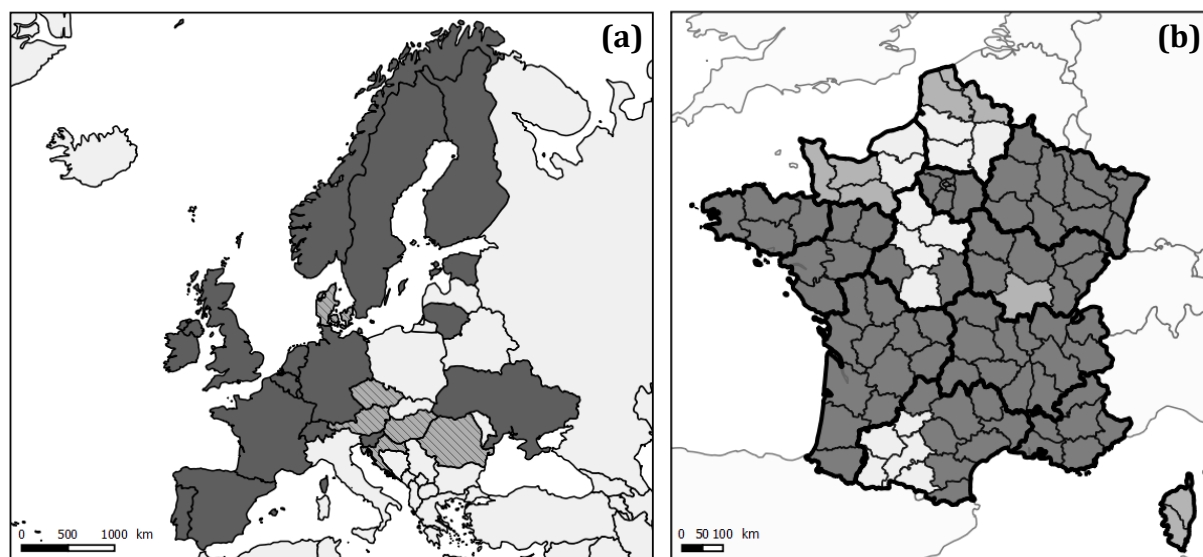


Figure 6 : (a) Carte des pays ayant intégré (noir) ou prévoyant une intégration (gris hachuré) au suivi des papillons d'Europe (BMS), et (b) couverture directe (noir) ou indirecte (gris foncé) des départements français par les portails de saisie de données naturalistes Biolovision.

En France, deux protocoles de suivi de Rhopalocères à l'échelle nationale ont été intégrés à cette dynamique européenne : le Suivi Temporel des Papillons de France (STERF) et le « suivi des milieux ouverts par les Rhopalocères » développé par les Réserves Naturelles de France (Langlois & Gilg, 2007). Comme les autres protocoles, il est basé sur le principe de suivi de transects fixes tel qu'initié par Pollard (1977). Un inventaire national des espèces de ce groupe a également été lancé par le Muséum National d'Histoire Naturel (MNHN) (Dupont, 2014a), visant à synthétiser et améliorer la connaissance de la répartition des espèces, et dans le cadre duquel un protocole standardisé a été défini afin de pallier aux limites dans la précision des suivis de transects (Dupont, 2014b). Des programmes similaires ont été mis en place pour les libellules, en particulier à l'occasion du premier Plan National d'Action (PNA) en faveur des Odonates lancé en 2011 (Dupont, 2010). Le Suivi Temporel des Libellules (STELI) a ainsi été lancé à partir de 2011 en vue de suivre la dynamique des communautés d'Odonates à partir de données collectées sur un réseau de sites, s'adressant à la fois aux gestionnaires d'espaces naturels et au grand public (Gourmand *et al.*, 2012). D'autres répondent plutôt à un besoin d'évaluation de l'état de conservation de certains milieux aquatiques, tels que le protocole RhoMéO (suivi des zones humides du bassin Rhône-Méditerranée), ou au suivi d'espèces représentant un enjeu particulier, comme c'est le cas sur le bassin de la Loire (Itrac-Bruneau *et al.*, 2016). En parallèle de ces suivis naturalistes, des projets plus participatifs ont été lancés afin d'obtenir des données sur les espèces communes et de suivre des milieux particulièrement anthropisés. C'est notamment le cas de

l'Observatoire des Papillons des Jardins (pilote par le MNHN), qui propose la réalisation de listes dont la résolution taxonomique est ajustée aux connaissances de l'observatoire (Fontaine *et al.*, 2016)

L'essor de ces différents programmes d'inventaire et de suivi reflète l'intérêt croissant de naturalistes et des scientifiques pour l'étude des Rhopalocères et des Odonates (New, 2014), et il offre une connaissance de leur répartition bien plus fine que pour d'autres groupes d'insectes (Troudet *et al.*, 2017). Cette dynamique s'est accompagnée de la publication régulière de guides d'indentification (Dijkstra & Lewington, 2006), de synthèses relatives à l'écologie des espèces (Cordoba-Aguilar, 2008) et d'atlas de répartition (Lafranchis *et al.*, 2015) qui permettent la mobilisation d'un plus grand nombre de volontaires. En parallèle, divers portails permettant la saisie de données naturalistes en ligne voient le jour, de même que des stratégies de centralisation de ces informations à l'échelle nationale (par ex. INPN, SINP, ...). Actuellement presque tous les départements français sont couverts par au moins un des portails de saisie construits sur le modèle Biolovision (<https://data.biolovision.net/>) (Fig.6b) et un portail national porté par la Ligue de Protection des Oiseaux (LPO), est en cours de mise en service. Les données fournies par la multiplication de ces réseaux d'observateurs représentent une opportunité pour évaluer les tendances des espèces à large échelle et construire des indicateurs robustes de la biodiversité (Brereton *et al.*, 2011). Ces jeux de données particulièrement volumineux constituent en effet une matière première particulièrement utile pour mesurer l'impact des changements environnementaux sur les communautés d'insectes à une échelle spatiale plus détaillée (Schmeller *et al.*, 2009). La centralisation, l'agrégation et l'analyse de ces données issues d'initiatives aux objectifs parfois différents représente également un challenge nécessitant l'utilisation de méthodes qui permettent de prendre en compte la variabilité de l'expérience des observateurs et l'hétérogénéité de la pression d'échantillonnage ou des protocoles utilisés (Van Strien *et al.*, 2010, Shmucki *et al.*, 2015).

2.6. Un déclin enregistré à l'échelle de l'Europe

Cette multiplication de données sur la répartition et l'abondance des espèces de Rhopalocères et d'Odonates a permis une évaluation plus fine de leur dynamique et de leur vulnérabilité. La dynamique de déclin signalée à l'échelle globale (Thomas *et al.*, 2004 ; Clausnitzer *et al.*, 2009) a ainsi pu être quantifiée à l'échelle de l'Europe à travers la production d'indicateurs,

de listes rouges et d'études nationales. Ces travaux ont permis de mettre en évidence une régression de l'aire de répartition et un risque d'extinction important pour de nombreuses espèces (Van Swaay *et al.*, 2010 ; Kalkman *et al.*, 2010) (Fig.7).

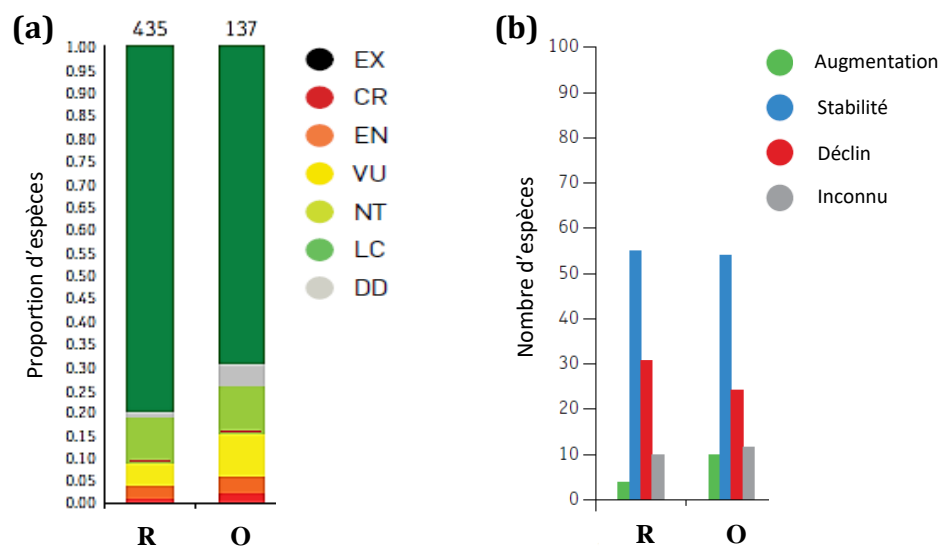


Figure 7 : Risque d'extinction **(a)** et dynamique des populations **(b)** des espèces de Rhopalocères (R) et d'Odonates (O) évaluées à l'échelle de l'Europe (modifié d'après Collen *et al.*, 2012). Les abréviations à la droite du graphe (a) correspondent aux catégories IUCN (cf liste des abréviations au début du document)

Sur la base de l'évaluation IUCN menée à l'échelle de l'Europe, 20% des espèces sont considérées comme menacées à presque menacées et environ 30% des espèces montrent une dynamique de déclin de leurs populations (Fig.7) (Collen *et al.*, 2012). L'indicateur d'abondance construit sur la base des données issues du programme BMS enregistre une régression de 50% entre 1990 et 2005 à l'échelle des pays européens contribuant au BMS (Van Swaay *et al.*, 2008). Ce déclin est particulièrement important dans les pays industrialisés d'Europe de l'Ouest depuis les années 1950 (Warren *et al.*, 2001). Les Rhopalocères ont ainsi montré un déclin de leur aire de répartition supérieur à celui des oiseaux et des plantes vasculaires à l'échelle de la Grande-Bretagne au cours de 40 dernières années (Thomas *et al.*, 2004). Il s'est traduit par une diminution de l'aire d'occurrence d'environ 70% des espèces et par une diminution de l'abondance pour 57% des espèces entre 1976 et 2015 (Fox *et al.*, 2015). Les Flandres, la Hollande et l'Allemagne constituent également des territoires montrant une régression particulièrement significative de l'aire des espèces de papillons de jour (Maes & Van Dyck, 2001 ; Wenzel *et al.*, 2006), comptabilisant même plusieurs extinctions régionales (Konvicka *et al.*, 2006 ; Pearse & Altermatt, 2013). Cette dynamique

concerne même des espèces considérées comme communes et très répandues à l'échelle de l'Europe (Van Dyck *et al.*, 2009), comme par exemple l'Azuré commun (*Polyommatus icarus*, Rottemburg, 1775) ou le Cuivré commun (*Lycaena phlaeas*, Linnaeus, 1760) (Léon-Cortés *et al.*, 1999 ; 2000). Un déclin de 60% des espèces liées aux pelouses semi-naturelles a également été enregistré en Finlande au cours des 50 dernières années (Kuussaari *et al.*, 2007).

Les Odonates, quant à eux, font partie des groupes d'espèces évalués qui présentent la plus grande proportion d'espèces menacées en Europe, avec les reptiles et les amphibiens (Essl *et al.*, 2013). Plus de 70% des espèces sont listées dans une catégorie de vulnérabilité (Near Threatened NT, Vulnerable VU, Endangered EN et Critically Endangered CR) dans au moins une des listes rouges publiées à l'échelle nationale au sein de l'Europe (Boudot & Kalkman, 2015). Plus de 25% des espèces sont considérées comme menacées à presque menacée à l'échelle de l'Europe et au moins 20% des espèces montrent une dynamique de déclin de leurs populations (Fig.7) (Kalkman *et al.*, 2010). Un déclin particulièrement important des Odonates a été reporté en Europe de l'Ouest entre 1950 et 1980 (Boudot & Kalkman, 2015), bien que certaines espèces liées à la dynamique des grands fleuves aient montré une importante résilience au cours des dernières années (par ex. le Gomphe à pattes jaunes, *Gomphus flavipes*, Charpentier, 1825) (Termaat *et al.*, 2015).

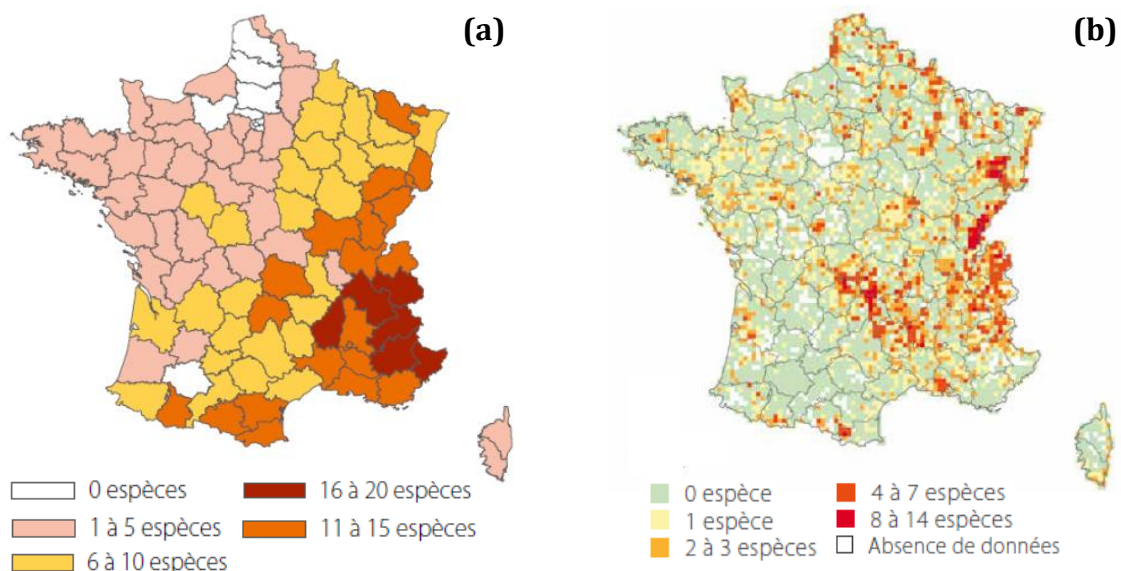


Figure 8 : Répartition des espèces menacées et quasi menacées **(a)** de papillons de jours et **(b)** de libellules en France métropolitaine selon les Listes rouges nationales (UICN *et al.*, 2014 ; 2016). Les papillons sont cartographiés à l'échelle départementale et les libellules à l'échelle de la maille 10x10km.

Malgré l'importance de la richesse et de l'endémisme que concentre la France pour les deux taxa étudiés, l'évaluation de leur risque d'extinction à l'échelle nationale est relativement récente et les études sur la dynamique des espèces à large échelle restent rares. Environ 14% des espèces de Rhopalocères et presque 30% des espèces d'Odonate sont considérées comme menacées à quasi-menacées (UICN France *et al.*, 2014 ; 2016). Un déclin important de la richesse spécifique est signalé dans plusieurs départements du nord-ouest de la France à la fin du 20^es (Dennis *et al.*, 2002 ; Dennis & Shreeve, 2003) et les enjeux de conservation actuels sont répartis de manière hétérogène sur le territoire (Fig.8). En effet le massif alpin concentre l'essentiel des enjeux pour les deux groupes. On retrouve également un nombre important d'espèces menacées sur le pourtour méditerranéen pour les papillons de jour et au niveau du Massif central et de l'est de la France pour les libellules.

3. Une diversité de réponses aux changements paysagers et climatiques

Ce déclin enregistré à l'échelle de l'Europe est principalement une conséquence d'une intensification des activités anthropiques, engendrent un changement important des habitats d'espèces à large échelle par différents processus combinés (Essens *et al.*, 2017). Ces derniers impactent principalement les communautés de Rhopalocères et d'Odonates à travers une destruction directe ou une altération des habitats de reproduction des espèces, une fragmentation des paysages ou une modification des conditions microclimatiques. L'enrichissement des milieux en nutriments conduit également à des changements dans la structure et la composition des communautés floristiques susceptibles d'affecter les papillons qui en dépendent (Marini *et al.*, 2009 ; Feest *et al.*, 2014). L'introduction et l'expansion d'espèces envahissantes a également un effet négatif sur de nombreuses espèces, par une action directe sur les individus (Fincke *et al.*, 2009) ou indirecte via une modification de leurs habitats (Samways & Sharratt, 2010 ; Gallien *et al.*, 2017). Ces différentes pressions sont sous-tendues à l'échelle globale par deux phénomènes principaux auxquels les papillons de jours et les libellules sont particulièrement sensibles : la modification de l'occupation des sols et le changement climatique (Travis, 2003 ; Stefanecu *et al.*, 2011 ; Ostberg *et al.*, 2015). Ces deux facteurs agissent en synergie. Leurs impacts relatifs sont parfois difficiles à mesurer, d'autant que leurs conséquences sur les différents organismes sont variables selon l'échelle et les espèces considérées (Boggs, 2016). Cependant, la prise en compte de ces effets combinés

est essentielle pour comprendre l'évolution des patrons de diversité à large échelle (Warren *et al.*, 2011 ; Titeux *et al.*, 2016).

3.1. Pertes et dégradations des habitats naturels

Le continent européen est soumis à d'importants changements d'occupation des sols et à un remaniement des paysages depuis le début de 20^{ème} siècle (Sirami *et al.*, 2010 ; Titeux *et al.*, 2016). Étant donné l'amplitude de ces changements, ils sont considérés comme un des principaux facteurs impliqués dans la diminution de la richesse et l'altération de la structure des communautés d'insectes (Stoate *et al.*, 2009 ; De Araújo *et al.*, 2015 ; Newbold *et al.*, 2015). L'urbanisation croissante et l'intensification des pratiques agricoles sont identifiées comme deux pressions anthropiques majeures pour les Rhopalocères et les Odonates (Warren & Bourne, 2011 ; Boudot & Kalkman, 2015). L'exode rural et la concentration d'une part croissante de la population dans les villes a conduit à une forte expansion des centres urbains au cours des dernières décennies ainsi qu'à une augmentation de la couverture végétale dans les campagnes (Antrop, 2004 ; Grimm *et al.*, 2008).

Amenant à une destruction directe ou une fragmentation des habitats naturels, ces processus ont des impact négatif sur la distribution et l'abondance de nombreux Rhopalocères européens (McKinney, 2008 ; Fontaine *et al.*, 2016). La simplification des paysages du fait de l'augmentation des surfaces de monocultures, de l'enrichissement artificiel des sols et de la suppression des haies est considérée comme une des premières causes de leur déclin (Van Dyck *et al.*, 2009). En parallèle de cette intensification agricole concentrée sur certains secteurs, les milieux les moins productifs autrefois utilisés pour l'élevage extensif sont progressivement abandonnés en lien avec le déclin des activités agro-pastorales (MacDonald *et al.*, 2000). Cette dynamique est particulièrement importante sur les reliefs méditerranéens, aux niveaux desquels les pelouses thermophiles calcaires sont progressivement recolonisées par des formations de fourrés et de garrigues (Sirami *et al.*, 2010). Si ces processus sont considérés par certains comme une opportunité de rétablir une plus grande part de naturalité dans les processus écosystémiques (Navarro & Pereira, 2015), ils constituent une menace immédiate pour les populations de nombreux Rhopalocères liés aux milieux ouverts et dont la présence est favorisée par une structure hétérogène du paysage (Slancarova *et al.*, 2016).

Les activités humaines ont également des impacts importants sur les milieux humides, entraînant de nombreuses destructions et dégradation de ces habitats fragiles à l'échelle du globe (Van Asselen *et al.*, 2013). La modification des réseaux hydrologiques lors de l'expansion des villes et l'augmentation de la charge de pollution ou de nutriments dans les eaux de surfaces vont également avoir des conséquences importantes sur les cortèges d'Odonates (Fitzpatrick *et al.*, 2007 ; Villalobos-Jiménez *et al.*, 2016). Bien que les Odonates réagissent moins à la présence de polluants chimiques que d'autres groupes d'insectes aquatiques (par ex. les Plécoptères et Trichoptères ; Chang *et al.*, 2014), certaines espèces peuvent être impactées par des concentrations élevées ainsi que par l'enrichissement trophique des milieux liées aux épandages d'engrais (Villalobos-Jiménez *et al.*, 2016). De plus, les projets de drainage, de conversion terres arables, d'extraction de tourbe ou de sylviculture ont conduits à une perte d'au moins 50% des zones humides européennes au cours des derniers siècles (Dixon *et al.*, 2016). La destruction directe des habitats de reproduction, la canalisation et la modification de la dynamique des cours d'eau, la dégradation des ripisylves ou encore l'introduction de poissons ont été à l'origine du déclin des populations de nombreuses espèces d'Odonates, en particulier durant la deuxième moitié du 20^{ème} siècle (Boudot & Kalkman, 2015).



Figure 9 : Imagos de trois espèces ayant connu un rétablissement suite à la restauration écologique de certains de leurs habitats dégradés : l'Azuré des moullières (*Maculinea alcon alcon*), le Gomphe à pattes jaunes (*Gomphus flavipes*) et la Leucorrhine à gros thorax (*Leucorrhinia pectoralis*) (de gauche à droite ; clichés : G.Delpon).

Il faut cependant noter ici que la restauration écologique des paysages peut s'avérer efficace et favoriser la recolonisation des espèces associées. La réouverture des milieux en cours d'enfrichement et leur entretien par des plans de fauches ou de pâturage permet le rétablissement de la richesse de certaines communautés de Rhopalocères liées aux pelouses calcaires thermophiles (Pöyry *et al.*, 2005 ; Bubova *et al.*, 2015). Appliqué sur des réseaux de

prairies humides, ce mode de gestion a été favorable au rétablissement des populations de l'Azuré des moullières (*Maculinea alcon alcon*, Denis & Schiffermüller, 1775) (Fig.9) aux Pays-Bas (WallisDeVries, 2004). Le rétablissement de plusieurs espèces, ayant quasiment disparu de certains territoires au siècle dernier (par ex. le Gomphe à pattes jaunes, *Gomphus flavipes*, Charpentier, 1825) (Fig.9), suite à une restauration des systèmes fluviaux dans l'ouest de l'Europe démontre l'importance du maintien des dynamiques naturelles pour la conservation des Odonates (Termaat *et al.*, 2015). La restauration des tourbières dégradées, notamment via leur remise en eau, peut permettre le rétablissement rapide des communautés d'Odonates typiques des eaux acides oligotrophes (Elo *et al.*, 2015) et permettre la recolonisation par des espèces menacées, comme par exemple la Leucorrhine à gros thorax (*Leucorrhinia pectoralis*, Charpentier, 1825) (Fig.9) dans certaines tourbières de l'est de la France (Montcorgé, 2007 ; Magnon, 2012).

3.2. Changements climatiques

Les changements climatiques mesurés à l'échelle globale depuis le début du 20^{ème} siècle constituent un des facteurs majeurs d'altération des patrons de diversité et de la composition des communautés animales et végétales (IPCC, 2014), résultant déjà en de multiples réponses biologiques documentées à diverses échelles spatiales (Parmesan, 2006 ; Garcia *et al.*, 2014). Dans ce cadre, les Rhopalocères et les Odonates sont considérés comme de bons intégrateurs des effets du climat et montrent plusieurs modes d'adaptation à ces changements (Hill *et al.*, 2002 ; Hassall, 2015). La modification de l'aire de répartition des espèces représente l'une des tendances les plus visibles et les plus étudiées (Chen *et al.*, 2011). Un décalage de cette aire de répartition vers des latitudes plus élevées a en particulier été documenté pour les deux taxa étudiés au niveau de l'hémisphère nord (Parmesan *et al.*, 1999 ; Hickling *et al.*, 2006), avec parfois des extensions de plusieurs kilomètres vers le nord en quelques dizaines d'années (Ott, 2010 ; Mason *et al.*, 2015). Bien que la réponse de chacune des espèces soit plus complexe à prévoir, notamment du fait de l'interaction entre le climat et d'autres facteurs environnementaux, les prédictions réalisées à partir des scénarios d'évolution du climat révèlent une diminution de l'aire de répartition de plusieurs espèces dans les prochaines décennies (Settele, 2008), avec des conséquences particulièrement négatives pour les espèces d'affinités euro-sibériennes (Franco *et al.*, 2006 ; De Knijf *et al.*, 2011). À l'inverse, plusieurs espèces d'origine africaine montrent une colonisation croissante vers le nord de l'Europe à la faveur du réchauffement climatique (De Knijf, & Anselin, 2010), comme c'est le cas pour

plusieurs Odonates tels que la Libellule écarlate (*Crocothemis erythraea*, Brulé, 1832), le Trithémis annelé (*Trithemis annulata*, Palisot de Beauvois, 1807) ou plus récemment encore le Trithémis à ailes ambrées (*Trithemis kirbyi*, Selys, 1891) (Boudot & Kalkman, 2015 Brouwer, 2016) (Fig.10). De la même manière, l'aire de distribution de plusieurs espèces de Rhopalocères européens se caractérise par une nette translation vers le nord, comme l'illustrent les cas de la Carte géographique (*Araschnia levana*, Linnaeus, 1758), du Nacré de la ronce (*Brenthis daphne*, Bergsträsser, 1780) ou du Tabac d'Espagne (*Argynnis paphia*, Linnaeus, 1758) (Parmesan *et al.*, 1999 ; Lafranchis *et al.*, 2015 ; Audusseau *et al.*, 2016). Les changements de distribution s'observent également sur l'axe altitudinal avec une remontée observée pour plusieurs espèces vers les sommets des massifs du sud de l'Europe (Konvicka *et al.*, 2003 ; Wilson *et al.*, 2007).

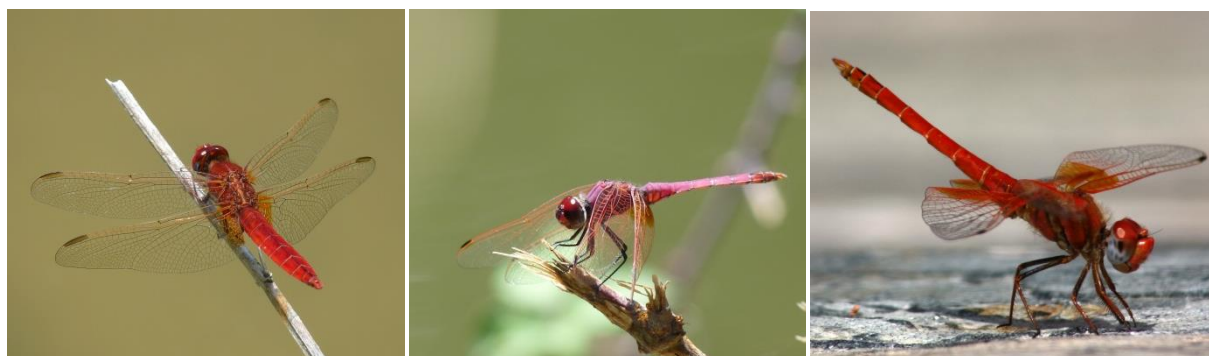


Figure 10 : Imagos de trois espèces d'Odonates d'origine africaine colonisant progressivement le sud de l'Europe depuis la fin du 20^e siècle : la Libellule écarlate (*Crocothemis erythraea*), le Trithémis annelé (*Trithemis annulata*) et le Trithémis à ailes ambrées (*Trithemis kirbyi*) (de gauche à droite ; clichés : G.Delpon et Charlesjsharp pour *T.kirbyi* (Creative Commons)).

Tous ces changements d'aires de distribution sont susceptibles à termes d'engendrer de larges modifications dans la structure des communautés (Lewhwaite *et al.*, 2016 ; De Palma *et al.*, 2017), en impactant parfois directement la niche des espèces locales (Audusseau *et al.*, 2016). La réponse des espèces s'exprime également à travers des tendances de diminution de la taille des individus (Gardner *et al.*, 2011), une augmentation de la fréquence des espèces les plus colorées dans les régions tempérées (Zeuss *et al.*, 2014) ou encore par des décalages de leur phénologie, avec des périodes de vols de plus en plus précoces (Diamond *et al.*, 2011 ; Altermatt 2012 ; Zografou *et al.* 2015). Chez les papillons de jour, ces modifications d'aire de distribution sont également susceptibles d'être associées à des déconnexions avec les aires de distribution de leur plantes-hôtes voire à des changements dans le cortège de plantes-hôtes (Schweiger *et al.*, 2008 ; Parmesan *et al.*, 2015). Pour les

espèces monophages, ces déconnexions d'aires de distribution pourraient même poser des problèmes de conservation.

Les changements climatiques semblent également conduire à une augmentation des événements météorologiques extrêmes, qui peuvent conduire à une indisponibilité temporaire de ressources auxquelles des espèces sténoèces (*cf glossaire*) pourraient avoir des difficultés à répondre (Maron *et al.*, 2015). Les sécheresses de plus en plus sévères en région méditerranéenne constituent aussi un exemple frappant d'impact négatif important à la fois sur les papillons de jours (Stefanescu *et al.*, 2011 ; De Palma *et al.*, 2017) et les libellules (Chase, 2007 ; Hassal & Thompson, 2008 ; Herzog & Hadrys, 2017). Des variations de température très localisées peuvent également modifier le microclimat sur les stations directement exploitées par les espèces (McDermott Long *et al.*, 2017). Des micro-refroidissements survenant au printemps de manière de plus en plus régulière dans l'hémisphère nord, semblent aussi avoir un effet négatif sur les espèces de papillons hibernant au stade d'œuf ou de larve, et nécessitant un fort apport d'énergie à cette période pour terminer leur cycle (WallisDeVries & Van Swaay, 2006 ; WallisDeVries, 2014).

3.3. Un gradient de réponse dépendant des traits d'histoire de vie

Toutes les espèces ne présentent pas les mêmes patrons de réponses face à ces deux facteurs et de nombreuses études ont montré qu'ils peuvent être fortement conditionnés par la combinaison de traits écologiques spécifiques (Angert *et al.*, 2010 ; Matilla *et al.*, 2011 ; Essens *et al.*, 2017). Du fait de leur richesse, les Rhopalocères et les Odonates présentent une grande variation des différents traits qui structurent leurs niches écologiques. Afin de simplifier la compréhension des patrons d'assemblage des communautés et de leur dynamique, les espèces sont généralement classées le long d'un continuum allant des généralistes aux plus spécialistes (Dapporto & Dennis, 2013 ; Bartonova *et al.*, 2014). La diversité des biotopes au sein desquels elles se reproduisent, leur spécialisation vis-à-vis de certaines ressources trophiques, leurs capacités de dispersion ou encore leur phénologie sont autant de traits qui permettent de classer les espèces le long de ce continuum (Carnicer *et al.*, 2013). Les espèces spécialisées montrent alors une sensibilité plus grande aux changements environnementaux (particulièrement à l'altération de leurs habitat), alors que les espèces à plus large valence écologique ont généralement de meilleures capacités de résilience (Powney *et al.*, 2015). Ces dernières montrent souvent une occupation plutôt continue de l'espace et

peuvent se maintenir au sein de paysages fortement altérés (Bartonova *et al.*, 2014). Ces tendances différentes conduisent à un remaniement progressif mais important de la structure des communautés au sein des paysages les plus anthropisés (Eskildsen *et al.*, 2015). La régression des espèces spécialistes du fait de la simplification de paysages et le maintien des espèces les plus euryèces (*cf glossaire*) va pouvoir engendrer un phénomène d'homogénéisation biotique (Olden & Rooney, 2006 ; Carvalheiro *et al.*, 2013 ; Mccune & Vellend, 2013), conduisant à un lissage de l'originalité des assemblages d'espèces pour conduire à une banalisation des communautés, observé chez les Rhopalocères (Ekroos *et al.*, 2010 ; Börshig *et al.*, 2013 ; Habel *et al.*, 2016) comme chez les Odonates (Rosset *et al.*, 2014).

Dans ce contexte actuel de changement global induisant des variations fortes des éléments de la biodiversité et de leurs interactions, ce travail de thèse a adopté pour objectif d'améliorer la connaissance de la réponse des communautés de Rhopalocères et d'Odonates face aux changements environnementaux à l'échelle de la France, en vue notamment d'une identification plus fine des enjeux de conservation que représentent les espèces et les territoires. Il tend principalement à mesurer les modifications récentes de répartition des espèces en lien avec les deux principales pressions environnementales que représentent les changements paysagers et climatiques, tout en intégrant les traits écologiques des différentes espèces considérées.

4. Les données d'occurrence à la base des stratégies de conservation opérationnelles

Ce contexte de modifications des environnements paysagers et climatiques oblige à la réalisation d'inventaires établis grâce un protocole rigoureux. Malgré les aléas météorologiques et situationnels lors de la réalisation de ces protocoles d'inventaires, leur répétition sur plusieurs jours doit permettre l'obtention d'une liste la plus complète possible des espèces présentes dans ce milieu. Cette exhaustivité est particulièrement importante lors de la réalisation des études d'impacts associées à des projets d'aménagement du territoire, car ces inventaires sont à la base de l'application de la loi de « reconquête de la biodiversité » (aout 2016) qui prévoit une absence de perte nette de biodiversité grâce à l'application de la séquence ERC (éviter-réduire-compenser). Ainsi, dans l'idéal, il est crucial que ces inventaires soient le plus complets possible et avec le moins de biais possibles. Or, la réalité

des inventaires montre qu'il existe plusieurs biais dans ces inventaires et qu'à défaut de les maîtriser, il faut au minimum les connaître et les contrôler.

4.1. De nombreux biais affectant la représentativité des inventaires

La mise en place de stratégies de conservations cohérentes et opérationnelles s'appuie sur une capacité à (1) mesurer un état initial (la richesse ou la structure des communautés, l'aire de répartition d'une espèce rare ou menacée, l'abondance de ses populations, ...), (2) quantifier l'impact des facteurs mentionnés dans le paragraphe précédent sur le compartiment mesuré, (3) suivre ce compartiment en vue d'évaluer l'efficacité des mesures d'atténuation mises en place (Braby & Williams, 2016). Les données biologiques et les méthodes mises en place pour les collecter auront donc une importance capitale sur la pertinence de ces mesures (Yoccoz *et al.*, 2001). Les données d'occurrence des espèces, leur abondance en un lieu et un temps donné et la richesse des assemblages constituent ainsi la matière première de la biologie de la conservation (Soberon *et al.*, 2007). Toutefois, ce type de données peut être affecté par de nombreux biais dont la non prise en compte peut amener à des erreurs importantes dans l'interprétation des résultats (Magurran & McGill, 2011).

Étant donné le coût humain et financier que représente la réalisation d'un inventaire biologique, il sera généralement impossible d'avoir accès à la richesse spécifique, en particulier dans le cas des insectes (Kellner & Swihart, 2014). En effet, toutes les espèces présentes en un lieu et en un temps donnés ne seront pas forcément détectées par un observateur. La probabilité de détection des espèces sera généralement imparfaite, pouvant conduire à des phénomènes de « fausse absence », et répartie de manière hétérogène au sein de la communauté (Bouligner *et al.*, 1998 ; MacKenzie *et al.*, 2006). De nombreux facteurs peuvent ainsi avoir une influence sur cette variabilité de la probabilité de détection, liées aux caractéristiques propres aux espèces (Dennis *et al.*, 2006) ou aux stades de développement considérés (Bried *et al.*, 2012), à la structure des sites échantillonnés (Dennis & Sparks, 2006) ou aux conditions d'échantillonnages elles-mêmes (Pellet, 2008 ; Nufio *et al.*, 2009) (Fig.11). Ces biais sont multipliés lors de la compilation de données issues de plusieurs sources (comme lors de la réalisation d'un atlas de répartition) en vue d'une analyse des patrons de distribution des espèces (Isaac & Pocock, 2015 ; Powney & Isaac, 2015). À l'hétérogénéité de l'effort d'échantillonnage viennent s'ajouter des problématiques liées à l'expérience des

observateurs ou à leurs conditions de prospection (Dennis & Thomas, 2000 ; Lukyanenko *et al.*, 2016). L'augmentation de la disponibilité des données biologiques pose également plusieurs problématiques liées aux procédures de gestion des sources et à leur validation (Dickinson *et al.*, 2010 ; Pocock *et al.*, 2015).

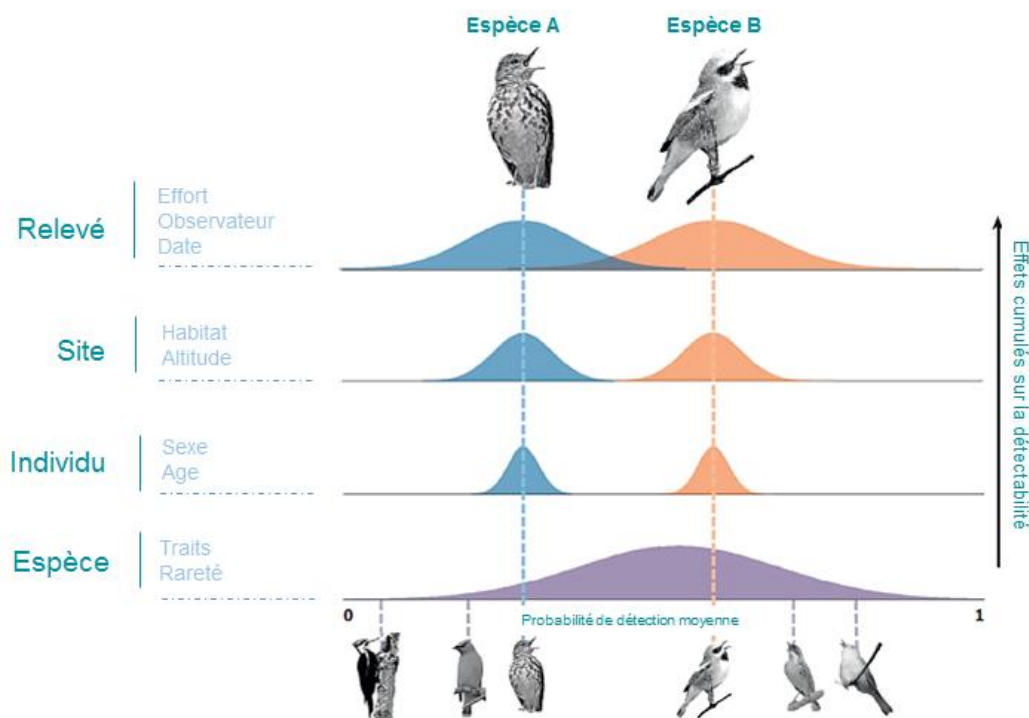


Figure 11 : Représentation théorique des facteurs pouvant affecter de manière cumulée la probabilité de détecter une espèce (d'après Iknayan *et al.*, 2014)

4.2. Mesurer l'impact de ces biais dans le cadre des stratégies courantes de conservation

Ces biais liés aux fausses absences, s'ils ne sont pas corrigés, peuvent conduire à une sous-estimation de la richesse d'un site ou à une mauvaise mesure de la distribution d'une espèce (Iknayan *et al.*, 2014). À un niveau spatial plus élevé, ils peuvent conduire à une mauvaise évaluation des enjeux de conservation d'un territoire ou à une mauvaise interprétation des patrons de répartition des espèces. Le coût de ces biais pour la conservation des espèces sera particulièrement important dans le cadre de la mise en place de mesures opérationnelles, où la non détection d'une population pourra conduire à une absence d'intervention ou à une destruction directe (Guillera-Arroita *et al.*, 2015). Ce dernier cas correspond typiquement au contexte de réalisation des études d'impacts sur l'environnement, qui constitue une des

opérations les plus courantes visant à limiter les conséquences négatives de l'aménagement du territoire sur les habitats naturels (Jay *et al.*, 2007). Instituée par la loi de 1976, la procédure de réalisation de ces études s'est précisée au fil du temps pour tendre dans leur mise à jour la plus récente (loi de 2016 sur la « reconquête de la biodiversité ») vers une « absence de perte nette » de biodiversité (espèces, habitats et fonctions) via l'application d'une séquence d'évitement, de réduction et de compensation (séquence ERC) des impacts du projet (Jacob *et al.*, 2014). En amont de cette séquence, les inventaires biologiques réalisés sur le site d'implantation du projet fournissent les données de bases qui permettront d'en évaluer l'impact et qui conditionnent dont *in fine* sa réalisation. D'une part ils visent à obtenir une estimation de la richesse et de la patrimonialité des cortèges d'espèces présents sur un site, d'autre part ils sont guidés par un objectif de détection des espèces protégées ou ciblées par un statut de conservation (par ex. classement liste rouge) et qui constitueront la contrainte majeure pour l'aménageur. Généralement réalisés en un nombre limité des passages et à partir de protocoles peu standardisés, les plans d'échantillonnage mis en place dans le cas de l'entomofaune passent par l'inventaire simultané de plusieurs taxa, avec des degrés de précisions différents. Les résultats issus de ce type de plans d'échantillonnage ne fournissent donc généralement qu'un aperçu limité de la diversité réellement présente sur un site (Field *et al.*, 2005 ; Lovell *et al.*, 2010). En lien avec la prise de conscience des biais liés à ce type d'inventaires, et parallèlement à l'émergence de la culture de l'évaluation de politiques publiques, une volonté de mesurer la qualité et la représentativité de ce type de relevés émerge depuis plusieurs années (Besnard & Salles, 2010).

Au cours des quarante dernières années, les méthodes d'analyse des données spécifiquement issues de suivis d'espèces animales ou végétales ont très largement évolué (Gimenez *et al.*, 2014). Plusieurs méthodes permettant d'intégrer les biais liés à l'imperfection de la détection ont progressivement vu le jour afin d'apporter une correction aux estimations de la répartition des espèces (MacKenzie *et al.*, 2006) ou de la richesse des communautés sur un ou plusieurs sites (Dorazio *et al.*, 2006 ; Colwell *et al.*, 2012). Les statistiques dites de « site-occupancy » constituent notamment un cadre d'analyse pertinent des données d'occurrence issues de visites de terrain répétées sur plusieurs sites (MacKenzie *et al.*, 2002). Initialement développés afin de quantifier la probabilité de détection et d'occurrence réelle d'une espèce, des techniques de modélisation plus avancées ont permis d'étendre leur application à des jeux de données incluant plusieurs espèces (Iknayan *et al.*, 2014). Elles permettent non seulement d'obtenir une estimation des paramètres spécifiques propres à

chacune de ces espèces, même pour les plus rares, mais également d'avoir accès à une valeur corrigée de la richesse des communautés qu'elles composent (Zipkin *et al.*, 2010). Des développements récents permettent également une extension à des échelles spatiales plus larges, facilitant l'analyse de jeux de données hétérogènes et minimisant les biais liés aux variations de l'effort d'échantillonnage dans le temps et dans l'espace (van Strien *et al.*, 2013 ; Bird *et al.*, 2014 ; Vogt-Schilb *et al.*, 2015). Ces nouvelles méthodes constituent une opportunité intéressante pour mesurer de façon plus précise et plus quantitative la fiabilité des relevés réalisés en conditions d'étude d'impact (Garrard *et al.*, 2015) et afin de préconiser des lignes directrices lors de la construction des plans d'inventaires permettant de maximiser cette fiabilité (Wintle *et al.*, 2012). Cette thèse vise à apporter des éléments à cette réflexion à travers l'application des modèles de « site-occupancy » afin de mesurer l'exhaustivité des pratiques actuelles d'échantillonnage de l'entomofaune dans le cadre des études d'impacts.

Objectifs et problématiques

Objectif général de la thèse

Cette thèse, financée par une bourse CIFRE (ANRT) et l'entreprise Biotope pour une période de 3 ans, a été réalisée dans le cadre d'une collaboration entre le Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175) et l'entreprise Biotope. Elle se positionne ainsi à l'interface entre écologie fondamentale et conservation appliquée. Elle porte des objectifs complémentaires d'amélioration des connaissances sur la structuration et la réponse des communautés de Rhopalocères et d'Odonates et de développement d'outils opérationnels pouvant permettre d'améliorer leur prise en compte dans les procédures d'évaluation environnementale.

À travers la valorisation des données biologiques acquises (souvent via des méthodes et un effort hétérogène, par des naturalistes ou des gestionnaires) au cours des dernières décennies sur la distribution spatiale (richesse, structure des communautés) et la niche écologique (en particulier la part biotique) de ces taxons, elle vise à contribuer à l'amélioration de la connaissance des tendances de leurs populations à l'échelle de la France et des phénomènes qui pourraient constituer des facteurs explicatifs de ces tendances (paysages, climats, traits, ...). Dans l'objectif d'alimenter une vision plus intégrée de leur conservation, ces patrons seront mis en lien avec les politiques de protection actuellement mises en place sur le territoire, afin d'en estimer la cohérence et d'évaluer les manques à combler. Au regard de l'importance de ce type de données pour l'établissement de politiques publiques cohérentes en termes de conservation de la biodiversité, il s'avère également essentiel d'être en mesure d'en évaluer la précision et la représentativité. Cette nécessité est d'autant plus grande dans le cadre des procédures ayant des conséquences immédiates sur l'évolution des paysages, comme c'est le cas pour la réalisation des études d'impact sur l'environnement, qui conditionnent l'aménagement local d'un territoire.

Problématiques

L'augmentation du nombre de programmes de suivi ou d'inventaire des Rhopalocères et des Odonates a permis, par l'agrégation de données opportunistes, d'avoir une vision plus large de la répartition des espèces (nationale, régionale, ...) et de pouvoir suivre son évolution au cours des époques. Cependant, l'exploitation de ces données sur des échelles importantes a généralement été limitée à une marge de l'aire de répartition des espèces (Grande-Bretagne,

Scandinavie, Espagne, Grèce, ...), en ne testant l'influence que d'un facteur environnemental (occupation des sols ou climat). À partir de données extraites d'atlas de répartition publiés à l'échelle de la France, le **premier chapitre** tentera de répondre aux problématiques suivantes :

- Quelles variations diachroniques récentes ont connu les communautés de Rhopalocères et Odonates, et quels sont leurs liens avec les principales pressions environnementales que constituent l'évolution des paysages et le changement climatique ?
- Dans quelle mesure l'hétérogénéité des traits d'histoires de vie des espèces conditionnent leur réponse à ces facteurs ?
- Quelle proportion des enjeux de conservation ainsi définis est-elle couverte par les politiques de conservation développées en France depuis les années 1990 ?

Cependant, les interactions biotiques constituent une des composantes de la niche des espèces ayant une forte influence sur leur réponse aux modifications de l'environnement. Une meilleure vision de la dynamique des Rhopalocères en Europe a permis de mettre en évidence une forte corrélation entre cette spécificité de la ressource nutritive des larves et l'intensité de leur réponse aux modifications de leurs habitats (déclin, expansion, ... à travers des processus de destruction directe, de diminution d'abondance, de désynchronisation des cycles, ...). Cependant, si la connaissance du régime alimentaire des espèces est plus précise, les relations entre espèces à travers le partage potentiel d'une même ressource restent peu explorées (en dehors d'études sur les processus de diversification à partir d'adaptations à des modes de défense chimique). La définition d'un statut de protection réglementaire pour une espèce conduit à une protection des habitats permettant sa reproduction et la persistance de ses populations, dont les plantes-hôtes sont une composante. À travers un recouvrement du régime alimentaire de leurs chenilles, ce type de protection pourrait favoriser le maintien d'autres Rhopalocères. Grâce à la construction du réseau d'interactions entre les papillons de jour et leurs plantes nourricières à l'échelle de la France, le **deuxième chapitre** permettra d'apporter des éléments de réponses aux problématiques suivantes :

- Le degré de cooccurrence, la similitude de l'habitat de reproduction et la distance taxonomique entre les Rhopalocères pourraient-ils expliquer les patrons d'associations avec leurs plantes-nourricières ?
- Existe-t-il une corrélation significative entre le degré de spécialisation d'un Rhopalocère et l'attractivité de ses plantes nourricières pour d'autres espèces ?

- Existe-t-il un lien entre la spécialisation trophique des Rhopalocères et leur risque d'extinction en France ?
- Les politiques françaises actuelles de protection permettent-elles, à travers le réseau projeté, une couverture indirecte des enjeux de conservation associés aux Rhopalocères ?

L'application des politiques de conservation dépend de la possibilité de mesurer la diversité biologique en un lieu et un temps donné et de l'évaluation de l'impact de mesures d'atténuation mises en place. Etant donné les nombreux biais affectant ce type de données et l'hétérogénéité de la probabilité de détection des espèces au sein d'une communauté, l'évaluation de la représentativité des données collectées est essentielle à la prise de décision pertinente. De plus, sachant l'importance que peut avoir la non-détection d'une espèce présente dans le cadre d'une étude d'impact sur le maintien de celle-ci, la définition de plans d'échantillonnages permettant de diminuer au mieux ces biais constitue un enjeu majeur. Bien que des préconisations aient été émises pour certains taxons très étudiés et particulièrement patrimoniaux (Tortue d'Herman, Lézard ocellé, ...), l'évaluation de l'exhaustivité de la pratique actuelle des bureaux d'études reste limitée, notamment dans le cas des insectes. Le **troisième chapitre** visera à développer des méthodes d'évaluation et des préconisations afin d'améliorer l'exhaustivité des inventaires entomologiques en conditions d'étude d'impact. S'appuyant sur une campagne de terrain réalisée sur le pourtour méditerranéen français et sur des méthodes de modélisation prenant en compte l'hétérogénéité de la détection des espèces, il s'attachera à explorer les problématiques suivantes :

- Quelle est la représentativité, par rapport à la communauté potentiellement présente sur un site, des listes d'espèces issues de la mise en place de protocoles d'inventaires entomologique dans le cadre d'une étude d'impact ?
 - L'intensité de l'effort d'échantillonnage appliqué lors de la réalisation d'une étude d'impact a-t-elle une influence significative sur l'exhaustivité des résultats ?
 - Cette exhaustivité est-elle homogène entre les espèces ?
 - Les caractéristiques des habitats présents au sein d'un site d'étude et les conditions de réalisation d'un relevé de terrain ont-elles une influence sur l'exhaustivité des inventaires ?
 - Quel effort d'échantillonnage moyen serait nécessaire pour assurer une détection fiable des espèces dans des conditions optimales d'inventaires ?

Liste des articles

Afin d'apporter des éléments de réponses à chacune de ces problématiques, le document de thèse se structure autour de trois chapitres, chacun composé d'un article dont le processus de publication est plus ou moins avancé.

Article 1

Delpon, G, Vogt-Schilb, H., Munoz, F., Richard, F. & Schatz, B. (2018) Diachronic variations in the distribution of butterflies and dragonflies linked to recent habitat changes in Western Europe. *Insect Conservation and Diversity*, article soumis (accepté après deuxième révision).

Article 2

Delpon, G., Dupont, P., Richard, F. & Schatz, B. Insight into butterfly-hostplant bipartite networks: using projected network as suitable tools for insect conservation. (en préparation avancée).

Article 3

Delpon, G., Besnard, A., Sannier, D., Richard, F. & Schatz, B. Multi-species occupancy model reveals the poor completeness of entomological surveys in environmental impact assessment. (en préparation avancée).

Chapitre 1

Diachronic variations in the distribution of butterflies and dragonflies linked to recent habitat changes in Western Europe

Le **premier chapitre** de cette thèse présente une étude portant sur la description des changements diachroniques de répartition des Rhopalocères et des Odonates à l'échelle de trois pays d'Europe de l'Ouest (France, Belgique et Luxembourg) entre 1980 et 2015. La connaissance de la répartition spatiale des espèces constitue en effet une donnée de base pour l'évaluation et la hiérarchisation de leurs enjeux de conservation. Dans le cas des Rhopalocères et des Odonates, cette répartition est de mieux en mieux documentée et plusieurs projets d'atlas nationaux ont vu le jour en Europe au cours des dernières décennies. Ils fournissent une image exhaustive des communautés d'insectes présentes au sein de différentes unités spatiales (maille, région administrative, ...) à un temps donné. Ils présentent désormais assez de recul dans l'acquisition des données naturalistes pour permettre la comparaison de ces différentes images et ainsi dégager des patrons d'évolution de ces communautés à l'échelle de plusieurs pays.

Les atlas publiés récemment en France ont pour l'instant été peu exploités dans cette optique. Cette étude a permis de valoriser les données compilées dans ces documents afin d'analyser la dynamique temporelle (apparition/disparition/stabilité) et le changement d'aire de distribution des espèces, en mettant en relation les dynamiques observées avec (1) les changements d'utilisation des sols et (2) les exigences écologiques des espèces. L'utilisation d'un modèle nul a permis de pallier à l'hétérogénéité spatiale de ces données. Les biais potentiels associés à la qualité des données utilisées sont également discutés.

Les résultats obtenus permettent d'identifier les secteurs géographiques et les groupes d'espèces ayant enregistré un déclin significatif et de révéler les principaux processus écologiques auxquels ce déclin peut être corrélé. La connaissance de cette hétérogénéité de la réponse des espèces est essentielle pour une allocation efficace des ressources dédiées à la conservation des insectes. D'un point de vue plus opérationnel, une estimation des enjeux de conservation liés aux différentes espèces ou à différents secteurs géographiques peut aussi permettre une meilleure orientation des prospections de terrain dans le cadre de la réalisation d'études d'impacts sur l'environnement.

Diachronic variations in the distribution of butterflies and dragonflies linked to recent habitat changes in Western Europe

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Abstract

1. In the context of ongoing global changes, it is crucial to characterize and understand the species distribution dynamics. Despite increasing emphasis on insects' conservation issues, evidence of distribution changes of insects over a wide range of bioclimatic conditions remains scarce in Western Europe.
2. We examined distribution changes of butterflies and dragonflies in three European countries over 34 years, determined the influence of environmental changes, especially land cover, and assessed how of species ecology related to distinct responses. We analyzed the diachronic variations by compiling occurrence data in France, Belgium and Luxembourg for 240 butterfly and 95 dragonfly taxa.
3. We found contrasting patterns of diachronic variation in butterfly and dragonfly distributions, i.e. a strong gradient of disappearance for butterflies (from northwest to southeast with significantly higher rate of disappearance in urbanized and intensive agriculture areas of northwestern France), whereas dragonflies showed lower and heterogeneous variation of occurrences, mainly related to alteration and regression of aquatic habitats.
4. Species responses appeared closely linked to their ecological preferences, with greater decline of habitat specialist species. Butterfly and dragonfly species are constrained by their dependence to hostplant species and to aquatic habitats, respectively, and proved to convey complementary insights on the influence of environmental changes on biodiversity dynamics.
5. Conservation priorities were identified across species and administrative units, revealing that almost 80% of the declining taxa were not listed on the current protection lists. Our results support the need to update current French policies in terms of insect conservation.

Key words: Insect conservation, land cover changes, range change, null models, diachronic analysis, ecological attributes.

I.1. Introduction

Ongoing global changes entail greater species extinction rates (De Vos *et al.*, 2015) and a general loss of biodiversity (Thomas *et al.*, 2004; Ceballos *et al.*, 2015). To forecast the future threats, it is crucial to understand how high anthropogenic pressure on habitats and resources determines the current species distribution dynamics. Identifying the drivers of these changes is also a key issue to determine priorities for conservation planning and to anticipate future distribution changes. Among these drivers, changes in land-cover and destruction of natural habitats is known to entail biodiversity loss (Foley *et al.*, 2005; Fischer & Lindenmayer, 2007), while global warming triggers local extinctions and range shifts to higher latitude and altitude (Hickling *et al.*, 2006; Chen *et al.*, 2011). Despite increasing research addressing local conservation issues (Margules & Pressey, 2000; Bottrill *et al.*, 2008), analyses of species distribution changes at the scale of several countries covering a wide range of bioclimatic conditions remain scarce (Schatz *et al.*, 2016). Species occur and persist under specific environmental conditions depending on the biological requirements making their ecological niche (Chase & Leibold, 2003). Species-specific abiotic and biotic preferences are expected to influence their response to environmental changes, and then to explain distribution changes according to their dispersal abilities (Thuiller *et al.*, 2005; Devictor *et al.*, 2008; Zhu *et al.*, 2012; but see Willis *et al.*, 2009 for successful assisted colonization).

In Western Europe, land cover deeply changed during the 20th century, with growing industrialization and urbanization and population concentration in expanding cities (Antrop, 2004; McKinney, 2008). Simultaneously, the intensification of agricultural practices has led to landscape homogenization and loss of natural habitats (Reidsma *et al.*, 2006). Parallel abandonment of extensive pastures in Mediterranean areas explained the progressive recolonization by shrublands and woodlands (Sirami *et al.*, 2010). During the same period, human activities have also largely impacted inland aquatic habitats, mostly by drainage and conversion to arable lands (Van Asselen *et al.*, 2013; Davidson, 2014), leading to a loss of almost 50% of wetlands areas in Europe during the last centuries (Pedro Silva *et al.*, 2007; Dixon *et al.*, 2016). This rapid evolution of Western Europe landscapes is recognized as a major driver of observed local changes in the richness and the composition of plant, vertebrate and insect communities (Biesmeijer *et al.*, 2006; Falcucci *et al.*, 2007). However, there is still a lack of integrated analysis of distribution changes at country-scale, aiming to investigate

effects of habitat changes along contrasted environmental gradients and the role of species ecological properties as co-determinants of temporal changes. Such analysis is crucial to go beyond descriptive assessment of richness decline, and for designing relevant conservation strategies based on ecological understanding of the distribution changes.

Among the different taxonomic groups considered in conservation strategies, insects have long been neglected (Dunn *et al.*, 2005; Fonseca, 2009), despite their key role in ecosystem functioning (Weisser & Siemann, 2004). As abundant and diversified prey for many vertebrates, butterflies and dragonflies are of importance in food chains, but are also involved in several major ecosystem functions, such as pollination and predation respectively (Corbet, 2004; Kühn *et al.*, 2005). To date, different studies have revealed a rapid response of these two taxa to environmental changes, especially in terms of changes in species distributions (Parmesan *et al.*, 1999; Grewe *et al.*, 2013) and community structure (Eskildsen *et al.*, 2015; Audusseau *et al.*, 2016; Habel *et al.*, 2016). Several species have declined in Europe because of habitat loss or fragmentation (Kalkman *et al.*, 2010; Van Swaay *et al.*, 2010). Their sensitivity could be linked to specific ecological requirements for their life cycle, with obligatory trophic interactions for butterflies (Herrando *et al.*, 2016), and a biphasic lifecycle including an aquatic larval stage for dragonflies (McPeck, 2008). Due to the variability of life-history traits across species, these two groups are considered as relevant biological models to characterize spatial and ecological patterns underlying changes in species assemblages (Carnicer *et al.*, 2013; Jaeschke *et al.*, 2013; Slancarova *et al.*, 2016) and are among the most monitored invertebrate taxa (Van Swaay *et al.*, 2008).

Species from these two groups cover a broad spectrum of ecological specialization, from localized specialists that are highly dependent on given habitat/ resource (trophic interactions, oviposition site) to largely distributed generalists, mobile over long distances (Hardy *et al.*, 2007; Bartonova *et al.*, 2014). In addition, this spectrum closely relates to species conservation status, and can explain the rarity and distribution changes of taxa (i.e. decline or expansion) (Nilsson *et al.*, 2008; Powney *et al.*, 2015). Often performed at the scale of a single country or bioclimatic area, most studies addressing the drivers of distribution change in European species have focused on the impact of climate change at the distribution margins, with particular emphasis on northern boundaries (often in UK or Scandinavia) (Hickling *et al.*, 2005; Flenner & Sahlén, 2008; Mattila *et al.*, 2011) or in Mediterranean region (Slancarova *et al.*, 2016), revealing for example expansion of several African species

to higher latitude (Ott, 2010; Brouwer, 2016). However, determinants of distribution changes are multiple, resulting from combined and diffuse effects of changes in land cover and climate across species range (Menéndez *et al.*, 2007; Stefanescu *et al.*, 2011a). Changes in European butterfly and dragonfly communities considering large gradients of contrasted bioclimatic conditions from Mediterranean areas to northern temperate regions, linked to high variations in local species pools and environmental pressures, have been poorly investigated (Parmesan *et al.*, 1999).

The aim of this study was to characterize diachronic changes during the last decades in butterfly and dragonfly fauna in three European countries. We compiled detection/non-detection data of 335 taxa (240 and 95 for butterflies and dragonflies, respectively) collected during the last thirty years in 108 administrative units (AU) of France, Belgium and Luxembourg (Lafranchis, 2000; Grand & Boudot, 2006; Grand *et al.*, 2014; Lafranchis *et al.*, 2015). We applied two null models (after Vogt-Schilb *et al.*, 2015) on the compiled distribution data to test the significance of appearance/disappearance dynamics in each spatial unit. We also estimated the intensity and direction of distribution changes per taxa in order to investigate differential responses to climate warming depending on their biogeographical background. We asked the following questions: (1) Do the butterfly and dragonfly distributions tend to expand or contract in Western Europe? (2) Is there a relationship between these patterns and recent changes in land cover? (3) Do taxa with narrower ecological niche and lower dispersal ability undergo higher rate of disappearance than highly mobile generalists? (4) Do southern taxa breeding in warmer habitats expand their range to higher latitude? (5) Are current conservation strategies (protection policies, evaluation of extinction risks) relevant regarding the highlighted distribution changes of studied taxa and knowing different vulnerable habitats?

I.2. Material & methods

I.2.1. Distribution data

We used published distribution maps of all 240 butterfly taxa (238 species and 2 subspecies) and all 95 dragonfly taxa (79 species and 16 subspecies) present in the 108 AU of France, Belgium and Luxembourg (see Suppl.S1.1 for a list of studied taxa). These AU constitute a basic level of implementation of conservation policies in the studied countries. They include

96 ‘départements’ in France, 11 regions in Belgium and Luxembourg considered as a single unit (Suppl.S1.2); these units have roughly a similar size, except three exceptions (the departments around Paris, ‘Territoire de Belfort’ and ‘Bruxelles’), which were removed from most of the analyses (see after). These data were extracted from two butterfly atlases (Lafranchis, 2000; Lafranchis *et al.*, 2015) and two dragonfly atlases (Grand & Boudot, 2006; Grand *et al.*, 2014), based on survey data over 35 and 34 years, respectively (before 1980 until 2015 for butterflies, before 1980 until 2014 for dragonflies) (Suppl.S1.3). These atlases provided two maps for each taxon: (1) one referring to its status (i.e., disappeared or present) in each AU between 1980 and the first published book (i.e., 2000 for butterflies, 2006 for dragonflies); (2) a second referring to its presence or absence in the current period (i.e., 2015 for butterflies, 2014 for dragonflies).

Authors of these atlases built these maps by compiling data taken from (1) literature citations (2) regional atlases, (3) collections, (4) conservation programs and (5) field observations. For the sake of consistency, we did not update these data using more recent sources. Nevertheless, given the diversity of data sources and the opportunistic nature of the observations, these datasets could show heterogeneity of sampling effort between AU, periods or species (Dennis *et al.*, 1999; Dennis & Thomas, 2000). In order to exclude the most poorly sampled AU, we counted the number of AU for which each taxon was observed and selected taxa with the highest value during both period (Maes & Van Dyck, 2001). For butterflies, this selection consists in ten taxa, i.e. *Anthocharis cardamines*, *Colias crocea*, *Gonepteryx rhamni*, *Maniola jurtina*, *Papilio machaon*, *Pararge aegeria*, *Pieris brassicae*, *Pieris rapae*, *Pieris napi* and *Polyommatus icarus*. The same method led to the selection of seven dragonfly taxa: *Anax imperator*, *Chalcolestes viridis viridis*, *Coenagrion puella*, *Libellula depressa*, *Orthetrum cancellatum*, *Sympetrum sanguineum* and *Sympetrum striolatum*. The observation of all these species, highly visible and occurring throughout Europe, at both studied period was used as a minimal surveying standard allowing the assessment of sampling coverage of each AU (Dapporto & Dennis, 2008; Dapporto *et al.*, 2015). This method led to the exclusion of two AU from the butterfly analysis (i.e. ‘Paris’ and ‘Territoire de Belfort’) and of three AU from the dragonfly analysis (i.e. ‘Paris’, ‘Tarn’ and ‘Tarn-et-Garonne’) (see Suppl.S1.2 for the location of these AU).

Three kinds of diachronic trends were defined for each taxa in each analyzed AU, by comparing the distribution maps from ancient and recent editions of the atlases: 1) ‘stable’

when a taxon was described as present in both editions, 2) ‘disappeared’ if a taxon was observed at least once before 1980 but had disappeared in the recent period, or 3) ‘newly appeared’ for a taxon with no reported occurrence in the past (i.e. before 2000 for butterflies, before 2006 for dragonflies), but with reported occurrence in the recent atlas edition (Suppl.S1.3). As a result, we defined disappearances on a 35-year period for butterflies and on a 34 period for dragonflies, while we defined appearances on a 15-year period for butterflies and on an 8-year period for dragonflies. Cases of rediscovery, i.e. taxa referenced as disappeared since 1980 in the first edition but present in the second, were associated to the ‘stable’ case.

Taxonomic revisions between the atlas editions were considered for both groups (Dijkstra & Kalkman, 2012; Dupont *et al.*, 2013). In our analysis, we ignored information about occasional presence or vagrancy and doubtful presence data (for details see Suppl.S1.4). Regarding the distribution maps of butterflies, there were some differences in data availability, *i.e.* (1) the two French AU ‘Corse-du-Sud’ and ‘Haute-Corse’ were considered as a single unit named ‘Corse’ (Suppl.S2), and (2) recent distribution data (after 2000) were not available for Belgium and Luxembourg in the second edition of the butterfly atlas (Lafranchis *et al.*, 2015); the analyses were thus restricted to France for this taxonomic group. Average latitudinal and longitudinal coordinates of each AU were calculated from their centroid using the QGIS software (Quantum GIS Development Team, 2015).

1.2.2. Land cover and habitat changes

To test the hypothesis that habitat changes are a major cause of butterfly and dragonfly decline during the last decades, we assessed the relationship between land cover changes and the diachronic variation in the distribution of taxa. We used Corine Land Cover (CLC) statistics in France, Belgium and Luxembourg established in 2012 (<http://land.copernicus.eu/pan-european/corine-land-cover/view.html>), temporally close to the recent map of presence (2014 for dragonflies; 2015 for butterflies). Based on CLC categories, we calculated the relative area (in % of the total area) of five main types of land cover (urban, agricultural, open natural, closed natural and wetland areas; Suppl.S1.5) in each AU using the QGIS software (Quantum GIS Development Team, 2015). Changes of these proportion in each AU between 1990 (the oldest available CLC data in our studied period) and 2012 were quantified and linked to taxa distribution changes.

I.2.3. Ecological attributes and protection status

We characterized ecological attributes (ten for butterfly and eight for dragonfly) expected to influence the distribution and the vulnerability of taxa: (1) habitat preferences (bioclimatic zonation, main breeding habitat, habitat specialization), (2) dependency to specific biotic interactions for butterflies (hostplant specialization, hostplant form, myrmecophily), (3) dispersal abilities, (4) voltinism (i.e. the number of generations completed within one year in the field), (5) taxonomy (classification of studied taxa at the family level) (Table 1.1, Suppl.S1.1). We synthesized data on these attributes from the available literature, with a correction of some indices to get closer to the conditions of the study area (e.g. main breeding habitat) and an extrapolation of the values of some traits for poorly studied species. Especially, dispersal abilities of European butterflies and dragonflies are currently known only in general terms and their estimation remains mainly based on assumptions for many taxa included in the present study.

We also compiled information on species protection and red list assessments were also compiled and confronted to recent taxa dynamics in order to assess their efficiency. Each taxon was defined as ‘unprotected’ or ‘protected’ at the national level based on the French list of protected insects (Lafranchis, 2015; Grand *et al.*, 2014). IUCN red lists were established at the French national level for butterfly (IUCN France *et al.*, 2014) and dragonfly taxa (IUCN France *et al.*, 2016). Taxa ranked as ‘Not evaluated’ (NE) or ‘Not applicable’ (NA: introduced or vagrant taxa) were excluded from the analysis.

Table 1.1: Ecological attributes of butterfly and dragonfly taxa used in the present analysis, with their detailed description and references.

Butterfly taxa		
<i>Attributes</i>	<i>Definition and categories of attributes</i>	<i>References</i>
Biogeographic background	Distribution of taxa regarding their range in Europe and the biogeographical origin of their host plants (1- northern Europe, 2- southern Europe, 3- mountain areas, 4- widespread across Europe)	Dennis <i>et al.</i> , 1991; Kudrna <i>et al.</i> , 2012
Bioclimatic zonation	Taxa ranked from their optimal affinity to main French altitudinal stages (1- hill, 2- meso-mediterranean, 3- supra-mediterranean, 4- mountain, 5- alpine-subalpine)	Dupont <i>et al.</i> , 2013
Main breeding habitat	Derived from local literature about French taxa (1- alpine grassland, 2- dry grassland, 3- humid grassland, 4- mesophile grassland, 5- shrubland, 6- forest)	Lafranchis, 2000; Lafranchis <i>et al.</i> , 2015
Habitat specialization	Adult habitat breadth based on the number of habitat exploited by adults at the European scale (1- generalist, 2- mid-generalist, 3- specialist)	Van Swaay <i>et al.</i> , 2006
Host plant specialization	Number of plant species fed on by caterpillars in France. Taxa ranked as 1- monophagous (using only one host plant species), 2- oligophagous (feeding on two to three host plant species) or 3- polyphagous (feeding on more than three host plants)	Lafranchis, 2000; Lafranchis <i>et al.</i> , 2015; Meister <i>et al.</i> , 2015
Host plant form	1- ephemerals and small herbaceous plants, 2- large herbaceous plants and grasses, 3- bushes, creepers and small trees, 4- large trees	Lafranchis, 2000; Dennis, 2012; Bartonova <i>et al.</i> , 2014; Lafranchis <i>et al.</i> , 2015
Voltnism	Average number of generation per year in Europe (0.5 generation, 1 generation, 1 or 2 generations, 2 generations, 2 to 3 generations, 3 to 4 generations)	López-Villalta, 2010; Dapporto & Dennis, 2013; Bartonova <i>et al.</i> , 2014; WallisDeVries, 2014; Lafranchis <i>et al.</i> , 2015
Dispersal abilities	Taxa dispersal abilities (1- low abilities, 2- medium abilities, 3- high abilities)	Based on European literature (Cowley <i>et al.</i> , 2001; Komonen, 2004; Päividen <i>et al.</i> , 2005; Stefanescu, 2011a, Dapporto & Dennis, 2013; Bartonova <i>et al.</i> , 2014) and adjusted for the study area based on expert evaluation (especially concerning Mediterranean species which are poorly documented)
Myrmecophily	Specificity of ant-lycaenid butterfly larvae interactions in Europe (1- myrmecoxenous, 2- facultative myrmecophilous, 3- steadily myrmecophilous, 4- obligatory myrmecophilous)	Fiedler, 1991 ; Pierce <i>et al.</i> , 2002; Fiedler, 2006; Cizek <i>et al.</i> , 2006; Dennis, 2012; Dapporto & Dennis, 2013; Lafranchis <i>et al.</i> , 2015)
Taxonomy	Classification of butterfly taxa at the family level (1- Hesperidae, 2- Papilionidae, 3- Pieridae, 4- Lycaenidae, 5- Nymphalidae, 6- Satyrinae). <i>Hamearis lucina</i> , the only species of Riodinidae in the study area, has been integrated to the Lycaenidae family	Lafranchis 2000; Dupont <i>et al.</i> , 2013; Lafranchis <i>et al.</i> , 2015
Dragonfly taxa		
<i>Attributes</i>	<i>Definition and categories of attributes</i>	<i>Reference</i>
Biogeographic background	Distribution of taxa regarding their range in Europe and bioclimatic preferences (1- northern Europe, 2- southern Europe, 3- mountain areas, 4- widespread across Europe)	Grand & Boudot, 2006; Boudot & Kalkman, 2015
Bioclimatic zonation	Taxa ranked from their optimal affinity to main French altitudinal stages (1- lowland, 2- hill, 3- mountain)	Grand & Boudot, 2006; Boudot & Kalkman, 2015
Freshwater type	Taxa categorized as 1- lentic (only breeding in standing water), 2- lotic (only breeding in running water) or 3- both (breeding in both standing and running water)	Hof <i>et al.</i> , 2006; Powney <i>et al.</i> , 2014
Main breeding habitat	1- stream, 2- river, 3- river and pond, 4- pond, 5- marsh and bog	Grand & Boudot, 2006; Powney <i>et al.</i> , 2014; Boudot & Kalkman, 2015
Habitat specialization	Taxa habitat breadth derived from the number of habitat exploited by dragonflies at the European scale. Classified as 1- specialist (using only one habitat type) or 2- generalist (using different habitat types)	Hof <i>et al.</i> , 2006; Powney <i>et al.</i> , 2014
Voltnism	Average number of generation per year in Europe (0.5 generation, 1 generation, 1 or 2 generations, 2 generations, 2 to 3 generations, 3 to 4 generations)	Corbet <i>et al.</i> , 2006; Powney <i>et al.</i> , 2014; WallisDeVries, 2014
Dispersal abilities	Taxa dispersal abilities (1- low abilities, 2- medium abilities, 3- high abilities)	Based on European literature (Chin & Taylor, 2009; Harabiš & Dolný, 2011; Jaeschke <i>et al.</i> , 2013; Dolný <i>et al.</i> , 2014) and adjusted for the study area based on expert evaluation (especially concerning Mediterranean species which are poorly documented)
Taxonomy	Classification of dragonfly taxa at the family level (1- Calopterygidae, 2- Lestidae, 3- Coenagrionidae, 4- Platycnemididae, 5- Aeshnidae, 6- Gomphidae, 7- Cordulegasteridae, 8- Corduliidae, 9- Libellulidae). <i>Macromia splendens</i> , the only species of Macromiidae in the study area, has been integrated to the Corduliidae family	Grand & Boudot, 2006; Djikstra & Kalkman, 2012 ; Boudot & Kalkman, 2015

I.2.4. Null models of appearance and disappearance

Two null models were designed from repeated random permutations of taxa occurrence status in atlases over the study period, to test significant distribution changes over time per AU and per taxon (after Vogt-Schilb *et al.*, 2015). The permutations generated random appearance/disappearance patterns that were compared to the real patterns, in order to identify significant distribution changes (Gotelli, 2001). In each model, some features were randomized whereas others were kept constant to test distinct hypotheses (see below precisions about features of each model). For both null models, the permutations were repeated 999 times and only concerned AU where a given taxon was present at least once during the studied period.

In *null model 1*, the status of each taxa (disappeared, stable or appeared) was permuted across AU. Therefore, the number of taxa that were considered as ‘disappeared’, ‘appeared’ or ‘stable’ in each AU varied randomly, while the number of AU where a given taxa was stable, had disappeared or had appeared, as well as the taxa richness of each AU, were kept constant. This model allowed testing whether there was more appearance or disappearance of taxa than expected by chance in each AU, by comparing the actual values with the null situation. The proportion of null values that fell above the actual number of taxa with disappearance/appearance status in each AU defined the P-value of the test, used to assess the significance of excess disappearance or appearance in each AU at $P < 0.05$ (Veech, 2012). In order to minimize the effect of spatial autocorrelation which could influence the spatial structure of (Legendre, 1993) appearance/disappearance patterns, the algorithm constrained the permutations of taxa status (disappeared, stable or appeared) to be more likely between neighboring units than between distant ones (Hardy, 2008; package ‘SpacodiR’ in R, function `resamp.3t`). The geographical coordinates of each AU centroid were used to measure distances between AU. Taxa that were characterized by only one status (disappeared, appeared or stable) on the entire study area did not contribute to the random permutations in *null model 1* (35 butterfly and 24 dragonfly taxa). Moreover, the change over the period of the average geographical coordinates for each taxon (average of AU coordinates where present) was compared to the change under the null model to assess significant change in the range of taxa and the direction of the change.

The *null model 2* shuffled the status of taxa within each AU. Contrary to the first model, the number of AU where each taxon was considered as disappeared, stable or appeared could vary at each permutation, while the number of taxa for each status was fixed in a given AU. The null model provided the null distribution of the number of AU where each taxon could appear or disappear over the study period. The differences between null values and real values allowed assessing whether each taxon shows more appearance or disappearance than expected by chance. To test the significance of these differences, the P-values were calculated as the proportion of null values greater than the number of AU where each taxon disappeared or appeared across the study area.

To address the relevance of taxa protection and red list assessments, the permutations procedure of model 2 was limited to French AU. In order to avoid biases linked to multiple comparisons among taxa or AUs (Pike, 2011), the ‘fdr’ method (false discovery rates) as designed by Benjamini & Hochberg (1995) was applied to adjust P-values.

1.2.5. Relating distribution changes to environmental contexts and taxa attributes

To identify the main drivers of butterfly and dragonfly range changes, a standardized effect size (SES) was defined to quantify the deviation between the null models and real appearance/disappearance patterns. This value was calculated from disappearance (SESdisp), appearance (SESapp) and range change (SESrange) information using the following formula:

$$SES = (x - \mu) / \sigma \quad (1)$$

where x is the actual observed value, μ and σ are the mean and standard deviation of the null values, respectively. To prevent statistical biases in null models, taxa observed in less than 10 AU during the studied period (47 butterfly and 13 dragonfly taxa) were not considered in following statistical analyses.

We calculated the SES values of each AU based on *null model 1* and compared the values to geographical and environmental characteristics of the AU. We performed a Spearman’s rank correlation test of the link between SES values and the mean coordinates of AU. Furthermore, we performed general least squares (gls) models to analyze the relationships between SES values and the proportion of each main type of land cover in 2012

while modeling spatial autocorrelation in residuals (Dormann *et al.*, 2007; Beguería & Pueyo, 2009). Five models were built with different spatial correlation structures (Gaussian, exponential, linear, rational quadratic and spherical structures) and the Akaike information criterion (AIC) was used to identify the best-fit model (Crawley, 2013). A second group of gls models was designed to study the link between SES values and the proportion change of each type of land use between 1990 and 2012, following the same methodology. In both cases, four AU ('Hauts-de-Seine', 'Seine-Saint-Denis', 'Val-de-Marne', 'Bruxelles') were excluded from the model due to their too high proportion of urban land cover (at least 88% in CLC data in 1990 and in 2012).

For each studied group, values of SESrange (given by the *null model 1*) were compared to a hypothetical null situation (i.e. situation with no range change corresponding to the 0 value on the X- and Y axis) to test whether the mean range of taxa has moved significantly or not toward a given cardinal direction. Because of the non-normality of the three kinds of SES values (SESdisp, SESapp, SESrange; Shapiro test, $P > 0.05$), Wilcoxon tests were used to perform the comparisons. These tests were also applied to evaluate range changes between taxa with different biogeographical backgrounds (Northern Europe vs. Southern Europe).

We calculated the SES values (SESdisp and SESapp) of each taxon based on *null model 2* and compared the values to the taxon ecological attributes. We performed Wilcoxon tests to compare these SES values of disappearance/appearance between pairs of modalities for each ecological attribute, protection status and red list ranks. For all paired Wilcoxon tests, P-values were corrected for multiple comparisons (Benjamini & Hochberg, 1995). The R software (R Development Core Team, 2015, version 3.2.1, package 'SpacodiR', 'nlme', 'fields') was used to design the null models and to perform statistical analyses. A diagrammatic representation of the framework used to analyze distribution changes and their link to environmental data and ecological attributes is presented in the Figure 1.1.

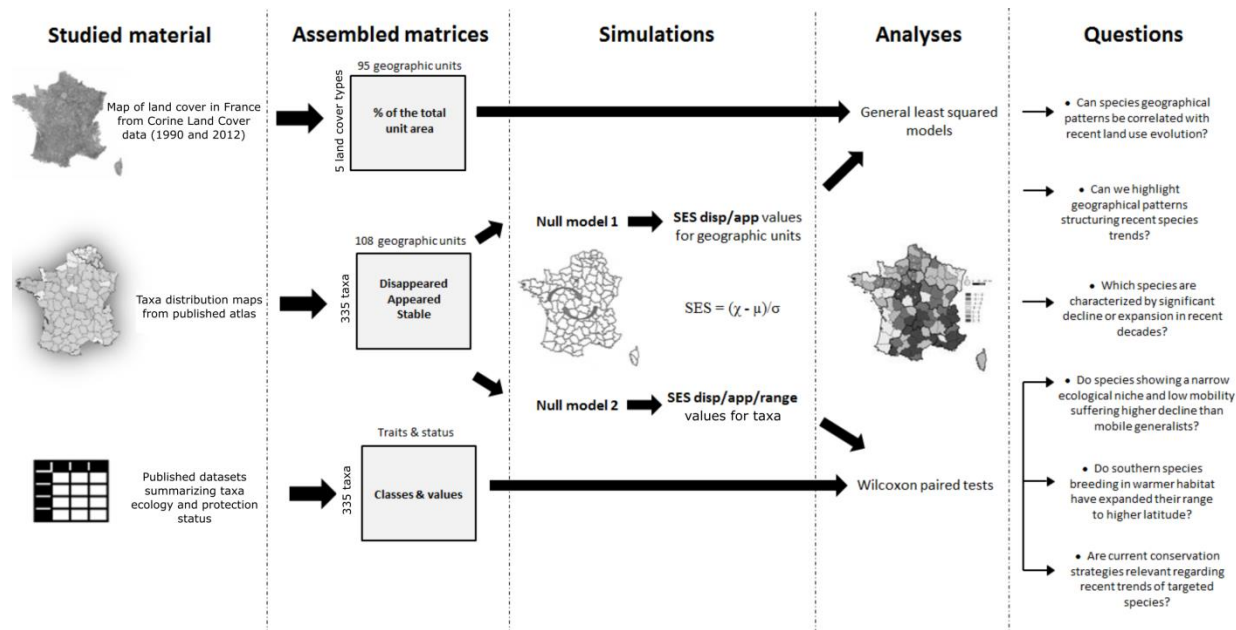


Figure 1.1: Diagrammatic representation of the analytical framework designed for the exploitation of distribution data. It summarizes the origin and the content of the different datasets, the analysis performed on the basis of null models simulations and their link with the main questions of the study.

I.3. Results

I.3.1. Spatial gradients of species richness and land cover patterns

Based on the most recent atlases, we synthesized species presence in each AU in order to evaluate the spatial distribution of the richness of each taxon. We observed significant variation of species richness among AU. There was a strong spatial gradient of butterfly richness, with an increasing number of taxa from north to the southeast of the study area, with mountainous units (Alps and Eastern Pyrenees) displaying highest richness (with a maximum value of 200 taxa in the AU ‘Hautes-Alpes’), whereas the AU around Paris show the lowest values (with less than 30 taxa in each of the three AU surrounding this unit) (Suppl.S1.6). For dragonflies, richness variation was less pronounced but still high, with more taxa in the Massif Central area and along the southern Atlantic coastline (center of France) than in northeast of the study area, and a gradient going from more than 70 taxa to less than 30 taxa in the French AU surrounding Paris (Suppl.S1.6).

There was also a latitudinal gradient of land cover patterns. Northwestern units were characterized by high proportion of urban areas (up to 25% in some AU) and agricultural areas (between 50 to 70%), while shrubland and forest areas were dominant (between 50 to 60% for at least 10 AU) in southeastern France. During the last two decades, urbanization increased in each AU of the study area, with an average extension of urban areas above 5400 ha (20% of the initial area) between 1990 and 2012. Increasing closure of natural or abandoned agricultural areas in Mediterranean landscapes was a second major trend during the period, with an average increase of more than 5200 ha (2% of the initial area) of closed natural area in the 10 AU located in Mediterranean bioclimatic belt (see Suppl.S1.2).

1.3.2. Geographical patterns of taxa appearance and disappearance

Based on *null model 1*, we found contrasting patterns of appearance/disappearance in AU among butterfly and dragonfly taxa. There was a strong latitudinal gradient of decline for butterflies in France, showing highest SESdisp mainly in northwest and in some AU of eastern France (Fig. 1.2a). Some other isolated AU with high recent urbanization also showed important (but non-significant) SES value of disappearance in the south of the study area. We found significant positive and negative correlation of butterfly SESdisp values with latitude and longitude of French AU, respectively (Spearman's correlation; $r_s=0.62$, $P < 0.001$ for latitude; $r_s=-0.34$, $P < 0.001$ for longitude). A total of 17 neighboring AU in the northwest of the study area had higher ($P < 0.05$) disappearance number than predicted by the model (Fig. 1.2a). Significant appearances of butterfly taxa were more punctual and rather located in the western half of France (Fig. 1.2b). This result was confirmed by the significant and negative correlation between SESapp values and the mean longitude of French AU ($r_s=-0.29$, $P < 0.01$) but without significant relationship with latitude ($r_s=0.06$, $P > 0.05$). Only three AU showed a significantly ($P < 0.05$) higher number of appearances than by chance (Fig. 1.2b).

For dragonflies, we found more heterogeneous patterns of disappearance, with AU showing important SESdisp values globally scattered on the entire study area (Fig. 1.2c). Highest disappearance rates were mainly located in Northern France, Belgium and Luxembourg, with a significant value for one AU in the northwest of Paris ($P < 0.001$). SESdisp was positively correlated to the latitude of these AU (Spearman's correlation; $r_s=0.21$, $P < 0.05$) but not to longitude ($r_s=-0.03$, $P > 0.05$). Dragonfly taxa showed important disparities of appearance dynamics, with recording high appearance rates dispersed across the

study area and sometimes surrounded by AU with few appearances (Fig. 1.2d). No AU was significant regarding appearance; moreover, SESapp was not correlated with latitude ($r_s=0.02$, $P > 0.05$) or longitude of AU ($r_s=-0.0004$, $P > 0.05$).

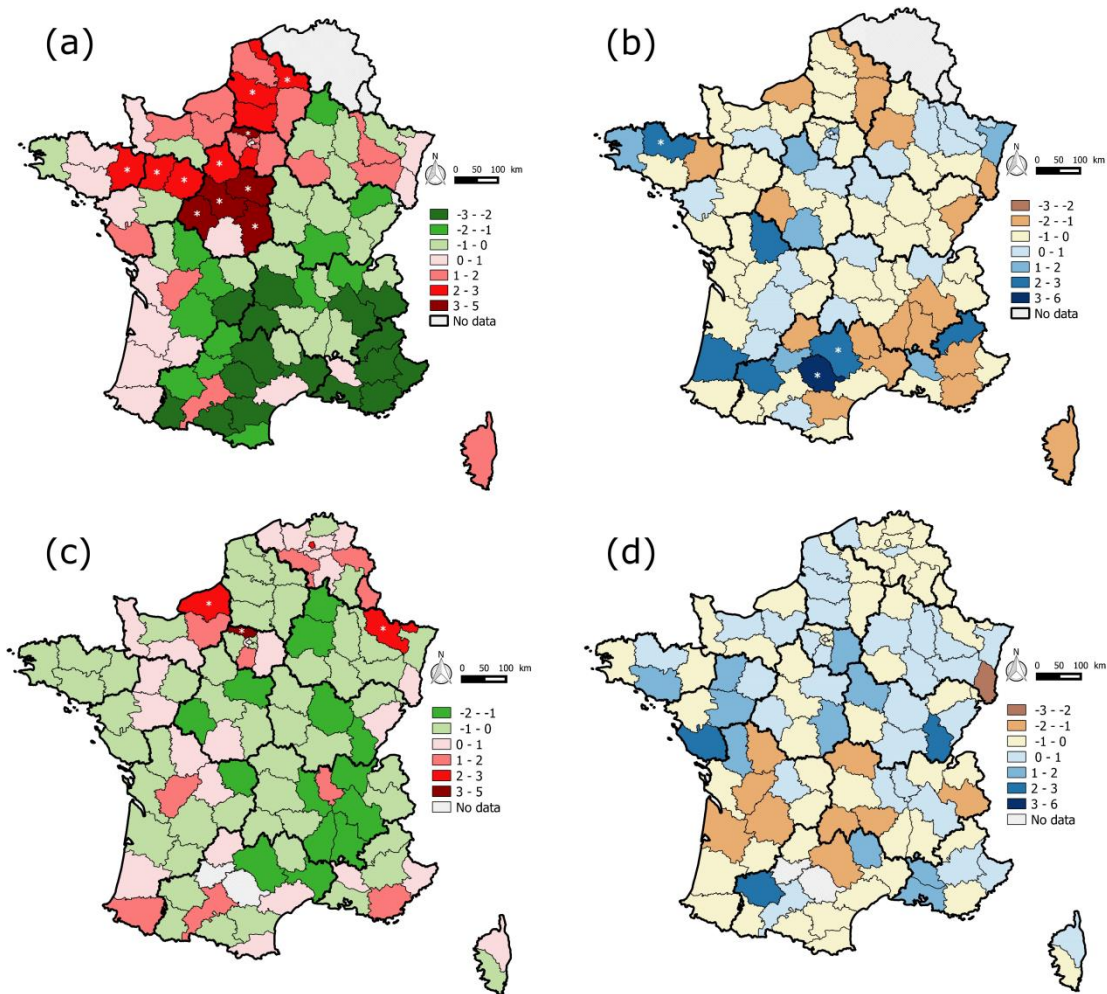


Figure 1.2 : Geographical patterns of butterfly (a and b) and dragonfly (c and d) trends of disappearance (a and c, SESdisp) and appearance (b and d, SESapp) across AU. Study area was limited to France for butterflies and includes Belgium and Luxembourg for dragonflies. Positive values of SES correspond to AU showing more changes than expected by chance whereas negative values indicate units with fewer changes than expected by chance. * designates units showing a significant number of disappearances or appearances at $P < 0.05$ (with P-values corrected for multiple comparisons with 'fdr' method). Different color levels correspond to intervals of SES values ranked by the minimum, first quartile (25%), median (50%), third quartile (75%) and maximum of their distribution. Bold lines correspond to the French "euroregions" as defined in 2015.

I.3.3. Links to land cover and habitat changes

For butterfly taxa, SESdisp was positively related to the proportion of urban and agricultural areas in AU in 2012, but not to the proportion of natural areas (Table 1.2). SESapp was negatively related to urban, open natural and closed natural areas (Table 1.2). Regarding the variation of land cover types from 1990 to 2012, SESdisp of butterflies was positively related to the variation of urban areas whereas a significant negative relationship was evidenced between the variation of closed natural areas and butterfly appearances (Table 1.2).

Table 1.2 : Influence of recent land-covers (i.e. proportions of land-cover types in 2012) and its variation (i.e. changes in the proportions of land-cover types between 1990 and 2012) on butterfly and dragonfly dynamics of disappearance and appearance. SES values of disappearance and appearance in each administrative unit taken from the *null model 1* were analyzed using general least squared models. After a selection based on AIC values, models were fitted with exponential, spherical and rational quadratic correlation structures (indicated in brackets under each tested trend). Proportions of main types of land cover in each administrative unit in 2012 were used as explanatory variables. Coefficient estimations from the linear models were coded as * for Pvalue < 0.05, ** for P-value < 0.01 and *** for P-value < 0.001.

Studied group	Trend	Coefficient	Recent land-cover				Land-cover variation			
			Estimate	SE	T-value	P-value	Estimate	SE	T-value	P-value
Butterflies	Disappearance (Exponential)	(Intercept)	-4.49	2.05	-2.18	0.03 **	-0.83	0.64	-1.29	0.20
		Urban area	0.09	0.04	2.3	0.02 **	0.63	0.24	2.6	0.01 **
		Agricultural area	0.07	0.02	2.87	0.005 **	0.02	0.07	0.34	0.73
		Closed natural area	0.04	0.25	1.52	0.13	-0.21	0.24	-0.88	0.37
		Open natural area	0.04	0.03	1.4	0.16	-0.13	0.11	-1.2	0.23
		Wetland area	-0.12	0.02	-0.52	0.59	-1.93	1.74	-1.11	0.27
	Appearance (Spherical) (Rational)	(Intercept)	3.05	1.06	2.87	0.005 **	-0.12	0.25	-0.48	0.62
		Urban area	-0.09	0.03	-3.17	0.002 **	-0.28	0.18	-1.56	0.12
		Agricultural area	-0.02	0.01	-1.9	0.06	-0.03	0.05	-0.53	0.59
		Closed natural area	-0.05	0.01	-3.45	0.0009 ***	-0.54	0.17	-3.09	0.003 **
		Open natural area	-0.04	0.01	-2.5	0.01 **	-0.08	0.07	-1.1	0.27
		Wetland area	-0.04	0.18	-0.22	0.83	1.52	1.35	1.12	0.26
Dragonflies	Disappearance (Rational)	(Intercept)	-1.83	0.90	-2.03	0.045	-0.74	0.20	-3.75	0.0003 ***
		Urban area	0.10	0.02	5.12	0.0001 ***	0.63	0.15	4.32	0.0001 ***
		Agricultural area	0.01	0.01	1.20	0.23	-0.04	0.04	-0.88	0.38
		Closed natural area	0.02	0.01	1.64	0.10	-0.13	0.15	-0.86	0.39
		Open natural area	0.02	0.01	1.49	0.14	0.001	0.06	0.02	0.98
		Wetland area	-0.45	0.14	-3.25	0.0016 **	-1.23	1.13	-1.09	0.28
	Appearance (Exponential)	(Intercept)	-0.77	0.98	-0.78	0.43	-0.23	0.18	-1.27	0.21
		Urban area	0.005	0.02	0.26	0.79	0.11	0.14	0.75	0.46
		Agricultural area	0.02	0.01	1.77	0.08	0.04	0.04	1.07	0.29
		Closed natural area	0.003	0.01	0.26	0.79	0.03	0.15	0.24	0.81
		Open natural area	0.008	0.01	0.56	0.58	-0.09	0.06	-1.48	0.15
		Wetland area	-0.18	0.14	-1.54	0.22	0.22	1.13	0.20	0.84

For dragonfly taxa, SESdisp was positively related to the proportion of urban areas and negatively related to the proportion of wetland areas in AU in 2012 (Table 1.2). SESdisp was also positively related to the variation of urban area from 1990 to 2012 (Table 1.2). Conversely, SESapp was neither related to any of the land cover variables, nor to their variation between 1990 and 2012 (Table 1.2).

1.3.4. Distribution changes

Based on *null model 1*, SESrange allowed testing and assessing the direction of butterfly and dragonfly distribution changes in the study area (*i.e.* France for butterflies; entire area for dragonflies). In both cases, few taxa showed significant distribution shift, with only 6% showing latitudinal shift and about 5% showing longitudinal shift. The average SESrange among taxa was negative in latitude (Wilcoxon test, $P < 0.001$ for butterflies, $P < 0.05$ for dragonflies), revealing a global tendency of southward shift (Fig. 1.3), while no significant difference was found for longitude (Wilcoxon test, $P > 0.05$). In addition, the distribution changes were not related to the biogeographical background of taxa in our study area (Wilcoxon test, $P > 0.05$; Fig. 1.3).

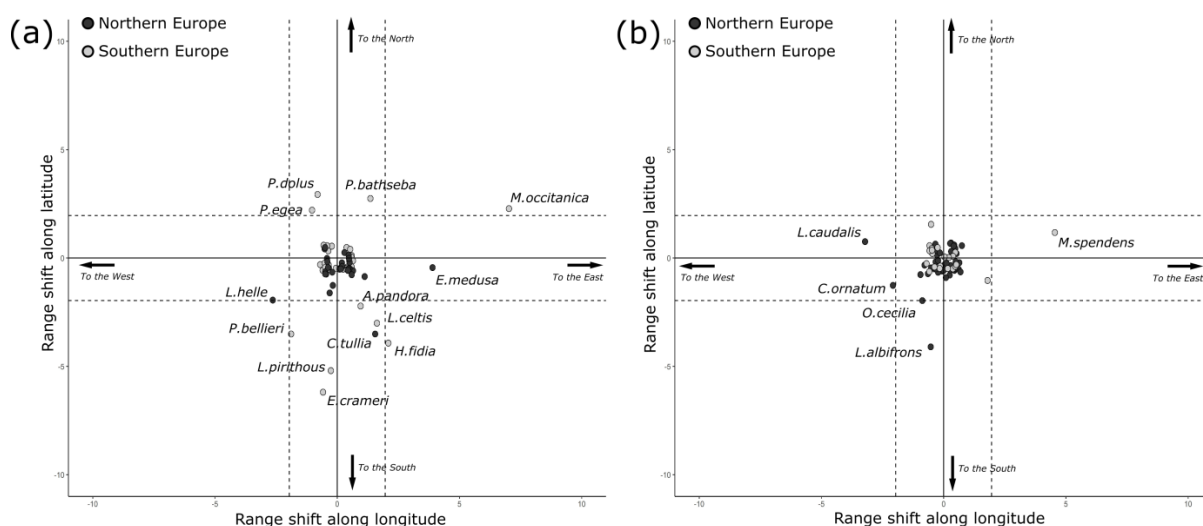


Figure 1.3 : Butterfly (a) and dragonfly (b) range changes across AU regarding their biogeographic preferences. Analyzes were limited to taxa from northern and southern Europe. Each point corresponds to a taxon SESrange, from the null model 1. The ordinate axis represents latitudinal changes, with northward shifts for positive values and southward shifts for negative values. The abscissa axis represents longitudinal changes, with eastward shifts for positive values and westward shifts for negative values. Names are shown for taxa with a significant change. The 95% confidence interval is represented by dashed lines, with the limits of -1.96 and 1.96 on both axes. P-values were corrected for multiple comparisons with the 'fdr' method.

I.3.5. Influence of ecological attributes of taxa

Based on *null model 2*, we estimated the SES values of disappearance/appearance for each taxon (Suppl.S1.7 and S1.8). Almost half of the butterfly taxa showed positive SESdisp value, among which 50 showed significant disappearance in the study area (20% of analyzed taxa). We found variation of SESdisp depending on the main breeding habitat of taxa (Wilcoxon test, $P < 0.001$, Table 1.3). Taxa breeding in dry grasslands tended to show more frequent disappearance in the AU, while taxa associated to mesophilous grasslands showed less frequent disappearance. Conversely, we found positive values of SESapp for nearly 40% of butterfly taxa, among which 17 taxa (7% of analyzed taxa) had significantly more appearances ($P < 0.05$) than expected by chance. Regarding breeding habitat, mesophile taxa tended to have lower SESapp values (Wilcoxon test, $P < 0.001$). Regarding other butterfly life history traits, SESdisp values were significantly higher for taxa showing distribution centered in Northern or Southern Europe, or an important affinity with Mediterranean and mountain bioclimatic zones, or a high degree of habitat specialization, or a narrow hostplant range (monophageous and oligophageous taxa), or a small number of generations per year (i.e. univoltine to bivoltine taxa) or low dispersal abilities (Wilcoxon tests, $P < 0.001$, Table 1.3). Specifically, the myrmecophilous Lycaenid taxa (steadily and obligatory myrmecophilous) had more pronounced disappearance rate (Wilcoxon tests, $P < 0.01$). Biogeographic background, preferential bioclimatic zone, breeding habitat, host plant specialization, voltinism, and dispersal abilities also significantly influenced the averaged SESapp values (Wilcoxon test, $P < 0.001$), with taxa with high rate of appearance showing similar ecological features than declining ones (Table 1.3). However, the taxonomy and host plant forms did not influence taxa disappearance and appearance rates (Wilcoxon test, $P > 0.05$).

For dragonflies, SESdisp values were positive for almost of analyzed taxa (16 taxa, $P < 0.05$). We found variation of SESdisp depending on main breeding habitats (Wilcoxon test, $P < 0.001$). The association to marshes and bogs, and to a lesser extent to rivers, was linked to a significantly higher decline of taxa (Wilcoxon test, $P < 0.001$). Positive values of SESapp concerned a lower proportion (29%) of studied taxa and only 11 dragonfly taxa showed significantly more appearance than expected by chance ($P < 0.05$). SESapp varied depending on taxon ecology (Wilcoxon test, $P < 0.001$), with significantly higher SESapp values for taxa breeding in rivers and significantly lower for ubiquitous taxa able to develop in both rivers and ponds. Dragonfly averaged tendencies (SESdisp and SESapp) were also significantly

influenced by several taxa traits. The degree of habitat specialization and the colonized freshwater type had major influence on taxa patterns, with a higher number of disappearances for specialists of lentic or lotic waters than for generalists able to colonize both types of waters (Table 1.4). Taxa known for their low number of generations per year (i.e. semivoltines and univoltines) and constrained to Northern or Southern Europe showed significantly higher number of disappearances than multivoltine and widespread taxa. Moreover, taxa with higher rate of appearance showed similar ecological features than declining ones. In particular, specialists breeding in a narrow range of habitats had higher appearance rate than generalists, especially taxa associated to lotic environment. Bioclimatic zonation, mobility and taxonomy did not significantly influence dragonfly disappearance and appearance rates (Wilcoxon test, $P > 0.05$).

I.3.6. Taxa protection status

Based on *null model 2*, we found similar relationships of disappearance/appearance with protection status in France for the two groups of organisms (Suppl.S1.7 and S1.8). Protected taxa displayed more frequent disappearance over the period (Wilcoxon test, $P < 0.001$). Results for appearance were more contrasted, with a significantly higher mean value of SESapp for protected dragonfly taxa ($P < 0.001$), while protection status was not significantly linked with diachronic variations of butterflies ($P > 0.05$).

Comparison of appearance/disappearance SESvalues between taxa with different IUCN status also indicated a difference in terms of SESdisp for butterflies and dragonflies ($P < 0.001$). Species considered as threatened (VU, EN and CR) showed a higher number of disappearances than species classified as 'Least Concern' (LC). However, there was no significant relationship between mean SESapp and IUCN statuses ($P > 0.05$).

Table 1.3 : Disappearance and appearance trends of butterfly taxa regarding their ecological attributes. Species trends correspond to median SES values (from null model 2) ("IQR" indicating the interquartile range of the variable). Significant differences between categories of each attribute were evaluated by Wilcoxon paired-tests, with P-values corrected by fdr method. Modalities featuring different letters have been shown as significantly different.

Attribute	Disappearance			Appearance		
	Significance	Median	IQR	Significance	Median	IQR
Distribution region						
Widespread	a	- 0.80	5.30	a	- 1.03	1.84
Northern Europe	b	1.80	3.17	b	0.07	1.46
Southern Europe	bc	1.15	3.73	b	0.48	2.06
Moutain areas	ac	0.42	1.44	b	- 0.54	0.73
Bioclimatic zonation						
Hill	a	- 1.24	5.15	a	- 0.78	2.07
Meso-mediterranean	bc	0.63	4.03	ab	0.21	1.30
Supra-mediterranean	c	1.55	2.42	ab	0.80	1.81
Mountain	bc	1.50	2.82	b	- 0.08	1.96
Alpine-subalpine	b	0.43	1.59	ab	- 0.55	0.03
Main breeding habitat						
Mesophile grassland	a	- 2.76	4.06	a	- 1.09	2.10
Dry grassland	b	2.14	3.49	b	0.22	2.10
Humid grassland	bc	0.97	2.89	bc	0.14	1.59
Alpine grassland	c	0.42	1.41	bc	- 0.53	0.06
Shrubland	c	- 0.74	2.22	ac	- 0.69	1.58
Forest	c	0.26	3.99	ac	- 0.58	1.54
Habitat specialization						
Specialist	a	0.56	3.49	a	- 0.17	1.51
Mid-Generalist	a	0.63	3.88	a	- 0.45	1.91
Generalist	b	- 4.18	0.39	b	- 1.82	0.64
Host plant specialization						
Monophagous	a	1.03	2.70	a	- 0.45	1.05
Oligophagous	a	0.62	3.52	a	0.07	1.75
Polyphagous	b	- 0.84	4.93	b	- 0.75	1.88
Host plant form						
Small herbaceous	a	0.60	3.80	a	- 0.35	1.86
Large herbaceous	a	0.35	4.59	a	- 0.60	1.65
Bushes	a	- 0.87	4.03	a	- 1.26	1.51
Large trees	a	- 0.29	2.65	a	0.26	1.66
Voltinism						
1 generation	a	0.62	3.64	a	- 0.48	1.43
1 or 2 generations	a	0.54	2.59	ab	- 0.05	1.94
2 generations	a	- 0.42	4.95	ab	- 0.71	1.93
2 to 3 generations	b	- 3.18	2.84	bc	- 1.07	2.26
3 to 4 generations	b	- 4.33	1.42	c	- 1.83	0.44
Mobility						
Low abilities	a	0.89	3.60	a	0.51	2.16
Medium abilities	b	- 0.002	3.06	b	- 0.50	1.30
High abilities	c	- 3.03	5.69	c	- 1.29	1.38
Myrmecophily						
Obligatory myrmecophilous	a	2.65	2.65	a	2.65	2.65
Steadily myrmecophilous	a	1.90	2.27	a	1.90	2.27
Facultative myrmecophilous	b	- 0.45	2.20	a	- 0.45	2.20
Myrmecoxenous	b	0.07	2.24	a	0.07	2.24
Taxonomy						
Hesperiidae	a	0.84	6.59	a	0.32	2.13
Papilionidea	a	- 0.84	1.43	a	- 0.82	0.42
Pieridae	a	- 0.74	6.25	a	- 0.92	1.42
Lycaenidae	a	0.42	2.66	a	- 0.02	2.37
Nymphalidae	a	- 0.13	4.65	a	- 0.45	1.50
Satyrinae	a	0.78	4.10	a	- 0.60	1.30

Table 1.4 : Disappearance and appearance trends of dragonfly taxa regarding their ecological attributes. Species trends correspond to median SES values (from null model 2) ("IQR" indicating the interquartile range of the variable). Significant differences between categories of each attribute were evaluated by Wilcoxon paired-tests, with P-values corrected by fdr method. Modalities featuring different letters have been shown as significantly different.

Attribute	Disappearance			Appearance		
	Significance	Median	IQR	Significance	Median	IQR
Distribution region						
Widespread	a	- 2.12	0.73	a	- 1.91	0.37
Northern Europe	b	0.91	3.01	b	- 0.54	2.29
Southern Europe	b	- 0.04	1.75	b	0.25	2.10
Mountain areas	b	0.72	2.73	b	- 0.36	1.91
Bioclimatic zonation						
Lowland	a	- 0.41	2.78	a	- 0.74	2.84
Hill	a	- 0.61	1.79	a	- 0.98	0.81
Mountain	a	0.72	2.73	a	- 0.36	1.92
Freshwater type						
Lentic	a	0.28	3.54	a	- 0.88	2.30
Lotic	a	- 0.10	2.36	a	- 0.37	2.49
Both types	b	- 0.96	1.51	b	- 1.90	1.35
Main breeding habitat						
Stream	bc	- 0.43	1.97	bc	- 0.62	1.62
River	ac	1.19	1.68	a	3.01	3.42
River and pond	b	- 0.96	1.51	b	- 1.90	1.35
Pond	bc	- 0.43	2.22	bc	- 1.15	1.46
Marsh and bog	a	1.79	2.45	ac	- 0.08	2.40
Habitat specialization						
Specialist	a	0.61	3.10	a	- 0.58	2.04
Generalist	b	- 1.25	1.68	b	- 1.90	1.39
Voltinism						
0.5 generation	a	0.36	3.12	a	- 0.04	2.96
1 generation	ac	- 0.25	2.49	bc	- 1.07	1.82
2 generations	b	- 2.12	0.47	bc	- 1.91	0.39
2 to 3 generations	bc	- 1.37	0.80	ac	- 1.90	1.25
Mobility						
Low abilities	a	0.03	3.72	a	- 0.87	2.35
Medium abilities	a	0.12	3.44	a	- 0.65	2.08
High abilities	a	- 0.69	1.35	a	- 0.98	2.41
Taxonomy						
Calopterygidae	a	- 0.98	1.19	a	- 1.48	0.43
Lestidae	a	0.13	1.22	a	- 0.74	1.25
Coenagrionidae	a	- 1.13	3.58	a	- 1.28	1.65
Platycnemididae	a	- 0.09	0.91	a	0.37	1.19
Aeshnidae	a	0.01	1.86	a	- 1.02	1.32
Gomphidae	a	0.61	2.69	a	- 0.41	4.46
Cordulegastridae	a	- 1.30	0.75	a	- 0.66	0.95
Corduliidae	a	0.29	2.08	a	0.93	2.23
Libellulidae	a	- 0.47	4.02	a	- 1.15	2.53

I.4. Discussion

I.4.1. Changes in taxa distribution linked to land cover changes

Based on a diachronic analysis of occurrence data gathered in three European countries, we found major distribution changes of butterfly and dragonfly taxa at the scale of France, Belgium and Luxembourg between 1980 and 2015. Although none of the taxa went extinct in the area during this period, we found contrasted disappearance and appearance patterns among AU and taxa, with a large proportion of AU affected by diversity loss and differences of spatial responses among the two studied groups. Butterfly distribution patterns were structured by a latitudinal gradient of disappearance, with more frequent disappearance in northwestern France; whereas species pool in southern AU remained relatively stable (Fig. 1.2a). These patterns confirmed trends pointed by former studies of butterfly distribution in northern France (Dennis & Shreeve, 2003) and pertain to a broader context of butterfly decline in the industrialized countries of northwestern Europe since 1950 (Maes & Van Dyck, 2001; Warren *et al.*, 2001; Wenzel *et al.*, 2006). The results also pointed a reinforcement of latitudinal disparities by several butterfly taxa appearances in some AU from southwestern France (Fig. 1.2b). Conversely, dragonflies showed more heterogeneous patterns, with hotspots of taxa disappearance and appearance scattered throughout the entire territory, without clear spatial gradient (Fig. 1.2c and d).

We identified a significant link between the spatial changes of butterfly and dragonfly assemblages and the recent variation of land cover within the study area (Ostberg *et al.*, 2015). The increasing proportion of urban areas over the last three decades was highly correlated to observed biodiversity loss (Table 1.2). Through destruction and fragmentation of natural habitats (Grimm *et al.*, 2008), the progressive extension of cities and transport infrastructures is known to have a negative impact on the distribution and abundance of many European butterfly species (Konvicka *et al.*, 2006; Ramírez-Restrepo & MacGregor-Fos, 2017). Moreover, most butterflies breed in open natural areas (Van Swaay *et al.*, 2006) and their occupancy is highly dependent on the vegetation structure, which influences the availability of nectar and host plants (Van Halder *et al.*, 2017). This dependence is consistent with the significant correlation between local disappearances of butterfly and the extent of agricultural areas (Table 1.2). Landscape simplification because of agricultural intensification (e.g. increase of monoculture surface, nitrogen deposition, removal of hedges) is considered

as a primary cause of butterfly decline in Europe (Van Dyck *et al.*, 2009; Warren & Bourn, 2011) and has been related to functional homogenization of butterfly communities (Börschig *et al.*, 2013; Eskildsen *et al.*, 2015). However, the progression of woodlands in the Mediterranean area did not entail significant decline of butterflies, contrarily to other European regions (Stefanescu *et al.*, 2011a). Such absence of correlation could be explained by the progressive nature of secondary successions in Mediterranean area and by the coarse spatial resolution of species occurrence data.

Similarly, dragonflies showed a significantly higher decline in AU comprising a reduced proportion of wetlands (especially bogs and rivers) (Table 1.2). At the scale of France, a decline of 67% of wetland areas has been reported within the last century (Pedro Silva *et al.* 2007). These habitats are critical for dragonfly fauna and have suffered from the establishment of industrial activities in alluvial lowlands, the multiplication of drainages and the increasing water demand during the second half of the 20th century (Boudot & Kalkman, 2015). Decrease in larval habitat availability potentially related to these direct destructions (Elo *et al.*, 2015) could be enhanced by the alteration of hydrological systems and the deterioration of water quality by the concentration of pollutants linked to urban activities (Ferrerias-Romero *et al.*, 2009; Villalobos-Jiménez *et al.*, 2016). In such a context of human exploitation of wetlands, changes in the composition of fish communities by the introduction of some predatory species (e.g. *Pesca fluviatilis*, *Salvelinus fontinalis*) could be an additional pressure for some dragonfly taxa, impacting the local structure of their communities (Mauersberger, 2010; Wittwer *et al.*, 2010). This specific response of butterflies and dragonflies to different landscape factors, related with distinctive features of their life cycle, highlights the advantage to use them in complementarity to assess responses of open-field and aquatic ecosystems to large scale environmental changes (Sahlén & Ekestubbe, 2001; Briers & Biggs, 2003; Thomas, 2005).

I.4.2. Ecological attributes associated to the diachronic variations of taxa

Trait-based analysis revealed that butterfly and dragonfly assemblages are structured along a specialist-generalist continuum regarding main ecological attributes (Carnicer *et al.*, 2013; Powney *et al.*, 2015). Taxa characterized by a narrow ecological niche showed the highest distribution changes in the face of changing land-uses (Tables 1.3 & 1.4). Specialists and mid-generalists' taxa in terms of breeding habitat were more subject to decline, especially when

they also occupied sensitive habitats (dry or humid grasslands, bogs, rivers). The area of these habitats drastically decreased during the second half of the 20th century through anthropogenic pressures (Janišová *et al.*, 2011; Elo *et al.*, 2015) and the availability of species resources shaping their niches was altered (Johansson *et al.*, 2006; Warren *et al.*, 2011). Because specialist taxa showed also globally low dispersal abilities (Bartonova *et al.*, 2014; WallisDeVries, 2014), their increasingly fragmented distribution then hindered recolonization and increased local demographic stochasticity. At the community level, these declining specialist species are progressively replaced by generalists able to colonize landscape with an increasing rate of natural habitat disturbance (Ekroos *et al.* 2010; Ricouart *et al.* 2013; Ball-Damerow *et al.* 2014).

In the case of butterflies, the specificity of trophic interactions between caterpillars and their host plants needs also to be considered in regard to this sensitivity to environmental changes. Because of the strict trophic dependence constraining their adaptability to environmental changes, monophagous and oligophagous taxa are known to be more sensitive to the degradation of their habitats (Komonen *et al.*, 2004; Stefanescu *et al.*, 2011a) and to have higher extinction risk (Hardy *et al.*, 2007; Pearse & Altermatt, 2013). This sensitivity is further increased when specific associations with ants are obligatory during the life cycle, as for some Lycaenidae. Our results emphasize the need of taking into account processes of co-extinction in the study of diversity trends (Koh *et al.*, 2004).

Low dispersal abilities were also related to the sensitivity of taxa to land cover changes. Species dispersal abilities play a major role in community dynamics, and habitat loss or fragmentation is likely to reduce colonization of new area after local environmental changes (Stevens *et al.*, 2010; Matilla *et al.*, 2011). Therefore, butterflies with low or medium dispersal abilities displayed higher rate of disappearance during the last decades (Table 1.3). This low dispersal often characterized habitat specialist species, able to maintain their population in small suitable patches, but often strongly responds to their degradation (Komonen *et al.*, 2004; Päivinen *et al.*, 2005). Similar trends have been reported for dragonflies (McCauley *et al.*, 2014), even though no significant link between dispersal abilities and diachronic variation in the range of taxa has been revealed in our study, certainly because of incomplete or unprecise data used to assign species mobility (Harabiš & Dolný, 2011). However, resilience phenomena are still possible with punctual recolonization of habitats through climatic events particularly favorable to dispersal, and favored by the

presence of linear habitat system (*e.g.* road sides, riversides, long hedges and riparian forests ... etc.) (Oliver *et al.*, 2013; De Palma *et al.*, 2017).

Correlated with larval growth rate, voltinism is also considered as a major determinant of insect species vulnerability (Altermatt, 2010; Essens *et al.*, 2017). For both groups, taxa with a low number of generations per year displayed higher decline than taxa producing several generations a year (Tables 1.3 & 1.4). Multivoltine species can produce more progeny per year, allowing more successful dispersion and colonization of new suitable areas (Stevens *et al.*, 2012; Slancarova *et al.*, 2016) and lower demographic risk.

1.4.3. Patterns of appearance and potential sampling bias

Ecological attributes related to more pronounced decline were also related to the highest values of appearance (Tables 1.3 & 1.4). Because of the difficulty of accurately measuring sampling coverage of each AU between the both studied periods, these patterns should be discussed with caution. The recent rise of citizen sciences at the European scale can be related to increasing number of observation concerning butterflies and dragonflies between the both studied periods (Silvertown *et al.*, 2009; Powney & Isaac, 2015). Nevertheless, spatial and temporal heterogeneity of the sampling effort often characterizes atlases compiling data from various naturalist sources (Romo *et al.*, 2006; Robertson *et al.*, 2010; Isaac *et al.*, 2015). It is often difficult to distinguish appearances revealing true expansions of species ranges from those consisting in the new detection of a population well established (Schatz *et al.*, 2016). In addition, localized and specialist species were often considered as priority conservation targets, and their presence often lead to higher attention to protect their habitat and to improve the knowledge about their range (Dapporto & Dennis, 2013). With the aim to discriminate such biases in diachronic analysis, a first study of butterfly distribution in France (Dennis & Shreeves, 2003) allowed to list AU considered as potentially under-recorded (from Lafranchis, 2000), mainly localised in southwestern France. The presence in this region of AU showing highest values of SESapp suggests the potential existence of this ‘false appearance’, as already mentionned for orchids in Vogt-Schilb *et al.* (2015). Despite the use of null models and the exclusion of the obviously undersurveyed units, appearance events remain clearly dependent of the relative sampling efforts in the different AU and during each studied period, revealing the limits of using compiled opportunistic data to assess precise

species dynamics without correcting for potential heterogeneity in sampling coverage (Van Strien *et al.*, 2010; Barwell *et al.*, 2015).

I.4.4. Taxa distribution changes

The analysis of butterflies and dragonflies distribution changes in Western Europe brought contrasted conclusions compared to previous observations at the northern margins of taxa distribution, where the rise of temperatures has been correlated with an extension of southern taxa to higher latitude during last decades (Pöyry *et al.*, 2009; Ott, 2010; Devictor *et al.*, 2012). At the scale of our study area, the mean shift of taxa's range centroids was found to be directed towards lower latitudes, without contrast between northern and southern taxa. These diachronic variations could be related to the major decline of many taxa in the northern part of France and in Belgium, which led to a contraction of taxa range toward the south of the study area. Our results thus rather underlined the effect of land-use changes on the spatial reorganization of butterfly and dragonfly communities (Fernández-Chacon *et al.*, 2014; Murphy & Romanuk, 2014). However, the measured response to climate change depends on the spatial resolution used to describe species presence (Angert *et al.*, 2011). Working at the scale of AU, without indices on changes in abundance or density, could make difficult the detection of species distribution change. Local conditions could enable the persistence of relictual populations of taxa in some units, keeping it as 'stable' in our dataset, whereas it actually undergoes a reduction of the core area of its range (Jump *et al.*, 2009). Secondly, our study area corresponds to the center of the range of many taxa. Significant shifts are often more difficult to detect when considering core area rather than range limits, especially when these shifts are estimated from the displacement of range centroid like in our case. Third, as we did not investigate altitudinal gradients, species upward shifts toward mountain areas could remain undetected, buffering their response to climate change (Konvicka *et al.*, 2003; Wilson *et al.*, 2005; Lenoir *et al.*, 2008).

I.4.5. Conservation issues

The observed changes in butterfly and dragonfly distributions resulted in a reinforcement of spatial contrasts in species richness within our study area between the present hotspots and AU with lower presence (Suppl.S1.6). As evidenced by recent synthesis (IUCN *et al.*, 2014, 2016), these hotspots concentrate many taxa with high risk of extinction. In the current context of climate change and increasing anthropogenic pressures affecting these areas, patterns of distribution change should be taken into account in the definition of insect's conservation priorities. Habitats closure and global warming could have a major impact on the conservation status of mountain specialist communities, which are gradually replaced by expanding lowland species in some European area (MacDonald *et al.*, 2000; Jiménez-Alfaro *et al.*, 2014). This dynamic has already a significant impact on butterfly communities in Spain and Southern Balkans (Stefanescu *et al.*, 2011b; Slancarova *et al.*, 2016) and could lead to the progressive decline of some localized or endemic taxa over the next few years (Sirami *et al.*, 2010). The predicted rise of temperatures in the next few decades also constitutes a significant threat to the availability of water resources in the Mediterranean basin, which is considered as a major issue for the persistence of several dragonfly and hostplant populations (Hassal & Thompson, 2008; Stefanescu *et al.*, 2011a). Revealing this trend, 18 out of the 22 dragonflies' species currently threatened in Europe are preferentially Mediterranean taxa, and affected by greater demand of water for human activities and by the increased duration of dry periods (Kalman *et al.*, 2010).

Although protection policies targeting these taxa have already been established, this study provides new insights into their relevance and efficiency over the recent period. Protected taxa remain among the most endangered taxa subject to decline in our study, questioning the ability of the protection status of taxa to stop the decline. In addition, almost 80% of the taxa showing a significant decline were not currently listed on protection lists (Suppl.S1.7 and S1.8), advocating for an update of French conservation policies (Schatz *et al.*, 2014). Moreover, such update needs considering differences of species sensitivity based on their ecological attributes in the current context of environmental changes (Mattila *et al.*, 2011). In this regard, our study provides an integrative perspective on distribution changes of butterfly and dragonfly taxa at the scale of several European countries, related to both environmental changes and taxon ecological properties, which should convey ecological relevance for the design of appropriate conservation strategies.

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Supplementary materials 1

Supplementary material S1.1: List of butterfly (A) and dragonfly (B) taxa (species and subspecies) included in the present study and values for their ecological attributes, protection statut and red list assessment at the scale of study area.

(À consulter dans la partie “Annexes” du manuscrit de thèse).

Supplementary material S1.2: Location and index of geographic units in France, Belgium and Luxembourg.

Supplementary material S1.3: Defined statuses of butterfly and dragonfly taxa in each geographic unit between the past and the recent period, according to their detection history.

Supplementary material S1.4: List of butterfly and dragonfly taxa excluded from the present analysis.

Supplementary material S1.5: Main land cover types and corresponding Corine Land Cover (CLC) categories and nomenclature considered in this study.

Supplementary material S1.6: Butterfly (a and b) and dragonfly (c and d) species richness in each administrative unit of the study area in 1980 (a and c) and 2015 (b and d).

Supplementary material S1.7: List of butterfly species observed in at least 10 French 'departements' during the studied period and showing a significant SES value of disappearance or appearance according to *null model 2*.

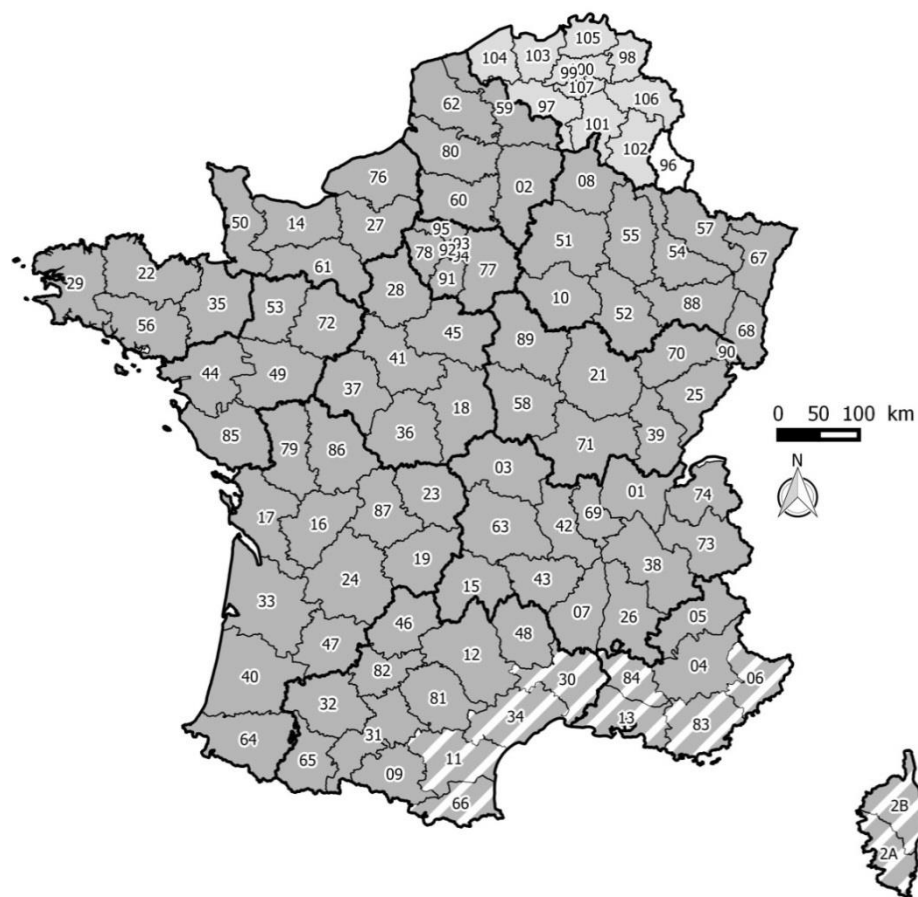
Supplementary material S1.8: List of dragonfly species observed in at least 10 French 'departements' during the studied period and showing a significant SES value of disappearance or appearance according to *null model 2*.

Supplementary material S1.1: Ce supplément volumineux n'étant pas indispensable à la compréhension du chapitre a été déplacé dans la partie « Annexes » du manuscrit de thèse par soucis de clarté.

Table A. List of butterfly taxa (species and subspecies) included in the present study and values for their ecological attributes, protection statut and red list assessment at the scale of study area: family (Hesp – Hesperiiidae, Lyc – Lycaenidae, Nymph – Nymphalidae, Pap – Papilionidae, Pier – Peridae, Rio – Riodinidae, Sat – Satyrinae), biogeographic background (Wide – widespread, North – northern Europe, South – southern Europe, Mount – mountain areas), bioclimatic zonation (Hill – hill zone, Meso – meso-mediterranean, Supra – supra-mediterranean, Mount – mountainous, Alp – alpine-subalpine), main breeding habitat (Alpine – alpine grassland, Dry – dry grassland, Humid – humid grassland, Meso – mesophile grassland, Shrub – shrubland), habitat specialization (Gen – generalist, Mid – mid-generalist, Spe - specialist), host plant specialization (1 – monophageous, 2 – oligophageous, 3 - polyphageous), host plant form (1 – ephemeral and small herbaceous, 2 – large herbaceous, 3 – bushes, 4 – large trees), mobility (1 – low abilities, 2 – medium abilities, 3 – high abilities), voltinism (1 - 0.5 generation, 2 - 1 generation, 3 - 1 or 2 generations, 4 - 2 generations, 5 - 2 to 3 generations, 6 - 3 to 4 generations), myrmecophily (1 – myrmecoxenous, 2 – facultative myrmecophilous, 3 – steadily myrmecophilous, 4 – obligatory myrmecophilous, 5 – no known interaction with ants), French protection status (Un – unprotected, Pr – protected), IUCN categories LC – least concern, NT – near threatened, VU – vulnerable, EN – endangered, CR – critically endangered).

Table B. List of dragonfly taxa (species and subspecies) included in the present study and values for their ecological attributes, protection statut and red list assessment at the scale of study area: family (Aesh – Aeshnidae, Calo – Calopterygidae, Cgstr – Cordulegastridae, Coen – Coenagrionidae, Culid – Corduliidae, Gom – Gomphidae, Lest – Lestidae, Lib – Libellulidae, Macr – Macromiidae, Platy – Platycnemididae), biogeographic background (Wide – widespread, North – northern Europe, South – southern Europe, Mount – mountain areas), bioclimatic zonation (Low – lowland, Hill – hill zone, Mount – mountainous), freshwater type (Lent. - lentic, Lot. - lotic, Both), main breeding habitat (Str. – stream, Riv. – river, Po. – pond, RivPo. – river and pond, Bog – marsh and bog), habitat specialization (Gen – generalist, Spe - specialist), mobility (1 – low abilities, 2 – medium abilities, 3 – high abilities), voltinism (1 – 0.5 generation, 2 – 1 generation, 3 – 1 or 2 generations, 3 – generations, 4 – 2 to 3 generations, 5 – 3 to 4 generations), French protection status (Un – unprotected, Pr – protected), IUCN categories LC – least concern, NT – near threatened, VU – vulnerable, EN – endangered, CR – critically endangered, RE – regionally extinct).

Supplementary material S1.2: Location and index of geographic units in France, Belgium and Luxembourg. Geographic units were defined as 96 ‘départements’ in France and 11 regions in Belgium, while Luxembourg was considered as a single geographic unit. Numbers on the maps are linked to the administrative name of each unit. Bold lines correspond to national limits and to the French “euroregions” as defined in 2015. White stripes cover geographical units included in the Mediterranean belt.



1 - Ain	51 - Marne
2 - Aisne	52 - Haute-Marne
3 - Allier	53 - Mayenne
4 - Alpes de Haute-Provence	54 - Meurthe-et-Moselle
5 - Hautes-Alpes	55 - Meuse
6 - Alpes-Maritimes	56 - Morbihan
7 - Ardèche	57 - Moselle
8 - Ardennes	58 - Nièvre
9 - Ariège	59 - Nord
10 - Aube	60 - Oise
11 - Aude	61 - Orne
12 - Aveyron	62 - Pas-de-Calais
13 - Bouches du Rhône	63 - Puy-de-Dôme
14 - Calvados	64 - Pyrénées-Atlantiques
15 - Cantal	65 - Hautes-Pyrénées
16 - Charente	66 - Pyrénées-Orientales
17 - Charente Maritime	67 - Bas-Rhin
18 - Cher	68 - Haut-Rhin
19 - Corrèze	69 - Rhône
2A - Corse du Sud	70 - Haute-Saône
2B - Haute-Corse	71 - Saône-et-Loire
21 - Côte d'Or	72 - Sarthe
22 - Côtes d'Armor	73 - Savoie
23 - Creuse	74 - Haute-Savoie
24 - Dordogne	75 - Paris
25 - Doubs	76 - Seine-Maritime
26 - Drôme	77 - Seine-et-Marne
27 - Eure	78 - Yvelines
28 - Eure-et-Loir	79 - Deux-Sèvres
29 - Finistère	80 - Somme
30 - Gard	81 - Tarn
31 - Haute-Garonne	82 - Tarn-et-Garonne
32 - Gers	83 - Var
33 - Gironde	84 - Vaucluse
34 - Hérault	85 - Vendée
35 - Ille-et-Vilaine	86 - Vienne
36 - Indre	87 - Haute-Vienne
37 - Indre-et-Loire	88 - Vosges
38 - Isère	89 - Yonne
39 - Jura	90 - Territoire-de-Belfort
40 - Landes	91 - Essonne
41 - Loir-et-Cher	92 - Hauts-de-Seine
42 - Loire	93 - Seine-St-Denis
43 - Haute-Loire	94 - Val-de-Marne
44 - Loire-Atlantique	95 - Val-d'Oise
45 - Loiret	96 - Luxembourg
46 - Lot	97 - Hainaut
47 - Lot-et-Garonne	98 - Limbourg
48 - Lozère	99 - Bruxelles
49 - Maine-et-Loire	100 - Brabant-Flamand
50 - Manche	101 - Namur
	102 - Luxembourg Belge
	103 - Flandre-Orientale

Supplementary material S1.3: Supplementary material S1.2: Location and index of geographic units in France, Belgium and Luxembourg. Geographic units were defined as 96 ‘départements’.

	Before 1980	First atlas publication	Last atlas publication	Species status
<i>Butterfly data sources</i>		<i>Lafranchis 2000</i>	<i>Lafranchis et al. 2015</i>	
<i>Dragonfly data sources</i>		<i>Grand & Boudot 2006</i>	<i>Grand et al. 2014</i>	
	Observed	Observed or absent	Observed	Stable
<i>Species detection history in each geographic unit</i>	Absent	Observed	Observed	Stable
	Observed	Observed or absent	Absent	Disappeared
	Absent	Absent	Observed	Newly appeared

Supplementary material S1.4: Supplementary material S1.2: Location and index of geographic units in France, Belgium and Luxembourg. Geographic units were defined as 96 ‘départements’.

Some butterfly species indicated by Lafranchis et al. (2015) as part of the French fauna were not presented in the first published distribution atlas (Lafranchis 2000), because of several taxonomic revisions between the two publications (review in France by Dupont et al., 2013). Due to this lack of information, 11 butterfly species were excluded from the analysis: *Spialia therapne*, *Pyrgus malvoides*, *Iphiclides feisthamelii*, *Leptidea reali*, *Leptidea juvernica*, *Plebejus bellieri*, *Lasiommata paramegera*, *Hipparchia alcyone*, *Hipparchia genava*, *Erebia sthenyo*, *Aricia montensis*.

In the case of sub-species elevation to species rank, data concerning the recent period (Lafranchis et al. 2015) were pooled and analyzed under the former nominal species.

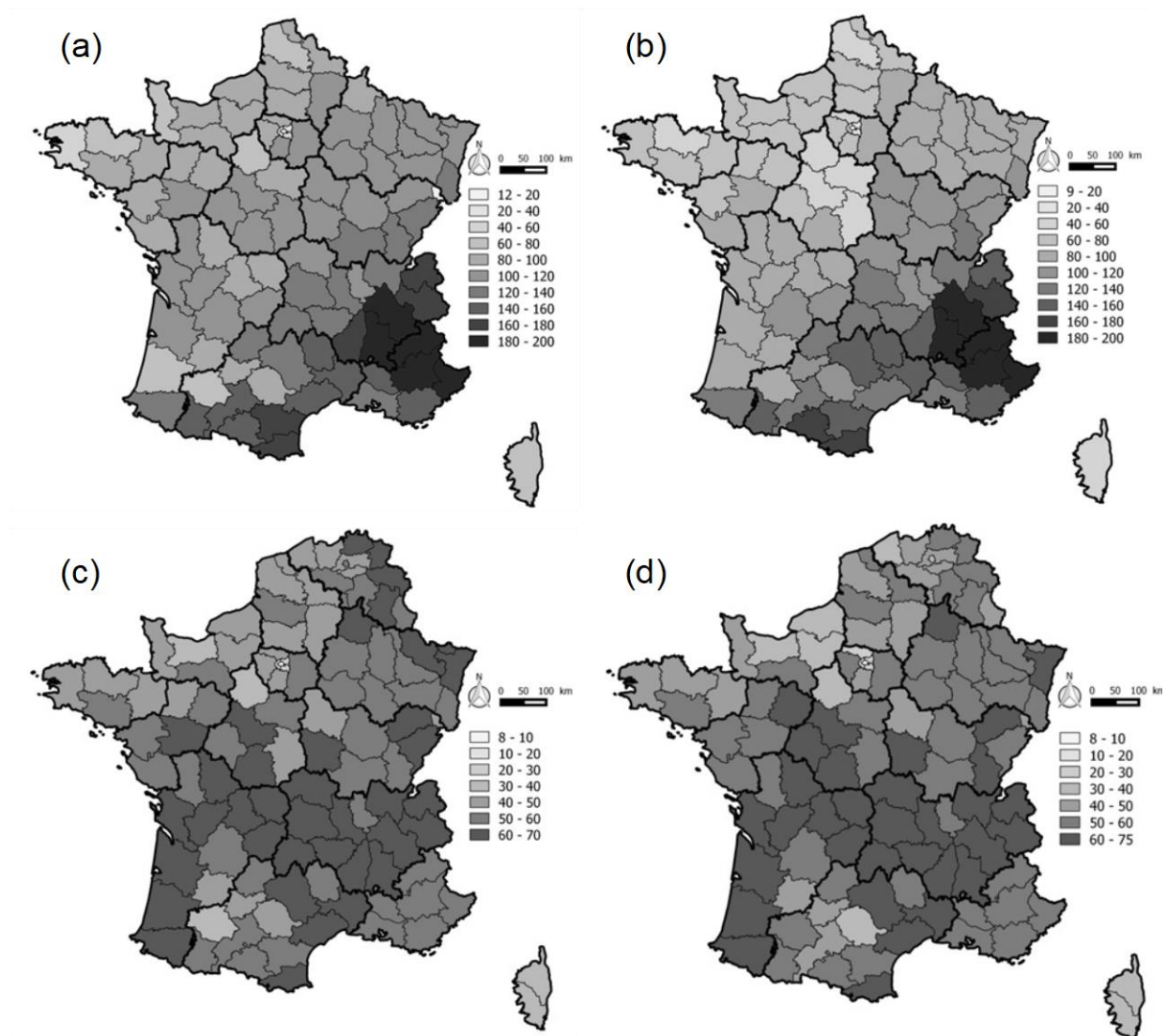
Six species for which the presence in France is considered doubtful were removed from the present work: *Erebia styx*, *Erebia tyndarus*, *Gegenes pumilio*, *Melitaea ornata*, *Polyommatus nivescens*, *Plebejus pylaon*

Four long-distance migrant species only known as punctual visitor in the study area were removed from the present work: *Anax junius*, *Danaus plexippus*, *Nymphalis xanthomelas*, *Vanessa virginiensis*

Supplementary material S1.5: Main land cover types and corresponding Corine Land Cover (CLC) categories and nomenclature considered in this study.

CLC code	Description
<i>Urban areas</i>	
111	Continuous urban fabric
112	Discontinuous urban fabric
121	Industrial or commercial units
122	Road and rail networks and associated land
123	Port areas
124	Airports
131	Mineral extraction sites
132	Dump sites
133	Construction sites
141	Green urban areas
142	Sport and leisure facilities
<i>Agricultural areas</i>	
211	Non irrigated arable land
212	Permanently irrigated land
213	Rice fields
221	Vineyards
222	Fruit trees and berry plantations
223	Olive groves
<i>Closed natural areas</i>	
311	Broad-leaved forests
312	Coniferous forests
313	Mixed forests
322	Moors and heathlands
323	Sclerophyllous vegetation
324	Transitional woodland-shrubs
<i>Open natural areas</i>	
321	Natural grasslands
231	Pastures
<i>Wetland areas</i>	
411	Inland marshes
412	Peat bogs
511	Water courses
512	Water bodies

Supplementary material S1.6: Butterfly (a and b) and dragonfly (c and d) species richness in each administrative unit of the study area in 1980 (a and c) and 2015 (b and d). Bold lines correspond to the French “euroregions” as defined in 2015.



Supplementary material S1.7: List of butterfly species observed in at least 10 French 'departements' during the studied period and showing a significant SES value of disappearance or appearance according to null model 2. Values were considered as significant for P-values < 0.05, after a correction for multiple comparisons using 'fdr' method. For each species, table indicates values of SESdisp or SES app, the number of 'departements' where the species was noted as appeared or disappeared (Obs.units), the total number of administrative units where the species was observed at least once (Total units), the ratio between these two values (Ratio), its main breeding habitat (Habitat) and its status regarding the French protection list.

Taxa	SES value	Obs.units/Total units	Ratio	Habitat	Protection
Disappearance					
<i>Chazara briseis</i>	14.26	51/74	69	Dry grassland	Unprotected
<i>Pontia daplidice</i>	14.19	58/88	66	Mesophile grassland	Unprotected
<i>Coenonympha hero</i>	10.72	28/30	93	Humid grassland	Protected
<i>Polygonia egea</i>	10.37	9/12	75	Dry grassland	Unprotected
<i>Pyrgus cirsii</i>	8.67	29/62	47	Dry grassland	Unprotected
<i>Carcharodus floccifer</i>	7.12	21/51	41	Mesophile grassland	Unprotected
<i>Ephydryas maturna</i>	6.75	17/21	81	Forest	Protected
<i>Pyrgus carthami</i>	6.66	23/58	40	Dry grassland	Unprotected
<i>Lopinga achine</i>	6.37	28/66	42	Forest	Protected
<i>Maculinea alcon alcon</i>	6.34	26/63	41	Humid grassland	Protected
<i>Hyponephele lycaon</i>	6.30	8/23	35	Dry grassland	Unprotected
<i>Argynnis niobe</i>	5.60	22/64	34	Mesophile grassland	Unprotected
<i>Pyrgus alveus</i>	5.26	23/68	34	Mesophile grassland	Unprotected
<i>Euchloe crameri</i>	5.23	21/65	32	Dry grassland	Unprotected
<i>Pyrgus serratulae</i>	5.03	22/68	32	Dry grassland	Unprotected
<i>Polyommatus theristes</i>	4.81	22/67	33	Dry grassland	Unprotected
<i>Boloria euphrosyne</i>	4.78	27/84	32	Forest	Unprotected
<i>Coenonympha tullia</i>	4.67	10/21	48	Humid grassland	Protected
<i>Lampides boeticus</i>	4.51	24/79	30	Shrubland	Unprotected
<i>Pyrgus onopordi</i>	4.49	7/27	26	Dry grassland	Unprotected
<i>Parnassius apollo</i>	4.12	8/32	25	Dry grassland	Protected
<i>Carcharodus baeticus</i>	4.07	4/13	31	Dry grassland	Unprotected
<i>Polyommatus dorylas</i>	4.003	10/42	24	Dry grassland	Unprotected
<i>Hipparchia statilinus</i>	3.90	18/62	29	Dry grassland	Unprotected
<i>Erebia aethiops</i>	3.71	11/41	27	Forest	Unprotected
<i>Maculinea teleius</i>	3.63	9/25	36	Humid grassland	Protected
<i>Limenitis populi</i>	3.57	21/65	32	Forest	Unprotected
<i>Hipparchia fagi</i>	3.49	18/71	25	Forest	Unprotected
<i>Coenonympha oedippus</i>	3.43	9/22	41	Humid grassland	Protected
<i>Cupido osiris</i>	3.42	6/28	21	Dry grassland	Unprotected
<i>Pyrgus armoricanus</i>	3.24	21/82	26	Dry grassland	Unprotected
<i>Iolanas iolas</i>	3.22	3/12	25	Forest	Unprotected
<i>Hamaeris lucina</i>	2.94	12/33	36	Humid grassland	Unprotected
<i>Hipparchia semele</i>	3.78	25/87	29	Dry grassland	Unprotected
<i>Euchloe simplonia</i>	3.02	3/13	23	Alpine grassland	Unprotected
<i>Satyrus actaea</i>	3.17	4/21	19	Dry grassland	Unprotected
<i>Scolitantides orion</i>	2.99	6/29	21	Dry grassland	Unprotected
<i>Pieris manni</i>	2.88	9/44	20	Dry grassland	Unprotected

<i>Hyponephele lupina</i>	3.25	3/12	25	Dry grassland	Unprotected
<i>Pseudophilotes baton</i>	3.005	18/75	24	Dry grassland	Unprotected
<i>Melitaea aurelia</i>	2.89	11/30	37	Dry grassland	Unprotected
<i>Polyommatus damon</i>	2.83	4/19	21	Dry grassland	Unprotected
<i>Colias palaeno</i>	2.41	3/11	27	Humid grassland	Protected
<i>Hipparchia fida</i>	2.35	3/16	19	Shrubland	Unprotected
<i>Brenthis hecate</i>	3.27	5/27	19	Dry grassland	Unprotected
<i>Syrichthus proto</i>	2.79	3/13	23	Dry grassland	Unprotected
<i>Plebejus idas</i>	2.68	18/77	23	Dry grassland	Unprotected
<i>Maculineaalcon rebeli</i>	2.69	11/45	24	Dry grassland	Protected
<i>Melitaea parthenoides</i>	2.79	21/85	25	Dry grassland	Unprotected
<i>Satyrus ferula</i>	2.38	4/28	14	Dry grassland	Unprotected
<i>Boloria napaea</i>	2.19	2/10	20	Alpine grassland	Unprotected
Appearance					
<i>Cacyreus marshalli</i>	20.30	32/51	63	Mesophile grassland	Unprotected
<i>Scolitantides orion</i>	6.90	8/29	28	Dry grassland	Unprotected
<i>Cupido alcetas</i>	6.58	11/50	22	Mesophile grassland	Unprotected
<i>Satyrrium pruni</i>	6.15	11/73	15	Forest	Unprotected
<i>Pieris mannii</i>	5.26	8/44	18	Dry grassland	Unprotected
<i>Melitaea diamina</i>	5.14	10/75	13	Humid grassland	Unprotected
<i>Maculineaalcon rebeli</i>	4.87	6/45	13	Dry grassland	Protected
<i>Brenthis daphne</i>	4.67	9/73	12	Shrubland	Unprotected
<i>Maculineaalconalcon</i>	4.42	8/63	13	Humid grassland	Protected
<i>Pyrgus armoricanus</i>	4.20	10/82	12	Dry grassland	Unprotected
<i>Lycaena dispar</i>	2.98	6/58	10	Humid grassland	Protected
<i>Lasiommata petropolitana</i>	2.99	2/14	14	Forest	Unprotected
<i>Satyrus ferula</i>	2.99	4/28	14	Dry grassland	Unprotected
<i>Carcharodus lavatherae</i>	2.78	3/26	12	Dry grassland	Unprotected
<i>Plebejus argyrognomon</i>	2.75	4/48	8	Dry grassland	Unprotected
<i>Pyrgus bellieri</i>	2.88	2/14	14	Dry grassland	Unprotected
<i>Apatura iris</i>	2.64	7/85	8	Forest	Unprotected
<i>Satyrrium spini</i>	2.62	5/54	9	Shrubland	Unprotected

Supplementary material S1.8: List of dragonfly species observed in at least 10 French 'departements' during the studied period and showing a significant SES value of disappearance or appearance according to null model 2. Values were considered as significant for P-values < 0.05, after a correction for multiple comparisons using 'fdr' method. For each species, table indicates values of SESdisp or SES app, the number of 'departements' where the species was noted as appeared or disappeared (Obs.units), the total number of administrative units where the species was observed at least once (Total units), the ratio between these two values (Ratio), its main breeding habitat (Habitat) and its status regarding the French protection list.

Species	SES value	Obs.units/Total units	Ratio	Habitat	Protection
Disappearance					
<i>Sympetrum depressiusculum</i>	11.39	17/43	40	Pond	Unprotected
<i>Leucorrhinia rubicunda</i>	5.38	8/20	40	Marsh & Bog	Unprotected
<i>Coenagrion hastulatum</i>	4.61	7/36	19	Marsh & Bog	Unprotected
<i>Leucorrhinia pectoralis</i>	4.12	10/61	16	Marsh & Bog	Protected
<i>Coenagrion ornatum</i>	4.12	2/10	20	Stream	Unprotected
<i>Epitheca bimaculata</i>	3.31	6/42	14	Pond	Unprotected
<i>Brachytron pratense</i>	3.21	9/89	10	Pond	Unprotected
<i>Leucorrhinia caudalis</i>	2.52	5/41	12	Pond	Protected
<i>Lestes macrostigma</i>	3.04	2/11	18	Marsh & Bog	Unprotected
<i>Coenagrion lunulatum</i>	2.63	2/11	18	Marsh & Bog	Unprotected
<i>Leucorrhinia albifrons</i>	2.44	3/15	20	Marsh & Bog	Protected
<i>Aeshna isoceles</i>	2.52	8/79	10	Pond	Unprotected
<i>Gomphus flavipes</i>	2.61	4/33	12	River	Protected
<i>Onychogomphus uncatus</i>	2.44	4/47	9	Stream	Unprotected
<i>Calopteryx virgo virgo</i>	2.40	7/64	11	Stream	Unprotected
<i>Sympetrum pedemontanum</i>	2.31	5/38	13	River & Pond	Unprotected
Appearance					
<i>Hemianax ephippiger</i>	20.40	34/62	55	Pond	Unprotected
<i>Leucorrhinia pectoralis</i>	12.82	20/61	33	Marsh & Bog	Protected
<i>Gomphus flavipes</i>	11.43	13/33	39	River	Protected
<i>Leucorrhinia caudalis</i>	8.06	12/41	29	Pond	Protected
<i>Trithemis annulata</i>	6.77	7/19	37	River & Pond	Unprotected
<i>Gomphus graslinii</i>	5.49	7/29	24	River	Protected
<i>Coenagrion ornatum</i>	3.77	3/10	30	Stream	Unprotected
<i>Ophiogomphus cecilia</i>	3.64	4/23	17	River	Protected
<i>Oxygastra curtisii</i>	3.11	8/77	10	River & Pond	Protected
<i>Coenagrion caeruleescens</i>	2.58	3/19	16	Stream	Unprotected
<i>Somatochlora arctica</i>	2.60	3/34	9	Marsh & Bog	Unprotected

Chapitre 2

Insight into butterfly-hostplant bipartite networks: using projected network as suitable tools for insect conservation

Ce **deuxième chapitre** s'intègre directement dans la suite des conclusions issues du chapitre 1 en termes de lien entre les exigences écologiques des espèces et leur capacité de réponse aux changements globaux. Les ressources trophiques constituent une des composantes essentielles de la niche des espèces. Du fait des interactions étroites qu'ils entretiennent avec leurs plantes nourricières au cours de leur phase larvaire, les Rhopalocères constituent un modèle d'étude approprié pour mener une investigation plus poussée de la relation entre le degré de spécificité de ces relations et l'état de conservation des espèces.

Ce travail est basé sur la première analyse d'un jeu de données faisant la synthèse de toutes les plantes nourricières mentionnées pour chacun des Rhopalocères présents en France entre le 19^{ème} siècle et la période actuelle. La mise à disposition de ce jeu de données par le MNHN a offert l'opportunité de construire un réseau d'interactions bipartite entre 241 papillons de jours et 527 plantes utilisées comme ressources trophiques par leurs chenilles.

Dans un objectif de recherche plus fondamental, une première étape a visé à décrire la structure de ce réseau afin de dégager les patrons d'associations entre les Rhopalocères et leur plantes nourricières, de les comparer avec les patrons observés dans d'autres régions du globe et de tenter d'identifier les principaux facteurs (évolutifs, écologiques, géographiques) qui les conditionnent. Le lien entre la position des Rhopalocères au sein de ce réseau et leur risque d'extinction a été exploré dans une deuxième étape, à travers le calcul de métriques simples (degré, degré moyen de partenaires, ...). Le réseau projeté des Rhopalocères a enfin été utilisé pour visualiser les relations entre espèces à travers le partage des mêmes plantes nourricières et estimer le bénéfice potentiel des listes de protection actuelles pour la couverture indirecte des principaux enjeux de conservation.

D'un point de vue plus opérationnel, la connaissance précise des ressources qui composent l'habitat des espèces doit être un prérequis indispensable au développement de mesures de conservation et à la définition des protocoles qui visent à les détecter ou à les suivre dans le temps. Le jeu de données compilé dans cette analyse fournit des éléments précis et essentiels pour une meilleure localisation de ces habitats, permettant une meilleure évaluation de la capacité d'accueil d'un site lors de la réalisation d'une étude d'impact sur l'environnement ou de la mise en place d'une mesure de compensation écologique.

Insight into butterfly-hostplant bipartite networks: using projected network as suitable tools for insect conservation

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Abstract

1. The butterflies are herbivorous insects with varying degrees of specificity to hostplant depending on the species. Host-range is an essential component of their ecological niche and the specificity of the link with hostplants have an important influence on species patterns of presence.
2. In the present study, we investigate the structure of the bipartite network between 241 French butterflies and 527 hostplants interactions, characterized by 768 nodes and 1094 two-species links. Our aim is (i) to identify the determinants of species host-range, (ii) to assess the relationships between the position of butterfly species in this network and their conservation issue and (iii) to explore projected links between butterflies through hostplant to evaluate potential coverage of these conservation issues through the current lists of protected species.
3. Our results reveal a highly modular structure of butterfly-hostplant network, significantly correlates with butterfly's taxonomic distances. Modules are constrained by the privileged association of certain butterfly families with certain hostplant families. This structure appears strongly conserved among different regions of the world, with a great similarity in the concerned taxa.
4. The analysis showed a significant relationship between extinction risk of butterflies in France and a high level of host specificity. The lack of correlation between the butterfly's degree and the average degrees of their hostplants showed that the hosts of specialist butterflies were not necessarily exclusive to them. Protected butterfly species were indirectly related to few other butterflies through the projected network. These indirect partners themselves were not highly dependent to the shared hostplants and they did not represent significant conservation issues. This pattern could allow deducing (i) a low potential of indirect protection through the current lists, and (ii) a weak influence of the sharing of the same resource on the extinction risk of two distinct butterfly species.
5. Network models help to map the relationship of butterflies with hostplants and to focus attention to potential biodiversity losses and potential homogenization.

Key words: Plant-insect interactions, herbivory, bipartite network, modularity, conservation.

II.1. Introduction

Protect ecosystem integrity and species diversity is at the core of all conservation or restoration management actions. Protecting rare, threatened or emblematic species has guided conservation strategies since the emergence of conservation biology (Jenkins & Ricklefs, 2011). Some taxa support, through the dependence of associated partners, a significant diversity and could be considered as "keystone" species in the local ecosystem (Mills *et al.*, 1993). The interaction among species in their community has an increasing weight in the assessment of conservation priorities and helps to go from species –centered approaches to systemic conservation strategies (Jordán *et al.*, 2007; Cadotte *et al.*, 2011). Facing cost-effective issues of such strategies (Layock *et al.*, 2009), this initially species-centered view has progressively evolved towards a more integrative vision, going towards the conservation of ecosystem functions and the biotic interactions that underlie them (Heleno *et al.*, 2012; Pollock *et al.*, 2017). Beyond the list of its elements (genes, species, habitats, landscapes), biodiversity also concerns complex networks of ecological interactions, from mutual (*e.g.* plant-pollinator) to antagonistic (*e.g.* host-parasite) (Montoya *et al.*, 2006; Ings *et al.*, 2009), as well as from direct to indirect (Williams *et al.*, 2002). Investigating the structure of these networks and their stability is now seen as an important way to understanding community structure (Albrecht *et al.*, 2017; Bascompte & Jordano, 2007; Thébault & Fontaine, 2010). This growing interest in biotic interactions has also increased with a better awareness of co-extinction processes (Koh *et al.*, 2004a; Dunn *et al.*, 2009). The decline of a species in response to environmental changes will inevitably lead to the cascading effects on specifically associated partners (Allesina & Bodini, 2004; Dunne & Williams, 2009). As consequence, global changes favor a general homogenization of species and interactions, *i.e.* generalist species and opportunist interactions (Albrecht *et al.*, 2017; Bascompte & Jordano, 2007; Eskildsen *et al.*, 2015).

In such context, measuring changes in biodiversity requires relevant and specific methods (Vogt-Schilb *et al.*, 2016; Joffard *et al.*, submitted). During the last decade, network approaches have been developed to model the complexity of biotic interactions (Proulx *et al.*, 2005; Bascompte, 2010). By representing the topology of associations (links) between species (nodes) from two groups of organisms (Latapy *et al.*, 2008), bipartite ecological networks have been used to address important ecological (Bastolla *et al.*, 2009), functional (Coux *et al.*, 2016) or evolutionary issues (Krasnov *et al.*, 2012). Many diverse metrics have

been introduced to evidence general patterns in bipartite networks such as centrality (Martín González *et al.*, 2010), modularity (Olesen *et al.*, 2007), nestedness (Staniczenko *et al.*, 2013) or robustness and stability facing potential environmental change (Pocock *et al.*, 2012). The study of relationships between species through their projected network has also provided new insight about complex community assemblages through indirect interactions, such as facilitation or competition (Nacher & Akutsu, 2013; Taudière *et al.*, 2015). This new analytical framework was seen as an opportunity to narrow the gap between concepts in ecology and applied conservation biology (Harvey *et al.*, 2017). Indeed, several studies have used network analysis to investigate the effects of habitat alterations and land use changes on biotic interactions (Weiner *et al.*, 2014; Villa-Galaviz *et al.*, 2012; Staniczenko *et al.*, 2017). Several authors recently advocated for the application of these theoretical metrics to the field of applied conservation biology in order to develop more relevant planning and monitoring (Tylianakis *et al.*, 2010; Kaiser-Bunbury & Blüthgen, 2015). In this context, the relationships between plants and insects, largely present in different ecosystems, have been the subject of particular attention (Evans *et al.*, 2017), especially by the study of plant-pollinator (Astegiano *et al.*, 2015) and herbivorous plants interaction networks (De Araújo, 2016).

With more than 900,000 species on earth, insects are the most diverse group of organisms (Footitt & Adler, 2009) and form the basis of most food webs (Strong *et al.*, 1984; Moir *et al.*, 2014). About half of the insect species described are specifically related to plants through herbivory (Speight *et al.*, 1999; War *et al.*, 2012). These trophic interactions constitute one of the most important energy flows in terrestrial ecosystems (Metcalf *et al.*, 2014; Forister *et al.*, 2015) and strongly influence the biomass and diversity of plant communities (Carson & Root, 2000; Bagchi *et al.*, 2014). Herbivorous insects generally show significant conservatism in their interactions with hostplants (Fontaine & Thébault, 2015), resulting from coevolution and fine adaptation to plants' defenses (Cagnolo *et al.*, 2011; Jensen *et al.*, 2011; Ibanez *et al.*, 2016). These evolutionary histories have led to a high specificity of many taxa for the exploitation of a particular plant species or genus (Richards *et al.*, 2015; Moir *et al.*, 2016). Because of this often specific links, plants represent essential nodes that condition the robustness of many networks and the maintenance of a wide diversity of herbivorous insects (Koh *et al.*, 2004b; Fonseca, 2009; Schleuning *et al.*, 2016).

Lepidoptera represent the largest lineage of herbivorous organisms, whose diversification has accompanied the explosive radiation of angiosperms (Regier *et al.*, 2013;

Vila, 2014; Schatz *et al.*, 2017). Most species feed on plants during at least a part of their larval stage, with a variable specificity depending on the considered taxonomic group or geographic area (Dyer *et al.*, 2007; Muto-Fujita *et al.*, 2017). Butterflies constitute one of the best studied groups of Lepidoptera at the scale of Europe in terms of ecology and distribution (Thomas, 2005; Lewis & Senior, 2011). The bipartite interactions linking host plants to the butterfly species are known more and more extensively within several countries (Robinson *et al.*, 2010; Ferrer-Paris *et al.*, 2013; Eskildsen *et al.*, 2015; Muto-Fujita *et al.*, 2017). Host range is an essential component of butterfly biology and the distribution of these resources significantly conditions the suitability of habitats (Dennis *et al.*, 2006; Vanreusel & Van Dyck, 2007). The specificity of the plant-butterfly link also shapes spatio-temporal patterns of species (Cizek *et al.*, 2006; Altermatt, 2010; Slove & Janz, 2011), and plays important role on the stability of its populations (León-Cortés *et al.*, 2003; Komonen *et al.*, 2004) and on metapopulation-specific parameters, such as colonization or local dispersal processes (Krämer *et al.*, 2012; Fourcade & Öckinger, 2017; Salz & Fartmann, 2017).

Butterflies show a general decline at the scale of Europe since the beginning of the last century, both in terms of range and size of populations (Warren *et al.*, 2001; Habel *et al.*, 2016; Delpon *et al.*, in press). The most specialized species present the largest regression, and several local to regional extinctions could be related to the negative impacts of landscape changes on hostplant populations (Hardy *et al.*, 2007; Pearse & Altermatt, 2013; Brunbjerg *et al.*, 2017). Several studies also showed a strong correlation between the local richness of floristic communities and the specific richness of butterflies in thermophilous habitat (Hawkins & Porter, 2003; Cremene *et al.*, 2005), and the decrease of the first is usually followed by an impoverishment of butterfly communities (Haddad *et al.*, 2009, Pöyry *et al.*, 2009). However, the topological characteristics of the butterfly-hostplant interaction network, which partly underlie the structuring of butterfly communities, have been poorly investigated in Europe. Studies of the link between population dynamics and hostplant range are usually centered on a unique butterfly species (Krauss *et al.*, 2005; Krämer *et al.*, 2012; Cormont *et al.*, 2013). Strategies built around community modules, including all closely interdependent species, have been developed to allow more consistent conservation of some iconic butterfly species (Hochberg *et al.*, 1996; Mouquet *et al.*, 2005). However, no synthesis of butterfly-plant interactions has been exploited in order to evaluate the indirect links between butterfly species, through a sharing of host plants, from an integrated conservation perspective.

In the present study, we describe the structure of a large ecological bipartite network of butterfly-hostplant interactions at the scale of France. Using projected networks, the indirect links between butterflies through shared hostplants are analyzed. We pay a particular attention to protected species, in order to analyze their position within the interaction network. This network was constructed from a qualitative dataset summarizing field records of caterpillar's development of 241 French butterfly species on 527 plant species, based on an exhaustive literature review. More especially, we address the following questions: (1) Could the association patterns of butterflies be predicted by the degree of co-occurrence, the similarity of breeding habitat and the taxonomic distance of butterfly? (2) Is there a significant correlation between the degree of specialization of a butterfly species and the attractiveness of its hostplants for other species? (3) Is there a correlation between butterfly specialization and their extinction risk? (4) Do current protection policies allow, through the projected network, an indirect coverage of conservation issues associated with butterflies?

II.2. Material & methods

II.2.1. Butterfly-hostplant interaction matrix

The present study was focused on the analysis of a large dataset that summarized hostplant species consumed by French butterfly species during their larval stage. This dataset was assembled by one of the coauthors (P.D.), on the basis of a literature review including 79 references (specific studies, regional syntheses, atlas of biodiversity, online databases ...) published between 1887 and today in eight European countries (France, Germany, England, Belgium, Spain, Italy, Sweden, Switzerland), but only targeting butterfly and plant species present in France. The interaction data collected are only qualitative and coded in the form of an incidence matrix (observation (1) or non-observation (0) of caterpillars feeding on a plant). The strength of each interaction could not be quantified and local variations in butterfly diet within the study area (*e.g.* Meister *et al.*, 2015) were not taken into account. The dataset was constructed only with field observations, and interactions observed within farms or greenhouses were excluded. Duplicate interactions due to synonymy and those involving taxa identified at higher ranks than species (*i.e.* genera or families) were also excluded. Butterfly and plant species names have been homogenized based on the most recent taxonomic reference at the scale of the study area (TaxRef v.10.0, www.inpn.mnhn.fr). Subspecies and varieties have been systematically reduced to specific resolution.

This database grouped 2232 interactions between 249 species of butterflies and 830 species of plants. All the observations for which the nature of the data or the initial source could not be clearly identified were removed from the analysis. In the end, this led to a database of 1094 interactions between 241 butterfly species (distributed among 6 families; Suppl.S2.1) and 527 plant species (distributed among 53 families; Suppl.S2.2). This represents 92% of butterfly species currently referenced in France (Lafranchis *et al.*, 2015). The exploited hostplants represent approximately 27% of families and 9% of species referenced in France for these families (Bock *et al.*, 2013).

II.2.2. Distance matrices

Three matrices were assembled to represent different components of the distance separating each of the butterfly species included in the analysis: geographic distance, ecological distance, and taxonomic distance. The first matrix was extracted from the most recent synthesis of butterfly distribution at the scale of the study area (Lafranchis *et al.*, 2015). According to this synthesis, France was divided into 96 administrative units (AU, called "departments"). Species range was based on AUs where butterflies occurred between 2000 and 2015.

A matrix of ecological distance between different butterfly species was constructed by extracting the characteristics of their main breeding habitats known in France (Lafranchis *et al.*, 2015). These features have been summarized into 6 major habitat types in which each species has been ranked (1) if the species breeds in the habitat, (0) if not): (1) mesophilous grasslands, (2) dry grasslands, (3) humid grasslands, (4) alpine grasslands, (5) shrublands, (6) forests.

In order to test the influence of butterfly taxonomy on their proximity within the interaction network, a taxonomic distance matrix between butterfly species was constructed and used as a proxy for their phylogenetic distance (Koehler *et al.*, 2012). Using a method already applied for the analysis of several ecological networks (Rezende *et al.*, 2007; Bellay *et al.*, 2015), the matrix of taxonomic distance (MTD) was calculated on the basis of the following equation:

$$MTD = Md - (F_{\omega} + Sf_{\omega} + G_{\omega} + Sp_{\omega}) \quad (1)$$

where Md is the maximum distance found in the butterfly database (maximum distance = 4, referring to the taxonomic category class) and F_ω , Sf_ω , G_ω and Sp_ω are matrices for each taxonomic category (family, subfamily, genus and species, respectively) generated by the function *weight.taxo* available in package Ape (Paradis *et al.*, 2004) for R. The lower the value of the index calculated between two species, the closer they are within the taxonomic classification. Therefore, species within the same genus exhibit a value of taxonomic distance (td) equal to 1, different genera have $td= 2$, different subfamilies have $td= 3$ and different families have $td= 4$. The name currently used for each taxonomic degree has been extracted from the French taxonomic reference system TaxRef (TaxRef v.10.0, www.inpn.mnhn.fr).

II.2.3. Species conservation status

The protection status and IUCN red list of each butterfly species was compiled from the most recent assessments at the scale of the study area (Suppl.S2.1). Each species was defined as “unprotected” or “protected” at the national level based on the French list of protected insects (<https://inpn.mnhn.fr/programme/reglementation>). According to their red list categories (UICN France *et al.*, 2014), they were classified as “least concern” (LC), “near threatened” (NT), “vulnerable” (VU), “endangered” (EN), “critically endangered” (CR), and “extinct” (at the French scale) (EX). Species categorized as VU, EN or CR were grouped into a “threatened” category for our analysis. Taxa ranked as ‘not evaluated’ (NE) or ‘not applicable’ (NA: introduced or vagrant taxa) were excluded from the analysis.

II.2.4. Analysis of bipartite and projected networks

An ecological bipartite network was constructed from the butterfly-hostplant association matrix using the package Igraph (Csárdi & Nepusz, 2006) in the R software (R 3.3.3, R Development Core Team, 2015) and the software GEPHI v.0.9.1 (Bastian *et al.*, 2009). Following network theory terminology, we estimated the degree of each butterfly species in the bipartite network k_b as the number of hostplant species with which they interact (with k_p corresponding to hostplant bipartite degree). This value was considered as a proxy of butterfly diet specialization (seen in this paper as the extent of the theoretical biotic part of the niche of butterfly species). In order to explore the attractiveness of the butterfly resource for other species, we estimated the mean degree of plants associated with each butterfly in the bipartite network c_b (defined as “partner specialization” of b by Taudière *et al.*, 2015). The projected network of butterflies was also constructed to visualize the indirect interactions established

between these species through the sharing of one or more hostplants. In order to quantify the importance of this sharing, the projected degree l_b was calculated for each butterfly species as the number of partners to which it was indirectly related in the projected network. This projected network allowed us to explore the potential indirect coverage of butterfly conservation issues through the sharing of a resource with a protected species.

From these values k and c , we developed an index (D) allowing to quantify the level of dependence of the partners of a butterfly species in the projected network to the hostplants they shared with this species. Assuming that the interactions between a butterfly and each of its hostplants have the same weight in the bipartite network (no primary/secondary host differentiation), a butterfly with a high degree k_b will be less dependent to each hostplant. The value of D of a butterfly was calculated by estimating the average degree of species related to each of its hostplants, using the following equation:

$$D_b = \frac{\sum_p^1 c_p}{k_b} \quad (2)$$

where D_b corresponded to the average dependence of the indirect partners of the butterfly b , c_p corresponded to the partner specialization of each of the plants p with which b interacts in the bipartite network and k_b corresponded to the degree of b . In order to avoid an artificial inflation of D_b , species b was not taken into account when calculating the value of c_p for each of its plants (D_b could not be calculated for butterfly species with a projected degree of zero). Given this formulation, a butterfly characterized by a low value of D was associated, in the projected network, with species highly dependent of the same hostplants (see Suppl.S2.3).

II.2.5. Null models

We simulated randomized network through two different null models in order to test the significance of patterns observed in the network structure, following the method of Taudière *et al.* (2015). The null model 1 consisted in a simple randomization, fixing only the total dimensions of the network while maintaining a mean degree of butterflies and plants in the bipartite network identical to that of the observed network. The null model 2 randomized the links between species while fixing the degree distribution within the bipartite network (the degree of each species was identical to that in the observed network). Null model 1 has been

implemented through the *permatfull* function of the Vegan package in R and the null model 2 with the *quasiswap* method of the *permatswap* function of the same package (with 999 permutations for each model) (Patefield, 1981). The estimation of the deviation from the simulated value allowed to evaluate whether the *k*, *c* and *l* values of the different species are higher or lower than expected by chance. It was calculated in each case from the following equation:

$$SES = \frac{(x-\mu)}{\sigma} \quad (3)$$

where *x* is the actual observed value (of *k*, *c* or *l*), μ is the mean of the null values, and σ is the standard deviation of null values. The use of these two models allowed to evaluate the part of the observed patterns which was solely related to the degree distribution within the network.

II.2.6. Network topology

In order to describe the structure of the butterfly-hostplant network, the modularity (*M*) of the bipartite network was analyzed through the algorithm of Newman & Girvan (2003) implemented in the NETCARTO software (Guimerà & Amaral, 2005). This value, ranging from 0 to 1, refers to a measure of the level at which species appear to be organized in modules. These modules corresponded to subsets of species that tend to interact more with each other than with other species of the network (Krause *et al.*, 2003). The significance of this measurement was evaluated using the same software, which generated random network simulations (999 randomizations) with the same degree distribution among species (Guimerà *et al.*, 2004). The membership of each species of the network to some module was estimated using the Igraph package in R, through a partitioning of the network allowing a maximization of the modularity (*i.e.* partitions of the original graph were only allowed if they increased modularity) (Newman, 2006). The role of each plant species in the network structure was also evaluated according to its topological properties. The position of each species has been defined by the crossing of the estimated values of within module degree (*z*, position relative to the other species of the module) and among-module connectivity (*c*, connection with the species of the other modules) (Santamaría *et al.*, 2014). These values were calculated using the NETCARTO software and the plant species were divided into four categories according to Olesen *et al.* (2007) (peripherals, connectors, module hubs and network hubs).

II.2.7. Statistical analysis

A Mantel test was performed to test the influence of geographical, ecological and taxonomic distance between butterfly species on their position within the network. Each of these explanatory matrices as well as the butterfly-plant association matrix were converted into dissimilarity matrices using the Jaccard index available function *vegdist* of the Vegan package (Oksanen et al., 2014). Mantel test was run using 9 999 randomizations and Spearman's rank correlation. In order to evaluate the link between butterfly specialization and their vulnerability, the degree k_b in the bipartite network was compared between butterflies characterized by different IUCN categories by means of a Kruskal-Wallis H test, followed by pairwise comparisons by the Wilcoxon rank-sum test, with p-values adjusted using the 'fdr' correction (Benjamini & Hochberg, 1995). We compared the degrees of butterflies in the bipartite network (k_b), their degree in the projected network (l_b), the mean degree of their hostplants (c_b) and the specialization of their indirect partner (D_b) between protected and unprotected species, using Wilcoxon's signed-rank tests. Finally, a Fisher's exact test was performed to assess independence between the coverage of species by current protection policies (directly protected, indirectly protected through the proposed network, unprotected) and their classification within the IUCN categories.

II.3. Results

II.3.1. Topological features of the network

The bipartite butterfly-hostplant interaction network consists in 768 nodes (241 butterflies and 527 plants) and 1094 links (Fig.2.1). Most butterflies interact with few plants. About 75% of the species feed on one to five hostplants and about 17% of the species are monophagous, specialized on a single plant resource. The degree of butterflies in the bipartite network ranges from 1 to 29 (*Callophrys rubi* has the higher number of hostplants), with an average value of 4.53 ± 4.25 (Suppl.S2.4a). Plants show an even higher degree of specialization, with about 95% of the species being consumed by only 1 to 5 butterflies, and 60% by a single species. Their degree varied between 1 and 27 (*Festuca ovina* was consumed by the highest number of species), with an average value of 2.08 ± 2.19 (Suppl.S2.4b).

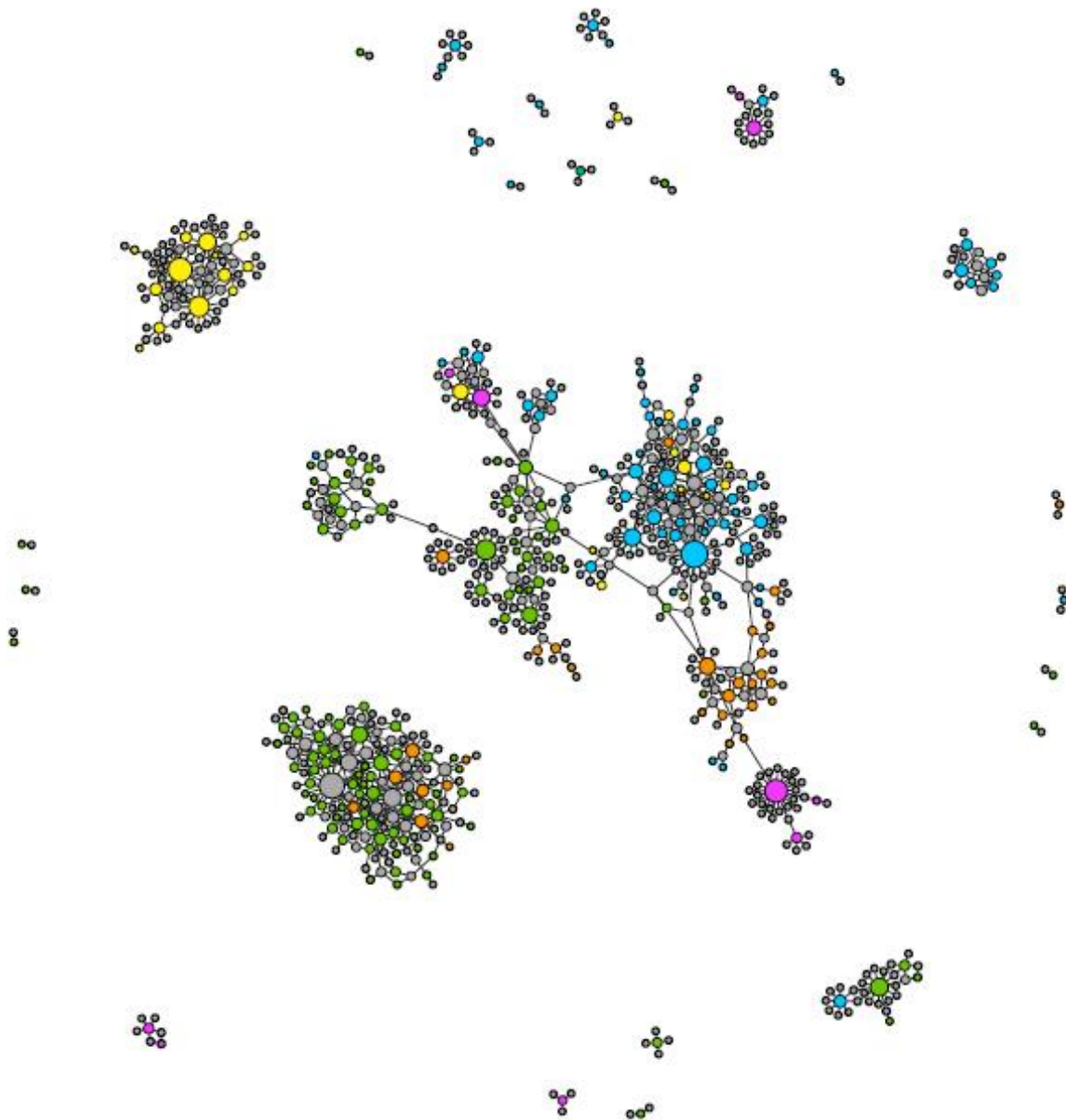


Figure 2.1 : Graphical representation of the bipartite butterfly-hostplants network based on the spatialization algorithm Force Atlas 2 (Jacomy et al., 2014) implemented in the software GEPHI (Bastian et al., 2009). Circles correspond to species of butterflies and hostplants and their size is proportional to species' degrees. Grey circles represent hostplants and colored circles correspond to butterfly families: Lycaenidae in blue, Papilionidae in purple, Pieridae in yellow, Nymphalidae in green, Hesperidae in orange and Riodinidae in cyan.

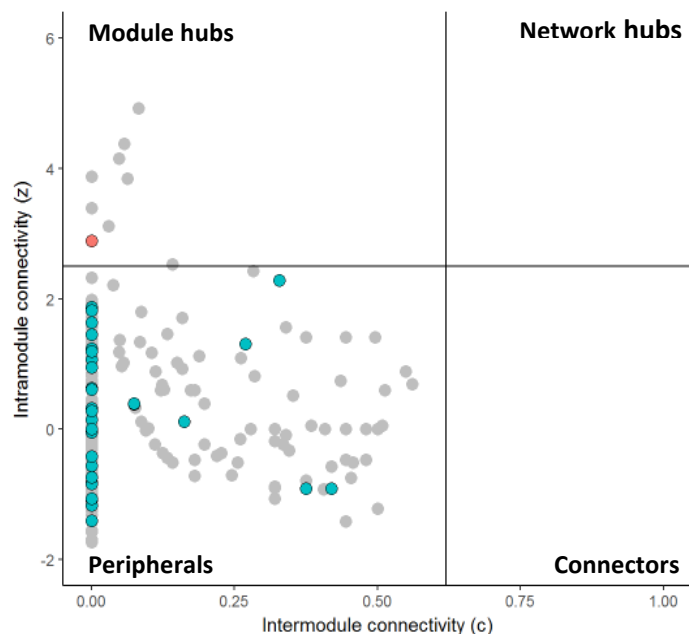


Figure 2.2: Role of each plant in the bipartite butterfly-hostplant network based on a modularity analysis. Solid lines correspond to the limits between each topological role, as defined by Olesen et al., (2007). Colored dots correspond to plants hosting protected butterfly species and grey dots represent other plant species.

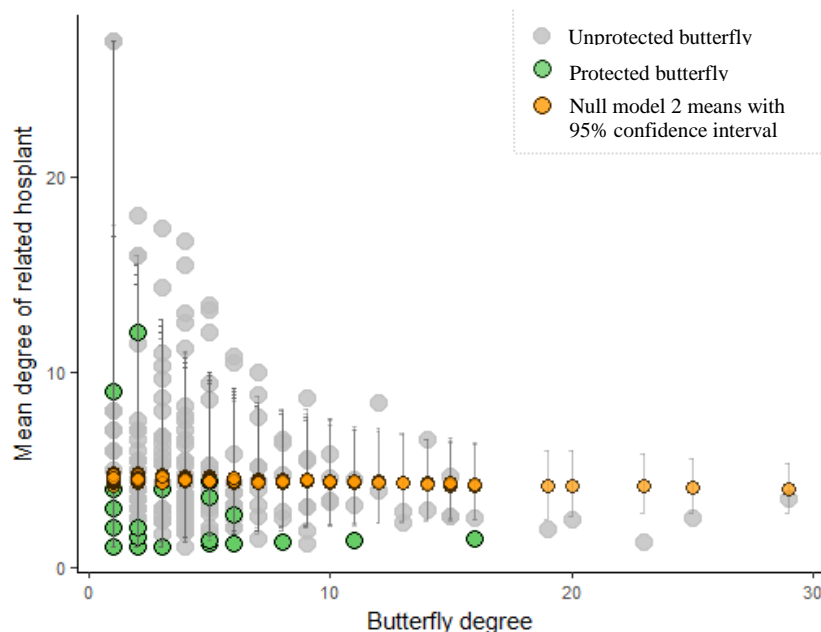


Figure 2.3: Distribution of butterfly species according to their degree in the bipartite network (k_b) and to the mean degree of their related hostplants (c_b). Green dots correspond to protected butterfly species ($n = 26$) and grey dots represent unprotected species ($n = 215$). Orange dots correspond to the mean position of butterfly species according to the null model 2, in which links are randomly distributed at fixed bipartite degree. Grey bars correspond to their 95% confidence intervals.

The studied network had a significant modular structure ($M = 0.852$) made of 39 modules (Suppl.S2.5). About 20 independent modules, containing between one to six butterfly species, were identified. They were mainly composed by butterflies with a low degree, which belonged to three families: Lycaenidae, Nymphalidae and Papilionidae (Fig.2.1). The two largest modules, including more than 10 species of butterflies, were completely independent of the rest of the network, which was structured into a set of interconnected modules. The modules mainly associated butterflies belonging to the same family (and usually to the same subfamily) and consuming taxonomically related plants. Most butterfly species (60%), regardless of their degree, were feeding on plants belonging to the same family. Hostplant preferences differed clearly among butterfly subfamilies. Some butterfly subfamilies consumed plants from many families but a low diversity of species within each family, while others were specialists from certain families and generalists within this family (Suppl.S2.6). Satyrinae (Nymphalidae) and Hesperinae (Hesperiidae) specifically interacted with the Poaceae plant family (as well as some Cyperaceae and Juncaceae) and were grouped in an independent module with high hostplant species richness (Suppl.S2.6; Suppl.S2.7). Pieridae also showed a strong specificity in terms of plant families and a privileged association with Brassicaceae, with species of Pierinae grouped in an independent module. Nymphalidae and Lycaenidae consumed the greatest diversity of plant families, although the majority of their hostplants belonged to the Fabaceae (Suppl.S2.6). Most Lycaeninae species were grouped in an independent module in which they interacted only with plants of the genus *Rumex* (Polygonaceae). Pyrginae (Hesperiidae) were strongly related to Rosaceae and Papilionidae mainly consumed Apiaceae, Rutaceae, Aristolochiaceae and Papaveraceae (Suppl.S2.7).

Among the 53 plant families present in the butterfly-plant network, three families centralized about half of the links with butterflies: Poaceae (23% of total links), Fabaceae (17%) and Rosaceae (10%). The modularity analysis showed that the majority of plant species (518 species) had a peripheral role in the structure of the network (Fig.2.2). Only nine species were considered as hubs, characterized by a central role in the cohesion of their module: *Bromus erectus*, *Colutea arborescens*, *Dorycnium pentaphyllum*, *Festuca ovina*, *Festuca rubra*, *Lotus corniculatus*, *Medicago sativa*, *Onobrychis supina*, *Potentilla neummanniana*. They corresponded to five Fabaceae, three Poaceae and one Rosaceae (Fig.2.2). They were all consumed by at least eight species of butterflies (with an average degree of 12 ± 6).

II.3.2. Correlation between distance matrices

The application of Mantel's tests revealed a significant and positive correlation between the distance matrix constructed from butterflies host range and the geographic, ecological and taxonomic distance matrices (Mantel tests, $P < 0.001$). However, despite their significance, correlations between butterfly host ranges and the similarity of species distribution and habitats remained low (Mantel tests, $r_s=0.06$ and $r_s=0.07$ respectively). Taxonomic relatedness of butterfly species showed the higher correlation with their host range (Mantel tests, $r_s=0.34$).

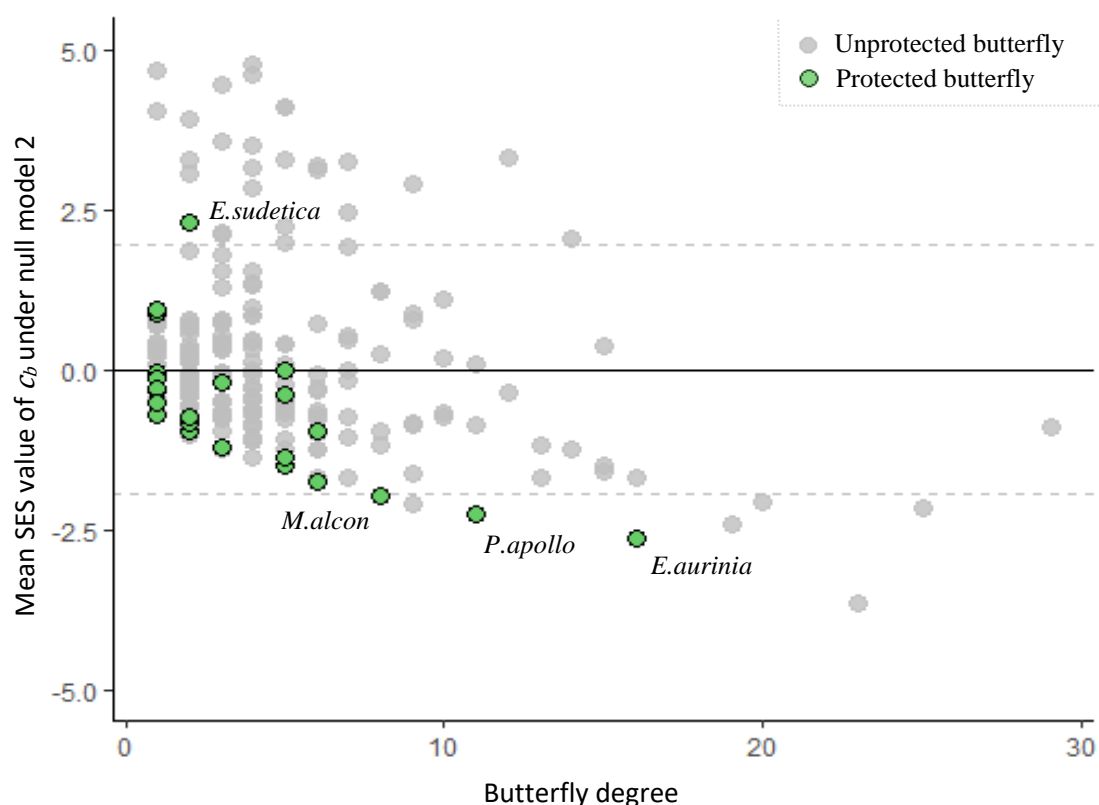


Figure 2.4 : Distribution of butterfly species according to their degree in the bipartite network (k_b) and to the standard effect size (SES) of the mean degree of their related hostplants (c_b) with respect to its value in null model 2. Both dotted lines indicate the significance of species deviation to the null value of c_b . Species located between these lines show no difference between the observed and null situation. Species located above the upper line interact with significantly more plants hosting a large number of butterflies than expected in random situation. Species located below the lower line interact with significantly more plants hosting a few butterflies than expected in random situation. Green dots correspond to protected butterfly species ($n = 26$) and grey dots represent unprotected species ($n = 215$). The name of protected species with a significant SES value is indicated.

II.3.3. Hostplant mean degree and projected network

A significant variation of the mean degree of related hostplant (c_b) was observed for butterflies, with some monophagous species grouped in independent modules ($c_b = 1$) and some species related to highly consumed plants ($c_b = 27$ for the maximum value, which mainly concerned Satyrinae). Most butterfly species interact with plants consumed by less than 10 species (on average $c_b = 4.86 \pm 3.96$). There was no significant correlation between the bipartite degree k_b of butterfly species and the mean number of butterflies feeding on their hostplants c_b (Spearman's correlation, $r_s=0.04$, $P > 0.05$; Fig.2.3). The variances of both parameters were significantly higher in the analyzed network than in the random situation simulated through null model 1 (random k_b ranged between 4 and 5, random c_b ranged between 3 and 3.15). Simulations based on the random model with fixed degree (null model 2) did not reveal a correlation between the degree k_b and the average degree of the hostplants c_b (Fig.2.3). The distribution of the butterfly degrees did not seem to impose a strong constraint on the structure of the network and the real c_b values showed a range of variation greater than expected according to this random model. However, the majority of butterfly species (75%) did not deviate significantly from the null value of c_b simulated by the null model 2 (Fig.2.4). Only 25 butterfly species had more hostplants heavily consumed than expected by chance, and 8 species more specific hostplants than expected by chance, given their bipartite degree. Eighteen species of butterflies were not linked to any other species across their projected network (Fig.2.5). The projected degree (l_b) of other species ranged from one to 45 (the highest values were for Satyrinae and Hesperinae), with an average of 10.61 ± 10.97 . The average dependence of the indirect partners of these butterflies in the projected network (D_b) ranged from one (high dependence the same hostplants) to 25 (low dependence to the shared hostplants), with an average of 7.66 ± 3.98 (Fig.2.5). There was no significant correlation between the projected degree of butterfly species and the average dependence of their indirect partners D_b (Spearman's correlation, $r_s=0.04$, $P > 0.05$).

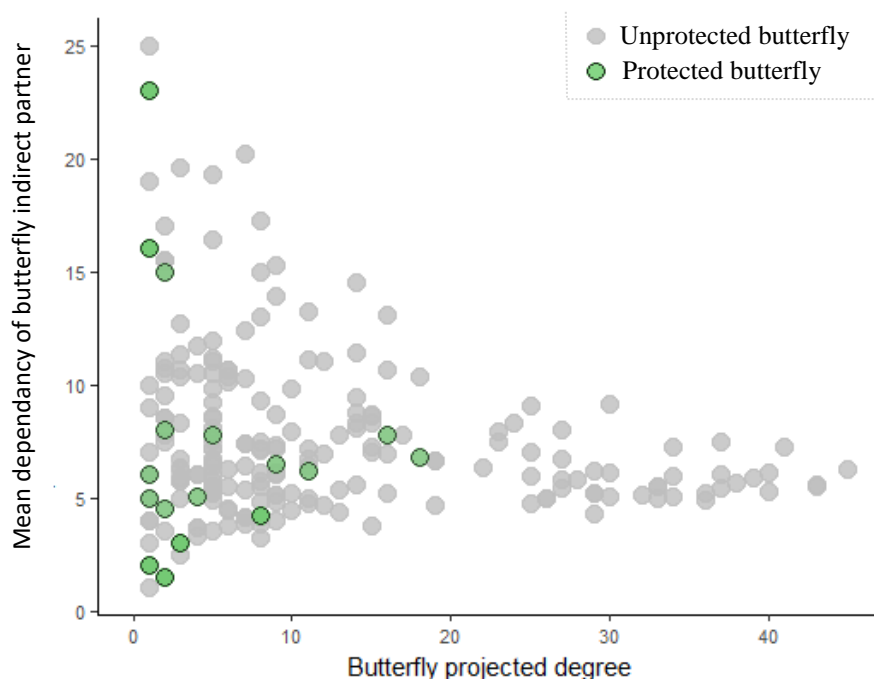


Figure 2.5 : Distribution of butterfly species according to their degree in the projected network (l_b) and to the mean dependency of their indirect partners (D_b). Green dots correspond to protected butterfly species ($n = 26$) and grey dots represent unprotected species ($n = 215$).

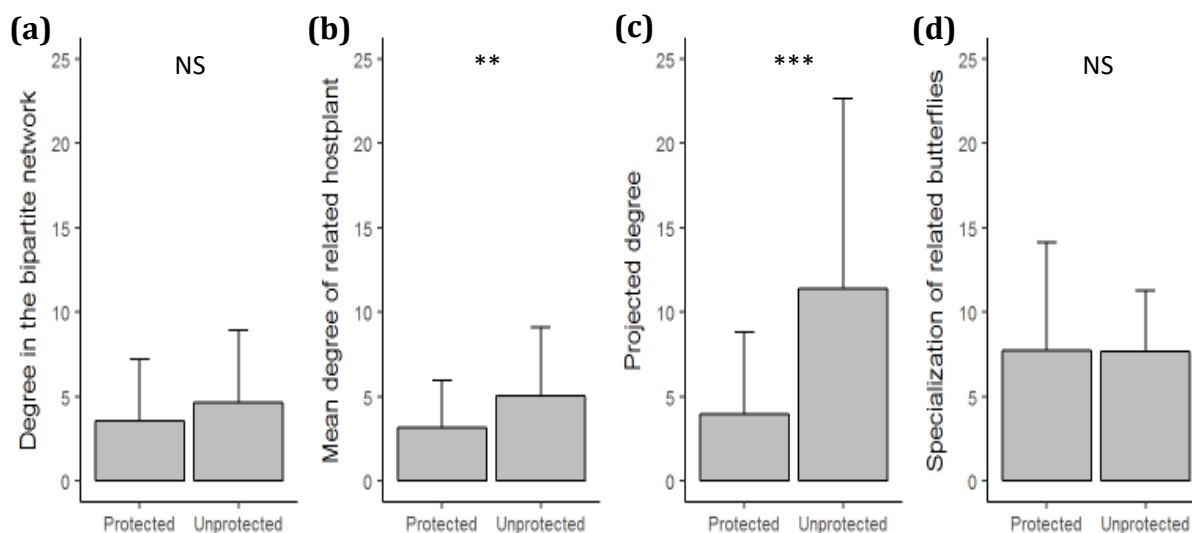


Figure 2.6 : Mean values (\pm SE) of **(a)** degree in the bipartite network (k_b), **(b)** mean degree of related hostplant (c_b), **(c)** projected degree (l_b) and **(d)** specialization of related butterflies (D_b), compared between protected ($n = 26$) and unprotected ($n = 215$) butterflies. Asterisks indicates significant differences between both groups (***: $P < 0.001$, *: $P < 0.05$, NS: $P > 0.05$, Wilcoxon's signed-rank tests).

II.3.4. Conservation issues and protected species

The comparison of the degree of species in the bipartite network according to their IUCN category revealed a significant link between species specialization and their risk of extinction. Species classified as Least Concern showed a significantly higher mean degree (4.98 ± 4.45) to Near Threatened species (2.23 ± 1.68) and Threatened species (2.47 ± 2.32) (Kruskal-Wallis test, $P < 0.01$).

Twenty-six protected butterfly species were included in the butterfly-plant interaction network. They interacted with 77 plant species. Almost all these plants (99%) had a peripheral role in the network (Fig.2.2). Protected butterflies interacted indirectly with a total of 54 butterfly species across the projected network (which we called “indirectly protected”). Protected species had a relatively low bipartite degree (k_p) (3.58 ± 3.62) but did not show a significant difference with the rest of the network (4.65 ± 4.31) (Wilcoxon test, $P > 0.05$; Fig.2.6). The mean degree of their hostplants (c_p) was significantly lower (3.15 ± 2.78) than the other butterflies in the network (5.08 ± 4.04) (Wilcoxon test, $P < 0.01$; Fig.2.6) and three species (*Euphydryas aurinia*, *Maculinea alcon* and *Parnassius apollo*) had a value of c_p significantly lower than expected by chance (Fig.2.4). The correlation between the bipartite degree of protected butterflies and the average degree of their host plants was significant and negative (Spearman’s correlation, $r_s = -0.39$, $P < 0.05$). This revealed a tendency for less specialized protected species to share their resources with a limited number of butterflies (Fig.2.3). The projected degree of protected butterflies was also significantly lower than that of unprotected ones (Wilcoxon test, $P < 0.001$; Fig.2.6), with an average of $3.96 (\pm 4.85)$ and $11.41 (\pm 11.24)$ respectively. The average dependence of the indirect partners of these protected butterflies in the projected network (D_b) (7.74 ± 6.40) was very close to the average of the complete network, and did not show a significant difference with unprotected species (7.64 ± 3.66) (Wilcoxon test, $P > 0.05$; Fig.2.6). The few species interacting indirectly with butterflies’ dependent of the same hostplants (*i.e.* with a low D_b value) (Fig.2.5) were in fact linked together within independent modules in the projected network (*e.g.* *Lycaena helle* and *Boloria eunomia*; *Maculinea teleius* and *Maculinea nausithous*).

Table 2.1: Vulnerability of the studied butterfly species according to their coverage by the current national protection lists. 'Directly protected' species are included on these lists, 'Indirectly protected' species are indirectly linked to protected butterflies through a shared host plant, 'Unprotected' species are neither listed nor linked to protected species. Butterfly vulnerability corresponds to their IUCN status on the French red list ("Threatened" corresponds to categories VU, EN and CR).

IUCN categories	Directly protected	Indirectly protected	Unprotected
Least Concern	13	52	143
Near Threatened	6	0	11
Threatened	7	1	8

The coverage of butterfly species by the current protection lists varied significantly depending on their IUCN categories in France (Fisher test, $P < 0.01$; Table 2.1). Half of the directly protected species were Near Threatened and Threatened. The high majority of other species in these two categories were unprotected. The potentially “indirectly protected” species were for 98% Least Concern species.

II.4. Discussion

In this study, we constructed the interaction network connecting French butterflies to their host plants, from a large original and verified dataset. This first analysis of these relations at the scale of France allowed describing the specific structure of this network, likely to have an influence on the recent dynamics of the species, and to identify the main explanatory factors of this structure. Taxonomic relationships between butterflies appeared to have a significant influence on their tendency to share a resource, and the most closely related species generally have a close relationship with related plants. Due to this conservatism, which is expressed by a modular structure, the majority of plants do not constitute potentially key resources for large butterfly assemblages. This structure was put in perspective with the vulnerability and protection status of butterfly species in order to contribute to the development of a more systemic view of butterfly conservation. From this work, we showed the higher vulnerability of the most specialized butterflies as compared to generalists and some potential limits of the current protection lists.

II.4.1. Butterfly diet constrained by taxonomic distances

The analysis of the association matrix revealed a structuration of the butterflies and their hostplants in a highly modular network (Fig.2.1), significantly different from a random situation (null model 1). Patterns of indirect interactions between butterflies through a sharing of trophic resources are therefore particularly constrained, leading to the existence of several entirely independent modules. This highly modular structure seems to be a common trend of antagonistic networks, especially in the case of plant-herbivore insect interactions (Thébaud & Fontaine, 2010). The existence of modules has been related to the high proportion of specialized insect and interaction range boundaries that determine modules are mainly imposed by the phylogeny of hostplants (Weiblen *et al.*, 2006; Cagnolo *et al.*, 2011). This type of conservatism also seems to be at the base of the structure of the analyzed network. Identified modules were mainly composed by related species (genus, subfamilies, families), both on the side of plants and that of butterflies. The important correlation between the overlap of butterfly host ranges and their taxonomic proximity, as evidenced by the comparison of distance matrices, confirmed these observations. This type of congruence between the phylogeny of butterflies and plants has already been described through a review of several datasets at the global scale (Ferrer-Paris *et al.*, 2013).

This structure appears strongly conserved among different regions for which more complete butterfly-hostplant matrices are available, with a great similarity of the patterns of associations (Munguira *et al.*, 2009). The small proportion of plants consumed by butterflies at the scale of a territory (between 20 and 30% of plant families; Ferrer-Paris *et al.*, 2013) and the significant butterfly richness associated with Fabaceae, Poaceae and Rosaceae seem to be constants whatever the explore areas worldwide (Ackery, 1991; Tiple *et al.*, 2011; Muto-Fujita *et al.*, 2017). The main modules, *i.e.* Satyrinae / Hesperinae with Poaceae, Pierinae with Brassicaceae, Lycaenidae with Fabaceae are also conserved (Munguira *et al.*, 2009; Ferrer-Paris *et al.*, 2013; Muto-Fujita *et al.*, 2017). Such modules contribute to spatially segregate butterflies' families in different habitats; for example, with Satyrinae / Hesperinae are mainly present in open areas dominated by grasses (Poaceae). These patterns reveal an evolutionary signal probably constrained by coevolution processes, related to an adaptation of butterflies to the chemical mediation (defenses, pollinator attraction) of plants (Muto Fujita *et al.*, 2017). The specificity of the chemical compounds used by different plant taxa could be a more conservative trait than their phylogeny (Wahlberg, 2001; Endara *et al.*, 2017). The hypothesis

of radiation events of some butterfly lineages following a host-shift, allowing the exploitation of a new group of host plants, has been advanced in order to describe the diversification of the butterflies, especially at the scale temperate regions (Fordyce, 2010; Condamine *et al.*, 2012).

II.4.2. Butterflies vulnerability and network metrics

Apart from some common Poaceae (*e.g.* *Bromus erectus*, *Festuca ovina*, *Festuca rubra*), which may host a wide variety of Satyrinae, the majority of host plants did not show a central position within the network or even within a module (Fig.2.2). Shifts in plant distribution patterns would not lead to a significant deconstruction of the butterfly communities. Indeed, the modular structure of antagonistic networks is generally considered as a characteristic favorable to a higher robustness (Thébaud & Fontaine, 2010). In most cases, it leads to a reduction of the propagation of negative cascades effects throughout the network in the case of local extinctions. The simulation of extinction cascades on a butterfly-plant dataset, taking into account the level of plant abundance, showed a significant delay between the decrease in plant richness and that of the butterfly communities associated with them (Pearse & Altermatt, 2013). The extinction of a plant may only affect a small proportion of the network, with a greater or lesser impact depending on the degree of specialization of the indirect butterfly partners.

More, the study of the butterfly-hostplant network did not reveal any significant correlation between the degree of butterfly species and the average degree of their hostplants, and this last value showed few significant deviations as compared to a random situation (null model 2; Fig.2.3). The most generalist butterflies feed on many plants characterized by a low k_p degree, with significant deviation to null situation for some of them (*e.g.* *Euphydryas aurinia*; Fig.2.4). Butterflies with the highest degree k_b values in the bipartite network (*e.g.* *Callophrys rubi*, *Papilio machaon*, *Pieris brassicae*, *Pieris rapae*) accumulate a large proportion of hostplants that are exclusive to them. In contrast, the most specialized butterflies did not show a strong tendency to be isolated in individual modules and some of them feed on more attractive plants (*i.e.* high value of c_b) than expected by chance (*e.g.* *Hipparchia fagi*; Fig.2.4). Therefore, these specialist species do not seem to be linked to plants free from any potential competitor within the butterfly communities. These patterns are in agreement with recent studies concluding in the little influence of interspecific competition in the specialization process and the structuring of butterfly-plant networks (Nakadai *et al.*, 2017).

However, the disappearance of certain plants in the network may have a high impact on the most specialized butterflies which depend on it. Several species of the studied network are monophagous and some are isolated within independent modules. Analyses thus showed a significant link between the level of specificity (*i.e.* low degree k_b) and the risk of extinction of butterflies. Constrained by the very narrow range of resources required for their development, specialized species will have low capacity to respond to environmental changes and will be particularly vulnerable to landscape structure alteration (Komonen *et al.*, 2004; Stefanescu *et al.*, 2011). In addition to the direct extinction that may result from the degradation of hostplant populations (Pearse & Altermatt, 2013), the decrease in their density or the mismatch between their phenology and that of butterflies (for example under climate changes) could have important consequences for the survival of the most specialized butterfly species, in particular within fragmented landscapes (Schweiger *et al.*, 2008; Brunbjerg *et al.*, 2017; Guardiola *et al.*, 2017). In addition, some characteristics of the hostplants may condition the response of the butterfly species, in particular by constraining their phenology, the speed of their development or their voltinism (Dennis *et al.*, 2004; Cizek *et al.*, 2006; Altermatt, 2010). Monophagous butterflies, which present *a priori* less possibility of range or host shift, could therefore be strongly constrained by these characteristics.

II.4.3. Patterns of potential indirect protection

The construction of the projected network provided an insight of indirect interactions that could link several species of butterflies sharing the same host plants. It has been used as a tool to investigate the potential role of umbrella species which could be associated with the species currently protected in France (26 protected butterflies in the network). Since these lists require the protection of the habitat and resources needed to complete the life cycle of the target species, this work aimed at estimating the indirect benefits of protecting hostplants for the conservation of key issues associated with butterflies. Most of the protected species showed a low k_b degree, indicating a tendency for specialization. In contrast, hostplants on which they feed were almost exclusively peripheral nodes of the network (Fig.2.2). This induces a weak sharing of these plants with other interacting butterflies, and was reflected by a low mean degree of partners (c_b) for most of them (Fig.2.3). The average value of this parameter was significantly lower than in the rest of the network (Fig.2.6) and, although few protected species showed a significant deviation from the null model 2, about 75% of them tended to

feed on less attractive plants than expected by chance (Fig.2.4). As a result, the protected species showed very little potential indirect interactions with other butterflies in the network (*i.e.* low value of lb ; Fig.2.6). The protection of hostplants as resources for the maintenance of protected butterfly species is unlikely to favor a great diversity of butterflies.

In addition, the few butterflies indirectly linked to the protected species did not show a strong dependence on shared hostplants (*i.e.* low value of D_b ; Fig.2.6). In general, they had a host range close to the population average, thus including several species of hostplants on which they can theoretically be distributed. The study of the status of these “indirectly protected” butterflies revealed that the majority of them were not concerned by a risk of extinction (Table 2.1). Most endangered species were not covered by the current statuses, whether directly or through indirect potential protection. This pattern could allow to deduce (1) a low benefit from the current protection lists for butterflies representing a real conservation issue and which would not be directly covered, and (2) a weak influence of the sharing of the same resource on the extinction risk of two distinct butterfly species. In a perspective limited to their biotic niche, the vulnerability of butterfly species could in this case be mainly dependant on the specificity of their caterpillars for one or a few host plants rather than by the specific characteristics of these plants.

II.4.4. Limits of the analyzed datas

Given the nature of the data used for the construction of the studied association matrix, it is important to make some considerations about their quality. Interaction networks built from literature reviews can indeed be seen as a summary of "potential" interactions on a given scale, derived from punctual observations in time and space and allowing to deduce the possibility for two species to interact when they are in co-occurrence (Delmas *et al.*, 2017). Since the interactions synthesized in our work cover a large geographical area, it is possible that one species of butterfly does not meet all the referenced hostplants across its entire range. Some hostplants may have a more restricted distribution and may be only consumed by a few populations of the butterfly species following local adaptation (Srinivasan *et al.*, 2007; Meister *et al.*, 2015). In addition, our dataset does not take into account the interaction strengths between butterflies and their different hostplants, limiting the analysis to the topological structure of the network. Given these limits, indirect sharing of resources among butterflies must therefore be considered as a potentiality related to an overlap of theoretical

niches, limited by the hypothesis of a temporal and spatial co-occurrence of the involved species (Pocock *et al.*, 2012).

The nature of the analyzed data may also lead to some biases in favor of an underestimation of hostplant species, related to the non-detection of certain interactions because of heterogeneous sampling effort (Gibson *et al.*, 2011; Costa *et al.*, 2016). On the other hand, given the floristic diversity in the studied area and the difficulty of identifying some groups, it is possible that a part of the interactions results from misidentification of a plant by an entomologist (*i.e.* false presence). It seems particularly important to take this potential bias into consideration when analyzing the Stayrinae-Poaceae module, in which some data may be related to inaccurate identification of plants. However, predictive models based on this type of network have shown a high robustness to these both sources of bias (Pearse & Altermatt, 2015). Given the diversity of sources and the period covered, our dataset can therefore be considered as a comprehensive basis to describe the general patterns of association despite potential biases.

II.4.5. Contribution to integrative butterfly conservation

Network models help to map the relationship of butterflies with host plants, and then to document the component of biodiversity devoted to the interactions among species. As such, network models may be a useful tool for assessing one component of herbivore extinction risk (Pearse & Altermatt, 2013). This approach centered on the biotic niche of the species allows identifying the component of species vulnerability linked solely to its host range and to the sharing of these hostplants. The projected network also constitutes an efficient tool to explore potential indirect conservation, in a perspective of identifying "umbrella" species in the context of resources allocated to biodiversity conservation (New, 1997). Species-specific characteristics, related to their location in this bipartite network, need to be integrated into a more holistic conservation strategy, to avoid too much simplification of the processes conditioning their vulnerability.

Hostplants are only one component of species' habitat, and their presence alone is not enough to ensure the presence and abundance of butterfly populations associated with them. Other essential resources compose species micro-habitats and filter their occupancy (Dennis, 2010). This is expressed by the often much wider distribution of the hostplant as compared to

that of its consumer (Quinn *et al.*, 1998). These other factors, for example related to landscape structure or connectivity, often have a more significant, or at least more visible, influence on species decline than the regression of host plant populations (Pearse & Altermatt, 2013). In particular, the influence of the specificity of the adult diet on the status of species is increasingly explored. Although the specificity of the caterpillar diet constitutes the most restrictive variable (Altermatt & Pearse, 2011), specialist species in the larval stage are often also specialists in the adult state (Hardy *et al.*, 2007); this double food dependence makes their conservation challenging. Since the nectariferous plants required for adults can be different from caterpillars' hostplant and influence their response to habitat changes (Tudor *et al.*, 2004), the processes that condition the risk of local extinction of populations of a species are probably more complex and requires the crossing of several layers of specificity (Astegiano *et al.*, 2017).

Nevertheless, interaction networks are essential tools for better prediction of potential biodiversity losses and potential homogenization in the face of large-scale reshaping of natural habitats. They allow for example the demonstration of cascades of potential extinctions or the destructuring of the links between species which underlie the diversity of the ecosystems, which can occur well before any decline in species richness (Dainese *et al.*, 2017). The synthesis of interaction data and the first analysis of the butterfly-hostplant bipartite network conducted in this study contribute to the improvement of the knowledge of the resources that condition the presence of butterflies and how they affect their conservation status. This knowledge is an important basis for the formulation of effective conservation management programs (Dennis *et al.*, 2008).

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Supplementary materials 2

Supplementary material S2.1: List of 241 butterfly species included in the butterfly-hostplant interaction network.

(À consulter dans la partie “Annexes” du manuscrit de thèse).

Supplementary material S2.2: List of 527 plant species included in the butterfly-hostplant interaction network.

(À consulter dans la partie “Annexes” du manuscrit de thèse).

Supplementary material S2.3: Illustration of the estimation of the index D.

Supplementary material S2.4: Histogram of the distribution of **(a)** butterflies and **(b)** plants degrees within the bipartite butterfly-hostplant interaction network.

Supplementary material S2.5: Graphical representation of modules in the bipartite butterfly-hostplants network.

Supplementary material S2.6: Specialization patterns of butterfly subfamilies composing the analyzed butterfly-hostplant interaction network.

Supplementary material S2.7: Graphical representation of the bipartite butterfly families-hostplants families network.

Supplementary material S2.1: Ce supplément volumineux n'étant pas indispensable à la compréhension du chapitre a été déplacé dans la partie « Annexes » du manuscrit de thèse par soucis de clarté.

List of 241 butterfly species included in the butterfly-hostplant interaction network. The higher taxonomic levels (family and subfamily) are shown on the basis of the most recent revision. The main breeding habitat and conservation status (protection, category on the French red list (LR), range trends, significance of decline) of each species are summarized. The degree (k), the projected degree (l) and the average degree of the partners (c) were calculated for each species. Each species was assigned to one of the modules (Mod) structuring the network.

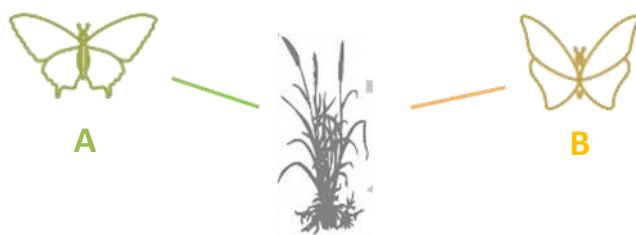
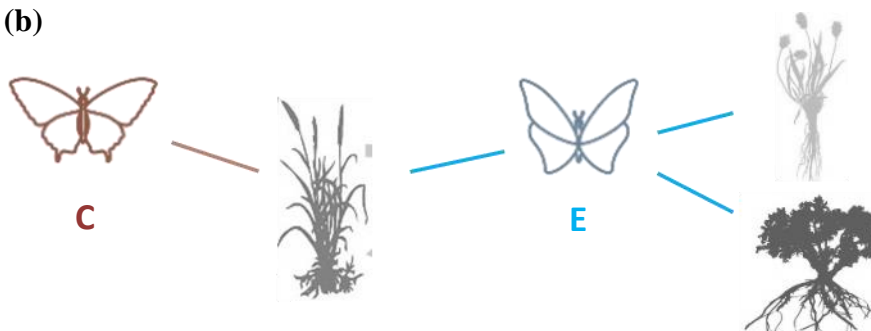
Supplementary material S2.2: Ce supplément volumineux n'étant pas indispensable à la compréhension du chapitre a été déplacé dans la partie « Annexes » du manuscrit de thèse par soucis de clarté.

List of 527 plant species included in the butterfly-hostplant interaction network. The higher taxonomic levels (order, family, and subfamily) are shown on the basis of the most recent revision. The degree (k), the projected degree (l) and the average degree of the partners (c) were calculated for each species. Each species was assigned to one of the modules structuring the network.

Supplementary material S2.3: Illustration of the estimation of the index D .

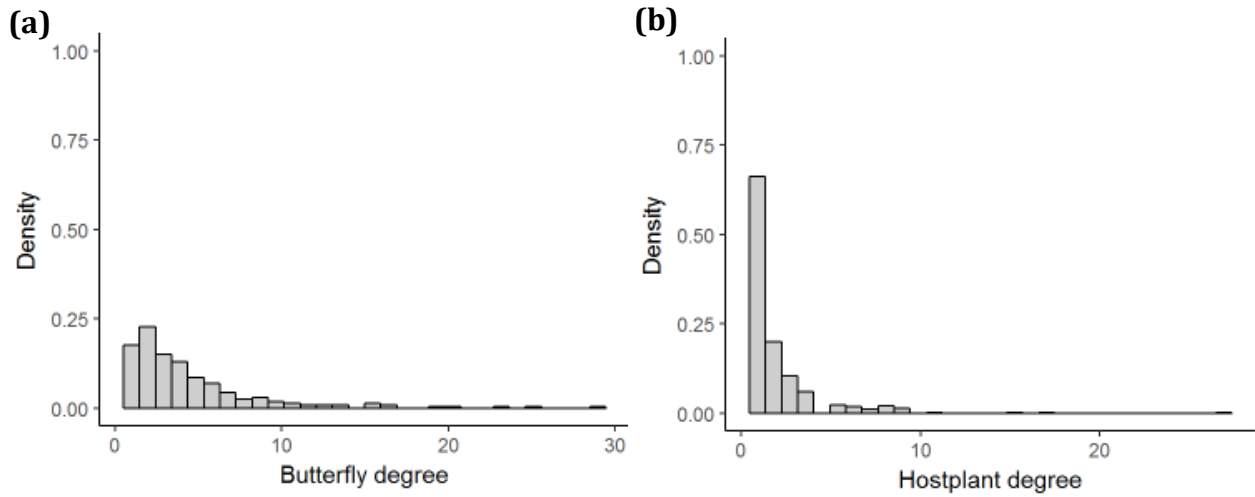
The index D , developed in the present study, allowing to index (D) allowing to quantify the level of dependence of the partners of a butterfly species in the projected network to the hostplants they shared with this species. The value of D of a butterfly was calculated by estimating the average degree of butterfly species related to each of its hostplants. The value of D_b for a butterfly b is given by the sum of the average degree of each of its host plants in the bipartite network (c), divided by its own degree in the bipartite network (k_b).

In the example below **(a)**, butterfly A shares its single hostplant with a butterfly B. This butterfly B has no other hostplant. The value of the index D for butterfly A will therefore be low, indicating that indirect partners (here B) is a specialist of the same resource. In example **(b)**, the butterfly C shares its single hostplant with the butterfly E, which also consume two other hostplants. The value of the index D for C will therefore be higher than that of A, indicating that its indirect partners (here E) have a lower degree of specialization on its hostplants (E is not monophagous and can consume two other plants).

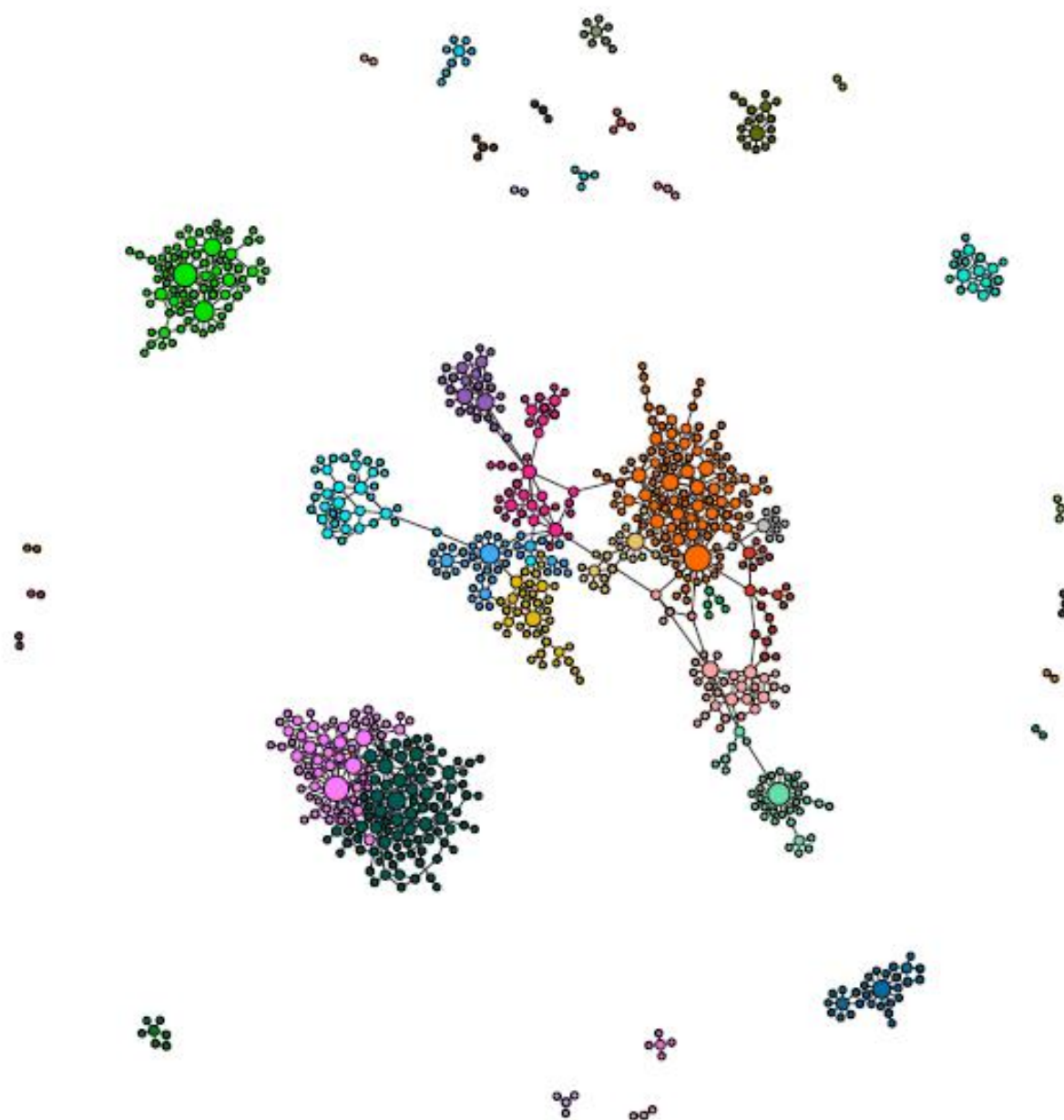
(a)**(b)**

Plant designs taken from Levine *et al.*, 2017. Butterfly designs created by Alena Artemova for the Noun Project (<https://thenounproject.com>).

Supplementary material S2.4: Histogram of the distribution of **(a)** butterflies and **(b)** plants degrees within the bipartite butterfly-hostplant interaction network.



Supplementary material S2.5: Graphical representation of modules in the bipartite butterfly-hostplants network based on the spatialization algorithm *Force Atlas 2* (Jacomy *et al.*, 2014) implemented in the software GEPHI (Bastian *et al.*, 2009). Circles correspond to species of butterflies and hostplants and their size is proportional to species' degrees. Different colors correspond to the different modules identified through the software NETCARTO (Guimera & Amaral, 2005).



Supplementary material S2.6: Specialization patterns of butterfly subfamilies composing the analyzed butterfly-hostplant interaction network. The number of butterfly species in each subfamily composing the network (Recorded Richness) was compared with their species richness in France (French richness). The number of orders, families and hostplant species which interacted with each butterfly subfamily was summarized.

Butterfly subfamilies	French richness	Recorded richness	Number of associated hostplant orders	Number of associated hostplant families	Number of associated hostplant species
Apaturinae	2	2	2	2	9
Charaxinae	1	1	1	1	2
Coliadinae	7	7	3	3	24
Danainae	2	1	1	1	1
Dismorphiinae	4	3	1	1	8
Heliconiinae	19	19	5	6	55
Hesperiinae	6	6	1	2	42
Heteropterinae	2	2	1	1	6
Libytheinae	1	1	1	2	2
Limenitinae	3	3	2	2	8
Lycaeninae	7	7	1	1	31
Melitaeinae	15	14	5	11	71
Nymphalinae	12	10	7	13	56
Papilioninae	5	5	3	3	48
Parnassinae	5	5	3	4	23
Pierinae	15	15	4	6	121
Polyommatainae	46	44	17	21	189
Pyrginae	22	22	4	5	87
Riodininae	1	1	1	1	3
Satyrinae	73	61	1	3	230
Theclinae	12	12	8	10	78

Supplementary material S2.7: Graphical representation of the bipartite butterfly families-hostplants families network based on the spatialization algorithm *Force Atlas 2* (Jacomy *et al.*, 2014) implemented in the software GEPHI (Bastian *et al.*, 2009). Circles correspond to families of butterflies and hostplants and their size is proportional to total families' degrees. The width of the links is proportional to the number of species pairs of the two related families interacting in the butterfly-hostplant network. Green circles represent hostplant families and orange circles butterfly families.



Chapitre 3

Multi-species occupancy model reveals the poor completeness of entomological surveys in environmental impact assessment

Ce **troisième chapitre** se place directement dans une perspective de recherche appliquée. Il vise à répondre à une demande croissante de données permettant de quantifier la représentativité des inventaires réalisés dans le cadre des études d'impacts sur l'environnement. Etant donné la limitation financière de la pression d'échantillonnage souvent mise en place dans le cadre de ces inventaires et les biais liés à l'imperfection de la détectabilité propre aux données biologiques, cette quantification permettrait d'évaluer la qualité de la mesure des impacts d'un projet et la pertinence de la séquence ERC programmée par l'aménageur.

Afin de répondre à cette problématique des inventaires entomologiques ont été réalisés sur plusieurs sites méditerranéens, sur la base de plans d'échantillonnage incluant toutes les contraintes auxquelles sont soumis les bureaux d'études en environnement lors de la construction de leurs offres (compétitivité, enjeux ciblés, potentialités d'accueil du site, ...). Les prospections de terrain ont ainsi été ciblées non seulement sur la recherche des Rhopalocères et des Odonates, mais ont également inclus un inventaire des espèces d'Orthoptères et de cigales afin de correspondre aux pratiques courantes des bureaux d'études dans le sud de la France.

La richesse spécifique détectée sur chaque site et la distribution observée pour chacune des espèces ont été comparées à des valeurs potentielles, estimées à travers des modèles statistiques permettant de corriger les biais liés à l'hétérogénéité de la détection. Ces modèles sont particulièrement pertinents pour extraire le maximum d'informations de matrices d'occurrence multi-espèces incluant plusieurs espèces rares et offrent la possibilité d'intégrer des covariables environnementales et celles propres aux conditions de réalisation de ces relevés susceptibles d'influencer la qualité des inventaires.

À terme, les résultats issus de cette étude sont susceptibles de permettre le développement d'outils méthodologiques et commerciaux permettant d'améliorer la qualité des plans d'échantillonnage en condition d'étude d'impact, voire même d'être par la suite présentés aux services instructeurs en vue d'harmoniser les pratiques des bureaux d'études à l'échelle nationale.

Multi-species occupancy model reveals the poor completeness of entomological surveys in environmental impact assessment

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Abstract

1. Imperfect species detection is likely to induce serious biases in conventional estimators of species distributions and species richness. Such biases are a major issue in the case of environmental impact assessment (EIA) as failure to detect a threatened species actually present on a site may lead to direct destruction of its local populations.
2. We aimed to obtain an initial evaluation of the completeness of the entomological surveys carried out under EIA, both in terms of total species richness and of threatened species detection. We conducted insect surveys at 20 sites located in the French Mediterranean area. They were targeted on four groups of insects (butterflies, dragonflies, grasshoppers and cicadas) and the sampling period was here doubled for each site in order to evaluate the link between the completeness of these results and the sampling effort. Collected data were analyzed under a multi-species occupancy models (MSOM), allowing estimating the potential richness of the community and the occurrence probability of each observed species, by taking into account biases related to the heterogeneity of their detection.
3. The results showed a significant discrepancy between the estimated species richness and the detected richness. Almost 50% of the potential richness remained undetected under classical condition of EIA and species occurring on a site had on average less than 30% of chance to be detected. Sampling coverage was dependent on the number of visits conducted on the site and was variable according to the conservation status of species. Survey conditions had a significant influence on species-specific detection probability.
4. Our results emphasize the need for field protocols that accommodate estimation of detection error when conduction entomological surveys in EIA. The significance of biases related to imperfect detection has demonstrated the importance of this type of scoping study for a better measurement of the risks linked to the project development. Such information could help the regulator to advocate minimum survey requirements guaranteeing the quality of EIA studies. The number of visit, their spread over the year and the time at which they will be carried out will then constitute important parameters for the establishment of cost-efficient sampling design which provide reliable knowledge.

Key words: Environmental impact assessment, imperfect detection, survey effort, sampling coverage, species richness, Mediterranean, hierarchical model.

III.1. Introduction

Species occurrence is a primary biodiversity datum of central importance in ecology and wildlife management (MacKenzie, 2005a; Soberon *et al.*, 2007). Depending on the scale at which they are collected, occurrence data can be aggregated into several metrics, comparable through time and space to access basic information about the response of species to environmental changes (Yoccoz *et al.*, 2001; Powney & Isaac, 2015). The count of the number of occurring species on the same site, namely species richness, is for instance one of the most widely used metric of biodiversity (Gotelli & Colwell, 2011). The presence of a same species within several sampling units informs about its distribution (Royle & Nichols, 2003; Gaston & He, 2011; Bird *et al.*, 2014). These metrics are widely used for a range of taxa to monitor some target species, to highlight their response to perturbations or to management actions (Tyre *et al.*, 2003; MacKenzie, 2005b). It is also on the basis of these measures that the main conservation issues within a site of interest or a region could be identified, and that operational measures could be constructed to reduce and mitigate the impact of the alteration of their habitat (Gotelli & Colwell 2001; Johnson *et al.*, 2004; DeWan & Zipkin, 2010).

In the vast majority of cases, a complete survey on a site is impossible, especially because of the limited human investment and financial cost necessary to reach such completeness (Kéry & Plattner, 2007; Kellner & Swihart, 2014). Occurrence are typically not observed perfectly and these data will be subject to biases related to "false absence" events, *i.e.* a species may be undetected in a survey even when it is actually present within a site (MacKenzie *et al.*, 2006; Miller *et al.*, 2011). Failure to take into account the imperfection and variability of species detection will lead to confusion between true absences (reflecting actual species occurrence) and false absences leading to artificially zero-inflated data sets (Tyre *et al.*, 2003; Martin *et al.*, 2005). Because some species could be particularly cryptic or rare the probability of detection could show a wide heterogeneity in a community (Bouligner *et al.*, 1998; Iknayan *et al.*, 2014), which could lead to bias in the estimation of species richness (Chao & Jost, 2012). In addition, the probability of detecting a species is rarely constant in time and space (Yoccoz *et al.*, 2001; Moore *et al.*, 2014). It can widely vary with site-specific environmental conditions (Iknayan *et al.*, 2014), with observer experience (Nichols *et al.*, 2000; Fitzpatrick *et al.*, 2009) or depending on the conditions under which field session are conducted (Chen *et al.*, 2009; Petitot *et al.*, 2014). Biological and ecological characteristics of

different species (life history traits, life cycle, period of activity...) (Rovero *et al.*, 2014; Potoka *et al.*, 2016)

These biases could significantly affect the quality of the results of studies based on occurrence data, such as species distribution or habitat modeling (Gu & Swihart, 2004; Lahoz-Monfort *et al.*, 2014; Guillera-Arroita, 2017), identification of the processes that govern meta-populations dynamics (*e.g.* colonization, extinction or dispersal; Moilanen, 2002), monitoring of rare or vulnerable species (Chadès *et al.*, 2008; Kéry & Schmidt, 2008; DeWan & Zipkin, 2010), planning management measures for invasive (Hauser & McCarthy, 2009; Regan *et al.*, 2011) or endangered species (Wintle *et al.*, 2004 ; MacKenzie 2005a). Hence, the importance of understanding and accounting for imperfect detection extends to major decision-making bodies (MacKenzie *et al.*, 2006; Cruickshank *et al.*, 2016).

This is particularly crucial in the case for environmental impact assessment (EIA) procedures, which use this type of occurrence and richness data to inform decision makers about the environmental consequences of project developments and provide elements allowing to avoid, reduce and mitigate for adverse impacts (Jay *et al.*, 2007). The main purpose of the EIA was to determine whether development can be allowed to proceed at a site despite the risk of adversely affecting one or several threatened species that might occupy the site (Ritter *et al.*, 2017). Failure to detect a species actually present (or underestimation of its presence) on a site may lead to a decision favorable to the project and thus to direct destruction of its local populations, which may have a significant negative impact on many endangered species (Garrard *et al.*, 2015). The lack of quality or completeness of data from EIA may therefore have a significant cost in terms of conservation (Guillera-Arroita *et al.*, 2015). It reveals the need for methodological framework developments by the regulator in order to set a minimum survey effort or sampling conditions (Garrard *et al.*, 2008; Wintle *et al.*, 2012). The development of cost-efficient sampling plans for EIAs, currently mainly focused on optimizing the competitiveness of structures in charge of the surveys, requires the respect of a trade-off between the costs of the surveys and the quality of the results (Moore *et al.*, 2014). However, the quality of the results of the current practice of EIA remains poorly evaluated in terms of sampling coverage and level of detection bias.

Many methods have been developed in recent decades to deal with imperfect detection when estimating species richness or species distribution (Mazerolle *et al.*, 2007; Bailey *et al.*,

2014). For instance, the methods based on accumulation curves of incidence data as a function of sampling effort were developed to obtain an unbiased estimate of richness (Soberon & Llorente, 1993; Gotelli & Colwell, 2011) or to compare several sites that have been surveyed under different efforts (Colwell *et al.*, 2012; Hsieh *et al.*, 2016). However, none of these methods consider the direct effect of detection biases and of the heterogeneity of detection probabilities between species on the estimation of species richness (Bouligner *et al.*, 1998; Kéry & Royle, 2008; Iknayan *et al.*, 2014).

Site-occupancy models, initially developed to address single-species issues, have known increasing success since the beginning of the century (MacKenzie *et al.*, 2006; Bailey *et al.*, 2014). From a history of detection of a species collected through repeated visits to several sites, these models allow estimating species occurrence while accounting for imperfect species detection and assessing the variation of these both quantities as a function of relevant environmental variables (MacKenzie *et al.*, 2002; MacKenzie & Royle 2005). Various extensions of these single species models have been proposed to estimate community-level metrics and dynamics. Multi-species occupancy models (MSOM thereafter) allow estimating unbiased occurrence and detectability of each surveyed species and use these estimates to draw conclusions at the community level (*i.e.* species richness) in the same framework (Dorazio & Royle, 2005). This relatively recent modelling framework have been used to test the effect of different management regimes (Zipkin *et al.*, 2010; Carrillo-Rubio *et al.*, 2014), evaluate biodiversity metrics and meta-community structure (Dorazio *et al.*, 2011; Mihaljevic *et al.*, 2015) or improve monitoring programs (DeWan & Zipkin, 2010). Recent extensions allow incorporating effects of several covariates (Kéry & Royle, 2008), multiple states (Kéry *et al.*, 2009), dynamic processes (Dorazio *et al.*, 2010) and effect of species abundance (Tobler *et al.*, 2015). MSOMs could constitute a relevant method for valuing multi-species incidence data in order to obtain a baseline for the evaluation of biological survey results (both in terms of community richness and specific occurrence), and to draw up guidelines for the implementation of cost-efficient protocols (Wintle *et al.*, 2012).

Biases related to imperfect species detectability, are now widely documented and taken into account when studying the occurrence or species richness of a large number of taxa, including plants (Shefferson *et al.*, 2006; Chen *et al.*, 2013), fishes (Holtrop *et al.*, 2010; Anderson *et al.*, 2012), amphibians (DeSolla *et al.*, 2005; Schmidt, 2005), reptiles (Durso *et al.*, 2011; McGrath *et al.*, 2015), large mammals (Rovero *et al.*, 2014; Bowler *et al.*, 2016),

bats (Gorressen *et al.*, 2008) or birds (Olea & Mateo-Tomas, 2011; Tingley & Beissinger, 2013). Unfortunately, inferential biases for insect sampling are often neglected and applications of correcting methods are still few (Kellner & Swihart, 2014; Alabano *et al.*, 2015). However, the detection in insect can notably vary between species according to their visual appearance (color, size ...), their behavior (height of flight ...) (Dennis *et al.*, 2006), their occupation of space during the day (Dennis & Sparks, 2006) or the life stage considered during surveys (Alliberti Lubertazzi & Ginsberg, 2009; Bried *et al.*, 2012a). The heterogeneity of the detection of insects is also governed by survey conditions, in particular by the date of the visits (Pellet, 2008), the number of visits and their duration (Bried *et al.* 2012b), the period of the day at which they are performed (Scalercio *et al.*, 2009), the weather conditions during the visit (Bried & Pellet, 2012), the experience of the observers (Lewandowski & Specht, 2015) or the spatial distribution of survey locations on a site (Nufio *et al.*, 2009). Given the large proportion of species characterized by low densities or low probability of detection (Driscoll, 2010; New, 2010), the actual entomological richness of a given site is particularly difficult or impossible to achieve with limited effort (Foggo *et al.*, 2003).

Long neglected in the field of conservation biology despite the significant amount of biodiversity they represent (Dunn, 2005), insects are now recognized as major components of the functioning of a wide variety of ecosystems (Prather *et al.* 2013; Yang & Graton, 2014), largely affected by global change (Fonseca, 2009). Due to their great diversity, a large part of which remains undescribed, insect conservation is still a challenge in terms of evaluation and ranking of conservation priorities (New, 2010). At the European level, only a few popular groups, for which biology and distribution are particularly well documented, have been evaluated and concentrate the majority of conservation efforts (Leandro *et al.*, 2017). Butterflies, dragonflies and grasshoppers are notably among the most studied taxa in Western Europe (Isaac & Pocock, 2015). Because of this legal protection covering certain species, these taxa belong to the groups commonly surveyed during the realization of EIAs. These surveys aim to specifically searching for these protected or vulnerable and, to a lesser extent, to estimate the richness and the patrimoniality of the species assemblages present on the site. The sampling effort is adjusted according to the conservation issues potentially occurring on the site and especially according to economic constraints (Field *et al.*, 2005). In the most common cases, surveys are conducted through a limited number of visits, focusing on the periods of activity of protected or vulnerable species, in order to maximize their detection,

and during which the three taxa are sought in simultaneous ways. Despite the various detection biases mentioned above and the rise of the culture of public policy evaluation, the quality of the results resulting from this current practice of entomological inventories under EIA conditions remains little evaluated at present.

The aim of the present study was to assess the completeness of the entomological surveys carried out under classical conditions of EIA, both in terms of total species richness and of protected or vulnerable species detection. We conducted insect surveys under EIA conditions at 20 sites located in the French Mediterranean area. The surveys were targeted on four groups of insects (butterflies, dragonflies, grasshoppers and cicadas) commonly followed in this type of study in the area, where conservation issues are particularly high (diversity, endemism ...). In order to evaluate the link between the completeness of these results and the sampling effort, the number of day of EIA in each site was doubled by a survey carried out under closed conditions. Incidence data from these two levels of effort were analyzed under a MSOM, estimating the potential richness of the community and the occurrence probability of each observed species, correcting biases related to the heterogeneity of their detection. These estimates were used as reference values to calculate the completeness of the results and in particular to answer the following questions: (1) Is there a significant gap between the potential richness of insect communities present at the sampled sites and the richness observed in classical EIA conditions? (2) To what extent is this gap limited by the increase in sampling effort applied to a site? (3) Are detection biases evenly distributed within the sampled community? (4) Which characteristics of the surveyed sites and the survey conditions have an influence on the proportion of observed richness and the probability of species detection? (5) What average effort would be required to ensure reliable detection of species under optimal survey conditions?

III.2. Material & methods

III.2.1. Study area and site-level habitat variables

This study was conducted in the Languedoc and Provence regions, located in southern continental France. The study area extended along the Mediterranean Sea, between Narbonne (Lat. 43°11'N, Long. 3°00'E) in the west and Toulon (Lat. 43°07'N, Long. 5°55'E) in the east, within an area of about 80km from the coastline to the Cevennes region in Languedoc

and Luberon massif in Provence (Lat. 44°03'N for the northern site) (Fig.3.1). This area shows a Mediterranean climate, characterized by dry summers and mild winters, with a maximum rainfall in autumn (Debussche *et al.*, 1999).

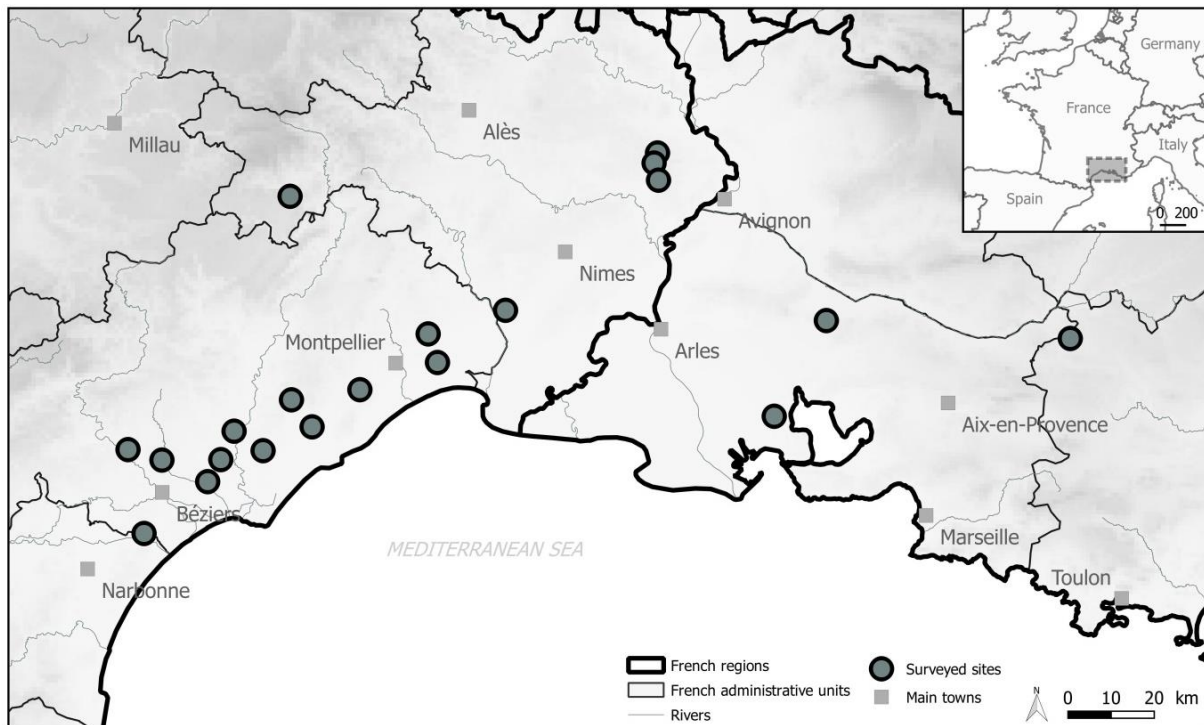


Figure 3.1 : Map of the study area in southern France.

Twenty sites were selected for the collection of entomological data, based on the location of development projects (commercial area, highway or railway, photovoltaic power station, wind turbine ...) requiring biological surveys as part of an EIA. In order to allow consistent modeling of community structure and species parameters (see below), we selected sites located within landscapes showing similar characteristics. These landscapes were mainly structured by disturbances related to human activities (agriculture, grazing, forestry ...) and the important dynamics of secondary successions that followed the abandonment of most of these practices in the second half of the 20th century, as shown by Sirami *et al.*, (2010) for a sector comprised within the global area of these twenty selected sites. The perimeter of selected sites mainly included a mosaic of thermophilous habitats *i.e.* xeric grasslands, dry wastelands, scrublands and woodlands mostly dominated by the holm oak (*Quercus ilex*). Aquatic habitats within sites were represented by sunny streams, large slow-flowing rivers and temporary wetlands.

A majority of these sites (N=13) were located in coastal plain at less than 100m altitude, but seven of them corresponded to sectors with stronger topographic variation, located from 150m to 650m above sea level. They were distant from each other by at least 2.5 km (measured from their centroids) and their average area was 540 ha (ranging from 9 ha to 950 ha) (Suppl.S3.1). They displayed an important variability in the diversity of natural habitats they covered, going from five to 65 natural habitats on a site. This diversity was measured on each site from a mapping of natural habitats, identified on the basis of botanical field surveys and following the Corine Land Cover nomenclature. These mapped data were also used to calculate the proportion of the site area occupied by closed habitats (*e.g.* shrubland, hedge, sclerophyllous vegetation, transitional woodland-shrubs, forest...). This proportion varied widely between sites, ranging from less than 1% for the most opened to 98% for the most wooded site. These site-level habitat variables were calculated using the Qgis mapping software (Quantum GIS Development Team, 2015).

III.2.2. Surveyed taxa

Four groups of insects were surveyed in each studied site: (1) butterflies (Lepidoptera: Papilionoidea) and burnet moths (Lepidoptera: Zygaenidae), (2) dragonflies (Odonata), (3) grasshoppers (Orthoptera), and (4) cicadas (Hemiptera: Cicadidae) (Table 3.1). These groups belonged to the most studied insect taxa in the context of EIAs. These groups also include a significant number of species targeted by regulatory protection policies (representing around 65% of the protected entomological diversity in France, www.legifrance.gouv.fr) or considered as highly vulnerable at the scale of the French Mediterranean area. Papilionoidea and Zygaenidae were treated in the same group in the following analyzes. For more clarity, they were grouped under the term "butterfly" in the rest of the paper.

The French diversity of these taxa is highly variable, ranging from 22 species for cicadas to 231 species for butterflies (Puissant, 2006; Lafranchis *et al.*, 2015) (Table 3.1). The Mediterranean area, which is the richest region in Europe in terms of invertebrate species diversity (Blondel *et al.*, 2010), is a hotspot of diversity across France for the studied taxa. About 80% of the national species richness of each of these groups is present in the two regions covered by the study area (Table 3.1). These two regions also included a significant proportion of the range of many protected or vulnerable species (IUCN France *et al.*, 2014; 2016). Given the known range of species and their ecological requirements (Puissant, 2006;

Grand *et al.*, 2014; Lafranchis *et al.*, 2015; Sardet *et al.*, 2015), the diversity of these four groups potentially present within the targeted landscapes of the study area represented between 60 and 75% of their regional richness (Table 3.1).

Table 3.1 : List of surveyed taxa. The known species richness of each group was summarized at the scale of France ('*nat.*') and of studied regions ('**Reg.**', Languedoc and Provence). 'Land.' refers to the potential number of species which could be observed in surveyed habitat types (based on local atlases and species ecological requirements). The total number of species observed during the present study ('Obs.')

Surveyed taxa	Order	Reg. / <i>nat.</i>	Land.	Obs.	Obs.Cons.	Sampled life stage and survey methods
Papilionoideae	Lepidoptera	231 / 262	140	93	7	Adult, larvae, eggs (vis.) ; hostplant (vis.)
Zygaenidae	Lepidoptera	22 / 26	15	9	1	Adult (vis.) ; hostplant (vis.)
Odonata	Odonata	76 / 96	57	46	9	Adult (vis.) ; exuviae (col.)
Orthoptera	Orthoptera	207 / 244	126	71	15	Adult (vis. and ac.) ; larvae (vis.)
Cicadidae	Hemiptera	18 / 22	12	8	1	Adult (vis. and ac.) ; exuviae (col.)

Two categories of species were distinguished within these four taxa according to the conservation issue they represented: (1) species considered as conservation issues ('covered'), which combined 'protected' species (taken from the French legislation) and 'vulnerable' species at the national or local level, and (2) species with no conservation status ('uncovered'). Vulnerable species have been identified according to their patrimonial status, their scarcity or the region's responsibility for their conservation. This information was collected from several sources: (1) national red lists (Sardet & Defaut, 2004; IUCN France *et al.*, 2014; 2016) and regional red lists (Bence *et al.*, 2011; Bence, 2014), (2) lists of species considered as indicator for the designation of zone of high ecological interest (<https://inpn.mnhn.fr/programme/inventaire-znieff/presentation>), (3) national (Dupont, 2010) and regional action plans (OPIE *et al.*, 2011; Lambret *et al.*, 2011), (4) national (Grand *et al.*, 2014; Lafranchis *et al.*, 2015; Sardet *et al.*, 2015) or regional distribution atlases (Jaulin *et al.*, 2011; Papazian *et al.*, 2017). This typology was used by the company to define the sampling strategy on each of the sites monitored.

Table 3.2 : Posterior estimates of the species richness for each surveyed site, as estimated under the MSOM (with mean, standard deviation, CI_{95%}). The number of species observed during field surveys was also included for each site, under the classical and doubled conditions. ‘Surveys’ refers to the number of visits conduction during the classical EIA.

Site	Locality	Surveys	Classical EIA condition	Doubled EIA conditions	MSOM predictions			
					Mean	Standard deviation	CI 2.5%	CI 97.5%
1	Lieuran-lès-Béziers	5	93	109	147.78	7.41	135	164
2	Mauguio	4	49	68	121.68	7.02	109	136
3	Lespignan	4	63	76	112.65	6.51	101	126
4	Fabrègues	3	60	77	123.43	6.92	111	138
5	Montdardier	4	86	99	131.74	6.14	121	145
6	Rians	3	80	98	136.53	6.83	124	151
7	Gallargues-le-Montueux	2	33	47	110.60	7.65	96	126
8	Pézenas	2	52	72	126.21	7.13	113	141
9	Bessan	2	53	62	121.92	7.48	108	137
10	Saint-Thibéry	2	75	79	132.75	7.28	119	148
11	Pinet	9	79	94	124.71	6.63	113	139
12	Poussan	9	93	110	132.84	6.01	122	146
13	Murviel-lès-Béziers	5	114	127	160.87	7.16	148	176
14	Saint-Pargoire	7	91	103	135.68	6.66	124	150
15	Saint-Victor-la-Coste	4	81	90	119.55	6.38	108	133
16	Lamanon	4	56	63	102.64	6.67	90	116
17	Istres	3	56	65	125.39	7.78	111	141
18	Valliguières	2	50	64	111.47	7.35	98	127
19	Saint-Hilaire-d'Ozilhan	2	48	59	113.05	7.51	99	128
20	Vendargues	3	55	64	114.18	6.98	101	129

III.2.3. Data collection and survey conditions

Data were collected over two consecutive years: 8 sites were sampled in 2015 and 12 sites in 2016. Insect communities were surveyed at each site through a sampling plan involving repeated visits, all performed during the same year for a given site. The number of visits was very variable between sites, ranging from 2 to 9 visits with a mean of 3.95 (\pm 2.16) visits by site (Table 3.2). The number of visits was fixed for each site following the usual procedure of a consultant in ecological engineering carrying out an EIA, according to the importance of the conservation issues potentially present on the site and the budget allocated by the developer. All visits were conducted between the beginning of April and the beginning of August. They were distributed within this interval according to the period when the highest diversity of each sampled taxa was detectable and to the phenology of species that were of conservation concern potentially present on each site. The visits were conducted under favorable weather conditions for insect activity. Rainy or cloudy days (cloud cover estimated to be greater than 50%), with low or too high temperatures (generally below 15° C or above 35° C) and high winds (greater than 20 km/ h) have been avoided (Pollard & Yates, 1993; Kéry & Plattner,

2007). The majority of visits were made during the day, between 10:00 am and 18:00 pm, but night surveys (between 22:00 pm and 02:00 am) were performed on some sites to maximize detection of some grasshopper species particularly active at night (concerned 10 sites and 11 visits). The length of survey varied a lot between the different visits, comprised between 2h and 8h of survey on the same site, spread out over a whole day or only part of the day (morning, afternoon or night according to the time the visit started).

The observer did not follow a fixed route during the surveys, but rather attempted complete coverage of the diversity of natural habitats present within the site, by prioritizing the habitats of species which representing conservation issue or areas potentially displaying the greater entomological diversity (*e.g.* heterogeneous habitats...). Although such wandering surveys are not standardized, they constitute a low-cost method allowing to collect data on species occupancy over large area, which is the main focus of EIAs (Longcore *et al.*, 2010 ; Taron & Ries, 2015). Repeated visits were carried out by three professional observers (GD and SD, authors of the present paper, and one other person from the Biotope compagny), considered to have similar skills and experience, with only one of them surveying a site during a visit.

A combination of several sampling techniques was used during each visit to allow detection of the different taxa studied (Table 3.1). The search for adult stages (with sometimes temporary capture to identify the most cryptic species) was preferred for all taxa. Caterpillars and host plants of butterflies and exuviae of dragonflies and certain cicadas have been occasionally sought. Mating calls produced by a large number of Orthoptera and Cicada were also used for the acoustic detection of some of the most cryptic species (Jeliazkov *et al.*, 2016). All detected individuals have been identified at the specific level according to the most recent taxonomic reference available at the scale of France (TaxRef v.10.0, www.inpn.mnhn.fr).

In order to test the influence of sampling effort on inventories completeness in the case of EIA, the number of visits performed at each surveyed site has been multiplied by two. For each visit, a duplicate was made between 1 and 14 days after the initial visit, in similar conditions (in terms of weather conditions, time of beginning, and duration of the visit...). The same sampling technics were applied through wandering surveys to obtain occupation data for each species. Although survey routes frequently cannot be closely replicated according to this

type of survey, the observer has tried to cover an area and a diversity of habitats as close as possible to the conditions of the initial visit. All the duplicates were made by the same observer (GD), generally different from the observer from the initial visit but who has the same skills and level experience (expert entomologist with professional training). Considering these duplicates, a total of four to 18 replicated visits per surveyed site were thus available for analyses. These spatial and temporal replicated visits were used to construct the species-specific detection histories that were used for the implementation of occupancy model (as described below).

III.2.4. Multi-species occupancy model

The completeness of EIA entomological surveys was evaluated by estimating the difference between the observed species richness (for the whole community and each species category) from the two levels of effort applied (classical and doubled) and the number of species potentially occurring on each site, accounting for those undetected during sampling. We used a MSOM to estimate this unknown total species richness of the insect community (Dorazio & Royle, 2005; Dorazio *et al.*, 2006).

The MSOM is an extension of the single-species occupancy model (MacKenzie *et al.*, 2002) to all species in a community, whether or not they were detected during sampling (Sanderling *et al.*, 2014). Occupancy models produce estimates of two probability-based parameters: detection (p), which is defined as the probability of detecting a species given that it is present at a site and available for capture; and occurrence (Ψ), which is the probability that a species is present at a site during sampling (Bailey *et al.*, 2014) (Suppl.S3.2). Sampling design through repeated visits is then a basic requirement to the distinction between true absence and non-detection (MacKenzie *et al.*, 2006). Given their structure, these models are referred as hierarchical (Royle & Dorazio, 2008), with these both parameters estimating from two linked processes: the ecological process (site occupied vs. unoccupied) and the detection process (species detected vs. undetected at occupied sites) (Guillera-Arroita *et al.*, 2014; Gimenez *et al.*, 2014). The MSOM expands these levels across all detected species and allows taking into account partially or never detected species through addition of a third hierarchical component corresponding to community process (Dorazio *et al.*, 2011; Iknayan *et al.*, 2014).

Species-level and community-level attributes are then combining into the same modeling framework, with species treated as random effects governed by ‘hyper-parameters’ of the community (Hunt *et al.*, 2013). The detection and occupancy probabilities of each species are then assumed to come from this community-level distribution and are used to inform the mean and variance of this distribution. By combining all individual species through this community hierarchical process, precision of species-specific estimates is improved, leading to a more efficient use of data resulting from multispecies surveys. Such ‘data shrinkage’ (Hobbs & Hooten, 2015) allows to made inference for rare species with a limited number of detections that otherwise would be difficult or impossible to model on their own (Zipkin *et al.*, 2009; Tingley & Beissinger, 2013). It could give significant advantages over SSOMs, provided that occurrence responses of species integrated in a same model can conceivably come from a common distribution (Sauer & Link, 2002).

Ecological equivalence constitutes one of the main assumptions of MSOM aiming to estimate occurrence of non-detected species (Dorazio *et al.*, 2006). Such equivalence must be considered in the sense that species should be likely to respond similarly, but not identically, to changes in their environment or habitat (Dorazio *et al.*, 2011). Although the occurrence may vary significantly between each species, all species are related in the sense that they belong to a larger community of ecologically similar species. The survey of taxa mainly breeding in open habitats, at the level of sites located within equivalent landscape entities allowed us to limit the potential biases related to the non-respect of this hypothesis. Site-occupancy analyses may also be susceptible to bias from violations of population closure (Kendall, 1999; Rota *et al.*, 2009). Since the surveys were conducted during a single flying season, we assumed community closure between the first and the last visit on a site. The assumptions of independence of sampling units and absence of false positive (i.e. species falsely detected in an unoccupied site following misidentification) (MacKenzie *et al.*, 2006) were also considered respected due to the distance between sites and the experience of the observers.

III.2.5. Modeling framework

We implemented a single season MSOM similar to that used by Zipkin *et al.* (2010) to estimate species and community responses to site covariates and survey covariates. We let $z(i, j)$ denote true occurrence status modelling as a binary variable in which $z(i, j) = 1$ when

species i occupies the site j , and $z(i, j) = 0$ otherwise. This occurrence state was assumed to be the outcome of a Bernoulli random variable, denoted by:

$$z(i, j) \sim \text{Bernoulli}(\psi_{i,j}) \quad (1)$$

where $\psi_{i,j}$ is the probability that species i occurs at site j . As occurrence is imperfectly observed, the occurrence state $z(i, j)$ is usually not known with certainty. Instead, we observed data $x(i, j, k)$ for species i at site j during replicate visit k . Conditional on the outcome of the occurrence state, this detection process was also modelled as a Bernoulli random variable:

$$x(i, j, k) \sim \text{Bernoulli}(p_{i,j,k} \times z(i, j)) \quad (2)$$

where $p_{i,j,k}$ is the detection probability of species i for the k th visit at site j , given that species i is in fact present at site j (i.e. $z(i, j) = 1$). The probability of detecting the species i at site j will then be zero if the species does not occupy site j , since $z(i, j) = 0$.

We considered that the occurrence ($\psi_{i,j}$) and detection ($p_{i,j,k}$) probabilities varied by species and were influenced by habitat and survey covariates, respectively. These effects were incorporated into the model using the logit link function (Kéry & Royle, 2008). Each covariate was centered and scaled prior to analysis. Covariates standardization allowed direct comparison of model coefficients as effect sizes relative to variation in each covariate (Hunt *et al.*, 2013). We modeled species-specific occurrence probabilities as a function of three habitat covariates: *area* was the area of the surveyed site (in ha); *divhabitat* covariate corresponded to the number of natural habitat present within the site (in number of natural habitats); *propclosed* was defined as the proportion of closed habitats within the site (varied from 0% to 100%). The first two covariates were only included as *linear effect* on occurrence, since we did not have strong a priori reasons for expecting non-linear effects. However, we had both *linear* and *quadratic effect* for the third covariate (*propclosed*²) in order to include possible intermediate response of species occurrence to this habitat characteristic. We used the following equation to relate these species-specific habitat covariates and occupancy to the hierarchical models described above:

$$\text{logit}(\psi_{i,j}) = u_i + a1_i \text{area}_j + a2_i \text{divhabitat}_j + a3_i \text{propclosed}_j + a4_i \text{propclosed}_j^2 \quad (3)$$

where u_i correspond to the occurrence probability (on the logit-scale) for species i in sites with ‘average’ values of habitat covariates (given their standardization). The coefficients a_{1i} , a_{2i} , a_{3i} and a_{4i} were the effects of each habitat covariates on species i respectively.

In the same way, species-specific detection probabilities were assumed to vary based on three survey covariates: *date* of the visits (linear and quadratic effects in order to detect potential optimum in species activities during the surveyed season, expressed in Julian date); *hour* at which each visit started (linear effects, in hours); *length* of each visit (linear effects, in hours). We modelled the effects of these covariates on detection probability with a logit function:

$$\text{logit}(p_{i,j,k}) = v_i + b_{1i} \text{date}_{jk} + b_{2i} \text{date}_{jk}^2 + b_{3i} \text{hour}_{jk} + b_{4i} \text{length}_{jk} \quad (4)$$

where v_i correspond to the detection probability (on the logit-scale) for species i at ‘average’ values of survey covariates, modeled by the coefficients b_i .

Species-specific occurrence and detection parameters were random effects governed by a common community-level hyper-parameter. Each parameter was modeled as drawn from a normal distribution described by the community mean (μ) and standard deviation (σ) hyper-parameters. For example, we specified species-specific occurrence as:

$$u_i \sim N(\mu_u, \tau_u) \quad (5)$$

where μ_u is mean occurrence from the community and τ_u the standard deviation between species. The distribution of hyper-parameters was specified in the same way for each a_i and b_i covariate effect.

The total richness was estimated using a data augmentation procedure (Divino *et al.*, 2011; Broms *et al.*, 2016) which allows estimating the number of species in the community including those never detected during visits (Royle *et al.*, 2007; Royle & Dorazio, 2012). This process consists in an addition of an arbitrarily large number of all-zero detection histories corresponding to hypothetical undetected species (Kéry & Royle, 2008). Zero-inflated version

of the model could then be seen as a ‘super-community’ (M) from which the observed community (n) was drawn. Using this method, we assumed a uniform $(0, M)$ prior for N , the ‘true’ species richness, where M was a fixed constant chosen to be much greater than the number of observed species (n). Considering the number of insect species detected during our visits and the potential species richness of the studied landscapes in our study area (Table 3.1), we added 200 species with zero encounter history to the observed community. The occurrence process was modified as:

$$z(i, j) \sim \text{Bernoulli}(\psi_{i,j} \times \omega_i), \quad (6)$$

$$\omega_i \sim \text{Bernoulli}(\Omega)$$

where i was a vector including all the specie from 1 to M and ω_i was the probability of a species from the ‘super-community’ to be available to capture (Dorazio *et al.*, 2006). If $\omega_i = 0$, species was unavailable to capture and cannot occur in the study area ($\psi_{i,j} = 0$). If $\omega_i = 1$, species is a member of the observable a community and had a probability $\psi_{i,j}$ to occur in the area. The estimation of the parameter Ω , which governed the distribution of this probability, was an indirect way to have access to N . We estimated this species richness including unobserved species at the scale of the study area, as well as at each visited sites. Species richness was also estimated for each taxonomic group and conservation class in each visited sites.

III.2.6. Model implementation

The model was implemented in a Bayesian framework using the BUGS language and run in JAGS (Plummer, 2003) from the R software (R Development Core Team, 2015) through the package *jagsUI* (Kellner, 2015). Given the lack of prior knowledge of a parameter’s true value, parameters and hyper-parameters were implemented with non-informative priors (Link *et al.*, 2002; Mata *et al.*, 2014). We used a uniform distribution from 0 to 1 for community-level parameter Ω , and for the community mean (μ) of species-specific occurrence and detection probabilities (u_i and v_i). The means of the site-specific (a_i) and survey-specific (b_i) effects were given normal priors with mean zero and variance 1,000. The community standard deviations (σ) of all these parameters were given gamma priors as *gamma* (0.1, 0.1).

We ran eight parallel chains of 150,000 iterations, after a burn-in of 50,000 iterations and thinned the posterior chains by 50. We assessed convergence by visual assessment of MCMC chains and by using the Gelman-Rubin statistic ('Rhat'), with values <1.1 considered acceptable (Gelman & Hill, 2007). An assessment of model fit to the actual dataset was performed using a *Bayesian p-value* approach and an estimation of a 'lack-of-fit' statistics (Kéry & Schaub, 2012; Broms *et al.*, 2016) (Suppl.S3.3). In contrast to the frequentist models for which the use of model selection criteria is widespread, there is currently no consensus regarding the appropriate methods for covariates selection or model comparison in the framework of complex hierarchical models (Hooten & Hobbs, 2015; Broms *et al.*, 2016). The importance of the effects of these covariates on species-level occurrence and detection probabilities were assessed based on posterior distributions of a_i and b_i parameters, considering non-significance if their 95% posterior credibility interval (CI_{95%}) included zero (Burton *et al.*, 2012; Chen *et al.*, 2013).

III.2.7. Minimum survey effort requirements

In an operational approach, we aimed to use species-specific detection probabilities given by the MSOM to estimate minimum survey effort required to ensure some degree of confidence in the representativeness of an EIA results. We followed the analytical framework developed by Wintle *et al.* (2012), based on the estimation of the probability that a species was present on a site given that it was not detected following a certain number of visits ($\Pr(\textit{presence}|\textit{non detection})$). By distinguishing the part of apparent absence linked to detection defects from those related to true absences, this method allowed to determine the number of sequential non-detections necessary to achieve a pre-specified level of confidence in the inference of species true absence. In addition to the prior fixation of this confidence level, this method required a prior knowledge of the detectability of the species (which may be dependent on the level of some covariates) and its prevalence within the study area (i.e. its expected rate of occurrence, which could be seen as a measure of the favorability of the area for the species) (Petitot *et al.*, 2014). According to this method, the minimum number of sequential non-detection required to infer the absence of a species (n^*) is then estimate as:

$$n^* = \frac{\log\left(\frac{\alpha}{1-\alpha}\right) - \log\left(\frac{\gamma}{1-\gamma}\right)}{\log(1-p')} \quad (7)$$

where γ was the prior probability that the species is present on the site (prevalence), p' corresponded to the prior probability of detecting the species given it is present and α was the posterior probability that the site is occupied given species was unobserved (which represents the level of confidence).

We used this equation to estimate the minimum number of visits without detection required to be 95% sure that a species is absent from a site. Because of the lack of knowledge on regional prevalence for the studied species pool, species-specific occurrence probabilities ($\psi_{i,j}$) were used as prior belief of species prevalence. Inference was therefore limited to sites presenting the same characteristics (in terms of landscape, climate...) than the present survey area, and the prevalence could be seen as a measure of the favorability of such characteristics to target species (species with high prevalence had more chance to occur in the site). The species-specific probability ($p_{i,j,k}$) estimated from the MSOM were used as prior detection probability p' . Considering the three survey covariates included in the simulation (date, hour, length), the value of $p_{i,j,k}$ was chosen for a combination of covariate level leading to the higher probability of detection of each species, respectively. The minimum survey effort requirement was thus estimated for the case of repeated visits conducted under survey conditions considered as optimal. This number was estimated for each of the 227 species observed on at least one surveyed site. In order to ensure a certain level of accuracy of these estimates, the species observed in less than two visits in doubled EIA conditions were excluded from this part of the analysis (representing 22 species).

III.2.8. Statistical analysis

The results from the two applied sampling plans, classical EIA and doubled EIA, were compared in terms of observed species richness and sampling coverage. The species richness estimated from the MSOM was used as a reference value for defining the completeness of classical and doubled surveys. This sampling coverage was calculated at the community level as well as at the site level. Given the non-normality of the data, classical EIA, double EIA and MSOM richness were compared from a non-parametric rank-based Friedman test (Oja, 2010). The sampling coverage of the first two modalities was compared using Wilcoxon's signed-rank test. These comparisons were repeated for each group of species (taxonomy or conservation status). The sign and the significance of the correlation between the mean value

of sampling coverage by sites and habitat covariates (*i.e.* site area, habitat diversity and percentage of closure) were estimated with a Spearman's rank correlation test.

Considering the species-specific level, the mean occurrence and detection probabilities were compared between these same groups by means of a Kruskal-Wallis H test, followed by pairwise comparisons by the Wilcoxon rank-sum test, with p-values adjusted using the 'fdr' correction (Benjamini & Hochberg, 1995). An absolute bias value in observed occurrence was also calculated for each species (Kéry & Royle, 2008). This bias value corresponds to the difference between the observed occurrence of each species (the proportion of sites at which they were observed) and their mean occurrence probability, estimated from the MSOM (ψ). Absolute bias value was used as an indicator of sampling coverage at the specific scale. Two values of this bias were calculated: one from the occurrence observed under classical EIA conditions, and another from the occurrence observed under doubled EIA conditions. These values were compared through a Wilcoxon signed-rank test. Absolute bias was also compared between the different groups of species defined above (Kruskal-Wallis H test and pairwise comparisons by the Wilcoxon rank-sum test).

Estimates of the minimum number visits required to certify the absence of a species were compared across species according to their conservation status. These comparisons were made from a Kruskal-Wallis H test, followed by a comparison of the Wilcoxon rank-sum test, with p-adjusted values using the 'fdr' correction. All these analyses were performed using the R software (R 3.3.3, R Development Core Team, 2015).

III.3. Results

III.3.1. Observed richness

Field surveys allowed collecting more than 4300 incidence data from 158 visits across the 20 studied sites. A total of 227 insect species were observed on all visits: 102 butterflies (45%), 46 dragonflies (20%), 71 grasshoppers (30%) and 8 cicadas (4%) (Table 3.1). This richness represents approximately 41% of the total number of known species in the biogeographic region, and 65% of the estimated gamma diversity for the landscapes targeted by the present study (Table 3.1). Among the observed species, 33 species were covered by conservation status (10 protected species and 23 vulnerable species) (14.5%). Twenty-two species (all taxa

combined) were only detected during a single visit (even under doubled conditions). Conversely, four species accounted for almost one-tenth of the observations (*Lasiommata megera*, *Pieris rapae*, *Polyommatus icarus* and *Tettigonia viridissima*).

Higher species richness was observed under doubled EIA conditions, with 10 species more than under classical EIA conditions (217 species observed in this last case). At the scale of the studied sites, the doubling of the sampling effort allowed to detect an average number of species significantly greater than under classical EIA conditions (Friedman test, $P < 0.001$) (Fig.3.2a). An average of 60.35 species (± 20.57 species) was observed per site under classical EIA conditions while 81.3 species (± 21.20 species) were detected on average under doubled EIA conditions (Table 3.2); that corresponds to a gain of 20.95 species (+25.8 %). Butterflies and uncovered species showed the higher difference of observed species between classical and doubles conditions (6.7 and 12.1 respectively).

Table 3.3 : Posterior estimates of the mean species richness per site for the community ('All taxa') and each group of species (as defined in Materials and methods), as estimated under the MSOM (with mean, standard deviation, CI95%). The mean number of species observed during field surveys was also included for each site, under the classical and doubled conditions.

Surveyed taxa	Classical EIA condition	Doubled EIA conditions	MSOM predictions			
			Mean	Standard deviation	CI 2.5%	CI 97.5%
All taxa	68.35	81.30	125.28	15.09	100	171
Lepidoptera	31.00	37.70	55.61	8.81	29	73
Odonata	9.70	11.85	17.06	9.84	5	35
Orthoptera	24.60	27.95	38.32	4.38	30	46
Cicadidae	3.50	3.75	5.25	1.28	2	7
Covered species	3.84	4.25	7.44	2.81	2	13
Uncovered species	65.05	77.15	108.10	11.73	88	137

III.3.2. Estimated richness and sampling coverage

The goodness-of-fit test showed an adequate fit of the MSOM to the data ($p = 0.75$, lack of fit = 1.01, see Suppl S3.3 for detailed results). The model estimated 313.9 species in the surveyed community on the whole study area ($CI_{95\%} = 271 - 382$; Suppl S3.4). The average richness per site was estimated at 125.28 species (Table 3.3), ranging from 102 to 160 species depending on the site considered (Table 3.2). Butterfly estimated richness is the highest, with an average of 55.61 species per site, compared to only 5.65 for cicadas (Table 3.3). Estimated richness was significantly higher than observed richness under classical and doubled EIA conditions, regardless of the group of species considered (Friedman test, $P < 0.001$) (Fig.3.2a).

When considering these estimated richness values as the upper limit of potential site richness, sampling coverage showed significant variability among survey methods (i.e. classical vs doubled), sites and species groups. At the community level, sampling coverage was significantly higher in doubled EIA conditions (Wilcoxon test, $P < 0.001$), with an average of 64.17% ($\pm 11.33\%$) of species detected at one site, whereas only 53.82% ($\pm 11.76\%$) of species were detected in average under classical EIA conditions (Fig.3.2b). Regardless of the group of species considered, the sampling coverage never exceeded 75% (Fig.3.3). We could not find significant difference between taxonomic groups when comparing their average sampling coverage per site, regardless of the survey conditions applied (Kruskall test, $P > 0.05$; Fig.3.3a). On the other hand, although the species covered by a conservation status do not differ from those not covered in terms of sampling coverage under classical EIA conditions (Wilcoxon test, $P > 0.05$), they had a significantly lower average sampling coverage under doubled EIA conditions (Wilcoxon test, $P < 0.05$), with an average of 51.43% of detected species per site ($\pm 26.11\%$) (Fig.3.3b). Cicadas were the only species group that showed no significant increase in the average sampling coverage when changing from classical to doubled EIA conditions (Wilcoxon test, $P > 0.05$). For all other groups, sampling coverage significantly increased with double visits (Wilcoxon test, $P < 0.05$; Fig.3.3).

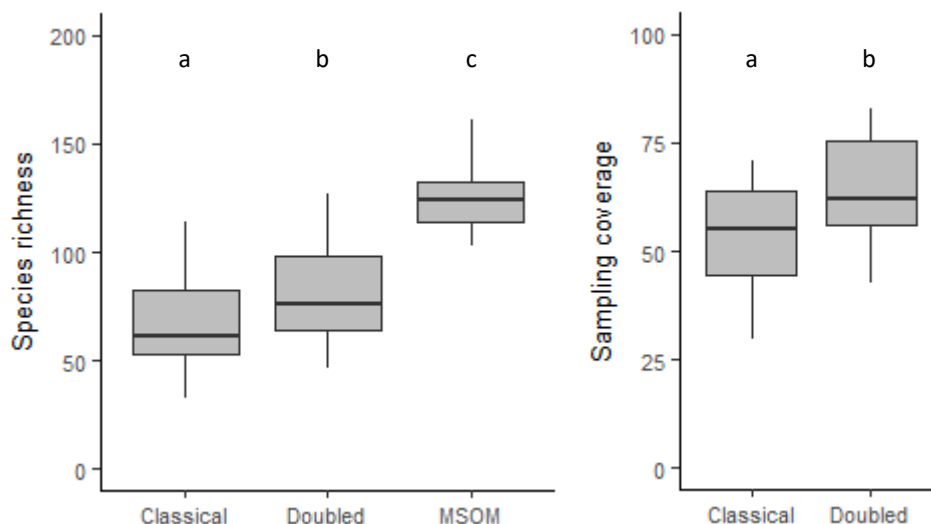


Figure 3.2 : Mean values of species richness (a) and sampling coverage (b) among surveyed sites under classical and doubled EIA conditions. The observed species richness was also compared to mean posterior estimates of the hierarchical MSOM. Sampling coverage was calculated with MSOM estimated richness considered as maximum reference value. Different letters refer to a significant difference ($P < 0.05$) between modalities according to non-parametric rank-based Friedman test (a) and Wilcoxon’s signed-rank test (b).

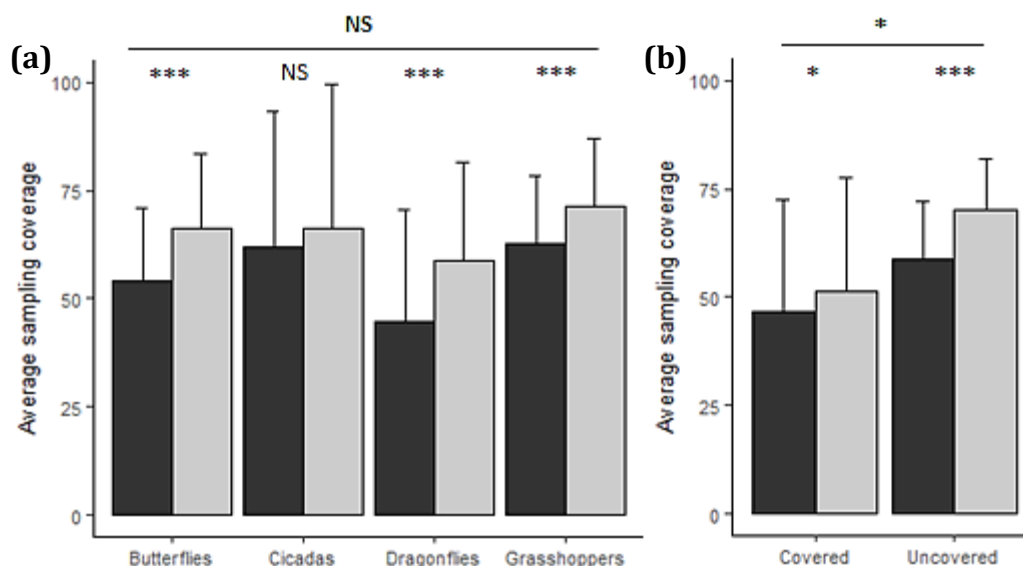


Figure 3.3 : Mean values (\pm SE) of sampling coverage among insects’ species observed under classical (dark bars) and doubled (light bars) EIA conditions, depending on their taxonomic group (a) and to their conservation status (b). Taxonomic groups are categorized into butterflies ($n = 102$), cicadas ($n = 8$), dragonflies ($n = 46$) and grasshoppers ($n = 71$). Conservation status are categorized into covered species ($n = 33$) and uncovered species ($n = 194$). Asterisks indicates significant differences of sampling coverage between classical EIA and doubled EIA in each species group (under the line) and between these groups (above the line) (***: $P < 0.001$, *: $P < 0.05$, NS: $P > 0.05$, pairwise Wilcoxon tests).

III.3.3. Correlations with survey effort and habitat covariates

The correlation between the sampling coverage at each site and the value of the measured habitat covariates was analyzed for each of the two survey conditions (i.e. classical vs doubled) (Fig.4). A significant positive correlation was found between this sampling coverage in classical condition and the area of the surveyed site (Spearman's correlation; $r_s=0.49$, $P < 0.05$). The average coverage also seemed positively correlated to the habitat diversity present on the site, but this correlation is not significant (Spearman's correlation; $r_s=0.36$, $P > 0.05$). No correlation was found between the proportion of closed habitats at a site and the average sampling coverage (Spearman's correlation; $r_s=0.14$, $P > 0.05$). Although conducting double visits increased the sampling coverage on each site, it did not lead to any change in the correlation between this coverage and habitat covariates (Fig.3.4b).

A significant correlation was also identified between the number of visits conducted on a site and the sampling coverage (Spearman's correlation; $r_s=0.81$, $P < 0.001$). Estimates of species richness were more complete for sessions with higher number of visits, both in classical and doubled conditions (Fig.4). The number of visits performed to a site also showed a strong correlation with several habitat covariates of this site. The largest number of visits was made (following classical EIA requirements) to sites with the largest area (Spearman's correlation; $r_s=0.52$, $P > 0.05$) and greatest diversity of natural habitats (Spearman's correlation; $r_s=0.54$, $P < 0.05$) (Suppl.S3.5).

III.3.4. Hyper-parameters of the community

When considering all insect species together at the community level, posterior hyper-parameters of occurrence and detection probabilities were globally low (mean value of 0.373 and 0.141 respectively) but very variable within the species pool ($CI_{95\%} = 0.162 - 0.559$ and $0.184 - 0.998$ respectively) (Table 3.4). At the community level, the correlation between average species occurrence and habitat covariates was positive, generally suggesting that surveyed insects' species were more likely to occur on large sites with a large proportion of closed habitat. The confidence interval of the response to habitat diversity was distributed almost equally around 0 ($CI_{95\%} = -0.22 - 0.255$), minimizing the role of this covariate as a driver of species occurrence. In contrast, area and proportion of closed habitat did not include the 0 value in their confidence interval, indicating a strong effect of these covariates on

species occurrence (Table 3.4). We also noted the significance of the quadratic effect of the "closure" parameter, indicating an optimum of occurrence probabilities species for an intermediate closure value (Suppl.S3.6a).

Table 3.4: Community-level summaries of the hyper-parameters for the detection and occupancy covariates (mean, standard deviation (SD), CI_{95%}). The direction (+ or -) of the effect of site and survey covariates was indicated for those showing a significant influence on occurrence and detection.

Community level hyper-parameter		Mean	SD	CI 2.5%	CI 97.5%	Sign.
ψ	Occurrence probability	0.373	0.103	0.162	0.559	
$\mu a1$	Area	0.268	0.103	0.066	0.469	(+)
$\mu a2$	Habitat diversity	0.199	0.121	-0.220	0.255	
$\mu a3$	Closure proportion (linear)	0.412	0.163	0.095	0.736	(+)
$\mu a4$	Closure proportion (quadratic)	-0.420	0.140	-0.701	-0.146	(-)
p	Detection probability	0.141	0.021	0.184	0.998	
$\mu b1$	Date (linear)	-0.307	0.158	-0.619	0.005	
$\mu b2$	Date (quadratic)	-1.367	0.105	-1.584	-1.168	(-)
$\mu b3$	Survey hour	-0.546	0.063	-0.672	-0.422	(-)
$\mu b4$	Survey length	0.023	0.037	-0.050	0.096	

Among the covariates related to the visit conditions (date, time, length), the length of the visit showed an average positive correlation with detection probability, although it was not significant (CI_{95%} = -0.05 - 0.096) (Table 3.4). The time at which the visit was started also strongly influenced the average detection probability, with a higher probability when the visit was started early (Suppl S3.6b). The date of the visit also had a negative but more variable influence on the average probability of detection of the community, reflecting the difference of activity period between species (Table 3.4). In addition, this covariate exhibited a significant quadratic effect (CI_{95%} = -1.58 - -1.17), reflecting a detection optimum over the field season.

III.3.5. Species-specific occurrence and detection

The naïve occurrence (proportion of sites where a given species was present) calculated from the observations made under classical EIA conditions varied according to the species considered, ranging from 0.05 for species located on a single site to 1 for species widespread on all sites (Suppl.S3.7). The value calculated after doubling the number of visits showed a similar range of variation between species. The observed occurrence of about 60% of the

species was higher under doubled EIA conditions, with an average of two new sites of presence (species occurrence increase in average of 0.09). Mean probabilities of occurrence estimated by hierarchical modelling varied widely among species, with values ranging from 0.07 (*Decticus verrucivorus monspelliensis*) to 0.98 (*Euchorthippus elegantulus*) (Suppl.S3.7).

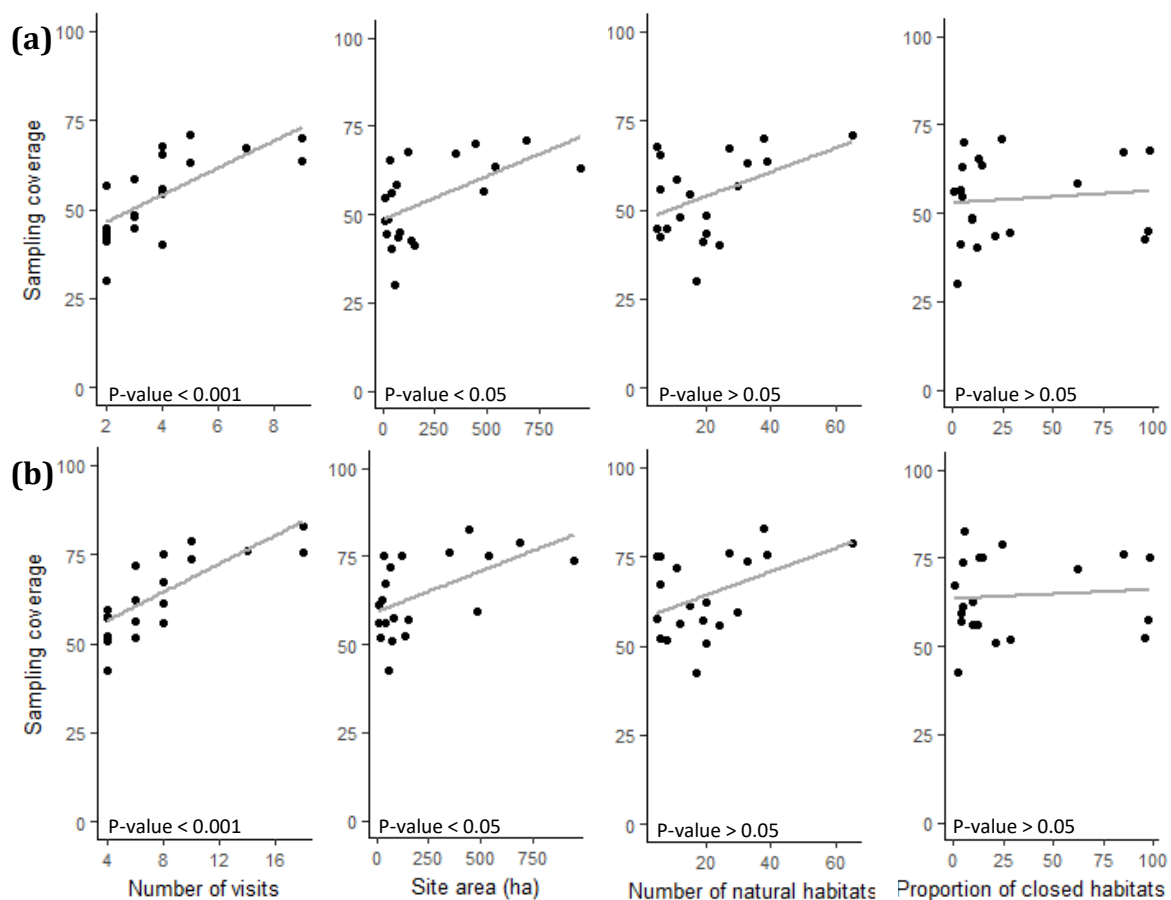


Figure 3.4 : Relationship between observed sampling coverage among sites and several site-level parameters, including habitat covariates included in the hierarchical model and the number of visits performed on the site. The upper line **(a)** correspond to sampling coverage observed under classical EIA conditions and the lower line **(b)** correspond to sampling coverage observed under doubled EIA conditions. P-values indicate the significance of a Spearman correlation test performed between the observed sampling coverage and each habitat covariate. The regression curve was adjusted through the function *geom_smooth* of the package *ggplot2* with argument *method = 'lm'*.

Absolute bias between naïve occupancy and the ones estimated with the MSOM ranged from 0.01 to -0.79 under classical EIA conditions and between 0.01 and -0.64 under double EIA conditions. The average bias in occurrence of the entire species pool was significantly lower under doubled conditions (Wilcoxon test, $P < 0.001$). Cicadas were the only species group without significant reduction in this bias when sampling effort was doubled (Fig.3.5). The absolute bias in occurrence differ significantly between the different taxonomic groups (Kruskall test, $P < 0.05$; Fig.3.5a), with a bias significantly higher for butterflies (-0.21 ± 0.14 under classical EIA, -0.16 ± 0.14 under doubled EIA) then dragonflies (-0.28 ± 0.17 under classical EIA, -0.22 ± 0.14 under doubled EIA) regardless of the sampling condition (i.e. classical or doubled). On the other hand, species covered by a conservation status (-0.15 ± 0.12 under classical EIA, -0.13 ± 0.10 under doubled EIA) showed a significantly lower bias than uncovered species (-0.27 ± 0.16 under classical EIA, -0.21 ± 0.13 under doubled EIA), under standard conditions and doubled conditions (Wilcoxon test, $P < 0.05$; Fig.3.5b).

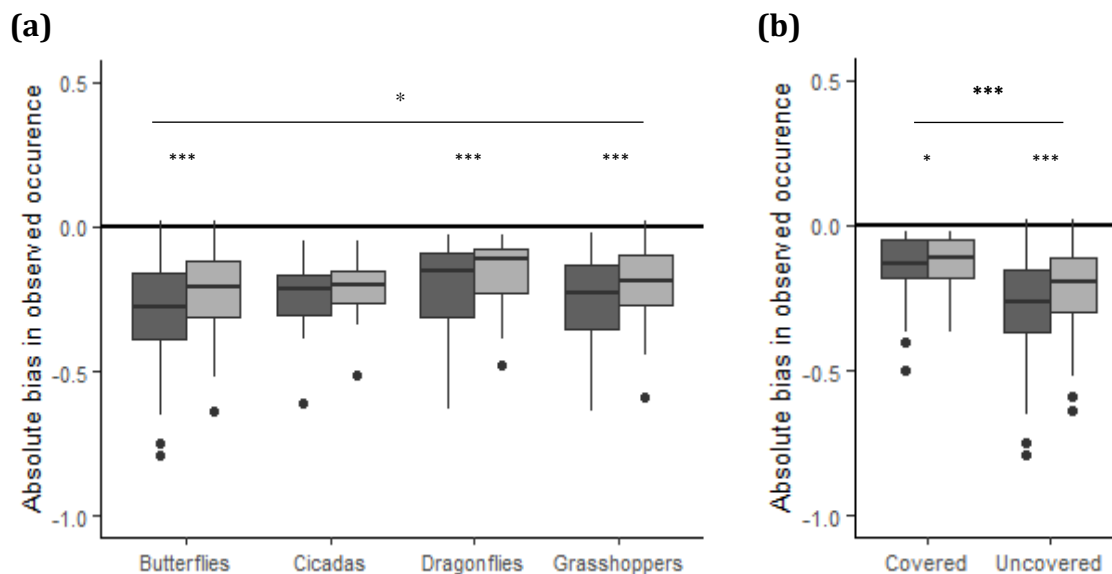


Figure 3.5 : Absolute bias in occurrence among insects' species observed under classical (dark boxes) and doubled (light boxes) EIA conditions, depending on their taxonomic group **(a)** and to their conservation status **(b)**. Absolute bias corresponded to the difference between mean species-specific occurrence probabilities and the observed occurrence in a given survey condition (classical or doubled). Taxonomic groups are categorized into butterflies ($n = 102$), cicadas ($n = 8$), dragonflies ($n = 46$) and grasshoppers ($n = 71$). Conservation status are categorized into covered species ($n = 33$) and uncovered species ($n = 194$). Asterisks indicates significant differences of sampling coverage between classical EIA and doubled EIA in each species group (under the line) and between these groups (above the line) (***: $P < 0.001$, *: $P < 0.05$, NS: $P > 0.05$, pairwise Wilcoxon tests).

Species-specific detection probabilities were mainly low, with greater than 80% of observed species having mean detection probabilities of less than 0.5 per visit in the study area (Suppl S3.7). This probability varied between 0.01 (*Callophrys rubi*) and 0.93 (*Decticus albifrons*). Comparison of the different taxonomic groups showed a significantly lower mean detection probability for butterflies (0.20 ± 0.17) than for dragonflies (0.33 ± 0.22) and grasshoppers (0.29 ± 0.21) (Wilcoxon test, $P < 0.001$; Fig.3.6a). In contrast, no significant difference was noticeable between species covered by conservation status and uncovered species (Wilcoxon test, $P > 0.05$; Fig.3.6b).

The estimation of the average posterior of the parameters a and b from the hierarchical model made it possible to evaluate the importance and the direction (positive or negative) of species response to the different habitat and visit covariates in term of occurrence and detection (Suppl S3.8 and S3.9). The mean species-specific effect of site area ($a1$) on the probabilities of occurrence was positive for all species, varying from 0.12 (*Argynnis paphia*) to 0.42 (*Issoria lathonia*). Yet, the $CI_{95\%}$ of this parameter for all species included the zero value, revealing an absence of strong significant effect. Species response in terms of occurrence was more variable for habitat diversity ($a2$). This parameter varied between -0.84 (*Dociostaurus jagoi*) and 0.90 (*Calliptamus wattenwylanus*) without any significant trend (almost 54% showed positive response and 46% showed negative response). The proportion of closed habitat ($a3$) had mostly a positive linear effect on species-specific occurrence probabilities, with a variation between -0.91 (*Libellula fulva*) and 1.93 (*Anthocharis euphenoides*) and 13 species showing a significant positive response. Moreover, all species were marked by a negative quadratic effect ($a4$) (without significant response), which indicated an occurrence maximized for intermediate values of closure.

The influence of visit date ($b1$) on species-specific detection probabilities was characterized by a high variability, going from -5.24 (*Melanargia occitanica*) to 4.58 (*Euchorthippus elegantulus*) and with 60% of the species showing a negative response. A high proportion of species (44%) had a $CI_{95\%}$ that did not overlap zero, which highlighted the importance of planning visits for insect detection. The majority of these species (64%) decrease of their detection probability throughout the year. A negative quadratic response to this covariate ($b2$) was also revealed for all species, with a significant value for 61% of them. Detection probabilities of a proportion of species were then maximized for intermediate date values. These values were highly variable across species, in relation to their phenology and

the variability of their detection according to their life stage. Regarding their mean values, cicadas and grasshoppers were mostly detectable in summer (July-August) whereas butterflies and dragonflies showed higher detection probabilities earlier in the season (May-June) (Suppl S3.6c). The time were the visit was conducted ($b3$) had a negative effect on almost 93% of the species, with a significant response for 26% of them. The value this parameter varied between -1.41 (*Euchorthippus elegantulus*) and 0.68 (*Uromenus rugosicollis*). Probability of false-absence was globally higher during visits started in the afternoon or conducted during the night for the four studied taxonomic groups (Suppl S3.6c). Some species (7%) showed positive (but non-significant) response to this covariate. A large part of these species were grasshoppers characterized by mainly nocturnal activity, detectable through their mating calls. Finally, detection probabilities were positively correlated to the effect of visit length ($b4$) for almost 65% of the studied species. This parameter varied from -0.39 (*Platypleis acutipennis*) to 0.34 (*Leptidea sinapis*) and was significant for only two species. The value of the mean detection probability was almost constant after one to seven hours of survey for each taxonomic group (Suppl.S3.6c).

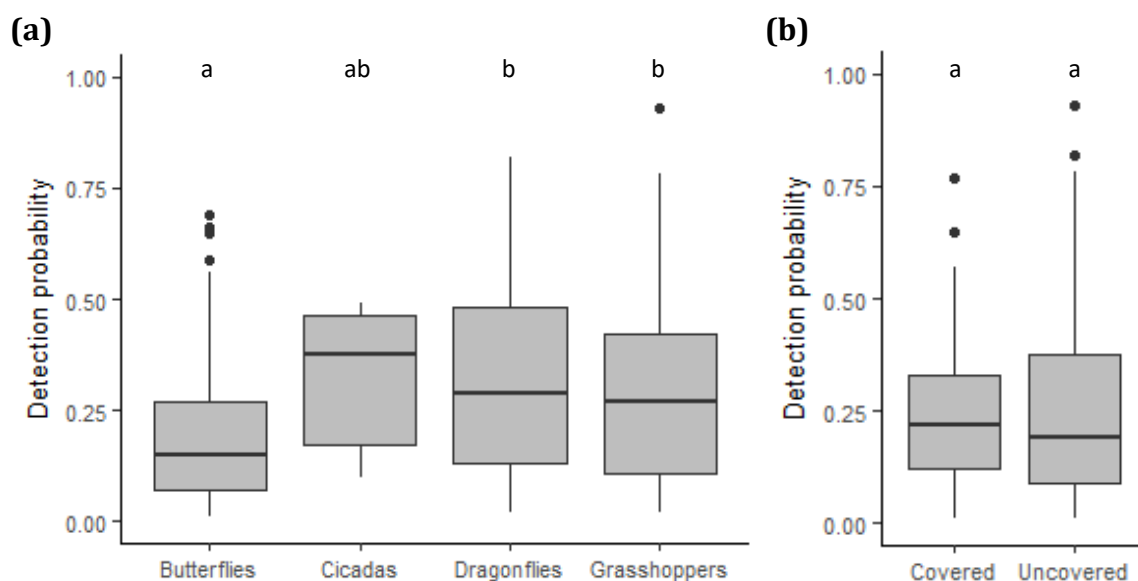


Figure 3.6 : Mean posterior estimates of detection probability among insects' species depending on their taxonomic group (a) and to their conservation status (b). Taxonomic groups are categorized into butterflies (n = 102), cicadas (n = 8), dragonflies (n = 46) and grasshoppers (n = 71). Conservation status are categorized into covered species (n = 33) and uncovered species (n = 194). Different letters refer to a significant difference ($P < 0.05$) between modalities according to pairwise Wilcoxon's signed-rank tests.

III.3.6. Minimum survey effort requirement

The mean number of required minimum visits was $7.15 (\pm 9.94)$, with great variability across species, ranging from 0.2 (*Prionotropis azami*) to 72.9 (*Pieris manii*) visits (Suppl S3.7). The value estimated for several species showed a particularly large confidence interval ($CI_{95\%}$). This lack of precision could be link to the method of modelling through data shrinkage, allowing estimating the detection probabilities of species for which very little field data has been collected. There was no significant difference in terms of minimum effort requirements between the surveyed taxonomic groups (Kruskall test, $P > 0.05$; Fig.3.7a). On the other hand, the average number of visits required to certify the absence of a species covered by a conservation status was significantly lower (2 ± 1.86 visits) than for uncovered species (7.39 ± 9.98 visits) (Wilcoxon test, $P < 0.001$; Fig.3.7b).

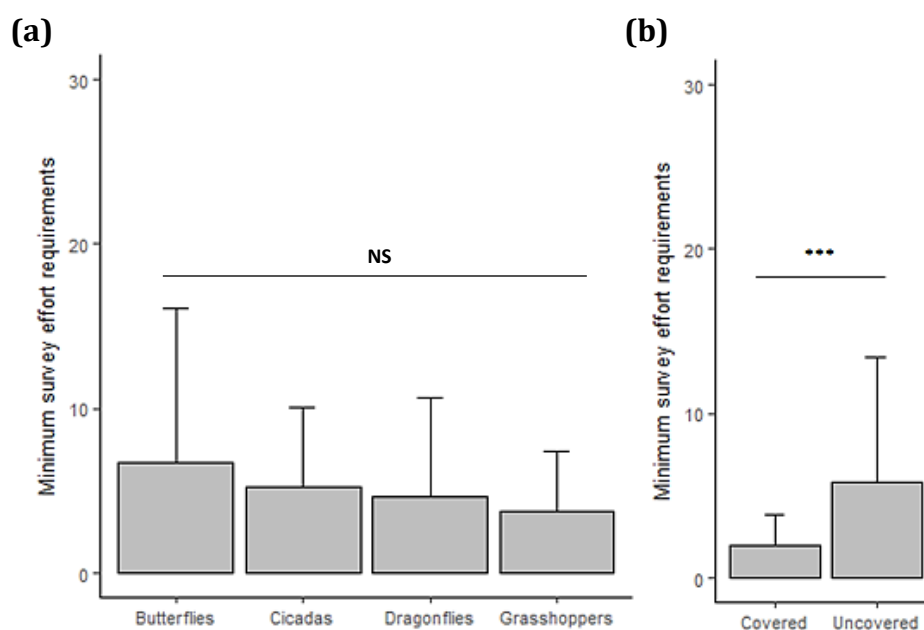


Figure 3.7 : Mean values (\pm SE) of minimum survey effort requirements among insect's species depending on their taxonomic group **(a)** and to their conservation status **(b)**. These values were estimated on the base of species-specific detection probabilities obtained through the MSOM under optimal survey conditions (i.e. for values of survey covariates maximizing detection probability). Taxonomic groups are categorized into butterflies ($n = 102$), cicadas ($n = 8$), dragonflies ($n = 46$) and grasshoppers ($n = 71$). Conservation status are categorized into covered species ($n = 33$) and uncovered species ($n = 194$). Asterisks indicates significant differences of sampling coverage between classical EIA and doubled EIA in each species group (under the line) and between these groups (above the line) (***: $P < 0.001$, *: $P < 0.05$, NS: $P > 0.05$, pairwise Wilcoxon tests).

III.4. Discussion

This study highlights the significant influence of the imperfection of insect detection on the quality of entomological surveys under EIA conditions. They reveal a major gap between survey results and the potential richness on a site, with in average one in two species which will remain undetected after the application of this type of classical effort. This bias remains significant when focusing on protected or vulnerable species (with a detection of less than 60% of the potential species), even if it was significantly fewer than for uncovered species. We showed that the doubling the sampling effort allowed a significant increase in survey completeness, but the average difference with the potential richness remains important. Given the estimated correlation between species-specific parameters and covariates links with survey conditions, it seems more relevant to fragment available resources into shorter visits, spread throughout the season and including at least a night visit, rather than spending more time on a site.

III.4.1. Representativeness of EIAs and sampling effort

We have been able to demonstrate the impossibility of establishing a complete list of the insect species present on a site from the number of visits defined under a classical EIA, whatever the taxonomic group considered. In the majority of cases (*i.e.* 15 out of 20 sites) the sampling design was limited to only 2 to 4 visits on the site during the year (Table 3.2). Although the richness was better covered on some sites than others (70% of the species detected for the most exhaustive, Table 3.2), one in two potential species will remain on average undetected after the application of this type of classical effort (Fig.3.1b). The lists of species established through the usual recommendations show a significant bias and represent only a truncated view of the diversity occupying a site, even though visits are made by experienced entomologists with a good knowledge of the area. This result is not totally unexpected with regard to knowledge about the richness and structure of insect communities. Many species occurred in low density, with populations established on relatively limited surface habitat areas (Paivinen *et al.*, 2005; New, 2010). This relative rarity, coupled with cryptic habits and often short flight periods, could limit the detection probabilities of these species if they are not specifically researched (Mao & Colwell, 2005). This part of the community will remain difficult to observe, even in the case of abundant resources allocated to the realization of many visits (Kéry & Plattner, 2007). Estimating species richness within

diversified entomological communities will usually require a particularly costly effort (Foggo *et al.*, 2003; Coddington *et al.*, 2009). If we take the example of butterflies, except from results obtained for poorer assemblages in Northern Europe (Wikström *et al.*, 2009), a minimum of ten field surveys seems generally necessary to approach 90% of the richness of sites in temperate climates, under standardized sampling conditions (Dennis *et al.*, 1999; Jonason *et al.*, 2010; Hardersen & Corezzola, 2014). Considering the entomological diversity of the Mediterranean area and the lack of standardization in EIA surveys (research of different taxa during a same visit, priority research of threatened species habitats ...), it is likely that the effort need to achieve such completeness is even higher.

The significant increase in the proportion of species detected following the double visits shows the influence of sampling effort on the quality of the results. However, although species lists were more representative of the potential richness of the sites, the average difference with this richness remains important even after double visits (Fig. 3.1b). Given the cost of a field visit, this relatively limited benefit in terms of completeness questions the relevance of increasing the sampling effort to improve representativeness of EIA inventories. From a certain threshold, it may become difficult to increase the number of species detected, and the cost of extra effort is likely to exceed the gain from further counts (Heliölä & Kuussaari, 2005). Given that the effort available when conducting an EIA is highly constrained by developer's funding, the goal of complete sampling coverage seems unrealistic. The large difference between the observed richness in double condition and the estimated richness gives an idea of the investment that would then be needed. However EIA do not claim such a degree of completeness, but rather aim to obtain an estimate of the richness and originality of the species assemblages present on the site. Depending on the objective of the study, a certain degree of effort reduction, with non-detection of a part of the community, may be acceptable, as long as the significance of the desired trends can be observed (Loos *et al.*, 2014). Species subsets can provide a reliable surrogate for the full community and reduced effort can allow detecting a representative assemblage of species (Bried *et al.*, 2012b). In the case of EIAs, this quantification of the relationship between the intensity of the sampling effort and sampling coverage may allow the regulator to fix the minimum effort required to reach an acceptable representativeness threshold during design of the sampling plan, which could optimize the cost-quality balance (Garrard *et al.*, 2015).

III.4.2. Going further asymptotic richness

Although the description of the main species assemblages is an important goal sought an EIA (in particular because their richness or their originality can guide the implementation of reduction measures if the project is accepted), the main objective remains the detection of species covered by conservation status. But the effort required for better sampling coverage or more optimal detection may be different depending on the status or rarity of species (MacKenzie & Royle, 2005; MacKenzie *et al.*, 2005). The distinction of several groups of species (taxonomy, conservation issue) in the MSOM allowed us to estimate sampling coverage in terms of detected richness for each of them. Although the average sampling coverage was lower for dragonflies, the results did not show any significant difference between the surveyed taxonomic groups (Fig.3.3a). Conclusions were similar to the results for the total community, both for the importance of the bias and for the relative benefit of increasing sampling effort (Table 3.3). On the other hand, sampling coverage was significantly dependent on the status of the species (covered/uncovered). On average, the proportion of undetected species was greater for covered species and the impact of survey conditions (classical vs doubled), although significant, was more limited (Fig.3.3b). Less than 60% of covered species were detected on average at a site, even after double visits. However, we must note the great variability of this completeness, related to the low number of potential species present on average per site (7.44 species). Since the absolute difference was small (4.25 species observed under doubled conditions), the least new species observed may lead to a significant increase in sampling coverage.

The modeling framework used in the present study also provided the opportunity to go beyond the simple estimation of an asymptotic richness, giving access to the occupancy patterns of individual species driving species richness (Honkanen *et al.*, 2011). The estimation of the difference between the occurrences observed during the visits and that ones estimated by the model allowed us to measure the intensity of the biases related to the heterogeneity of the probability of detection within the community. While the increase in sampling effort has improved to some extent the average detection of the different species groups, the importance of bias will vary depending on the taxonomic group and the species conservation status (Fig.3.5). This bias was significantly more important for butterflies and for uncovered species. Contrary to the general pattern known for threatened species (MacKenzie *et al.*, 2005; Guillera-Aroita *et al.*, 2010), they have been observed on a good proportion of the sites at

which they occurred. This result could be explained by the fact that their detectability was higher on average than the uncovered species (although not significant) (Fig.3.6b). The EIA-specific study design pays greater attention to covered species, preferably targeting their period of activity and the habitats that are favorable to their presence on a site (Jay *et al.*, 2007). Our results thus demonstrate some effectiveness of the current conditions toward this objective. However, some inaccuracy remains, and some covered species are characterized by a particularly important absolute occupation bias (e.g. value of -0.5 for *Saga pedo* (Orthoptera, Pallas 1771)). As with most sampled species, absolute detectability was still relatively low with high variability across species (Fig.3.6). An observer has on average less than one chance in two to detect a species occurring on a site, during a visit made for median values of covariates. This potentially strong propensity for false absences is commonly encountered in insects (Mata *et al.*, 2014) and has already been demonstrated for butterflies, despite surveys focused solely on this taxon and more standardized conditions (Dorazio *et al.*, 2006; Kéry & Plattner, 2007). The risk of direct population destruction of these undetected species increases the importance of considering these biases when assessing the impact of a project. Although the increase in sampling effort has allowed a significant increase in the average detection of these species at their sites of presence (Fig.3.5b), the benefit remains limited for a significant proportion of covered species (i.e. no change in absolute bias occurrence between classical and doubled EIA conditions for 80% of them). It therefore seems necessary to adjust this increase in effort by a more cost-efficient allocation of resources. Detection probability can be improved by adjusting the sampling conditions, adapted to the local peculiarities of the sites. The study of the correlation between probabilities of occurrence and detectability and the different covariates incorporated into the hierarchical model allowed us to identify these optimal conditions.

III.4.3. Influence of the local context of the sites

Our results show that larger sites host a larger number of species, and species detected during our visits have a higher probability of being present on those sites (Table 3.4). This relationship between area and species richness is already documented in some insect groups surveyed in our study (Steffan-Dewenter & Tscharntke, 2000; Öckinger & Smith, 2006; Ruggiero *et al.* 2008). A site with a large area is more likely to cover the home range of several species and to include diverse natural habitats (as shown by the strong positive correlation between these two variables in our study; Suppl.S3.5). Consistent with this

pattern, the greater the number of identified natural habitats, the higher the potential richness of a site estimated by the MSOM (Table 3.2, Suppl.S3.1). However, our results do not reveal any significant influence of this parameter on species occurrence (Table 3.4, Suppl.S3.6). The heterogeneity of the natural habitats on a site leads in the majority of the cases to the multiplication of the niches available for the invertebrates (Tew *et al.*, 2003). The diversification of available resources, particularly plants communities (Haddad *et al.*, 2009), allows the co-occurrence of a larger number of species within the same area. However, within this community each species will respond specifically to certain factors that will favor its presence (habitat, biotic interactions...) (Rosin *et al.*, 2012), without necessarily depending on the absolute diversity of habitats on the site.

The degree of closure of the sites seems to be one of the habitat parameters which significantly influence the composition of the entomological community (Table 3.4, Fig.3.4). Each species has its own optimum of occurrence along this closure gradient linked to its specific requirements (e.g. *Aiolopus puissantii* (Orthoptera, Defaut 2005) linked to the most open sites, *Isophya pyrenaea* (Orthoptera, Audinet-Serville 1838) with a higher occurrence in sites dominated by woodland), and a large part of the community seems to be favored by intermediate values (Suppl S3.6). These intermediate conditions allow the coexistence of several stages of succession on the same locality. Because most species generally use several types of adjacent habitats, such coexistence gives them access to complementary resources or to micro-habitats required for some specific phases of their life cycle (e.g. dragonflies occur preferentially along edges during their maturation) (Van Halder *et al.*, 2011 ; Ushida & Ushimaru, 2014).

In a rather counter-intuitive way, our results showed a significant positive correlation between site covariates that favor species richness and sampling coverage (Fig.3.4). Larger sites showing a greater diversity of habitats were, on average, surveyed with greater precision. But in the majority of cases, the more diverse a community will be, the more its real richness will be difficult to observed (Gotelli & Colwell, 2011). The relationship observed in our study seems to be related to the correlation between site area and sampling effort, with larger site receiving more visits (Suppl S3.5). Such increase in sampling effort could have increased the performance of the surveys, notably by providing better coverage of the time window favorable to the sampled groups.

III.4.4. Adjustment of survey conditions to maximize species detection

Although the mean probability of detection was low for the majority of the species, this parameter shows a significant variation according to the conditions of each visit. The date and time at which the visits were carried out have the most significant influence on species detection and will therefore constitute important levers for improving the quality of EIA results (Table 3.4, Suppl S3.9). The influence of the visit's date showed in particular the greatest heterogeneity within the community. Species presented various detection optimum, with some threatened species almost perfectly detectable during precise periods of the year (i.e. *Zerynthia polyxena* (Rhopalocera, Denis & Schiffermüller 1775) for visits conduct in early April). Time of the year in which surveys will be undertaken constitute a major issue for the detection of species covered by conservation status and the spreading of visits throughout the season is necessary to improve the sampling coverage (Bell *et al.*, 2014; Petitot *et al.*, 2014).

The starting time of survey had a more homogeneous influence and visits started early in the day seemed to improve the detection of a high number of species, whatever the visit length. However, each species shows its own daily cycle of activity (Hassall & Thompson, 2008) and some threatened species will be much better detected in later passages (i.e. *Saga pedo*, with an optimal detection probability when visits were conducted at 24 pm). The realization of at least one nocturnal visit (as it is already the case in some EIAs conducted in the Mediterranean area) seems justified in relation to these issues, although this effort is not sufficient to ensure perfect detection.

On the other hand, visits length did not appear as a significant parameter for the quality of EIAs results. The majority of species did not show any particular response to this factor in terms of detection probability. The variations of the number of visits and of their length are generally two methods of resources allocation on which it is possible to play simultaneously (Bried *et al.*, 2012b; Hardersen & Corezzola, 2014). From our results, it seems more relevant to fragment available resources into shorter visits, spread throughout the season and including at least a night visit, rather than spending more time on a site (Dettmers *et al.*, 1999).

The estimation of the minimum survey effort required to attest the absence of each species provides a first view of the investment required to obtain representative results, under the assumption of visits made under optimal conditions for detecting target species. These requirements seemed already important for a high number of species (Suppl S3.7). For many species, these needs appeared unrealistic with respect to the constraints and objectives of an EIA. However, the minimum requirements of most threatened species seem to fit within EIA framework (Fig.3.7b).

III.4.5. Hierarchical model as a decision-making tool for the regulator

Considering the results of our study, MSOMs seem to be a relevant tool for measuring the completeness of biological surveys, allowing to consider the variability related to species-specific response. The fact that the estimates fitted well to our data (Suppl S3.2) and the consistency of the estimated richness values (given the potentialities of the studied landscapes; Table 3.1), despite the relatively limited number of input data, shows their potential for the valorization of incidence data collected through wandering surveys. Moreover, analysis of multi-species data can be challenging because sampling techniques often identify numerous species with few detections (Zipkin *et al.*, 2010). Unlike less diverse groups, the richness of insect communities makes it difficult to obtain accurate data for all species in a single visit (Sewell *et al.*, 2012; Petitot *et al.*, 2014). The bayesian shrinkage process allows overcoming this limit by going beyond a simple aggregation of individual estimates, which can give biased results (Zipkin *et al.*, 2009; Clark *et al.*, 2014). Where analyzes based on rarefaction curves have shown their limits (Kobitz *et al.*, 2017), MOSM could become a decision-making tool in the context of EIA and insect conservation (Sauer *et al.*, 2013; Mata *et al.*, 2017).

Nevertheless, accuracy of species-specific estimates will always be limited by the amount of available data (Zipkin *et al.*, 2009). In the present case, the low number of sites (i.e. 20 sites) linked to a heterogeneous number of visits should lead us to consider some numerical results with caution, especially with regard to the estimation of the minimum effort requirements (which show a very high standard deviation for some species sparsely observed). Our work should be considered as a "preliminary" study, allowing to alert regulators about the main biases of current EIA survey conditions and to extract valid guidelines for the studied landscapes (i.e. Mediterranean area). This study could be improved

in the future by carrying out more investigations and declined over a wider variety of conditions through recent developments in MSOM (multi-region models, guild distinction ...) (Sutherland *et al.*, 2016; Tenan *et al.*, 2017).

III.4.6. Conclusion

Our results emphasize the need for field protocols that accommodate estimation of detection error when conducting entomological multi-species surveys in the case of EIA. They highlight the benefit of using reference values to quantify the completeness of the results from these studies in order to obtain a more precise assessment of the risks associated with the project for the conservation of threatened insects. Given that the flexibility is particularly limited in the context of EIA due to the limited available resources, the establishment of guidelines for optimal allocation is essential in order to maximize the value of data from multi-taxa surveys (Field *et al.*, 2005; Lovell *et al.*, 2010). The number of visits, their spread over the year and the time at which they will be carried out will then constitute important parameters for the establishment of minimum standard guaranteeing the quality of studies.

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Supplementary materials 3

Supplementary material S3.1: Site description and sampling summaries.

Supplementary material S3.2: Illustration of the Multi-Species Occupancy Model framework.

Supplementary material S3.3: Goodness-of-fit test for single season multi-species occupancy models

Supplementary material S3.4: Estimated species richness.

Supplementary material S3.5: Correlation index between the habitat covariates measured at the scale of the sampled sites and the total number of visits made per site.

Supplementary material S3.6: Posterior estimates of community level occurrence (a) and detection (b) probabilities as a function of site (a) and survey (b) covariates.

Supplementary material S3.7: Posterior estimates of the species-specific occurrence and detection probabilities of insect species as estimated under the MSOM.
(À consulter dans la partie “Annexes” du manuscrit de thèse).

Supplementary material S3.8: Posterior estimates for the effect of site covariates on observed insect species as estimated under the MSOM.
(À consulter dans la partie “Annexes” du manuscrit de thèse).

Supplementary material S3.9: Posterior estimates for the effect of visit covariates on observed insect species as estimated under the MSOM.
(À consulter dans la partie “Annexes” du manuscrit de thèse).

Supplementary material S3.1: Site description and sampling summaries. 'Habitat' indicates the number of natural habitats included in the limit of the site (described from field surveys using the CLC nomenclature), 'Closure' refers to the proportion of the site area occupied by closed habitat (dense shrubland, forest) and 'Surveys' to the number of visits conduction during the classical EIA.

N°	Locality	Lat.	Long.	Administrative unit	Region	Area	Altitude	Habitat	Closure	Surveys	Year	Start date	End date
1	Lieuran-lès-Béziers	N 43°25'08.4"	E 003°14'20.8"	Herault	Languedoc	950.09	40	33	4.36	5	2015	Apr 14th	Jun 29th
2	Mauguio	N 43°37'00.5"	E 004°00'34.2"	Herault	Languedoc	38.9	3	24	11.90	4	2015	Apr 10th	Jun 11th
3	Lespignan	N 43°16'22.4"	E 003°10'21.0"	Herault	Languedoc	43.79	20	6	0.27	4	2015	Apr 20th	Jul 2nd
4	Fabrègues	N 43°33'04.3"	E 003°46'30.0"	Herault	Languedoc	25.83	20	20	9.48	3	2015	Apr 9th	Jun 24th
5	Montdardier	N 43°55'38.6"	E 004°35'34.1"	Gard	Languedoc	59.31	642	6	13.05	4	2015	Apr 15th	Jul 19th
6	Rians	N 43°36'22.7"	E 005°45'22.3"	Var	Provence	63.63	390	11	62.42	3	2015	Apr 11th	Jul 23th
7	Gallargues-le-Montueux	N 43°43'09.1"	E 004°10'07.3"	Gard	Languedoc	58.37	15	17	1.90	2	2015	Apr 10th	Jul 8th
8	Pézenas	N 43°38'26.5"	E 003°25'26.0"	Herault	Languedoc	156.55	22	19	4.17	2	2015	Apr 13th	Jul 10th
9	Bessan	N 43°21'40.0"	E 003°25'36.5"	Herault	Languedoc	73.63	45	20	21.35	2	2016	Jun 30th	Aug 4th
10	Saint-Thibéry	N 43°23'42.7"	E 003°24'59.8"	Herault	Languedoc	486.83	35	30	3.77	2	2016	Apr 25th	Jul 4th
11	Pinet	N 43°24'15.8"	E 003°30'34.2"	Herault	Languedoc	541	50	39	14.32	9	2016	Apr 7th	Jul 25th
12	Poussan	N 43°29'18.2"	E 003°40'13.4"	Herault	Languedoc	443.69	80	38	5.37	9	2016	Apr 4th	Jul 8th
13	Murviel-lès-Béziers	N 43°26'23.3"	E 003°08'39.8"	Herault	Languedoc	685.44	47	65	23.95	5	2016	Apr 6th	Apr 27th
14	Saint-Pargoire	N 43°31'39.7"	E 003°31'12.0"	Herault	Languedoc	365.11	195	27	85.20	7	2016	Apr 4th	Jul 12th
15	Saint-Victor-la-Coste	N 44°03'52.2"	E 004°38'23.3"	Gard	Languedoc	102.67	248	5	98.28	4	2016	Apr 20th	Jul 13th
16	Lamanon	N 43°42'01.1"	E 005°05'25.8"	Bouches-du-Rhones	Provence	9.1	120	15	4.72	4	2016	May 20th	Jul 24th
17	Istres	N 43°29'56.0"	E 004°57'07.2"	Bouches-du-Rhones	Provence	16.18	10	8	28.12	3	2016	May 05th	Jul 22th
18	Valliguières	N 44°00'31.7"	E 004°34'43.7"	Gard	Languedoc	85.78	235	5	97.61	2	2016	May 13th	Jul 14th
19	Saint-Hilaire-d'Ozilhan	N 43°58'10.2"	E 004°35'26.9"	Gard	Languedoc	136.01	190	6	95.99	2	2016	May 26th	Jul 14th
20	Vendargues	N 43°39'19.8"	E 003°58'06.2"	Herault	Languedoc	12.88	52	12	9.39	3	2016	Apr 18th	Jul 18th

Supplementary material S3.2: Illustration of the Multi-Species Occupancy Model framework.

species i	Site k								ω_i
	Observed				Partially observed				
	1	2	...	J	1	2	...	J	
1	X_{11}	X_{12}	...	X_{1J}	Z_{11}	Z_{12}	...	Z_{1J}	ω_1
2	X_{21}	X_{22}	...	X_{2J}	Z_{21}	Z_{22}	...	Z_{2J}	ω_2
...
n	X_{n1}	X_{n2}	...	X_{nJ}	Z_{n1}	Z_{n2}	...	Z_{nJ}	ω_n
$n+1$	0	0	...	0	$Z_{n+1,1}$	$Z_{n+1,2}$...	$Z_{n+1,J}$	ω_{n+1}
...
...
N	0	0	...	0	Z_{N1}	Z_{N2}	...	Z_{NJ}	ω_N
$N+1$	0	0	...	0	$Z_{N+1,1}$	$Z_{N+1,2}$...	$Z_{N+1,J}$	ω_{N+1}
...
...
M	0	0	...	0	Z_{M1}	Z_{M2}	...	Z_{MJ}	ω_M

Fig.1. Conceptualization of the super-community of M species used in data augmentation process of the Multi-Species Occupancy Model (MSOM) framework. x comprises a matrix of n rows of observed visit frequencies and $M-n$ rows of unobserved (all-zero) visit frequencies (the *detection process*). z denotes a matrix of species- and site-specific occurrence parameters (the *ecological process*). ω denotes a vector of parameters that indicate membership in the community of N species available to capture (adapted from Dorazio *et al.*, 2011).

		<i>Detection process</i>				<i>Ecological process</i>				ω_i
		Site 1	Site 2	Site 3	Site 4					
		1 2 3	1 2 3	1 2 3	1 2 3					
Observed data	Sp 1	1 1 1	0 0 1	0 1 0	0 0 0	1	1	1	0	1
	Sp 2	0 0 0	1 0 1	0 0 1	1 0 0	1	1	1	1	1
	3	0 1 1	0 0 0	0 1 0	0 1 1	1	1	1	1	1
	4	1 0 1	1 0 0	1 1 1	1 0 1	1	1	1	1	1
	n	1 0 1	1 0 0	0 0 0	0 0 1	1	1	0	1	1
Data augmentation		0	0	0	0	0	1	1	0	1
		0	0	0	0	1	0	1	0	1
		0	0	0	0	1	0	0	0	1
		0	0	0	0	0	1	1	0	1
		0	0	0	0	0	1	1	1	1
		0	0	0	0	1	1	0	0	1
		0	0	0	0	0	0	0	1	1
	N	0	0	0	0	1	0	0	1	1
		0	0	0	0	0	0	0	0	0
		0	0	0	0	0	0	0	0	0
		0	0	0	0	0	0	0	0	0
M	0	0	0	0	0	0	0	0	0	

Fig.2. Schematic representation of the hierarchical Multi-Species Occupancy Model (MSOM) framework. The *detection process* consists in an incidence data (k visits per site, n observed species) for a number of sites (four in this example), where 1 mean a species was detect during a visit at a site and 0 means that the species was not detected. This matrix was augmented with a virtual large number of zeros to produce a super-community of M fixed species. Such statistical trick allowed simplifying the estimation of the number of species that occupied the sites but never detected during visits. This estimation problem was converted to the distinction of augmented species that were a part of the real community and those that were just extra zero. The distinction was performed through the estimation of an inclusion probability (ω_i). The MSOM estimates species detection and inclusion probabilities within a Bayesian framework using MCMC (Markov Chain Monte Carlo) algorithm. The *ecological process* was represented by a matrix of species presence/absence at each site. This matrix was only partly observed in the *detection process*, because of possible species non-detection. “Sampling” zeros (species undetected at each visit on a site) indicated in grey in the *detection process* may reflected a true absence (in red in the *ecological process*) or simply a non-detection of a present species (in green in the *ecological process*). The inclusion probability ω_i was the probability that a species from the super-community (M) forms a part of the regional community. The “true species richness” of the regional community was then estimated as a sum over the vector ω . In the present example, $n = 5$ species were detected, and the virtual richness of the super-community was fixed to $M = 17$ species by data augmentation. The model estimated the true species richness as $N = 13$ species (5 observed and 8 unobserved), based on the input incidence matrix.

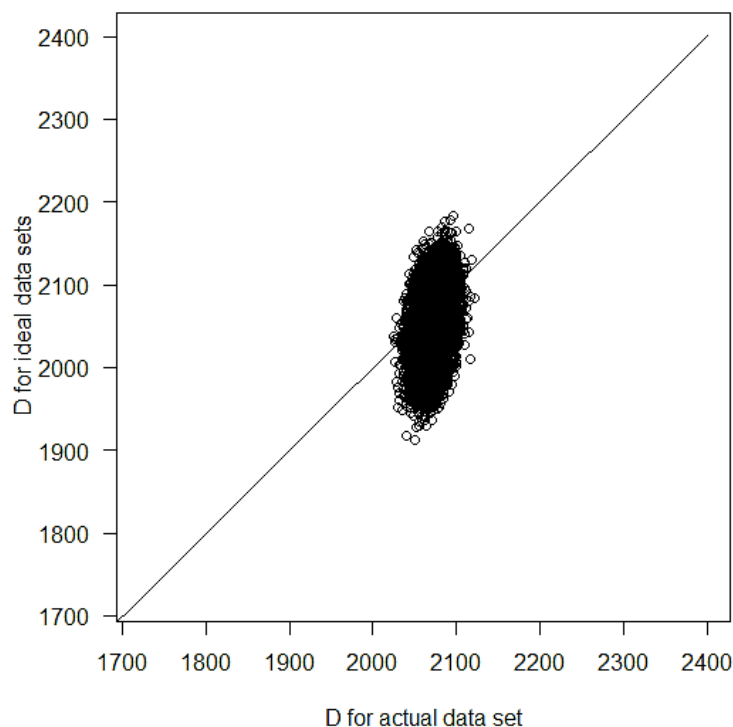
Supplementary material S3.3: Goodness-of-fit test for single season multi-species occupancy models

We assessed model fit using a *Bayesian p-value* (Gelman *et al.*, 1996). We defined a discrepancy measure D following Zipkin *et al.*, 2009:

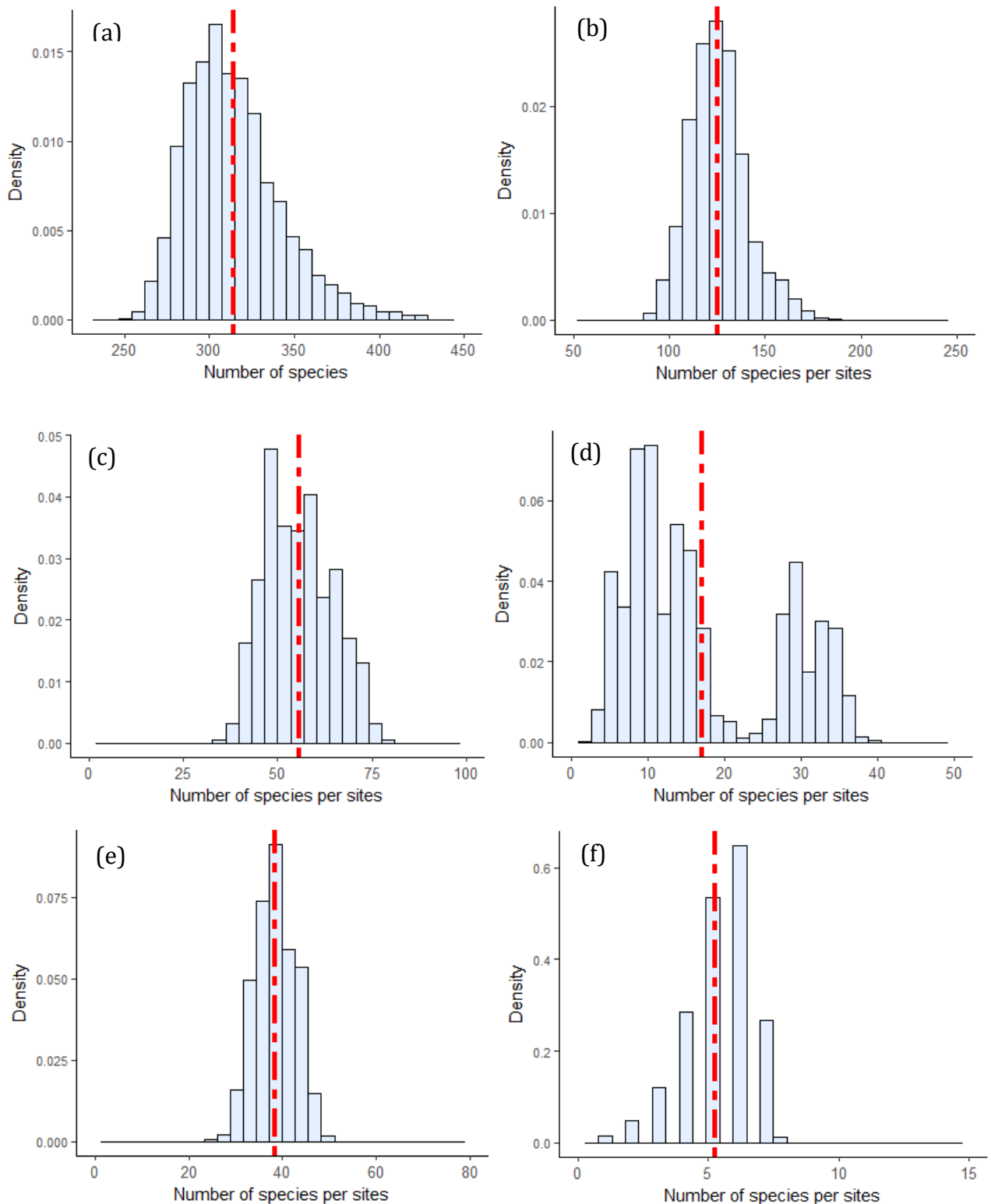
$$D = \sum_i (x_i - p_i)^2$$

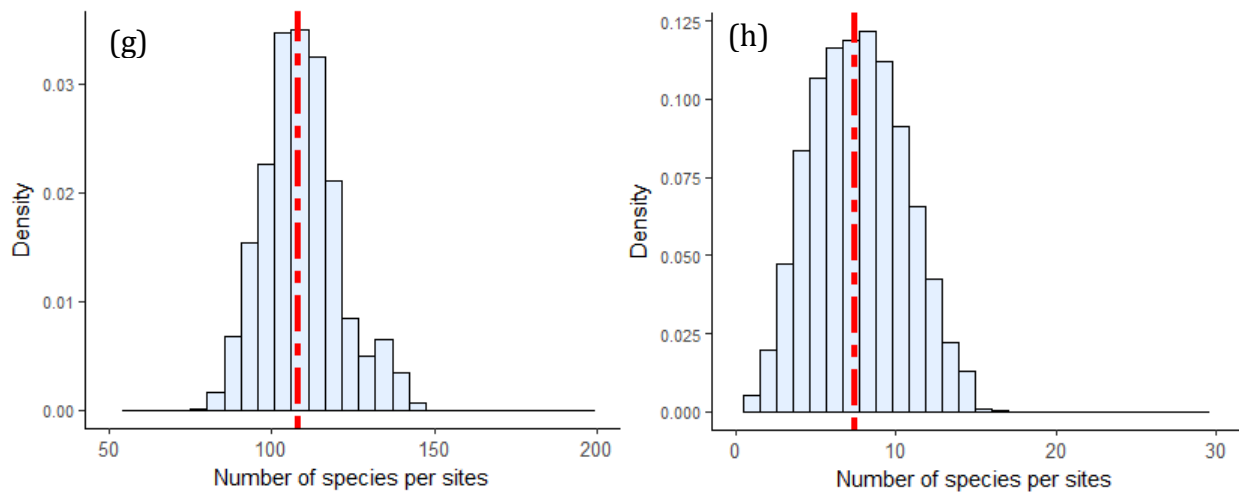
for the observations x_i and their expected values p_i under the MSOM. This discrepancy statistic was computed at each iteration of the MCMC algorithm. A reference distribution was computed by simulating data sets from the posterior distribution and computing the discrepancy measure, D^{sim} , for the simulated data set. The *Bayesian p-value* was calculated as the proportion of times that the deviance of the observed data, D , was greater than the deviance of detections D^{sim} predicted from the model: $\Pr(D > D^{sim})$. Values larger than 0.95 or smaller than 0.05 indicate that the model did not fit well the data. We also calculated a “lack-of-fit” statistics D/D^{sim} which is expected to be equal to 1 if the model fits the data perfectly (Kéry & Schaub, 2012).

For our dataset, the *Bayesian p-value* was estimated at 0.75 and the “lack-of-fit” statistic was estimated as 1.01. These values suggesting that the MSOM provided an adequate description of the input data.

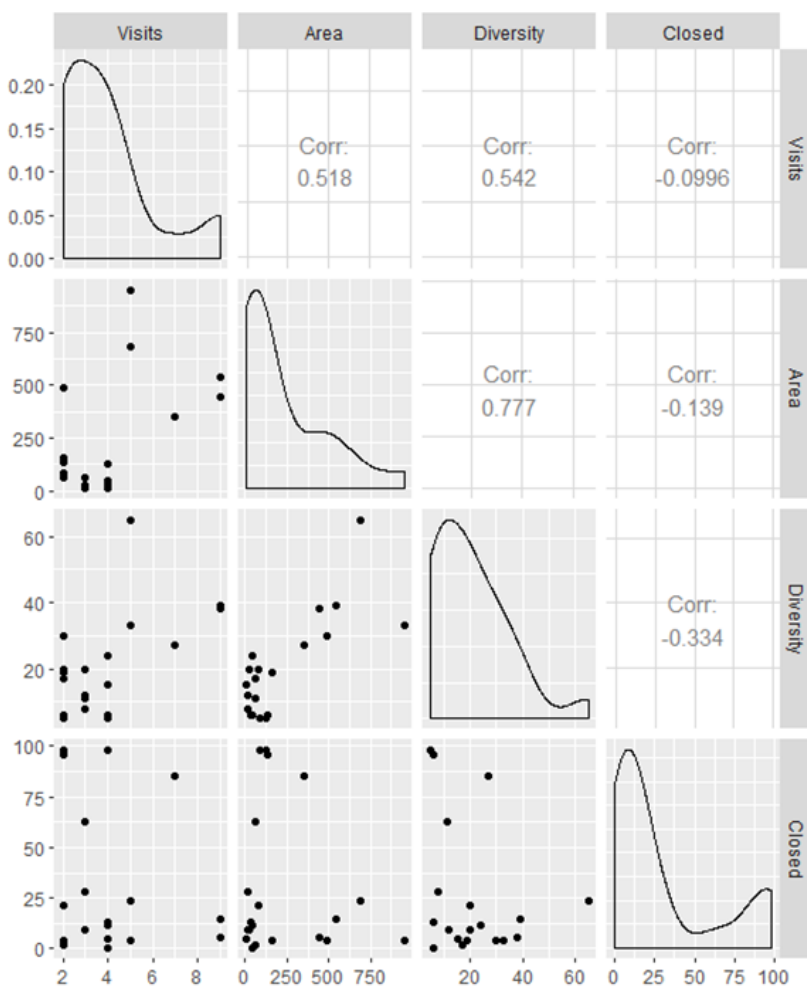


Supplementary material S3.4: Estimated species richness of the community (a), at the scale of each site (b), of butterflies (c), of dragonflies (d), of grasshoppers (e), of cicadas (f), of species uncovered by conservation status (g) and of species covered by conservation status (h). Red lines indicate the mean response and colored bars the posterior distribution (i.e., 100% credible interval).

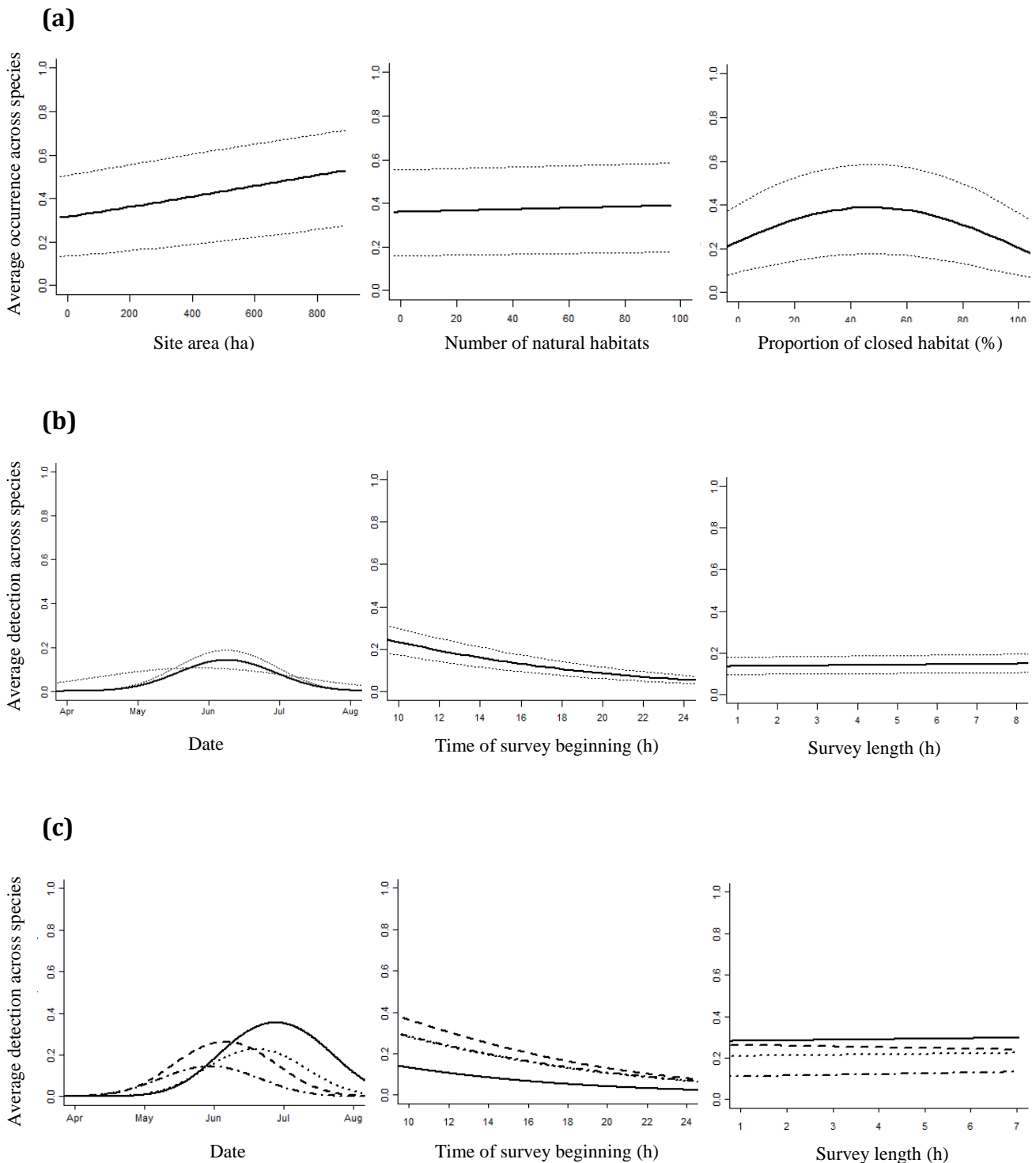




Supplementary materials S3.5: Correlation index between the habitat covariates measured at the scale of the sampled sites and the total number of visits made per site.



Supplementary materials S3.6: Posterior estimates of community level occurrence (a) and detection (b) probabilities as a function of site (a) and survey (b) covariates. Solid line represents the posterior mean community response and dotted lines represent the CI_{95%} of the posterior mean. The mean detection probabilities estimated for different taxonomic groups, on the base of species-specific posterior estimates, were also presented as a function of survey covariates (c). Line types correspond to different taxonomic groups (dotdash: butterflies, solid: cicadas, dashed: dragonflies, dotted: grasshoppers).



Supplementary material S3.7 : Ce supplément volumineux n'étant pas indispensable à la compréhension du chapitre a été déplacé dans la partie « Annexes » du manuscrit de thèse par soucis de clarté.

Posterior estimates of the species-specific occurrence and detection probabilities of insect species as estimated under the MSOM (with mean, standard deviation, $CI_{95\%}$). All the species detected at least during a visit during the survey were listed and grouped according to their taxonomic group. 'Conservation status' refers to the three categories of specific-level conservation issues as described in Materials & methods. The number of observations (count) was also included for each species, under the classical and doubled surveys. For these both modalities, absolute bias in occurrence indicates the difference between the proportion of sites where each species was detected and its occurrence probability, as estimated through the MSOM. The minimum effort requirements to ensure species absence (with a 95% confidence index) were estimated for values of covariables allowing an optimal detectability.

Supplementary material S3.8 : Ce supplément volumineux n'étant pas indispensable à la compréhension du chapitre a été déplacé dans la partie « Annexes » du manuscrit de thèse par soucis de clarté.

Posterior estimates for the effect of site covariates on observed insect species as estimated under the MSOM (with mean, standard deviation, $CI_{95\%}$): a1 – linear effect of the site area (ha); a2 – linear effect of habitat diversity; a3 – linear effect of the proportion of closed habitats (%); a4 – quadratic effect of the proportion of closed habitats (%). Grey cells indicate species with confidence interval not containing zero (considered as indicative of significant response to the parameter).

Supplementary material S3.9 : Ce supplément volumineux n'étant pas indispensable à la compréhension du chapitre a été déplacé dans la partie « Annexes » du manuscrit de thèse par soucis de clarté.

Posterior estimates for the effect of visit covariates on observed insect species as estimated under the MSOM (with mean, standard deviation, $CI_{95\%}$): b1 – linear effect of the visit date; b2 – quadratic effect of the visit date; b3 – linear effect of the visit hour; b4 – linear effect of the visit length. Grey cells indicate species with confidence interval not containing zero (considered as indicative of significant response to the parameter).

Discussion générale

L'accumulation de données de suivi à long terme et l'important développement des programmes de sciences participatives au cours des deux dernières décennies a permis un accroissement important du nombre de données sur la répartition et l'écologie des Rhopalocères et des Odonates à l'échelle de l'Europe (Lukyanenko *et al.*, 2016). Ces deux groupes étant considérés comme des indicateurs écologiques pertinents, cette connaissance plus fine offre l'opportunité de dépasser certaines problématiques liées aux déficits de données qui limitent la construction de stratégies de conservation efficaces de l'entomofaune (Cardoso *et al.*, 2011a). L'hétérogénéité de ces jeux de données, collectés via des protocoles différents ne visant pas les mêmes objectifs et à travers un effort d'inventaire très variable, a pu constituer une limite à leur pleine exploitation. Les récents développements techniques et méthodologiques offrent désormais l'opportunité de corriger ces biais afin d'analyser des patrons d'assemblage des communautés à des échelles spatiales et temporelles plus larges (Robertson *et al.*, 2010 ; Gimenez *et al.*, 2014).

Dans cette optique de valorisation des données naturalistes, ce travail de thèse a permis de décrire la dynamique récente des différentes espèces de Rhopalocères et d'Odonates à l'échelle de la France et d'identifier les principaux facteurs environnementaux qui la conditionne. Il apporte ainsi des éléments en faveur d'une vision plus intégrée de la conservation de ces taxons, en prenant en compte l'hétérogénéité spatiale des enjeux de conservation et des pressions anthropiques. À travers une perspective d'analyse « multi-espèces », il permet également de contribuer au changement de perspectives des programmes de conservation des insectes, nécessitant de se dégager d'une vision « espèce-centrée » et d'améliorer la prise en compte des interactions biotiques qui sous-tendent la structure des communautés (Harvey *et al.*, 2017). Ce travail offre une vision plus large intégrant la variabilité de la réponse des espèces au sein des communautés, en lien avec leurs caractéristiques écologiques, et des liens indirects qu'elles peuvent entretenir à travers un recouvrement de leur niche trophique. Se positionnant à l'interface entre la recherche en écologie et la conservation appliquée, cette thèse contribue à l'articulation entre problématiques fondamentales et besoins opérationnels, en permettant à la fois une meilleure compréhension des mécanismes de structuration des communautés d'insectes et la formulation de recommandations pour une meilleure application locale des politiques de conservation. Le renforcement de ce lien constitue un enjeu majeur de la biologie de la conservation, pouvant permettre d'appuyer la mise en place de stratégies d'inventaire, d'optimiser la conservation en se basant sur une connaissance solide des systèmes biologiques

et de faciliter les retours d'expériences afin d'alimenter les développements méthodologiques (Sunderland et al., 2009).

Changements de répartition des espèces et hétérogénéité des enjeux de conservation

Le **Chapitre 1** a permis de décrire les patrons de changements de répartition des Rhopalocères et des Odonates à l'échelle de la France au cours des 35 dernières années et d'identifier les principaux processus qui les conditionnent, en lien avec les changements environnementaux et l'écologie des espèces. L'application de modèles nuls à des données diachroniques issues d'atlas de répartition a offert la possibilité de prendre en compte l'hétérogénéité des assemblages d'espèces à l'échelle du territoire et la variabilité de la réponse des différentes espèces au sein de ces assemblages (Schatz *et al.*, 2016). Cette étude a mis en évidence de forts contrastes spatiaux dans la dynamique de ces deux groupes, avec des phénomènes de déclin particulièrement fort pour les Rhopalocères dans les départements du nord-ouest de la France et des variations d'occurrences plus faibles et plus hétérogènes pour les Odonates. Les résultats ont aussi révélé l'influence prépondérante des changements d'occupation des sols sur l'appauvrissement des communautés de ces deux taxa. Longtemps considéré comme un facteur ayant des impacts très localisés sur la diversité (Newbold *et al.*, 2015), cette modification des paysages est particulièrement profonde sur une large part du territoire français et constitue une pression majeure pour l'entomofaune. L'urbanisation est particulièrement impliquée dans le déclin des espèces, avec une réponse propre des Rhopalocères à l'extension des secteurs d'agriculture intensive et des Odonates à la régression des zones humides. Cette double réponse face à l'urbanisation montre l'intérêt de l'analyse conjointe de deux taxa à l'écologie différente, permettant de couvrir les différentes composantes du paysage affectées par les activités humaines (Cleary *et al.*, 2004 ; Herrando *et al.*, 2016 ; Zeuss *et al.*, 2017). L'influence du climat semble plus limitée ou masquée par ces phénomènes à l'échelle de l'aire d'étude. Les espèces étendant leur aire vers le nord de l'Europe doivent en effet s'appuyer sur l'existence d'habitats potentiellement favorables, que l'artificialisation des paysages peut limiter. La majorité des espèces actuellement en expansion sont des ubiquistes peu exigeantes dans le choix de leurs habitats (Parmesan *et al.*, 1999 ; Mattila *et al.*, 2011).

La connaissance de cette hétérogénéité spatiale dans la dynamique des distributions d'espèces constitue un point important pour la planification de stratégies de conservation cohérentes, permettant l'allocation la plus pertinente des ressources humaines et financières. Les résultats issus de cette analyse montrent notamment une concentration progressive des enjeux de conservation sur certaines régions abritant encore des communautés diversifiées et la majorité des espèces menacées. C'est notamment le cas du pourtour méditerranéen et des secteurs d'altitude du sud et de l'est de la France. Ces régions sont actuellement soumises à des pressions susceptibles de s'accroître dans les prochaines années. Sur un même territoire, l'artificialisation de certains secteurs s'intensifie, en lien avec une concentration de la population ou des activités récréatives), quand d'autres évoluent progressivement vers la fermeture du milieu. Parallèlement, du fait de l'accroissement des épisodes de sécheresse et de la pression de prélèvement pour les activités humaines, la ressource en eau tend à devenir limitante pour de nombreuses espèces notamment d'Odonates. Ce travail fournit ainsi des premiers éléments de priorisation des secteurs qui nécessitent une concentration des efforts de conservation. Ces dynamiques paysagères soulignent également la nécessité de mettre en place des mesures spécifiques pour tenter de contrôler ces pressions liées aux changements d'occupation des sols. Les listes d'espèces protégées constituent un des leviers d'actions principaux pour une prise en compte des enjeux liés à la conservation de la biodiversité dans la politique d'aménagement. À travers la procédure d'étude des impacts sur l'environnement, la détection d'espèces présentes sur ces listes constitueront un poids réglementaire pouvant conduire à la mise en place de procédures de réduction, d'évitement ou de compensation. La déclinaison de la liste nationale des insectes protégés en plusieurs listes régionales pourrait par exemple permettre de prendre en compte l'hétérogénéité des enjeux, en augmentant la liste initiale par un lot d'espèces constituant localement un enjeu important (Schatz *et al.*, 2014).

La compilation d'une base de traits écologiques a également permis de révéler une hétérogénéité dans la réponse des espèces aux changements d'occupation des sols en lien avec les caractéristiques de leurs niches écologiques. Ces résultats permettent d'identifier les espèces présentant les taux de déclin les plus significatifs (principalement des spécialistes peu mobiles ou celles impliquées dans des interactions obligatoires) et fournir des éléments pouvant contribuer à une hiérarchisation plus cohérente des enjeux de conservation. Sur l'ensemble des espèces ayant enregistré un déclin significatif au cours des 35 dernières années, presque 80% ne sont couvertes par aucun statut de protection réglementaire. À

l'image des recherches récentes menées à l'échelle de l'Europe (Cardoso, 2012 ; Leandro *et al.*, 2017), ces résultats plaident ainsi fortement en faveur d'une réévaluation des politiques publiques en matière de conservation mises en place en France et le développement d'une procédure facilitant la réévaluation de ces statuts à partir des résultats scientifiques d'identifications des vulnérabilités spécifiques et des menaces environnementales et humaines. La dernière mise à jour des listes de protection d'espèces date de la dernière décennie (2007), et elle ne constituait alors qu'une simple reprise de la première liste émise en 1993 pour les deux groupes étudiés. Bien que les Rhopalocères et les Odonates représentent l'essentiel des organismes couverts par ces listes, plusieurs espèces ont été sélectionnées pour leur aspect emblématique (par ex. l'Apollon, *Parnassius apollo* ; Samways, 1994) ou bien sur la base d'évaluation principalement valable pour le nord de l'Europe (par ex. l'Agrion de Mercure, *Coenagrion mercuriale*, Charpentier, 1840). Bien que certains projets sortant de ce cadre réglementaire et plus cohérents avec les évaluations des enjeux réels aient été développés avec succès (par ex. le PNA en faveur des Odonates), la majeure partie des leviers institutionnels restent fortement liées à ces listes d'espèces protégées. Si d'espèces protégées par le droit français (ou de leurs habitats) constitue un des arguments les plus forts pour la définition des stratégies d'évitement, de réduction, et compensation dans le cadre des études d'impacts, la question de la représentativité de ces listes vis-à-vis de la vulnérabilité de la diversité entomologique devient critique.

Au-delà de ces conclusions, plusieurs biais liés au manque de résolution du jeu de données ont limité l'interprétation de certains résultats. L'absence d'information sur la répartition spatiale et temporelle de l'effort d'échantillonnage rend en effet difficile la quantification de l'exhaustivité et de la comparabilité des données. Plusieurs méthodes de correction, propres à ce type de bases de données hétérogènes, existent ou sont en cours de développement. Certaines se basent notamment sur l'utilisation d'indices non paramétriques de richesse asymptotique afin de calculer un nombre d'espèces potentiellement présente, servant de seuil pour évaluer l'exhaustivité de la connaissance de la maille (Romo *et al.*, 2006 ; Bruno *et al.*, 2012). Cependant, leur application nécessite d'avoir accès à des données brutes ou au moins à un nombre de données par unité de surface, utilisé comme proxy pour représenter l'effort d'échantillonnage (Lobo, 2008). Les atlas de répartition utilisés comme base du présent travail ne présentent qu'une agrégation de données à l'échelle départementale. Toutefois les programmes de centralisation des données naturalistes actuellement pilotés par le MNHN dans le cadre de l'INPN et du SINP pourraient offrir prochainement une alternative

intéressante pour affiner les résultats issus de cette étude à l'avenir. Actuellement très avancés pour ce qui est des Rhopalocères et des Odonates (P.Dupont, *comm.pers.*), ces programmes pourraient donner accès à une base plus complète des données ponctuelles ou maillées à l'échelle de la France, collectées à partir d'un réseau de référents répartis sur le territoire et via un contact avec les associations naturalistes locales. Cette base pourrait permettre d'affiner notre compréhension des variations de présence de ces taxa en intégrant dans les analyses statistiques plusieurs caractéristiques de ces inventaires comme l'effort d'échantillonnage par unité de surface (secteur ou département par exemple), la focalisation sur certaines espèces protégées en défaveur des espèces communes, la couverture spatiale des différents habitats, les conditions de réalisation de ces inventaires. Cette future base de données plus complète est donc prometteuse d'une meilleure connaissance et il faut espérer que les mesures de conservation associées soient à la hauteur de cette connaissance.

Rôle de la spécificité des interactions biotiques dans la réponse des espèces

Cette première partie a mis en évidence l'influence significative de la position des espèces le long du continuum spécialistes-généralistes sur leurs capacités de réponse aux changements d'occupation du sol. Parmi les traits constitutifs de ce continuum, le degré de spécificité de la ressource trophique des espèces de Rhopalocères montre une variabilité importante, avec un déclin significativement plus fort des espèces monophages ou oligophages. Les plantes-nourricières sont en effet une des ressources majeures qui composent l'habitat des papillons de jour (Turlure, 2009). Afin de préciser les processus moteurs des patrons décrits dans ce premier chapitre, l'influence de cette part biotique de la niche des Rhopalocères sur leur état de conservation à l'échelle de la France a été explorée plus en détail dans le **Chapitre 2** à travers l'utilisation des métriques propres à la topologie des réseaux d'interactions.

Cette étude a permis de valoriser un important jeu de données (agrégé par P. Dupont du SNPN au MNHN) faisant la synthèse de toutes les plantes nourricières mentionnées pour chacun des Rhopalocères présents en France entre le 19^{ème} siècle et la période actuelle. Cette synthèse a permis de construire un réseau d'interactions bipartite entre 241 papillons de jours et 527 plantes utilisées comme ressources trophiques par leurs chenilles. Elle a permis d'effectuer une première description des patrons d'association des espèces et des facteurs qui

les conditionnent (par ex. géographiques, écologiques, évolutifs, ...). Le réseau d'interactions s'est caractérisé par une structure significativement modulaire, qui semble principalement liée à l'histoire évolutive des espèces. En effet, les herbivores montrent une forte tendance à former des réseaux marqués un fort conservatisme phylogénétique, issus de phénomènes de coévolution et d'adaptation à l'exploitation de certaines ressources (Fontaine & Thébaud, 2015). Dans le cas du réseau analysé durant cette thèse, les Rhopalocères appartenant à la même sous-famille ont tendance à s'associer préférentiellement au sein de modules composés de plantes généralement de la même famille. De plus, ce type de patrons et les relations spécifiques entre certaines sous-familles de Rhopalocères et familles de plantes-hôtes se révèlent extrêmement conservés à l'échelle du globe (Ferrer-Paris *et al.*, 2013). Ils semblent conditionnés par une adaptation de certains Rhopalocères aux défenses chimiques développées spécifiquement par certaines espèces de plantes pour limiter l'impact de l'herbivorie (Muto-Fujita *et al.*, 2017). La diversité de ces molécules de défense pourrait même constituer un trait beaucoup plus conservatif que la phylogénie des plantes (Endara *et al.*, 2017). La forte similarité des résultats obtenus dans ce chapitre combinée aux données consultées dans des régions où la richesse et la composition de communautés de Rhopalocères est très différente pose des questions sur les processus évolutifs à large échelle qui ont conduit à l'émergence de ces patrons. Etant donné la faible proportion de familles de plantes consommées dans ces différentes régions, l'identification des caractéristiques communes des familles non exploitées et des facteurs susceptibles d'expliquer cette absence d'exploitation pourrait constituer une perspective de recherche fondamentale pertinente.

Du point de vue de la conservation des papillons de jour, cette thèse a permis de révéler un lien significatif entre le degré des Rhopalocères (le nombre de plantes qu'ils consomment) et leur risque d'extinction à l'échelle de la France. Les espèces qui sont intimement liées à une ou quelques plantes nourricières sont beaucoup plus vulnérables à l'évolution des paysages. Toutefois, la structure du réseau se caractérise par une absence de corrélation entre ce degré des Rhopalocères et le degré moyen des plantes-hôtes qu'ils consomment. La ressource indispensable aux espèces monophages ne leur est donc pas forcément exclusive et tous les papillons de jours associés à la même plante ne présenteront pas forcément le même déclin. Le réseau projeté des Rhopalocères a également été généré afin d'évaluer les possibilités de couverture indirectes des enjeux de conservation à travers les listes actuelles d'espèces protégées. En effet, les papillons de jour sont souvent considérés comme des espèces parapluies, dont la conservation permettrait d'assurer celles de tous les

groupes liés aux mêmes ressources (Braby & Williams, 2016). La perspective du réseau projeté permet d'évaluer le bénéfice potentiel de l'interdiction de destruction des habitats espèces protégées (incluant leurs plantes nourricières), telle que prévue par la loi française. Les papillons actuellement protégés se sont révélés peu reliés aux autres espèces à travers le réseau projeté. De plus, le développement d'un indice de spécificité des partenaires indirects n'a pas révélé de forte dépendance des Rhopalocères liés aux espèces protégées vis-à-vis des ressources qu'ils partagent avec celles-ci. Il s'agit principalement d'espèces oligophages ou polyphages, qui sont donc potentiellement susceptibles de répartir leurs effectifs sur plusieurs espèces de plantes nourricières. Sachant que ces partenaires indirects sont majoritairement peu menacés, la couverture indirecte des enjeux de conservation via le groupe d'espèces actuellement protégées paraît limitée, et ces dernières ne semblent pas constituer des espèces parapluies pertinentes du simple point de vue de leurs ressources trophiques.

Cet axe de recherche a permis d'assembler un vaste jeu de données, incluant non seulement la synthèse des interactions papillons-plantes nourricières à l'échelle de la France mais également de nombreuses informations relatives à l'écologie, à la biologie, à la répartition ou au statut des espèces qui composent chacun de ces compartiments. Ces informations ont été synthétisées à partir d'atlas de répartition récents, de guides de terrain décrivant l'écologie des espèces, d'études scientifiques tentant de décrire les processus qui conditionnent l'assemblage des communautés de Rhopalocères (par ex. Bartonova *et al.*, 2014), de référentiels taxonomiques, de politiques de conservation des insectes et des habitats naturels (par ex. listes de protection, plantes indicatrices pour la définition des habitats d'intérêts communautaires dans le cadre de Natura 2000, ...) ou encore de bases de données sur la chorologie et l'écologie des plantes (Julve, 2002), en s'attachant à rester proches des conditions de la zone d'étude. Cette synthèse pourra constituer une base de travail pour développer de nouveaux questionnements sur les facteurs qui structurent le réseau d'interactions, et le croisement de ces différentes sources pourrait permettre d'éclairer des processus plus évolutifs ou propres à l'écologie des communautés (Muto-Fujita *et al.*, 2017 ; Nakadai *et al.*, 2017).

Un travail préliminaire a notamment pu être engagé dans le cadre de cette thèse afin de mobiliser ce jeu de données pour décrire l'impact de certaines dynamiques paysagères sur les communautés de Rhopalocères, à travers le prisme des changements de structure engendrés au sein des assemblages de plantes qu'ils consomment (Welti *et al.*, 2017). Des perspectives sur

l'étude de l'impact des successions secondaires liées à la déprise agricole, actuellement considérées comme un des facteurs de déclin et d'homogénéisation biotique pour les Rhopalocères en Europe (Stefanescu *et al.* 2011), ont notamment pu être explorées. En effet, contrairement aux impacts de l'intensification des pratiques agricoles, la réponse des invertébrés à la fermeture des milieux ouverts n'a été que peu étudiée en Europe (Cremene *et al.*, 2005), et notamment sur le pourtour méditerranéen (Slancarova *et al.*, 2016). Pour les Rhopalocères, ces travaux se basent principalement sur la comparaison de données d'inventaires d'imagos collectés sur des sites montrant divers degrés de fermeture paysagère (Stefanescu *et al.*, 2009). Seule une étude menée en région tropicale sur la base d'un échantillonnage des chenilles a permis de comparer les paramètres descriptifs des réseaux Rhopalocères-plantes nourricières sur des parcelles à différents stades de succession et elle a montré une forte résilience du système (Villa-Galavitz *et al.*, 2012). La base de données synthétisée dans le cadre de cette thèse pourrait fournir un point de départ pour répondre à ce type de problématiques. Elle permettrait de développer une approche plus holistique de ces dynamiques, en évaluant l'évolution de la structure du réseau et de la composition des communautés de Rhopalocères à travers la définition de plusieurs stades de successions potentiels.

D'un point de vue plus opérationnel, la connaissance précise des ressources qui composent l'habitat des espèces doit être un prérequis indispensable au développement de mesures de conservation et à la définition des protocoles qui visent à les détecter ou à les suivre dans le temps (Dennis, 2010). Les informations sur la liste des plantes-hôtes consommées et sur le degré de dépendance à chacune d'elle fournissent des éléments pour une meilleure localisation de ces habitats ou une meilleure évaluation de la capacité d'accueil d'un site. Dans le cadre de la politique européenne Natura 2000, le MNHN a récemment développé un programme d'évaluation de l'état de conservation des milieux ouverts agropastoraux, dont l'une des composantes passe par l'étude de l'intégrité des communautés de papillons de jour (Maciejewski *et al.*, 2015). Cette intégrité est calculée à partir de la mesure de l'écart entre les communautés observées et les communautés potentielles sur le site. La composition des communautés potentielles sur un site est alors évaluée à partir de plusieurs filtres appliqués à un pool d'espèces connues à l'échelle du département où se trouve le site. Ces filtres fonctionnent sur la base du croisement de plusieurs traits propres aux espèces : habitats colonisés, phénologie, degré de sténoécie, capacités de dispersion, ... (Dupont, 2015). Cette base de traits peut également être utilisée pour la validation de données

d'inventaires, en lien avec la pression d'échantillonnage appliquée sur le terrain (Dupont, 2014b). De la même manière, la description actualisée du régime alimentaire des chenilles présentée dans le deuxième chapitre de cette thèse pourrait s'intégrer au sein de ce type de méthodes prédictives de la richesse ou de la composition des cortèges de Rhopalocères sur un site. Ce type d'outils pourrait permettre d'exploiter les résultats issus d'inventaires floristiques et la probabilité de cooccurrence de certaines espèces de Rhopalocères afin de contribuer à l'évaluation de l'exhaustivité des inventaires.

Evaluation et amélioration des plans d'échantillonnage pour une mesure plus fiable des impacts sur l'environnement

Ces problématiques liées au manque et à la mesure de l'exhaustivité des inventaires biologiques représentent un des enjeux majeurs de la conservation appliquée, qui se développe en grande partie sur la base de données d'occurrence ou de mesures d'abondance d'espèces. Le **Chapitre 3** a permis de se placer en amont de la description des différents patrons à large échelle étudiés dans les chapitres précédents, en questionnant la représentativité des données d'occurrence collectées localement sur le terrain vis-à-vis de l'occupation réelle de l'espace par les insectes. S'intégrant dans une optique d'évaluation des politiques publiques, cette étude s'est ainsi attachée à quantifier l'exhaustivité des plans d'échantillonnage de l'entomofaune mis en place dans le cadre des études d'impacts. Ces plans pâtissent du poids des enjeux commerciaux dans la réalisation des études, lié aux objectifs de compétitivité des bureaux d'étude. Un équilibre est recherché entre une résolution suffisante des résultats de terrain pour une évaluation sérieuse des impacts et le maintien d'un coût le plus réduit possible. Toutefois cette qualité restait actuellement peu évaluée dans le cas particulier des insectes, qui constituent des groupes riches incluant de nombreuses espèces cryptiques et nécessitant le croisement de plusieurs méthodes d'échantillonnage.

Les visites de terrain qui ont permis de collecter les données analysées dans ce chapitre ont été réalisées sur la base de plans d'échantillonnage spécifiquement élaboré pour la réalisation d'études d'impacts. Le nombre de passages réalisés sur chaque site, la durée de ces passages, l'horaire auquel ils ont été conduits et les groupes d'insectes échantillonnés ont ainsi été définis conformément aux pratiques courantes du bureau d'étude Biotope en région Méditerranéenne. Les Orthoptères et les cigales sont ainsi venus s'ajouter aux deux taxa ciblés par la présente thèse (Rhopalocères et Odonates) afin de pas s'éloigner des standards de

ces études. Bien que ce prérequis ait amené une hétérogénéité importante dans la pression d'échantillonnage appliquée sur les différents sites, elle offre une vision de l'exhaustivité des inventaires entomologiques en conditions d'étude d'impact en prenant en compte les contraintes réelles auxquelles est soumis le bureau d'étude lors de la construction de ses offres.

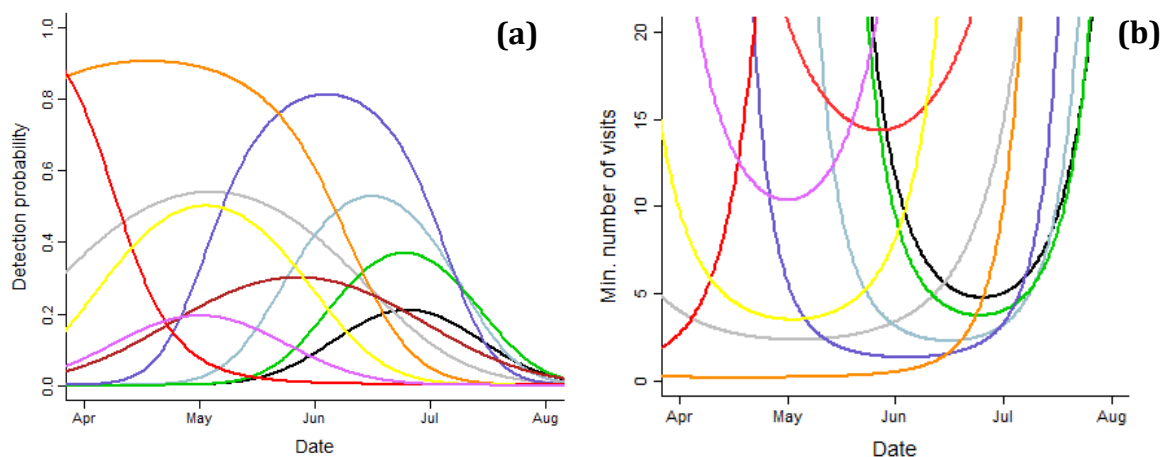


Figure 12 : Probabilité de détection **(a)** et nombre minimum de passages nécessaire pour statuer sur l'absence **(b)** des différentes espèces protégées observées (associées aux différentes couleurs) au cours des inventaires présentés dans le chapitre 3 en fonction de la date. Réalisée à partir des estimations issues du MSOM.

Le modèle d'occupation multi-espèces implémenté a permis d'obtenir des estimations de la richesse potentielle de la communauté, par site, par groupe taxonomique et en fonction du statut des espèces. Ces données ont été utilisées comme valeurs de références pour quantifier le degré d'exhaustivité moyen des relevés effectué sur un site dans le cadre d'une étude d'impact. La probabilité de détection et le biais absolu dans la connaissance de l'occupation ont pu être calculés pour chacune des espèces observées, et leur valeur moyenne a été comparée entre les différents taxa. Les résultats ont mis en évidence un décalage élevé entre les données collectées et la diversité entomologique potentiellement présente sur un site. Presque 50% de cette diversité est susceptible de ne pas être détectée en moyenne et une espèce présente sur un site aura en moyenne moins de 30% de chance d'être observée dans des conditions d'inventaire classique. L'estimation des probabilités d'occupation et de détection de chacune des espèces a également montré une différence de représentativité des données issues d'échantillonnages classiques en fonction de leur statut de conservation. Cette distinction est importante étant donné l'objectif particulier de détection des espèces protégées ou patrimoniales portés par les études d'impacts. Ce sont ces espèces qui constituent la

contrainte réglementaire majeure pour l'aménageur et qui conditionne l'importance des investissements qu'il devra apporter pour éviter, réduire ou compenser les impacts de son projet. L'estimation de leurs probabilités de détection via le modèle et l'étude de la variation de ce paramètre en fonction des conditions de réalisation des relevés (par ex. date, heure, durée, ...) apportent des éléments essentiels pour une répartition plus efficace de la pression d'inventaire.

Ces résultats ont montré la nécessité de prendre en compte les biais liés à la détectabilité des espèces dans la procédure de définition des plans d'échantillonnages en condition d'étude d'impact. Les analyses réalisées dans ce chapitre présentent l'avantage de pouvoir conduire au développement d'outils opérationnels à la fois pour les bureaux d'études et pour les différentes structures chargées de poser un avis durant l'instruction des dossiers d'études d'impacts (DREAL, DDTM, CNPN, ...). La connaissance du pourcentage d'exhaustivité moyen d'une étude dans des conditions environnementales précises (par ex. l'aire du site, la diversité des habitats, ...) fournit une mesure du degré d'incertitude associé aux résultats des inventaires en fonction de l'effort appliqué. Elle permet de porter un regard plus critique sur la représentativité de la mesure des impacts associés à un projet. L'accès aux probabilités de détection de chaque espèce et la description de leur variation en fonction des conditions du relevé apportent des éléments intéressants pour une répartition plus efficace de l'effort lors de la construction des plans d'inventaires, en vue de maximiser la détection des enjeux pressentis. La connaissance des dates auxquelles les espèces protégées sont les plus détectables peut par exemple permettre une meilleure répartition des passages au cours de la saison, en fonction des potentialités d'accueil du site (Fig.12a). Ces probabilités spécifiques peuvent également être utilisées afin de déterminer un nombre minimum de passages nécessaires pour statuer sur l'absence d'une espèce avec un certain degré de confiance (Fig.12b) (Wintle *et al.*, 2012). Ce type d'indice apporte des arguments pour fixer des conditions standard d'inventaire pour les espèces portant les enjeux les plus importants, ainsi que des éléments d'évaluation des inventaires réalisés avec un effort plus faible. *In fine*, l'interaction entre bureaux d'études et services instructeurs sur la base de ce type de travaux devrait aboutir à la définition de lignes directrices pour la planification et la réalisation des inventaires entomologiques dans le cadre des études d'impact, afin de fixer des conditions minimales en vue de garantir un certain degré de qualité. Les problématiques liées à la gestion de la superposition des préconisations pour les différentes espèces à enjeux potentielles sur un

même site nécessiteront d'être explorées dans le cadre du développement de ce type de lignes directrices.

Dans cette optique, les modèles de site-occupancy étendus à l'échelle multi-spécifique constituent un outil prometteur, offrant la possibilité de valoriser des données biologiques acquises suivant des plans d'échantillonnage parfois hétérogènes et pouvant comporter un nombre important d'espèces rares (notamment via les procédés de « shrinkage »). L'emboîtement des différents niveaux hiérarchiques permet d'aller plus loin que l'estimation d'une simple richesse asymptotique en dégageant les biais sous-jacents liés à l'hétérogénéité de la probabilité de détection au sein de la communauté biologique. Les processus qui conditionnent cette hétérogénéité peuvent ensuite être décrits par l'intégration de covariables ou la distinction de groupes d'espèces. Les MSOM constituent ainsi une opportunité appropriée pour le cadre précis des études d'impacts, dans lequel les enjeux ciblés par site sont généralement multiples et couplé à une nécessité d'avoir une vision plus large (même sommaire) de la richesse des communautés présentes.

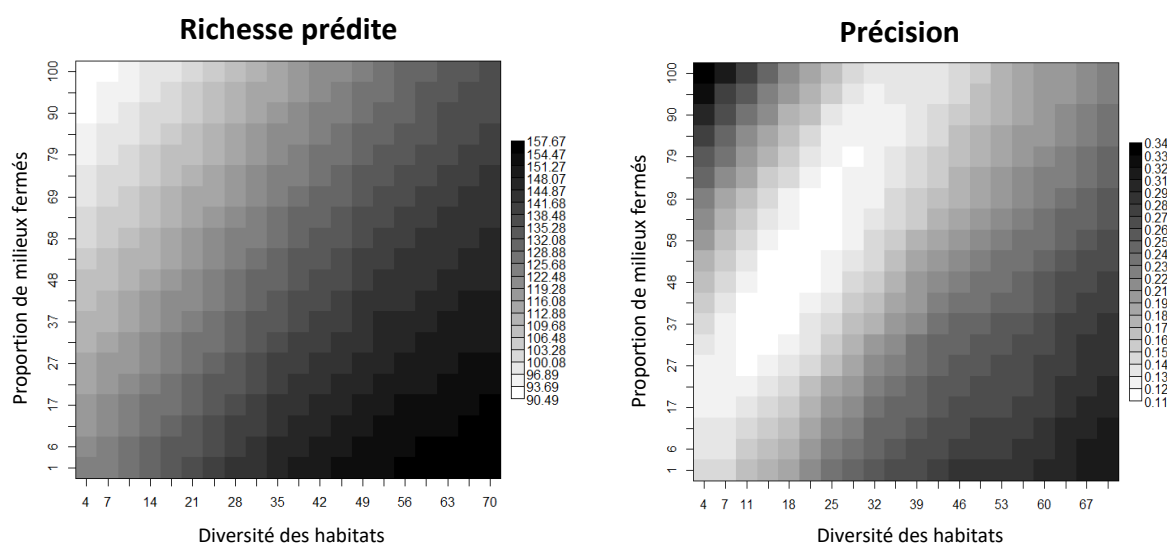


Figure 13 : Exemple de grille d'estimation de la richesse potentielle (à gauche) d'un site en fonction d'une combinaison de valeurs de deux variables d'habitats. La grille de droite représente la précision des estimations pour les différentes combinaisons (dépendante des valeurs réelles des données en entrée). Réalisées à partir des résultats du MSOM issues du chapitre 3.

L'intérêt croissant du cadre bayésien pour l'analyse des données en écologie a amené à une forte dynamique de recherche sur les MSOM au cours des 10 dernières années (Dorazio, 2016). Ces modèles sont applicables à des situations de plus en plus variées et incluent une diversité toujours plus grande de sources d'hétérogénéité de la détection des espèces. Ces

nouvelles techniques font apparaître plusieurs perspectives d'amélioration ou de précision des analyses d'exhaustivité menées dans le cadre de cette thèse. À partir des probabilités d'occupation des espèces calculées sur les différents sites à travers le MSOM, il est notamment possible de prédire une richesse spécifique potentielle pour diverses combinaisons de covariables propres à ces sites (par exemple quelle est la richesse potentielle d'un site de 50ha composé à 50% de milieux fermés ?) (Mata *et al.*, 2017) (Fig.13). Différents degrés de résolution peuvent être définis au niveau de l'échelle des covariables, mais la précision des estimations reste fortement dépendante de la richesse du jeu de données en entrée, notamment en termes de nombre de sites et de diversité des combinaisons de covariables (Zipkin *et al.*, 2009). Dans le cadre des études d'impacts, la production de grilles de combinaisons plus exhaustive pourrait fournir des outils pour réaliser une évaluation grossière de la richesse potentielle des communautés d'insectes sur un site d'étude. Ce type d'information permettrait un meilleur ajustement des plans d'échantillonnages mais aussi une mesure de l'exhaustivité des données obtenues à l'issue des inventaires. D'autres développements récents mériteraient d'être étudiés pour l'amélioration de ce cadre d'analyse, notamment la possibilité de traiter dans un même modèle plusieurs régions aux caractéristiques différentes (par ex. recouvrant différents biomes ou habitats, avec des pools d'espèces différents) (Sutherland *et al.*, 2016) ou la définition de groupes fonctionnels directement au sein de la structure hiérarchique du modèle (Tenan *et al.*, 2017).

Cette étude peut être considérée comme une étape préliminaire qui pourrait déboucher sur le développement d'outils méthodologiques et commerciaux au sein de l'entreprise, pouvant être par la suite proposés aux services instructeurs en vue d'harmoniser les pratiques des bureaux d'études à l'échelle nationale. Le jeu de données collecté dans le cadre de cette thèse nécessiterait alors d'être enrichi en incluant de nouveaux sites afin d'obtenir des résultats plus robustes sur le plan statistique, que ce soit pour le calcul de la richesse des communautés ou pour l'estimation des paramètres spécifiques. Cet enrichissement pourrait notamment permettre d'améliorer l'estimation de l'effort minimum requis pour assurer un certain degré de détection de certaines espèces d'intérêts (par ex. les espèces protégées), en incluant un nombre plus important de covariables propres aux relevés et susceptible de l'influencer (par ex. paramètres météorologiques, expérience de l'observateur, ...). Une extension à d'autres types de milieux, d'autres régions ou d'autres groupes faunistiques permettrait d'envisager une déclinaison de ce type d'outils d'évaluation à une échelle plus large. En effet, les résultats quantitatifs issus de cette étude ne sont valables que dans des

conditions comparables aux inventaires qui ont permis de les obtenir, à savoir un échantillonnage des quatre taxa mentionnés plus hauts sur un site de plaine méditerranéenne dominé par des formations de garrigues et de friches sèches.

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Glossaire

Akaike's information criterion (AIC) : estimateur de la qualité relative de modèles statistiques vis-à-vis d'un jeu de données. Etant donné un ensemble de modèle pour un même jeu de données, l'AIC estime la qualité de chacun de ces modèles, relativement aux autres modèles. L'évaluation se base sur le compromis entre la qualité de l'ajustement du modèle (« goodness of fit ») et sa complexité. Il n'apporte en revanche pas d'information sur la qualité absolue du modèle.

Bayesian shrinkage : processus statistique qui permet une précision accrue dans l'estimation d'un paramètre via une modélisation des paramètres à travers une distribution commune définie *a priori* (Link & Sauer, 1996). Les paramètres individuels sont ainsi estimés en prenant en compte la moyenne de cette distribution.

Bioindicateur écologique : espèce sensible aux impacts de certains stress environnementaux (par ex. l'altération des habitats naturels, leur fragmentation, le changement climatique, ...). Le suivi de ces espèces peut permettre de détecter ces stress et de déduire leur impact sur l'ensemble des organismes présentant une écologie proche de celles-ci. Papillons largement utilisés pour milieux ouverts.

Capture-marquage-recapture (mark-release-recapture) : méthode couramment utilisée en écologie afin d'estimer la taille et les paramètres démographiques d'une population animale (survie, colonisation, extinction ...). Elle se base sur la capture, le marquage et le relâché d'une partie de la population. Plus tard, une autre partie est capturée et le nombre d'individus marqués dans l'échantillon est compté.

Centralité (centrality) : mesure de l'influence d'une espèce au sein du réseau d'interaction dans lequel elle s'intègre. Cette mesure se découle en différents indices, en fonction de la définition donnée à « l'influence » (proche d'un nombre important de nœuds dans le réseau, point de connection entre de nombreux modules, ...) (Delmas *et al.*, 2017).

Communauté : Ensemble d'organismes n'ayant pas de relation de prédation directe ou indirecte entre eux, partageant un ou plusieurs facteurs limitants (ressource(s), prédateur(s), ...) et occupant un même espace de petite dimension au regard de leur mobilité et de leur dispersion (Laroche, 2014).

Connectance : nombre de liens réalisés dans un réseau d'interactions par rapport au nombre maximum de de lien possibles entre les nœuds qui le compose (Delmas *et al.*, 2017).

Conservatisme phylogénétique (phylogenetic conservatism) : interaction entre espèces étroitement apparentées avec des partenaires similaires. Dans le cas du réseau d'interaction papillon-plante nourricière, ce conservatisme s'exprime par le fait que plus deux papillons sont apparentés, plus ils partagent de plantes nourricières.

Courbe d'accumulation (species-accumulation curve) : représentation graphique du nombre moyen d'espèces rencontrées en fonction d'un effort d'échantillonnage croissant, qui facilite la comparaison des mesures de diversité (richesse spécifique, ...) entre des échantillons collectés avec un effort d'échantillonnage inégal (Gotelli & Colwell, 2011). L'effort est généralement mesuré par le nombre d'échantillons, de relevés réalisés ou d'individus observés.

- Degré (degree)** : nombre de partenaires d'un nœud donné au sein d'un réseau d'interaction (Latapy *et al.*, 2008).
- Degré projeté (projected degree)** : nombre de partenaires indirects dans le réseau projeté (Taudière *et al.*, 2015).
- Detectabilité (detectability)** : Probabilité de détecter un individu d'une espèce donné au niveau des sites, patchs ou unités d'échantillonnages qu'elle occupe (MacKenzie *et al.*, 2002).
- Espèce étendard (flagship species)** : espèces charismatiques populaires qui servent de symboles et de points de ralliement pour stimuler la sensibilisation et l'action en matière de conservation, telles que définies par Home *et al.*, 2009.
- Espèce parapluie (umbrella species)** : espèce dont l'étendue du territoire ou de la niche écologique permet la protection d'un grand nombre d'autres espèces si celle-ci est protégée (Noss, 1990).
- Estimateur non-paramétrique (nonparametric estimator)** : un estimateur qui n'assume pas de distribution sous-jacente pour les données sur lesquelles l'estimation est réalisée (Gotelli & Colwell, 2011).
- Etude d'impact sur l'environnement (Environmental Impact Assessment)** : processus visant à intégrer l'environnement dans l'élaboration d'un projet d'aménagement du territoire ou d'un document de planification via l'évaluation de leurs impacts potentiels en amont de leur mise en œuvre. Cette évaluation se base sur une première étape visant à établir l'état initial des milieux naturels au sein de l'emprise du projet à travers toutes leurs composantes (habitats, flore, faune, fonctions ...).
- Euryèce** : qualifie des espèces possédant une valence élevée par rapport à un facteur, tel que la température, le courant ou encore l'ensoleillement.
- Eutrophisation (eutrophication)** : Tendance à l'augmentation de la biomasse végétale dans un espace aquatique par ajout naturel ou non de nutriments, tels que des nitrates ou des phosphates. Cette forte augmentation du phytoplancton conduit à l'hypoxie du milieu et impacte négativement les autres compartiments de l'écosystème (invertébrés, poissons, ...).
- Exuvie (exuviae)** : enveloppe cuticulaire des larves d'Odonates de derniers stades laissés sur la végétation émergente ou sur le substrat de la berge au moment de l'émergence de l'imago. Les exuvies sont argement utilisées dans le cadre de l'étude des populations d'Odonates, du fait qu'elles constituent un indice robuste de reproduction des espèces au sein d'un habitat donné et qu'elles permettent une estimation semi-quantitative de la taille des populations.
- Fausse absence (false absence)** : désigne un événement au cours duquel un individu ou une espèce qui est présente sur un site donné n'y est pas détecté au cours d'un inventaire. Il peut être lié à une erreur d'observation ou au fait que les individus peuvent ne pas être disponibles à la détection durant la période des relevés.
- Hémimétabole** : désigne les taxons d'insectes qui ne subissent pas de métamorphose complète entre les stades larvaires et imaginaires mais dont la larve et l'adulte sont inféodés à des milieux différentes (par ex. larve aquatique et adulte aérien).
- Holométabole** : désigne les taxons d'insectes qui subissent une métamorphose complète, à travers les phases post-embryonnaires de la larve, la nymphe et de l'adulte.

- Hyperparamètre** : dans le cas d'un modèle hiérarchique impliquant un processus de "bayesian shrinkage", il s'agit d'un paramètre qui gouverne la distribution un niveau de la communauté, au sein de laquelle les probabilités propres à chaque espèce seront tirées (Dorazio *et al.*, 2006).
- Imago** : désigne le stade final d'un individu dont le développement se déroule en plusieurs phases (en général œuf, larve, imago). Ce terme est en général utilisé pour les arthropodes, mais aussi pour les amphibiens.
- Imbrication** (*nestedness*) : dans le cadre de l'analyse de réseaux, correspond à une disposition des partenaires selon des patrons emboîtés. Plus un réseau est imbriqué, plus les partenaires des espèces spécialistes sont également partenaires des généralistes.
- Matrice d'incidence** (*incidence matrix*) : en théorie des graphes, tableau représentant les liens qui unissent les différents sommets d'un graphe. Ce type de représentation est également largement utilisé en écologie, par exemple pour synthétiser les événements d'observation/non-observation (1/0) de plusieurs espèces sur différents sites, ou les interaction/non-interaction (1/0) entre plusieurs espèces appartenant à différents niveaux d'un réseau bipartite.
- Markov chain Monte Carlo (MCMC)** : classe d'algorithmes utilisés pour générer des échantillons aléatoires dépendants à partir de distributions statistiques (typiquement des distributions postérieures dans l'analyse bayésienne d'un modèle).
- Métapopulation** : Un groupe de populations locales instables interconnectées par des déplacements d'individus entre elles, tels que définis par Hanski & Gyllen (1991). Ce concept est d'une grande importance pour l'étude de la fragmentation et de la conservation de l'habitat.
- Modèle hiérarchique** (*hierarchical model*) : modèle statistique caractérisé par une séquence emboîtée de variables aléatoires, permettant de modéliser de manière assez flexible et transparente des jeux de données impliquant des dépendances complexes dans les données observées.
- Méthode d'échantillonnage** : méthode de collecte est un ensemble de techniques, de savoir-faire et/ou d'outils spécifiques mobilisés de manière logique (règles, étapes et principes) pour collecter des données associées à un paramètre à observer ou à un facteur écologique à prendre en compte.
- Modèles de Site-Occupancy** : tels que développés par MacKenzie *et al.* (2002), modèles exploitant les données de détection/non-détection d'une espèce collectée sur la base de visites répétées sur plusieurs sites d'échantillonnage afin d'estimer la probabilité qu'un site pris au hasard soit occupé par l'espèce, en prenant en compte sa probabilité de détection.
- Modèle nul** (*null model*) : en mathématiques, dans l'étude des propriétés statistiques des graphes, un modèle nul correspond à un graphe dont une partie des caractéristiques structurelles est fixée en fonction d'un graphe étudié, mais qui résultent pour le reste de processus aléatoires (Gotelli, 2001). Les modèles nuls sont utilisés pour des procédures de comparaison, afin de tester la significativité de la structure d'un réseau particulier.
- Module** : sous-ensemble d'un réseau d'interactions composé d'espèces qui établissent plus de liens entre elles qu'avec le reste du réseau.

- Modularité** : statistique mesurant la différence entre la fraction de liens intramodules du réseau étudié et la fraction de liens intramodules d'un réseau dont les liens seraient répartis aléatoirement (Newman & Girvan, 2003)
- Myrmecophilie** : capacité de vivre en association avec des fourmis. Chez les Lépidoptères, la myrmécophilie est très commune chez les larves et les pupes des familles de Lycaenidae et de Riodinidae.
- Natura 2000** : réseau de sites naturels ou semi-naturels européens visant à protéger des habitats ou des espèces présentant une grande valeur patrimoniale en tenant compte des activités humaines et des pratiques qui ont permis de les sauvegarder jusqu'à ce jour. Leur désignation et leurs modalités de gestion sont encadrées par des directives et des financements issus de l'Union Européenne.
- Niche écologique** : Hypervolume à n dimensions, où chaque dimension est une condition environnementale (abiotique ou biotique) qui limite la viabilité des individus de l'espèce, telle que définie par Hutchinson (1957).
- Occupation du sol** (*land-cover*) : ensemble des matériaux physiques occupant la surface de la Terre sur un espace donné, qu'ils soient naturels ou d'origine anthropiques, et incluant l'eau, le sol nu, l'herbe, les arbres, le pavage, les constructions, etc.
- Occupation** (*occupancy*) : proportion de sites, de patches ou d'unités d'échantillonnage occupés par une espèce donnée (c.-à-d. que l'espèce y est présente et qu'elle peut y être détectée) (MacKenzie *et al.*, 2002).
- Population** : Ensemble des individus d'une même espèce qui occupe simultanément le même milieu.
- Plan d'échantillonnage** (*sampling plan*) : plan d'étude détaillé expliquant comment les données doivent être collectées, organisées et analysées afin de mettre en évidence les éléments structurants des patrons et des processus écologiques (protocole de processus), ou plus largement de répondre à une question scientifique.
- Population fermée** : population considérée comme isolée de son environnement extérieur durant un intervalle de temps défini, donc que 100% des individus sont présents dans un espace bien délimité et qu'ils ne peuvent pas en sortir. Il n'y a donc ni migration (individus sortants), ni immigration (individus entrants) dans un pas de temps défini.
- Réseau bipartite** (*bipartite network*) : Réseau constitué de liens unissant uniquement des nœuds de deux classes différentes. Les interactions intra-classes ne sont ainsi pas possible. Dans le cas étudié dans le Chapitre 2, les Rhopalocères forment une classe ne pouvant interagir qu'avec des plantes-nourricières, qui forment l'autre classe.
- Réseau projeté** (*projected network*) : réseau constitué d'une unique classe de partenaires et issu de la projection d'un réseau bipartite (Latapy *et al.*, 2008). Permet de décrire les interactions indirectes entre les partenaires d'une même classe via les espèces appartenant à l'autre classe.
- Robustesse** (*Robustness*) : paramètre illustrant la vulnérabilité d'un réseau d'interaction à des processus d'extinction progressive d'un compartiment, dans un ordre plus ou moins contraint. Cette valeur est mesurée via une estimation d'aire sous la courbe qui figure la fraction d'espèces d'un compartiment qui survivent suite à l'extinction des espèces de l'autre compartiment une à une.

Sténoèce : espèce de faible valence écologique ne pouvant supporter que des variations limitées des facteurs écologiques (et présentant donc un intervalle de tolérance étroit pour l'ensemble des facteurs propres à son habitat).

Test d'ajustement (*goodness of fit test*) : paramètre qui décrit à quel point un modèle statistique s'ajuste bien à un jeu de données. Cette évaluation de l'ajustement permet typiquement d'estimer la divergence entre les valeurs observées (tirées du jeu de données) et les valeurs attendues sous le modèle.

Ténéral : qualifie l'imago de libellule fraîchement émergé, nécessitant de passer par une phase de maturation avant d'atteindre le stade reproducteur.

Trait d'histoire de vie (*life history trait*) : descripteurs biologiques et comportementaux quantitatifs (respiration, croissance, mode/rythme/stratégie de reproduction et alimentation) ou écologiques (préférendum de température, pH, humidité, ...) étudiées aux échelles spatiales de l'habitat et du paysage.

Uncorrected count : valeur issue du dénombrement d'individus ou d'espèces observés à partir d'inventaires de terrain n'ayant pas été statistiquement ajustée pour tenir compte des biais d'échantillonnage ou des sources d'imperfection de la détection.

Utilisation du sol (*land-use*) : modification par l'homme de son environnement naturel ou sauvage au niveau du sol quand il est transformé un environnement anthropisé ou semi-naturel (prairies, champs, pâturages, boisements exploités, constructions et autres implantations humaines...).

Variable latente (*latent variable*) : désigne un paramètre qui est déduit d'autres paramètres à l'aide de modèles statistiques et mais qui n'est pas directement observé par un échantillonnage.

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Annexes

Listes des annexes complémentaires aux chapitres

Les annexes des chapitres qui représentent des tableaux de données volumineux, n'apportant pas d'informations indispensables à la compréhension des chapitres, sont regroupées dans cette partie afin d'alléger la lecture du document.

Chapitre 1 : Diachronic variations in the distribution of butterflies and dragonflies linked to recent habitat changes in Western Europe

Supplementary material S1.1 : List of butterfly (A) and dragonfly (B) taxa (species and subspecies) included in the present study and values for their ecological attributes, protection statut and red list assessment at the scale of study area. *(page 249)*

Chapitre 2 : Insight into butterfly-hostplant bipartite networks: using projected network as suitable tools for insect conservation

Supplementary material S2.1: List of 241 butterfly species included in the butterfly-hostplant interaction network. *(page 260)*

Supplementary material S2.2: List of 527 plant species included in the butterfly-hostplant interaction network. *(page 269)*

Chapitre 3 : Multi-species occupancy model reveal the poor completeness of entomological surveys in environmental impact assessment

Supplementary material S3.7: Posterior estimates of the species-specific occurrence and detection probabilities of insect species as estimated under the MSOM. *(page 281)*

Supplementary material S3.8: Posterior estimates for the effect of site covariates on observed insect species as estimated under the MSOM. *(page 288)*

Supplementary material S3.9: Posterior estimates for the effect of visit covariates on observed insect species as estimated under the MSOM. *(page 295)*

Supplementary material S1.1: Par soucis de clarté, ce supplément volumineux, non indispensable à la compréhension du chapitre, est présenté dans la partie « Annexes » du manuscrit de thèse.

Table A. List of butterfly taxa (species and subspecies) included in the present study and values for their ecological attributes, protection statut and red list assessment at the scale of study area: family (Hesp – Hesperidae, Lyc – Lycaenidae, Nymph – Nymphalidae, Pap – Papilionidae, Pier – Pieridae, Rio – Riodinidae, Sat – Satyrinae), biogeographic background (Wide – widespread, North – northern Europe, South – southern Europe, Mount – mountain areas), bioclimatic zonation (Hill – hill zone, Meso – meso-mediterranean, Supra – supra-mediterranean, Mount – mountainous, Alp – alpine-subalpine), main breeding habitat (Alpine – alpine grassland, Dry – dry grassland, Humid – humid grassland, Meso – mesophile grassland, Shrub – shrubland), habitat specialization (Gen – generalist, Mid – mid-generalist, Spe - specialist), host plant specialization (1 – monophagous, 2 – oligophagous, 3 - polyphagous), host plant form (1 – ephemeral and small herbaceous, 2 – large herbaceous, 3 – bushes, 4 – large trees), mobility (1 – low abilities, 2 – medium abilities, 3 – high abilities), voltinism (1 - 0.5 generation, 2 - 1 generation, 3 - 1 or 2 generations, 4 - 2 generations, 5 - 2 to 3 generations, 6 - 3 to 4 generations), myrmecophily (1 – myrmecoxenous, 2 – facultative myrmecophilous, 3 – steadily myrmecophilous, 4 – obligatory myrmecophilous, 5 – no known interaction with ants), French protection status (Un – unprotected, Pr – protected), IUCN categories LC – least concern, NT – near threatened, VU – vulnerable, EN – endangered, CR – critically endangered).

Species/subspecies name	Family	Biogeographic background	Bioclimatic zonation	Main breeding habitat	Habitat specialization	Host plant specialization	Host plant form	Dispersal abilities	Voltinism	Myrmecophily	French protection status	IUCN categories
<i>Carcharodus alceae</i>	Hesp.	Wide.	Hill.	Meso.	Mid.	3	1	2	5	5	Un.	LC
<i>Carcharodus baeticus</i>	Hesp.	South.	Meso.	Dry.	Mid.	2	1	1	5	5	Un.	VU
<i>Carcharodus floccifer</i>	Hesp.	Wide.	Mount.	Meso.	Mid.	2	1	1	3	5	Un.	LC
<i>Carcharodus lavatherae</i>	Hesp.	South.	Supra.	Dry.	Spe.	2	1	1	2	5	Un.	NT
<i>Carterocephalus palaemon</i>	Hesp.	North.	Mount.	Forest	Mid.	2	2	1	2	5	Un.	LC
<i>Erynnis tages</i>	Hesp.	Wide.	Hill.	Meso.	Spe.	3	1	1	4	5	Un.	LC
<i>Hesperia coma</i>	Hesp.	Wide.	Hill.	Dry.	Mid.	1	2	1	2	5	Un.	LC
<i>Heteropterus morpheus</i>	Hesp.	North.	Hill.	Humid.	Mid.	1	2	1	2	5	Un.	LC
<i>Ochlodes sylvanus</i>	Hesp.	Wide.	Hill.	Forest	Gen.	3	2	2	4	5	Un.	LC
<i>Pyrgus alveus</i>	Hesp.	Wide.	Mount.	Meso.	Spe.	1	1	1	2	5	Un.	LC
<i>Pyrgus andromedae</i>	Hesp.	Mount.	Alp.	Dry.	Spe.	1	1	1	2	5	Un.	LC
<i>Pyrgus armoricanus</i>	Hesp.	Wide.	Hill.	Dry.	Spe.	3	1	1	4	5	Un.	LC
<i>Pyrgus bellieri</i>	Hesp.	South.	Mount.	Dry.	Mid.	3	1	1	2	5	Un.	LC

<i>Pyrgus cacaliae</i>	Hesp.	Mount.	Alp.	Humid.	Spe.	2	1	1	2	5	Un.	LC
<i>Pyrgus carlinae</i>	Hesp.	Mount.	Alp.	Meso.	Mid.	1	1	1	2	5	Un.	LC
<i>Pyrgus carthami</i>	Hesp.	Wide.	Hill.	Dry.	Spe.	2	1	1	2	5	Un.	LC
<i>Pyrgus cirsi</i>	Hesp.	South.	Hill.	Dry.	Spe.	2	1	1	2	5	Un.	NT
<i>Pyrgus malvae</i>	Hesp.	Wide.	Hill.	Meso.	Gen.	3	1	1	3	5	Un.	LC
<i>Pyrgus onopordi</i>	Hesp.	South.	Supra.	Dry.	Spe.	2	1	1	4	5	Un.	LC
<i>Pyrgus serratulae</i>	Hesp.	Wide.	Hill.	Dry.	Spe.	2	1	1	2	5	Un.	LC
<i>Pyrgus sidae</i>	Hesp.	South.	Meso.	Dry.	Mid.	1	1	1	2	5	Un.	LC
<i>Pyrgus warrenensis</i>	Hesp.	Mount.	Alp.	Alpine.	Mid.	2	1	1	2	5	Un.	VU
<i>Sloperia proto</i>	Hesp.	South.	Meso.	Dry.	Mid.	2	1	1	2	5	Un.	LC
<i>Spialia sertorius</i>	Hesp.	South.	Hill.	Dry.	Spe.	1	1	2	4	5	Un.	LC
<i>Thymelicus acteon</i>	Hesp.	Wide.	Hill.	Dry.	Spe.	3	2	1	2	5	Un.	LC
<i>Thymelicus lineola</i>	Hesp.	Wide.	Hill.	Meso.	Gen.	3	2	1	2	5	Un.	LC
<i>Thymelicus sylvestris</i>	Hesp.	Wide.	Hill.	Meso.	Gen.	2	2	2	2	5	Un.	LC
<i>Agriades glandon</i>	Lyc.	Mount.	Alp.	Alpine.	Spe.	3	1	1	2	4	Un.	LC
<i>Agriades optilete</i>	Lyc.	North.	Hill.	Humid.	Mid.	1	1	1	2	4	Un.	LC
<i>Agriades orbitulus</i>	Lyc.	Mount.	Alp.	Alpine.	Spe.	3	1	1	2	4	Un.	LC
<i>Agriades pyrenaica</i>	Lyc.	Mount.	Alp.	Alpine.	Mid.	1	1	1	2	4	Un.	LC
<i>Aricia agestis</i>	Lyc.	Wide.	Hill.	Meso.	Mid.	3	1	2	4	3	Un.	LC
<i>Aricia artaxerxes</i>	Lyc.	North.	Mount.	Meso.	Spe.	2	1	1	2	3	Un.	LC
<i>Aricia morronensis</i>	Lyc.	South.	Mount.	Dry.	Mid.	1	1	1	2	3	Un.	VU
<i>Aricia nicias</i>	Lyc.	North.	Alp.	Alpine.	Spe.	1	1	1	2	4	Un.	LC
<i>Callophrys avis</i>	Lyc.	South.	Meso.	Shrub.	Mid.	2	4	1	2	4	Un.	LC
<i>Callophrys rubi</i>	Lyc.	Wide.	Hill.	Shrub.	Gen.	3	3	1	2	4	Un.	LC
<i>Celastrina argiolus</i>	Lyc.	Wide.	Hill.	Forest	Mid.	3	3	2	5	3	Un.	LC
<i>Cupido alcetas</i>	Lyc.	South.	Hill.	Meso.	Mid.	2	1	2	5	3	Un.	LC
<i>Cupido argiades</i>	Lyc.	Wide.	Hill.	Humid.	Mid.	3	1	2	4	3	Un.	LC
<i>Cupido minimus</i>	Lyc.	Wide.	Hill.	Meso.	Spe.	3	1	2	4	2	Un.	LC
<i>Cupido osiris</i>	Lyc.	South.	Supra.	Dry.	Spe.	3	1	1	2	2	Un.	LC
<i>Cyaniris semiargus</i>	Lyc.	Wide.	Hill.	Meso.	Spe.	3	1	2	2	3	Un.	LC
<i>Eumedonia eumedon</i>	Lyc.	Mount.	Mount.	Forest	Mid.	3	1	1	2	3	Un.	LC
<i>Glaucopsyche alexis</i>	Lyc.	Wide.	Hill.	Meso.	Spe.	3	1	1	2	3	Un.	LC
<i>Glaucopsyche melanops</i>	Lyc.	South.	Meso.	Shrub.	Mid.	1	1	1	2	3	Un.	LC
<i>Iolana iolas</i>	Lyc.	South.	Supra.	Forest	Mid.	1	1	3	2	3	Un.	NT
<i>Laeosopis roboris</i>	Lyc.	South.	Meso.	Forest	Mid.	2	4	1	2	2	Un.	LC
<i>Lampides boeticus</i>	Lyc.	Wide.	Meso.	Shrub.	Mid.	3	1	3	5	3	Un.	LC
<i>Leptotes pirthous</i>	Lyc.	South.	Meso.	Dry.	Mid.	3	1	3	5	2	Un.	LC

<i>Lycaena dispar</i>	Lyc.	North.	Hill.	Humid.	Mid.	3	1	2	4	3	Pr.	LC
<i>Lycaena helle</i>	Lyc.	North.	Mount.	Humid.	Spe.	1	1	2	2	4	Pr.	NT
<i>Lycaena hippothoe</i>	Lyc.	North.	Mount.	Humid.	Spe.	2	1	2	3	4	Un.	LC
<i>Lycaena phlaeas</i>	Lyc.	Wide.	Hill.	Meso.	Gen.	3	1	3	5	4	Un.	LC
<i>Lycaena tityrus</i>	Lyc.	Wide.	Hill.	Meso.	Mid.	2	1	2	5	4	Un.	LC
<i>Lycaena virgaureaea</i>	Lyc.	Wide.	Mount.	Meso.	Mid.	2	1	2	2	4	Un.	LC
<i>Lycaena alciphrons</i>	Lyc.	Wide.	Hill.	Dry.	Spe.	2	1	2	2	4	Un.	LC
<i>Lysandra bellargus</i>	Lyc.	Wide.	Hill.	Dry.	Spe.	2	1	2	4	3	Un.	LC
<i>Lysandra coridon</i>	Lyc.	Wide.	Hill.	Dry.	Spe.	2	1	2	2	3	Un.	LC
<i>Lysandra hispana</i>	Lyc.	South.	Supra.	Dry.	Mid.	2	1	2	4	3	Un.	LC
<i>Maculineaalconalcon</i>	Lyc.	Wide.	Mount.	Humid.	Mid.	2	1	2	2	1	Pr.	NT
<i>Maculineaalconrebeli</i>	Lyc.	Wide.	Mount.	Dry.	Spe.	2	1	2	2	1	Pr.	LC
<i>Maculineaarion</i>	Lyc.	Wide.	Mount.	Dry.	Spe.	3	1	2	2	1	Pr.	LC
<i>Maculineaausithous</i>	Lyc.	North.	Hill.	Humid.	Spe.	1	1	2	2	1	Pr.	VU
<i>Maculineaateleius</i>	Lyc.	North.	Hill.	Humid.	Spe.	1	1	2	2	1	Pr.	VU
<i>Plebejusargus</i>	Lyc.	Wide.	Hill.	Dry.	Mid.	3	1	1	4	1	Un.	LC
<i>Plebejusargyrognomon</i>	Lyc.	Wide.	Hill.	Dry.	Spe.	2	1	2	4	3	Un.	LC
<i>Plebejusidas</i>	Lyc.	Wide.	Hill.	Dry.	Mid.	3	1	1	4	1	Un.	LC
<i>Polyommatusamandus</i>	Lyc.	North.	Mount.	Meso.	Spe.	3	1	2	2	2	Un.	LC
<i>Polyommatusdamon</i>	Lyc.	North.	Mount.	Dry.	Spe.	2	1	1	2	3	Un.	LC
<i>Polyommatusdaphnis</i>	Lyc.	South.	Hill.	Dry.	Spe.	2	1	2	2	3	Un.	LC
<i>Polyommatusdolos</i>	Lyc.	South.	Supra.	Dry.	Mid.	2	1	1	3	3	Un.	LC
<i>Polyommatusdorylas</i>	Lyc.	Wide.	Mount.	Dry.	Spe.	2	1	1	4	3	Un.	NT
<i>Polyommatuseros</i>	Lyc.	Mount.	Alp.	Alpine.	Spe.	3	1	1	2	3	Un.	LC
<i>Polyommatusescheri</i>	Lyc.	South.	Mount.	Dry.	Spe.	2	1	1	2	3	Un.	LC
<i>Polyommatusicarus</i>	Lyc.	Wide.	Hill.	Meso.	Gen.	3	1	3	5	3	Un.	LC
<i>Polyommatusripartii</i>	Lyc.	South.	Hill.	Dry.	Spe.	1	1	1	2	2	Un.	LC
<i>Polyommatusthersites</i>	Lyc.	Wide.	Hill.	Dry.	Spe.	2	1	1	4	2	Un.	LC
<i>Pseudophilotesbaton</i>	Lyc.	South.	Hill.	Dry.	Spe.	3	1	2	4	3	Un.	LC
<i>Quercusiaquercus</i>	Lyc.	Wide.	Hill.	Forest	Spe.	3	4	2	2	3	Un.	LC
<i>Satyriumacaciae</i>	Lyc.	Wide.	Hill.	Shrub.	Mid.	2	3	1	2	4	Un.	LC
<i>Satyriumesculi</i>	Lyc.	South.	Meso.	Shrub.	Mid.	3	4	1	2	3	Un.	LC
<i>Satyriumilicis</i>	Lyc.	Wide.	Hill.	Shrub.	Spe.	3	4	1	2	3	Un.	LC
<i>Satyriumpruni</i>	Lyc.	North.	Hill.	Forest	Spe.	2	3	1	2	3	Un.	LC
<i>Satyriumspini</i>	Lyc.	Wide.	Hill.	Shrub.	Mid.	3	3	1	2	3	Un.	LC
<i>Satyriumw-album</i>	Lyc.	Wide.	Hill.	Forest	Spe.	2	4	1	2	3	Un.	LC
<i>Scolitantidesorion</i>	Lyc.	Wide.	Mount.	Dry.	Mid.	2	1	1	3	2	Un.	LC

<i>Thecla betulae</i>	Lyc.	Wide.	Hill.	Forest	Mid.	2	3	1	2	3	Un.	LC
<i>Tomares ballus</i>	Lyc.	South.	Meso.	Shrub.	Mid.	3	2	1	2	2	Un.	VU
<i>Aglais io</i>	Nymph.	Wide.	Hill.	Meso.	Gen.	2	2	3	4	5	Un.	LC
<i>Aglais urticae</i>	Nymph.	Wide.	Hill.	Meso.	Gen.	2	2	3	5	5	Un.	LC
<i>Apatura ilia</i>	Nymph.	Wide.	Hill.	Forest	Spe.	3	4	2	3	5	Un.	LC
<i>Apatura iris</i>	Nymph.	Wide.	Hill.	Forest	Spe.	3	4	2	2	5	Un.	LC
<i>Araschnia levana</i>	Nymph.	North.	Hill.	Meso.	Mid.	1	2	2	4	5	Un.	LC
<i>Argynnis adippe</i>	Nymph.	Wide.	Mount.	Meso.	Mid.	3	1	2	2	5	Un.	LC
<i>Argynnis aglaja</i>	Nymph.	Wide.	Hill.	Meso.	Mid.	3	1	2	2	5	Un.	LC
<i>Argynnis elisa</i>	Nymph.	South.	Mount.	Forest	Mid.	1	1	2	2	5	Pr.	LC
<i>Argynnis niobe</i>	Nymph.	Wide.	Mount.	Meso.	Mid.	3	1	2	2	5	Un.	NT
<i>Argynnis pandora</i>	Nymph.	South.	Meso.	Dry.	Mid.	1	1	2	2	5	Un.	LC
<i>Argynnis paphia</i>	Nymph.	Wide.	Hill.	Forest	Spe.	3	1	2	2	5	Un.	LC
<i>Boloria aquilonaris</i>	Nymph.	North.	Mount.	Humid.	Spe.	2	1	2	2	5	Pr.	NT
<i>Boloria dia</i>	Nymph.	Wide.	Hill.	Meso.	Mid.	3	1	2	5	5	Un.	LC
<i>Boloria eunomia</i>	Nymph.	North.	Mount.	Humid.	Mid.	1	1	1	2	5	Pr.	LC
<i>Boloria euphrosyne</i>	Nymph.	Wide.	Mount.	Forest	Mid.	3	1	2	3	5	Un.	LC
<i>Boloria graeca</i>	Nymph.	Mount.	Alp.	Alpine.	Spe.	1	1	1	2	5	Un.	LC
<i>Boloria napaea</i>	Nymph.	Mount.	Alp.	Alpine.	Spe.	1	1	2	2	5	Un.	LC
<i>Boloria pales</i>	Nymph.	Mount.	Alp.	Alpine.	Spe.	2	1	2	2	5	Un.	LC
<i>Boloria selene</i>	Nymph.	Wide.	Hill.	Humid.	Mid.	2	1	2	3	5	Un.	NT
<i>Boloria titania</i>	Nymph.	North.	Mount.	Humid.	Spe.	2	1	1	2	5	Un.	LC
<i>Brenthis daphne</i>	Nymph.	South.	Hill.	Shrub.	Mid.	3	3	3	2	5	Un.	LC
<i>Brenthis hecate</i>	Nymph.	South.	Supra.	Dry.	Spe.	2	1	1	2	5	Un.	LC
<i>Brenthis ino</i>	Nymph.	Wide.	Mount.	Humid.	Spe.	1	2	2	2	5	Un.	LC
<i>Brintesia circe</i>	Nymph.	Wide.	Hill.	Forest	Mid.	3	2	3	2	5	Un.	LC
<i>Charaxes jasius</i>	Nymph.	South.	Meso.	Shrub.	Mid.	2	4	3	4	5	Un.	LC
<i>Danaus chrysippus</i>	Nymph.	South.	Meso.	Shrub.	Mid.	2	2	3	2	5	Un.	LC
<i>Euphydryas aurinia</i>	Nymph.	Wide.	Hill.	Humid.	Spe.	3	1	1	2	5	Pr.	LC
<i>Euphydryas cynthia</i>	Nymph.	Mount.	Alp.	Alpine.	Spe.	2	1	2	2	5	Un.	LC
<i>Euphydryas desfontainii</i>	Nymph.	South.	Supra.	Shrub.	Mid.	1	1	1	2	5	Pr.	VU
<i>Euphydryas intermedia</i>	Nymph.	Mount.	Mount.	Alpine.	Mid.	1	3	2	2	5	Un.	VU
<i>Euphydryas maturna</i>	Nymph.	North.	Hill.	Forest	Spe.	3	4	2	2	5	Pr.	EN
<i>Issoria lathonia</i>	Nymph.	Wide.	Hill.	Meso.	Gen.	3	1	3	5	5	Un.	LC
<i>Libythea celtis</i>	Nymph.	South.	Meso.	Forest	Mid.	1	3	3	3	5	Un.	LC
<i>Limenitis camilla</i>	Nymph.	Wide.	Hill.	Forest	Spe.	2	3	2	3	5	Un.	LC
<i>Limenitis populi</i>	Nymph.	North.	Hill.	Forest	Spe.	2	4	2	2	5	Un.	NT

<i>Limenitis reducta</i>	Nymph.	Wide.	Hill.	Forest	Spe.	3	3	2	4	5	Un.	LC
<i>Melitaea athalia</i>	Nymph.	Wide.	Hill.	Meso.	Mid.	3	1	1	2	5	Un.	LC
<i>Melitaea aurelia</i>	Nymph.	North.	Hill.	Dry.	Spe.	2	1	1	2	5	Un.	VU
<i>Melitaea cinxia</i>	Nymph.	Wide.	Hill.	Meso.	Spe.	3	1	1	4	5	Un.	LC
<i>Melitaea deione</i>	Nymph.	South.	Supra.	Dry.	Spe.	3	1	1	4	5	Un.	LC
<i>Melitaea diamina</i>	Nymph.	North.	Mount.	Humid.	Spe.	2	1	1	3	5	Un.	LC
<i>Melitaea didyma</i>	Nymph.	Wide.	Hill.	Dry.	Spe.	3	1	2	4	5	Un.	LC
<i>Melitaea parthenoides</i>	Nymph.	Wide.	Hill.	Dry.	Spe.	2	1	2	4	5	Un.	LC
<i>Melitaea phoebe</i>	Nymph.	Wide.	Hill.	Meso.	Spe.	3	1	2	4	5	Un.	LC
<i>Melitaea varia</i>	Nymph.	Mount.	Alp.	Alpine.	Mid.	2	1	2	2	5	Un.	LC
<i>Nymphalis antiopa</i>	Nymph.	Wide.	Hill.	Forest	Spe.	3	4	3	2	5	Un.	LC
<i>Nymphalis polychloros</i>	Nymph.	Wide.	Hill.	Forest	Mid.	3	4	3	2	5	Un.	LC
<i>Polygonia c-album</i>	Nymph.	Wide.	Hill.	Forest	Gen.	3	3	3	4	5	Un.	LC
<i>Polygonia egea</i>	Nymph.	South.	Meso.	Dry.	Mid.	1	1	3	4	5	Un.	EN
<i>Vanessa atalanta</i>	Nymph.	Wide.	Hill.	Meso.	Mid.	2	2	3	4	5	Un.	LC
<i>Vanessa cardui</i>	Nymph.	Wide.	Hill.	Meso.	Mid.	3	1	3	6	5	Un.	LC
<i>Iphiclides podalirius</i>	Pap.	Wide.	Hill.	Shrub.	Gen.	3	3	3	5	5	Un.	LC
<i>Papilio alexanor</i>	Pap.	South.	Supra.	Dry.	Mid.	2	1	2	2	5	Pr.	LC
<i>Papilio hospiton</i>	Pap.	South.	Meso.	Dry.	Mid.	2	1	2	2	5	Pr.	LC
<i>Papilio machaon</i>	Pap.	Wide.	Hill.	Meso.	Gen.	3	1	2	5	5	Un.	LC
<i>Parnassius apollo</i>	Pap.	North.	Mount.	Dry.	Mid.	3	1	3	2	5	Pr.	LC
<i>Parnassius corybas</i>	Pap.	Mount.	Alp.	Humid.	Spe.	2	1	2	2	5	Pr.	LC
<i>Parnassius mnemosyne</i>	Pap.	North.	Mount.	Forest	Spe.	2	1	2	2	5	Pr.	NT
<i>Zerynthia polyxena</i>	Pap.	South.	Meso.	Humid.	Mid.	3	1	2	2	5	Pr.	LC
<i>Zerynthia rumina</i>	Pap.	South.	Meso.	Shrub.	Mid.	1	1	2	2	5	Pr.	LC
<i>Anthocharis cardamines</i>	Pier.	Wide.	Hill.	Humid.	Gen.	3	1	2	2	5	Un.	LC
<i>Anthocharis euphenoides</i>	Pier.	South.	Meso.	Dry.	Mid.	1	1	2	2	5	Un.	LC
<i>Aporia crataegi</i>	Pier.	Wide.	Hill.	Shrub.	Mid.	3	3	2	2	5	Un.	LC
<i>Colias alfacariensis</i>	Pier.	Wide.	Hill.	Dry.	Spe.	2	1	3	5	5	Un.	LC
<i>Colias crocea</i>	Pier.	Wide.	Hill.	Meso.	Mid.	3	1	3	6	5	Un.	LC
<i>Colias hyale</i>	Pier.	Wide.	Hill.	Humid.	Mid.	2	1	3	5	5	Un.	LC
<i>Colias palaeno</i>	Pier.	North.	Mount.	Humid.	Spe.	2	1	3	2	5	Pr.	LC
<i>Colias phicomone</i>	Pier.	Mount.	Alp.	Alpine.	Spe.	1	1	3	2	5	Un.	LC
<i>Euchloe cramerii</i>	Pier.	South.	Hill.	Dry.	Mid.	3	1	1	4	5	Un.	LC
<i>Euchloe insularis</i>	Pier.	South.	Meso.	Meso.	Mid.	3	1	1	2	5	Un.	LC
<i>Euchloe simplonia</i>	Pier.	Mount.	Alp.	Alpine.	Mid.	2	1	2	2	5	Un.	LC
<i>Gonepteryx cleopatra</i>	Pier.	South.	Meso.	Shrub.	Mid.	1	3	3	3	5	Un.	LC

<i>Gonepteryx rhamni</i>	Pier.	Wide.	Hill.	Meso.	Gen.	2	3	3	2	5	Un.	LC
<i>Iberochloe tagis</i>	Pier.	South.	Supra.	Dry.	Mid.	3	1	1	2	5	Un.	NT
<i>Leptidea duponcheli</i>	Pier.	South.	Supra.	Dry.	Spe.	2	1	1	4	5	Un.	LC
<i>Leptidea sinapis</i>	Pier.	Wide.	Hill.	Meso.	Gen.	3	1	2	4	5	Un.	LC
<i>Pieris brassicae</i>	Pier.	Wide.	Hill.	Meso.	Gen.	3	1	3	6	5	Un.	LC
<i>Pieris bryoniae</i>	Pier.	Mount.	Mount.	Alpine.	Mid.	2	1	2	2	5	Un.	LC
<i>Pieris ergane</i>	Pier.	South.	Mount.	Dry.	Mid.	1	1	1	5	5	Pr.	VU
<i>Pieris mannii</i>	Pier.	South.	Hill.	Dry.	Mid.	3	1	3	5	5	Un.	LC
<i>Pieris napi</i>	Pier.	Wide.	Hill.	Meso.	Gen.	3	1	3	5	5	Un.	LC
<i>Pieris rapae</i>	Pier.	Wide.	Hill.	Meso.	Gen.	3	1	3	6	5	Un.	LC
<i>Pontia callidice</i>	Pier.	Mount.	Alp.	Alpine.	Spe.	2	1	2	2	5	Un.	LC
<i>Pontia daplidice</i>	Pier.	Wide.	Meso.	Meso.	Gen.	3	1	3	6	5	Un.	LC
<i>Hamaeris lucina</i>	Rio.	Wide.	Hill.	Forest	Mid.	3	1	2	3	4	Un.	LC
<i>Aphantopus hyperantus</i>	Sat.	Wide.	Hill.	Forest	Gen.	3	2	2	2	5	Un.	LC
<i>Arethusana arethusa</i>	Sat.	Wide.	Hill.	Dry.	Spe.	2	2	2	2	5	Un.	LC
<i>Chazara briseis</i>	Sat.	Wide.	Hill.	Dry.	Mid.	2	2	2	2	5	Un.	VU
<i>Coenonympha arcania</i>	Sat.	Wide.	Hill.	Forest	Mid.	3	2	2	2	5	Un.	LC
<i>Coenonympha corinna</i>	Sat.	South.	Meso.	Dry.	Mid.	1	2	2	3	5	Un.	LC
<i>Coenonympha darwiniana</i>	Sat.	Mount.	Alp.	Alpine.	Mid.	1	2	2	2	5	Un.	LC
<i>Coenonympha dorus</i>	Sat.	South.	Supra.	Shrub.	Spe.	2	2	2	2	5	Un.	LC
<i>Coenonympha gardetta</i>	Sat.	Mount.	Alp.	Alpine.	Spe.	1	2	2	2	5	Un.	LC
<i>Coenonympha glycerion</i>	Sat.	Wide.	Mount.	Dry.	Spe.	3	2	2	3	5	Un.	LC
<i>Coenonympha hero</i>	Sat.	North.	Mount.	Humid.	Mid.	2	2	1	2	5	Pr.	CR
<i>Coenonympha oedippus</i>	Sat.	North.	Hill.	Humid.	Mid.	2	2	1	2	5	Pr.	NT
<i>Coenonympha pamphilus</i>	Sat.	Wide.	Hill.	Meso.	Gen.	3	2	3	5	5	Un.	LC
<i>Coenonympha tullia</i>	Sat.	North.	Mount.	Humid.	Spe.	2	2	1	2	5	Pr.	EN
<i>Erebia aethiopellus</i>	Sat.	Mount.	Alp.	Alpine.	Mid.	1	2	1	2	5	Un.	LC
<i>Erebia aethiops</i>	Sat.	North.	Mount.	Forest	Spe.	3	2	2	2	5	Un.	LC
<i>Erebia alberganus</i>	Sat.	Mount.	Mount.	Meso.	Spe.	2	2	2	2	5	Un.	LC
<i>Erebia cassioides</i>	Sat.	Mount.	Alp.	Alpine.	Spe.	1	2	2	2	5	Un.	LC
<i>Erebia epiphron</i>	Sat.	North.	Mount.	Alpine.	Spe.	1	2	1	2	5	Un.	LC
<i>Erebia epistygne</i>	Sat.	Mount.	Supra.	Dry.	Mid.	1	2	1	2	5	Un.	NT
<i>Erebia euryale</i>	Sat.	Mount.	Mount.	Alpine.	Mid.	2	2	2	2	5	Un.	LC
<i>Erebia gorge</i>	Sat.	Mount.	Alp.	Alpine.	Spe.	2	2	2	2	5	Un.	LC
<i>Erebia gorgone</i>	Sat.	Mount.	Alp.	Alpine.	Mid.	1	2	2	2	5	Un.	LC
<i>Erebia lefebvrei</i>	Sat.	Mount.	Alp.	Alpine.	Mid.	1	2	2	2	5	Un.	NT
<i>Erebia ligea</i>	Sat.	North.	Mount.	Forest	Spe.	3	2	2	2	5	Un.	LC

<i>Erebia manto</i>	Sat.	Mount.	Alp.	Meso.	Spe.	2	2	2	2	5	Un.	LC
<i>Erebia medusa</i>	Sat.	North.	Mount.	Humid.	Spe.	2	2	2	2	5	Un.	LC
<i>Erebia melampus</i>	Sat.	Mount.	Alp.	Alpine.	Spe.	2	2	2	2	5	Un.	LC
<i>Erebia meolans</i>	Sat.	Mount.	Mount.	Meso.	Spe.	2	2	2	2	5	Un.	LC
<i>Erebia mnestra</i>	Sat.	Mount.	Alp.	Shrub.	Mid.	1	2	2	2	5	Un.	LC
<i>Erebia montana</i>	Sat.	Mount.	Alp.	Alpine.	Mid.	3	2	2	2	5	Un.	LC
<i>Erebia neoridas</i>	Sat.	Mount.	Mount.	Dry.	Mid.	1	2	2	2	5	Un.	LC
<i>Erebia oeme</i>	Sat.	Mount.	Mount.	Humid.	Spe.	3	2	2	2	5	Un.	LC
<i>Erebia ottomana</i>	Sat.	Mount.	Mount.	Shrub.	Mid.	1	2	2	2	5	Un.	LC
<i>Erebia pandrose</i>	Sat.	North.	Alp.	Alpine.	Spe.	2	2	1	2	5	Un.	LC
<i>Erebia pharte</i>	Sat.	Mount.	Alp.	Alpine.	Spe.	3	2	2	2	5	Un.	LC
<i>Erebia pluto</i>	Sat.	Mount.	Alp.	Alpine.	Mid.	2	2	2	2	5	Un.	LC
<i>Erebia pronoe</i>	Sat.	Mount.	Alp.	Alpine.	Spe.	2	2	2	2	5	Un.	LC
<i>Erebia rondoui</i>	Sat.	Mount.	Alp.	Alpine.	Mid.	1	2	1	2	5	Un.	LC
<i>Erebia scipio</i>	Sat.	Mount.	Alp.	Alpine.	Mid.	2	2	1	2	5	Un.	NT
<i>Erebia sudetica</i>	Sat.	Mount.	Mount.	Humid.	Spe.	1	2	1	2	5	Pr.	LC
<i>Erebia triarius</i>	Sat.	Mount.	Mount.	Dry.	Spe.	2	2	2	2	5	Un.	LC
<i>Hipparchia aristaeus</i>	Sat.	South.	Meso.	Shrub.	Mid.	1	2	2	2	5	Un.	LC
<i>Hipparchia fagi</i>	Sat.	Wide.	Hill.	Forest	Mid.	3	2	2	2	5	Un.	LC
<i>Hipparchia fidia</i>	Sat.	South.	Meso.	Shrub.	Mid.	3	2	2	2	5	Un.	LC
<i>Hipparchia neomiris</i>	Sat.	South.	Meso.	Dry.	Mid.	1	2	2	2	5	Un.	LC
<i>Hipparchia semele</i>	Sat.	Wide.	Hill.	Dry.	Mid.	3	2	2	2	5	Un.	LC
<i>Hipparchia statilinus</i>	Sat.	Wide.	Hill.	Dry.	Mid.	3	2	2	2	5	Un.	LC
<i>Hyponephele lupina</i>	Sat.	South.	Mount.	Dry.	Mid.	2	2	2	2	5	Un.	NT
<i>Hyponephele lycaon</i>	Sat.	Wide.	Meso.	Dry.	Mid.	2	2	2	2	5	Un.	LC
<i>Lasiommata maera</i>	Sat.	Wide.	Mount.	Forest	Mid.	3	2	2	4	5	Un.	LC
<i>Lasiommata megera</i>	Sat.	Wide.	Hill.	Dry.	Mid.	3	2	3	5	5	Un.	LC
<i>Lasiommata petropolitana</i>	Sat.	North.	Mount.	Forest	Spe.	2	2	2	3	5	Un.	LC
<i>Lopinga achine</i>	Sat.	North.	Hill.	Forest	Spe.	3	2	2	2	5	Pr.	NT
<i>Maniola jurtina</i>	Sat.	Wide.	Hill.	Meso.	Gen.	3	2	3	2	5	Un.	LC
<i>Melanargia galathea</i>	Sat.	Wide.	Hill.	Meso.	Gen.	3	2	2	2	5	Un.	LC
<i>Melanargia lachesis</i>	Sat.	South.	Hill.	Dry.	Mid.	3	2	2	2	5	Un.	LC
<i>Melanargia occitanica</i>	Sat.	South.	Hill.	Dry.	Spe.	3	2	2	2	5	Un.	LC
<i>Melanargia russiae</i>	Sat.	South.	Mount.	Dry.	Spe.	2	2	2	2	5	Un.	LC
<i>Minois dryas</i>	Sat.	Wide.	Hill.	Forest	Mid.	3	2	2	2	5	Un.	LC
<i>Oneis glacialis</i>	Sat.	Mount.	Alp.	Alpine.	Spe.	1	2	2	2	5	Un.	LC
<i>Pararge aegeria</i>	Sat.	Wide.	Hill.	Forest	Spe.	3	2	3	5	5	Un.	LC

<i>Pyronia bathseba</i>	Sat.	South.	Meso.	Shrub.	Mid.	2	2	2	2	5	Un.	LC
<i>Pyronia cecilia</i>	Sat.	South.	Meso.	Shrub.	Mid.	3	2	2	2	5	Un.	LC
<i>Pyronia tithonus</i>	Sat.	Wide.	Hill.	Meso.	Mid.	3	2	2	2	5	Un.	LC
<i>Satyurus actaea</i>	Sat.	South.	Supra.	Dry.	Mid.	2	3	2	2	5	Un.	LC
<i>Satyurus ferula</i>	Sat.	South.	Mount.	Dry.	Mid.	1	2	2	2	5	Un.	LC

Table B. List of dragonfly taxa (species and subspecies) included in the present study and values for their ecological attributes, protection statut and red list assessment at the scale of study area: family (Aesh – Aeshnidae, Calo – Calopterygidae, Cgstr – Cordulegastridae, Coen – Coenagrionidae, Culid – Corduliidae, Gom – Gomphidae, Lest – Lestidae, Lib – Libellulidae, Macr – Macromiidae, Platy – Platycnemididae), biogeographic background (Wide – widespread, North – northern Europe, South – southern Europe, Mount – mountain areas), bioclimatic zonation (Low – lowland, Hill – hill zone, Mount – mountainous), freshwater type (Lent. - lentic, Lot. - lotic, Both), main breeding habitat (Str. – stream, Riv. – river, Po. – pond, RivPo. – river and pond, Bog – marsh and bog), habitat specialization (Gen – generalist, Spe - specialist), mobility (1 – low abilities, 2 – medium abilities, 3 – high abilities), voltinism (1 – 0.5 generation, 2 – 1 generation, 3 – 1 or 2 generations, 3 – generations, 4 – 2 to 3 generations, 5 – 3 to 4 generations), French protection status (Un – unprotected, Pr – protected), IUCN categories LC – least concern, NT – near threatened, VU – vulnerable, EN – endangered, CR – critically endangered, RE – regionally extinct).

Species/subspecies name	Family	Biogeographic background	Bioclimatic zonation	Freshwater type	Main breeding habitat	Habitat specialization	Dispersal abilities	Voltinism	Protection statut	IUCN categories
<i>Aeshna affinis</i>	Aesh.	South.	Low.	Both	RivPo.	Gen.	3	1	Un.	LC
<i>Aeshna cyanea</i>	Aesh.	Wide.	Hill.	Lent.	Po.	Gen.	3	2	Un.	LC
<i>Aeshna grandis</i>	Aesh.	Mount.	Mount.	Lent.	Bog.	Spe.	2	1	Un.	LC
<i>Aeshna isoceles</i>	Aesh.	North.	Low.	Lent.	Po.	Spe.	2	2	Un.	LC
<i>Aeshna juncea</i>	Aesh.	Mount.	Mount.	Lent.	Bog.	Spe.	2	1	Un.	NT
<i>Aeshna mixta</i>	Aesh.	Wide.	Low.	Both	RivPo.	Gen.	3	2	Un.	LC
<i>Aeshna subartica elisabethae</i>	Aesh.	Mount.	Mount.	Lent.	Bog.	Spe.	2	1	Un.	NT
<i>Anax imperator</i>	Aesh.	Wide.	Low.	Lent.	Po.	Gen.	3	1	Un.	LC
<i>Anax parthenope</i>	Aesh.	South.	Low.	Lent.	Po.	Gen.	3	2	Un.	LC
<i>Boyeria irene</i>	Aesh.	South.	Low.	Lot.	Str.	Spe.	2	1	Un.	LC
<i>Brachytron pratense</i>	Aesh.	North.	Low.	Lent.	Po.	Spe.	2	1	Un.	LC

<i>Hemianax ephippiger</i>	Aesh.	South.	Low.	Lent.	Po.	Gen.	3	2	Un.	LC
<i>Calopteryx haemorrhoidalis</i>	Calo.	South.	Low.	Lot.	Str.	Spe.	1	2	Un.	LC
<i>Calopteryx splendens caprai</i>	Calo.	South.	Low.	Lot.	Str.	Spe.	1	2	Un.	LC
<i>Calopteryx splendens splendens</i>	Calo.	North.	Low.	Lot.	Str.	Spe.	1	2	Un.	LC
<i>Calopteryx virgo meridionalis</i>	Calo.	South.	Hill.	Lot.	Str.	Spe.	1	2	Un.	LC
<i>Calopteryx virgo virgo</i>	Calo.	North.	Hill.	Lot.	Str.	Spe.	1	2	Un.	LC
<i>Calopteryx xanthostoma</i>	Calo.	South.	Low.	Lot.	Str.	Spe.	1	2	Un.	LC
<i>Cordulegaster bidentata</i>	Cgstr.	Mount.	Mount.	Lot.	Str.	Spe.	3	1	Un.	LC
<i>Cordulegaster boltonii boltonii</i>	Cgstr.	Wide.	Hill.	Lot.	Str.	Spe.	3	1	Un.	LC
<i>Cordulegaster boltonii immaculifrons</i>	Cgstr.	South.	Hill.	Lot.	Str.	Spe.	3	1	Un.	LC
<i>Ceriagrion tenellum</i>	Coen.	South.	Hill.	Both	RivPo.	Gen.	1	2	Un.	LC
<i>Coenagrion caerulescens</i>	Coen.	South.	Low.	Lot.	Str.	Spe.	1	2	Un.	EN
<i>Coenagrion hastulatum</i>	Coen.	Mount.	Mount.	Lent.	Bog.	Spe.	1	1	Un.	VU
<i>Coenagrion lunulatum</i>	Coen.	Mount.	Mount.	Lent.	Bog.	Spe.	1	1	Un.	VU
<i>Coenagrion mercuriale</i>	Coen.	South.	Low.	Lot.	Str.	Spe.	1	1	Pr.	LC
<i>Coenagrion ornatum</i>	Coen.	North.	Low.	Lot.	Str.	Spe.	1	2	Un.	NT
<i>Coenagrion puella</i>	Coen.	Wide.	Low.	Lot.	Po.	Gen.	2	2	Un.	LC
<i>Coenagrion pulchellum</i>	Coen.	North.	Low.	Lot.	Po.	Spe.	2	2	Un.	VU
<i>Coenagrion scitulum</i>	Coen.	South.	Low.	Lent.	Po.	Spe.	2	2	Un.	LC
<i>Enallagma cyathigerum</i>	Coen.	Wide.	Low.	Lent.	Po.	Gen.	2	4	Un.	LC
<i>Erythromma lindenii</i>	Coen.	Wide.	Low.	Both	RivPo.	Gen.	1	4	Un.	LC
<i>Erythromma najas</i>	Coen.	North.	Low.	Lent.	Po.	Spe.	1	2	Un.	LC
<i>Erythromma viridulum</i>	Coen.	Wide.	Low.	Lent.	Po.	Spe.	1	4	Un.	LC
<i>Ischnura elegans</i>	Coen.	Wide.	Low.	Both	RivPo.	Gen.	2	4	Un.	LC
<i>Ischnura genei</i>	Coen.	South.	Low.	Both	RivPo.	Gen.	2	4	Un.	LC
<i>Ischnura graellsii</i>	Coen.	South.	Low.	Both	RivPo.	Gen.	2	5	Un.	VU
<i>Ischnura pumilio</i>	Coen.	Wide.	Low.	Lent.	Po.	Spe.	2	5	Un.	LC
<i>Nehalennia speciosa</i>	Coen.	North.	Low.	Lent.	Bog.	Spe.	1	2	Un.	CR
<i>Pyrrhosoma nymphula</i>	Coen.	Wide.	Low.	Both	RivPo.	Gen.	2	2	Un.	LC
<i>Cordulia aenea</i>	Culid.	North.	Hill.	Lent.	Po.	Gen.	2	1	Un.	LC

<i>Epitheca bimaculata</i>	Culid.	North.	Low.	Lent.	Po.	Spe.	2	1	Un.	LC
<i>Oxygastra curtisii</i>	Culid.	South.	Low.	Both	RivPo.	Gen.	2	1	Pr.	LC
<i>Somatochlora alpestris</i>	Culid.	Mount.	Mount.	Lent.	Bog.	Spe.	3	1	Un.	NT
<i>Somatochlora arctica</i>	Culid.	Mount.	Mount.	Lent.	Bog.	Spe.	3	1	Un.	NT
<i>Somatochlora flavomaculata</i>	Culid.	North.	Low.	Lent.	Bog.	Spe.	2	1	Un.	LC
<i>Somatochlora meridionalis</i>	Culid.	South.	Low.	Lot.	Str.	Spe.	3	2	Un.	NT
<i>Somatochlora metallica</i>	Culid.	North.	Hill.	Both	RivPo.	Gen.	2	1	Un.	LC
<i>Gomphus graslinii</i>	Gom.	South.	Low.	Lot.	Riv.	Spe.	2	1	Pr.	LC
<i>Gomphus flavipes</i>	Gom.	North.	Low.	Lot.	Riv.	Spe.	2	1	Pr.	LC
<i>Gomphus pulchellus</i>	Gom.	North.	Low.	Both	RivPo.	Gen.	2	1	Un.	LC
<i>Gomphus simillimus</i>	Gom.	South.	Low.	Lot.	Riv.	Spe.	2	1	Un.	LC
<i>Gomphus vulgatissimus</i>	Gom.	North.	Low.	Lot.	Str.	Spe.	2	1	Un.	LC
<i>Onychogomphus forcipatus forcipatus</i>	Gom.	North.	Low.	Lot.	Str.	Spe.	2	1	Un.	LC
<i>Onychogomphus forcipatus unguiculatus</i>	Gom.	South.	Hill.	Lot.	Str.	Spe.	2	1	Un.	LC
<i>Onychogomphus uncatus</i>	Gom.	South.	Low.	Lot.	Str.	Spe.	2	1	Un.	LC
<i>Ophiogomphus cecilia</i>	Gom.	North.	Low.	Lot.	Riv.	Spe.	2	1	Pr.	LC
<i>Chalcolestes viridis viridis</i>	Lest.	Wide.	Low.	Both	RivPo.	Gen.	1	2	Un.	LC
<i>Lestes barbarus</i>	Lest.	North.	Low.	Lent.	Po.	Spe.	3	2	Un.	LC
<i>Lestes dryas</i>	Lest.	Wide.	Hill.	Lent.	Bog.	Spe.	3	2	Un.	LC
<i>Lestes macrostigma</i>	Lest.	South.	Low.	Lent.	Bog.	Spe.	1	2	Un.	EN
<i>Lestes sponsa</i>	Lest.	North.	Hill.	Lent.	Po.	Spe.	2	2	Un.	NT
<i>Lestes virens vestalis</i>	Lest.	North.	Low.	Lent.	Po.	Spe.	1	2	Un.	LC
<i>Lestes virens virens</i>	Lest.	South.	Low.	Lent.	Po.	Spe.	1	2	Un.	LC
<i>Sympecma fusca</i>	Lest.	Wide.	Low.	Lent.	Po.	Gen.	2	2	Un.	LC
<i>Sympecma paedisca</i>	Lest.	North.	Low.	Lent.	Bog.	Spe.	1	2	Pr.	RE
<i>Crocothemis erythraea</i>	Lib.	South.	Low.	Both	RivPo.	Gen.	3	5	Un.	LC
<i>Leucorrhinia albifrons</i>	Lib.	North.	Low.	Lent.	Bog.	Spe.	2	1	Pr.	NT
<i>Leucorrhinia caudalis</i>	Lib.	North.	Low.	Lent.	Po.	Spe.	1	2	Pr.	LC
<i>Leucorrhinia dubia</i>	Lib.	Mount.	Mount.	Lent.	Bog.	Spe.	1	1	Un.	NT
<i>Leucorrhinia pectoralis</i>	Lib.	North.	Low.	Lent.	Bog.	Spe.	2	1	Pr.	NT

<i>Leucorrhinia rubicunda</i>	Lib.	North.	Low.	Lent.	Bog.	Spe.	2	1	Un.	RE
<i>Libellula depressa</i>	Lib.	Wide.	Low.	Both	RivPo.	Gen.	3	2	Un.	LC
<i>Libellula fulva</i>	Lib.	North.	Low.	Both	RivPo.	Gen.	2	1	Un.	LC
<i>Libellula quadrimaculata</i>	Lib.	Wide.	Hill.	Lent.	Po.	Gen.	2	2	Un.	LC
<i>Orthetrum albistylum</i>	Lib.	Wide.	Low.	Both	RivPo.	Gen.	3	2	Un.	LC
<i>Orthetrum brunneum</i>	Lib.	Wide.	Low.	Both	RivPo.	Gen.	2	2	Un.	LC
<i>Orthetrum cancellatum</i>	Lib.	Wide.	Low.	Both	RivPo.	Gen.	3	5	Un.	LC
<i>Orthetrum coerulescens anceps</i>	Lib.	South.	Hill.	Both	RivPo.	Gen.	3	2	Un.	LC
<i>Orthetrum coerulescens coerulescens</i>	Lib.	Wide.	Low.	Both	RivPo.	Gen.	3	2	Un.	LC
<i>Sympetrum danae</i>	Lib.	North.	Hill.	Lent.	Bog.	Spe.	3	4	Un.	VU
<i>Sympetrum depressiusculum</i>	Lib.	North.	Low.	Lent.	Po.	Spe.	2	2	Un.	EN
<i>Sympetrum flaveolum</i>	Lib.	Mount.	Mount.	Lent.	Bog.	Spe.	3	2	Un.	NT
<i>Sympetrum fonscolombii</i>	Lib.	South.	Low.	Lent.	Po.	Gen.	3	5	Un.	LC
<i>Sympetrum meridionale</i>	Lib.	South.	Low.	Lent.	Po.	Gen.	2	1	Un.	LC
<i>Sympetrum pedemontanum</i>	Lib.	North.	Low.	Both	RivPo.	Spe.	3	2	Un.	NT
<i>Sympetrum sanguineum</i>	Lib.	Wide.	Low.	Lent.	Po.	Gen.	2	4	Un.	LC
<i>Sympetrum striolatum</i>	Lib.	Wide.	Low.	Both	RivPo.	Gen.	3	2	Un.	LC
<i>Sympetrum vulgatum ibericum</i>	Lib.	South.	Low.	Lent.	Po.	Gen.	3	2	Un.	NT
<i>Sympetrum vulgatum vulgatum</i>	Lib.	North.	Low.	Lent.	Po.	Gen.	3	2	Un.	NT
<i>Trithemis annulata</i>	Lib.	South.	Low.	Both	RivPo.	Gen.	3	5	Un.	LC
<i>Macromia splendens</i>	Macr.	South.	Low.	Lot.	Riv.	Spe.	3	1	Pr.	VU
<i>Platycnemis acutipennis</i>	Platy.	South.	Low.	Both	RivPo.	Gen.	2	2	Un.	LC
<i>Platycnemis latipes</i>	Platy.	South.	Low.	Lot.	Riv.	Spe.	2	2	Un.	LC
<i>Platycnemis pennipes</i>	Platy.	North.	Low.	Both	RivPo.	Gen.	2	2	Un.	LC

Supplementary material S2.1: List of 241 butterfly species included in the butterfly-hostplant interaction network. The higher taxonomic levels (family and subfamily) are shown on the basis of the most recent revision. The main breeding habitat and conservation status (protection, category on the French red list (LR), range trends, significance of decline) of each species are summarized. The degree (k), the projected degree (l) and the average degree of the partners (c) were calculated for each species. Each species was assigned to one of the modules (Mod) structuring the network.

Species	Family	Subfamily	Main breeding habitat	Protection status	LR	National trend	Significant decline	k	l	c	D	Mod
<i>Aglais ichnusa</i>	Nymphalidae	Nymphalinae	mesophile grassland	Unprotected	LC	NA	NA	1	0	1	NA	A
<i>Aglais io</i>	Nymphalidae	Nymphalinae	mesophile grassland	Unprotected	LC	Stable	No	2	5	4	8.5	B
<i>Aglais urticae</i>	Nymphalidae	Nymphalinae	mesophile grassland	Unprotected	LC	Stable	No	1	5	6	7.2	B
<i>Agriades glandon</i>	Lycaenidae	Polyommatainae	alpine grassland	Unprotected	LC	Stable	No	3	0	1	NA	C
<i>Agriades optilete</i>	Lycaenidae	Polyommatainae	humid grassland	Unprotected	LC	Stable	No	1	2	3	15	D
<i>Agriades orbitulus</i>	Lycaenidae	Polyommatainae	alpine grassland	Unprotected	LC	Stable	No	2	0	1	NA	E
<i>Agriades pyrenaica</i>	Lycaenidae	Polyommatainae	alpine grassland	Unprotected	LC	Stable	No	1	0	1	NA	F
<i>Anthocharis cardamines</i>	Pieridae	Pierinae	humid grassland	Unprotected	LC	Stable	No	16	9	2.5	13.88	G
<i>Anthocharis euphenoides</i>	Pieridae	Pierinae	dry grassland	Unprotected	LC	Stable	No	1	6	7	10.66	G
<i>Apatura ilia</i>	Nymphalidae	Apaturinae	forest	Unprotected	LC	Stable	No	5	5	3.2	6.45	H
<i>Apatura iris</i>	Nymphalidae	Apaturinae	forest	Unprotected	LC	Stable	No	4	5	3.75	8.11	H
<i>Aphantopus hyperantus</i>	Nymphalidae	Satyrinae	forest	Unprotected	LC	Stable	No	2	8	5	7.1	I
<i>Aporia crataegi</i>	Pieridae	Pierinae	shrubland	Unprotected	LC	Stable	No	13	6	2.85	10.64	J
<i>Araschnia levana</i>	Nymphalidae	Nymphalinae	mesophile grassland	Unprotected	LC	Stable	No	1	5	6	7.2	B
<i>Arethusana arethusia</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Declining	No	3	38	17.33	5.62	I
<i>Argynnis adippe</i>	Nymphalidae	Heliconiinae	mesophile grassland	Unprotected	LC	Declining	No	1	3	4	6.33	K
<i>Argynnis aglaja</i>	Nymphalidae	Heliconiinae	mesophile grassland	Unprotected	LC	Stable	No	6	15	4.33	3.79	K
<i>Argynnis elisa</i>	Nymphalidae	Heliconiinae	forest	Protected	LC	Stable	No	1	0	1	NA	L
<i>Argynnis niobe</i>	Nymphalidae	Heliconiinae	mesophile grassland	Unprotected	NT	Declining	Yes	1	7	8	4.14	K
<i>Argynnis pandora</i>	Nymphalidae	Heliconiinae	dry grassland	Unprotected	LC	Stable	No	4	5	3	5.75	K
<i>Argynnis paphia</i>	Nymphalidae	Heliconiinae	forest	Unprotected	LC	Stable	No	5	5	3.4	5.5	K
<i>Aricia agestis</i>	Lycaenidae	Polyommatainae	mesophile grassland	Unprotected	LC	Stable	No	8	14	2.87	8.75	M

<i>Aricia artaxerxes</i>	Lycaenidae	Polyommatainae	mesophile grassland	Unprotected	LC	Declining	No	2	6	4	5.5	M
<i>Aricia montensis</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	NA	NA	1	5	6	9.2	M
<i>Aricia morronensis</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	VU	Stable	No	1	0	1	NA	N
<i>Aricia nicias</i>	Lycaenidae	Polyommatainae	alpine grassland	Unprotected	LC	Stable	No	1	1	2	6	O
<i>Boloria aquilonaris</i>	Nymphalidae	Heliconiinae	humid grassland	Protected	NT	Declining	No	2	0	1	NA	P
<i>Boloria dia</i>	Nymphalidae	Heliconiinae	mesophile grassland	Unprotected	LC	Stable	No	6	7	3.83	5.33	K
<i>Boloria eunomia</i>	Nymphalidae	Heliconiinae	humid grassland	Protected	LC	Declining	No	1	3	4	3	K
<i>Boloria euphrosyne</i>	Nymphalidae	Heliconiinae	forest	Unprotected	LC	Declining	Yes	7	12	4	4.69	K
<i>Boloria graeca</i>	Nymphalidae	Heliconiinae	alpine grassland	Unprotected	LC	Stable	No	1	7	8	4.14	K
<i>Boloria napaea</i>	Nymphalidae	Heliconiinae	alpine grassland	Unprotected	LC	Declining	Yes	1	7	8	4.14	K
<i>Boloria pales</i>	Nymphalidae	Heliconiinae	alpine grassland	Unprotected	LC	Declining	No	4	8	3.25	3.24	K
<i>Boloria selene</i>	Nymphalidae	Heliconiinae	humid grassland	Unprotected	NT	Declining	No	2	4	3	6	K
<i>Boloria titania</i>	Nymphalidae	Heliconiinae	humid grassland	Unprotected	LC	Declining	No	2	4	3	3.33	K
<i>Brenthis daphne</i>	Nymphalidae	Heliconiinae	shrubland	Unprotected	LC	Stable	No	3	3	2.66	19.58	Q
<i>Brenthis hecate</i>	Nymphalidae	Heliconiinae	dry grassland	Unprotected	LC	Declining	Yes	1	0	1	NA	R
<i>Brenthis ino</i>	Nymphalidae	Heliconiinae	humid grassland	Unprotected	LC	Stable	No	1	2	3	11	Q
<i>Brintesia circe</i>	Nymphalidae	Satyrinae	forest	Unprotected	LC	Declining	No	3	22	9.66	6.35	I
<i>Callophrys avis</i>	Lycaenidae	Theclinae	shrubland	Unprotected	LC	Stable	No	2	2	2	15.5	S
<i>Callophrys rubi</i>	Lycaenidae	Theclinae	shrubland	Unprotected	LC	Stable	No	29	37	3.48	7.45	D
<i>Carcharodus alceae</i>	Hesperiidae	Pyrginae	mesophile grassland	Unprotected	LC	Stable	No	9	1	1.22	19	B
<i>Carcharodus baeticus</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	VU	Declining	Yes	2	1	1.5	4	T
<i>Carcharodus floccifer</i>	Hesperiidae	Pyrginae	mesophile grassland	Unprotected	LC	Declining	Yes	4	3	1.75	5	T
<i>Carcharodus lavatherae</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	NT	Declining	No	3	2	1.66	8.5	T
<i>Carterocephalus palaemon</i>	Hesperiidae	Heteropterinae	forest	Unprotected	LC	Declining	No	4	12	4.25	6.96	I
<i>Celastrina argiolus</i>	Lycaenidae	Polyommatainae	forest	Unprotected	LC	Stable	No	15	16	2.6	13.06	U
<i>Charaxes jasius</i>	Nymphalidae	Charaxinae	shrubland	Unprotected	LC	Stable	No	2	2	2	15.50	S
<i>Chazara briseis</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	VU	Declining	Yes	4	34	11.25	5.07	V
<i>Coenonympha arcania</i>	Nymphalidae	Satyrinae	forest	Unprotected	LC	Stable	No	2	19	11.5	6.68	V
<i>Coenonympha darwiniana</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Stable	No	2	9	5.5	5.11	I
<i>Coenonympha dorus</i>	Nymphalidae	Satyrinae	shrubland	Unprotected	LC	Declining	No	4	5	2.75	5.16	I

<i>Coenonympha glycerion</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Stable	No	6	24	5.83	8.32	I
<i>Coenonympha hero</i>	Nymphalidae	Satyrinae	humid grassland	Protected	CR	Declining	Yes	1	8	9	4.25	I
<i>Coenonympha oedippus</i>	Nymphalidae	Satyrinae	humid grassland	Protected	NT	Declining	Yes	1	8	9	4.25	I
<i>Coenonympha pamphilus</i>	Nymphalidae	Satyrinae	mesophile grassland	Unprotected	LC	Stable	No	4	28	8.25	5.78	I
<i>Coenonympha tullia</i>	Nymphalidae	Satyrinae	humid grassland	Protected	EN	Declining	Yes	5	16	4.4	7.79	V
<i>Colias alfacariensis</i>	Pieridae	Coliadae	dry grassland	Unprotected	LC	Stable	No	4	10	5.5	5.20	D
<i>Colias crocea</i>	Pieridae	Coliadae	mesophile grassland	Unprotected	LC	Stable	No	10	27	5.8	8.02	D
<i>Colias hyale</i>	Pieridae	Coliadae	humid grassland	Unprotected	LC	Declining	No	2	9	7	8.68	D
<i>Colias palaeno</i>	Pieridae	Coliadae	humid grassland	Protected	LC	Declining	Yes	1	2	3	15	D
<i>Colias phicomone</i>	Pieridae	Coliadae	alpine grassland	Unprotected	LC	Stable	No	3	14	6.66	8.1	D
<i>Cupido alceas</i>	Lycanidae	Polyommatinae	mesophile grassland	Unprotected	LC	Stable	No	1	3	4	12.66	D
<i>Cupido argiades</i>	Lycanidae	Polyommatinae	humid grassland	Unprotected	LC	Stable	No	7	18	5.15	10.38	D
<i>Cupido minimus</i>	Lycanidae	Polyommatinae	mesophile grassland	Unprotected	LC	Declining	No	6	14	3.83	8.31	D
<i>Cupido osiris</i>	Lycanidae	Polyommatinae	dry grassland	Unprotected	LC	Declining	Yes	4	16	7	10.66	D
<i>Cyaniris semiargus</i>	Lycanidae	Polyommatinae	mesophile grassland	Unprotected	LC	Stable	No	4	11	3.75	6.7	D
<i>Danaus chrysippus</i>	Nymphalidae	Danainae	shrubland	Unprotected	LC	Declining	No	1	0	1	NA	W
<i>Erebia aethiopellus</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Stable	No	1	5	6	5.2	V
<i>Erebia aethiops</i>	Nymphalidae	Satyrinae	forest	Unprotected	LC	Declining	Yes	12	45	8.42	6.29	I
<i>Erebia alberganus</i>	Nymphalidae	Satyrinae	mesophile grassland	Unprotected	LC	Stable	No	2	29	18	6.21	V
<i>Erebia cassioides</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Stable	No	5	36	13.4	5.18	V
<i>Erebia epiphron</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Declining	No	6	36	10.83	4.92	V
<i>Erebia epistygne</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	NT	Stable	No	1	0	1	NA	X
<i>Erebia euryale</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Stable	No	14	43	6.57	5.57	V
<i>Erebia gorge</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Declining	No	5	13	5.2	4.41	V
<i>Erebia ligea</i>	Nymphalidae	Satyrinae	forest	Unprotected	LC	Stable	No	2	8	5	5.5	V
<i>Erebia medusa</i>	Nymphalidae	Satyrinae	humid grassland	Unprotected	LC	Declining	Yes	4	40	16.75	6.10	I
<i>Erebia melampus</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Stable	No	5	34	12	7.26	V
<i>Erebia meolans</i>	Nymphalidae	Satyrinae	mesophile grassland	Unprotected	LC	Declining	No	4	32	12.5	5.15	V
<i>Erebia mnestra</i>	Nymphalidae	Satyrinae	shrubland	Unprotected	LC	Stable	No	3	30	14.33	5.03	V
<i>Erebia montana</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Stable	No	4	33	13	5.51	V

<i>Erebia neoridas</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Declining	No	3	27	10.33	5.44	V
<i>Erebia oeme</i>	Nymphalidae	Satyrinae	humid grassland	Unprotected	LC	Stable	No	3	3	3	10.66	V
<i>Erebia ottomana</i>	Nymphalidae	Satyrinae	shrubland	Unprotected	LC	Stable	No	1	8	9	6.12	V
<i>Erebia pandrose</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Stable	No	4	16	6.5	5.22	V
<i>Erebia pharte</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Declining	No	6	37	10.5	6.04	V
<i>Erebia pluto</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Stable	No	4	11	4.75	4.96	V
<i>Erebia pronoe</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Declining	No	5	37	13.2	5.46	V
<i>Erebia scipio</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	NT	Stable	No	2	0	1	NA	Y
<i>Erebia sudetica</i>	Nymphalidae	Satyrinae	humid grassland	Protected	LC	Stable	No	2	18	12	6.78	V
<i>Erebia triarius</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Stable	No	2	29	16	5.21	V
<i>Erynnis tages</i>	Hesperiidae	Pyrginae	mesophile grassland	Unprotected	LC	Stable	No	4	16	7.5	6.98	D
<i>Euchloe crameri</i>	Pieridae	Pierinae	dry grassland	Unprotected	LC	Declining	Yes	6	9	3.16	15.27	G
<i>Euchloe insularis</i>	Pieridae	Pierinae	mesophile grassland	Unprotected	LC	Stable	No	3	5	3	16.38	G
<i>Euchloe simplonia</i>	Pieridae	Pierinae	alpine grassland	Unprotected	LC	Declining	Yes	5	8	2.8	13	G
<i>Eumedonia eumedon</i>	Lycaenidae	Polyommatainae	forest	Unprotected	LC	Declining	No	6	1	1.16	1	O
<i>Euphydryas aurinia</i>	Nymphalidae	Melitaeinae	humid grassland	Protected	LC	Stable	No	16	4	1.44	5.08	Z
<i>Euphydryas cynthia</i>	Nymphalidae	Melitaeinae	alpine grassland	Unprotected	LC	Stable	No	4	7	3	3.86	K
<i>Euphydryas desfontainii</i>	Nymphalidae	Melitaeinae	shrubland	Protected	VU	Stable	No	1	1	2	16	Z
<i>Euphydryas intermedia</i>	Nymphalidae	Melitaeinae	alpine grassland	Unprotected	VU	Stable	No	1	0	1	NA	AA
<i>Euphydryas maturna</i>	Nymphalidae	Melitaeinae	forest	Protected	EN	Declining	Yes	5	11	3.6	6.20	T
<i>Gegenes pumilio</i>	Hesperiidae	Hesperiinae	dry grassland	Unprotected	CR	NA	NA	1	1	2	9	I
<i>Glaucopsyche alexis</i>	Lycaenidae	Polyommatainae	mesophile grassland	Unprotected	LC	Declining	No	7	14	4.43	14.53	D
<i>Glaucopsyche melanops</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Declining	No	2	7	4.5	12.43	D
<i>Gonepteryx cleopatra</i>	Pieridae	Coliadinae	shrubland	Unprotected	LC	Stable	No	1	2	3	10.5	U
<i>Gonepteryx rhamni</i>	Pieridae	Coliadinae	mesophile grassland	Unprotected	LC	Stable	No	3	2	2.33	7.5	U
<i>Hamearis lucina</i>	Riodinidae	Riodininae	forest	Unprotected	LC	Declining	Yes	3	0	1	NA	AB
<i>Hesperia comma</i>	Hesperiidae	Hesperiinae	dry grassland	Unprotected	LC	Declining	No	5	34	9.4	5.93	V
<i>Heteropterus morpheus</i>	Hesperiidae	Heteropterinae	humid grassland	Unprotected	LC	Declining	No	2	8	5	4.12	I
<i>Hipparchia alcyone</i>	Nymphalidae	Satyrinae	forest	Unprotected	LC	NA	NA	3	9	4	6.07	I
<i>Hipparchia aristaeus</i>	Nymphalidae	Satyrinae	shrubland	Unprotected	LC	Stable	No	2	5	3.5	6.58	I

<i>Hipparchia fagi</i>	Nymphalidae	Satyrinae	forest	Unprotected	LC	Declining	Yes	4	39	15.5	5.85	V
<i>Hipparchia fidia</i>	Nymphalidae	Satyrinae	shrubland	Unprotected	LC	Stable	Yes	1	1	2	7	I
<i>Hipparchia semele</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Declining	Yes	7	40	8.86	5.31	I
<i>Hipparchia statilinus</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Declining	Yes	8	33	6.37	5.48	I
<i>Hyponephele lupina</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	NT	Declining	No	2	4	3	3.66	I
<i>Hyponephele lycaon</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Declining	Yes	2	29	16	5.21	V
<i>Iberochloe tagis</i>	Pieridae	Pierinae	dry grassland	Unprotected	NT	Declining	No	2	1	1.5	25	G
<i>Iolana iolas</i>	Lycaenidae	Polyommatinae	forest	Unprotected	NT	Declining	Yes	1	7	8	10.28	D
<i>Iphiclides feisthamelii</i>	Papilionidae	Papilioninae	shrubland	Unprotected	LC	NA	NA	3	5	4.3	11.15	J
<i>Iphiclides podalirius</i>	Papilionidae	Papilioninae	shrubland	Unprotected	LC	Stable	No	15	6	2.6	10.16	J
<i>Issoria lathonia</i>	Nymphalidae	Heliconiinae	mesophile grassland	Unprotected	LC	Stable	No	6	10	3	7.94	K
<i>Laeosopis roboris</i>	Lycaenidae	Theclinae	forest	Unprotected	LC	Stable	No	2	0	1	NA	AC
<i>Lampides boeticus</i>	Lycaenidae	Polyommatinae	shrubland	Unprotected	LC	Declining	Yes	11	14	3.18	11.45	D
<i>Lasiommata maera</i>	Nymphalidae	Satyrinae	forest	Unprotected	LC	Declining	No	5	33	8.6	4.95	I
<i>Lasiommata megera</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Stable	No	3	19	8	4.64	I
<i>Lasiommata petropolitana</i>	Nymphalidae	Satyrinae	forest	Unprotected	LC	Stable	No	1	26	27	4.96	V
<i>Leptidea duponcheli</i>	Pieridae	Dismorphiinae	dry grassland	Unprotected	LC	Declining	No	2	10	7	9.81	D
<i>Leptidea juvernica</i>	Pieridae	Dismorphiinae	shrubland	Unprotected	LC	NA	NA	2	11	7	7.15	D
<i>Leptidea sinapis</i>	Pieridae	Dismorphiinae	mesophile grassland	Unprotected	LC	Stable	No	4	15	6.25	8.68	D
<i>Leptotes pirithous</i>	Lycaenidae	Polyommatinae	dry grassland	Unprotected	LC	Declining	No	5	14	4.8	9.45	D
<i>Libythea celtis</i>	Nymphalidae	Libytheinae	forest	Unprotected	LC	Declining	No	2	1	1.5	10	H
<i>Limenitis camilla</i>	Nymphalidae	Limenitinae	forest	Unprotected	LC	Stable	No	2	2	2.5	7.75	Z
<i>Limenitis populi</i>	Nymphalidae	Limenitinae	forest	Unprotected	NT	Declining	Yes	1	1	2	5	H
<i>Limenitis reducta</i>	Nymphalidae	Limenitinae	forest	Unprotected	LC	Stable	No	5	2	2	10.75	Z
<i>Lopinga achine</i>	Nymphalidae	Satyrinae	forest	Protected	NT	Declining	Yes	3	9	4	6.5	I
<i>Lycaena alciphron</i>	Lycaenidae	Lycaeninae	dry grassland	Unprotected	LC	Declining	No	4	5	4.5	6.05	AD
<i>Lycaena dispar</i>	Lycaenidae	Lycaeninae	humid grassland	Protected	LC	Stable	No	6	5	2.66	7.76	AD
<i>Lycaena helle</i>	Lycaenidae	Lycaeninae	humid grassland	Protected	NT	Declining	No	1	3	4	3	K
<i>Lycaena hippothoe</i>	Lycaenidae	Lycaeninae	humid grassland	Unprotected	LC	Declining	No	3	5	5.33	5.3	AD
<i>Lycaena phlaeas</i>	Lycaenidae	Lycaeninae	mesophile grassland	Unprotected	LC	Stable	No	9	5	3.11	4.9	AD

<i>Lycaena tityrus</i>	Lycaenidae	Lycaeninae	mesophile grassland	Unprotected	LC	Stable	No	5	5	4	5.5	AD
<i>Lycaena virgaureae</i>	Lycaenidae	Lycaeninae	mesophile grassland	Unprotected	LC	Stable	No	3	5	5.33	5.3	AD
<i>Lysandra bellargus</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Stable	No	3	8	5.33	4.83	D
<i>Lysandra coridon</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Stable	No	3	8	4.33	3.83	D
<i>Lysandra hispana</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Declining	No	2	8	6.5	5.70	D
<i>Maculineaalcon</i>	Lycaenidae	Polyommatainae	humid grassland	Protected	NT	Declining	Yes	8	1	1.25	16	Z
<i>Maculinea arion</i>	Lycaenidae	Polyommatainae	dry grassland	Protected	LC	Stable	No	6	1	1.16	2	AE
<i>Maculinea nausithous</i>	Lycaenidae	Polyommatainae	humid grassland	Protected	VU	Declining	No	1	2	3	1.5	AF
<i>Maculinea teleius</i>	Lycaenidae	Polyommatainae	humid grassland	Protected	VU	Declining	Yes	1	2	3	1.5	AF
<i>Maniola jurtina</i>	Nymphalidae	Satyrinae	mesophile grassland	Unprotected	LC	Stable	No	2	2	2	3.5	I
<i>Melanargia galathea</i>	Nymphalidae	Satyrinae	mesophile grassland	Unprotected	LC	Stable	No	9	25	5.55	5.96	I
<i>Melanargia lachesis</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Declining	No	7	27	7.71	6.68	I
<i>Melanargia occitanica</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Declining	No	7	43	10	5.49	I
<i>Melanargia russiae</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Declining	No	3	19	8.66	6.63	I
<i>Melitaea athalia</i>	Nymphalidae	Melitaeinae	mesophile grassland	Unprotected	LC	Stable	No	6	8	3.16	7.14	T
<i>Melitaea aurelia</i>	Nymphalidae	Melitaeinae	dry grassland	Unprotected	VU	Declining	Yes	2	7	5.5	7.39	T
<i>Melitaea cinxia</i>	Nymphalidae	Melitaeinae	mesophile grassland	Unprotected	LC	Stable	No	2	7	5.5	6.39	T
<i>Melitaea deione</i>	Nymphalidae	Melitaeinae	dry grassland	Unprotected	LC	Declining	No	4	3	1.75	6.75	T
<i>Melitaea diamina</i>	Nymphalidae	Melitaeinae	humid grassland	Unprotected	LC	Declining	No	4	0	1	NA	AG
<i>Melitaea didyma</i>	Nymphalidae	Melitaeinae	dry grassland	Unprotected	LC	Declining	No	13	11	2.23	4.74	T
<i>Melitaea helvetica</i>	Nymphalidae	Melitaeinae	mesophile grassland	Unprotected	LC	Stable	No	4	8	3.5	7.5	T
<i>Melitaea parthenoides</i>	Nymphalidae	Melitaeinae	dry grassland	Unprotected	LC	Declining	Yes	2	7	5.5	7.39	T
<i>Melitaea phoebe</i>	Nymphalidae	Melitaeinae	mesophile grassland	Unprotected	LC	Stable	No	7	2	1.43	17	B
<i>Minois dryas</i>	Nymphalidae	Satyrinae	forest	Unprotected	LC	Declining	No	4	25	7.75	7.05	I
<i>Nymphalis antiopa</i>	Nymphalidae	Nymphalinae	forest	Unprotected	LC	Declining	No	7	5	2.57	6.75	H
<i>Nymphalis polychloros</i>	Nymphalidae	Nymphalinae	forest	Unprotected	LC	Stable	No	10	13	3.3	7.74	H
<i>Ochlodes sylvanus</i>	Hesperiidae	Hesperiinae	forest	Unprotected	LC	Stable	No	8	30	6.5	6.09	I
<i>Oeneis glacialis</i>	Nymphalidae	Satyrinae	alpine grassland	Unprotected	LC	Stable	No	1	26	27	4.96	V
<i>Papilio alexanor</i>	Papilionidae	Papilioninae	dry grassland	Protected	LC	Declining	No	2	1	1.5	23	AF
<i>Papilio hospiton</i>	Papilionidae	Papilioninae	dry grassland	Protected	LC	Stable	No	5	1	1.2	23	AF

<i>Papilio machaon</i>	Papilionidae	Papilioninae	mesophile grassland	Unprotected	LC	Stable	No	23	6	1.26	4.42	AF
<i>Pararge aegeria</i>	Nymphalidae	Satyrinae	forest	Unprotected	LC	Stable	No	7	25	5.14	4.76	I
<i>Parnassius apollo</i>	Papilionidae	Parnassinae	dry grassland	Protected	LC	Declining	Yes	11	2	1.36	4.5	AH
<i>Parnassius corybas</i>	Papilionidae	Parnassinae	humid grassland	Protected	LC	Declining	No	2	2	2	8	AH
<i>Parnassius mnemosyne</i>	Papilionidae	Parnassinae	forest	Protected	NT	Stable	No	3	0	1	NA	AI
<i>Pieris brassicae</i>	Pieridae	Pierinae	mesophile grassland	Unprotected	LC	Stable	No	20	8	2.4	15.01	G
<i>Pieris bryoniae</i>	Pieridae	Pierinae	alpine grassland	Unprotected	LC	Declining	No	3	6	3	10.33	G
<i>Pieris ergane</i>	Pieridae	Pierinae	dry grassland	Protected	VU	Declining	No	1	1	2	6	G
<i>Pieris manni</i>	Pieridae	Pierinae	dry grassland	Unprotected	LC	Declining	Yes	6	5	2	11.91	G
<i>Pieris napi</i>	Pieridae	Pierinae	mesophile grassland	Unprotected	LC	Stable	No	9	8	3.11	17.21	G
<i>Pieris rapae</i>	Pieridae	Pierinae	mesophile grassland	Unprotected	LC	Stable	No	25	11	2.48	13.25	G
<i>Plebejus argus</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Stable	No	15	30	4.66	9.15	D
<i>Plebejus argyrognomon</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Stable	No	2	5	4.5	7.55	D
<i>Plebejus bellieri</i>	Lycaenidae	Polyommatainae	shrubland	Unprotected	LC	Declining	No	2	1	1.5	3	D
<i>Plebejus idas</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Declining	Yes	11	25	4.45	9.09	D
<i>Polygonia c-album</i>	Nymphalidae	Nymphalinae	forest	Unprotected	LC	Stable	No	10	15	3.4	8.59	H
<i>Polygonia egea</i>	Nymphalidae	Nymphalinae	dry grassland	Unprotected	EN	Declining	Yes	1	1	2	4	B
<i>Polyommatus amandus</i>	Lycaenidae	Polyommatainae	mesophile grassland	Unprotected	LC	Declining	No	4	4	2	10.5	D
<i>Polyommatus damon</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Declining	Yes	3	11	6.66	11.14	D
<i>Polyommatus daphnis</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Stable	No	5	9	3.4	7.2	D
<i>Polyommatus dolus</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Stable	No	3	15	6.66	8.28	D
<i>Polyommatus dorylas</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	NT	Declining	Yes	2	2	2	8.5	D
<i>Polyommatus eros</i>	Lycaenidae	Polyommatainae	alpine grassland	Unprotected	LC	Stable	No	2	1	1.5	5	D
<i>Polyommatus escheri</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Declining	No	3	3	2.33	11.33	D
<i>Polyommatus icarus</i>	Lycaenidae	Polyommatainae	mesophile grassland	Unprotected	LC	Stable	No	12	23	3.92	7.97	D
<i>Polyommatus ripartii</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Declining	No	2	8	6	9.29	D
<i>Polyommatus thersites</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Declining	Yes	3	12	6.66	11.02	D
<i>Pontia callidice</i>	Pieridae	Pierinae	alpine grassland	Unprotected	LC	Declining	No	3	0	1	NA	AJ
<i>Pontia daplidice</i>	Pieridae	Pierinae	mesophile grassland	Unprotected	LC	Declining	Yes	8	5	2.5	19.29	G
<i>Pseudophilotes baton</i>	Lycaenidae	Polyommatainae	dry grassland	Unprotected	LC	Declining	Yes	2	1	1.5	6	AE

<i>Pyrgus alveus</i>	Hesperiidae	Pyrginae	mesophile grassland	Unprotected	LC	Declining	Yes	3	14	6	5.6	M
<i>Pyrgus andromedae</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	LC	Declining	No	2	3	2.5	8.33	Q
<i>Pyrgus armoricanus</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	LC	Declining	Yes	5	9	5.2	7.35	Q
<i>Pyrgus bellieri</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	LC	NA	NA	4	5	2.25	8.6	M
<i>Pyrgus cacaliae</i>	Hesperiidae	Pyrginae	humid grassland	Unprotected	LC	Declining	No	3	4	2.33	6	Q
<i>Pyrgus carlinae</i>	Hesperiidae	Pyrginae	alpine grassland	Unprotected	LC	Stable	No	3	9	4.33	4	M
<i>Pyrgus carthami</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	LC	Declining	Yes	3	9	6.66	5.11	Q
<i>Pyrgus cirsii</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	NT	Declining	Yes	3	9	5.66	4.83	Q
<i>Pyrgus malvae</i>	Hesperiidae	Pyrginae	mesophile grassland	Unprotected	LC	Stable	No	14	17	2.93	7.79	Q
<i>Pyrgus malvoides</i>	Hesperiidae	Pyrginae	mesophile grassland	Unprotected	LC	Stable	No	8	15	4.75	7.21	Q
<i>Pyrgus onopordi</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	LC	Declining	Yes	4	9	5.25	6.125	Q
<i>Pyrgus serratulae</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	LC	Declining	Yes	4	10	5.5	4.42	Q
<i>Pyrgus sidae</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	LC	Declining	No	1	6	7	4.5	Q
<i>Pyrgus warrenensis</i>	Hesperiidae	Pyrginae	alpine grassland	Unprotected	VU	Stable	No	2	3	2.5	2.5	M
<i>Pyronia bathseba</i>	Nymphalidae	Satyrinae	shrubland	Unprotected	LC	Stable	No	2	11	7.5	6.38	I
<i>Pyronia cecilia</i>	Nymphalidae	Satyrinae	shrubland	Unprotected	LC	Stable	No	2	5	3.5	3.5	I
<i>Pyronia tithonus</i>	Nymphalidae	Satyrinae	mesophile grassland	Unprotected	LC	Stable	No	3	13	6.33	5.37	I
<i>Quercusia quercus</i>	Lycaenidae	Theclinae	forest	Unprotected	LC	Stable	No	6	3	2.66	5.7	H
<i>Satyrium acaciae</i>	Lycaenidae	Theclinae	shrubland	Unprotected	LC	Declining	No	2	5	4	10.5	J
<i>Satyrium esculi</i>	Lycaenidae	Theclinae	shrubland	Unprotected	LC	Stable	No	6	3	2.5	5.875	H
<i>Satyrium ilicis</i>	Lycaenidae	Theclinae	shrubland	Unprotected	LC	Declining	No	5	3	3	6.27	H
<i>Satyrium pruni</i>	Lycaenidae	Theclinae	forest	Unprotected	LC	Stable	No	2	5	5	9.83	J
<i>Satyrium spini</i>	Lycaenidae	Theclinae	shrubland	Unprotected	LC	Declining	No	6	3	2	5.75	U
<i>Satyrium w-album</i>	Lycaenidae	Theclinae	forest	Unprotected	LC	Declining	No	2	3	2.5	10.33	H
<i>Satyrus actaea</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Declining	Yes	2	4	3.5	3.66	I
<i>Satyrus ferula</i>	Nymphalidae	Satyrinae	dry grassland	Unprotected	LC	Declining	No	3	27	11	5.79	V
<i>Scolitantides orion</i>	Lycaenidae	Polyommatae	dry grassland	Unprotected	LC	Declining	Yes	5	2	1.8	9.5	AH
<i>Sloperia proto</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	LC	Declining	Yes	2	0	1	NA	AK
<i>Spialia sertorius</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	LC	Stable	No	2	6	4	6.25	AF
<i>Spialia therapne</i>	Hesperiidae	Pyrginae	dry grassland	Unprotected	LC	NA	NA	1	4	5	11.75	AF

<i>Thecla betulae</i>	Lycaenidae	Theclinae	forest	Unprotected	LC	Declining	No	7	5	3.14	11.06	J
<i>Thymelicus acteon</i>	Hesperiidae	Hesperiinae	dry grassland	Unprotected	LC	Stable	No	9	29	5.44	4.26	I
<i>Thymelicus lineola</i>	Hesperiidae	Hesperiinae	mesophile grassland	Unprotected	LC	Stable	No	9	41	8.66	7.26	I
<i>Thymelicus sylvestris</i>	Hesperiidae	Hesperiinae	mesophile grassland	Unprotected	LC	Stable	No	10	23	4.6	7.46	I
<i>Tomares ballus</i>	Lycaenidae	Theclinae	shrubland	Unprotected	VU	Declining	No	9	7	1.88	20.21	AL
<i>Vanessa atalanta</i>	Nymphalidae	Nymphalinae	mesophile grassland	Unprotected	LC	Stable	No	4	6	2.5	3.8	B
<i>Vanessa cardui</i>	Nymphalidae	Nymphalinae	mesophile grassland	Unprotected	LC	Stable	No	19	15	1.94	7.06	B
<i>Zerynthia polyxena</i>	Papilionidae	Parnassinae	humid grassland	Protected	LC	Stable	No	5	1	1.4	2	AM
<i>Zerynthia rumina</i>	Papilionidae	Parnassinae	shrubland	Protected	LC	Stable	No	2	1	2	5	AM

Supplementary material S2.2: List of 527 plant species included in the butterfly-hostplant interaction network. The higher taxonomic levels (order, family, and subfamily) are shown on the basis of the most recent revision. The degree (k), the projected degree (l) and the average degree of the partners (c) were calculated for each species. Each species was assigned to one of the modules structuring the network.

Species	Order	Family	k	l	c	Module
<i>Achillea millefolium</i>	Asterales	Asteraceae	1	12	13	T
<i>Achnatherum calamagrostis</i>	Poales	Poaceae	1	8	9	I
<i>Adenocarpus complicatus</i>	Fabales	Fabaceae	2	13	9	D
<i>Aegilops ovata</i>	Poales	Poaceae	2	3	2.5	I
<i>Aethionema saxatile</i>	Brassicales	Brassicaceae	2	5	3.5	G
<i>Agrimonia eupatoria</i>	Rosales	Rosaceae	2	15	11	Q
<i>Agrostis canina</i>	Poales	Poaceae	1	7	8	I
<i>Agrostis capillaris</i>	Poales	Poaceae	8	30	6.1	I
<i>Agrostis curtisii</i>	Poales	Poaceae	1	4	5	V
<i>Agrostis stolonifera</i>	Poales	Poaceae	2	12	7.5	I
<i>Alcea rosea</i>	Malvales	Malvaceae	1	8	9	B
<i>Alliaria petiolata</i>	Brassicales	Brassicaceae	4	44	17.5	G
<i>Alnus glutinosa</i>	Fagales	Betulaceae	2	8	6	H
<i>Alopecurus pratensis</i>	Poales	Poaceae	1	9	10	I
<i>Althaea cannabina</i>	Malvales	Malvaceae	1	8	9	B
<i>Althaea officinalis</i>	Malvales	Malvaceae	1	8	9	B
<i>Alyssoides utriculata</i>	Brassicales	Brassicaceae	1	5	6	G
<i>Amelanchier ovalis</i>	Rosales	Rosaceae	2	16	14	J
<i>Ammophila arenaria</i>	Poales	Poaceae	2	13	8	I
<i>Androsace carnea</i>	Ericales	Primulaceae	1	2	3	C
<i>Androsace obtusifolia</i>	Ericales	Primulaceae	1	2	3	C
<i>Androsace villosa</i>	Ericales	Primulaceae	1	0	1	F
<i>Androsace vitaliana</i>	Ericales	Primulaceae	1	2	3	C
<i>Anethum graveolens</i>	Apiales	Apiaceae	1	22	23	AF
<i>Angelica sylvestris</i>	Apiales	Apiaceae	1	22	23	AF
<i>Anthoxanthum odoratum</i>	Poales	Poaceae	9	32	6.9	I
<i>Anthyllis montana</i>	Fabales	Fabaceae	1	1	2	D
<i>Anthyllis vulneraria</i>	Fabales	Fabaceae	3	15	6.3	D
<i>Apium graveolens</i>	Apiales	Apiaceae	1	22	23	AF
<i>Arabidopsis arenosa</i>	Brassicales	Brassicaceae	1	15	16	G
<i>Arabidopsis halleri</i>	Brassicales	Brassicaceae	1	2	3	G
<i>Arabis hirsuta</i>	Brassicales	Brassicaceae	2	21	12	G
<i>Arabis pauciflora</i>	Brassicales	Brassicaceae	1	15	16	G
<i>Arbutus andrachne</i>	Ericales	Ericaceae	1	1	6	S
<i>Arbutus unedo</i>	Ericales	Ericaceae	3	30	12.3	S
<i>Arctium lappa</i>	Asterales	Asteraceae	1	18	19	B
<i>Argentina anserina</i>	Rosales	Rosaceae	1	13	14	Q
<i>Aristolochia clematitis</i>	Piperiales	Aristolochiaceae	1	4	5	AL

<i>Aristolochia pallida</i>	Piperales	Aristolochiaceae	1	4	5	AL
<i>Aristolochia paucinervis</i>	Piperales	Aristolochiaceae	1	4	5	AL
<i>Aristolochia pistolochia</i>	Piperales	Aristolochiaceae	2	4	3.5	AL
<i>Aristolochia rotunda</i>	Piperales	Aristolochiaceae	2	4	3.5	AM
<i>Arrhenatherum elatius</i>	Poales	Poaceae	3	9	4.3	I
<i>Artemisia vulgaris</i>	Asterales	Asteraceae	2	26	14.5	B
<i>Asarina procumbens</i>	Lamiales	Plantaginaceae	1	3	4	T
<i>Astragalus alopecurus</i>	Fabales	Fabaceae	1	10	11	D
<i>Astragalus alpinus</i>	Fabales	Fabaceae	1	1	2	E
<i>Astragalus cicer</i>	Fabales	Fabaceae	1	5	6	D
<i>Astragalus danicus</i>	Fabales	Fabaceae	2	14	8	D
<i>Astragalus glycyphyllos</i>	Fabales	Fabaceae	3	12	5.7	D
<i>Astragalus incanus</i>	Fabales	Fabaceae	2	12	7.5	D
<i>Astragalus monspessulanus</i>	Fabales	Fabaceae	4	26	8.8	D
<i>Astragalus onobrychis</i>	Fabales	Fabaceae	2	5	3.5	D
<i>Astragalus penduliflorus</i>	Fabales	Fabaceae	1	5	6	D
<i>Astragalus sempervirens</i>	Fabales	Fabaceae	1	2	3	D
<i>Avenula pratensis</i>	Poales	Poaceae	3	10	5.3	V
<i>Avenula pubescens</i>	Poales	Poaceae	1	3	4	I
<i>Ballota nigra</i>	Lamiales	Labiaceae	2	4	3	T
<i>Barbarea vulgaris</i>	Brassicales	Brassicaceae	2	18	11	G
<i>Biscutella laevigata</i>	Brassicales	Brassicaceae	7	42	9.7	G
<i>Bistorta officinalis</i>	Caryophyllales	Polygonaceae	4	6	2.5	K
<i>Borago officinalis</i>	Lamiales	Boraginaceae	2	23	12.5	K
<i>Bothriochloa ischaemum</i>	Poales	Poaceae	1	7	8	I
<i>Brachypodium phoenicoides</i>	Poales	Poaceae	8	20	5.3	I
<i>Brachypodium pinnatum</i>	Poales	Poaceae	8	29	6.6	I
<i>Brachypodium retusum</i>	Poales	Poaceae	2	8	5.5	I
<i>Brachypodium rupestre</i>	Poales	Poaceae	3	4	2.7	I
<i>Brachypodium sylvaticum</i>	Poales	Poaceae	5	24	7.2	I
<i>Brassica napus</i>	Brassicales	Brassicaceae	2	23	14	G
<i>Brassica oleracea</i>	Brassicales	Brassicaceae	2	33	22.5	G
<i>Brassica rapa</i>	Brassicales	Brassicaceae	3	37	18	G
<i>Briza media</i>	Poales	Poaceae	4	24	9	I
<i>Bromus diandrus</i>	Poales	Poaceae	1	8	9	I
<i>Bromus erectus</i>	Poales	Poaceae	17	47	6.5	I
<i>Bromus sterilis</i>	Poales	Poaceae	4	18	7.3	I
<i>Buddleja davidii</i>	Scrophulariales	Buddlejaceae	1	14	15	U
<i>Bunias erucago</i>	Brassicales	Brassicaceae	1	19	20	G
<i>Bupleurum falcatum</i>	Apiales	Apiaceae	1	22	23	AF
<i>Buxus sempervirens</i>	Buxales	Buxaceae	1	14	15	U
<i>Cakile maritima</i>	Brassicales	Brassicaceae	3	36	17.7	G
<i>Calamagrostis epigejos</i>	Poales	Poaceae	1	2	3	V
<i>Calamagrostis varia</i>	Poales	Poaceae	1	13	14	V
<i>Calamagrostis villosa</i>	Poales	Poaceae	2	11	6.5	I
<i>Calluna vulgaris</i>	Ericales	Ericaceae	1	14	15	U

<i>Capparis spinosa</i>	Capparales	Capparaceae	1	19	20	G
<i>Cardamine hirsuta</i>	Brassicales	Brassicaceae	3	36	16.3	G
<i>Cardamine pratensis</i>	Brassicales	Brassicaceae	2	19	12.5	G
<i>Cardamine resedifolia</i>	Brassicales	Brassicaceae	1	2	3	AJ
<i>Carduus acanthoides</i>	Asterales	Asteraceae	1	18	19	B
<i>Carduus crispus</i>	Asterales	Asteraceae	1	18	19	B
<i>Carduus defloratus</i>	Asterales	Asteraceae	1	18	19	B
<i>Carduus nutans</i>	Asterales	Asteraceae	1	18	19	B
<i>Carduus tenuiflorus</i>	Asterales	Asteraceae	1	18	19	B
<i>Carex alba</i>	Poales	Cyperaceae	1	2	3	I
<i>Carex ferruginea</i>	Poales	Cyperaceae	3	14	7	V
<i>Carex flacca</i>	Poales	Cyperaceae	3	15	7.7	V
<i>Carex halleriana</i>	Poales	Cyperaceae	2	10	6	I
<i>Carex montana</i>	Poales	Cyperaceae	2	10	6	I
<i>Carex nigra</i>	Poales	Cyperaceae	1	11	12	I
<i>Carex sempervirens</i>	Poales	Cyperaceae	3	19	9.7	V
<i>Carex sylvatica</i>	Poales	Cyperaceae	1	1	2	V
<i>Celtis australis</i>	Rosales	Ulmaceae	2	10	6	H
<i>Centaurea decipiens</i>	Asterales	Asteraceae	1	6	7	B
<i>Centaurea jacea</i>	Asterales	Asteraceae	1	6	7	B
<i>Centaurea nigrescens</i>	Asterales	Asteraceae	1	6	7	B
<i>Centaurea scabiosa</i>	Asterales	Asteraceae	2	18	10	T
<i>Centranthus angustifolius</i>	Dipsacales	Caprifoliaceae	1	15	16	Z
<i>Centranthus ruber</i>	Dipsacales	Caprifoliaceae	1	15	16	Z
<i>Cephalaria leucantha</i>	Dipsacales	Caprifoliaceae	2	15	8.5	Z
<i>Cervaria rivini</i>	Apiales	Apiaceae	1	22	23	AF
<i>Chaenorrhinum minus</i>	Lamiales	Plantaginaceae	1	3	4	T
<i>Cichorium intybus</i>	Asterales	Asteraceae	1	24	25	G
<i>Cirsium arvense</i>	Asterales	Asteraceae	2	23	13	B
<i>Cirsium dissectum</i>	Asterales	Asteraceae	1	6	7	B
<i>Cirsium palustre</i>	Asterales	Asteraceae	1	18	19	B
<i>Cirsium vulgare</i>	Asterales	Asteraceae	2	23	13	B
<i>Clinopodium vulgare</i>	Lamiales	Labiaceae	1	5	6	AE
<i>Cochlearia danica</i>	Brassicales	Brassicaceae	1	24	25	G
<i>Coincya cheiranthos</i>	Brassicales	Brassicaceae	1	5	6	G
<i>Colutea arborescens</i>	Fabales	Fabaceae	8	49	9.1	D
<i>Comarum palustre</i>	Rosales	Rosaceae	1	13	14	Q
<i>Coriaria myrtifolia</i>	Cucurbitales	Coriariaceae	1	1	2	S
<i>Cornus sanguinea</i>	Cornales	Cornaceae	2	40	22	U
<i>Coronilla juncea</i>	Fabales	Fabaceae	1	5	6	D
<i>Coronilla minima</i>	Fabales	Fabaceae	1	28	29	D
<i>Coronopus dydimus</i>	Brassicales	Brassicaceae	1	24	25	G
<i>Corydalis cava</i>	Ranunculales	Papaveraceae	1	2	3	AI
<i>Corydalis intermedia</i>	Ranunculales	Papaveraceae	1	2	3	AI
<i>Corydalis solida</i>	Ranunculales	Papaveraceae	1	2	3	AI
<i>Corylus avellana</i>	Fagales	Corylaceae	1	9	10	H

<i>Corynephorus canescens</i>	Poales	Poaceae	3	9	4.3	I
<i>Cotoneaster integerrimus</i>	Rosales	Rosaceae	2	12	7.5	J
<i>Crambe maritima</i>	Brassicales	Brassicaceae	1	19	20	G
<i>Crataegus monogyna</i>	Rosales	Rosaceae	2	16	14	J
<i>Crithmum maritimum</i>	Apiales	Apiaceae	1	22	23	AF
<i>Cymbalaria muralis</i>	Lamiales	Plantaginaceae	1	12	13	T
<i>Cynanchum acutum</i>	Gentianales	Apocynaceae	1	0	1	W
<i>Cynara scolymus</i>	Asterales	Asteraceae	1	18	19	B
<i>Cynosurus cristatus</i>	Poales	Poaceae	2	13	8	I
<i>Cytisus scoparius</i>	Fabales	Fabaceae	3	44	18.3	D
<i>Cytisus spinosus</i>	Fabales	Fabaceae	1	28	29	D
<i>Dactylis glomerata</i>	Poales	Poaceae	6	35	8.8	I
<i>Daucus carota</i>	Apiales	Apiaceae	1	22	23	AF
<i>Deschampsia cespitosa</i>	Poales	Poaceae	2	16	9.5	V
<i>Deschampsia flexuosa</i>	Poales	Poaceae	2	8	6	V
<i>Descurainia tanacetifolia</i>	Brassicales	Brassicaceae	1	4	5	G
<i>Digitalis purpurea</i>	Lamiales	Plantaginaceae	2	15	9.5	T
<i>Diplotaxis tenuifolia</i>	Brassicales	Brassicaceae	5	43	13	G
<i>Dorycnium hirsutum</i>	Fabales	Fabaceae	2	35	19	AL
<i>Dorycnium pentaphyllum</i>	Fabales	Fabaceae	8	65	11.1	D
<i>Dorycnopsis gerardi</i>	Fabales	Fabaceae	5	11	4.6	D
<i>Dryas octopetala</i>	Rosales	Rosaceae	1	1	2	Q
<i>Echinopartum horridum</i>	Fabales	Fabaceae	1	28	29	D
<i>Echium vulgare</i>	Lamiales	Boraginaceae	1	18	19	B
<i>Elymus caninus</i>	Poales	Poaceae	1	3	4	I
<i>Elytrigia repens</i>	Poales	Poaceae	4	17	6.3	I
<i>Erica ciliaris</i>	Ericales	Ericaceae	1	6	7	D
<i>Erica cinerea</i>	Ericales	Ericaceae	1	14	15	D
<i>Erica tetralix</i>	Ericales	Ericaceae	1	28	29	D
<i>Eriophorum vaginatum</i>	Poales	Cyperaceae	1	4	5	V
<i>Erodium acaule</i>	Geraniales	Geraniaceae	1	7	8	M
<i>Erodium chium</i>	Geraniales	Geraniaceae	1	7	8	M
<i>Erodium cicutarium</i>	Geraniales	Geraniaceae	1	7	8	M
<i>Erodium glandulosum</i>	Geraniales	Geraniaceae	1	0	1	N
<i>Eruca sativa</i>	Brassicales	Brassicaceae	1	24	25	G
<i>Eruca vesicaria</i>	Brassicales	Brassicaceae	1	24	25	G
<i>Erucastrum incanum</i>	Brassicales	Brassicaceae	2	20	11.5	G
<i>Erucastrum nasturtiifolium</i>	Brassicales	Brassicaceae	1	4	5	G
<i>Erysimum ochroleucum</i>	Brassicales	Brassicaceae	1	2	3	AJ
<i>Euonymus europaeus</i>	Celastrales	Celastraceae	1	14	15	U
<i>Ferula communis</i>	Apiales	Apiaceae	1	4	5	AF
<i>Festuca cinerea</i>	Poales	Poaceae	1	0	1	X
<i>Festuca gigantea</i>	Poales	Poaceae	1	2	3	I
<i>Festuca halleri</i>	Poales	Poaceae	2	4	4.5	V
<i>Festuca liviensis</i>	Poales	Poaceae	3	10	5	V
<i>Festuca ovina</i>	Poales	Poaceae	27	47	4.9	V

<i>Festuca pallens</i>	Poales	Poaceae	1	3	4	V
<i>Festuca paniculata</i>	Poales	Poaceae	1	2	3	I
<i>Festuca pumila</i>	Poales	Poaceae	6	11	4.5	V
<i>Festuca rubra</i>	Poales	Poaceae	15	34	5.8	V
<i>Festuca trichophylla</i>	Poales	Poaceae	1	3	4	V
<i>Festuca valesiaca</i>	Poales	Poaceae	1	5	6	V
<i>Festuca violacea</i>	Poales	Poaceae	7	12	4.6	V
<i>Filago arvensis</i>	Asterales	Asteraceae	1	18	19	B
<i>Filipendula ulmaria</i>	Rosales	Rosaceae	3	15	7.7	Q
<i>Filipendula vulgaris</i>	Rosales	Rosaceae	1	0	4	R
<i>Foeniculum vulgare</i>	Apiales	Apiaceae	1	22	23	AF
<i>Fragaria vesca</i>	Rosales	Rosaceae	1	13	14	Q
<i>Frangula dodonei</i>	Rosales	Rhamnaceae	3	18	8	U
<i>Fraxinus angustifolia</i>	Lamiales	Oleaceae	1	1	2	AC
<i>Fraxinus excelsior</i>	Lamiales	Oleaceae	1	4	5	T
<i>Genista cinerea</i>	Fabales	Fabaceae	1	1	2	D
<i>Genista corsica</i>	Fabales	Fabaceae	1	1	2	D
<i>Genista pilosa</i>	Fabales	Fabaceae	1	28	29	D
<i>Genista sagittalis</i>	Fabales	Fabaceae	1	28	29	D
<i>Genista salzmannii</i>	Fabales	Fabaceae	1	14	15	D
<i>Genista tinctoria</i>	Fabales	Fabaceae	2	29	18	D
<i>Gentiana acaulis</i>	Gentianales	Gentianaceae	1	15	16	Z
<i>Gentiana alpina</i>	Gentianales	Gentianaceae	1	15	16	Z
<i>Gentiana asclepiadea</i>	Gentianales	Gentianaceae	1	7	8	Z
<i>Gentiana burseri</i>	Gentianales	Gentianaceae	1	7	8	Z
<i>Gentiana clusii</i>	Gentianales	Gentianaceae	1	15	16	Z
<i>Gentiana cruciata</i>	Gentianales	Gentianaceae	2	21	12	Z
<i>Gentiana lutea</i>	Gentianales	Gentianaceae	2	21	12	Z
<i>Gentiana pneumonanthe</i>	Gentianales	Gentianaceae	1	7	8	Z
<i>Gentiana punctata</i>	Gentianales	Gentianaceae	1	15	16	Z
<i>Gentianella campestris</i>	Gentianales	Gentianaceae	1	7	8	Z
<i>Gentianella germanica</i>	Gentianales	Gentianaceae	1	7	8	Z
<i>Gentianopsis ciliata</i>	Gentianales	Gentianaceae	1	7	8	Z
<i>Geranium cinereum</i>	Geraniales	Geraniaceae	1	5	6	O
<i>Geranium dissectum</i>	Geraniales	Geraniaceae	1	7	8	M
<i>Geranium phaeum</i>	Geraniales	Geraniaceae	1	5	6	O
<i>Geranium pratense</i>	Geraniales	Geraniaceae	1	5	6	O
<i>Geranium pyrenaicum</i>	Geraniales	Geraniaceae	1	5	6	O
<i>Geranium robertianum</i>	Geraniales	Geraniaceae	1	7	8	M
<i>Geranium rotundifolium</i>	Geraniales	Geraniaceae	1	7	8	M
<i>Geranium sanguineum</i>	Geraniales	Geraniaceae	1	5	6	O
<i>Geranium sylvaticum</i>	Geraniales	Geraniaceae	2	5	3.5	O
<i>Geum montanum</i>	Rosales	Rosaceae	1	2	3	M
<i>Halimium halimifolium</i>	Malvales	Cistaceae	1	14	15	D
<i>Hedera helix</i>	Apiales	Araliaceae	1	14	15	U
<i>Hedysarum boveanum</i>	Fabales	Fabaceae	4	36	12.5	D

<i>Hedysarum hedysaroides</i>	Fabales	Fabaceae	1	1	2	E
<i>Helianthemum apenninum</i>	Malvales	Cistaceae	1	3	4	M
<i>Helianthemum grandiflorum</i>	Malvales	Cistaceae	3	4	2.7	M
<i>Helianthemum hirtum</i>	Malvales	Cistaceae	1	3	4	M
<i>Helianthemum italicum</i>	Malvales	Cistaceae	2	2	2	M
<i>Helianthemum nummularium</i>	Malvales	Cistaceae	6	40	7.8	M
<i>Helianthemum oelandicum</i>	Malvales	Cistaceae	1	3	4	M
<i>Helichrysum stoechas</i>	Asterales	Asteraceae	1	14	15	D
<i>Helictochloa versicolor</i>	Poales	Poaceae	1	3	4	V
<i>Helictotrichon sedenense</i>	Poales	Poaceae	1	1	2	Y
<i>Helictotrichon setaceum</i>	Poales	Poaceae	1	1	2	Y
<i>Heracleum sphondylium</i>	Apiales	Apiaceae	1	22	23	AF
<i>Hippocrepis biflora</i>	Fabales	Fabaceae	1	8	9	AL
<i>Hippocrepis comosa</i>	Fabales	Fabaceae	8	24	5.6	D
<i>Hippocrepis conradiae</i>	Fabales	Fabaceae	2	3	2.5	D
<i>Hippocrepis scorpioides</i>	Fabales	Fabaceae	3	4	3.3	D
<i>Hippophae rhamnoides</i>	Rosales	Elaeagnaceae	1	10	11	D
<i>Holcus lanatus</i>	Poales	Poaceae	2	13	9.5	I
<i>Holcus mollis</i>	Poales	Poaceae	2	13	9.5	I
<i>Hornungia alpina</i>	Brassicales	Brassicaceae	1	2	3	AJ
<i>Humulus lupulus</i>	Rosales	Cannabaceae	2	9	6	B
<i>Hylotelephium maximum</i>	Saxifragales	Crassulaceae	1	4	5	AH
<i>Hyparrhenia hirta</i>	Poales	Poaceae	2	8	5	I
<i>Iberis amara</i>	Brassicales	Brassicaceae	1	5	6	G
<i>Iberis ciliata</i>	Brassicales	Brassicaceae	1	1	2	G
<i>Iberis pinnata</i>	Brassicales	Brassicaceae	2	25	13.5	G
<i>Iberis saxatilis</i>	Brassicales	Brassicaceae	1	8	9	G
<i>Iberis sempervirens</i>	Brassicales	Brassicaceae	1	5	6	G
<i>Ilex aquifolium</i>	Aquifoliales	Aquifoliaceae	1	14	15	U
<i>Isatis tinctoria</i>	Brassicales	Brassicaceae	4	37	13.3	G
<i>Kandis perfoliata</i>	Brassicales	Brassicaceae	1	7	8	G
<i>Knautia arvensis</i>	Dipsacales	Caprifoliaceae	1	15	16	Z
<i>Laburnum anagyroides</i>	Fabales	Fabaceae	1	28	29	D
<i>Laserpitium halleri</i>	Apiales	Apiaceae	1	4	5	AF
<i>Lathyrus latifolius</i>	Fabales	Fabaceae	1	10	11	D
<i>Lathyrus odoratus</i>	Fabales	Fabaceae	2	20	11.5	D
<i>Lathyrus pratensis</i>	Fabales	Fabaceae	3	6	3.3	D
<i>Lavatera arborea</i>	Malvales	Malvaceae	1	8	9	B
<i>Lepidium campestre</i>	Brassicales	Brassicaceae	1	15	16	G
<i>Lepidium didymum</i>	Brassicales	Brassicaceae	1	24	25	G
<i>Lepidium latifolium</i>	Brassicales	Brassicaceae	1	19	20	G
<i>Lepidium sativum</i>	Brassicales	Brassicaceae	1	24	25	G
<i>Lepidium villarsii</i>	Brassicales	Brassicaceae	1	15	16	G
<i>Ligustrum vulgare</i>	Lamiales	Oleaceae	1	4	5	T
<i>Linaria repens</i>	Lamiales	Scrophulariaceae	2	6	4	T
<i>Linaria vulgaris</i>	Lamiales	Plantaginaceae	3	18	7.7	T

<i>Lobularia maritima</i>	Brassicales	Brassicaceae	2	23	13	G
<i>Lolium perenne</i>	Poales	Poaceae	2	10	6	I
<i>Lonicera caerulea</i>	Dipsacales	Caprifoliaceae	1	0	1	AA
<i>Lonicera etrusca</i>	Dipsacales	Caprifoliaceae	2	17	10.5	Z
<i>Lonicera implexa</i>	Dipsacales	Caprifoliaceae	2	17	10.5	Z
<i>Lonicera japonica</i>	Dipsacales	Caprifoliaceae	1	4	5	Z
<i>Lonicera periclymenum</i>	Dipsacales	Caprifoliaceae	3	17	7.7	Z
<i>Lonicera xylostium</i>	Dipsacales	Caprifoliaceae	2	4	3.5	Z
<i>Lotus corniculatus</i>	Fabales	Fabaceae	11	65	9.5	D
<i>Lotus glaber</i>	Fabales	Fabaceae	1	14	15	D
<i>Lotus ornithopodioides</i>	Fabales	Fabaceae	1	8	9	AL
<i>Lotus pedunculatus</i>	Fabales	Fabaceae	3	17	7.7	D
<i>Lunaria annua</i>	Brassicales	Brassicaceae	3	42	20.3	G
<i>Lunaria rediviva</i>	Brassicales	Brassicaceae	1	8	9	G
<i>Luzula luzuloides</i>	Poales	Juncaceae	1	13	14	V
<i>Luzula nivea</i>	Poales	Juncaceae	1	11	12	I
<i>Lythrum salicaria</i>	Myrtales	Lythraceae	1	4	5	D
<i>Malus domestica</i>	Rosales	Rosaceae	2	16	14	J
<i>Malus pumila</i>	Rosales	Rosaceae	1	14	15	J
<i>Malus sylvestris</i>	Rosales	Rosaceae	1	14	15	J
<i>Malva alcea</i>	Malvales	Malvaceae	1	8	9	B
<i>Malva moschata</i>	Malvales	Malvaceae	2	25	14	B
<i>Malva neglecta</i>	Malvales	Malvaceae	1	8	9	B
<i>Malva parviflora</i>	Malvales	Malvaceae	1	8	9	B
<i>Malva sylvestris</i>	Malvales	Malvaceae	2	25	14	B
<i>Marrubium vulgare</i>	Lamiales	Labiaceae	1	1	2	T
<i>Matthiola sinuata</i>	Brassicales	Brassicaceae	1	5	6	G
<i>Medicago lupulina</i>	Fabales	Fabaceae	4	28	9.8	D
<i>Medicago minima</i>	Fabales	Fabaceae	1	11	12	D
<i>Medicago rigidula</i>	Fabales	Fabaceae	1	8	9	AL
<i>Medicago sativa</i>	Fabales	Fabaceae	8	53	10.4	D
<i>Medicago truncatula</i>	Fabales	Fabaceae	1	8	9	AL
<i>Melampyrum arvense</i>	Lamiales	Orobanchaceae	2	7	5	T
<i>Melampyrum pratense</i>	Lamiales	Orobanchaceae	1	5	6	T
<i>Melica ciliata</i>	Poales	Poaceae	2	13	8	I
<i>Melilotus albus</i>	Fabales	Fabaceae	1	10	11	D
<i>Melittis melissophyllum</i>	Lamiales	Labiaceae	1	12	13	T
<i>Milium effusum</i>	Poales	Poaceae	1	3	4	I
<i>Molinia caerulea</i>	Poales	Poaceae	9	23	3.9	I
<i>Morus alba</i>	Rosales	Moraceae	1	1	2	H
<i>Nardus stricta</i>	Poales	Poaceae	9	25	5.6	V
<i>Nasturtium officinale</i>	Brassicales	Brassicaceae	2	33	22.5	G
<i>Noccaea montana</i>	Brassicales	Brassicaceae	1	2	3	G
<i>Odontites luteus</i>	Lamiales	Orobanchaceae	2	14	8.5	T
<i>Oloptum miliaceum</i>	Poales	Poaceae	2	6	4	I
<i>Onobrychis caput-galli</i>	Fabales	Fabaceae	1	8	9	AL

<i>Onobrychis montana</i>	Fabales	Fabaceae	4	38	12.8	D
<i>Onobrychis saxatilis</i>	Fabales	Fabaceae	5	30	8.6	D
<i>Onobrychis supina</i>	Fabales	Fabaceae	9	50	8.6	D
<i>Onobrychis viciifolia</i>	Fabales	Fabaceae	7	33	7.4	D
<i>Ononis spinosa</i>	Fabales	Fabaceae	1	11	12	D
<i>Ononis striata</i>	Fabales	Fabaceae	1	28	29	D
<i>Onopordum acanthium</i>	Asterales	Asteraceae	1	18	19	B
<i>Opopanax chironium</i>	Apiales	Apiaceae	1	1	2	AF
<i>Origanum vulgare</i>	Lamiales	Labiaceae	1	5	6	AE
<i>Ostrya carpinifolia</i>	Fagales	Betulaceae	1	9	10	H
<i>Oxytropis campestris</i>	Fabales	Fabaceae	1	1	2	D
<i>Parietaria judaica</i>	Rosales	Urticaceae	2	3	2.5	B
<i>Parietaria officinalis</i>	Rosales	Urticaceae	1	3	4	B
<i>Pastinaca latifolia</i>	Apiales	Apiaceae	1	4	5	AF
<i>Pastinaca sativa</i>	Apiales	Apiaceae	1	22	23	AF
<i>Petroselinum crispum</i>	Apiales	Apiaceae	1	22	23	AF
<i>Peucedanum officinale</i>	Apiales	Apiaceae	2	26	14	AF
<i>Peucedanum palustre</i>	Apiales	Apiaceae	1	22	23	AF
<i>Phalaris arundinacea</i>	Poales	Poaceae	1	7	8	I
<i>Phaseolus vulgaris</i>	Fabales	Fabaceae	1	10	11	D
<i>Phillyrea latifolia</i>	Lamiales	Oleaceae	1	1	2	AC
<i>Phleum alpinum</i>	Poales	Poaceae	1	9	10	I
<i>Phleum pratense</i>	Poales	Poaceae	4	22	8.8	I
<i>Phlomis herba-venti</i>	Lamiales	Labiaceae	1	1	2	AK
<i>Phlomis lychnitis</i>	Lamiales	Labiaceae	1	1	2	AK
<i>Phragmites australis</i>	Poales	Poaceae	1	1	2	I
<i>Pimpinella saxifraga</i>	Apiales	Apiaceae	1	22	23	AF
<i>Pisum sativum</i>	Fabales	Fabaceae	1	10	11	D
<i>Plantago alpina</i>	Lamiales	Plantaginaceae	2	5	4	K
<i>Plantago atrata</i>	Lamiales	Plantaginaceae	1	3	4	K
<i>Plantago lanceolata</i>	Lamiales	Plantaginaceae	8	37	6.6	T
<i>Plantago media</i>	Lamiales	Plantaginaceae	3	12	5.7	T
<i>Poa alpina</i>	Poales	Poaceae	1	13	14	V
<i>Poa annua</i>	Poales	Poaceae	4	9	3.5	I
<i>Poa bulbosa</i>	Poales	Poaceae	1	4	5	I
<i>Poa minor</i>	Poales	Poaceae	2	4	4.5	V
<i>Poa nemoralis</i>	Poales	Poaceae	2	14	9.5	V
<i>Poa pratensis</i>	Poales	Poaceae	3	6	3	I
<i>Poa trivialis</i>	Poales	Poaceae	7	27	6.6	I
<i>Populus nigra</i>	Malpighiales	Salicaceae	3	14	7.3	H
<i>Populus tremula</i>	Malpighiales	Salicaceae	2	4	3	H
<i>Potentilla argentea</i>	Rosales	Rosaceae	2	15	10	Q
<i>Potentilla aurea</i>	Rosales	Rosaceae	1	2	3	Q
<i>Potentilla cinerea</i>	Rosales	Rosaceae	1	2	3	Q
<i>Potentilla crantzii</i>	Rosales	Rosaceae	2	5	3.5	Q
<i>Potentilla erecta</i>	Rosales	Rosaceae	4	18	6.8	Q

<i>Potentilla hirta</i>	Rosales	Rosaceae	7	11	4.1	Q
<i>Potentilla montana</i>	Rosales	Rosaceae	1	13	14	Q
<i>Potentilla neumanniana</i>	Rosales	Rosaceae	9	21	5.3	Q
<i>Potentilla pusilla</i>	Rosales	Rosaceae	5	9	5.4	Q
<i>Potentilla recta</i>	Rosales	Rosaceae	1	3	4	Q
<i>Potentilla reptans</i>	Rosales	Rosaceae	4	16	8	Q
<i>Potentilla sterilis</i>	Rosales	Rosaceae	1	13	14	Q
<i>Poterium sanguisorba</i>	Rosales	Rosaceae	5	38	9.6	AF
<i>Primula elatior</i>	Ericales	Primulaceae	1	2	3	AB
<i>Primula veris</i>	Ericales	Primulaceae	1	2	3	AB
<i>Primula vulgaris</i>	Ericales	Primulaceae	1	2	3	AB
<i>Prunella hyssopifolia</i>	Lamiales	Labiaceae	1	5	6	AE
<i>Prunella vulgaris</i>	Lamiales	Labiaceae	1	5	6	AE
<i>Prunus armeniaca</i>	Rosales	Rosaceae	3	18	11.7	J
<i>Prunus avium</i>	Rosales	Rosaceae	2	22	12.5	J
<i>Prunus domestica</i>	Rosales	Rosaceae	4	18	9.3	J
<i>Prunus dulcis</i>	Rosales	Rosaceae	3	16	10.3	J
<i>Prunus mahaleb</i>	Rosales	Rosaceae	4	18	9.5	J
<i>Prunus padus</i>	Rosales	Rosaceae	1	6	7	J
<i>Prunus persica</i>	Rosales	Rosaceae	3	18	11.7	J
<i>Prunus spinosa</i>	Rosales	Rosaceae	6	18	7	J
<i>Prunus tenella</i>	Rosales	Rosaceae	1	14	15	J
<i>Ptychotis saxifraga</i>	Apiales	Apiaceae	2	23	12.5	AF
<i>Pyrus communis</i>	Rosales	Rosaceae	3	24	12.7	J
<i>Pyrus spinosa</i>	Rosales	Rosaceae	2	16	14	J
<i>Quercus cerris</i>	Fagales	Fagaceae	1	5	6	H
<i>Quercus coccifera</i>	Fagales	Fagaceae	1	5	6	H
<i>Quercus ilex</i>	Fagales	Fagaceae	3	7	5.7	H
<i>Quercus petraea</i>	Fagales	Fagaceae	2	5	5.5	H
<i>Quercus pubescens</i>	Fagales	Fagaceae	4	16	6.8	H
<i>Quercus pyrenaica</i>	Fagales	Fagaceae	3	7	5.7	H
<i>Quercus robur</i>	Fagales	Fagaceae	3	7	5.7	H
<i>Quercus suber</i>	Fagales	Fagaceae	1	5	6	H
<i>Raphanus raphanistrum</i>	Brassicales	Brassicaceae	3	37	18	G
<i>Raphanus sativus</i>	Brassicales	Brassicaceae	1	24	25	G
<i>Rapistrum rugosum</i>	Brassicales	Brassicaceae	1	19	20	G
<i>Reseda lutea</i>	Brassicales	Resedaceae	3	36	17.7	G
<i>Rhamnus alaternus</i>	Rosales	Rhamnaceae	3	18	7.3	U
<i>Rhamnus alpina</i>	Rosales	Rhamnaceae	2	5	4.5	U
<i>Rhamnus cathartica</i>	Rosales	Rhamnaceae	2	5	4.5	U
<i>Rhamnus lycioides</i>	Rosales	Rhamnaceae	1	5	6	U
<i>Rhamnus pumila</i>	Rosales	Rhamnaceae	1	5	6	U
<i>Rhinanthus angustifolius</i>	Lamiales	Orobanchaceae	1	12	13	T
<i>Rhodiola rosea</i>	Saxifragales	Crassulaceae	3	13	6	AH
<i>Rhynchospora alba</i>	Poales	Cyperaceae	1	4	5	V
<i>Ribes rubrum</i>	Saxifragales	Grossulariaceae	1	9	10	H

<i>Robinia pseudoacacia</i>	Fabales	Fabaceae	2	21	12.5	U
<i>Rorippa amphibia</i>	Brassicales	Brassicaceae	1	24	25	G
<i>Rorippa sylvestris</i>	Brassicales	Brassicaceae	2	33	20.5	G
<i>Rosa canina</i>	Rosales	Rosaceae	1	6	7	J
<i>Rosmarinus officinalis</i>	Lamiales	Labiaceae	1	4	5	D
<i>Rubus fruticosus</i>	Rosales	Rosaceae	3	41	15.7	Q
<i>Rubus idaeus</i>	Rosales	Rosaceae	4	50	14.3	Q
<i>Rubus ulmifolius</i>	Rosales	Rosaceae	1	2	4	Q
<i>Rumex acetosa</i>	Caryophyllales	Polygonaceae	6	10	5	AD
<i>Rumex acetosella</i>	Caryophyllales	Polygonaceae	5	9	4.8	AD
<i>Rumex arifolius</i>	Caryophyllales	Polygonaceae	1	4	5	AD
<i>Rumex bucephalophorus</i>	Caryophyllales	Polygonaceae	1	8	9	AD
<i>Rumex conglomeratus</i>	Caryophyllales	Polygonaceae	2	9	7.5	AD
<i>Rumex crispus</i>	Caryophyllales	Polygonaceae	2	9	7.5	AD
<i>Rumex hydrolapathum</i>	Caryophyllales	Polygonaceae	1	5	6	AD
<i>Rumex intermedius</i>	Caryophyllales	Polygonaceae	2	8	6.5	AD
<i>Rumex obtusifolius</i>	Caryophyllales	Polygonaceae	3	10	6.7	AD
<i>Rumex pulcher</i>	Caryophyllales	Polygonaceae	2	9	7.5	AD
<i>Rumex scutatus</i>	Caryophyllales	Polygonaceae	5	9	4.8	AD
<i>Ruta corsica</i>	Sapindales	Rutaceae	1	4	5	AF
<i>Ruta graveolens</i>	Apiales	Apiaceae	1	22	23	AF
<i>Salix acuminata</i>	Malpighiales	Salicaceae	4	18	7.3	H
<i>Salix alba</i>	Malpighiales	Salicaceae	1	6	7	H
<i>Salix atrocinerea</i>	Malpighiales	Salicaceae	5	21	7.2	H
<i>Salix aurita</i>	Malpighiales	Salicaceae	1	3	4	H
<i>Salix caprea</i>	Malpighiales	Salicaceae	5	24	7.2	H
<i>Salix eleagnos</i>	Malpighiales	Salicaceae	1	6	7	H
<i>Salix purpurea</i>	Malpighiales	Salicaceae	1	6	7	H
<i>Sanguisorba officinalis</i>	Rosales	Rosaceae	3	1	1.3	AF
<i>Saxifraga aizoides</i>	Saxifragales	Saxifragaceae	1	1	2	AH
<i>Saxifraga bryoides</i>	Saxifragales	Saxifragaceae	1	10	11	AH
<i>Saxifraga exarata</i>	Saxifragales	Saxifragaceae	1	10	11	AH
<i>Scabiosa atropurpurea</i>	Dipsacales	Caprifoliaceae	1	15	16	Z
<i>Scabiosa columbaria</i>	Dipsacales	Dipsacaceae	1	15	16	Z
<i>Securigera varia</i>	Fabales	Fabaceae	6	23	6.7	D
<i>Sedum acre</i>	Saxifragales	Crassulaceae	1	10	11	AH
<i>Sedum album</i>	Saxifragales	Crassulaceae	2	12	8	AH
<i>Sedum anacampseros</i>	Saxifragales	Crassulaceae	1	10	11	AH
<i>Sedum anopetalum</i>	Saxifragales	Crassulaceae	1	10	11	AH
<i>Sedum ochroleucum</i>	Saxifragales	Crassulaceae	1	4	5	AH
<i>Sedum rupestre</i>	Saxifragales	Crassulaceae	1	10	11	AH
<i>Sedum sediforme</i>	Saxifragales	Crassulaceae	2	12	8	AH
<i>Selinum carvifolia</i>	Apiales	Apiaceae	1	22	23	AF
<i>Sempervivum arachnoideum</i>	Saxifragales	Crassulaceae	1	10	11	AH
<i>Sempervivum montanum</i>	Saxifragales	Crassulaceae	1	10	11	AH
<i>Sesamoides purpurascens</i>	Brassicales	Resedaceae	1	7	8	G

<i>Seseli libanotis</i>	Apiales	Apiaceae	1	22	23	AF
<i>Sesleria caerulea</i>	Poales	Poaceae	9	21	5.3	V
<i>Sideritis fruticulosa</i>	Lamiales	Labiaceae	1	2	3	T
<i>Sideritis hirsuta</i>	Lamiales	Labiaceae	1	2	3	T
<i>Silaum silaus</i>	Apiales	Apiaceae	1	22	23	AF
<i>Sinapis alba</i>	Brassicales	Brassicaceae	1	19	20	G
<i>Sinapis arvensis</i>	Brassicales	Brassicaceae	3	35	15.7	G
<i>Sison amomum</i>	Apiales	Apiaceae	1	22	23	AF
<i>Sisymbrium austriacum</i>	Brassicales	Brassicaceae	1	4	5	G
<i>Sisymbrium officinale</i>	Brassicales	Brassicaceae	3	21	9.3	G
<i>Sorbus aucuparia</i>	Rosales	Rosaceae	1	12	13	J
<i>Spartium junceum</i>	Fabales	Fabaceae	3	36	15.7	D
<i>Stachys officinalis</i>	Lamiales	Labiaceae	1	3	4	T
<i>Stachys pradica</i>	Lamiales	Labiaceae	1	3	4	T
<i>Stachys recta</i>	Lamiales	Labiaceae	3	17	6.7	T
<i>Stipa offneri</i>	Poales	Poaceae	4	9	3.8	I
<i>Stipa parviflora</i>	Poales	Poaceae	1	3	6	V
<i>Stipa pennata</i>	Poales	Poaceae	5	16	4.8	V
<i>Stipa tenacissima</i>	Poales	Poaceae	1	1	2	I
<i>Succisa pratensis</i>	Dipsacales	Dipsacaceae	1	15	16	Z
<i>Tamarix africana</i>	Caryophyllales	Tamaricaceae	1	14	15	U
<i>Thymus pulegioides</i>	Lamiales	Labiaceae	2	6	4	AE
<i>Thymus serpyllum</i>	Lamiales	Labiaceae	1	5	6	AE
<i>Thymus vulgaris</i>	Lamiales	Labiaceae	1	1	2	AE
<i>Thysselinum lancifolium</i>	Apiales	Apiaceae	1	22	23	AF
<i>Trifolium cherleri</i>	Fabales	Fabaceae	1	8	9	AL
<i>Trifolium medium</i>	Fabales	Fabaceae	1	3	4	D
<i>Trifolium ochroleucon</i>	Fabales	Fabaceae	1	3	4	D
<i>Trifolium pallescens</i>	Fabales	Fabaceae	1	2	3	D
<i>Trifolium pratense</i>	Fabales	Fabaceae	6	20	5.2	D
<i>Trifolium repens</i>	Fabales	Fabaceae	1	11	12	D
<i>Trigonella officinalis</i>	Fabales	Fabaceae	1	9	10	D
<i>Trinia glauca</i>	Apiales	Apiaceae	1	22	23	AF
<i>Tripodion tetraphyllum</i>	Fabales	Fabaceae	1	8	9	AL
<i>Tropaeolum majus</i>	Brassicales	Tropaeolaceae	4	44	17.5	G
<i>Turritis glabra</i>	Brassicales	Brassicaceae	1	15	16	G
<i>Ulex europaeus</i>	Fabales	Fabaceae	2	40	22	U
<i>Ulex minor</i>	Fabales	Fabaceae	4	36	11	D
<i>Ulex parviflorus</i>	Fabales	Fabaceae	1	11	12	D
<i>Ulmus glabra</i>	Rosales	Ulmaceae	1	1	2	H
<i>Ulmus minor</i>	Rosales	Ulmaceae	4	26	8.3	H
<i>Urtica atrovirens</i>	Rosales	Urticaceae	1	0	1	A
<i>Urtica dioica</i>	Rosales	Urticaceae	6	29	8.2	B
<i>Urtica urens</i>	Rosales	Urticaceae	1	3	4	B
<i>Vaccinium microcarpum</i>	Ericales	Ericaceae	1	1	2	P
<i>Vaccinium myrtillus</i>	Ericales	Ericaceae	1	28	29	D

<i>Vaccinium oxycoccos</i>	Ericales	Ericaceae	1	1	2	P
<i>Vaccinium uliginosum</i>	Ericales	Ericaceae	3	28	10.3	D
<i>Valeriana dioica</i>	Dipsacales	Caprifoliaceae	1	3	4	AG
<i>Valeriana montana</i>	Dipsacales	Caprifoliaceae	1	3	4	AG
<i>Valeriana officinalis</i>	Dipsacales	Caprifoliaceae	1	3	4	AG
<i>Valeriana tripteris</i>	Dipsacales	Caprifoliaceae	1	3	4	AG
<i>Verbascum nigrum</i>	Lamiales	Scrophulariaceae	1	12	13	T
<i>Veronica allionii</i>	Lamiales	Plantaginaceae	1	3	4	K
<i>Veronica austriaca</i>	Lamiales	Plantaginaceae	1	12	13	T
<i>Veronica chamaedrys</i>	Lamiales	Plantaginaceae	3	8	4.3	T
<i>Vicia cracca</i>	Fabales	Fabaceae	3	35	13.3	D
<i>Vicia tenuifolia</i>	Fabales	Fabaceae	1	3	4	D
<i>Vicia villosa</i>	Fabales	Fabaceae	1	3	4	D
<i>Viola alba</i>	Malpighiales	Violaceae	2	6	4.5	K
<i>Viola arvensis</i>	Malpighiales	Violaceae	1	5	6	K
<i>Viola biflora</i>	Malpighiales	Violaceae	2	4	3	K
<i>Viola calaminaria</i>	Malpighiales	Violaceae	1	5	6	K
<i>Viola calcarata</i>	Malpighiales	Violaceae	8	18	3.8	K
<i>Viola canina</i>	Malpighiales	Violaceae	4	10	6	K
<i>Viola cenisia</i>	Malpighiales	Violaceae	1	6	7	K
<i>Viola cornuta</i>	Malpighiales	Violaceae	1	3	4	K
<i>Viola corsica</i>	Malpighiales	Violaceae	1	0	1	L
<i>Viola hirta</i>	Malpighiales	Violaceae	4	9	5	K
<i>Viola kitaibeliana</i>	Malpighiales	Violaceae	2	7	5	K
<i>Viola odorata</i>	Malpighiales	Violaceae	4	9	5.5	K
<i>Viola palustris</i>	Malpighiales	Violaceae	2	6	4	K
<i>Viola reichenbachiana</i>	Malpighiales	Violaceae	3	8	6	K
<i>Viola riviniana</i>	Malpighiales	Violaceae	4	9	5	K
<i>Viola tricolor</i>	Malpighiales	Violaceae	4	13	5.5	K

Supplementary materials S3.7. Posterior estimates of the species-specific occurrence and detection probabilities of insect species as estimated under the MSOM (with mean, standard deviation, CI_{95%}). All the species detected at least during a visit during the survey were listed and grouped according to their taxonomic group. ‘Conservation status’ refers to the three categories of specific-level conservation issues as described in Materials & methods. The number of observations (count) was also included for each species, under the classical and doubled surveys. For these both modalities, absolute bias in occurrence indicates the difference between the proportion of sites where each species was detected and its occurrence probability, as estimated through the MSOM. The minimum effort requirements to ensure species absence (with a 95% confidence index) were estimated for values of covariables allowing an optimal detectability.

Scientific name	Group	Conservation status	Counts		Observed occurrence		Estimated occurrence				Estimated detection				Absolute bias in occurrence		Minimum effort requirement		
			Classical EIA	Doubled EIA	Classical EIA	Doubled EIA	Mean	SD	CI 2.5%	CI 97.5%	Mean	SD	CI 2.5%	CI 97.5%	Classical EIA	Doubled EIA	Median	CI 2.5%	CI 97.5%
<i>Cicada orni</i>	Cicada	Uncovered	26	53	0.75	0.75	0.91	0.08	0.7	1	0.46	0.08	0.31	0.61	-0.16	-0.16	1,4	0,9	2,7
<i>Cicadatra atra</i>	Cicada	Uncovered	18	35	0.6	0.65	0.88	0.1	0.64	1	0.49	0.09	0.32	0.65	-0.28	-0.23	3,7	2,1	8,0
<i>Lyristes plebejus</i>	Cicada	Uncovered	26	55	0.7	0.75	0.89	0.09	0.67	1	0.45	0.07	0.31	0.59	-0.19	-0.14	1,7	1,0	3,7
<i>Tettigettna argentata</i>	Cicada	Uncovered	13	20	0.55	0.6	0.94	0.07	0.73	1	0.18	0.06	0.08	0.33	-0.39	-0.34	5,8	3,3	12,2
<i>Tettigettna pygmaea</i>	Cicada	Uncovered	14	21	0.6	0.6	0.84	0.12	0.54	1	0.3	0.08	0.15	0.47	-0.24	-0.24	6,8	3,2	17,2
<i>Tibicina garricola</i>	Cicada	Uncovered	3	6	0.15	0.15	0.32	0.22	0.04	0.87	0.16	0.08	0.04	0.36	-0.17	-0.17	6,0	2,1	26,3
<i>Tibicina haematodes</i>	Cicada	Uncovered	2	5	0.1	0.2	0.71	0.24	0.21	1	0.1	0.08	0.02	0.31	-0.61	-0.51	15,8	4,8	60,5
<i>Tibicina tomentosa</i>	Cicada	Vulnerable	2	3	0.05	0.05	0.1	0.12	0.01	0.43	0.48	0.22	0.09	0.88	-0.05	-0.05	1,0	0,2	15,8
<i>Aeshna affinis</i>	Odonata	Uncovered	3	5	0.15	0.15	0.48	0.27	0.08	0.99	0.15	0.1	0.03	0.39	-0.33	-0.33	12,7	2,5	88,0
<i>Aeshna cyanea</i>	Odonata	Uncovered	1	2	0.05	0.1	0.46	0.32	0.03	1	0.07	0.07	0.01	0.29	-0.41	-0.36	20,1	3,0	187,1
<i>Aeshna isoceles</i>	Odonata	Uncovered	1	2	0.05	0.05	0.15	0.17	0.01	0.71	0.28	0.23	0.01	0.82	-0.1	-0.1	1,3	0,4	21,9
<i>Aeshna mixta</i>	Odonata	Uncovered	2	2	0.1	0.15	0.49	0.32	0.04	0.99	0.13	0.14	0.01	0.55	-0.39	-0.34	19,7	2,3	187,7
<i>Anax imperator</i>	Odonata	Uncovered	17	33	0.6	0.65	0.82	0.1	0.58	0.97	0.43	0.08	0.28	0.59	-0.22	-0.17	3,9	2,4	7,1
<i>Anax parthenope</i>	Odonata	Uncovered	8	13	0.3	0.3	0.48	0.18	0.18	0.88	0.33	0.12	0.13	0.57	-0.18	-0.18	3,3	1,5	10,3
<i>Boyeria irene</i>	Odonata	Uncovered	4	8	0.2	0.25	0.33	0.17	0.08	0.74	0.23	0.11	0.06	0.49	-0.13	-0.08	1,8	0,5	45,4
<i>Brachytron pratense</i>	Odonata	Vulnerable	1	2	0.05	0.05	0.16	0.19	0.01	0.79	0.07	0.09	0	0.33	-0.11	-0.11	2,1	0,4	106,9
<i>Calopteryx haemorrhoidalis</i>	Odonata	Uncovered	10	21	0.25	0.3	0.33	0.14	0.1	0.63	0.76	0.1	0.53	0.91	-0.08	-0.03	1,0	0,6	2,1
<i>Calopteryx xanthostoma</i>	Odonata	Uncovered	10	20	0.3	0.35	0.43	0.16	0.15	0.74	0.51	0.11	0.3	0.73	-0.13	-0.08	1,4	0,8	3,0
<i>Ceragrion tenellum</i>	Odonata	Uncovered	11	19	0.35	0.35	0.4	0.15	0.14	0.71	0.6	0.11	0.37	0.79	-0.05	-0.05	1,5	0,9	3,3
<i>Chalcolestes viridis</i>	Odonata	Uncovered	6	11	0.3	0.3	0.44	0.2	0.12	0.88	0.4	0.13	0.17	0.65	-0.14	-0.14	3,0	1,3	10,0
<i>Coenagrion caeruleum</i>	Odonata	Vulnerable	1	2	0.05	0.05	0.13	0.17	0	0.68	0.2	0.16	0.02	0.62	-0.08	-0.08	1,8	0,5	19,6
<i>Coenagrion mercuriale</i>	Odonata	Protected	8	14	0.2	0.2	0.25	0.13	0.05	0.55	0.32	0.13	0.11	0.59	-0.05	-0.05	1,6	0,8	4,3
<i>Coenagrion puella</i>	Odonata	Uncovered	6	7	0.2	0.2	0.43	0.24	0.08	0.96	0.15	0.08	0.04	0.35	-0.23	-0.23	8,1	3,1	28,8
<i>Cordulegaster boltonii</i>	Odonata	Uncovered	0	1	0	0.05	0.27	0.29	0.01	0.98	0.09	0.1	0	0.38	-0.27	-0.22	NA	NA	NA
<i>Crocothemis erythraea</i>	Odonata	Uncovered	10	21	0.3	0.35	0.44	0.14	0.18	0.72	0.74	0.1	0.53	0.9	-0.14	-0.09	1,2	0,7	2,3

<i>Enallagma cyathigerum</i>	Odonata	Uncovered	4	9	0.1	0.15	0.19	0.11	0.04	0.46	0.36	0.15	0.11	0.68	-0.09	-0.04	1,4	0,7	4,4
<i>Erythromma lindenii</i>	Odonata	Uncovered	14	31	0.3	0.3	0.33	0.13	0.1	0.61	0.82	0.09	0.62	0.95	-0.03	-0.03	0,7	0,5	1,3
<i>Gomphus graslinii</i>	Odonata	Protected	5	9	0.2	0.2	0.23	0.13	0.05	0.53	0.52	0.15	0.22	0.8	-0.03	-0.03	1,3	0,7	4,0
<i>Gomphus pulchellus</i>	Odonata	Uncovered	5	12	0.15	0.3	0.41	0.17	0.13	0.76	0.14	0.08	0.03	0.33	-0.26	-0.11	2,8	1,3	8,4
<i>Gomphus similimus</i>	Odonata	Uncovered	5	7	0.15	0.2	0.41	0.22	0.09	0.92	0.13	0.09	0.02	0.36	-0.26	-0.21	5,1	2,1	18,1
<i>Hemianax ephippiger</i>	Odonata	Uncovered	0	3	0	0.15	0.63	0.29	0.09	1	0.02	0.02	0	0.08	-0.63	-0.48	30,9	3,6	801,1
<i>Ischnura elegans</i>	Odonata	Uncovered	20	34	0.55	0.55	0.69	0.13	0.41	0.9	0.29	0.07	0.16	0.44	-0.14	-0.14	4,0	2,4	7,5
<i>Ischnura pumilio</i>	Odonata	Vulnerable	2	2	0.05	0.05	0.14	0.18	0	0.76	0.13	0.12	0.01	0.45	-0.09	-0.09	2,6	0,6	33,6
<i>Lestes barbarus</i>	Odonata	Uncovered	3	4	0.05	0.05	0.09	0.09	0	0.31	0.59	0.2	0.18	0.92	-0.04	-0.04	0,6	0,2	4,5
<i>Lestes virens</i>	Odonata	Uncovered	0	1	0	0.05	0.43	0.33	0.01	0.99	0.06	0.08	0	0.3	-0.43	-0.38	NA	NA	NA
<i>Libellula depressa</i>	Odonata	Uncovered	4	10	0.2	0.3	0.65	0.22	0.23	0.99	0.12	0.06	0.03	0.27	-0.45	-0.35	8,9	3,0	34,1
<i>Libellula fulva</i>	Odonata	Uncovered	10	16	0.35	0.45	0.7	0.18	0.31	0.98	0.22	0.07	0.1	0.39	-0.35	-0.25	6,6	3,0	17,2
<i>Macromia splendens</i>	Odonata	Protected	2	5	0.1	0.15	0.23	0.17	0.03	0.69	0.33	0.18	0.06	0.71	-0.13	-0.08	1,9	0,7	10,5
<i>Onychogomphus forcipatus</i>	Odonata	Uncovered	7	17	0.2	0.3	0.36	0.15	0.11	0.67	0.6	0.12	0.34	0.81	-0.16	-0.06	1,2	0,7	2,5
<i>Onychogomphus uncatatus</i>	Odonata	Vulnerable	4	8	0.15	0.2	0.33	0.18	0.07	0.77	0.29	0.14	0.08	0.6	-0.18	-0.13	3,5	1,4	12,4
<i>Orthetrum albistylum</i>	Odonata	Uncovered	1	1	0.05	0.05	0.38	0.32	0.01	0.99	0.06	0.07	0	0.27	-0.33	-0.33	NA	NA	NA
<i>Orthetrum brunneum</i>	Odonata	Uncovered	7	14	0.3	0.35	0.44	0.17	0.15	0.78	0.43	0.11	0.21	0.65	-0.14	-0.09	2,3	1,1	6,5
<i>Orthetrum cancellatum</i>	Odonata	Uncovered	13	25	0.45	0.55	0.66	0.14	0.36	0.89	0.39	0.09	0.22	0.57	-0.21	-0.11	3,7	2,0	8,2
<i>Orthetrum coerulescens</i>	Odonata	Uncovered	7	13	0.35	0.45	0.64	0.17	0.3	0.96	0.31	0.1	0.14	0.52	-0.29	-0.19	4,8	2,2	14,1
<i>Oxygastra curtisii</i>	Odonata	Protected	9	18	0.3	0.3	0.34	0.14	0.1	0.63	0.77	0.1	0.54	0.93	-0.04	-0.04	1,0	0,6	1,9
<i>Platycnemis acutipennis</i>	Odonata	Uncovered	15	36	0.3	0.5	0.62	0.14	0.34	0.86	0.5	0.1	0.32	0.68	-0.32	-0.12	1,5	0,9	2,7
<i>Platycnemis latipes</i>	Odonata	Uncovered	8	17	0.35	0.35	0.43	0.15	0.16	0.73	0.65	0.12	0.39	0.86	-0.08	-0.08	1,3	0,8	2,7
<i>Pyrrhosoma nymphula</i>	Odonata	Uncovered	10	20	0.25	0.3	0.36	0.15	0.11	0.66	0.18	0.09	0.05	0.39	-0.11	-0.06	1,7	0,9	4,0
<i>Sympecma fusca</i>	Odonata	Uncovered	3	4	0.1	0.1	0.19	0.18	0.01	0.71	0.1	0.08	0.01	0.3	-0.09	-0.09	5,5	1,5	36,7
<i>Sympetrum fonscolombii</i>	Odonata	Uncovered	18	36	0.55	0.6	0.73	0.13	0.45	0.93	0.34	0.06	0.22	0.47	-0.18	-0.13	6,2	1,9	39,1
<i>Sympetrum meridionale</i>	Odonata	Uncovered	6	10	0.2	0.3	0.56	0.22	0.19	0.98	0.26	0.12	0.08	0.52	-0.36	-0.26	4,2	1,7	15,8
<i>Sympetrum pedemontanum</i>	Odonata	Vulnerable	0	1	0	0.05	0.34	0.31	0.01	0.99	0.11	0.15	0	0.58	-0.34	-0.29	NA	NA	NA
<i>Sympetrum striolatum</i>	Odonata	Uncovered	8	18	0.3	0.55	0.83	0.13	0.51	1	0.29	0.09	0.14	0.49	-0.53	-0.28	5,6	2,8	13,5
<i>Trithemis annulata</i>	Odonata	Uncovered	4	11	0.2	0.25	0.3	0.14	0.08	0.62	0.56	0.14	0.28	0.82	-0.1	-0.05	1,6	0,8	4,3
<i>Acrotylus fischeri</i>	Orthoptera	Uncovered	7	17	0.25	0.4	0.54	0.16	0.23	0.85	0.08	0.05	0.02	0.21	-0.29	-0.14	2,4	1,4	5,1
<i>Acrotylus insubricus</i>	Orthoptera	Uncovered	14	27	0.35	0.4	0.6	0.16	0.28	0.88	0.05	0.03	0.01	0.13	-0.25	-0.2	3,0	1,8	5,4
<i>Aiolopus puissanti</i>	Orthoptera	Uncovered	7	14	0.25	0.4	0.66	0.19	0.27	0.98	0.32	0.09	0.15	0.51	-0.41	-0.26	5,6	2,4	16,3
<i>Aiolopus strepens</i>	Orthoptera	Uncovered	13	30	0.55	0.65	0.92	0.07	0.73	1	0.03	0.02	0.01	0.08	-0.37	-0.27	3,1	1,7	6,7
<i>Amedegnatiana vicheti</i>	Orthoptera	Vulnerable	3	5	0.05	0.05	0.08	0.07	0	0.27	0.65	0.19	0.23	0.94	-0.03	-0.03	0,3	0,1	1,0
<i>Anacridium aegyptium</i>	Orthoptera	Uncovered	35	57	0.8	0.85	0.92	0.06	0.76	1	0.2	0.05	0.11	0.3	-0.12	-0.07	3,2	1,8	6,8
<i>Antaxius sorrezensis</i>	Orthoptera	Vulnerable	1	1	0.05	0.05	0.42	0.33	0.02	0.99	0.07	0.09	0	0.34	-0.37	-0.37	NA	NA	NA
<i>Arachnocephalus vestitus</i>	Orthoptera	Uncovered	4	9	0.2	0.25	0.54	0.21	0.18	0.96	0.1	0.07	0.02	0.27	-0.34	-0.29	1,5	0,6	10,3
<i>Arcyptera kheili</i>	Orthoptera	Vulnerable	3	5	0.05	0.05	0.08	0.07	0	0.27	0.57	0.23	0.13	0.94	-0.03	-0.03	0,2	0,1	0,9
<i>Barbitistes fischeri</i>	Orthoptera	Uncovered	2	3	0.1	0.1	0.32	0.25	0.03	0.96	0.18	0.13	0.02	0.5	-0.22	-0.22	8,7	2,1	58,4
<i>Calliptamus barbarus</i>	Orthoptera	Uncovered	17	34	0.7	0.85	0.97	0.04	0.87	1	0.3	0.07	0.18	0.46	-0.27	-0.12	4,2	2,4	9,3

<i>Calliptamus italicus</i>	Orthoptera	Uncovered	10	18	0.45	0.55	0.82	0.14	0.48	1	0.27	0.09	0.13	0.46	-0.37	-0.27	6,0	2,6	17,7
<i>Calliptamus wattenwylianus</i>	Orthoptera	Uncovered	16	32	0.5	0.5	0.69	0.14	0.39	0.91	0.61	0.09	0.42	0.79	-0.19	-0.19	2,0	1,3	3,6
<i>Chorthippus binotatus</i>	Orthoptera	Vulnerable	0	1	0	0.05	0.4	0.32	0.01	0.99	0.08	0.1	0	0.39	-0.4	-0.35	NA	NA	NA
<i>Chorthippus brunneus</i>	Orthoptera	Uncovered	33	62	0.95	0.95	0.98	0.03	0.91	1	0.73	0.06	0.61	0.83	-0.03	-0.03	3,1	2,2	5,0
<i>Chorthippus vagans</i>	Orthoptera	Uncovered	10	19	0.4	0.45	0.62	0.16	0.29	0.9	0.28	0.09	0.12	0.48	-0.22	-0.17	1,8	0,7	9,6
<i>Conocephalus fuscus</i>	Orthoptera	Uncovered	0	2	0	0.1	0.46	0.31	0.04	0.99	0.13	0.14	0.01	0.54	-0.46	-0.36	16,8	1,8	201,3
<i>Decticus albifrons</i>	Orthoptera	Uncovered	36	74	0.7	0.75	0.81	0.1	0.58	0.96	0.93	0.03	0.86	0.97	-0.11	-0.06	1,3	0,9	2,3
<i>Decticus verrucivorus</i>	Orthoptera	Vulnerable	2	4	0.05	0.05	0.07	0.08	0	0.27	0.57	0.19	0.19	0.89	-0.02	-0.02	0,3	0,1	1,8
<i>Depressotetrix depressa</i>	Orthoptera	Uncovered	2	5	0.1	0.15	0.3	0.19	0.05	0.79	0.02	0.03	0	0.09	-0.2	-0.15	1,6	0,5	24,4
<i>Dociostaurus genei</i>	Orthoptera	Vulnerable	4	10	0.2	0.25	0.39	0.17	0.11	0.77	0.18	0.11	0.04	0.47	-0.19	-0.14	1,1	0,5	7,5
<i>Dociostaurus jagoi</i>	Orthoptera	Uncovered	11	20	0.55	0.6	0.73	0.13	0.43	0.94	0.32	0.1	0.16	0.53	-0.18	-0.13	2,5	1,3	6,9
<i>Dociostaurus maroccanus</i>	Orthoptera	Uncovered	6	10	0.2	0.2	0.33	0.16	0.09	0.7	0.4	0.13	0.16	0.67	-0.13	-0.13	2,7	1,1	10,1
<i>Ephippiger diurnus</i>	Orthoptera	Uncovered	28	56	0.75	0.9	0.96	0.04	0.85	1	0.61	0.08	0.45	0.75	-0.21	-0.06	2,8	1,5	7,8
<i>Ephippiger provincialis</i>	Orthoptera	Vulnerable	1	1	0.05	0.05	0.38	0.31	0.01	0.99	0.08	0.1	0	0.39	-0.33	-0.33	NA	NA	NA
<i>Euchorthippus chopardi</i>	Orthoptera	Uncovered	9	12	0.3	0.3	0.61	0.19	0.23	0.96	0.19	0.08	0.07	0.36	-0.31	-0.31	6,7	2,7	22,5
<i>Euchorthippus declivus</i>	Orthoptera	Uncovered	3	6	0.1	0.15	0.21	0.12	0.04	0.51	0.49	0.18	0.15	0.83	-0.11	-0.06	0,9	0,4	4,3
<i>Euchorthippus elegantulus</i>	Orthoptera	Uncovered	20	39	0.8	0.85	0.98	0.03	0.89	1	0.28	0.08	0.15	0.44	-0.18	-0.13	2,1	1,3	4,2
<i>Eumodicogryllus bordigalensis</i>	Orthoptera	Uncovered	15	25	0.35	0.6	0.89	0.1	0.63	1	0.17	0.05	0.09	0.28	-0.54	-0.29	5,9	2,1	29,9
<i>Gryllomorpha dalmatina</i>	Orthoptera	Uncovered	1	2	0.05	0.05	0.12	0.16	0	0.61	0.19	0.16	0.02	0.59	-0.07	-0.07	1,8	0,3	38,0
<i>Gryllotalpa vineae</i>	Orthoptera	Vulnerable	1	1	0.05	0.05	0.19	0.24	0.01	0.94	0.12	0.15	0	0.57	-0.14	-0.14	NA	NA	NA
<i>Gryllus bimaculatus</i>	Orthoptera	Uncovered	2	7	0.1	0.25	0.69	0.22	0.24	1	0.06	0.04	0.01	0.17	-0.59	-0.44	6,8	2,1	34,7
<i>Gryllus campestris</i>	Orthoptera	Uncovered	5	14	0.2	0.4	0.72	0.17	0.34	0.99	0.1	0.05	0.03	0.21	-0.52	-0.32	3,5	1,2	23,5
<i>Isophya pyrenaea</i>	Orthoptera	Uncovered	6	9	0.25	0.25	0.47	0.24	0.1	0.97	0.05	0.03	0.01	0.14	-0.22	-0.22	5,5	2,2	17,9
<i>Leptophyes punctatissima</i>	Orthoptera	Uncovered	12	20	0.55	0.55	0.76	0.13	0.46	0.97	0.31	0.1	0.14	0.53	-0.21	-0.21	3,1	1,6	7,4
<i>Locusta cinerascens</i>	Orthoptera	Uncovered	23	33	0.55	0.6	0.86	0.12	0.57	1	0.16	0.04	0.09	0.26	-0.31	-0.26	5,2	2,1	20,9
<i>Mogoplistes brunneus</i>	Orthoptera	Uncovered	1	1	0.05	0.05	0.27	0.29	0.01	0.98	0.09	0.1	0	0.4	-0.22	-0.22	NA	NA	NA
<i>Nemobius sylvestris</i>	Orthoptera	Uncovered	9	16	0.3	0.35	0.57	0.16	0.26	0.89	0.12	0.06	0.04	0.26	-0.27	-0.22	3,4	1,2	16,0
<i>Oecanthus pellucens</i>	Orthoptera	Uncovered	9	18	0.45	0.45	0.88	0.12	0.58	1	0.09	0.05	0.02	0.22	-0.43	-0.43	2,9	1,3	10,1
<i>Oedaleus decorus</i>	Orthoptera	Uncovered	14	29	0.6	0.65	0.9	0.09	0.66	1	0.31	0.08	0.17	0.49	-0.3	-0.25	3,9	2,2	8,3
<i>Oedipoda caeruleascens</i>	Orthoptera	Uncovered	20	43	0.8	0.85	0.97	0.04	0.86	1	0.42	0.08	0.26	0.59	-0.17	-0.12	2,5	1,7	4,4
<i>Oedipoda charpentieri</i>	Orthoptera	Vulnerable	1	2	0.05	0.05	0.18	0.22	0.01	0.92	0.29	0.21	0.02	0.76	-0.13	-0.13	3,1	0,5	71,6
<i>Oedipoda germanica</i>	Orthoptera	Uncovered	16	33	0.65	0.7	0.94	0.06	0.76	1	0.29	0.08	0.16	0.46	-0.29	-0.24	2,8	1,8	4,8
<i>Omocestus petraeus</i>	Orthoptera	Vulnerable	1	3	0.05	0.05	0.12	0.13	0.01	0.46	0.31	0.2	0.04	0.77	-0.07	-0.07	0,9	0,3	8,2
<i>Omocestus raymondi</i>	Orthoptera	Uncovered	27	56	0.75	0.75	0.86	0.09	0.64	0.97	0.6	0.08	0.44	0.75	-0.11	-0.11	1,7	1,2	2,6
<i>Omocestus rufipes</i>	Orthoptera	Uncovered	37	76	0.9	1	0.98	0.02	0.92	1	0.56	0.08	0.39	0.72	-0.08	0.02	2,0	1,5	2,9
<i>Paratettix meridionalis</i>	Orthoptera	Uncovered	22	41	0.45	0.45	0.55	0.14	0.27	0.82	0.42	0.1	0.23	0.62	-0.1	-0.1	1,5	0,9	2,4
<i>Pezotettix giornaie</i>	Orthoptera	Uncovered	14	17	0.55	0.55	0.91	0.1	0.64	1	0.16	0.05	0.07	0.28	-0.36	-0.36	8,1	2,8	41,2
<i>Phaneroptera nana</i>	Orthoptera	Uncovered	3	4	0.15	0.2	0.79	0.2	0.31	1	0.05	0.04	0.01	0.16	-0.64	-0.59	22,0	5,6	121,5
<i>Pholidoptera femorata</i>	Orthoptera	Uncovered	24	38	0.5	0.65	0.82	0.11	0.55	0.98	0.44	0.07	0.3	0.57	-0.32	-0.17	3,5	1,6	12,1

<i>Platycleis affinis</i>	Orthoptera	Uncovered	22	47	0.6	0.7	0.85	0.09	0.62	0.98	0.62	0.08	0.46	0.76	-0.25	-0.15	2,1	1,1	6,1
<i>Platycleis albopunctata</i>	Orthoptera	Uncovered	13	22	0.55	0.6	0.79	0.12	0.49	0.97	0.38	0.09	0.21	0.57	-0.24	-0.19	4,8	2,6	11,1
<i>Platycleis falx</i>	Orthoptera	Vulnerable	6	8	0.15	0.15	0.36	0.23	0.06	0.92	0.27	0.11	0.1	0.52	-0.21	-0.21	7,3	2,0	38,8
<i>Platycleis intermedia</i>	Orthoptera	Uncovered	9	21	0.4	0.5	0.92	0.09	0.68	1	0.14	0.06	0.06	0.28	-0.52	-0.42	3,8	1,6	17,7
<i>Platycleis sabulosa</i>	Orthoptera	Uncovered	1	1	0.05	0.05	0.49	0.33	0.02	1	0.05	0.06	0	0.21	-0.44	-0.44	NA	NA	NA
<i>Platycleis tessellata</i>	Orthoptera	Uncovered	20	34	0.65	0.75	0.91	0.08	0.71	0.99	0.45	0.08	0.3	0.61	-0.26	-0.16	4,8	2,6	10,8
<i>Prionotropis azami</i>	Orthoptera	Protected	2	4	0.05	0.05	0.08	0.08	0	0.28	0.38	0.22	0.05	0.84	-0.03	-0.03	0,2	0,1	3,2
<i>Pteronemobius heydenii</i>	Orthoptera	Uncovered	4	4	0.1	0.1	0.19	0.15	0.02	0.6	0.29	0.18	0.04	0.7	-0.09	-0.09	2,0	0,7	12,9
<i>Pyrgomorpha conica</i>	Orthoptera	Uncovered	9	19	0.35	0.35	0.59	0.16	0.27	0.9	0.09	0.05	0.03	0.2	-0.24	-0.24	3,5	2,0	8,0
<i>Ramburiella hispanica</i>	Orthoptera	Uncovered	12	26	0.4	0.55	0.77	0.13	0.47	0.98	0.27	0.08	0.12	0.45	-0.37	-0.22	1,8	0,9	6,3
<i>Saga pedo</i>	Orthoptera	Protected	10	25	0.4	0.6	0.9	0.11	0.61	1	0.27	0.06	0.17	0.4	-0.5	-0.3	7,6	3,3	23,5
<i>Sepiana sepium</i>	Orthoptera	Uncovered	2	4	0.05	0.05	0.09	0.08	0.01	0.3	0.51	0.23	0.11	0.91	-0.04	-0.04	0,3	0,2	1,5
<i>Sphingonotus caeruleus</i>	Orthoptera	Uncovered	8	16	0.35	0.45	0.87	0.12	0.55	1	0.16	0.06	0.07	0.29	-0.52	-0.42	7,3	2,9	26,0
<i>Stenobothrus fischeri</i>	Orthoptera	Vulnerable	3	6	0.1	0.1	0.18	0.13	0.02	0.5	0.46	0.2	0.11	0.84	-0.08	-0.08	1,1	0,5	3,6
<i>Tetrix ceperoi</i>	Orthoptera	Vulnerable	1	5	0.05	0.1	0.18	0.13	0.02	0.51	0.15	0.11	0.02	0.44	-0.13	-0.08	1,7	0,7	7,1
<i>Tetrix undulata</i>	Orthoptera	Uncovered	1	1	0.05	0.05	0.28	0.29	0.01	0.98	0.04	0.05	0	0.17	-0.23	-0.23	NA	NA	NA
<i>Tettigonia viridissima</i>	Orthoptera	Uncovered	55	107	0.9	0.95	0.97	0.04	0.86	1	0.78	0.04	0.69	0.86	-0.07	-0.02	2,5	1,5	5,7
<i>Thyreonotus corsicus</i>	Orthoptera	Uncovered	3	6	0.15	0.2	0.53	0.25	0.11	0.99	0.09	0.05	0.02	0.23	-0.38	-0.33	8,7	2,7	41,5
<i>Tylopsis lilifolia</i>	Orthoptera	Uncovered	27	54	0.7	0.85	0.96	0.04	0.85	1	0.69	0.07	0.55	0.82	-0.26	-0.11	2,9	1,7	6,6
<i>Uromenus rugosicollis</i>	Orthoptera	Uncovered	4	10	0.2	0.3	0.54	0.2	0.18	0.94	0.21	0.1	0.06	0.43	-0.34	-0.24	3,3	1,4	11,3
<i>Yersinella raymondii</i>	Orthoptera	Uncovered	2	2	0.05	0.05	0.2	0.14	0.03	0.56	0.29	0.19	0.04	0.73	-0.15	-0.15	1,4	0,5	9,6
<i>Anthocharis cardamines</i>	Papilionoideae	Uncovered	8	17	0.35	0.4	0.63	0.15	0.31	0.9	0.02	0.01	0	0.05	-0.28	-0.23	1,8	0,8	5,3
<i>Anthocharis euphenoides</i>	Papilionoideae	Uncovered	9	18	0.25	0.3	0.31	0.15	0.07	0.63	0.07	0.06	0.01	0.22	-0.06	-0.01	0,9	0,6	1,9
<i>Aporia crataegi</i>	Papilionoideae	Uncovered	4	16	0.2	0.55	0.95	0.07	0.74	1	0.04	0.02	0.01	0.1	-0.75	-0.4	13,7	7,1	30,9
<i>Arethusana arethusa</i>	Papilionoideae	Uncovered	1	3	0.05	0.1	0.38	0.27	0.04	0.98	0.08	0.08	0.01	0.3	-0.33	-0.28	3,9	0,6	149,7
<i>Argynnis adippe</i>	Papilionoideae	Uncovered	1	4	0.05	0.1	0.16	0.15	0.01	0.58	0.25	0.16	0.04	0.64	-0.11	-0.06	1,3	0,3	18,3
<i>Argynnis aglaja</i>	Papilionoideae	Uncovered	0	1	0	0.05	0.4	0.33	0.01	0.99	0.08	0.1	0	0.4	-0.4	-0.35	NA	NA	NA
<i>Argynnis niobe</i>	Papilionoideae	Uncovered	0	1	0	0.05	0.39	0.32	0.01	0.99	0.08	0.1	0	0.36	-0.39	-0.34	NA	NA	NA
<i>Argynnis paphia</i>	Papilionoideae	Uncovered	4	7	0.2	0.25	0.66	0.22	0.22	0.99	0.17	0.1	0.04	0.42	-0.46	-0.41	7,3	2,8	25,1
<i>Aricia agestis</i>	Papilionoideae	Uncovered	34	72	0.9	0.95	0.97	0.03	0.89	1	0.45	0.06	0.33	0.57	-0.07	-0.02	5,1	3,5	7,7
<i>Boloria dia</i>	Papilionoideae	Uncovered	2	4	0.1	0.15	0.51	0.27	0.09	0.99	0.05	0.04	0	0.17	-0.41	-0.36	15,7	3,9	83,9
<i>Boloria euphrosyne</i>	Papilionoideae	Uncovered	1	2	0.05	0.05	0.1	0.12	0	0.44	0.12	0.12	0.01	0.47	-0.05	-0.05	0,3	0,0	###
<i>Brenthis daphne</i>	Papilionoideae	Uncovered	1	2	0.05	0.05	0.21	0.23	0.01	0.92	0.2	0.18	0.01	0.67	-0.16	-0.16	3,9	0,9	38,7
<i>Brintesia circe</i>	Papilionoideae	Uncovered	20	39	0.65	0.8	0.95	0.05	0.82	1	0.59	0.08	0.43	0.74	-0.3	-0.15	3,1	2,0	5,5
<i>Callophrys rubi</i>	Papilionoideae	Uncovered	12	22	0.45	0.45	0.76	0.16	0.41	0.99	0.01	0.01	0	0.04	-0.31	-0.31	4,6	2,3	11,3
<i>Carcharodus alceae</i>	Papilionoideae	Uncovered	36	67	0.8	0.9	0.94	0.05	0.81	1	0.3	0.06	0.19	0.41	-0.14	-0.03	3,0	1,8	5,8
<i>Celastrina argiolus</i>	Papilionoideae	Uncovered	18	38	0.45	0.7	0.91	0.09	0.68	1	0.2	0.05	0.12	0.31	-0.46	-0.21	10,1	5,8	19,1
<i>Charaxes jasius</i>	Papilionoideae	Uncovered	4	4	0.15	0.15	0.34	0.26	0.03	0.97	0.17	0.12	0.03	0.49	-0.19	-0.19	7,5	2,1	40,3
<i>Chazara briseis</i>	Papilionoideae	Vulnerable	1	2	0.05	0.05	0.14	0.18	0	0.76	0.22	0.17	0.02	0.63	-0.09	-0.09	1,8	0,4	24,4
<i>Coenonympha arcania</i>	Papilionoideae	Uncovered	1	3	0.05	0.1	0.37	0.27	0.04	0.98	0.13	0.12	0.01	0.45	-0.32	-0.27	6,9	1,6	53,9

<i>Coenonympha dorus</i>	Papilionoideae	Uncovered	8	16	0.4	0.4	0.67	0.17	0.33	0.97	0.3	0.1	0.12	0.52	-0.27	-0.27	3,9	2,1	8,8
<i>Coenonympha pamphilus</i>	Papilionoideae	Uncovered	5	12	0.15	0.25	0.48	0.18	0.16	0.86	0.07	0.04	0.01	0.18	-0.33	-0.23	3,9	1,3	26,0
<i>Colias alfahariensis</i>	Papilionoideae	Uncovered	11	19	0.3	0.4	0.63	0.16	0.29	0.92	0.17	0.06	0.06	0.31	-0.33	-0.23	5,2	2,8	11,6
<i>Colias crocea</i>	Papilionoideae	Uncovered	32	66	0.85	0.9	0.97	0.04	0.86	1	0.33	0.06	0.23	0.44	-0.12	-0.07	6,3	4,3	9,7
<i>Cupido minimus</i>	Papilionoideae	Uncovered	3	7	0.15	0.15	0.14	0.1	0.01	0.41	0.12	0.1	0.01	0.38	0.01	0.01	0,7	0,3	3,0
<i>Erebia epistygne</i>	Papilionoideae	Vulnerable	1	1	0.05	0.05	0.23	0.26	0.01	0.96	0.06	0.08	0	0.31	-0.18	-0.18	NA	NA	NA
<i>Erynnis tages</i>	Papilionoideae	Uncovered	3	5	0.1	0.1	0.15	0.1	0.02	0.41	0.16	0.12	0.02	0.47	-0.05	-0.05	0,2	0,1	3,0
<i>Euchloe crameri</i>	Papilionoideae	Uncovered	4	7	0.15	0.2	0.6	0.25	0.15	0.99	0.03	0.03	0	0.1	-0.45	-0.4	14,7	5,0	52,6
<i>Glaucopsyche alexis</i>	Papilionoideae	Uncovered	7	12	0.3	0.35	0.77	0.17	0.4	1	0.04	0.03	0.01	0.1	-0.47	-0.42	9,1	4,2	24,2
<i>Glaucopsyche melanops</i>	Papilionoideae	Uncovered	9	19	0.35	0.4	0.68	0.16	0.34	0.96	0.02	0.02	0	0.07	-0.33	-0.28	4,5	2,5	9,3
<i>Gonepteryx cleopatra</i>	Papilionoideae	Uncovered	27	61	0.6	0.6	0.7	0.13	0.41	0.91	0.48	0.08	0.34	0.63	-0.1	-0.1	2,1	1,5	3,1
<i>Gonepteryx rhanni</i>	Papilionoideae	Uncovered	5	6	0.2	0.2	0.66	0.26	0.16	1	0.03	0.03	0	0.1	-0.46	-0.46	21,7	5,7	97,6
<i>Hipparchia fagi</i>	Papilionoideae	Uncovered	5	10	0.2	0.3	0.5	0.2	0.16	0.91	0.14	0.08	0.04	0.34	-0.3	-0.2	2,4	0,9	12,7
<i>Hipparchia fidia</i>	Papilionoideae	Uncovered	2	7	0.1	0.2	0.37	0.22	0.06	0.91	0.17	0.1	0.04	0.41	-0.27	-0.17	4,6	1,6	22,1
<i>Hipparchia semele</i>	Papilionoideae	Uncovered	5	10	0.15	0.25	0.62	0.22	0.21	0.99	0.22	0.1	0.07	0.45	-0.47	-0.37	5,3	2,4	15,5
<i>Iphiclides podalirius</i>	Papilionoideae	Uncovered	23	59	0.55	0.95	0.97	0.03	0.88	1	0.23	0.05	0.14	0.33	-0.42	-0.02	4,9	2,8	10,5
<i>Issoria lathonia</i>	Papilionoideae	Uncovered	1	4	0.05	0.1	0.18	0.17	0.01	0.69	0.08	0.07	0.01	0.26	-0.13	-0.08	4,1	1,3	20,3
<i>Lampides baeticus</i>	Papilionoideae	Uncovered	1	1	0.05	0.05	0.44	0.33	0.02	0.99	0.05	0.06	0	0.21	-0.39	-0.39	NA	NA	NA
<i>Lasiommata megera</i>	Papilionoideae	Uncovered	55	103	1	1	0.98	0.02	0.92	1	0.56	0.07	0.43	0.68	0.02	0.02	2,7	2,0	3,9
<i>Leptidea sinapis</i>	Papilionoideae	Uncovered	25	49	0.5	0.6	0.73	0.13	0.44	0.93	0.23	0.06	0.13	0.36	-0.23	-0.13	2,3	1,3	5,1
<i>Leptotes pirithous</i>	Papilionoideae	Uncovered	1	3	0.05	0.15	0.67	0.27	0.13	1	0.06	0.04	0.01	0.17	-0.62	-0.52	26,3	6,7	127,1
<i>Libythea celtis</i>	Papilionoideae	Uncovered	1	2	0.05	0.1	0.44	0.31	0.03	0.99	0.03	0.03	0	0.11	-0.39	-0.34	41,0	7,2	###
<i>Limenitis reducta</i>	Papilionoideae	Uncovered	14	32	0.4	0.65	0.86	0.11	0.6	1	0.3	0.07	0.17	0.45	-0.46	-0.21	5,5	3,5	9,5
<i>Lycæna alciphron</i>	Papilionoideae	Uncovered	1	2	0.05	0.1	0.43	0.3	0.04	0.99	0.06	0.06	0	0.24	-0.38	-0.33	20,1	3,5	164,3
<i>Lycæna phlaeas</i>	Papilionoideae	Uncovered	33	59	0.8	0.8	0.92	0.06	0.76	0.99	0.32	0.06	0.2	0.46	-0.12	-0.12	3,7	2,4	6,4
<i>Lysandra bellargus</i>	Papilionoideae	Uncovered	4	10	0.15	0.35	0.8	0.17	0.39	1	0.14	0.07	0.04	0.3	-0.65	-0.45	11,8	5,1	33,1
<i>Lysandra coridon</i>	Papilionoideae	Uncovered	2	5	0.1	0.15	0.45	0.25	0.09	0.98	0.09	0.07	0.01	0.28	-0.35	-0.3	3,1	0,7	50,6
<i>Lysandra hispana</i>	Papilionoideae	Uncovered	14	28	0.4	0.45	0.62	0.15	0.3	0.89	0.27	0.08	0.13	0.44	-0.22	-0.17	2,5	1,5	5,0
<i>Maniola jurtina</i>	Papilionoideae	Uncovered	24	44	0.75	0.8	0.97	0.03	0.87	1	0.55	0.07	0.4	0.69	-0.22	-0.17	4,0	2,6	7,0
<i>Melanargia galathea</i>	Papilionoideae	Uncovered	3	5	0.1	0.1	0.22	0.16	0.03	0.65	0.34	0.2	0.05	0.77	-0.12	-0.12	1,5	0,6	6,0
<i>Melanargia lachesis</i>	Papilionoideae	Uncovered	22	42	0.7	0.8	0.87	0.09	0.65	0.98	0.69	0.07	0.54	0.82	-0.17	-0.07	2,3	1,6	3,7
<i>Melanargia occitanica</i>	Papilionoideae	Uncovered	14	25	0.4	0.4	0.59	0.16	0.28	0.88	0.11	0.06	0.03	0.26	-0.19	-0.19	2,1	1,2	4,2
<i>Melitaea athalia</i>	Papilionoideae	Uncovered	4	9	0.1	0.15	0.14	0.11	0.01	0.41	0.5	0.18	0.16	0.83	-0.04	0.01	0,7	0,4	1,7
<i>Melitaea cinxia</i>	Papilionoideae	Uncovered	24	48	0.8	0.9	0.97	0.04	0.86	1	0.18	0.04	0.1	0.28	-0.17	-0.07	7,7	5,1	12,5
<i>Melitaea didyma</i>	Papilionoideae	Uncovered	26	45	0.75	0.9	0.98	0.03	0.9	1	0.51	0.07	0.37	0.65	-0.23	-0.08	4,4	3,0	6,9
<i>Melitaea phoebe</i>	Papilionoideae	Uncovered	10	22	0.35	0.55	0.87	0.12	0.56	1	0.15	0.05	0.07	0.26	-0.52	-0.32	10,5	5,3	23,0
<i>Nymphalis polychloros</i>	Papilionoideae	Uncovered	1	1	0.05	0.05	0.2	0.25	0	0.95	0.04	0.05	0	0.19	-0.15	-0.15	NA	NA	NA
<i>Ochlodes sylvanus</i>	Papilionoideae	Uncovered	4	5	0.15	0.2	0.68	0.25	0.19	1	0.09	0.07	0.02	0.26	-0.53	-0.48	14,3	4,0	59,8
<i>Papilio machaon</i>	Papilionoideae	Uncovered	35	64	0.7	0.7	0.82	0.11	0.57	0.97	0.35	0.07	0.23	0.49	-0.12	-0.12	2,6	1,8	4,4
<i>Pararge aegeria</i>	Papilionoideae	Uncovered	37	77	0.75	0.85	0.94	0.06	0.79	1	0.3	0.06	0.19	0.43	-0.19	-0.09	2,7	1,6	5,1

<i>Pieris brassicae</i>	Papilionoideae	Uncovered	24	42	0.6	0.75	0.93	0.07	0.74	1	0.13	0.04	0.06	0.22	-0.33	-0.18	6,0	3,0	14,8
<i>Pieris mannii</i>	Papilionoideae	Uncovered	2	5	0.1	0.25	0.89	0.14	0.49	1	0.05	0.03	0.01	0.12	-0.79	-0.64	72,9	19,2	###
<i>Pieris napi</i>	Papilionoideae	Uncovered	8	21	0.35	0.6	0.86	0.12	0.55	1	0.08	0.04	0.03	0.17	-0.51	-0.26	9,0	3,7	28,4
<i>Pieris rapae</i>	Papilionoideae	Uncovered	54	100	0.9	1	0.98	0.02	0.92	1	0.53	0.07	0.39	0.66	-0.08	0.02	2,5	1,9	3,4
<i>Plebejus argus</i>	Papilionoideae	Uncovered	3	4	0.15	0.15	0.41	0.26	0.07	0.98	0.23	0.17	0.03	0.66	-0.26	-0.26	4,8	1,2	38,2
<i>Plebejus idas</i>	Papilionoideae	Uncovered	1	1	0.05	0.05	0.4	0.33	0.01	0.99	0.08	0.11	0	0.4	-0.35	-0.35	NA	NA	NA
<i>Polygonia c-album</i>	Papilionoideae	Uncovered	2	7	0.1	0.25	0.7	0.23	0.23	1	0.03	0.03	0	0.1	-0.6	-0.45	16,1	2,8	150,9
<i>Polyommatus daphnis</i>	Papilionoideae	Vulnerable	1	2	0.05	0.05	0.2	0.22	0.01	0.9	0.15	0.14	0.01	0.52	-0.15	-0.15	3,4	0,6	78,4
<i>Polyommatus dolus</i>	Papilionoideae	Vulnerable	1	2	0.05	0.05	0.17	0.19	0.01	0.79	0.19	0.18	0.01	0.66	-0.12	-0.12	1,6	0,3	59,5
<i>Polyommatus escheri</i>	Papilionoideae	Uncovered	5	9	0.15	0.2	0.35	0.18	0.08	0.75	0.3	0.13	0.09	0.6	-0.2	-0.15	2,0	1,0	4,9
<i>Polyommatus icarus</i>	Papilionoideae	Uncovered	49	96	1	1	0.98	0.02	0.92	1	0.65	0.06	0.54	0.76	0.02	0.02	3,4	2,4	5,2
<i>Polyommatus thersites</i>	Papilionoideae	Uncovered	1	1	0.05	0.05	0.39	0.32	0.01	0.99	0.08	0.1	0	0.36	-0.34	-0.34	NA	NA	NA
<i>Pontia daplidice</i>	Papilionoideae	Uncovered	22	43	0.45	0.55	0.72	0.13	0.44	0.93	0.36	0.07	0.24	0.5	-0.27	-0.17	4,8	2,8	9,5
<i>Pseudophilotes baton</i>	Papilionoideae	Uncovered	13	25	0.45	0.45	0.64	0.15	0.33	0.9	0.06	0.03	0.01	0.14	-0.19	-0.19	3,2	1,9	6,1
<i>Pyrgus bellieri</i>	Papilionoideae	Uncovered	0	1	0	0.05	0.35	0.31	0.01	0.99	0.07	0.09	0	0.36	-0.35	-0.3	NA	NA	NA
<i>Pyrgus malvoides</i>	Papilionoideae	Uncovered	7	11	0.35	0.4	0.84	0.15	0.47	1	0.04	0.02	0.01	0.1	-0.49	-0.44	15,4	5,7	44,3
<i>Pyrgus serratulae</i>	Papilionoideae	Uncovered	1	1	0.05	0.05	0.3	0.3	0.01	0.98	0.06	0.08	0	0.31	-0.25	-0.25	NA	NA	NA
<i>Pyrgus sidae</i>	Papilionoideae	Vulnerable	1	2	0.05	0.05	0.08	0.11	0	0.34	0.27	0.21	0.02	0.76	-0.03	-0.03	0,3	0,1	15,9
<i>Pyronia bathseba</i>	Papilionoideae	Uncovered	24	45	0.65	0.7	0.81	0.1	0.57	0.95	0.52	0.09	0.34	0.69	-0.16	-0.11	1,8	1,2	2,9
<i>Pyronia cecilia</i>	Papilionoideae	Uncovered	21	42	0.65	0.75	0.87	0.08	0.67	0.98	0.66	0.08	0.5	0.79	-0.22	-0.12	2,0	1,3	3,3
<i>Pyronia tithonus</i>	Papilionoideae	Uncovered	1	2	0.05	0.05	0.21	0.22	0.01	0.91	0.15	0.14	0.01	0.52	-0.16	-0.16	3,5	0,6	82,5
<i>Quercusia quercus</i>	Papilionoideae	Uncovered	1	3	0.05	0.1	0.26	0.23	0.02	0.93	0.13	0.11	0.01	0.43	-0.21	-0.16	4,2	1,0	38,5
<i>Satyrium esculi</i>	Papilionoideae	Uncovered	11	22	0.5	0.6	0.81	0.12	0.53	0.98	0.42	0.1	0.23	0.61	-0.31	-0.21	3,6	2,0	8,2
<i>Satyrium ilicis</i>	Papilionoideae	Uncovered	6	9	0.25	0.3	0.53	0.22	0.15	0.97	0.23	0.12	0.06	0.52	-0.28	-0.23	4,4	2,1	12,0
<i>Satyrium spini</i>	Papilionoideae	Uncovered	7	13	0.3	0.3	0.53	0.18	0.19	0.87	0.25	0.11	0.08	0.5	-0.23	-0.23	2,4	1,3	5,2
<i>Satyryus ferula</i>	Papilionoideae	Uncovered	1	2	0.05	0.05	0.19	0.21	0.01	0.88	0.24	0.19	0.02	0.71	-0.14	-0.14	2,5	0,6	33,1
<i>Spialia sertorius</i>	Papilionoideae	Uncovered	12	30	0.4	0.65	0.93	0.08	0.7	1	0.13	0.04	0.05	0.23	-0.53	-0.28	6,3	4,0	11,1
<i>Thymelicus acteon</i>	Papilionoideae	Uncovered	18	40	0.6	0.75	0.96	0.05	0.83	1	0.45	0.08	0.31	0.6	-0.36	-0.21	4,1	2,8	6,5
<i>Thymelicus lineolus</i>	Papilionoideae	Uncovered	0	1	0	0.05	0.32	0.32	0.01	0.99	0.08	0.1	0	0.37	-0.32	-0.27	NA	NA	NA
<i>Thymelicus sylvestris</i>	Papilionoideae	Uncovered	7	11	0.3	0.3	0.69	0.22	0.25	1	0.15	0.07	0.05	0.31	-0.39	-0.39	9,2	3,7	26,8
<i>Vanessa atalanta</i>	Papilionoideae	Uncovered	11	23	0.4	0.5	0.81	0.14	0.46	0.99	0.03	0.02	0.01	0.09	-0.41	-0.31	5,8	1,8	35,1
<i>Vanessa cardui</i>	Papilionoideae	Uncovered	18	42	0.6	0.8	0.96	0.05	0.82	1	0.11	0.04	0.05	0.2	-0.36	-0.16	6,4	4,2	10,4
<i>Zerynthia polyxena</i>	Papilionoideae	Protected	15	28	0.5	0.5	0.75	0.14	0.43	0.96	0.01	0.01	0	0.02	-0.25	-0.25	0,9	0,6	1,6
<i>Zerynthia rumina</i>	Papilionoideae	Protected	9	17	0.25	0.25	0.38	0.15	0.12	0.69	0.13	0.07	0.03	0.31	-0.13	-0.13	2,0	1,2	4,0
<i>Zygaena ephialtes</i>	Zygaenidae	Uncovered	1	4	0.05	0.1	0.09	0.1	0	0.35	0.38	0.19	0.07	0.77	-0.04	0.01	0,5	0,2	4,7
<i>Zygaena erythrus</i>	Zygaenidae	Uncovered	3	4	0.15	0.15	0.49	0.3	0.07	0.99	0.16	0.12	0.02	0.47	-0.34	-0.34	8,9	2,1	56,8
<i>Zygaena fausta</i>	Zygaenidae	Uncovered	6	14	0.25	0.35	0.6	0.2	0.22	0.96	0.17	0.07	0.06	0.34	-0.35	-0.25	4,4	2,2	11,0
<i>Zygaena filipendulae</i>	Zygaenidae	Uncovered	14	26	0.4	0.4	0.58	0.17	0.25	0.9	0.24	0.08	0.1	0.41	-0.18	-0.18	2,3	1,3	4,6
<i>Zygaena lavandulae</i>	Zygaenidae	Uncovered	13	25	0.4	0.5	0.71	0.15	0.38	0.94	0.06	0.04	0.01	0.16	-0.31	-0.21	3,2	1,9	6,5
<i>Zygaena occitanica</i>	Zygaenidae	Uncovered	3	7	0.15	0.3	0.7	0.23	0.22	1	0.11	0.06	0.03	0.26	-0.55	-0.4	10,1	3,8	33,0

<i>Zygaena rhadamanthus</i>	Zygaenidae	Protected	3	5	0.15	0.15	0.33	0.2	0.06	0.82	0.05	0.05	0	0.19	-0.18	-0.18	3,5	1,3	14,9
<i>Zygaena sarpedon</i>	Zygaenidae	Uncovered	8	9	0.35	0.35	0.87	0.13	0.51	1	0.1	0.05	0.03	0.21	-0.52	-0.52	14,6	5,5	44,9
<i>Zygaena transalpina</i>	Zygaenidae	Uncovered	1	1	0.05	0.05	0.33	0.32	0.01	0.99	0.08	0.09	0	0.34	-0.28	-0.28	NA	NA	NA

Supplementary materials S3.8. Posterior estimates for the effect of site covariates on observed insect species as estimated under the MSOM (with mean, standard deviation, CI_{95%}): a1 – linear effect of the site area (ha); a2 – linear effect of habitat diversity; a3 – linear effect of the proportion of closed habitats (%); a4 – quadratic effect of the proportion of closed habitats (%). Grey cells indicate species with confidence interval not containing zero (considered as indicative of significant response to the parameter).

Scientific name	Group	Conservation status	Area (a1)				Habitat diversity (a2)				Linear closed habitat (a3)				Quadratic closed habitat (a4)			
			Mean	SD	CI 2.5%	CI 97.5%	Mean	SD	CI 2.5%	CI 97.5%	Mean	SD	CI 2.5%	CI 97.5%	Mean	SD	CI 2.5%	CI 97.5%
<i>Cicadatra atra</i>	Cicada	Uncovered	0.22	0.29	-0.37	0.78	0.14	0.58	-0.95	1.35	0.17	0.75	-1.27	1.69	-0.43	0.39	-1.2	0.35
<i>Cicada orni</i>	Cicada	Uncovered	0.2	0.29	-0.41	0.74	-0.09	0.55	-1.15	1.03	1.01	0.77	-0.48	2.55	-0.29	0.4	-1.03	0.56
<i>Lyristes plebejus</i>	Cicada	Uncovered	0.21	0.28	-0.36	0.77	-0.06	0.53	-1.08	1.02	1.1	0.76	-0.36	2.66	-0.28	0.39	-0.99	0.56
<i>Tettigetta alba argentata</i>	Cicada	Uncovered	0.24	0.29	-0.36	0.81	-0.02	0.62	-1.2	1.26	0.35	0.86	-1.3	2.11	-0.42	0.4	-1.22	0.4
<i>Tettigetta pygmaea</i>	Cicada	Uncovered	0.17	0.29	-0.43	0.72	-0.21	0.53	-1.25	0.87	1.02	0.76	-0.44	2.57	-0.23	0.4	-0.98	0.63
<i>Tibicina garricola</i>	Cicada	Uncovered	0.35	0.28	-0.2	0.94	0.85	0.6	-0.26	2.09	0.01	0.82	-1.67	1.59	-0.51	0.4	-1.34	0.25
<i>Tibicina haematodes</i>	Cicada	Uncovered	0.22	0.29	-0.38	0.78	-0.03	0.56	-1.12	1.14	0.39	0.89	-1.37	2.19	-0.51	0.42	-1.4	0.29
<i>Tibicina tomentosa</i>	Cicada	Vulnerable	0.21	0.28	-0.36	0.75	-0.43	0.62	-1.73	0.72	-0.12	0.81	-1.78	1.39	-0.46	0.39	-1.25	0.3
<i>Aeshna affinis</i>	Odonata	Uncovered	0.22	0.28	-0.35	0.77	-0.25	0.61	-1.44	0.96	-0.16	0.85	-1.84	1.56	-0.5	0.4	-1.34	0.27
<i>Aeshna cyanea</i>	Odonata	Uncovered	0.28	0.28	-0.28	0.86	0.28	0.59	-0.87	1.45	1.05	0.87	-0.64	2.81	-0.29	0.39	-1.04	0.55
<i>Aeshna isocela</i>	Odonata	Uncovered	0.21	0.28	-0.38	0.75	-0.36	0.62	-1.67	0.79	0.34	0.8	-1.27	1.89	-0.56	0.4	-1.43	0.18
<i>Aeshna mixta</i>	Odonata	Uncovered	0.26	0.28	-0.29	0.82	0.03	0.66	-1.26	1.35	0.09	0.88	-1.66	1.86	-0.49	0.41	-1.34	0.29
<i>Anax imperator</i>	Odonata	Uncovered	0.34	0.28	-0.2	0.9	0.8	0.61	-0.32	2.08	0.17	0.65	-1.1	1.47	-0.4	0.36	-1.11	0.33
<i>Anax parthenope</i>	Odonata	Uncovered	0.28	0.27	-0.25	0.8	-0.11	0.54	-1.13	0.98	0.17	0.65	-1.11	1.44	-0.39	0.36	-1.12	0.33
<i>Boyeria irene</i>	Odonata	Uncovered	0.36	0.27	-0.16	0.92	0.53	0.52	-0.45	1.62	-0.38	0.74	-1.94	1.01	-0.5	0.38	-1.31	0.23
<i>Brachytron pratense</i>	Odonata	Vulnerable	0.2	0.28	-0.39	0.74	-0.07	0.61	-1.31	1.12	0.14	0.83	-1.57	1.73	-0.51	0.41	-1.36	0.27
<i>Calopteryx haemorrhoidalis</i>	Odonata	Uncovered	0.33	0.26	-0.18	0.87	0.54	0.49	-0.38	1.55	-0.47	0.71	-1.97	0.84	-0.52	0.38	-1.33	0.2
<i>Calopteryx xanthostoma</i>	Odonata	Uncovered	0.36	0.27	-0.15	0.91	0.72	0.54	-0.26	1.87	-0.5	0.69	-1.96	0.78	-0.55	0.39	-1.4	0.18
<i>Ceragrion tenellum</i>	Odonata	Uncovered	0.34	0.27	-0.18	0.89	0.72	0.53	-0.23	1.84	-0.63	0.72	-2.17	0.7	-0.5	0.39	-1.33	0.24
<i>Chalcolestes viridis</i>	Odonata	Uncovered	0.31	0.27	-0.22	0.86	0.27	0.61	-0.85	1.57	-0.69	0.76	-2.27	0.74	-0.48	0.39	-1.29	0.28
<i>Coenagrion caeruleum</i>	Odonata	Vulnerable	0.31	0.28	-0.25	0.88	0.65	0.58	-0.45	1.83	0.38	0.85	-1.33	2.02	-0.51	0.41	-1.38	0.27
<i>Coenagrion mercuriale</i>	Odonata	Protected	0.3	0.26	-0.21	0.84	0.54	0.5	-0.41	1.58	-0.12	0.72	-1.62	1.23	-0.56	0.39	-1.42	0.16
<i>Coenagrion puella</i>	Odonata	Uncovered	0.35	0.28	-0.17	0.92	0.68	0.6	-0.45	1.94	-0.21	0.83	-1.88	1.37	-0.51	0.4	-1.37	0.24
<i>Cordulegaster boltonii</i>	Odonata	Uncovered	0.31	0.28	-0.25	0.89	0.54	0.62	-0.65	1.81	0.4	0.9	-1.37	2.19	-0.49	0.41	-1.34	0.29
<i>Crocothemis erythraea</i>	Odonata	Uncovered	0.24	0.26	-0.29	0.75	0.16	0.46	-0.73	1.08	-0.33	0.65	-1.7	0.91	-0.64	0.39	-1.5	0.06
<i>Enallagma cyathigerum</i>	Odonata	Uncovered	0.3	0.27	-0.23	0.84	-0.13	0.51	-1.15	0.84	-0.45	0.74	-2.00	0.91	-0.47	0.38	-1.28	0.26
<i>Erythromma lindenii</i>	Odonata	Uncovered	0.33	0.27	-0.19	0.87	0.55	0.5	-0.37	1.59	-0.47	0.7	-1.97	0.82	-0.51	0.38	-1.32	0.21
<i>Gomphus graslinii</i>	Odonata	Protected	0.42	0.28	-0.09	1.02	0.55	0.52	-0.42	1.62	-0.33	0.74	-1.88	1.07	-0.48	0.38	-1.28	0.26

<i>Gomphus pulchellus</i>	Odonata	Uncovered	0.25	0.27	-0.27	0.79	0.29	0.5	-0.66	1.29	-0.58	0.7	-2.05	0.74	-0.51	0.38	-1.33	0.2
<i>Gomphus simillimus</i>	Odonata	Uncovered	0.39	0.28	-0.13	0.98	0.4	0.54	-0.63	1.5	0.37	0.73	-1.08	1.84	-0.52	0.39	-1.35	0.21
<i>Hemianax ephippiger</i>	Odonata	Uncovered	0.28	0.29	-0.29	0.85	0.08	0.67	-1.23	1.42	0.99	0.84	-0.68	2.65	-0.25	0.4	-1.01	0.63
<i>Ischnura elegans</i>	Odonata	Uncovered	0.3	0.27	-0.23	0.86	0.66	0.55	-0.34	1.84	-0.09	0.59	-1.26	1.05	-0.52	0.36	-1.29	0.18
<i>Ischnura pumilio</i>	Odonata	Vulnerable	0.28	0.28	-0.29	0.83	0.09	0.62	-1.13	1.3	1.13	0.79	-0.38	2.75	-0.34	0.39	-1.09	0.48
<i>Lestes barbarus</i>	Odonata	Uncovered	0.21	0.28	-0.36	0.74	-0.45	0.62	-1.73	0.7	-0.13	0.8	-1.79	1.35	-0.46	0.39	-1.28	0.29
<i>Lestes virens</i>	Odonata	Uncovered	0.23	0.29	-0.35	0.79	-0.32	0.68	-1.69	1.03	0.02	0.9	-1.76	1.81	-0.43	0.4	-1.25	0.36
<i>Libellula depressa</i>	Odonata	Uncovered	0.33	0.28	-0.2	0.89	0.07	0.64	-1.16	1.37	0.74	0.74	-0.66	2.27	-0.28	0.39	-1.00	0.56
<i>Libellula fulva</i>	Odonata	Uncovered	0.29	0.27	-0.25	0.85	0.34	0.58	-0.76	1.54	-0.91	0.78	-2.48	0.6	-0.52	0.4	-1.38	0.22
<i>Macromia splendens</i>	Odonata	Protected	0.3	0.27	-0.24	0.85	0.5	0.53	-0.49	1.58	-0.18	0.77	-1.76	1.26	-0.5	0.39	-1.32	0.25
<i>Onychogomphus forcipatus</i>	Odonata	Uncovered	0.4	0.27	-0.1	0.98	0.75	0.54	-0.23	1.89	-0.41	0.71	-1.88	0.91	-0.54	0.39	-1.37	0.19
<i>Onychogomphus uncutus</i>	Odonata	Vulnerable	0.3	0.26	-0.22	0.84	0.49	0.53	-0.53	1.59	-0.17	0.75	-1.71	1.26	-0.56	0.39	-1.39	0.17
<i>Orthetrum albistylum</i>	Odonata	Uncovered	0.36	0.28	-0.18	0.95	0.12	0.67	-1.17	1.47	0.12	0.91	-1.7	1.9	-0.44	0.41	-1.27	0.35
<i>Orthetrum brunneum</i>	Odonata	Uncovered	0.33	0.27	-0.18	0.89	0.7	0.55	-0.29	1.89	-0.63	0.73	-2.15	0.71	-0.5	0.39	-1.32	0.23
<i>Orthetrum cancellatum</i>	Odonata	Uncovered	0.22	0.27	-0.32	0.73	-0.06	0.49	-1.01	0.92	-0.81	0.65	-2.15	0.41	-0.61	0.39	-1.47	0.08
<i>Orthetrum coerulescens</i>	Odonata	Uncovered	0.29	0.27	-0.24	0.83	0.37	0.54	-0.67	1.49	-0.62	0.74	-2.11	0.81	-0.57	0.39	-1.41	0.14
<i>Oxygastra curtisii</i>	Odonata	Protected	0.32	0.26	-0.19	0.85	0.53	0.5	-0.4	1.56	-0.49	0.7	-1.95	0.8	-0.52	0.39	-1.34	0.2
<i>Platynemesis acutipennis</i>	Odonata	Uncovered	0.32	0.27	-0.2	0.87	0.38	0.5	-0.56	1.4	-0.28	0.6	-1.49	0.9	-0.61	0.38	-1.45	0.08
<i>Platynemesis latipes</i>	Odonata	Uncovered	0.31	0.26	-0.19	0.83	0.27	0.48	-0.65	1.25	-0.56	0.68	-2.00	0.7	-0.56	0.39	-1.39	0.15
<i>Pyrrhosoma nymphula</i>	Odonata	Uncovered	0.32	0.26	-0.19	0.86	0.52	0.5	-0.43	1.56	-0.46	0.7	-1.9	0.82	-0.53	0.38	-1.35	0.18
<i>Sympetrum fonscolombii</i>	Odonata	Uncovered	0.18	0.28	-0.39	0.71	-0.45	0.51	-1.48	0.56	-0.71	0.63	-1.99	0.5	-0.43	0.37	-1.18	0.29
<i>Sympetma fusca</i>	Odonata	Uncovered	0.32	0.28	-0.23	0.9	0.65	0.57	-0.4	1.82	1.11	0.76	-0.36	2.65	-0.38	0.39	-1.15	0.4
<i>Sympetrum meridionale</i>	Odonata	Uncovered	0.24	0.27	-0.31	0.78	-0.28	0.56	-1.37	0.85	0.06	0.69	-1.27	1.48	-0.37	0.38	-1.11	0.4
<i>Sympetrum pedemontanum</i>	Odonata	Vulnerable	0.22	0.28	-0.36	0.77	-0.29	0.66	-1.65	1.00	0.38	0.89	-1.36	2.14	-0.51	0.41	-1.37	0.27
<i>Sympetrum striolatum</i>	Odonata	Uncovered	0.29	0.28	-0.24	0.85	0.2	0.59	-0.92	1.42	0.8	0.76	-0.66	2.34	-0.29	0.38	-1.02	0.53
<i>Trithemis annulata</i>	Odonata	Uncovered	0.37	0.27	-0.13	0.92	0.49	0.51	-0.45	1.52	-0.42	0.73	-1.92	0.93	-0.5	0.39	-1.32	0.24
<i>Acrotylus fischeri</i>	Orthoptera	Uncovered	0.13	0.28	-0.46	0.64	-0.72	0.54	-1.84	0.27	1.02	0.63	-0.15	2.32	-0.29	0.37	-1.00	0.48
<i>Acrotylus insubricus</i>	Orthoptera	Uncovered	0.37	0.27	-0.14	0.93	0.55	0.52	-0.42	1.64	0.15	0.63	-1.1	1.37	-0.51	0.37	-1.28	0.2
<i>Aiolopus puissanti</i>	Orthoptera	Uncovered	0.27	0.27	-0.28	0.81	0.18	0.55	-0.88	1.32	-0.87	0.8	-2.48	0.67	-0.5	0.39	-1.32	0.23
<i>Aiolopus strepens</i>	Orthoptera	Uncovered	0.31	0.28	-0.24	0.87	0.38	0.64	-0.82	1.69	0.03	0.85	-1.59	1.77	-0.56	0.41	-1.41	0.22
<i>Amedegnatiiana vicheti</i>	Orthoptera	Vulnerable	0.21	0.28	-0.37	0.76	-0.45	0.61	-1.74	0.68	-0.14	0.8	-1.79	1.35	-0.47	0.39	-1.28	0.28
<i>Anacridium aegyptium</i>	Orthoptera	Uncovered	0.3	0.28	-0.26	0.87	0.38	0.63	-0.82	1.66	0.07	0.73	-1.3	1.6	-0.29	0.38	-1.02	0.51
<i>Antaxius sorrezensis</i>	Orthoptera	Vulnerable	0.24	0.29	-0.35	0.8	-0.3	0.68	-1.69	1.02	0.22	0.91	-1.59	2.04	-0.46	0.41	-1.31	0.34
<i>Arachnocephalus vestitus</i>	Orthoptera	Uncovered	0.24	0.28	-0.33	0.79	0.23	0.52	-0.76	1.28	0.64	0.75	-0.78	2.18	-0.41	0.37	-1.15	0.34
<i>Arcyptera kheili</i>	Orthoptera	Vulnerable	0.22	0.28	-0.35	0.77	-0.26	0.59	-1.47	0.85	0.84	0.75	-0.64	2.33	-0.53	0.38	-1.34	0.19
<i>Barbitistes fischeri</i>	Orthoptera	Uncovered	0.24	0.28	-0.32	0.81	-0.13	0.63	-1.39	1.1	1.37	0.83	-0.24	3.08	-0.36	0.4	-1.13	0.47
<i>Calliptamus barbarus</i>	Orthoptera	Uncovered	0.24	0.29	-0.34	0.81	-0.02	0.63	-1.26	1.24	0.59	0.83	-1.01	2.27	-0.31	0.39	-1.06	0.52

<i>Calliptamus italicus</i>	Orthoptera	Uncovered	0.25	0.27	-0.29	0.79	-0.1	0.56	-1.2	1.03	0.73	0.75	-0.71	2.26	-0.23	0.4	-0.96	0.65
<i>Calliptamus wattenwylanus</i>	Orthoptera	Uncovered	0.39	0.28	-0.14	0.98	0.9	0.59	-0.14	2.16	-0.02	0.62	-1.27	1.17	-0.54	0.37	-1.32	0.16
<i>Chorthippus binotatus</i>	Orthoptera	Vulnerable	0.23	0.28	-0.34	0.78	-0.32	0.68	-1.71	1.02	0.19	0.91	-1.65	1.97	-0.48	0.41	-1.32	0.3
<i>Chorthippus brunneus</i>	Orthoptera	Uncovered	0.27	0.29	-0.29	0.85	-0.01	0.64	-1.26	1.26	0.51	0.82	-1.06	2.17	-0.32	0.39	-1.07	0.51
<i>Chorthippus vagans</i>	Orthoptera	Uncovered	0.23	0.27	-0.32	0.75	-0.38	0.5	-1.4	0.58	1.4	0.69	0.11	2.83	-0.19	0.39	-0.89	0.68
<i>Conocephalus fuscus</i>	Orthoptera	Uncovered	0.19	0.29	-0.41	0.75	-0.27	0.67	-1.59	1.05	0.17	0.87	-1.53	1.92	-0.52	0.41	-1.35	0.25
<i>Decticus albifrons</i>	Orthoptera	Uncovered	0.37	0.28	-0.15	0.97	0.34	0.54	-0.67	1.45	0.14	0.57	-0.99	1.27	-0.26	0.36	-0.94	0.5
<i>Decticus verrucivorus</i>	Orthoptera	Vulnerable	0.28	0.28	-0.27	0.85	0.11	0.58	-1.06	1.22	1.14	0.75	-0.31	2.63	-0.36	0.38	-1.1	0.43
<i>Depressotetrix depressa</i>	Orthoptera	Uncovered	0.34	0.27	-0.19	0.9	-0.53	0.57	-1.7	0.53	0.64	0.69	-0.71	2.01	-0.3	0.38	-1.03	0.5
<i>Dociopterus genei</i>	Orthoptera	Vulnerable	0.14	0.28	-0.47	0.67	-0.78	0.59	-2.01	0.28	1.1	0.68	-0.17	2.5	-0.33	0.37	-1.05	0.44
<i>Dociopterus jagoi</i>	Orthoptera	Uncovered	0.2	0.27	-0.34	0.71	-0.84	0.53	-1.95	0.13	0.91	0.66	-0.33	2.26	-0.13	0.41	-0.84	0.8
<i>Dociopterus maroccanus</i>	Orthoptera	Uncovered	0.28	0.26	-0.24	0.82	-0.51	0.54	-1.62	0.49	-0.1	0.67	-1.43	1.19	-0.48	0.37	-1.25	0.24
<i>Ephippiger diurnus</i>	Orthoptera	Uncovered	0.29	0.28	-0.28	0.86	0.22	0.64	-1.01	1.53	0.81	0.81	-0.76	2.47	-0.32	0.39	-1.06	0.5
<i>Ephippiger provincialis</i>	Orthoptera	Vulnerable	0.23	0.28	-0.35	0.79	-0.19	0.67	-1.55	1.11	0.83	0.89	-0.9	2.59	-0.44	0.41	-1.26	0.39
<i>Euchorthippus chopardi</i>	Orthoptera	Uncovered	0.33	0.29	-0.22	0.91	0.76	0.61	-0.36	2.02	0.85	0.75	-0.61	2.42	-0.49	0.39	-1.29	0.28
<i>Euchorthippus declivus</i>	Orthoptera	Uncovered	0.15	0.27	-0.44	0.65	-0.49	0.56	-1.65	0.52	-0.39	0.73	-1.91	0.97	-0.52	0.39	-1.36	0.2
<i>Euchorthippus elegantulus</i>	Orthoptera	Uncovered	0.27	0.28	-0.3	0.84	0.04	0.65	-1.21	1.36	0.56	0.84	-1.03	2.28	-0.31	0.4	-1.06	0.53
<i>Eumodicogryllus bordigalensis</i>	Orthoptera	Uncovered	0.32	0.28	-0.22	0.89	0.43	0.63	-0.76	1.74	-0.04	0.84	-1.64	1.72	-0.52	0.4	-1.36	0.26
<i>Gryllus bimaculatus</i>	Orthoptera	Uncovered	0.34	0.29	-0.21	0.93	0.59	0.65	-0.65	1.89	0.53	0.81	-1.02	2.18	-0.38	0.4	-1.17	0.44
<i>Gryllus campestris</i>	Orthoptera	Uncovered	0.25	0.27	-0.3	0.8	-0.51	0.6	-1.7	0.72	-0.1	0.71	-1.48	1.34	-0.37	0.38	-1.14	0.4
<i>Gryllomorpha dalmatina</i>	Orthoptera	Uncovered	0.31	0.28	-0.23	0.89	0.65	0.58	-0.44	1.85	0.38	0.84	-1.31	2.01	-0.52	0.41	-1.38	0.27
<i>Gryllotalpa vineae</i>	Orthoptera	Vulnerable	0.21	0.28	-0.38	0.75	-0.19	0.62	-1.45	1.01	-0.04	0.84	-1.74	1.56	-0.45	0.4	-1.28	0.33
<i>Isophya pyrenaea</i>	Orthoptera	Uncovered	0.29	0.28	-0.26	0.84	0.08	0.6	-1.06	1.32	1.22	0.73	-0.2	2.72	-0.15	0.4	-0.87	0.7
<i>Leptophyes punctatissima</i>	Orthoptera	Uncovered	0.17	0.28	-0.42	0.71	-0.3	0.5	-1.3	0.65	1.08	0.71	-0.23	2.58	-0.28	0.38	-0.99	0.51
<i>Locusta cinerascens</i>	Orthoptera	Uncovered	0.35	0.29	-0.2	0.95	0.19	0.56	-0.9	1.34	0.38	0.78	-1.11	2.00	-0.36	0.38	-1.11	0.43
<i>Mogoplistes brunneus</i>	Orthoptera	Uncovered	0.31	0.28	-0.26	0.89	0.55	0.61	-0.63	1.82	0.39	0.9	-1.41	2.15	-0.48	0.41	-1.32	0.33
<i>Nemobius sylvestris</i>	Orthoptera	Uncovered	0.28	0.26	-0.24	0.81	-0.2	0.47	-1.14	0.71	0.79	0.66	-0.47	2.14	-0.5	0.38	-1.27	0.21
<i>Oecanthus pellucens</i>	Orthoptera	Uncovered	0.24	0.29	-0.35	0.81	-0.15	0.58	-1.26	1.06	0.52	0.82	-1.05	2.18	-0.33	0.39	-1.07	0.47
<i>Oedipoda caerulescens</i>	Orthoptera	Uncovered	0.28	0.28	-0.28	0.85	0.07	0.65	-1.2	1.36	0.63	0.84	-1.00	2.31	-0.31	0.4	-1.06	0.54
<i>Oedipoda charpentieri</i>	Orthoptera	Vulnerable	0.22	0.29	-0.37	0.77	-0.41	0.63	-1.72	0.78	-0.07	0.85	-1.75	1.57	-0.45	0.39	-1.27	0.33
<i>Oedaleus decorus</i>	Orthoptera	Uncovered	0.25	0.28	-0.31	0.8	-0.47	0.65	-1.73	0.88	0.88	0.81	-0.69	2.48	-0.29	0.39	-1.01	0.55
<i>Oedipoda germanica</i>	Orthoptera	Uncovered	0.3	0.28	-0.26	0.87	0.1	0.62	-1.13	1.36	0.85	0.85	-0.8	2.56	-0.31	0.39	-1.05	0.52
<i>Omocestus petraeus</i>	Orthoptera	Vulnerable	0.22	0.28	-0.36	0.76	-0.44	0.62	-1.74	0.7	0.05	0.81	-1.6	1.58	-0.53	0.39	-1.38	0.2
<i>Omocestus raymondi</i>	Orthoptera	Uncovered	0.37	0.27	-0.15	0.93	0.16	0.53	-0.84	1.26	1.15	0.7	-0.14	2.62	-0.22	0.39	-0.94	0.61
<i>Omocestus rufipes</i>	Orthoptera	Uncovered	0.26	0.28	-0.3	0.82	-0.01	0.64	-1.26	1.27	0.48	0.82	-1.11	2.14	-0.31	0.4	-1.06	0.53
<i>Paratettix meridionalis</i>	Orthoptera	Uncovered	0.32	0.27	-0.19	0.87	0.58	0.51	-0.36	1.64	-0.28	0.64	-1.6	0.92	-0.69	0.4	-1.61	0.01
<i>Pezotettix giornae</i>	Orthoptera	Uncovered	0.29	0.28	-0.26	0.86	0.03	0.72	-1.39	1.45	0.58	0.8	-0.95	2.23	-0.28	0.39	-1.04	0.55

<i>Phaneroptera nana</i>	Orthoptera	Uncovered	0.22	0.29	-0.39	0.78	-0.31	0.72	-1.72	1.1	0.61	0.88	-1.11	2.4	-0.38	0.4	-1.15	0.45
<i>Pholidoptera femorata</i>	Orthoptera	Uncovered	0.37	0.28	-0.15	0.96	0.47	0.57	-0.57	1.64	0.68	0.7	-0.62	2.16	-0.27	0.38	-1.00	0.53
<i>Platycleis affinis</i>	Orthoptera	Uncovered	0.34	0.28	-0.19	0.93	0.64	0.61	-0.47	1.94	-0.87	0.64	-2.17	0.34	-0.46	0.36	-1.2	0.24
<i>Platycleis albopunctata</i>	Orthoptera	Uncovered	0.18	0.28	-0.4	0.72	-0.72	0.54	-1.8	0.32	1.08	0.7	-0.24	2.52	-0.22	0.39	-0.94	0.65
<i>Platycleis falx</i>	Orthoptera	Vulnerable	0.29	0.28	-0.27	0.87	0.17	0.58	-0.94	1.37	-0.34	0.81	-2.02	1.21	-0.47	0.4	-1.3	0.3
<i>Platycleis intermedia</i>	Orthoptera	Uncovered	0.27	0.29	-0.29	0.84	0.25	0.64	-0.97	1.57	0.08	0.89	-1.62	1.91	-0.49	0.41	-1.34	0.32
<i>Platycleis sabulosa</i>	Orthoptera	Uncovered	0.29	0.29	-0.27	0.87	0.24	0.68	-1.09	1.61	0.17	0.93	-1.68	2.03	-0.43	0.41	-1.28	0.38
<i>Platycleis tessellata</i>	Orthoptera	Uncovered	0.27	0.28	-0.29	0.83	0.1	0.58	-1.01	1.3	-0.59	0.69	-1.94	0.77	-0.49	0.38	-1.27	0.22
<i>Prionotropis azami</i>	Orthoptera	Protected	0.22	0.28	-0.36	0.77	-0.26	0.6	-1.49	0.84	0.83	0.74	-0.63	2.33	-0.53	0.39	-1.37	0.21
<i>Pteronemobius heydenii</i>	Orthoptera	Uncovered	0.25	0.27	-0.3	0.78	0.34	0.52	-0.67	1.36	0.42	0.76	-1.11	1.89	-0.61	0.41	-1.52	0.12
<i>Pyrgomorpha conica</i>	Orthoptera	Uncovered	0.2	0.27	-0.36	0.71	-0.23	0.51	-1.22	0.78	0.38	0.63	-0.85	1.64	-0.51	0.37	-1.29	0.2
<i>Ramburiella hispanica</i>	Orthoptera	Uncovered	0.19	0.28	-0.4	0.73	-0.48	0.55	-1.56	0.65	0.68	0.7	-0.65	2.1	-0.28	0.38	-0.99	0.51
<i>Saga pedo</i>	Orthoptera	Protected	0.32	0.28	-0.23	0.91	0.2	0.61	-1.00	1.42	0.59	0.79	-0.92	2.21	-0.29	0.4	-1.04	0.55
<i>Sepiana sepium</i>	Orthoptera	Uncovered	0.22	0.28	-0.36	0.76	-0.44	0.61	-1.73	0.69	0.07	0.78	-1.53	1.56	-0.53	0.4	-1.39	0.2
<i>Sphingonotus caeruleus</i>	Orthoptera	Uncovered	0.31	0.28	-0.23	0.89	0.39	0.63	-0.8	1.68	-0.11	0.85	-1.73	1.61	-0.53	0.4	-1.36	0.23
<i>Stenobothrus fischeri</i>	Orthoptera	Vulnerable	0.19	0.28	-0.39	0.72	-0.58	0.59	-1.82	0.49	0.54	0.7	-0.85	1.89	-0.58	0.39	-1.42	0.14
<i>Tetrix ceperoi</i>	Orthoptera	Vulnerable	0.35	0.27	-0.17	0.92	-0.23	0.55	-1.35	0.82	0.04	0.75	-1.49	1.44	-0.56	0.39	-1.4	0.16
<i>Tetrix undulata</i>	Orthoptera	Uncovered	0.37	0.29	-0.17	0.96	0.1	0.65	-1.19	1.41	0.1	0.88	-1.66	1.81	-0.45	0.4	-1.28	0.34
<i>Tettigonia viridissima</i>	Orthoptera	Uncovered	0.28	0.28	-0.29	0.84	-0.01	0.62	-1.22	1.24	0.51	0.79	-1.02	2.12	-0.28	0.4	-1.02	0.6
<i>Thyreonotus corsicus</i>	Orthoptera	Uncovered	0.37	0.29	-0.17	0.98	0.81	0.65	-0.45	2.15	0.69	0.79	-0.85	2.28	-0.38	0.39	-1.14	0.41
<i>Tylopsis lilifolia</i>	Orthoptera	Uncovered	0.27	0.28	-0.28	0.84	0.06	0.62	-1.14	1.3	0.32	0.83	-1.25	2.05	-0.38	0.39	-1.14	0.41
<i>Uromenus rugosicollis</i>	Orthoptera	Uncovered	0.3	0.28	-0.24	0.86	0.37	0.53	-0.64	1.44	-0.37	0.79	-1.95	1.19	-0.51	0.39	-1.33	0.23
<i>Yersinella raymondii</i>	Orthoptera	Uncovered	0.19	0.28	-0.4	0.72	-0.65	0.6	-1.92	0.42	0.09	0.75	-1.43	1.53	-0.61	0.4	-1.48	0.12
<i>Anthocharis cardamines</i>	Papilionoideae	Uncovered	0.32	0.27	-0.19	0.88	0.03	0.49	-0.91	1.00	0.62	0.64	-0.62	1.88	-0.45	0.37	-1.21	0.27
<i>Anthocharis euphenoides</i>	Papilionoideae	Uncovered	0.19	0.28	-0.39	0.72	-0.52	0.55	-1.67	0.49	1.93	0.69	0.66	3.37	-0.15	0.4	-0.86	0.73
<i>Aporia crataegi</i>	Papilionoideae	Uncovered	0.27	0.28	-0.3	0.83	0.03	0.63	-1.2	1.32	0.58	0.82	-1.03	2.21	-0.3	0.4	-1.07	0.55
<i>Arethusana arethusana</i>	Papilionoideae	Uncovered	0.21	0.29	-0.39	0.76	-0.49	0.65	-1.81	0.78	0.54	0.82	-1.05	2.15	-0.49	0.4	-1.33	0.28
<i>Argynnis adippe</i>	Papilionoideae	Uncovered	0.21	0.28	-0.38	0.76	-0.42	0.6	-1.69	0.7	1.35	0.75	-0.04	2.91	-0.33	0.38	-1.06	0.45
<i>Argynnis aglaja</i>	Papilionoideae	Uncovered	0.23	0.29	-0.35	0.78	-0.31	0.68	-1.69	1.01	0.19	0.91	-1.62	1.98	-0.47	0.41	-1.32	0.34
<i>Argynnis niobe</i>	Papilionoideae	Uncovered	0.23	0.28	-0.35	0.79	-0.2	0.68	-1.58	1.13	0.82	0.9	-0.91	2.62	-0.44	0.41	-1.25	0.38
<i>Argynnis paphia</i>	Papilionoideae	Uncovered	0.12	0.29	-0.51	0.67	-0.68	0.67	-2.02	0.65	0.71	0.79	-0.8	2.34	-0.36	0.39	-1.13	0.46
<i>Aricia agestis</i>	Papilionoideae	Uncovered	0.27	0.28	-0.29	0.83	0.08	0.64	-1.14	1.39	0.11	0.83	-1.45	1.83	-0.41	0.39	-1.18	0.39
<i>Boloria dia</i>	Papilionoideae	Uncovered	0.31	0.28	-0.24	0.87	-0.35	0.64	-1.61	0.91	0.34	0.82	-1.27	1.97	-0.5	0.41	-1.35	0.28
<i>Boloria euphrosyne</i>	Papilionoideae	Uncovered	0.22	0.28	-0.36	0.76	-0.27	0.61	-1.53	0.87	0.83	0.76	-0.65	2.38	-0.52	0.39	-1.35	0.21
<i>Brenthis daphne</i>	Papilionoideae	Uncovered	0.22	0.28	-0.36	0.77	-0.26	0.63	-1.56	0.96	0.84	0.83	-0.76	2.52	-0.48	0.4	-1.3	0.29
<i>Brintesia circe</i>	Papilionoideae	Uncovered	0.28	0.28	-0.28	0.84	0.28	0.62	-0.9	1.57	-0.32	0.73	-1.75	1.13	-0.53	0.39	-1.34	0.2
<i>Callophrys rubi</i>	Papilionoideae	Uncovered	0.35	0.27	-0.17	0.92	0.32	0.56	-0.74	1.46	0.81	0.78	-0.65	2.43	-0.32	0.39	-1.06	0.48

<i>Carcharodus alceae</i>	Papilionoideae	Uncovered	0.29	0.28	-0.25	0.86	0.26	0.6	-0.87	1.5	-0.35	0.65	-1.68	0.89	-0.38	0.36	-1.1	0.34
<i>Celastrina argiolus</i>	Papilionoideae	Uncovered	0.29	0.28	-0.26	0.86	0.19	0.6	-0.98	1.39	0.35	0.79	-1.16	2.02	-0.29	0.39	-1.03	0.54
<i>Chazara briseis</i>	Papilionoideae	Vulnerable	0.28	0.28	-0.29	0.84	0.08	0.61	-1.15	1.25	1.11	0.79	-0.41	2.69	-0.33	0.39	-1.08	0.46
<i>Charaxes jasius</i>	Papilionoideae	Uncovered	0.27	0.28	-0.28	0.83	0.25	0.55	-0.82	1.35	1.47	0.79	-0.07	3.08	-0.2	0.39	-0.9	0.65
<i>Coenonympha arcania</i>	Papilionoideae	Uncovered	0.19	0.29	-0.41	0.75	-0.53	0.64	-1.84	0.7	0.56	0.81	-0.99	2.2	-0.52	0.41	-1.37	0.25
<i>Coenonympha dorus</i>	Papilionoideae	Uncovered	0.23	0.28	-0.35	0.78	0.25	0.52	-0.76	1.3	0.49	0.67	-0.83	1.85	-0.57	0.39	-1.39	0.16
<i>Coenonympha pamphilus</i>	Papilionoideae	Uncovered	0.29	0.27	-0.24	0.84	-0.34	0.52	-1.39	0.65	0.76	0.69	-0.54	2.18	-0.46	0.39	-1.24	0.32
<i>Colias alfacariensis</i>	Papilionoideae	Uncovered	0.23	0.27	-0.32	0.76	0.01	0.49	-0.95	0.97	1.57	0.72	0.25	3.1	-0.33	0.38	-1.07	0.48
<i>Colias crocea</i>	Papilionoideae	Uncovered	0.25	0.28	-0.31	0.8	-0.07	0.62	-1.27	1.19	0.6	0.82	-0.96	2.24	-0.3	0.4	-1.05	0.55
<i>Cupido minimus</i>	Papilionoideae	Uncovered	0.2	0.28	-0.38	0.74	-0.55	0.59	-1.78	0.53	1.58	0.69	0.28	2.98	-0.26	0.37	-0.95	0.51
<i>Erebia epistygne</i>	Papilionoideae	Vulnerable	0.22	0.28	-0.37	0.76	-0.41	0.65	-1.74	0.83	0.15	0.85	-1.57	1.79	-0.51	0.4	-1.35	0.25
<i>Erynnis tages</i>	Papilionoideae	Uncovered	0.2	0.28	-0.39	0.71	-0.55	0.58	-1.8	0.51	0.57	0.69	-0.81	1.89	-0.58	0.39	-1.42	0.13
<i>Euchloe crameri</i>	Papilionoideae	Uncovered	0.35	0.28	-0.19	0.92	0.17	0.65	-1.09	1.52	0.54	0.8	-0.98	2.18	-0.41	0.4	-1.2	0.39
<i>Glaucopsyche alexis</i>	Papilionoideae	Uncovered	0.34	0.28	-0.2	0.9	0.15	0.64	-1.09	1.46	0.48	0.81	-1.09	2.1	-0.52	0.4	-1.35	0.27
<i>Glaucopsyche melanops</i>	Papilionoideae	Uncovered	0.25	0.27	-0.29	0.79	0.19	0.51	-0.78	1.22	1.23	0.75	-0.15	2.78	-0.36	0.38	-1.11	0.44
<i>Gonepteryx cleopatra</i>	Papilionoideae	Uncovered	0.38	0.27	-0.12	0.93	0.24	0.49	-0.7	1.26	1.41	0.65	0.21	2.78	-0.19	0.39	-0.89	0.66
<i>Gonepteryx rhamni</i>	Papilionoideae	Uncovered	0.27	0.28	-0.29	0.83	0.13	0.56	-0.94	1.28	0.65	0.82	-0.93	2.34	-0.33	0.39	-1.08	0.47
<i>Hipparchia fagi</i>	Papilionoideae	Uncovered	0.25	0.28	-0.3	0.79	-0.02	0.5	-1.01	0.95	1.64	0.75	0.24	3.18	-0.26	0.38	-0.96	0.58
<i>Hipparchia fidia</i>	Papilionoideae	Uncovered	0.34	0.28	-0.2	0.94	0.63	0.57	-0.45	1.79	1.27	0.74	-0.16	2.76	-0.29	0.39	-1.02	0.53
<i>Hipparchia semele</i>	Papilionoideae	Uncovered	0.2	0.28	-0.38	0.74	-0.39	0.6	-1.56	0.82	0.53	0.75	-0.92	2.06	-0.4	0.4	-1.19	0.39
<i>Iphiclides podalirius</i>	Papilionoideae	Uncovered	0.28	0.28	-0.28	0.85	0.06	0.64	-1.17	1.37	0.47	0.8	-1.05	2.1	-0.28	0.4	-1.03	0.58
<i>Issoria lathonia</i>	Papilionoideae	Uncovered	0.42	0.28	-0.1	1.02	0.62	0.56	-0.42	1.77	0.11	0.81	-1.52	1.67	-0.5	0.4	-1.33	0.25
<i>Lampides baeticus</i>	Papilionoideae	Uncovered	0.3	0.29	-0.26	0.87	0.26	0.68	-1.04	1.64	0.26	0.92	-1.56	2.09	-0.46	0.41	-1.33	0.36
<i>Lasiommata megera</i>	Papilionoideae	Uncovered	0.26	0.28	-0.31	0.83	-0.01	0.65	-1.27	1.29	0.48	0.82	-1.09	2.15	-0.32	0.39	-1.06	0.52
<i>Leptotes pirithous</i>	Papilionoideae	Uncovered	0.35	0.28	-0.19	0.94	0.32	0.72	-1.07	1.75	0.48	0.83	-1.13	2.14	-0.35	0.4	-1.13	0.5
<i>Leptidea sinapis</i>	Papilionoideae	Uncovered	0.39	0.27	-0.12	0.98	0.26	0.51	-0.69	1.3	1.41	0.67	0.16	2.84	-0.2	0.39	-0.9	0.66
<i>Libythea celtis</i>	Papilionoideae	Uncovered	0.31	0.28	-0.24	0.88	0.56	0.63	-0.66	1.85	0.15	0.91	-1.63	1.96	-0.47	0.41	-1.32	0.31
<i>Limenitis reducta</i>	Papilionoideae	Uncovered	0.37	0.28	-0.16	0.95	0.44	0.6	-0.71	1.67	1.29	0.77	-0.21	2.86	-0.28	0.38	-1.00	0.54
<i>Lycaena alciphron</i>	Papilionoideae	Uncovered	0.25	0.28	-0.34	0.8	-0.1	0.67	-1.45	1.22	1.24	0.88	-0.49	3.01	-0.36	0.4	-1.13	0.46
<i>Lycaena phlaeas</i>	Papilionoideae	Uncovered	0.31	0.28	-0.25	0.89	0.43	0.6	-0.68	1.68	-0.5	0.67	-1.89	0.78	-0.68	0.39	-1.53	0.01
<i>Lysandra bellargus</i>	Papilionoideae	Uncovered	0.22	0.28	-0.34	0.77	-0.6	0.7	-1.97	0.82	0.41	0.81	-1.12	2.11	-0.35	0.4	-1.11	0.48
<i>Lysandra coridon</i>	Papilionoideae	Uncovered	0.25	0.28	-0.31	0.79	0.08	0.52	-0.93	1.13	0.54	0.8	-1.02	2.15	-0.54	0.4	-1.4	0.21
<i>Lysandra hispana</i>	Papilionoideae	Uncovered	0.26	0.26	-0.26	0.79	0.12	0.47	-0.8	1.07	0.78	0.64	-0.43	2.1	-0.24	0.38	-0.93	0.55
<i>Maniola jurtina</i>	Papilionoideae	Uncovered	0.27	0.28	-0.29	0.85	0.05	0.63	-1.16	1.35	0.39	0.85	-1.25	2.1	-0.35	0.4	-1.13	0.51
<i>Melitaea athalia</i>	Papilionoideae	Uncovered	0.2	0.28	-0.38	0.74	-0.54	0.6	-1.8	0.56	1.57	0.7	0.27	3.02	-0.26	0.38	-0.98	0.53
<i>Melitaea cinxia</i>	Papilionoideae	Uncovered	0.28	0.28	-0.28	0.85	0.07	0.64	-1.19	1.38	0.56	0.82	-1.03	2.2	-0.29	0.4	-1.04	0.55
<i>Melitaea didyma</i>	Papilionoideae	Uncovered	0.27	0.28	-0.3	0.85	0.02	0.64	-1.23	1.31	0.51	0.82	-1.06	2.18	-0.3	0.39	-1.06	0.53

<i>Melanargia galathea</i>	Papilionoideae	Uncovered	0.19	0.28	-0.41	0.71	-0.59	0.59	-1.83	0.5	0.55	0.72	-0.87	1.98	-0.57	0.39	-1.4	0.17
<i>Melanargia lachesis</i>	Papilionoideae	Uncovered	0.34	0.28	-0.18	0.92	0.5	0.59	-0.58	1.74	0.49	0.65	-0.76	1.78	-0.15	0.39	-0.85	0.72
<i>Melanargia occitanica</i>	Papilionoideae	Uncovered	0.25	0.26	-0.27	0.77	0.34	0.5	-0.6	1.38	0.69	0.6	-0.48	1.88	-0.4	0.36	-1.12	0.32
<i>Melitaea phoebe</i>	Papilionoideae	Uncovered	0.32	0.28	-0.23	0.88	0.4	0.65	-0.84	1.73	0.04	0.75	-1.4	1.62	-0.36	0.39	-1.11	0.44
<i>Nymphalis polychloros</i>	Papilionoideae	Uncovered	0.3	0.28	-0.24	0.87	0.58	0.6	-0.57	1.82	0.4	0.88	-1.35	2.13	-0.5	0.4	-1.36	0.27
<i>Ochlodes sylvanus</i>	Papilionoideae	Uncovered	0.17	0.29	-0.43	0.72	-0.57	0.7	-1.99	0.84	0.46	0.81	-1.1	2.11	-0.33	0.39	-1.08	0.47
<i>Papilio machaon</i>	Papilionoideae	Uncovered	0.28	0.28	-0.27	0.83	0.33	0.55	-0.69	1.5	-0.36	0.6	-1.57	0.8	-0.33	0.37	-1.04	0.43
<i>Pararge aegeria</i>	Papilionoideae	Uncovered	0.29	0.28	-0.25	0.86	0.24	0.62	-0.95	1.54	0.13	0.74	-1.29	1.65	-0.32	0.39	-1.06	0.49
<i>Pieris brassicae</i>	Papilionoideae	Uncovered	0.3	0.28	-0.25	0.87	0.2	0.63	-1.02	1.45	0.59	0.8	-0.97	2.2	-0.31	0.39	-1.04	0.53
<i>Pieris mammi</i>	Papilionoideae	Uncovered	0.26	0.29	-0.32	0.83	-0.01	0.68	-1.35	1.36	0.42	0.86	-1.24	2.17	-0.33	0.4	-1.09	0.5
<i>Pieris napi</i>	Papilionoideae	Uncovered	0.25	0.28	-0.29	0.8	-0.1	0.57	-1.2	1.08	-0.11	0.74	-1.51	1.47	-0.33	0.39	-1.08	0.48
<i>Pieris rapae</i>	Papilionoideae	Uncovered	0.26	0.28	-0.3	0.83	0.00	0.64	-1.25	1.26	0.49	0.83	-1.1	2.15	-0.32	0.4	-1.06	0.53
<i>Plebejus argus</i>	Papilionoideae	Uncovered	0.22	0.28	-0.34	0.76	-0.3	0.61	-1.5	0.91	-0.12	0.81	-1.7	1.52	-0.55	0.41	-1.41	0.21
<i>Plebejus idas</i>	Papilionoideae	Uncovered	0.23	0.29	-0.36	0.8	-0.32	0.68	-1.7	1.02	0.19	0.9	-1.61	1.96	-0.47	0.41	-1.33	0.32
<i>Polygonia c-album</i>	Papilionoideae	Uncovered	0.25	0.28	-0.33	0.8	0.06	0.55	-1.03	1.17	0.65	0.83	-0.97	2.32	-0.38	0.39	-1.16	0.41
<i>Polyommatus daphnis</i>	Papilionoideae	Vulnerable	0.23	0.29	-0.36	0.78	-0.4	0.64	-1.71	0.8	0.09	0.85	-1.63	1.72	-0.51	0.4	-1.36	0.26
<i>Polyommatus dolus</i>	Papilionoideae	Vulnerable	0.22	0.29	-0.37	0.77	-0.25	0.63	-1.55	0.94	0.84	0.81	-0.72	2.49	-0.49	0.4	-1.31	0.26
<i>Polyommatus escheri</i>	Papilionoideae	Uncovered	0.2	0.28	-0.38	0.73	-0.6	0.57	-1.8	0.44	1.52	0.73	0.21	3.03	-0.3	0.39	-1.04	0.52
<i>Polyommatus icarus</i>	Papilionoideae	Uncovered	0.26	0.29	-0.3	0.83	-0.01	0.65	-1.27	1.27	0.48	0.84	-1.14	2.2	-0.31	0.4	-1.07	0.53
<i>Polyommatus thersites</i>	Papilionoideae	Uncovered	0.23	0.29	-0.35	0.79	-0.2	0.67	-1.54	1.11	0.81	0.89	-0.93	2.58	-0.43	0.41	-1.25	0.38
<i>Pontia daplidice</i>	Papilionoideae	Uncovered	0.33	0.27	-0.2	0.89	0.61	0.56	-0.38	1.81	-0.2	0.62	-1.45	0.99	-0.53	0.37	-1.3	0.16
<i>Pseudophilotes baton</i>	Papilionoideae	Uncovered	0.21	0.27	-0.34	0.73	-0.52	0.49	-1.54	0.42	1.15	0.68	-0.11	2.55	-0.24	0.39	-0.96	0.6
<i>Pyronia bathseba</i>	Papilionoideae	Uncovered	0.41	0.28	-0.11	1.01	0.1	0.51	-0.86	1.16	0.79	0.65	-0.44	2.11	-0.21	0.37	-0.89	0.59
<i>Pyrgus bellieri</i>	Papilionoideae	Uncovered	0.24	0.29	-0.35	0.8	-0.22	0.67	-1.56	1.08	0.83	0.89	-0.91	2.61	-0.44	0.4	-1.26	0.36
<i>Pyronia cecilia</i>	Papilionoideae	Uncovered	0.32	0.28	-0.22	0.91	0.6	0.59	-0.47	1.84	-0.31	0.62	-1.55	0.86	-0.42	0.36	-1.14	0.28
<i>Pyrgus malvoides</i>	Papilionoideae	Uncovered	0.26	0.28	-0.29	0.82	-0.04	0.7	-1.39	1.38	0.1	0.84	-1.5	1.83	-0.45	0.4	-1.27	0.36
<i>Pyrgus serratulae</i>	Papilionoideae	Uncovered	0.23	0.29	-0.36	0.79	-0.23	0.66	-1.58	1.05	0.83	0.85	-0.83	2.57	-0.47	0.41	-1.3	0.36
<i>Pyrgus sidae</i>	Papilionoideae	Vulnerable	0.24	0.28	-0.32	0.8	-0.29	0.61	-1.57	0.86	1.12	0.76	-0.34	2.67	-0.28	0.38	-1.01	0.52
<i>Pyronia tithonus</i>	Papilionoideae	Uncovered	0.23	0.28	-0.35	0.78	-0.4	0.64	-1.73	0.81	0.11	0.84	-1.56	1.71	-0.5	0.4	-1.36	0.26
<i>Quercusia quercus</i>	Papilionoideae	Uncovered	0.21	0.29	-0.37	0.76	-0.39	0.64	-1.71	0.84	1.34	0.8	-0.19	3.00	-0.31	0.39	-1.05	0.5
<i>Satyrrium esculi</i>	Papilionoideae	Uncovered	0.22	0.27	-0.33	0.75	0.28	0.54	-0.77	1.38	1.38	0.73	0.01	2.88	-0.26	0.39	-0.99	0.56
<i>Satyrus ferula</i>	Papilionoideae	Uncovered	0.22	0.28	-0.37	0.76	-0.42	0.63	-1.71	0.76	0.11	0.83	-1.55	1.69	-0.52	0.4	-1.37	0.25
<i>Satyrrium ilicis</i>	Papilionoideae	Uncovered	0.22	0.28	-0.34	0.76	-0.15	0.51	-1.17	0.86	1.58	0.77	0.11	3.14	-0.28	0.38	-0.99	0.52
<i>Satyrrium spini</i>	Papilionoideae	Uncovered	0.18	0.28	-0.4	0.7	-0.64	0.55	-1.79	0.38	1.02	0.68	-0.25	2.45	-0.3	0.38	-1.04	0.49
<i>Spialia sertorius</i>	Papilionoideae	Uncovered	0.29	0.28	-0.27	0.85	0.14	0.63	-1.11	1.43	0.77	0.82	-0.8	2.4	-0.26	0.4	-1.00	0.61
<i>Thymelicus acteon</i>	Papilionoideae	Uncovered	0.27	0.28	-0.29	0.84	0.17	0.63	-1.04	1.46	0.00	0.85	-1.58	1.75	-0.45	0.4	-1.26	0.36
<i>Thymelicus lineolus</i>	Papilionoideae	Uncovered	0.24	0.29	-0.33	0.8	-0.25	0.67	-1.62	1.06	1.11	0.86	-0.56	2.87	-0.25	0.4	-0.99	0.6

<i>Thymelicus sylvestris</i>	Papilionoideae	Uncovered	0.31	0.28	-0.24	0.88	-0.12	0.64	-1.37	1.18	0.19	0.79	-1.3	1.85	-0.32	0.38	-1.06	0.48
<i>Vanessa atalanta</i>	Papilionoideae	Uncovered	0.28	0.28	-0.27	0.84	0.21	0.58	-0.92	1.41	-0.3	0.71	-1.7	1.12	-0.37	0.38	-1.11	0.41
<i>Vanessa cardui</i>	Papilionoideae	Uncovered	0.28	0.29	-0.28	0.86	0.18	0.66	-1.1	1.51	0.38	0.8	-1.17	2.01	-0.31	0.4	-1.08	0.55
<i>Zerynthia polyxena</i>	Papilionoideae	Protected	0.37	0.28	-0.17	0.95	0.8	0.61	-0.31	2.06	-0.01	0.7	-1.38	1.38	-0.42	0.38	-1.2	0.34
<i>Zerynthia rumina</i>	Papilionoideae	Protected	0.26	0.27	-0.27	0.78	0.41	0.49	-0.53	1.42	0.9	0.61	-0.3	2.12	-0.54	0.37	-1.32	0.14
<i>Zygaena ephialtes</i>	Zygaenidae	Uncovered	0.23	0.28	-0.35	0.77	-0.44	0.61	-1.72	0.69	1.48	0.74	0.08	2.98	-0.14	0.39	-0.84	0.71
<i>Zygaena erythrus</i>	Zygaenidae	Uncovered	0.18	0.28	-0.42	0.71	-0.6	0.68	-1.95	0.75	0.36	0.75	-1.08	1.89	-0.28	0.39	-1.02	0.53
<i>Zygaena fausta</i>	Zygaenidae	Uncovered	0.28	0.27	-0.26	0.84	0.44	0.54	-0.59	1.55	1.22	0.7	-0.09	2.68	-0.23	0.39	-0.93	0.6
<i>Zygaena filipendulae</i>	Zygaenidae	Uncovered	0.39	0.27	-0.12	0.94	-0.13	0.53	-1.15	0.97	0.59	0.64	-0.66	1.88	-0.15	0.4	-0.85	0.74
<i>Zygaena lavandulae</i>	Zygaenidae	Uncovered	0.26	0.27	-0.28	0.79	0.1	0.5	-0.87	1.1	1.59	0.71	0.27	3.1	-0.25	0.38	-0.97	0.59
<i>Zygaena occitanica</i>	Zygaenidae	Uncovered	0.33	0.28	-0.22	0.9	0.02	0.66	-1.26	1.34	1.16	0.81	-0.44	2.8	-0.21	0.4	-0.94	0.67
<i>Zygaena rhadamanthus</i>	Zygaenidae	Protected	0.2	0.28	-0.36	0.74	-0.35	0.58	-1.55	0.74	1.28	0.75	-0.13	2.87	-0.49	0.4	-1.32	0.31
<i>Zygaena sarpedon</i>	Zygaenidae	Uncovered	0.3	0.28	-0.26	0.87	0.17	0.61	-0.99	1.42	-0.11	0.9	-1.83	1.71	-0.5	0.41	-1.36	0.3
<i>Zygaena transalpina</i>	Zygaenidae	Uncovered	0.24	0.29	-0.35	0.8	-0.25	0.68	-1.64	1.08	1.12	0.85	-0.54	2.83	-0.25	0.39	-0.98	0.59

Supplementary materials S3.9. Posterior estimates for the effect of visit covariates on observed insect species as estimated under the MSOM (with mean, standard deviation, CI_{95%}): b1 – linear effect of the visit date; b2 – quadratic effect of the visit date; b3 – linear effect of the visit hour; b4 – linear effect of the visit length. Grey cells indicate species with confidence interval not containing zero (considered as indicative of significant response to the parameter).

Scientific name	Group	Conservation status	Linear date (b1)				Quadratic date (b2)				Hour (b3)				Length (b4)			
			Mean	SD	CI 2.5%	CI 97.5%	Mean	SD	CI 2.5%	CI 97.5%	Mean	SD	CI 2.5%	CI 97.5%	Mean	SD	CI 2.5%	CI 97.5%
<i>Cicada orni</i>	Cicada	Uncovered	1,96	0,5	1,1	2,88	0,07	0,3	-0,5	0,61	-1,09	0,28	-1,67	-0,55	-0,02	0,18	-0,38	0,33
<i>Cicadatra atra</i>	Cicada	Uncovered	1,39	0,5	0,38	2,49	-2,17	0,7	-3,5	-0,98	-0,72	0,29	-1,3	-0,18	-0,01	0,19	-0,39	0,37
<i>Lyristes plebejus</i>	Cicada	Uncovered	1,53	0,4	0,77	2,34	0,24	0,2	-0,19	0,68	-0,6	0,26	-1,12	-0,1	-0,01	0,17	-0,35	0,33
<i>Tettigettna argentata</i>	Cicada	Uncovered	2,52	0,8	1,15	4,07	-2,12	0,8	-3,73	-0,67	-1,09	0,34	-1,79	-0,46	0,02	0,19	-0,36	0,41
<i>Tettigettna pygmea</i>	Cicada	Uncovered	0,25	0,6	-0,8	1,33	-1,24	0,5	-2,33	-0,31	-0,72	0,32	-1,36	-0,11	-0,01	0,19	-0,38	0,36
<i>Tibicina garricola</i>	Cicada	Uncovered	1,34	0,9	-0,42	3,3	-1,49	0,8	-3,16	-0,04	-0,4	0,39	-1,18	0,34	0,07	0,22	-0,35	0,5
<i>Tibicina haematodes</i>	Cicada	Uncovered	0,13	1	-1,8	2,04	-1,83	0,8	-3,54	-0,38	-0,73	0,45	-1,65	0,14	0,14	0,21	-0,27	0,58
<i>Tibicina tomentosa</i>	Cicada	Vulnerable	0,85	1,7	-2,24	4,3	-1,68	1	-3,59	0,13	-0,09	0,49	-1,06	0,88	-0,02	0,23	-0,48	0,43
<i>Aeshna affinis</i>	Odonata	Uncovered	0,44	0,9	-1,31	2,31	-1,03	0,7	-2,49	0,21	-0,34	0,42	-1,16	0,47	-0,07	0,21	-0,51	0,33
<i>Aeshna cyanea</i>	Odonata	Uncovered	1,39	1,3	-1,1	4,11	-1,73	0,9	-3,65	-0,03	-0,5	0,48	-1,45	0,42	0,08	0,22	-0,36	0,52
<i>Aeshna isocoles</i>	Odonata	Uncovered	1,9	1,4	-0,75	4,87	-1,34	0,9	-3,19	0,42	-0,82	0,51	-1,84	0,19	0,04	0,23	-0,4	0,5
<i>Aeshna mixta</i>	Odonata	Uncovered	0,1	1,4	-2,67	2,79	-2,04	0,9	-3,93	-0,44	-0,56	0,5	-1,55	0,41	-0,03	0,22	-0,49	0,4
<i>Anax imperator</i>	Odonata	Uncovered	-0,94	0,5	-1,92	-0,02	-1,34	0,4	-2,06	-0,7	-0,72	0,32	-1,36	-0,11	0,01	0,18	-0,36	0,36
<i>Anax parthenope</i>	Odonata	Uncovered	-0,45	0,8	-1,95	1,02	-1,37	0,6	-2,56	-0,36	-0,81	0,42	-1,65	-0,02	0,03	0,2	-0,38	0,43
<i>Boyeria irene</i>	Odonata	Uncovered	0,97	0,9	-0,7	2,69	0,09	0,4	-0,78	0,96	-0,54	0,45	-1,42	0,34	-0,13	0,21	-0,56	0,27
<i>Brachytron pratense</i>	Odonata	Vulnerable	-1,12	1,4	-3,94	1,7	-0,04	0,6	-1,22	1,19	-0,36	0,54	-1,41	0,72	0	0,23	-0,46	0,46
<i>Calopteryx haemorrhoidalis</i>	Odonata	Uncovered	-1,15	0,8	-2,78	0,4	-1,24	0,4	-2,12	-0,42	-0,27	0,45	-1,14	0,61	-0,22	0,21	-0,66	0,17
<i>Calopteryx xanthostoma</i>	Odonata	Uncovered	-2,02	0,7	-3,54	-0,63	-1,78	0,5	-2,74	-0,94	-0,82	0,43	-1,66	-0,01	-0,09	0,2	-0,51	0,3
<i>Ceragrion tenellum</i>	Odonata	Uncovered	-0,25	0,8	-1,87	1,4	-2,08	0,7	-3,54	-0,81	-0,84	0,38	-1,6	-0,12	-0,07	0,21	-0,49	0,32
<i>Chalcolestes viridis</i>	Odonata	Uncovered	0	1	-1,85	2,05	-2,07	0,8	-3,77	-0,54	-0,49	0,39	-1,27	0,26	-0,22	0,22	-0,68	0,18
<i>Coenagrion caerulescens</i>	Odonata	Vulnerable	1,39	1,4	-1,36	4,3	-1,77	0,9	-3,67	-0,06	-0,84	0,51	-1,84	0,15	0,06	0,22	-0,38	0,5
<i>Coenagrion mercuriale</i>	Odonata	Protected	-1,61	1	-3,56	0,17	-0,66	0,4	-1,5	0,11	-0,25	0,46	-1,16	0,66	-0,27	0,21	-0,72	0,12
<i>Coenagrion puella</i>	Odonata	Uncovered	-0,6	0,9	-2,44	1,2	-1,11	0,6	-2,34	-0,07	-0,58	0,43	-1,46	0,24	0,07	0,21	-0,34	0,48
<i>Cordulegaster boltonii</i>	Odonata	Uncovered	0,84	1,5	-1,99	3,8	-1,73	0,9	-3,63	-0,03	-0,64	0,51	-1,66	0,34	0,03	0,22	-0,41	0,48
<i>Crocothemis erythraea</i>	Odonata	Uncovered	-0,46	0,7	-1,82	0,89	-1,48	0,5	-2,47	-0,6	-0,8	0,42	-1,63	0	0,02	0,21	-0,39	0,43
<i>Enallagma cyathigerum</i>	Odonata	Uncovered	-0,7	1,2	-3,13	1,69	-0,45	0,5	-1,5	0,59	-0,47	0,48	-1,42	0,48	0,22	0,21	-0,18	0,65
<i>Erythromma lindenii</i>	Odonata	Uncovered	-1,96	0,9	-3,81	-0,29	-1,26	0,4	-2,16	-0,46	-0,53	0,46	-1,43	0,37	-0,02	0,2	-0,41	0,37
<i>Gomphus graslinii</i>	Odonata	Protected	0,47	1	-1,51	2,46	-1,97	0,8	-3,71	-0,54	-0,67	0,49	-1,63	0,28	-0,06	0,22	-0,5	0,36
<i>Gomphus pulchellus</i>	Odonata	Uncovered	-2,84	1	-4,92	-0,98	-1,24	0,5	-2,15	-0,41	-0,65	0,47	-1,6	0,26	-0,01	0,19	-0,39	0,37
<i>Gomphus simillimus</i>	Odonata	Uncovered	-1,93	1	-4,07	-0,03	-1,22	0,5	-2,33	-0,22	-0,72	0,5	-1,72	0,25	0,05	0,22	-0,37	0,48
<i>Hemianax ephippiger</i>	Odonata	Uncovered	0,1	1	-1,92	2,01	0,18	0,5	-0,72	1,09	-0,71	0,48	-1,68	0,2	-0,02	0,21	-0,44	0,39
<i>Ischnura elegans</i>	Odonata	Uncovered	-1,14	0,6	-2,26	-0,11	-0,45	0,3	-0,95	0,03	-0,48	0,34	-1,15	0,16	0,02	0,17	-0,32	0,35
<i>Ischnura pumilio</i>	Odonata	Vulnerable	-2,26	1,3	-4,99	0,26	-1,35	0,7	-2,72	-0,09	-0,56	0,53	-1,62	0,46	0,04	0,22	-0,39	0,48
<i>Lestes barbarus</i>	Odonata	Uncovered	0,03	1,6	-2,93	3,15	-1,6	0,9	-3,39	0,07	-0,11	0,49	-1,06	0,86	-0,01	0,23	-0,48	0,43
<i>Lestes virens</i>	Odonata	Uncovered	-1,27	1,4	-4,06	1,5	-1,6	0,8	-3,32	-0,03	-0,44	0,52	-1,48	0,55	0	0,22	-0,45	0,43

<i>Libellula depressa</i>	Odonata	Uncovered	-2,1	0,9	-3,92	-0,51	-1,25	0,5	-2,17	-0,42	-0,42	0,44	-1,3	0,44	-0,04	0,2	-0,45	0,34
<i>Libellula fulva</i>	Odonata	Uncovered	-1,69	0,8	-3,18	-0,27	-1,25	0,4	-2,11	-0,47	-0,28	0,37	-1,01	0,43	-0,15	0,2	-0,56	0,22
<i>Macromia splendens</i>	Odonata	Protected	1,55	1,3	-0,94	4,19	-2	0,9	-3,9	-0,32	-0,77	0,48	-1,73	0,17	0,01	0,22	-0,43	0,44
<i>Onychogomphus forcipatus</i>	Odonata	Uncovered	-1,89	0,8	-3,53	-0,35	-2,54	0,6	-3,87	-1,41	-0,94	0,44	-1,83	-0,1	-0,04	0,21	-0,46	0,36
<i>Onychogomphus uncatulus</i>	Odonata	Vulnerable	-1,15	1	-3,14	0,8	-1,37	0,6	-2,62	-0,3	-0,46	0,47	-1,38	0,46	-0,08	0,21	-0,51	0,33
<i>Orthetrum albistylum</i>	Odonata	Uncovered	-1,05	1,5	-3,91	1,83	-1,72	0,9	-3,49	-0,14	-0,52	0,52	-1,54	0,5	0,03	0,22	-0,42	0,47
<i>Orthetrum brunneum</i>	Odonata	Uncovered	0,39	0,8	-1,26	2,05	-1,72	0,7	-3,22	-0,41	-0,79	0,38	-1,56	-0,05	-0,12	0,21	-0,55	0,28
<i>Orthetrum cancellatum</i>	Odonata	Uncovered	-0,87	0,6	-2,04	0,2	-0,59	0,3	-1,19	-0,05	-0,45	0,35	-1,13	0,23	-0,11	0,19	-0,49	0,25
<i>Orthetrum coerulescens</i>	Odonata	Uncovered	0,66	0,8	-0,77	2,16	-1,74	0,7	-3,22	-0,46	-0,71	0,37	-1,45	0	0,01	0,2	-0,39	0,41
<i>Oxygastra curtisii</i>	Odonata	Protected	-1,04	0,9	-2,85	0,69	-2,03	0,6	-3,32	-0,9	-0,63	0,48	-1,57	0,3	-0,06	0,22	-0,5	0,36
<i>Platynemis acutipennis</i>	Odonata	Uncovered	-2,22	0,6	-3,52	-1,05	-1,08	0,3	-1,72	-0,5	-0,57	0,38	-1,33	0,15	-0,39	0,2	-0,81	-0,02
<i>Platynemis latipes</i>	Odonata	Uncovered	-0,43	0,9	-2,15	1,22	-2,64	0,8	-4,29	-1,24	-0,95	0,46	-1,87	-0,06	-0,05	0,21	-0,47	0,35
<i>Pyrhosoma nymphula</i>	Odonata	Uncovered	-2,43	1	-4,45	-0,64	-0,65	0,4	-1,49	0,12	-0,36	0,46	-1,26	0,56	-0,04	0,2	-0,44	0,34
<i>Sympecma fusca</i>	Odonata	Uncovered	0,02	1	-2,05	2,01	-0,1	0,5	-1,11	0,85	-0,83	0,48	-1,81	0,09	0,16	0,22	-0,26	0,6
<i>Sympetrum fonscolombii</i>	Odonata	Uncovered	0,12	0,5	-0,77	0,99	0,04	0,2	-0,4	0,47	-0,15	0,29	-0,72	0,42	0,08	0,17	-0,25	0,43
<i>Sympetrum meridionale</i>	Odonata	Uncovered	0,04	0,7	-1,43	1,48	-1,62	0,7	-3,1	-0,41	-0,98	0,43	-1,85	-0,18	-0,08	0,22	-0,53	0,35
<i>Sympetrum pedemontanum</i>	Odonata	Vulnerable	1,23	1,4	-1,46	4,13	-1,44	0,9	-3,31	0,27	-0,6	0,51	-1,62	0,39	0,02	0,22	-0,43	0,46
<i>Sympetrum striolatum</i>	Odonata	Uncovered	-0,85	0,6	-2,16	0,35	-2,3	0,7	-3,67	-1,1	-0,87	0,37	-1,62	-0,17	-0,05	0,2	-0,44	0,33
<i>Trithemis annulata</i>	Odonata	Uncovered	-0,34	1	-2,29	1,56	-2,34	0,8	-3,99	-0,91	-0,61	0,49	-1,57	0,33	0	0,21	-0,43	0,42
<i>Acrotylus fischeri</i>	Orthoptera	Uncovered	-3,45	1	-5,42	-1,7	-1,37	0,4	-2,26	-0,56	-0,82	0,47	-1,76	0,09	0,2	0,21	-0,19	0,62
<i>Acrotylus insubricus</i>	Orthoptera	Uncovered	-3,83	1	-5,86	-2,03	-1,11	0,4	-1,84	-0,43	-0,25	0,42	-1,09	0,58	0,12	0,18	-0,23	0,49
<i>Aiolopus puissanti</i>	Orthoptera	Uncovered	-0,21	0,7	-1,66	1,27	-2,11	0,7	-3,63	-0,81	-0,53	0,36	-1,26	0,15	-0,07	0,2	-0,48	0,32
<i>Aiolopus strepens</i>	Orthoptera	Uncovered	-1,31	0,7	-2,84	0	0,07	0,3	-0,52	0,65	-0,69	0,41	-1,51	0,11	0,08	0,18	-0,26	0,43
<i>Amedegnatiana vicheti</i>	Orthoptera	Vulnerable	-1,32	1,5	-4,24	1,56	-1,84	0,8	-3,53	-0,29	-0,66	0,5	-1,66	0,3	0,03	0,23	-0,41	0,48
<i>Anacridium aegyptium</i>	Orthoptera	Uncovered	-1,11	0,5	-2,06	-0,26	-0,13	0,2	-0,57	0,28	-0,62	0,32	-1,28	-0,01	0,07	0,17	-0,26	0,42
<i>Anaxiulus sorzezensis</i>	Orthoptera	Vulnerable	1,06	1,5	-1,76	4,06	-1,47	0,9	-3,33	0,19	-0,08	0,49	-1,03	0,88	-0,05	0,22	-0,51	0,37
<i>Arachnocephalus vestitus</i>	Orthoptera	Uncovered	3,54	1,1	1,68	5,88	-0,97	0,8	-2,62	0,48	-1,19	0,4	-2,02	-0,43	0,01	0,21	-0,41	0,42
<i>Arcyptera kheili</i>	Orthoptera	Vulnerable	-2,5	1,4	-5,35	-0,04	-0,93	0,9	-2,68	0,86	-0,8	0,55	-1,9	0,26	0,1	0,23	-0,33	0,57
<i>Barbitistes fischeri</i>	Orthoptera	Uncovered	-0,33	1,2	-2,66	2,01	-2,11	0,9	-3,95	-0,51	-0,28	0,48	-1,21	0,66	0,1	0,22	-0,32	0,54
<i>Calliptamus barbarus</i>	Orthoptera	Uncovered	2,62	0,6	1,52	3,88	-1,51	0,6	-2,81	-0,3	-0,83	0,27	-1,38	-0,31	-0,02	0,18	-0,37	0,34
<i>Calliptamus italicus</i>	Orthoptera	Uncovered	2,06	0,8	0,67	3,7	-2,12	0,8	-3,76	-0,67	-0,44	0,31	-1,06	0,15	-0,1	0,2	-0,51	0,27
<i>Calliptamus wattenwylanus</i>	Orthoptera	Uncovered	2,41	0,7	1,12	3,83	-3,06	0,8	-4,62	-1,65	-0,49	0,3	-1,09	0,09	0,07	0,2	-0,33	0,46
<i>Chorthippus binotatus</i>	Orthoptera	Vulnerable	-0,17	1,5	-3,12	2,81	-1,91	0,9	-3,78	-0,25	-0,61	0,52	-1,65	0,41	0,08	0,22	-0,35	0,52
<i>Chorthippus brunneus</i>	Orthoptera	Uncovered	-2,16	0,5	-3,14	-1,28	-2,34	0,4	-3,11	-1,65	-0,45	0,27	-0,99	0,06	-0,02	0,17	-0,37	0,32
<i>Chorthippus vagans</i>	Orthoptera	Uncovered	2,13	0,7	0,89	3,55	-0,84	0,6	-2,12	0,29	-1,06	0,36	-1,79	-0,39	0,09	0,19	-0,28	0,48
<i>Conocephalus fuscus</i>	Orthoptera	Uncovered	0,94	1,3	-1,43	3,56	-1,64	0,9	-3,47	-0,03	-0,56	0,5	-1,59	0,41	0	0,22	-0,45	0,44
<i>Decticus albifrons</i>	Orthoptera	Uncovered	1,52	0,6	0,43	2,77	-1,41	0,5	-2,46	-0,46	-0,06	0,39	-0,81	0,73	0,1	0,21	-0,29	0,52
<i>Decticus verrucivorus</i>	Orthoptera	Vulnerable	-0,57	1,3	-3,02	1,97	-1,8	0,8	-3,46	-0,34	-0,36	0,5	-1,33	0,62	-0,02	0,22	-0,47	0,41
<i>monspelliensis</i>	Orthoptera	Uncovered	-1,9	1,3	-4,62	0,47	-0,06	0,6	-1,23	1,11	-0,47	0,54	-1,52	0,59	0,02	0,22	-0,42	0,47
<i>Depressotetrix depressa</i>	Orthoptera	Uncovered	3,62	1,1	1,55	6,01	-1,21	0,9	-3,03	0,5	-1,03	0,42	-1,87	-0,21	0	0,21	-0,42	0,42
<i>Doclostaurus genei</i>	Orthoptera	Vulnerable	3,26	0,9	1,68	5,07	-2,03	0,9	-3,76	-0,42	-0,59	0,33	-1,24	0,04	0,06	0,2	-0,33	0,46
<i>Doclostaurus jagoi</i>	Orthoptera	Uncovered	0,42	0,8	-1,13	1,98	-1,36	0,7	-2,77	-0,15	-0,48	0,42	-1,32	0,33	-0,03	0,21	-0,45	0,37
<i>Doclostaurus maroccanus</i>	Orthoptera	Uncovered	1,76	0,5	0,92	2,69	-0,75	0,5	-1,74	0,08	0,31	0,29	-0,24	0,9	0	0,18	-0,35	0,36
<i>Ephippiger diurnus</i>	Orthoptera	Uncovered	0,83	1,5	-1,88	3,76	-1,71	0,9	-3,63	0,02	-0,56	0,51	-1,58	0,45	0,04	0,22	-0,4	0,48
<i>Ephippiger provincialis</i>	Orthoptera	Vulnerable	2,01	0,8	0,55	3,74	-1,33	0,7	-2,81	-0,05	-0,22	0,32	-0,86	0,4	0,05	0,2	-0,34	0,46
<i>Euchorthippus chopardi</i>	Orthoptera	Uncovered																

<i>Lysandra bellargus</i>	Papilionoidea	Uncovered	-0,62	0,8	-2,1	0,79	-1,29	0,6	-2,48	-0,28	-0,69	0,42	-1,55	0,12	0,12	0,2	-0,27	0,52
<i>Lysandra coridon</i>	Papilionoidea	Uncovered	3,1	1,2	0,86	5,68	-1,29	0,9	-3,11	0,41	-0,91	0,44	-1,79	-0,08	0,04	0,22	-0,38	0,48
<i>Lysandra hispana</i>	Papilionoidea	Uncovered	-3,09	0,7	-4,58	-1,74	-1,63	0,4	-2,36	-0,97	-0,48	0,37	-1,23	0,23	-0,09	0,19	-0,47	0,28
<i>Maniola jurtina</i>	Papilionoidea	Uncovered	-2,93	0,6	-4,14	-1,81	-2,81	0,5	-3,8	-1,94	-0,34	0,3	-0,95	0,24	-0,01	0,18	-0,36	0,35
<i>Melanargia galathea</i>	Papilionoidea	Uncovered	-0,59	1,2	-2,89	1,69	-2,38	0,9	-4,17	-0,8	-0,95	0,51	-1,98	0,02	0,18	0,23	-0,25	0,65
<i>Melanargia lachesis</i>	Papilionoidea	Uncovered	-0,31	0,5	-1,36	0,72	-3,09	0,7	-4,52	-1,86	-0,85	0,29	-1,43	-0,3	0,07	0,19	-0,31	0,45
<i>Melanargia occitanica</i>	Papilionoidea	Uncovered	-5,24	1	-7,39	-3,36	-2,35	0,5	-3,3	-1,52	-0,5	0,44	-1,36	0,35	-0,05	0,19	-0,43	0,32
<i>Melitaea athalia</i>	Papilionoidea	Uncovered	-1,18	0,9	-2,95	0,51	-1,83	0,7	-3,31	-0,5	-0,91	0,51	-1,92	0,07	0,11	0,21	-0,31	0,55
<i>Melitaea cinxia</i>	Papilionoidea	Uncovered	-1,18	0,5	-2,1	-0,32	-0,3	0,2	-0,71	0,11	-0,51	0,31	-1,14	0,1	0,01	0,16	-0,3	0,32
<i>Melitaea didyma</i>	Papilionoidea	Uncovered	-1,32	0,5	-2,23	-0,46	-1,93	0,4	-2,74	-1,2	-0,58	0,29	-1,16	-0,02	0,17	0,18	-0,18	0,52
<i>Melitaea phoebe</i>	Papilionoidea	Uncovered	-1,32	0,6	-2,52	-0,22	-0,73	0,3	-1,33	-0,19	-0,48	0,37	-1,23	0,21	0,04	0,18	-0,32	0,4
<i>Nymphalis polychloros</i>	Papilionoidea	Uncovered	-1,04	1,4	-3,82	1,46	-0,2	0,6	-1,4	0,94	-0,43	0,53	-1,47	0,6	0,03	0,23	-0,4	0,48
<i>Ochlodes sylvanus</i>	Papilionoidea	Uncovered	-1,94	1,1	-4,11	0,05	-2,11	0,7	-3,67	-0,78	-0,74	0,48	-1,7	0,18	0,03	0,21	-0,38	0,47
<i>Papilio machaon</i>	Papilionoidea	Uncovered	-1,73	0,5	-2,74	-0,79	-0,62	0,2	-1,08	-0,19	-0,72	0,32	-1,37	-0,11	-0,05	0,17	-0,38	0,28
<i>Pararge aegeria</i>	Papilionoidea	Uncovered	-1,35	0,4	-2,23	-0,52	-0,24	0,2	-0,67	0,18	-0,75	0,31	-1,38	-0,16	0,05	0,17	-0,27	0,38
<i>Pieris brassicae</i>	Papilionoidea	Uncovered	-1,24	0,5	-2,28	-0,3	-0,23	0,2	-0,68	0,2	-0,55	0,34	-1,23	0,1	0,01	0,17	-0,31	0,34
<i>Pieris mannii</i>	Papilionoidea	Uncovered	-0,43	0,8	-2,09	1,11	-0,64	0,5	-1,7	0,27	-0,23	0,43	-1,08	0,59	-0,01	0,21	-0,42	0,4
<i>Pieris napi</i>	Papilionoidea	Uncovered	-0,99	0,6	-2,29	0,2	-0,2	0,3	-0,77	0,34	-0,7	0,39	-1,49	0,03	-0,09	0,18	-0,45	0,25
<i>Pieris rapae</i>	Papilionoidea	Uncovered	-2,12	0,5	-3,03	-1,28	-0,61	0,2	-1,07	-0,14	-0,58	0,28	-1,14	-0,04	0,03	0,17	-0,3	0,38
<i>Plbejus argus</i>	Papilionoidea	Uncovered	-0,37	1,4	-3,21	2,22	-2,29	0,9	-4,06	-0,73	-0,78	0,49	-1,76	0,15	0,11	0,22	-0,31	0,55
<i>Plbejus idas</i>	Papilionoidea	Uncovered	-0,25	1,5	-3,19	2,7	-1,9	0,9	-3,79	-0,23	-0,61	0,51	-1,64	0,39	0,07	0,22	-0,36	0,52
<i>Polygonia c-album</i>	Papilionoidea	Uncovered	-1,06	0,9	-2,98	0,63	-0,15	0,4	-0,97	0,64	-0,47	0,47	-1,4	0,44	-0,01	0,2	-0,42	0,39
<i>Polyommatus daphnis</i>	Papilionoidea	Vulnerable	2,07	1,5	-0,79	5,19	-1,27	0,9	-3,15	0,46	-0,6	0,5	-1,59	0,35	-0,01	0,22	-0,46	0,42
<i>Polyommatus dolus</i>	Papilionoidea	Vulnerable	2,53	1,5	-0,25	5,74	-1,21	1	-3,13	0,58	-0,63	0,53	-1,67	0,41	0,05	0,22	-0,4	0,49
<i>Polyommatus escheri</i>	Papilionoidea	Uncovered	-0,12	0,9	-1,84	1,67	-2,6	0,9	-4,4	-1,01	-1,02	0,47	-1,97	-0,12	0,25	0,22	-0,15	0,71
<i>Polyommatus icarus</i>	Papilionoidea	Uncovered	-0,59	0,4	-1,28	0,09	-0,45	0,2	-0,81	-0,09	-0,75	0,25	-1,25	-0,27	-0,14	0,16	-0,46	0,16
<i>Polyommatus thersites</i>	Papilionoidea	Uncovered	0,83	1,5	-1,92	3,8	-1,71	0,9	-3,63	0,03	-0,56	0,51	-1,57	0,44	0,04	0,22	-0,39	0,48
<i>Pontia daplidice</i>	Papilionoidea	Uncovered	0,06	0,4	-0,71	0,81	-0,06	0,2	-0,46	0,32	-0,54	0,28	-1,1	0,01	0,07	0,17	-0,26	0,4
<i>Pseudophilotes baton</i>	Papilionoidea	Uncovered	-3,16	0,9	-5,06	-1,51	-0,83	0,4	-1,55	-0,18	-0,37	0,42	-1,21	0,43	0,14	0,19	-0,22	0,52
<i>Pyrgus bellieri</i>	Papilionoidea	Uncovered	1,78	1,5	-0,95	4,84	-1,21	0,9	-3,09	0,52	-0,57	0,51	-1,57	0,43	0,03	0,22	-0,41	0,48
<i>Pyrgus malvoides</i>	Papilionoidea	Uncovered	-2,55	1	-4,63	-0,75	-0,87	0,4	-1,72	-0,09	-0,34	0,45	-1,23	0,54	0,11	0,19	-0,27	0,5
<i>Pyrgus serratulae</i>	Papilionoidea	Uncovered	-1,82	1,4	-4,65	0,76	-1,06	0,8	-2,64	0,57	-0,49	0,53	-1,54	0,55	0,03	0,22	-0,42	0,47
<i>Pyrgus sidae</i>	Papilionoidea	Vulnerable	-2,92	1,6	-6,16	-0,09	-1,03	1	-2,97	0,98	-0,65	0,56	-1,75	0,43	0,05	0,23	-0,4	0,51
<i>Pyronia bathseba</i>	Papilionoidea	Uncovered	-3,43	0,7	-4,75	-2,19	-2,34	0,4	-3,16	-1,6	-0,78	0,33	-1,44	-0,15	-0,07	0,18	-0,44	0,27
<i>Pyronia cecilia</i>	Papilionoidea	Uncovered	1,47	0,5	0,51	2,48	-2,21	0,6	-3,43	-1,12	-1,17	0,3	-1,77	-0,6	-0,08	0,2	-0,48	0,3
<i>Pyronia tithonus</i>	Papilionoidea	Uncovered	2,07	1,5	-0,77	5,16	-1,27	0,9	-3,18	0,49	-0,6	0,5	-1,61	0,37	-0,01	0,22	-0,46	0,42
<i>Quercusia quercus</i>	Papilionoidea	Uncovered	1,76	1,3	-0,58	4,37	-1,41	0,9	-3,24	0,27	-0,84	0,5	-1,86	0,13	0,05	0,22	-0,38	0,5
<i>Satyrjum esculi</i>	Papilionoidea	Uncovered	-1,95	0,7	-3,3	-0,68	-3,16	0,7	-4,67	-1,87	-0,71	0,36	-1,44	-0,03	-0,05	0,19	-0,44	0,33
<i>Satyrjum ilicis</i>	Papilionoidea	Uncovered	0,28	0,9	-1,39	2,01	-2,46	0,9	-4,27	-0,88	-0,77	0,45	-1,66	0,09	0,2	0,21	-0,2	0,63
<i>Satyrjum spini</i>	Papilionoidea	Uncovered	-2,77	0,9	-4,62	-1,1	-2,92	0,7	-4,42	-1,58	-1,04	0,46	-1,98	-0,18	0,13	0,2	-0,26	0,54
<i>Satyrus ferula</i>	Papilionoidea	Uncovered	-0,55	1,5	-3,58	2,39	-2,03	0,9	-3,86	-0,41	-0,8	0,53	-1,86	0,23	0,14	0,22	-0,28	0,59
<i>Spialia sertorius</i>	Papilionoidea	Uncovered	-1,91	0,6	-3,11	-0,82	-0,96	0,3	-1,53	-0,43	-0,82	0,38	-1,59	-0,09	0,2	0,17	-0,13	0,55
<i>Thymelicus acteon</i>	Papilionoidea	Uncovered	-2,01	0,5	-3,08	-1	-2,11	0,4	-2,97	-1,37	-0,54	0,31	-1,17	0,05	0,15	0,18	-0,19	0,52
<i>Thymelicus lineolus</i>	Papilionoidea	Uncovered	-0,18	1,4	-2,95	2,7	-1,91	0,9	-3,83	-0,19	-0,61	0,52	-1,64	0,4	0	0,22	-0,44	0,44
<i>Thymelicus sylvestris</i>	Papilionoidea	Uncovered	-1,41	0,8	-3,01	0,07	-1,32	0,5	-2,37	-0,42	-0,51	0,42	-1,37	0,28	0,1	0,2	-0,28	0,51
<i>Vanessa atalanta</i>	Papilionoidea	Uncovered	-3,34	1	-5,39	-1,54	-0,81	0,4	-1,54	-0,12	0,07	0,42	-0,75	0,91	-0,08	0,18	-0,45	0,27

<i>Vanessa cardui</i>	Papilionoideae	Uncovered	-2,27	0,6	-3,53	-1,15	-0,69	0,3	-1,2	-0,2	-0,44	0,36	-1,16	0,25	0,1	0,16	-0,22	0,43
<i>Zerynthia polyxena</i>	Papilionoideae	Protected	-1,37	1,1	-3,68	0,61	0,73	0,5	-0,16	1,63	-0,64	0,47	-1,56	0,26	0,2	0,2	-0,18	0,6
<i>Zerynthia rumina</i>	Papilionoideae	Protected	-3,23	0,9	-5,15	-1,55	-1,29	0,4	-2,08	-0,58	-0,72	0,45	-1,63	0,14	0	0,19	-0,38	0,38
<i>Zygaena ephialtes</i>	Zygaenidae	Uncovered	2,27	1,4	-0,23	5,14	-1,45	1	-3,42	0,36	-0,46	0,52	-1,47	0,56	0,09	0,22	-0,35	0,55
<i>Zygaena erythrus</i>	Zygaenidae	Uncovered	0	1,1	-2,09	2,13	-2,11	0,9	-3,92	-0,52	-0,86	0,47	-1,83	0,02	0	0,23	-0,46	0,45
<i>Zygaena fausta</i>	Zygaenidae	Uncovered	-2,79	0,8	-4,51	-1,23	-2,04	0,5	-3,12	-1,09	-0,67	0,44	-1,56	0,15	0,02	0,2	-0,37	0,42
<i>Zygaena filipendulae</i>	Zygaenidae	Uncovered	-3,75	0,9	-5,51	-2,16	-2,16	0,4	-3,06	-1,34	-0,58	0,4	-1,4	0,19	-0,07	0,19	-0,46	0,3
<i>Zygaena lavandulae</i>	Zygaenidae	Uncovered	-5,09	1,1	-7,29	-3,15	-2,04	0,4	-2,93	-1,25	-0,45	0,43	-1,32	0,37	-0,02	0,19	-0,4	0,34
<i>Zygaena occitanica</i>	Zygaenidae	Uncovered	1,47	1	-0,34	3,46	-2,05	0,9	-3,85	-0,42	-0,69	0,4	-1,52	0,06	0,2	0,21	-0,2	0,64
<i>Zygaena rhadamanthus</i>	Zygaenidae	Protected	-3,14	1,3	-5,73	-0,83	-1,21	0,6	-2,38	-0,13	-0,77	0,51	-1,78	0,21	0,18	0,22	-0,23	0,63
<i>Zygaena sarpedon</i>	Zygaenidae	Uncovered	-3,13	1	-5,21	-1,28	-2,66	0,7	-4,14	-1,39	-0,42	0,44	-1,29	0,41	-0,01	0,2	-0,43	0,38
<i>Zygaena transalpina</i>	Zygaenidae	Uncovered	-0,65	1,4	-3,45	2,22	-1,88	0,9	-3,72	-0,23	-0,61	0,53	-1,66	0,43	0	0,22	-0,44	0,44

Abstract

Insects are still poorly considered in biodiversity conservation programs, despite their major role in the functioning of terrestrial ecosystems. Because of their great diversity, and a great lack of knowledge of community structuring patterns, the conservation of these organisms faces major challenges related to the evaluation and prioritization of issues as well as the estimation of the species richness of communities. Because they constitute two groups of insects particularly impacted by environmental changes, butterflies and dragonflies are an important part of protected insects in Europe. In this context of low consideration of entomological diversity in conservation biology, this thesis aims to (1) measure the recent dynamics (decline, stability or expansion) of these two taxa in France, and to identify the climatic and ecological factors likely to condition them, (2) for butterflies, to use a fine description of the interactions network between the larvae and their hostplants to question the conservation status according to a systemic approach (3) and finally, with a clearly operational objective, to evaluate the links between the information gains and the efforts / sampling costs mobilized during environmental impact assessments.

The comparative study of the temporal dynamics of the populations of these two taxa was carried out at the scale of three countries of Western Europe through a diachronic analysis of the species distribution patterns on a time step of 35 years. This work has highlighted a strong correlation between the artificialisation of landscapes (urbanization, agricultural intensification, regression of wetlands) and the decline of many species, mainly characterized by strict ecological requirements and currently unprotected. On this same scale, the analysis of the architecture of the interactions network between butterfly larvae and their food plants revealed a modular structure in relation to the taxonomy of the partners, as well as a link between the degree specialization and species vulnerability (although the similarity of the species' diet did not seem to condition their conservation status). A final part was focused on the evaluation of the completeness of entomological surveys carried out during environmental impact assessments. A systematic and calibrated return procedure, on sites sampled in Mediterranean scrublands, allowed highlighting the limits of the current protocols in the estimation of species richness and the detection of protected or vulnerable species.

This thesis contributes to the articulation between fundamental issues and operational needs, by allowing both a better understanding of the structuring mechanisms of insect communities and the formulation of recommendations for a better local application of conservation policies

Key words: distribution, diachronic analysis, life history traits, biotic interactions, detectability, environmental impact assessment.

Résumé

Les insectes sont encore aujourd'hui peu pris en compte dans les programmes de conservation de la biodiversité, malgré leur rôle majeur dans le fonctionnement des écosystèmes terrestres. Du fait de leur grande diversité, et d'une grande méconnaissance des patrons de structuration des communautés, la conservation de ces organismes se heurte à des problématiques liées à l'évaluation et à la hiérarchisation des enjeux ainsi qu'à l'estimation de la richesse spécifique des communautés. Parce qu'ils constituent deux groupes d'insectes particulièrement impactés par les changements environnementaux, les Rhopalocères et les Odonates constituent une part importante des insectes protégés en Europe. Dans ce contexte de faible prise en compte de la diversité entomologique en biologie de la conservation, cette thèse a eu pour objectifs (1) de mesurer les dynamiques récentes (déclin, stabilité ou essor) de ces deux taxa en France, et d'identifier les facteurs climatiques et écologiques susceptibles de les conditionner, (2) pour les Rhopalocères, d'utiliser une description fine des réseaux d'interaction entre les larves et leurs plantes-nourricières pour questionner les statuts de conservation selon une approche systémique (3) et enfin, dans un objectif résolument opérationnel, d'évaluer les liens entre les gains d'informations et les efforts/coûts d'échantillonnage mobilisés au cours des études d'impacts.

L'étude comparative des dynamiques temporelles des populations de ces deux taxons a été réalisée à l'échelle de trois pays d'Europe de l'Ouest grâce à une analyse diachronique des patrons de répartition des espèces sur un pas de temps de 35 ans. Ce travail a mis en évidence une forte corrélation entre l'artificialisation des paysages (urbanisation, intensification agricole, régression des zones humides) et le déclin de nombreuses espèces, majoritairement caractérisées par des exigences écologiques strictes et actuellement non protégées. A cette même échelle, l'analyse de l'architecture du réseau d'interactions entre les larves de Rhopalocères et leurs plantes nourricières a quant à elle révélé une structure modulaire en relation avec la taxonomie des partenaires, ainsi qu'un lien entre le degré de spécialisation et la vulnérabilité des espèces (sans que la similarité du régime alimentaire des espèces ne semble conditionner leur statut de conservation). Une dernière partie a été ciblée sur l'évaluation du degré d'exhaustivité des inventaires entomologiques réalisés lors d'études d'impact réalisées en amont d'aménagements. Une procédure de repasse systématique et calibrée, sur des sites échantillonnés en garrigue méditerranéenne, a permis de mettre en évidence les limites des protocoles actuels, en termes d'estimation de la richesse spécifique et de détection d'espèces à enjeux. Sur cette base, des recommandations sont formulées pour optimiser les protocoles d'échantillonnage à mettre en œuvre pour la détection des espèces à enjeux.

Cette thèse contribue à l'articulation entre problématiques fondamentale et besoins opérationnels, en permettant à la fois une meilleure compréhension des mécanismes de structuration des communautés d'insectes et la formulation de recommandations pour une meilleure application locale des politiques de conservation.

Mots clés : répartition, analyse diachronique, traits d'histoire de vie, interactions biotiques, détectabilité, étude d'impact