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Le rôle de la diversité et des perturbations environnementales sur la stabilité temporelle des communautés animales en milieu naturel

Théophile Olivier

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Théophile OLIVIER

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Le rôle de la diversité et des perturbations environnementales sur la stabilité temporelle des communautés animales en milieu naturel

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Pour plus de détails concernant les remerciements, voir Bacon (2017), Jeanmougin (2017), Thévenin (2018), Martin (2019).

Résumé

La stabilité des communautés est un sujet qui a largement été abordé théoriquement et expérimentalement, notamment chez les plantes pour comprendre la relation entre la diversité d'une communauté et la stabilité de sa biomasse. Il existe cependant beaucoup moins d'études de la relation diversité/stabilité dans les communautés naturelles, notamment lorsqu'il s'agit de communautés animales. Or, dans le contexte actuel de changements globaux, et du fait des services écosystémiques apportés par les communautés animales, à travers notamment la dispersion des graines, la pollinisation ou encore le contrôle des ravageurs, il devient primordial de comprendre quels mécanismes régissent la stabilité des communautés animales et donc la stabilité des fonctions et services écosystémiques, ainsi que les impacts de la dégradation des habitats ou encore du changement climatique. Lors de cette thèse, je me suis d'abord intéressé à la relation diversité – stabilité dans des communautés naturelles de chauves-souris, d'oiseaux et de papillons et à l'impact de la dégradation des habitats sur cette relation. Chez ces trois taxons différents, j'ai pu mettre en évidence que la perte de diversité, ainsi que la dégradation des habitats via l'urbanisation et l'intensification agricole, sont liées à une diminution de la stabilité temporelle de l'abondance des communautés, et ce via des mécanismes distincts. Dans un second temps, je me suis intéressé à l'un des principaux mécanismes de la stabilité des communautés : la synchronie entre les fluctuations temporelles des espèces. J'ai pu montrer que la similarité de traits entre espèces de papillons, comme les ressources utilisées ou la période de vol des adultes, ainsi que la variabilité climatique augmentent la synchronie, en interaction avec le contexte paysager. Enfin, j'ai étudié le lien entre la synchronie entre espèces à l'échelle régionale et les tendances temporelles d'abondance des espèces, dans l'objectif de relier des groupes d'espèces synchrones aux tendances temporelles des espèces. Cette approche nous a permis d'évaluer l'impact des potentielles extinctions des espèces en déclin sur la synchronie entre espèces à l'échelle régionale et donc sur les dynamiques compensatoires à cette échelle.

Mots clés : relation diversité – stabilité, synchronie, papillons, oiseaux, chauves-souris, communautés animales, traits, changements globaux, dégradation des habitats, climat

Summary

Community stability has been extensively studied both theoretically and experimentally, especially in plant communities to examine the relationship between species diversity and stability of biomass. But the diversity – stability relationship has received less attention in natural communities, particularly in animals. However, in the context of global changes and given the ecosystem services provided by animal communities such as seed dispersal, pollination or pest control, it is of a primary importance to understand the drivers of community, hence ecosystem services, stability and the impact of habitat degradation or climate change. In this thesis, I first focused on the diversity – stability relationship in natural communities of bats, birds and butterflies, and I studied the impact of habitat degradation. For these three taxa, I found a negative effect of diversity loss, urbanization and agricultural intensification on the temporal stability of community abundance, through different mechanisms. Second, I focused on one of the main drivers of community stability: synchrony among species temporal fluctuations. We showed that trait similarity between butterfly species such as food resources of adult flight period affect synchrony among species, in addition to the impact of environmental conditions such as landscape and climate. Finally, I studied the synchrony among species at a regional scale, with the aim to link groups of synchronous species to species temporal trends. This approach allowed me to assess the effect of potential extinction of declining species on compensatory dynamics at regional scale.

Key words: Diversity – stability relationship, synchrony, butterflies, birds, bats, natural communities, species traits, global changes, habitat degradation, weather

Liste des publications

Olivier T., Thébault E., Elias M., Fontaine B., Fontaine C. Negative effects of habitat degradation and diversity loss on the stability of animal communities, *In review in Nature Communications*

Olivier T., Fontaine C., Thébault E., Giraud C., Roy D. B., Porcher E. Combined effects of traits, habitat context and weather variability on interspecific synchrony in common butterflies of Great Britain. *In preparation*

Olivier T., Thépault S., Fontaine C., Porcher E., Thébault E., Roy D. B., Giraud C. Regional compensatory dynamics among butterfly species in Great Britain are not affected by long-term temporal trends. *In preparation*

Liste des communications

Olivier T., Thébault E., Elias M., Fontaine B., Fontaine C. The diversity – stability relationship: from theory to natural communities. ICCB: 27th International Congress for Conservation Biology; August 2-6 août 2015; Montpellier, France. (Oral)

Olivier T., Thébault E., Elias M., Fontaine B., Fontaine C. The diversity – stability relationship: from theory to natural communities. SFécologie 2016; 24-28 octobre 2016; Marseille, France. (Oral)

Olivier T., Thébault E., Elias M., Fontaine B., Fontaine C. The diversity – stability relationship: from theory to natural communities. YNHM 2017; 7-11 février 2017; Paris, France. (Oral)

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Introduction

Les fonctions et services écosystémiques à l'épreuve du changement global

Les fonctions des écosystèmes correspondent à l'ensemble des processus écologiques qui contrôlent les flux de matière et d'énergie au sein des écosystèmes, comme la production et le recyclage de biomasse, la pollinisation, et sont le résultat du mode de vie et des traits fonctionnels des espèces (Bengtsson, 1998; Cardinale et al., 2012; Potts et al., 2010; Schulze and Mooney, 2012). La diversité et la quantité des fonctions réalisées vont en partie être liées à l'abondance, la biomasse et la diversité des espèces au sein d'un écosystème. Par exemple, une plus grande diversité de pollinisateurs permettra la pollinisation d'une plus grande diversité de plantes, et une plus grande abondance de pollinisateurs sera responsable d'un plus grand effort de pollinisation (Potts et al., 2010). Les espèces qui ont les mêmes fonctions au sein d'un écosystème peuvent être regroupées en groupes fonctionnels (Schulze and Mooney, 2012). La diversité de groupes fonctionnels au sein des écosystèmes reflète la diversité en fonctions réalisées dans les écosystèmes.

De ces fonctions, l'être humain tire des bénéfiques, appelés services écosystémiques (Costanza et al., 1997; Fisher et al., 2009; Westman, 1977). Comme exemples on peut citer la pollinisation qui est assurée par les insectes permet la reproduction des plantes et donc la production de nourriture, le contrôle des ravageurs par des prédateurs protège les cultures, ou encore la dépollution des eaux par des plantes permet le recyclage des eaux usées (Fisher et al., 2009; Wallace, 2007). La qualité et la quantité des services écosystémiques vont dépendre du fonctionnement des écosystèmes dans lesquels ils sont prélevés, et être liés à la biodiversité présente au sein de ces écosystèmes (Beaumont et al., 2007; Cardinale et al., 2011; Duffy et al., 2017; Hooper et al., 2005; Loreau et al., 2001; O'Connor et al., 2017).

L'intensité de l'exploitation des écosystèmes par les activités humaines a considérablement augmenté au cours des cinquante dernières années (Millennium Ecosystem Assessment, 2005). De cette intensification des activités humaines résultent les changements globaux. Les changements globaux désignent les perturbations des conditions environnementales dues aux activités humaines, comme le réchauffement climatique, la pollution de l'eau et de l'air (Chapin III et al., 2000). En plus de dégrader les conditions abiotiques, les changements globaux sont également responsables de la dégradation des habitats et du déclin de la biodiversité (Cardinale et al., 2012; Chapin III et al., 2000).

Toutes ces perturbations peuvent avoir d'importantes conséquences sur les fonctions et services écosystémiques assurés au sein des écosystèmes, et notamment sur leur stabilité. La stabilité renvoie à la capacité d'un système écologique à se maintenir dans son état de référence à travers le temps et en présence de variations des conditions environnementales (Grimm and Wissel, 1997). Si l'on veut maintenir les fonctions des écosystèmes et les services écosystémiques qui en découlent dans un contexte d'augmentation des perturbations, il est nécessaire de comprendre l'impact des changements globaux sur la stabilité des communautés qui assurent ces fonctions.

Mesurer la stabilité temporelle des communautés d'espèces

En l'absence de perturbations extérieures, les composantes d'un système écologique, comme l'abondance totale d'une communauté, vont tendre vers un état appelé état d'équilibre et qui dépend des conditions initiales des abondances des espèces de la communauté. Cet état d'équilibre peut être un point (ou un vecteur dans le cas de plusieurs espèces), auquel cas l'abondance des espèces ne change pas en l'absence de perturbations. Il peut également être dynamique en raison des interactions entre espèces (Ives and Carpenter, 2007; Kendall et al., 1999; Krebs et al., 1995).

Lorsque l'on veut mesurer la stabilité d'un système, on peut s'intéresser à plusieurs caractéristiques de ce système, comme sa stabilité temporelle, sa résistance ou encore sa

résilience (Figure 1) (Grimm and Wissel, 1997; Ives and Carpenter, 2007; McCann, 2000). La **résistance** d'un système écologique correspond à sa capacité à rester proche de son état d'équilibre malgré une perturbation. Plus l'écart avec l'état d'équilibre est faible, plus le système est stable. La **résilience** d'un système écologique représente le temps que met le système à retourner à son état d'équilibre après une perturbation, et à quel point le système parvient à revenir à un état proche de l'état d'équilibre initial. Un temps de retour à l'équilibre court est synonyme de système stable. La **stabilité temporelle** fait référence à l'amplitude des variations générées par des perturbations répétées au cours du temps autour de l'état d'équilibre du système. Un système stable est un système avec des variations de faible amplitude. Enfin, selon l'intensité de la perturbation, on peut observer des changements d'état d'équilibre. Dans ce cas la stabilité du système reflète la probabilité de passer de l'état d'équilibre initial à un nouvel état d'équilibre. Plus la probabilité de changer d'état est faible, plus le système est stable. Le nouvel état d'équilibre peut lui être plus ou moins stable que l'état d'équilibre précédent.

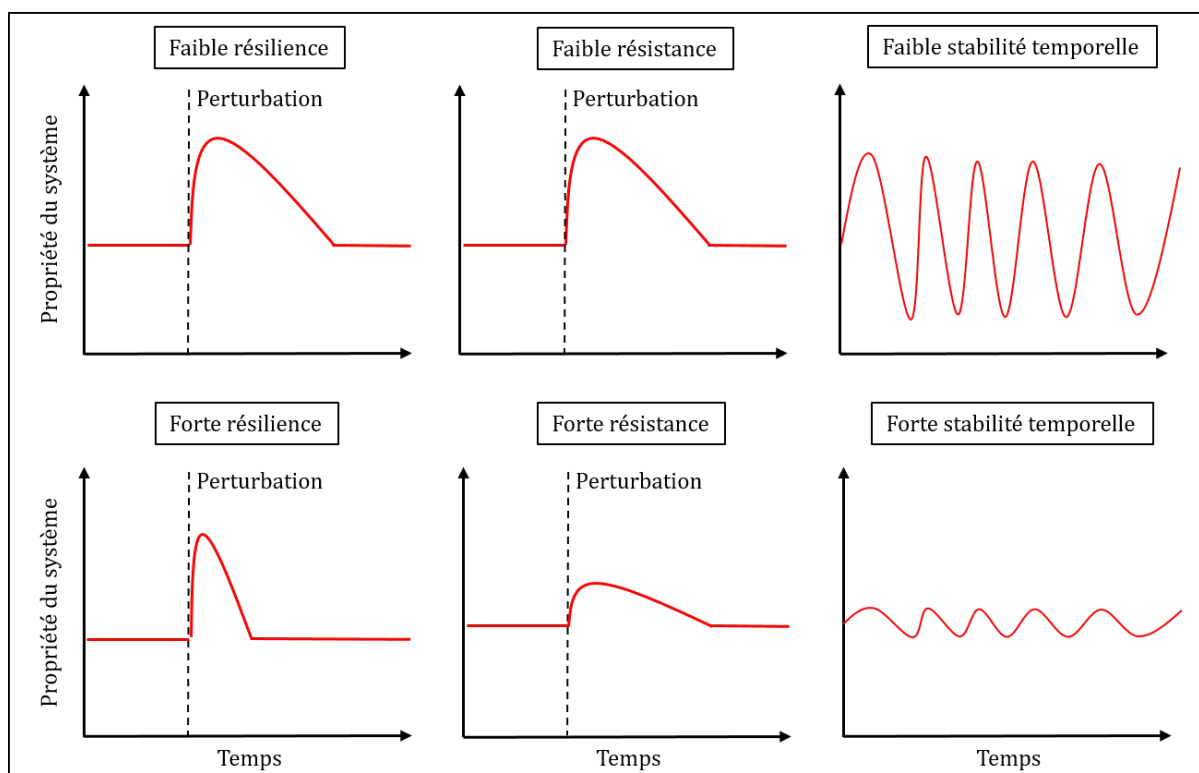


Figure 1. Différents types et niveaux de stabilité d'une propriété d'un système écologique.

Dans cette thèse, je me suis intéressé à la stabilité temporelle de l'abondance totale de communautés animales naturelles. J'ai fait l'hypothèse que les variations temporelles d'abondance peuvent représenter un proxy des variations temporelles de la quantité de fonctions réalisée par ces communautés, en réponses à des perturbations environnementales issues des changements globaux.

La stabilité temporelle de l'abondance totale d'une communauté se calcule communément via l'inverse du coefficient de variation CV, ici de l'abondance d'une communauté :

$$S = \frac{1}{CV} = \frac{\mu}{\sigma}$$

Avec S la stabilité de l'abondance de la communauté, σ l'écart type et μ la moyenne de l'abondance. Plus l'inverse du coefficient de variation est grand, plus la communauté est stable. Récemment, Thibaut and Connolly (2013) ont décomposé la stabilité temporelle des communautés en deux composantes : la stabilité temporelle moyenne pondérée de ses populations et la synchronie entre les fluctuations de ses populations. Cette décomposition permet d'écrire la stabilité temporelle de la communauté sous la forme :

$$S = \frac{1}{CV_c} = \frac{1}{CV_s * \sqrt{\varphi}}$$

Avec CV_c le coefficient de variation de la communauté, CV_s le coefficient de variation moyen pondéré des populations de la communauté et φ la synchronie entre les fluctuations des populations de la communauté. CV_s peut s'écrire de la façon suivante :

$$CV_s = \sum_i \frac{\mu(i) \sigma(i)}{\mu_c \mu(i)}$$

Avec $\mu(i)$ l'abondance moyenne de la population i , μ_c l'abondance moyenne de la communauté et $\sigma(i)$ l'écart-type de la population i . Ce coefficient de variation moyen pondéré de l'abondance des populations correspond à l'inverse de la stabilité temporelle moyenne pondérée par l'abondance relative des populations dans la communauté. La stabilité temporelle de la communauté augmente avec la stabilité temporelle moyenne pondérée des populations. La synchronie reflète quant à elle la corrélation entre les fluctuations des

populations. La stabilité temporelle de la communauté augmente lorsque la synchronie diminue, ou que l'asynchronie augmente (Figure 2).

Ainsi, le développement de Thibaut and Connolly (2013) permet de séparer les effets des conditions environnementales sur les différentes composantes de la stabilité des communautés, afin de préciser les mécanismes sous-jacents. La diversité des communautés ou les perturbations environnementales peuvent affecter indépendamment et simultanément la stabilité des populations, et la synchronie entre leurs fluctuations.

La première composante de la stabilité temporelle de l'abondance totale des communautés reflète la stabilité moyenne pondérée des populations qui composent les communautés. On peut séparer cette composante en deux parties :

$$\frac{\sigma(i)}{\mu(i)}$$

Soit le coefficient de variation des populations, l'inverse de la stabilité des populations. Une communauté composée de populations stables sera plus stable qu'une communauté composée de populations instables. Cependant, une augmentation de la stabilité moyenne des populations n'est pas forcément accompagnée d'une augmentation de la stabilité de la communauté, et dépend de la répartition de l'abondance totale (ou de la biomasse) de la communauté à travers les différentes espèces :

$$\frac{\mu(i)}{\mu_c}$$

Cette mesure de l'abondance relative de chaque espèce dans la communauté, aussi appelée « evenness », pondère le rôle de chaque population, et distingue la contribution des espèces dominantes et des espèces rares dans une communauté. Ainsi la stabilité de la communauté reflète plus de la stabilité des espèces dominantes par rapport aux espèces rares si la répartition de l'abondance totale est très déséquilibrée. Tandis qu'une communauté avec une répartition équitable de l'abondance a une stabilité proche de la stabilité moyenne de ses populations.

La seconde composante de la stabilité des communautés est la synchronie entre les fluctuations des populations qui constituent cette communauté, ou synchronie entre espèces. La synchronie entre espèces reflète la corrélation entre les fluctuations temporelles de plusieurs populations. La stabilité d'une communauté augmente lorsque la synchronie entre espèces diminue (l'asynchronie augmente), du fait de dynamiques compensatoires (Gonzalez and Loreau, 2009; Yachi and Loreau, 1999) (Figures 2 et 3).

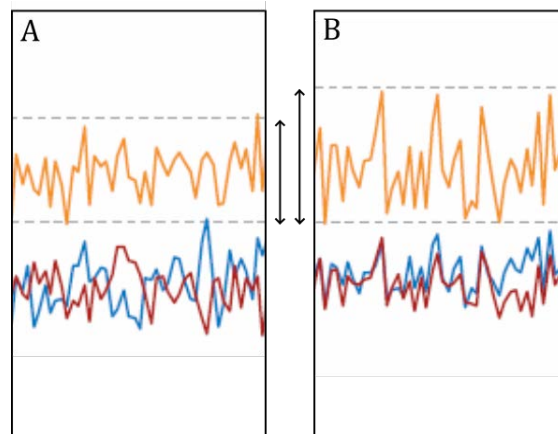


Figure 2. Différents niveaux de synchronie entre espèces (rouge et bleu) au cours du temps, et leur impact sur la variabilité de l'abondance totale (jaune). (A) Populations avec de fortes dynamiques compensatoires, générant de l'asynchronie. Lorsqu'une population décroît, la diminution de sa densité est compensée par la croissance de l'autre population. (B) Populations avec une forte synchronie. Il n'y a pas de dynamique compensatoire, et les fluctuations de densité à l'échelle de la communauté sont plus importantes (extrait de Gonzalez and Loreau (2009)).

Dans la suite de cette introduction je vais décrire la relation entre la diversité et la stabilité temporelle des communautés, et les mécanismes liés à la stabilité des populations et à la synchronie entre espèces. Dans un second temps je détaillerai comment les perturbations environnementales peuvent affecter la stabilité temporelle de l'abondance totale des communautés.

La relation entre diversité et stabilité des communautés

La relation entre la diversité et la stabilité a été abondamment étudiée depuis les travaux théoriques de MacArthur (1955) et le débat suscité par les prédictions de (May, 1973, 1972) en contradiction avec celles de MacArthur. MacArthur prédit que les communautés plus riches sont plus stables, du fait d'un plus grand nombre d'interactions proies-prédateurs, ce qui diminue la force de chacune d'elles et permet des fluctuations moins importantes des populations (MacArthur 1955). Cette démonstration théorique pose les bases d'une relation positive entre diversité et stabilité. Elle s'inscrit dans la démarche de MacArthur d'expliquer les observations de variations d'abondance des espèces au cours du temps, et met en avant le rôle des interactions entre espèces. Elton (1958) prédit lui que les communautés plus pauvres sont plus sensibles aux perturbations, avec une plus grande probabilité que des populations s'éteignent, augmentant ainsi le risque d'invasion. Cette prédiction provenait de l'observation que les communautés simplifiées par l'agriculture montraient de plus grandes fluctuations et de plus nombreuses invasions, et que les forêts boréales, moins riches, étaient plus sujettes aux explosions démographiques d'insectes que les riches forêts tropicales. Elton fait donc intervenir les perturbations et le lien entre diversité et capacité de résister à ces perturbations.

Puis dans les années 70, Gardner and Ashby (1970), May (1972) et Pimm and Lawton (1978) prédisent qu'une augmentation de la complexité diminue la probabilité d'équilibres stables. Ces nouvelles théories sont à l'origine du débat sur la relation entre la diversité et la stabilité temporelle de la biomasse ou de l'abondance des communautés. Ce débat va produire des résultats contrastés sur la relation diversité – stabilité entre les études, notamment sur des communautés de plantes, de plancton ou d'arthropodes (Frank and McNaughton, 1991; Hurd and Wolf, 1974; Hurd et al., 1971; Margalef, 1968; McNaughton, 1968; Mcnaughton, 1978; McNaughton, 1985; Mellinger and McNaughton, 1975; Singh and Misra, 1969; Smedes and Hurd, 1981; Zaret, 1982).

Aujourd'hui il existe un consensus sur l'existence d'une relation positive entre la richesse et la stabilité des communautés, notamment depuis les travaux expérimentaux sur les communautés de plantes (Tilman and Downing, 1994). Cette relation a été prédite théoriquement (Yachi and Loreau, 1999) (Figure 3), montrée expérimentalement sur la stabilité de la biomasse totale de communautés de plantes (Hector et al., 2010; Kuiters, 2013; Tilman et al., 2006) et expérimentalement et empiriquement sur l'abondance totale de communautés animales (Downing et al., 2014; Schaefer et al., 2012; Thibaut et al., 2012) (Figure 4).

Cependant, l'existence de tels résultats contradictoires depuis le début de l'étude de la relation entre diversité et stabilité temporelle suggère une relation dépendante du contexte dans lequel se place l'étude et du type de communauté étudié (Jiang and Pu, 2009) (Figure 4). La diversité des traits des espèces, de leurs interactions et des conditions environnementales selon les milieux peut expliquer ces variations. Cela montre l'importance de continuer à étudier le lien entre diversité et stabilité temporelle, notamment dans le contexte des changements globaux et de l'impact des perturbations environnementales sur la biodiversité.

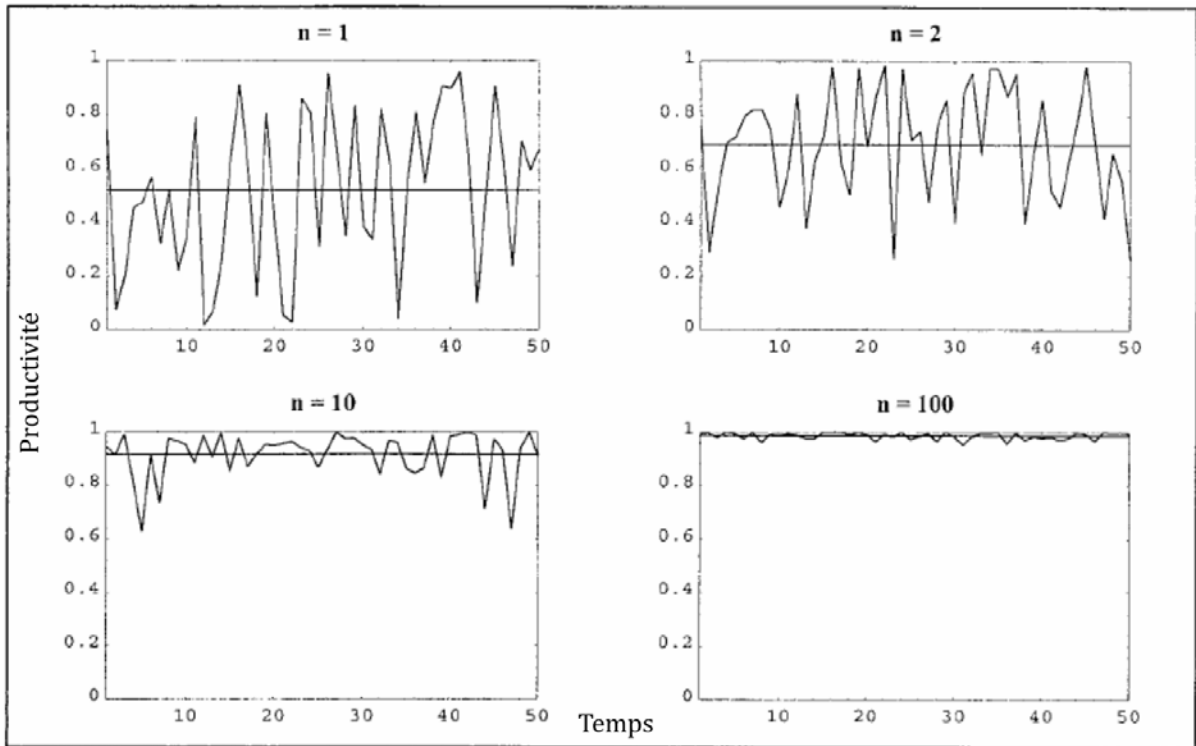


Figure 3. Variabilité temporelle de la productivité en fonction du nombre d'espèces d'après Yachi and Loreau (1999). Il est prédit une augmentation de la stabilité temporelle avec l'augmentation du nombre d'espèces n .

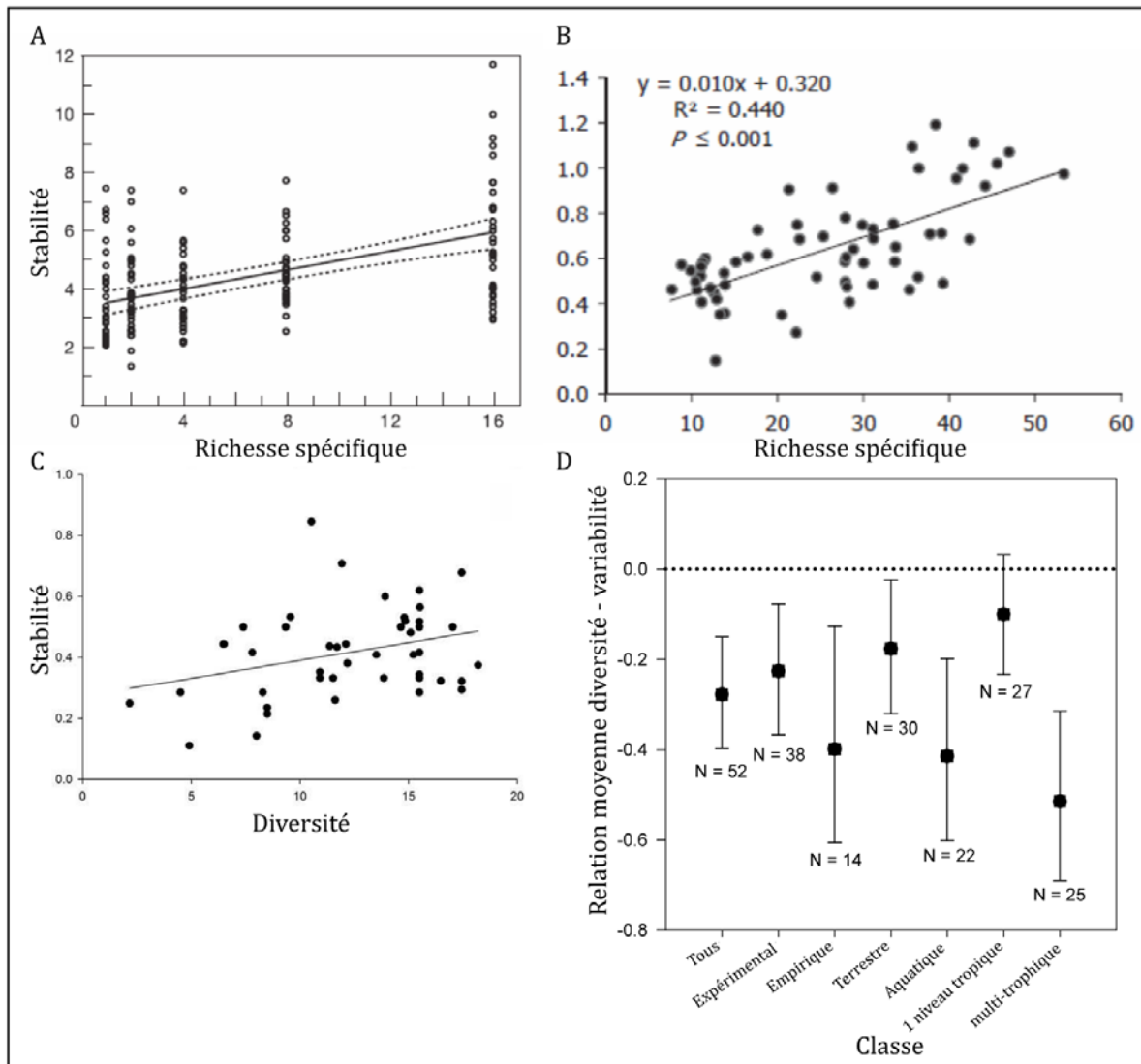


Figure 4. Relation positive entre la richesse spécifique et la stabilité de la biomasse de communautés de plantes montrée expérimentalement par Tilman et al. (2006) (A) et Kuiters, (2013) (B), et (C) relation positive entre la diversité et la stabilité de l'abondance de communautés de poissons par Schaefer et al. (2012). (D) montre l'effet moyen de la relation diversité – variabilité des communautés à travers des études expérimentales, empiriques, terrestres, aquatiques, et portant sur un ou plusieurs niveaux trophiques. Hormis pour les études sur un seul niveau trophique, la moyenne et l'écart type de l'effet moyen est toujours inférieur à 0, indiquant une relation négative entre diversité et variabilité, donc une relation positive entre diversité et stabilité (extrait de Jiang and Pu, 2009).

D'autre part, les mécanismes mis aujourd'hui en avant s'inscrivent dans la continuité des hypothèses développées par MacArthur et Elton, à savoir les interactions entre espèces et les réponses des espèces aux variations des conditions environnementales. Si on fait le lien avec la partie précédente concernant les différentes composantes de la stabilité temporelle, la diversité des communautés peut affecter soit la stabilité moyenne pondérée des populations soit la synchronie entre espèces en modifiant les interactions entre espèces et les réponses des espèces aux variations des conditions environnementales.

La relation entre diversité et stabilité des populations

Comme détaillé précédemment, la stabilité des populations peut affecter la stabilité des communautés via des changements du coefficient de variation moyen des populations et de l'abondance ou biomasse relative des espèces dans la communauté (evenness). Les études sur la relation entre diversité et stabilité des populations ont montré des résultats contrastés (Hooper et al., 2005). D'après une méta-analyse de Jiang and Pu (2009), la relation entre la diversité et la stabilité des populations semble dépendre du contexte dans lequel les études se placent (Figure 5).

Les études basées sur des communautés à plusieurs niveaux trophiques mettent en évidence une relation positive entre diversité et stabilité des populations (Jiang and Pu, 2009). Ce résultat suit ceux de Thébault and Loreau (2005, 2006) qui ont montré que la relation diversité – stabilité des populations au sein d'une communauté dépend des interactions entre niveaux trophiques. Ces résultats mettent en avant l'augmentation d'interactions trophiques faibles avec l'augmentation de la diversité, qui stabilise les populations, et est en accord avec les hypothèses initiales de MacArthur (1955) concernant un rôle stabilisateur de l'augmentation des relations proies-prédateurs via une diminution de la pression de prédation sur chaque espèce.

L'augmentation de la diversité peut entraîner une augmentation de la compétition entre espèces et ainsi déstabiliser les populations (Loreau and de Mazancourt, 2013). Cependant, la

complémentarité, comme par exemple l'utilisation de ressources différentes par les plantes, peut diminuer la compétition entre espèces et stabiliser les communautés. Cadotte et al. (2012) ont ainsi montré un lien positif entre diversité phylogénétique et stabilité des populations, expliqué par l'utilisation de ressources différentes par des espèces phylogénétiquement éloignées. La diversité phylogénétique, en reflétant la diversité de traits entre les espèces, pourrait expliquer les relations entre diversité et stabilité des populations dues aux interactions entre espèces autrement que la richesse spécifique, habituellement utilisée comme mesure de diversité. De plus, l'effet de sélection peut modifier les rapports de dominance entre espèces et affecter la stabilité moyenne pondérée des populations en lien avec la diversité (Loreau and Hector, 2001).

Les interactions entre espèces comme les relations proies – prédateurs et la compétition semblent être les principaux mécanismes influençant la relation entre la diversité des communautés et la stabilité des populations. La méta-analyse de Jiang and Pu (2009) montre des différences notables entre études expérimentales et empiriques, ou entre études comportant un ou plusieurs niveaux trophiques. Mougi and Kondoh (2012) prédisent que la diversité d'interactions entre espèces augmente la probabilité d'un équilibre stable localement. Les assemblages d'espèces utilisés en conditions expérimentales peuvent s'avérer être peu représentatifs la complexité des assemblages en milieux naturels (Díaz et al., 2003). Les études en milieu naturel et prenant en compte différents taxons sont ainsi nécessaires pour intégrer l'ensemble des interactions qui stabilisent les populations dans les communautés naturelles.

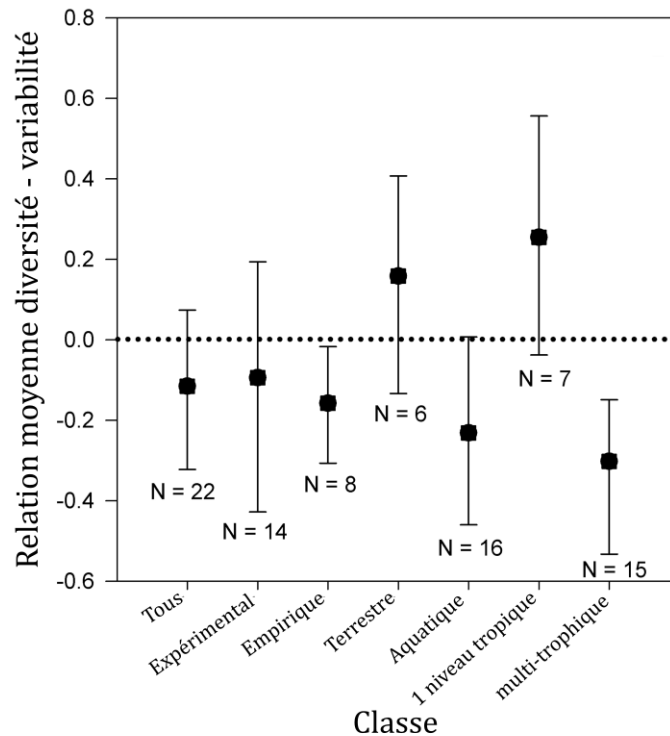


Figure 5. Effet moyen de la relation diversité – variabilité des populations à travers des études expérimentales, empiriques, terrestres, aquatiques, et portant sur un ou plusieurs niveaux trophiques. Contrairement aux communautés, l’effet moyen de la relation diversité – stabilité des populations est contrasté, et dépend du contexte de l’étude (extrait de Jiang and Pu (2009)).

La relation entre diversité et synchronie entre espèces

Le rôle stabilisateur de l’asynchronie à l’échelle des communautés et sa relation positive avec la richesse spécifique ont été montrés, expérimentalement comme empiriquement (Downing et al., 2014; Hector et al., 2010; Morin et al., 2014; Sasaki et al., 2019). Les dynamiques compensatoires peuvent être le résultat d’interactions entre espèces ou de réponses différentes aux variations des conditions environnementales (Gonzalez and Loreau, 2009; Loreau and de Mazancourt, 2008, 2013). Cependant, la similarité des réponses des espèces aux variations des conditions environnementales semble être le principal mécanisme qui influence l’asynchronie entre espèces (Ives et al., 1999; Tredennick et al., 2017).

La variation des réponses aux conditions environnementales implique des traits de réponses différents entre les espèces, relatifs au comportement ou aux conditions physiologiques (Hofmann and Todgham, 2010; Oliver et al., 2015). Par exemple, les traits des arbres liés à leur sensibilité à la sécheresse (O'Brien et al., 2014), les traits des abeilles qui ont un effet sur leurs réponses à la perte d'habitat, l'agriculture ou les feux (Williams et al., 2010), ou les traits des plantes qui influencent leur croissance et leur survie selon les conditions de ressources (Reich, 2014). En augmentant la diversité d'une communauté cela augmente les chances que celle-ci contienne des espèces capables de réagir différemment aux conditions environnementales. La diversité phylogénétique, en reflétant une diversité de traits de réponses différents aux conditions environnementales, pourrait expliquer une stabilisation des communautés via l'asynchronie entre fluctuations des populations. Le lien entre synchronie et similarité de traits a déjà été mis en évidence, par exemple avec le type de ressource utilisée par les chenilles de papillons (Raimondo et al., 2004a). Les espèces se nourrissant du même type de plantes montraient une plus grande synchronie entre elles qu'avec les espèces se nourrissant sur d'autres types de plantes.

Perturbations, diversité et stabilité des communautés d'espèces

Pour résumer, les interactions entre espèces et les réponses des espèces aux variations des conditions environnementales vont affecter la stabilité temporelle des communautés. Des changements de diversité, en terme de richesse ou de diversité de traits, peuvent affecter ces interactions, par exemple en diminuant les pressions de prédation, ainsi que diversifier les réponses aux conditions environnementales en augmentant la diversité de traits de réponses au sein des communautés. On peut s'attendre à ce que les interactions et les traits de réponses varient selon les groupes taxonomiques, suggérant l'importance d'étudier la relation diversité – stabilité dans des communautés de taxons différents et dans des conditions naturelles. De plus dans un contexte de changements globaux, les perturbations environnementales pourraient affecter directement la stabilité temporelle des communautés via la stabilité des populations et l'asynchronie, mais aussi via des changements d'abondance et de diversité. Il est donc nécessaire d'intégrer ces perturbations afin de comprendre leur

impact sur la stabilité temporelle des communautés, pouvant refléter la stabilité des fonctions des écosystèmes.

Dès le début de l'intérêt pour la relation diversité - stabilité, MacArthur suppose que les fluctuations des populations pourraient être influencées par des variations environnementales de la disponibilité en énergie, ou des variations de la mortalité (MacArthur, 1955). Dans le contexte actuel des changements globaux, les perturbations environnementales induites par les activités humaines peuvent modifier les conditions environnementales et leurs variations, et affecter à de multiples niveaux la stabilité des communautés et donc le fonctionnement des écosystèmes. Si les effets des perturbations anthropiques sur la diversité, l'abondance ou la biomasse des communautés sont déjà connus (Ceballos et al., 2015; Inger et al., 2015), leurs effets directs sur les composantes de la stabilité des communautés le sont moins. De plus, certaines études montrent des effets directs des perturbations sur la stabilité des populations ou la synchronie (Blüthgen et al. 2016; Oliver et al. 2010), lorsque d'autres études montrent un effet via la diversité des communautés (Hautier et al., 2015).

Ces perturbations peuvent être de différentes natures et affecter les écosystèmes de plusieurs façons (Bender et al., 1984). Par exemple, des événements climatiques extrêmes, ou des pollutions vont perturber le système étudié de façon brève et plus ou moins importante selon son intensité. Le système va être affecté au moment de cet événement, avec potentiellement un retour vers son état initial selon ses caractéristiques. Ces perturbations sont appelées **perturbations ponctuelles** (« pulse » en anglais) (Figure 6A). Les **perturbations permanentes** (« press » en anglais) (Figure 6B), sont elles installées dans le temps et affectent progressivement le système. L'augmentation de la température dans un milieu, ou la dégradation des habitats par l'urbanisation ou l'agriculture sont des perturbations permanentes. Les perturbations permanentes vont ainsi éloigner le système de son état initial, par exemple en diminuant l'abondance des populations d'une communauté. Que ce soit pour les perturbations ponctuelles ou permanentes, la réaction du système va dépendre de ses caractéristiques, comme le nombre d'espèces. Ainsi, après une perturbation ponctuelle, le

système aura dévié de son état initial plus ou moins selon sa résistance, et pourra y revenir plus ou moins selon sa résilience. La répétition de perturbations ponctuelles va faire plus ou moins osciller le système autour de son état initial selon sa stabilité temporelle. En présence d'une perturbation permanente, le système va s'écartier progressivement de son état initial (Ives and Carpenter, 2007).

Des changements de diversité peuvent également être vus comme des perturbations. Ainsi, l'invasion d'un écosystème par une espèce exotique va perturber l'état dans lequel se trouvait l'écosystème avant l'invasion (Figure 6D). Les perturbations peuvent entraîner un changement définitif d'état d'équilibre (May, 1977; Scheffer and Carpenter, 2003), comme lors d'extinction d'espèces (Figure 6C). L'extinction d'une espèce suite à une perturbation va engendrer une nouvelle perturbation, du fait de la perte de sa fonction dans le système, mais également des interactions que les autres espèces avaient avec elle.

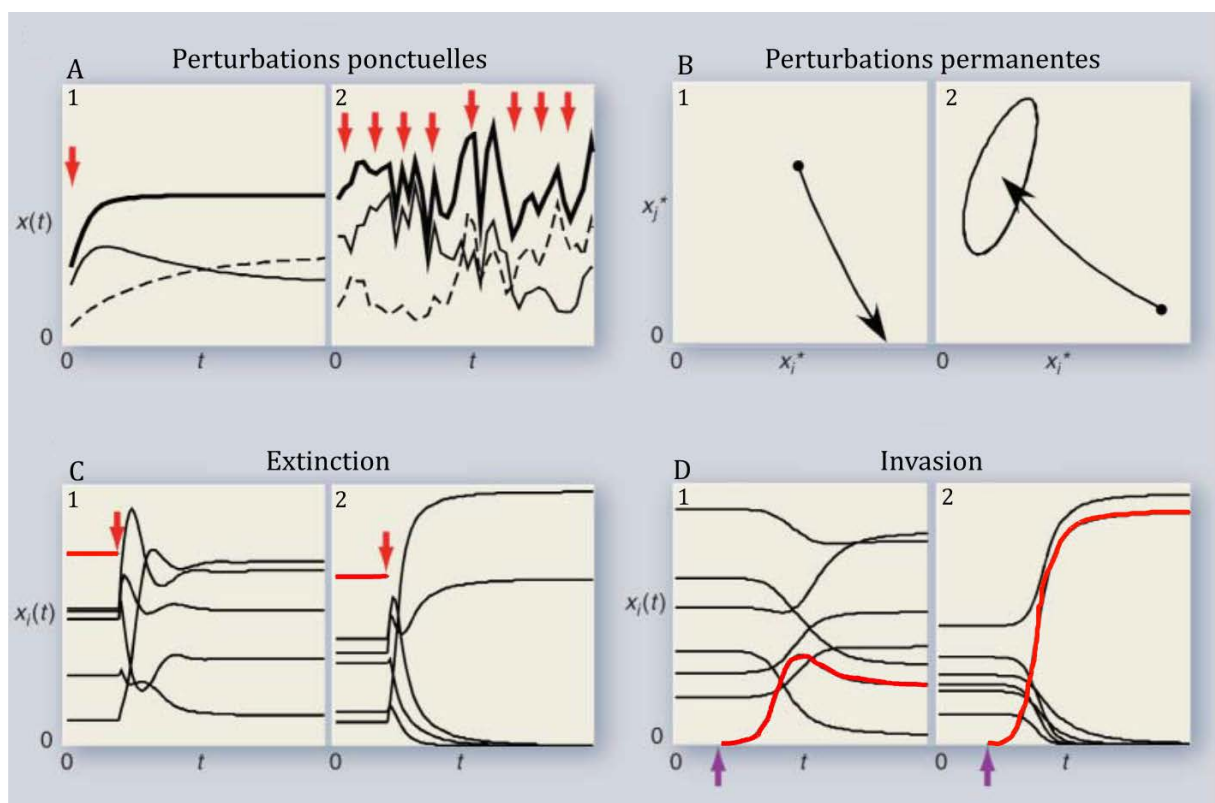


Figure 6. Exemples de perturbations (extrait de Ives and Carpenter (2007)). Les flèches représentent le moment où la perturbation a lieu. Pour les perturbations ponctuelles (A), chaque courbe correspond à l'évolution de la densité d'une espèce au cours du temps. A.1

représente la réponse des espèces à une perturbation ponctuelle, et A.2 correspond à une répétition de perturbations ponctuelles qui à chaque fois modifient la densité des espèces. Une perturbation ponctuelle peut ainsi conduire à l'extinction d'une ou plusieurs espèces. Pour les perturbation permanentes (B), les deux figures représentent l'évolution des densités à l'équilibre de deux espèces en présence d'une perturbation continue, par rapport à leur point d'équilibre initial. B.1 la perturbation mène à l'extinction d'une des deux espèces. B.2 la perturbation mène à un nouvel équilibre (cyclique dans ce cas) où les deux espèces coexistent. L'extinction d'une espèce (C), représentée par la droite rouge, peut mener à des changements de densités des autres espèces présentes. C.1 toutes les espèces restantes survivent, mais dans un état différent de celui initial, C.2 l'extinction de l'espèce entraîne par la suite l'extinction d'autres espèces. Comme pour l'extinction, l'invasion (D) par une espèce peut modifier la densité à l'équilibre des autres espèces du milieu (D.1), jusqu'à l'extinction de certaines d'entre elles et donc un changement par rapport à l'état initial (D.2).

Les perturbations environnementales sont responsables de déclin d'abondance des espèces. L'impact des changements globaux sur l'abondance des espèces est l'un des plus médiatisés (Foucart 2018). Par exemple, des études ont montré que 41% des espèces d'insectes sont en déclin (Sánchez-Bayo and Wyckhuys, 2019), ainsi que les espèces d'oiseaux communs en Europe (Inger et al., 2015). Le déclin peut à terme mener à l'extinction d'espèces. Le rôle des changements globaux sur les extinctions est assez bien documenté (Ceballos et al., 2015; Pimm et al., 2014), avec par exemple la perte de 50% de l'aire de distribution de mammifères (Ceballos and Ehrlich, 2002), représentant des extinctions locales.

En plus d'affecter la quantité des fonctions réalisées par les espèces (Potts et al., 2010), ces déclin et extinctions peuvent également affecter la stabilité temporelle des communautés via la stabilité des populations et l'asynchronie. Les déclin d'abondance peuvent modifier les rapports de dominance au sein des communautés et affecter la stabilité moyenne pondérée des populations. De plus, les extinctions auxquels les déclin peuvent conduire vont déstabiliser les communautés via la diminution de la diversité (Hautier et al., 2015). L'assemblage des communautés, notamment la diversité des traits fonctionnels, est influencé

par les conditions environnementales dans lesquelles se trouvent les communautés (Lebrija-Trejos et al., 2010). La dégradation des habitats et la simplification des paysages du fait de l'agriculture ou de l'urbanisation peuvent orienter le filtre environnemental sur les communautés (Gámez-Virués et al., 2015). En diminuant la diversité de traits, ces perturbations peuvent affecter la diversité de réponses aux variations des conditions environnementales. Enfin, les perturbations environnementales peuvent affecter directement les deux composantes de la stabilité temporelle des communautés, la stabilité des populations et la synchronie entre espèces. Par exemple, l'intensification de l'utilisation des sols (Blüthgen et al. 2016) et l'eutrophisation (Hautier et al. 2014) augmentent la synchronie entre espèces au sein des communautés. Oliver et al. (2010) ont montré eux que la diminution de la diversité des habitats diminue la stabilité des populations de papillons.

Cependant, si l'impact des perturbations anthropiques sur le déclin de la biodiversité est relativement bien documenté (Pimm et al., 1995; Sala et al., 2000), celui sur la stabilité des communautés est encore mal connu (Donohue et al., 2016), notamment en ce qui concerne le rôle des traits des espèces. Comprendre comment les perturbations dues aux changements globaux affectent la stabilité temporelle des communautés, proxy de la stabilité temporelle des fonctions des écosystèmes est primordial afin d'orienter les politiques de conservation et de gestion vers des décisions efficaces pour maintenir le fonctionnement des écosystèmes et les services qu'ils fournissent stables.

Contexte de la thèse

Ma thèse s'inscrit dans ce contexte de l'étude de l'impact des changements globaux sur la stabilité des communautés, proxy du fonctionnement des écosystèmes, et vise à mettre en évidence les différents mécanismes sous-jacents, comme le rôle de la diversité et des traits des espèces. Dans le cadre de cette thèse, je me suis intéressé à la stabilité temporelle de l'abondance totale de communautés naturelles de chauves-souris, d'oiseaux et de papillons. Les fonctions exercées par ces trois taxons animaux, comme la pollinisation, le contrôle des ravageurs ou encore la dispersion des graines ont une importance dans le fonctionnement des

écosystèmes, et d'autant plus dans le contexte de changements globaux. L'utilisation de communautés naturelles m'a de plus permis d'analyser des assemblages d'espèces naturels dans une grande gamme de conditions environnementales.

La relation diversité – stabilité dans les communautés animales naturelles et l'impact de la dégradation des habitats

La 1^{ère} partie de ma thèse a consisté à intégrer la relation diversité – stabilité dans le contexte des perturbations environnementales. J'ai utilisé des mesures de richesse spécifique et de diversité phylogénétique pour refléter la diversité des communautés. L'intensification de l'usage des sols est responsable de la dégradation et de la simplification des habitats. En offrant moins de quantité et de diversité d'habitats, ces changements sont responsables de la diminution de la diversité et de la simplification des communautés (Ekroos et al., 2010; Gámez-Virués et al., 2015). J'ai ainsi intégré des mesures d'urbanisation et d'intensification agricole comme perturbations environnementales. Afin de séparer les différents effets et potentiels mécanismes, j'ai utilisé la décomposition de Thibaut and Connolly (2013), pour regarder les liens entre perturbation, diversité et les deux composantes de la stabilité des communautés, la stabilité moyenne pondérée des populations ou la synchronie en fluctuations des populations.

Le rôle de la similarité de traits des espèces et des conditions environnementales sur la synchronie locale

Les seconde et troisième parties de ma thèse se sont focalisées sur les mécanismes de la synchronie entre espèces de papillons. La synchronie est un des mécanismes principaux de la stabilité des communautés (Loreau and de Mazancourt, 2013; Thibaut and Connolly, 2013). La synchronie reflète des réponses des espèces plus ou moins différentes aux conditions environnementales (Tredennick et al., 2017). Ces différences de réponses aux variations des conditions environnementales peuvent être liées à des différences de traits de réponses des espèces. La synchronie augmente entre les espèces qui partagent les mêmes traits de réponse (Raimondo et al., 2004a, 2004b). Il est nécessaire de comprendre quels sont ces traits de

réponses, afin d'orienter les politiques de gestion et de conservation favorisant une diversité qui permet des dynamiques compensatoires, et donc la stabilisation des communautés et des fonctions qu'elles assurent. Dans cette optique de compréhension mécaniste basée sur les traits des espèces, j'ai analysé à une échelle locale le rôle de la similarité de traits entre espèces sur la synchronie. J'ai utilisé des traits relatifs à la disponibilité en ressources, et aux conditions environnementales subies par les individus. J'ai également intégré les conditions environnementales dans mes analyses, comme le contexte d'habitat et la variabilité interannuelle du climat, afin de mettre en évidence de potentiels interactions entre traits des espèces et conditions environnementales sur la synchronie locale entre espèces.

Impact des tendances temporelles sur la stabilité des communautés via la synchronie entre espèces à l'échelle régionale

Un des impacts majeurs des changements globaux est le déclin de la biodiversité, ou la diminution au cours du temps de l'abondance globale des espèces. La conséquence à terme d'un déclin d'abondance peut être la disparition de l'espèce, localement, régionalement ou globalement. Selon si les espèces en déclin sont également des espèces synchrones, le déclin de la biodiversité dû aux changements globaux pourrait avoir un effet déstabilisateur à large échelle, à cause de la perte d'une partie de la dynamique compensatoire générée par l'asynchronie entre espèces. Dans la 3^{ème} partie de ma thèse j'ai cherché à voir si on pouvait identifier des groupes d'espèces synchrones à l'échelle régionale, et si les tendances temporelles des espèces pouvaient affecter le potentiel de dynamiques compensatoires à l'échelle régionale. Dans le cas où les espèces en déclin se retrouveraient dans les mêmes groupes de synchronie, le déclin du aux perturbations anthropiques pourrait déstabiliser les communautés à l'échelle régionale à cause de l'extinction de groupes d'espèces synchrones et donc une diminution du potentiel de dynamiques compensatoires à l'échelle régionale.

Chapitre 1. Relation diversité-stabilité dans les communautés animales naturelles et l'impact de la dégradation des habitats

Contexte

Pour tester les prédictions des études théoriques, la relation diversité-stabilité a été abondamment étudiée, principalement en conditions expérimentale et sur des communautés de plantes. Ces études ont permis de mettre en évidence une relation positive entre la richesse des communautés de plantes et la stabilité de leur biomasse. Cet intérêt pour les plantes vient du rôle de la biomasse de plantes dans le fonctionnement des écosystèmes et les flux d'énergie, mais également du service écosystémique de la provision de nourriture pour l'être humain via l'agriculture. Cependant, ces résultats ne peuvent être généralisés à l'ensemble des communautés, notamment animales. Ensuite, en manipulant des assemblages d'espèces aléatoires, ces études expérimentales pourraient ne pas refléter les communautés naturelles. Enfin, dans le contexte des changements globaux, il faut intégrer les perturbations environnementales aux études sur la relation entre diversité et stabilité des communautés afin de comprendre comment ces perturbations peuvent affecter la stabilité temporelle des communautés. Dans ce 1^{er} chapitre, je me suis intéressé à la relation diversité – stabilité dans les communautés naturelles de trois taxons animaux, les chauves-souris, les oiseaux et les papillons. Ces taxons ont des rôles importants dans le fonctionnement des écosystèmes, comme la dispersion des graines, la pollinisation ou le contrôle des ravageurs. De plus, j'ai intégré deux perturbations environnementales qui sont la dégradation des habitats via l'intensification agricole et l'urbanisation, qui sont des perturbations anthropiques connues pour affecter les communautés.

Résultats

Dans cette étude j'apporte plusieurs résultats qui contribuent à la compréhension de la stabilité des communautés :

- Je mets en évidence une relation positive entre diversité et stabilité de l'abondance des communautés pour les trois taxons étudiés. Cette relation positive est trouvée pour la richesse spécifique comme pour la diversité phylogénétique, et passe principalement par un effet sur l'asynchronie entre les fluctuations des populations. Ce résultat renforce l'hypothèse que la diversité des réponses aux variations des conditions environnementales est un des principaux mécanismes de la relation diversité – stabilité. Favoriser la diversité de traits fonctionnels pourrait stabiliser les communautés animales.
- La relation entre la diversité et la stabilité des populations montre des résultats contrastés entre les taxons, avec une relation négative chez les oiseaux, l'absence de relation chez les chauves-souris et une relation positive chez les papillons.
- La dégradation des habitats via l'urbanisation et l'intensification agricole déstabilise les communautés des trois taxons étudiés, principalement en déstabilisant les populations qui constituent ces communautés plus qu'en affectant leur diversité.

Ces résultats suggèrent que pour maintenir des communautés stables en dépit des changements globaux, il est nécessaire de maximiser une diversité d'espèces capables de réagir différemment aux variations environnementales (hypothèse de l'assurance), et de maintenir des conditions d'habitats qui stabilisent les populations. Cela implique de comprendre précisément les traits de réponses des espèces qui concernent les réponses aux conditions environnementales, mais également les types de paysages qui maximisent la stabilité des populations.

Negative effects of habitat degradation and diversity loss on the stability of animal communities

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Abstract

Despite growing concern over consequences of global changes, we still know little about potential interactive effects of anthropogenic perturbations and diversity loss on the stability of local communities, especially for taxa other than plants. Here we show that habitat degradation and diversity loss both destabilize bat, bird and butterfly communities but in different ways: while diversity loss translates into greater population synchrony, habitat degradation mainly decreases population stability. In addition to highlight the stabilizing effects of diversity on ecologically important and overlooked taxa, our results further reveal new pathways linking anthropogenic activities to diversity and stability.

Keywords: Diversity, temporal stability, birds, bats, butterflies, natural communities, habitat degradation

Main Text

Temporal stability of biomass or abundance can vary greatly across local communities, and the causes of such variations remain poorly understood¹. The stability of plant and animal community abundances is important for the maintenance of ecosystem processes and services over time, as these communities are involved in key functions such as primary and secondary productions, pollination and pest control². In the past decades, research on the stability of community properties and ecosystem processes has mainly focused on consequences of ongoing biodiversity loss, often on plant communities^{2,3}, revealing a negative effect of diversity loss on the temporal stability of communities⁴⁻⁶. This destabilizing effect of diversity loss appears mainly related to lower asynchrony among population dynamics in species poor communities^{5,6}. Recently, a few studies brought to light the importance of other major anthropogenic changes, such as nutrient eutrophication and climate warming, on plant community stability and associated primary production⁷⁻¹⁰. While some of these studies highlight that anthropogenic changes affect ecosystem stability mainly via changes in biodiversity^{7,11}, other studies suggest independent effects of diversity and environmental changes on stability¹². Resolving this discrepancy is key to our understanding of the mechanisms by which global changes affect the stability of ecosystem functions and services¹³, and therefore to our ability to mitigate adverse effects. The elaboration of efficient conservation plans. Furthermore, while animal communities provide key ecosystem function and services, such as seed dispersal or pollination, the vast majority of published studies focused on plant communities, resulting in a knowledge gap regarding animal communities.

At a global scale, the conversion and degradation of habitats related to human activities are recognized as major drivers of local diversity loss, urban and intensive agricultural land-use being most detrimental¹⁴. Despite the paramount importance of habitat degradation on biodiversity, only a few recent studies have investigated the consequences of land-use intensity on the temporal stability of population abundances or community total abundances^{15,16}, i.e., the total number of individuals present in a community, across all species of this community.

To investigate the mechanisms by which diversity loss and habitat degradation affect community stability, we analyzed the inter-annual abundance fluctuations of 152 bat, 269 bird and 130 butterfly communities across France, monitored following standardized protocols over six, 17 and 11 years, respectively (Fig. 1, Supplementary Table 1, see Methods). While bats and insectivorous birds are recognized as important for pest control^{17,18}, butterflies contribute to pollination¹⁹ and frugivorous birds are essential for plant dispersal¹⁸. We analyzed the landscape surrounding these communities and distinguished two habitat degradation gradients reflecting (1) urbanization, with an increase of urban and sealed soil areas to the detriment of semi-natural and agricultural areas (hereafter, urbanization), and (2) agricultural intensification, with an increase of cropland areas and agricultural inputs to the detriment of landscape heterogeneity, woodland areas and semi-natural open areas (Supplementary Fig. 1-2, see Methods). We computed local community species richness and phylogenetic diversity (see Methods), as there is still debate on which aspect of diversity better relates to community stability^{20,21}. We then partitioned community stability, measured as the inverse of the coefficient of variation of community abundance across time, into a population asynchrony and a population stability component²² (see Methods). Those complementary components of community stability have different implications. Lower population stability increases species extinction risks while lower population asynchrony reduces the insurance effect of diversity on the provision of ecosystem functions and services²³. While both components appear to be key to the stability of experimental plant communities^{4,5}, their relative contributions to variations in stability of natural communities experiencing various perturbation regimes is poorly known. We used structural equation modeling to quantify how both components of community stability are affected by local diversity and habitat degradation, as well as to disentangle the direct and indirect (i.e. mediated by diversity changes) effects of habitat degradation on community stability (see Methods).

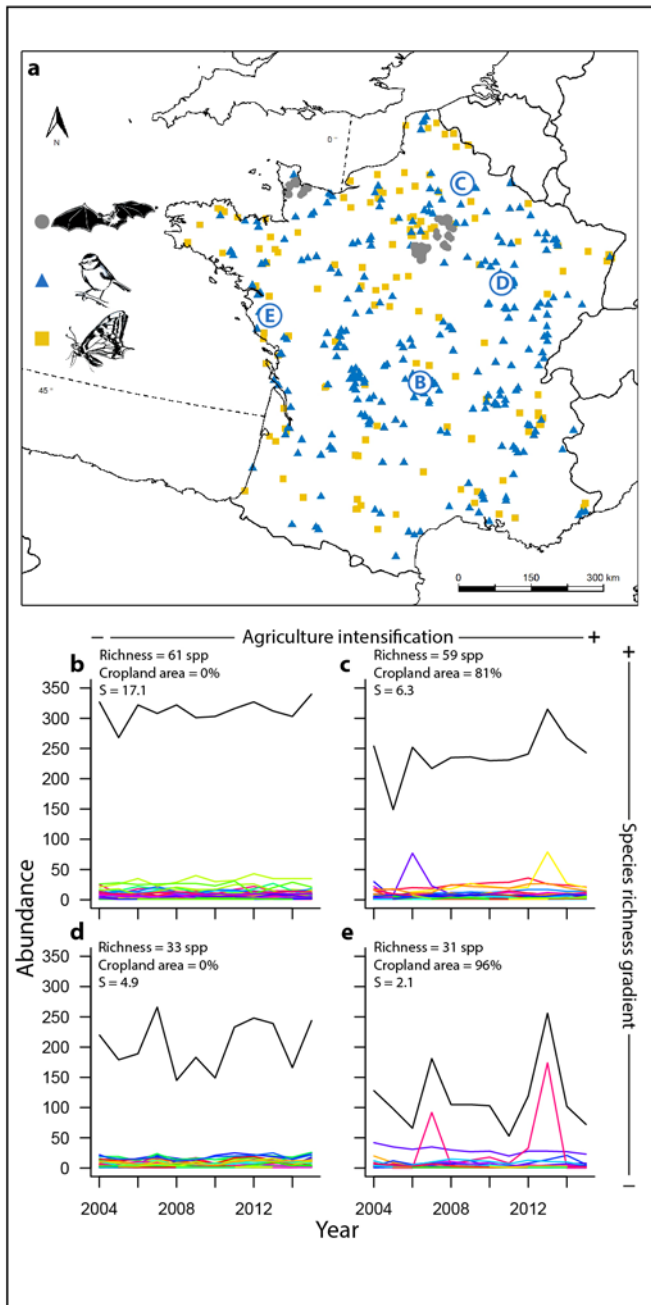


Fig. 1. Datasets. (a) Spatial distribution of the monitored bat, bird and butterfly communities across France. Circled letters correspond to the bird communities with contrasted levels of species richness and agricultural intensification plotted in (b), (c), (d), (e). Each colored line represents a given species abundance time series and black lines represent total community abundance time series. Richness, surrounding cropland area, and stability index (S , computed as the inverse of the coefficient of variation) of the total community abundance time series are given for each bird community.

Our results show that both diversity loss and habitat degradation destabilize communities (Fig. 2) with overall effects of similar magnitude (Table 1). The structural equation modelling further reveals that the loss of both species richness and phylogenetic diversity destabilizes bat, bird and butterfly communities, and that this is mainly channelled by a decrease in population asynchrony (Table. 1 and Supplementary Tables 2-4, Fig. 3 and Supplementary Fig. 3-5). This extends classical results found for experimental plant communities^{4,5} to animal taxa and brings new support to the phylogenetic insurance hypothesis²⁰, suggesting that phylogeny can be used as a proxy to assess the dynamical response of populations to environmental variations and perturbations. The effects of species richness and phylogenetic diversity on population stability are much weaker and more contrasted among the three taxa (Table 1 and Supplementary Tables 2-4, Fig. 3 and Supplementary Fig. 3-5), reflecting previous theoretical and experimental findings on plants and plankton, which predict varying diversity – population stability relationships depending on the community context considered^{24,25}.

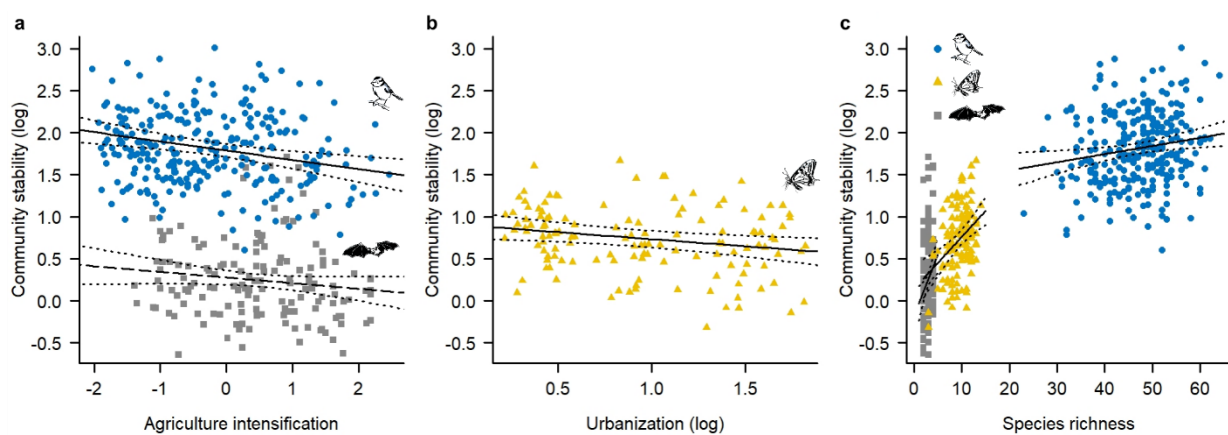





Fig. 2. Standard regression between community stability and agricultural intensification (a), urbanization (b) and local species richness (c) for bird (a, c), bat (a,c) and butterfly (b, b) communities. Solid and dashed lines represent significant and marginally significant (p -value = 0.06) regression lines, respectively. Non-significant relationships where p -value > 0.06 are not shown. Dotted lines correspond to associated 95% confidence intervals.

Table 1. Strength of the different paths by which diversity loss and habitat degradation affect the stability of bat, bird and butterfly local communities.

Effects on community stability			
Diversity loss:			
Total effects	-0.433	-0.224	-0.513
Richness effects	-0.195	-0.139	-0.347
Phylogenetic diversity effects	-0.238	-0.085	-0.166
Effects via population stability	NS	0.076	-0.172
Effects via population asynchrony	-0.433	-0.299	-0.341
Habitat degradation:			
Total effects	-0.320	-0.246	-0.319
Urbanization effects	-0.078	NS	-0.319
Agricultural intensification effects	-0.243	-0.246	NS
Effects via diversity	0.016	-0.028	-0.092
Effects via population stability	-0.336	-0.218	-0.227
Effects via population asynchrony	NS	NS	NS

Footnote: the strength of each path is calculated from the standardized coefficients of the structural equation models, multiplying coefficients along a path and summing the results over the different paths. Total effects refer to the sum of the effects by which species richness and phylogenetic diversity loss, or urbanization and agricultural intensification, affect community stability. Effects via a variable are the sum of the effects of diversity loss / habitat degradation on community stability that are channelled by a direct effect on this variable. NS stands for non-significant effects.

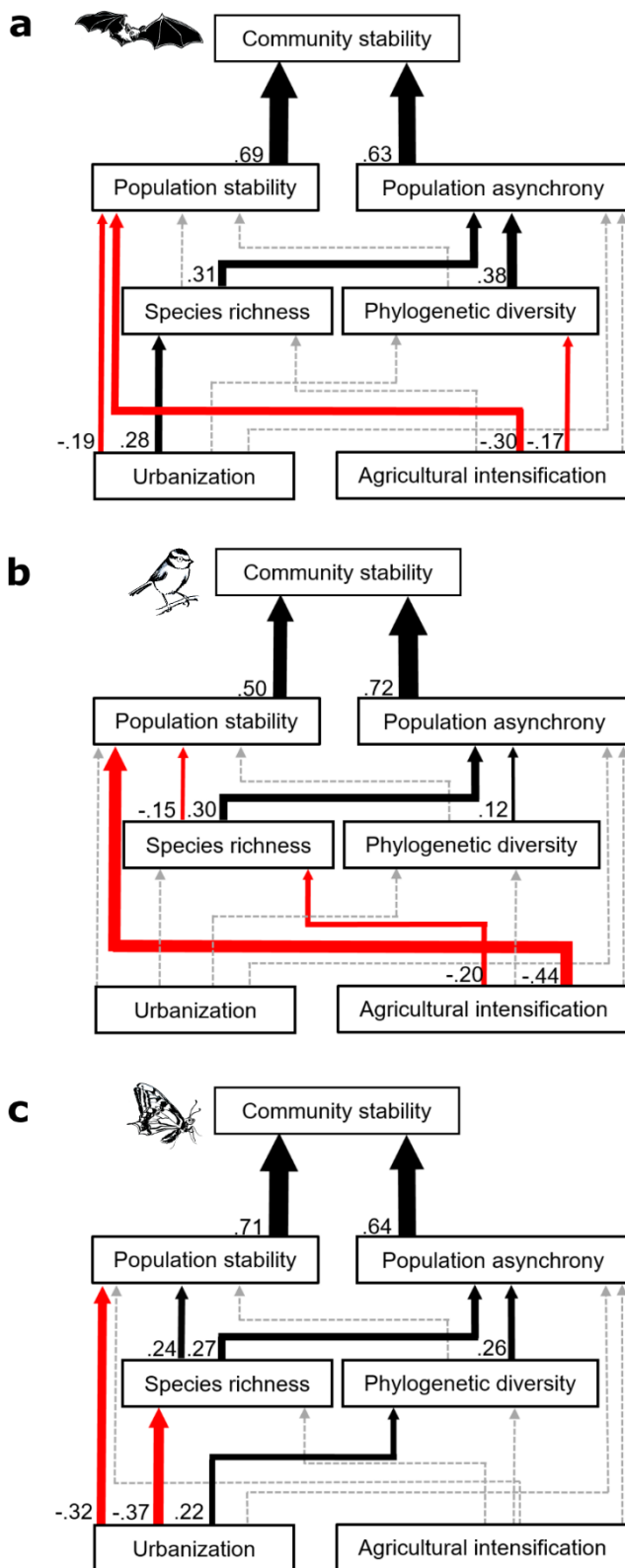


Fig. 3. Effects of habitat degradation and local diversity on community stability estimated by structural equation models, for (a) bat, (b) bird and (c) butterfly communities. Urbanization and agricultural intensification are independent variables while species richness, phylogenetic diversity, population stability, population asynchrony and community stability are dependent

variables. Black and red arrows represent positive and negative relationships, respectively, with relationship strength depicted by arrow width. Solid and grey dashed arrows represent significant relationships and non-significant relationships, respectively (Supplementary Tables 4, 6, 8, see Methods). Standardized coefficients are shown next to the arrow basis.

Our results further highlight that two major drivers of habitat degradation, urbanization and agricultural intensification, decrease community stability mainly via a decrease in population stability, this for all three taxa (Table 1, Fig. 3 and Supplementary Fig. 3-5). The mechanisms linking habitat degradation to population stability may be related to the diversity and availability of resources for species^{16,26}. Overall, less degraded habitats with more diverse and abundant resources such as food supply, nesting or breeding site, hunting territory are likely to result in larger and more stable populations. Mean population abundances of bats and butterflies decline in parallel with population stability in degraded habitats (Supplementary Fig. 7 and 9), reflecting the fact that mean population stability is lower in communities with low mean population abundance (Supplementary Fig. 6) as expected from Taylor's power law²⁷ (see Methods). For birds, however, the destabilizing effect of agriculture is not related to decreased mean population abundances, but to an increase in the temporal variance of populations in areas with intensive agricultural land-use (Supplementary Fig. 8). Moreover, while butterfly community stability is mainly impacted by urbanization, bird and bat communities are mostly destabilized by agricultural intensification (Fig. 2a-b, Table 1) as known from previous studies on butterflies²⁸ and birds^{29,30}. This result could also stem from different levels of habitat degradation as butterfly communities were sampled in more urbanized areas than were bird and bat communities (Supplementary Fig. 1-2).

Although habitat degradation directly affects the diversity of all three taxa, the effects of habitat degradation on community stability via population stability are 21, 8 and 2.5 times stronger than those mediated via its effects on diversity for bats, birds and butterflies, respectively (Table 1, Fig. 3 and Supplementary Fig. 3-5). These results contrast with previous findings on plants, butterflies and birds indicating that anthropogenic perturbations effects on community stability were mainly channelled by direct changes in diversity⁵ or population asynchrony¹⁵. Those contrasted findings across studies may stem from the fact that habitat

degradation affects the diversity of bat, bird and butterfly communities in slightly more complex and contrasted ways than it affects their stability. Agricultural intensification decreases bird community species richness, consistently with previous findings²⁹. While urbanization sharply decreases butterfly species richness, it slightly increases bird and butterfly community phylogenetic diversity and bat community species richness. Such positive effects have already been shown for moderate levels of urbanization, where urban exploiters and exotic species can mix with urbanophobe species^{31,32}. Such results also echo previous findings highlighting complex patterns of species richness variation along urbanization or agricultural gradients associated with non-random changes in community composition^{31,33}.

Our results extend to animals the classical diversity-stability relationship found for plants^{5,6} and further uncover a population-level destabilizing effect of habitat degradation. Moreover, by increasing the risks of extinction through the destabilization of populations, habitat degradation may also enhance the negative effect of diversity loss on community stability. Besides advancing our understanding of the stability of animal communities and thereby the functions and services they deliver, our findings are also relevant for biodiversity conservation and management as they identify different pathways affecting community stability on which conservation policies might act. Finally, by providing numerous long-term time series of local communities under real perturbation regimes, citizen science monitoring-programs emerge as a major tool to further our understanding of the dynamical consequences of current global change.

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Authors contributions

TO, CF, ET and BF designed the study; T.O. managed the datasets and performed the statistical analyses with contributions from ET, CF and BF; M.E. built the butterfly and the bird phylogenetic trees; all authors interpreted the results and participated in writing.

Competing interests

The authors declare no competing interests.

Data and materials availability

Upon acceptance, data and R code will be available on GitHub.

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Methods

Community dynamics datasets. Yearly butterfly, bird and bat abundance data were obtained across France from nationwide citizen science monitoring schemes, part of the “Vigie Nature” program [<http://vigienature.mnhn.fr/>].

For bat communities, we used data from the French bat-monitoring program [<http://vigienature.mnhn.fr/page/vigie-chiro>], a citizen-science program running since 2006³⁴. Briefly, volunteers record bat activity using ultrasound recorder while driving at a constant low-speed (25 ± 5 km/h) along 30 km circuits on low-traffic roads for security and representative of the different land-cover types in the area. These circuits are divided into ten 2-km transects where bats are recorded, separated by 1-km road portions where recording is not carried out. Surveys start 30 min after sunset and last approximately 1.5 h. Weather conditions have to be suitable for the survey to be carried out: no rain, wind speed below 7 m/s, temperature above 12°C. Bat activity is recorded through echolocation calls with ultrasound detectors connected to a digital recorder. Volunteers were trained to classify echolocation calls to the most accurate taxonomic level using Syrinx 2.6 [<http://SyrinxPC.com/>]³⁵. Data validation was done by program coordinators at MNHN for recordings with uncertain identification. Following previous works (e.g.³⁶), the abundance of each bat species in a 2-km road transect was defined as the number of bat pass per species (a bat pass corresponds to a trigger of the bat detector in time expansion). We used data from transects surveyed between June 15th and July 31st (seasonal bat activity peak) from four to six years between 2006 and 2012. This represented a total of 152 local bat communities, where a total of seven species were recorded (Supplementary Table1).

For bird communities, we used data from the French Breeding Bird Survey [<http://www.vigie-plume.fr/>]³⁷, a monitoring program relying on keen birdwatchers to count birds annually in a given plot. Plots are squares of 2x2km² randomly selected by the national coordinator, within which the surveyor places 10 points separated by at least 300m, in order to cover all the habitats present in the plot. Each plot is surveyed twice a year, the first session (to record non-migrant birds and short distance migrants) between April 1st and May 8th, the second (to record trans-saharian migrants) between May 9th and June 30th, with at least four weeks between both sessions. Surveying dates must be the same (+/- 5 days) every year, and counting takes place in the morning, starting 30 min after sunrise, with points always visited

in the same order. At each point, the volunteer spends 5 minutes recording all birds seen or heard. Following previous work (e.g.³⁷), yearly species abundance at a site was calculated as the sum of the maximum number of individuals detected per point over the two sessions. For this study, plots surveyed at least eight years between 2001 and 2017 were selected, representing 269 local bird communities and 75 common species (Supplementary Table 1).

For butterflies, we used data from the French garden butterfly observatory [<http://vigienature.mnhn.fr/page/operation-papillons>]³⁸. Participants identify and count Lepidoptera in gardens, from a closed list of 28 common species or species groups (27 butterflies and one common diurnal moth, *Macroglossum stellatarum*). Since some of the taxa targeted by this scheme group several look-alike species (“species groups”), we only kept the 13 butterflies and 1 moth identified at species level for our analyses (Supplementary Table 1). The temporal variability of the butterfly community restricted to these 14 species reflects that of the entire community (Supplementary Fig. 10). For each species, abundances are recorded monthly, as the maximum number of butterflies seen simultaneously during the month. Counting takes place from March to October, but for this study, gardens that had been monitored in July at least seven years between 2007 and 2018 were selected, except for the year 2014 for the butterfly dataset because of a crash of the database server, representing 130 local butterfly communities.

Our data selection presented and analyzed in the main text totalized 551 sites (DATASET 1), with variations in the number of years across sites and taxa. This leads to 65, 7 and 80 sites with time series of respectively 4, 5, and 6 years for bats; 3, 14, 37, 32, 29, 33, 49, 30, 30 and 12 sites with time series of respectively 8, 9, 10, 11, 12, 13, 14, 15, 16 and 17 years for birds; and 34, 12, 10, 17 and 57 sites with time series of respectively 7, 8, 9, 10 and 11 years for butterflies.

To test the robustness of our results to the presence of gaps in the time series, we also ran our analyses on two subsets of the dataset that included only time series of the same duration and with no missing year. The first subset was restricted to the longest fully overlapping observation period with no gap common to all sites, leading to times series of 4, 8 and 7 years for bats, butterflies and birds, respectively (DATASET 2). The second one was restricted to sites having the longest fully overlapping observation period with no gap, leading to time series of 5, 12 and 11 years, for bats, birds and butterflies, respectively. This last data selection

procedure reduced the number of sites included to 87, 106 and 57, for bats, birds and butterflies, respectively (DATASET 3). The analysis of the three datasets gave qualitatively similar results (Supplementary Tables 2 - 10), confirming the robustness of our results to both the presence of gaps and the number of communities studied.

Species richness and phylogenetic diversity of local communities. For each local community, we estimated the species richness as the total number of species seen in a community during the survey period. We also calculated the Chao index³⁹ to account for imperfect detections (Supplementary Fig. 14) with R package «vegan»⁴⁰. The use of either species richness estimates did not change qualitatively the results of the following analysis (Supplementary Tables 2-10) and only species richness is presented in the main text. We assessed the phylogenetic diversity of each community using the Mean Pairwise Distance index (MPD) weighted by species abundances⁴¹. As the weighted MPD was correlated to species richness for bat and butterfly communities, all analyses were performed using the residuals of the weighted MPD against the species richness (Supplementary Fig. 15).

The weighted MPD calculations were based on ultrametric molecular phylogenetic trees⁴². For bats we used the phylogenetic tree provided by Shi & Raboski (2015)⁴³ (Supplementary Fig. 11). For birds we extracted 1000 trees from the phylogeny published by Jetz et al. (2012)⁴⁴ and computed the Maximum Clade Credibility tree with branch lengths equal to the median of the branch lengths of the 1000 trees using TreeAnnotator 1.7.5⁴⁵ and without burnin. The resulting tree was well supported, with 93% of the nodes having a Bayesian Posterior Probability > 0.9 (Supplementary Fig. 12). For butterflies, we downloaded published sequences for the following genes: cytochrome oxidase c subunit 1 (COI, 657 bp), elongation factor 1 alpha (EF1 α , 1239 bp), glyceraldehyde 3-phosphate dehydrogenase (GAPDH, 690 bp), ribosomal protein S5 (RPS5, 616 bp), wingless (wg, 402 bp) (Supplementary Table 11). Sequences were aligned using CodonCode Aligner 6.0.2 [<http://www.codoncode.com>], and the different genes were concatenated. Phylogenetic analyses were performed in a Bayesian framework using BEAST 1.8.1. The dataset was partitioned by gene. Unlinked GTR+ Γ model of nucleotide substitution and uncorrelated lognormal clocks were implemented for all partitions. The MCMC analysis was run for 100 million generations, and sampled every 100,000 generation, which resulted in 1000 trees. After checking for convergence, we applied

a 10% burnin and extracted the Maximum Clade Credibility tree with branch lengths equal to the median of those of all trees using Tree Annotator 1.8.1⁴⁵. Because in preliminary runs Papilionoideae monophyly was not recovered (basal relationships were poorly resolved), we enforced monophyly for this group. The MCC tree where Papilionoideae monophyly was enforced was well resolved, with all Bayesian posterior probabilities >0.99 (Supplementary Fig. 13).

Community stability, population stability and population asynchrony. To investigate the mechanisms by which habitat degradation and community diversity might affect the stability of local communities, we calculated the temporal stability of each of these communities as the inverse of the coefficient of variation of the community abundance across time. The temporal stability of a community abundance decreases when the coefficient of variation of the community abundance increases. To quantify the respective contribution of population asynchrony and stability to community stability, we followed Thibaut & Connolly (2013)²² and partitioned the coefficient of variation of community abundance CV into the product of an index of population synchrony φ developed by Loreau & de Mazancourt (2008)⁴⁶ and the mean coefficient of variation of the population abundance (mean population variability) weighted by their relative abundances \overline{CV}_w , as:

$$CV = \overline{CV}_w \sqrt{\varphi} \quad (1)$$

With:

$$\overline{CV}_w = \sum_i \frac{\mu_i \sigma_i}{\mu \mu_i} = \sum_i \frac{\mu_i}{\mu} CV_i$$

And:

$$\varphi = \frac{\sigma^2}{(\sum_i \sigma_i)^2}$$

With σ^2 representing the variance of the abundance of the community, σ_i the standard deviation of the abundance of the population i in the community, μ the temporal mean of the abundance of the community, μ_i the temporal mean of the abundance of the population i and CV_i the coefficient of variation of the abundance of population i . The population synchrony

index φ ranges from 0 (maximum asynchrony) to 1 (maximum synchrony). To get an asynchrony index that increases with population asynchrony, and population and community indices that increase with population and community stability, respectively, we used the inverses of the synchrony index and of the weighted mean coefficient of variation of population abundance. To achieve normality, we log-transformed the coefficient of variation of community, the coefficient of variation of population and the synchrony index for the three taxa.

Following equation (1), we always have:

$$\text{Community stability} = \frac{1}{2} \text{Population asynchrony} + \text{Population stability}$$

Where

$$\text{Community stability} = -\log(\text{CV}),$$

$$\text{Population asynchrony} = -\log(\varphi) \text{ and}$$

$$\text{Population stability} = -\log(\overline{CV_w}).$$

Assessing habitat degradation. To characterize and quantify habitat degradation, we first used Corine Land Cover 2006 [<https://www.data.gouv.fr/fr/datasets/corine-land-cover-occupation-des-sols-en-france/>] to quantify the percentages of cover occupied by five land-use categories within buffers surrounding the study sites: urban, cropland, heterogeneous agriculture, woodland and semi-natural open areas (Supplementary Table 12).

Second, to account for the intensity of both urban and agricultural land uses, we calculated the area of sealed soil from the European Soil Sealing V2 [<http://www.eea.europa.eu/data-and-maps/explore-interactive-maps/european-soil-sealing-v2>] (hereafter, urbanization) and an index of agricultural practice intensity (hereafter, agricultural intensification) following the European Union agri-environmental indicator of intensification-extensification [http://ec.europa.eu/eurostat/statistics-explained/index.php/Agri-environmental_indicator_-_intensification_-_extensification]. This last indicator is defined as the sum of expenses in k€ for fertilizers, pesticides, livestock food and veterinarian medics per year. It was calculated for each year and administrative region using data from the Agricultural Network of Account Information (RICA) [<http://agreste.agriculture.gouv.fr/enquetes/reseau-d-information-comptable/>]. For each site, we took the mean over the 2006-2013 period of the administrative region where the site was located.

Third, to account for landscape complexity, we calculated a Shannon diversity index on the area of each land-use category of the level 3 of Corine land cover 2006 (Supplementary Table 12).

To calculate the area and percentage of cover associated to each of our landscape variables, we used 3 buffer sizes per taxa: buffers of radius 250, 500 and 1000m around the transect for bat and around the garden for butterfly communities, and squares of 2, 2.5 and 3km of side for bird communities. These differences in size and shape among taxa accommodate for the shape of the sampled area and the scale at which landscape is known to affect those taxa^{34,47,48}. The use of either of the 3 buffer sizes in our statistical analyses (see below) did not change qualitatively our results (Supplementary Table 2-10).

For each time series selection we performed a Principal Component Analysis (PCA) on all these landscape variables for all the monitored communities, followed by a Varimax rotation⁴⁹ to ease the interpretation. The two first dimensions were used to characterize habitat degradation by an urbanization and an agricultural intensification gradients. These two first dimensions accounted for 28.4 and 23.4 percent of the total variation for both the dataset used in the main text and the dataset with short uninterrupted time series (Supplementary Fig. 1), and for 29.4 and 24.2 percent of the overall variation for the dataset with long uninterrupted time series (Supplementary Fig. 2). To achieve normality, we log-transformed the urbanization gradient for the three taxa and for the two PCA.

Statistical analysis. To assess the relationship between habitat degradation and community stability, we first fitted for each taxonomic group (1) a linear model with the two habitat degradation gradient as explanatory variables (Fig. 2a-b) and (2) a linear model with species richness as explanatory variable (Fig. 2c).

To quantify the direct and indirect effects of habitat degradation on community stability, structural equation modeling was performed in two steps:

First, for each taxonomic group and related buffer sizes, we built a set of 5 linear models to assess the effects of urbanization and agricultural intensification on species richness (model 1) and phylogenetic diversity (model 2), the effects of urbanization, agricultural intensification, species richness and phylogenetic diversity on population stability (model 3) and asynchrony (model 4), and the effects of the population stability and asynchrony on community stability (model 5).

Second, to disentangle direct and indirect relationships among variables, and compare the strength of significant relationships, we conducted piecewise Structural Equation Modeling (SEM)⁵⁰ for each taxonomic group and related buffer size. We used Shipley's test of d-separation to assess the overall fit of the SEM⁵¹. The strength of a path from a variable on another is the product of the strength of each significant relationship along the path. The overall effect of a variable on another one is the sum of the paths joining the two variables. For each taxon, the analysis presented in the main text correspond to that performed with the buffer size leading to the lowest AIC. All results remain qualitatively similar for all scales (Supplementary Tables 2-10).

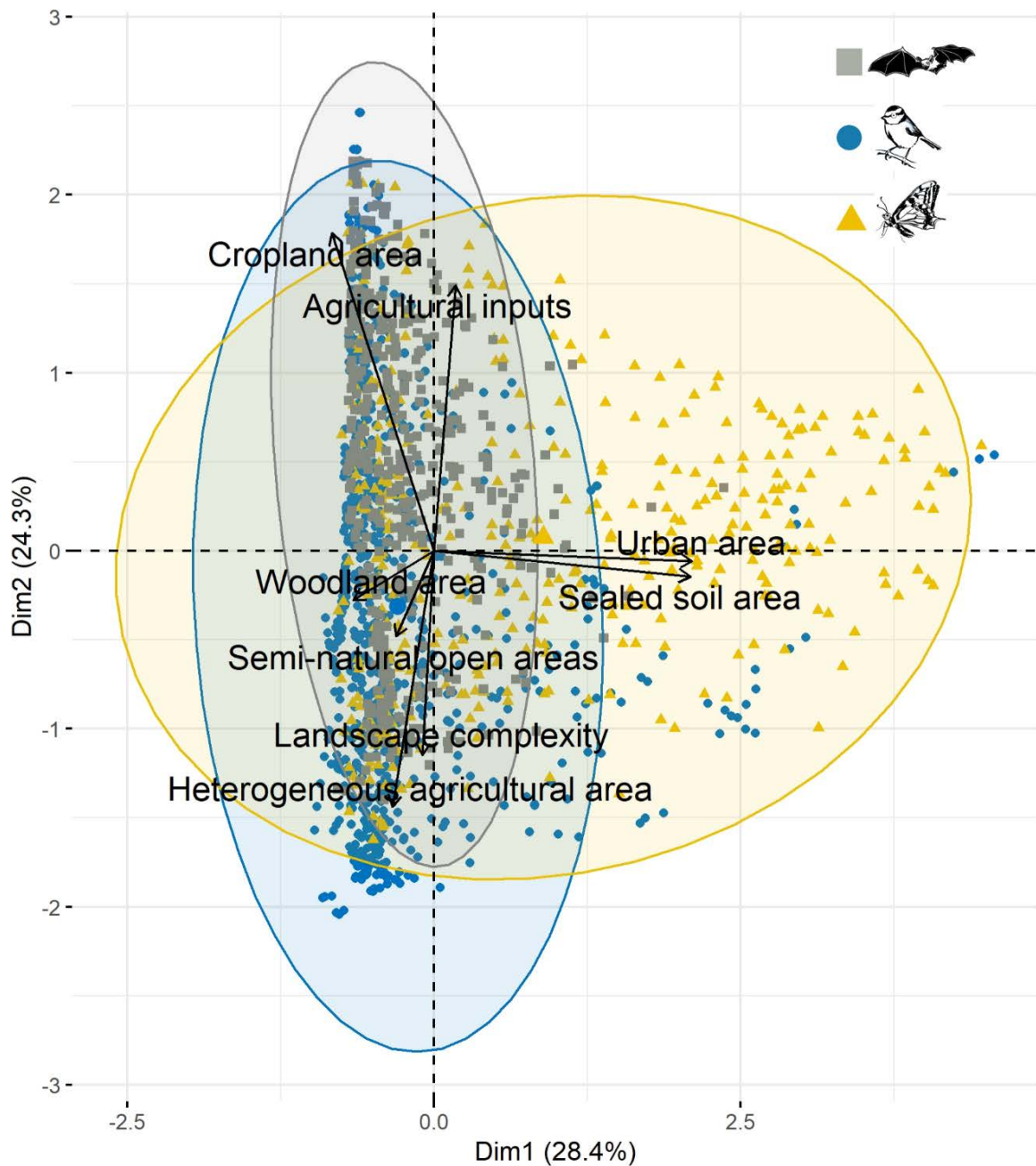
For all statistical analyses, spatial autocorrelation was accounted for. For bird and butterfly communities we used generalized least squares with exponential and gaussian spatial correlation structures respectively⁵². Because bat communities were aggregated in two distinct geographical regions, we used linear mixed-models with region as random effect (Ile-de-France or Manche)⁵².

To further our understanding of the effect of habitat degradation on population stability, we estimated the mean-variance scaling for each taxon by performing a linear mixed-model explaining the log of the variance of population abundances by the log of the mean population abundances, with both species and site as a random effect. We found a slope of 1.61-/+ 0.029 for bats, 1.09-/+ 0.004 for birds and 1.09-/+ 0.018 for butterflies, meaning that the stability of communities increases with the mean population abundance of the communities²². We verified these predictions by looking at the relationships between the temporal stability of populations and the mean population abundance for each taxon using linear models identical to those used in the path analyses (Supplementary Fig. 6). In addition, we tested whether habitat degradation gradients were correlated to either the mean population abundance of the communities or its standard deviation (Supplementary Fig. 7-9). Statistical analyses were performed using the R software⁵³, with libraries «PiecwiseSEM v1.2.0»⁵⁰, «nlme»⁵⁴, «picante»⁵⁵, «ape»⁵⁶, «ade4»⁵⁷, «lmerTest»⁵⁸.

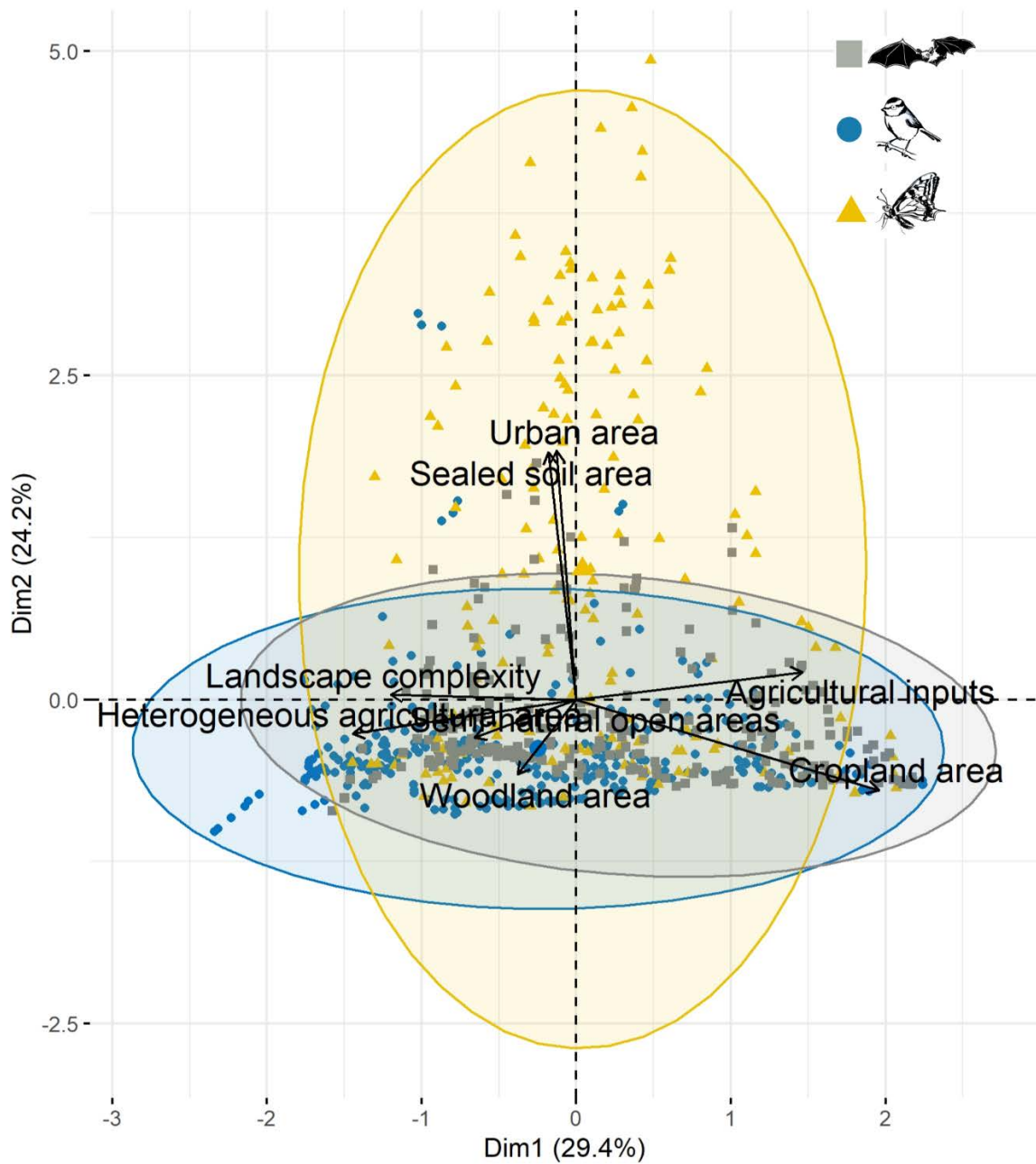
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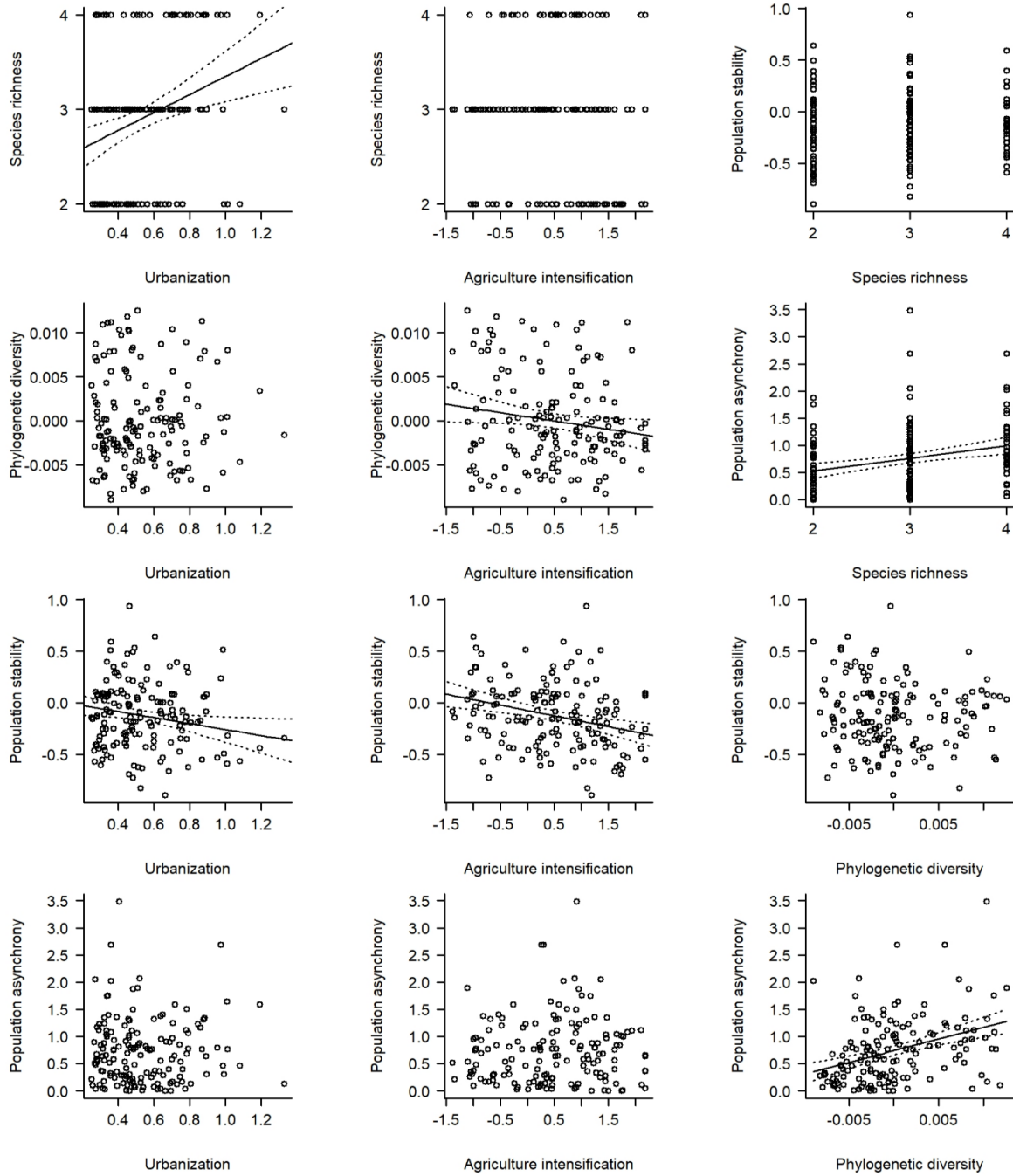
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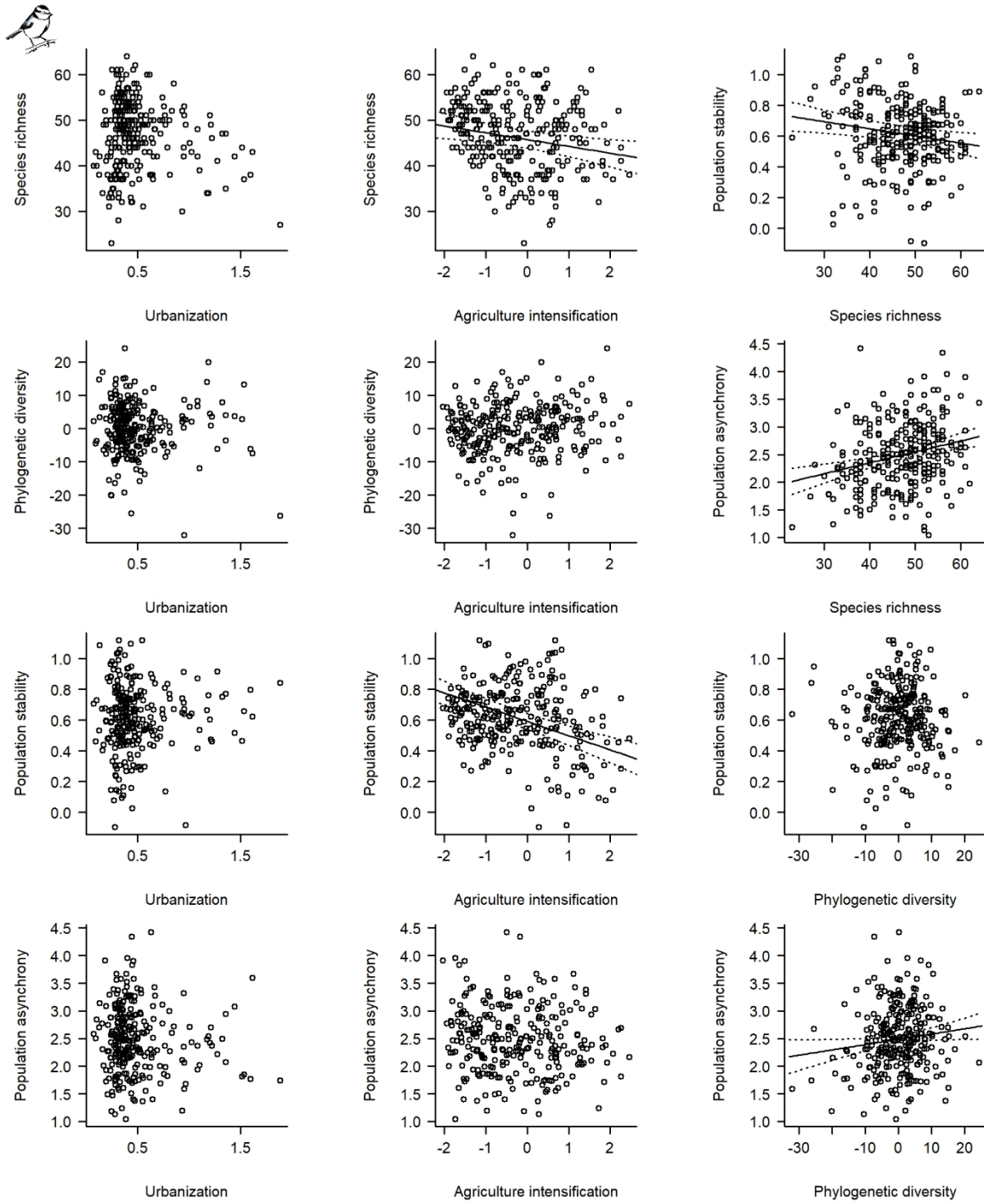
Supplementary Fig. 1. Graphical representation of the 2 first axis of the Principal Component Analysis for datasets that include 551 sites. Each point is a site and each ellipse contains 95% of the sites of the corresponding colored taxa. Each axis is a linear combination of the explanatory variables. Each arrow corresponds to the contribution of the variable to the two axes.



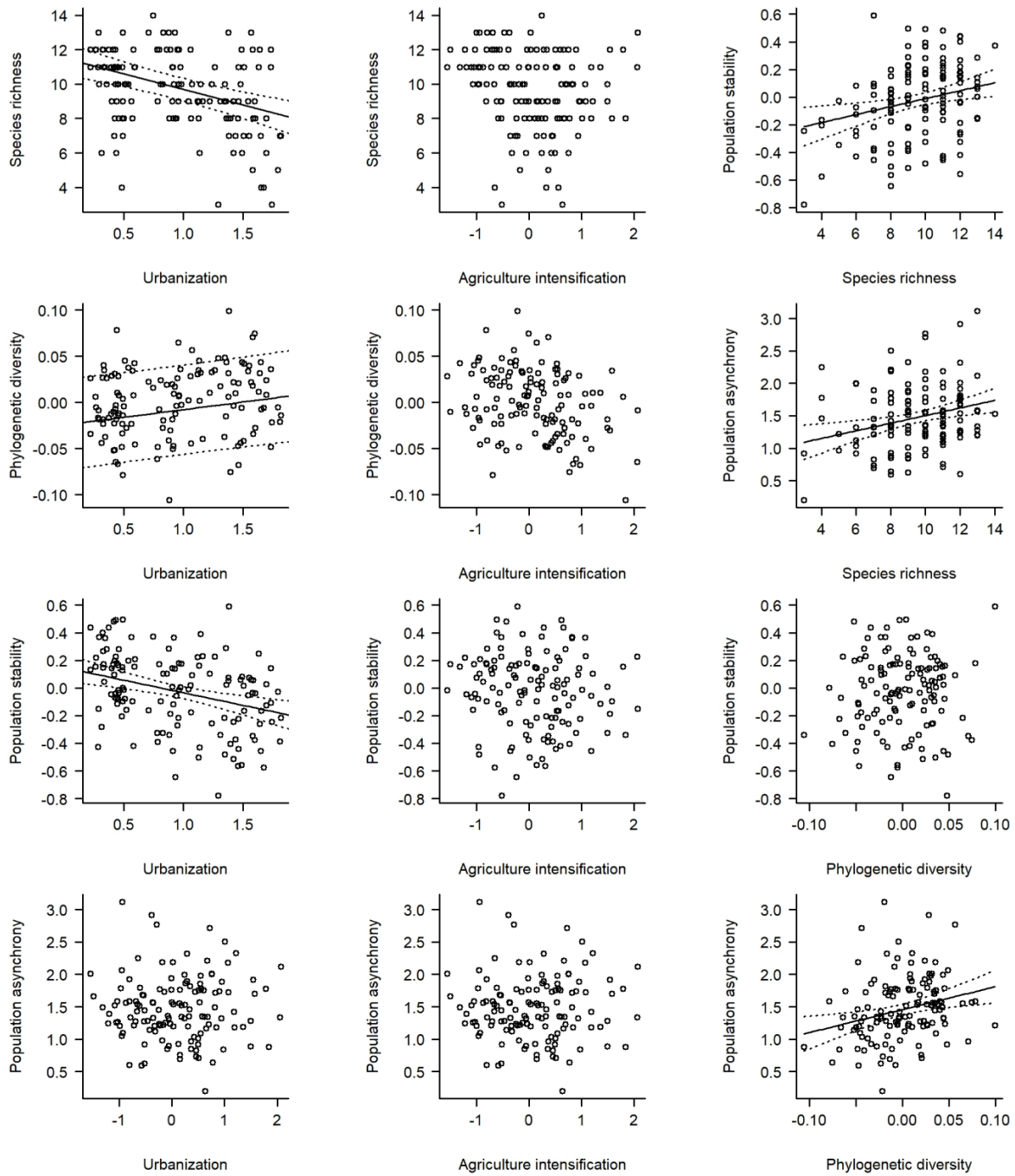
Supplementary Fig. 2. Graphical representation of the 2 first axis of the Principal Component Analysis for dataset with the longest time series without gap. Each point is a site and each ellipse contains 95% of the sites of the corresponding colored taxa. Each axis is a linear combination of the explanatory variables. Each arrow corresponds to the contribution of the variable to the two axes.



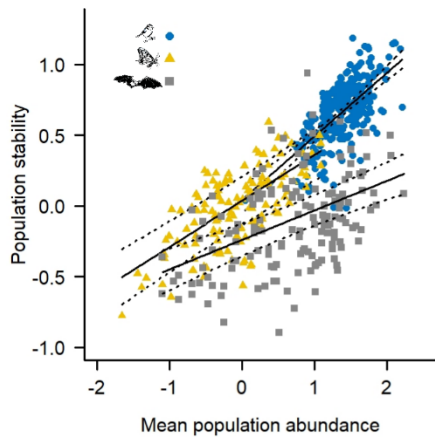
Supplementary Fig. 3. Relationships tested in the structural equation model used for bat communities. Significant relationships and their 95% confidence intervals are represented by solid and dotted lines respectively. Population stability, asynchrony and urbanization are log-transformed.



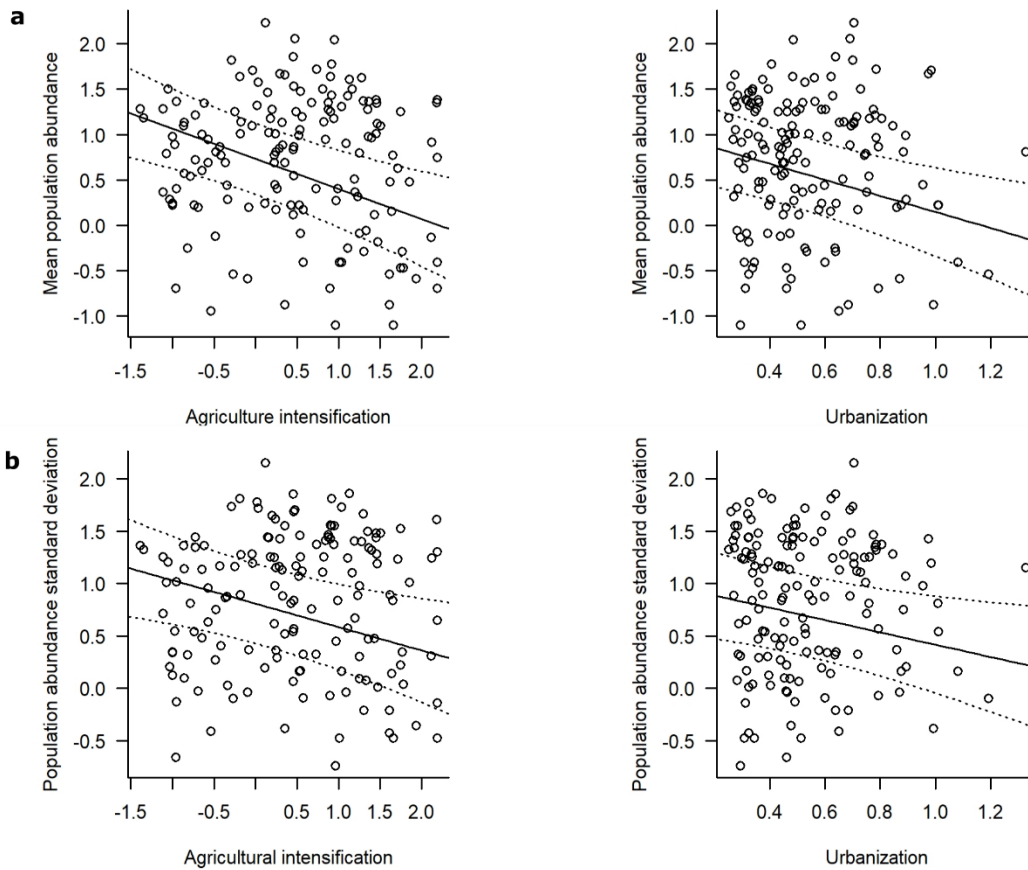
Supplementary Fig. 4. Relationships tested in the structural equation model used for bird communities. Significant relationships and their 95% confidence intervals are represented by solid and dotted lines respectively. Population stability, asynchrony and urbanization are log-transformed.



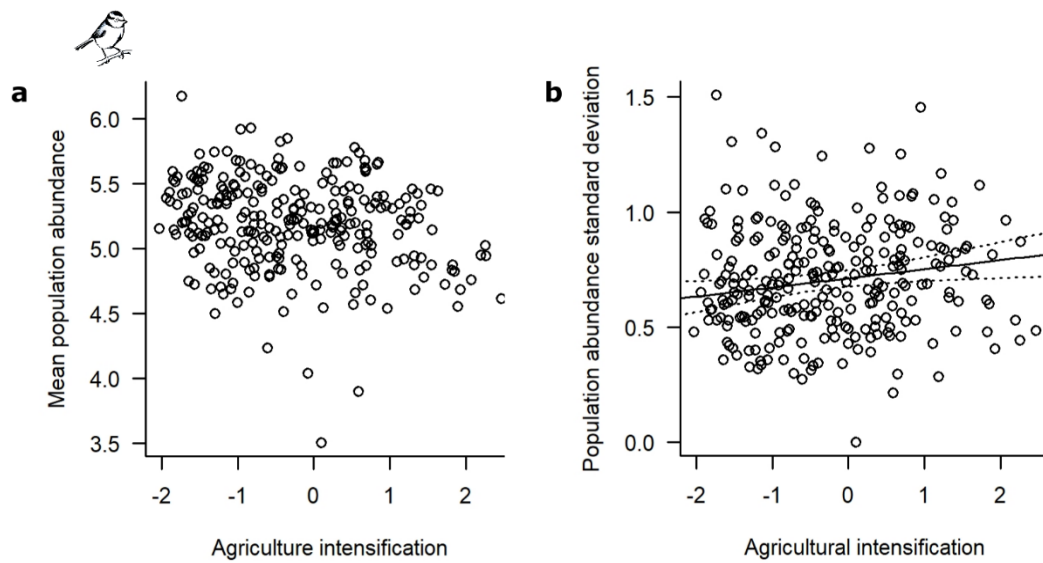
Supplementary Fig. 5. Relationships tested in the structural equation model used for butterfly communities. Significant relationships and their 95% confidence intervals are represented by solid and dotted lines respectively. Population stability, asynchrony and urbanization are log-transformed.



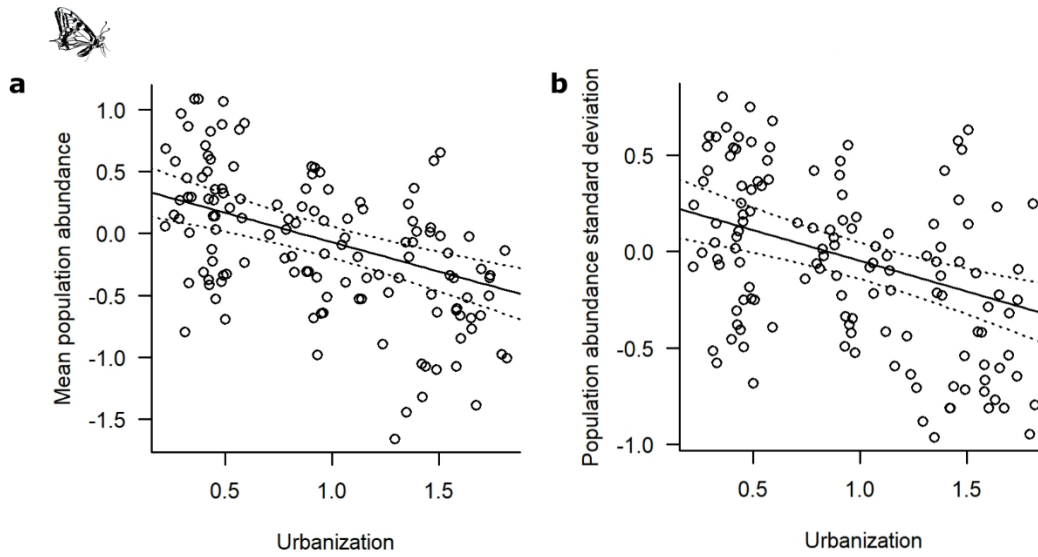
Supplementary Fig. 6. Relationships between population stability and community mean population abundance for bird, bat and butterfly communities. Black lines represent significant relationships and dotted lines represent 95% confidence intervals. Population stability and community mean population abundance are log-transformed.



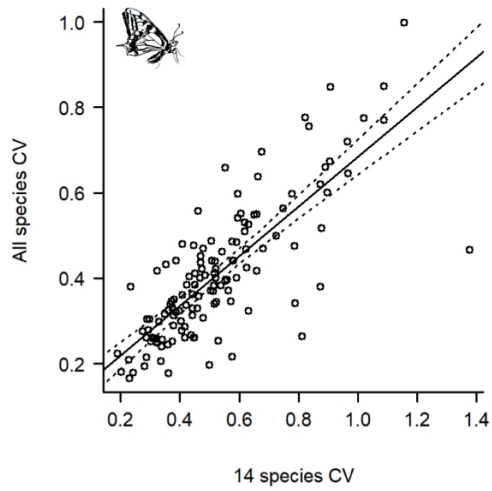
Supplementary Fig. 7. Relationships between habitat degradation and the community mean population abundance (a) and the average standard deviation of population abundances (b) for bat communities. Significant relationships and their 95% confidence intervals are represented by solid and dotted lines respectively. The community mean population abundance and the average standard deviation of population abundances are log-transformed.



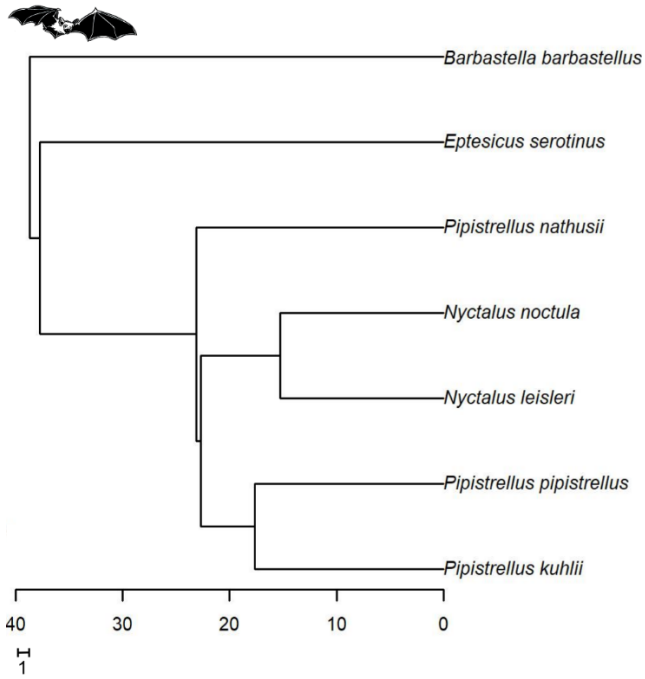
Supplementary Fig. 8. Relationships between habitat degradation and the community mean population abundance (a) and the average standard deviation of population abundances (b) for bird communities. Significant relationships and their 95% confidence intervals are represented by solid and dotted lines respectively. The community mean population abundance and the average standard deviation of population abundances are log-transformed.



Supplementary Fig. 9. Relationships between habitat degradation and the mean population abundance (a) and the average standard deviation of population abundances (b) for butterfly communities. Significant relationships and their 95% confidence intervals are represented by solid and dotted lines respectively. The community mean population abundance and the average standard deviation of population abundances are log-transformed.



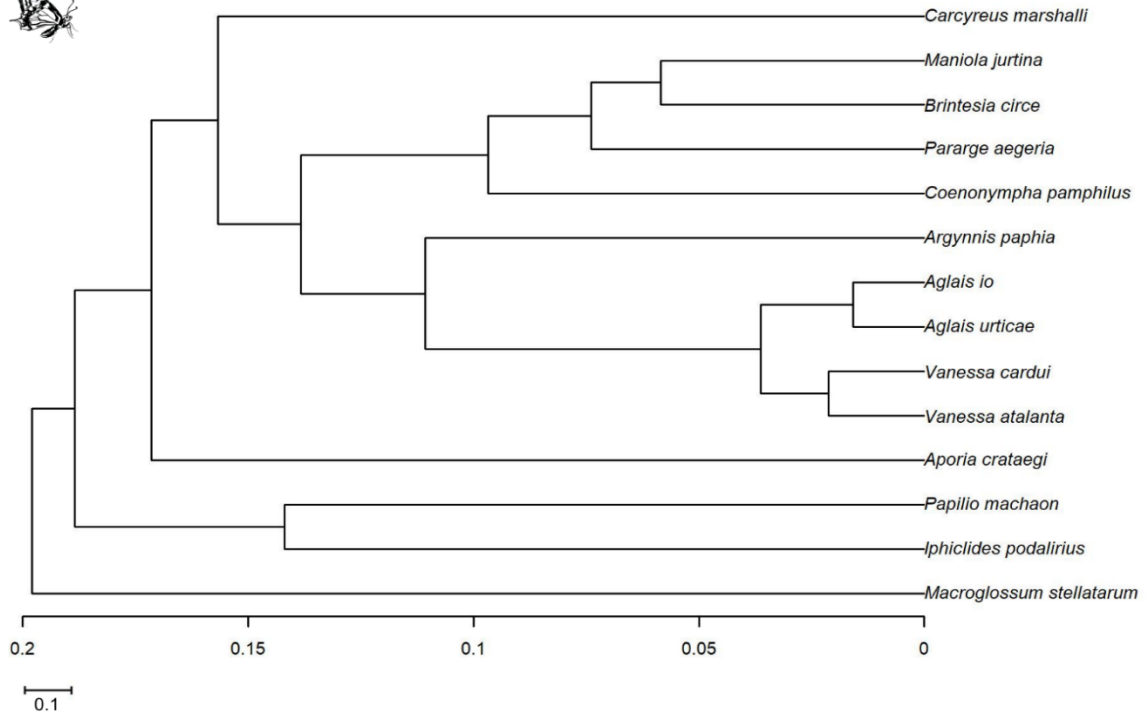
Supplementary Fig. 10. Relationship between the coefficients of variation of the total abundance of the entire butterfly communities and the butterfly communities restricted to the 14 species that could be identified with certainty (estimate = 0.58, p -value <0.001). Regression line and its 95% confidence intervals are represented by solid and dotted lines.



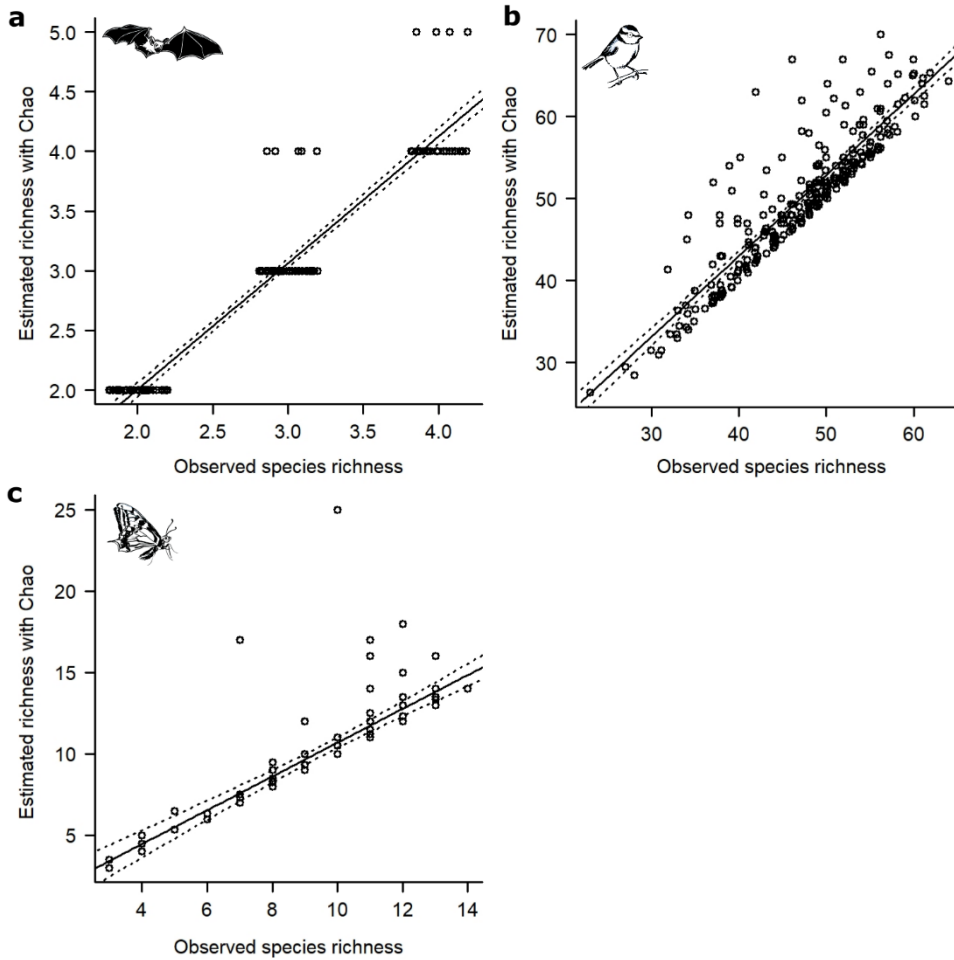
Supplementary Fig. 11. Phylogenetic tree of bat species present in our communities, based on Shi & Rabowski⁴³. Branch lengths are in number of substitutions per nucleotide.



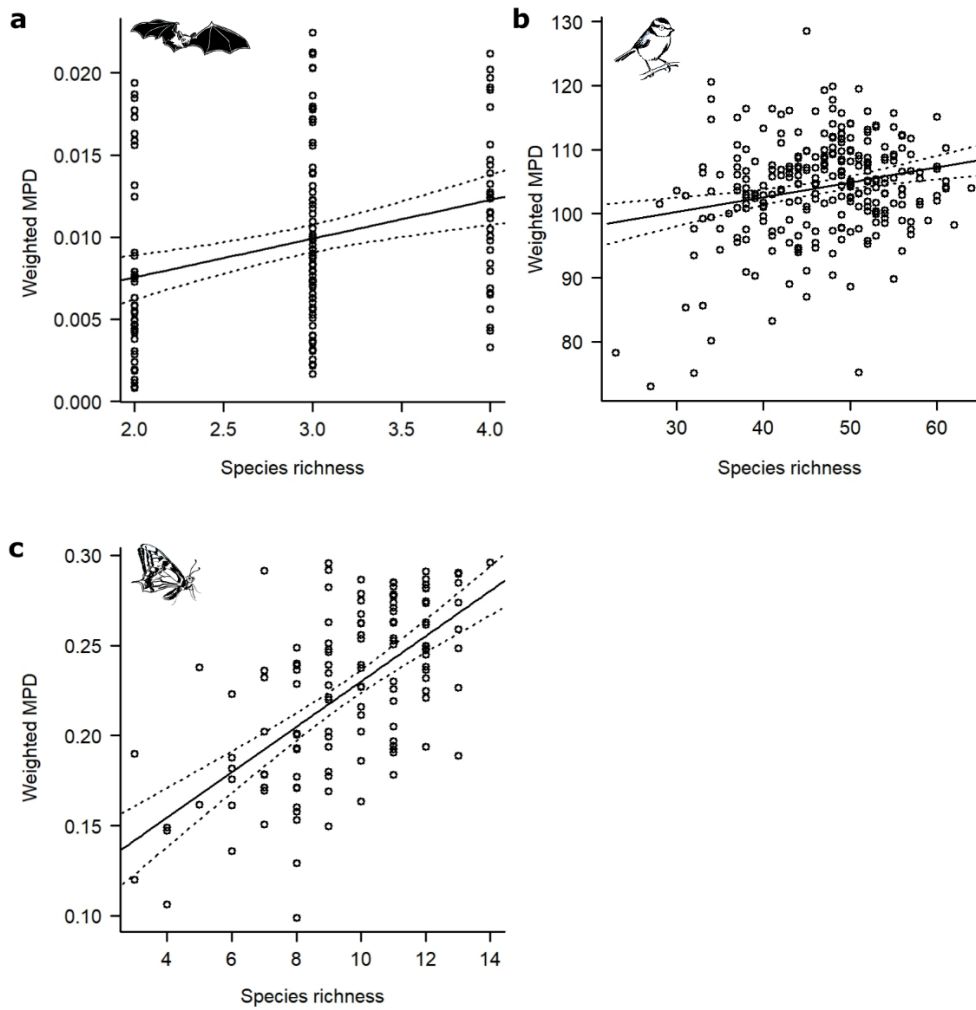
Supplementary Fig. 12. Phylogenetic tree of bird species present in our communities. Branch lengths are in millions years.



Supplementary Fig. 13. Phylogenetic tree of butterfly species present in our communities. Branch lengths are in number of substitutions per nucleotide.



Supplementary Fig. 14. Relationship between species richness and Chao index for local communities of (a) bats (estimate = 1.06, p-value < 0.001), (b) birds (estimate = 0.98, p-value < 0.001) (c) and butterflies (estimate = 1.04, p-value < 0.001). Regression lines and their 95% confidence intervals are represented by solid and dotted lines respectively.



Supplementary Fig. 15. Relationship between species richness and mean phylogenetic distance for local communities of (a) bats (estimate = 0.002, p -value <0.001), (b) birds (estimate = 0.23, p -value <0.001) (c) and butterflies (estimate = 0.01, p -value <0.001). Regression lines and their 95% confidence intervals are represented by solid and dotted lines respectively for significant relationships. The Weighted MPD is in million years for birds and in number of substitutions per nucleotide for bats and butterflies.

Supplementary Table 1. Species for bat, bird and butterfly local communities.



<i>Nyctalus leisleri</i>	<i>Coturnix coturnix</i>	<i>Regulus ignicapilla</i>	<i>Macroglossum stellatarum</i>
<i>Nyctalus noctula</i>	<i>Alectoris rufa</i>	<i>Regulus regulus</i>	<i>Iphiclides podalirius</i>
<i>Eptesicus serotinus</i>	<i>Perdix perdix</i>	<i>Phylloscopus bonelli</i>	<i>Papilio machaon</i>
<i>Pipistrellus pipistrellus</i>	<i>Buteo buteo</i>	<i>Phylloscopus collybita</i>	<i>Aporia crataegi</i>
<i>Pipistrellus nathusii</i>	<i>Vanellus vanellus</i>	<i>Phylloscopus sibilatrix</i>	<i>Cacyreus marshalli</i>
<i>Pipistrellus kuhlii</i>	<i>Columba palumbus</i>	<i>Phylloscopus trochilus</i>	<i>Argynnis paphia</i>
<i>Barbastella barbastellus</i>	<i>Streptopelia decaocto</i>	<i>Hippolais polyglotta</i>	<i>Aglais io</i>
	<i>Cuculus canorus</i>	<i>Sylvia atricapilla</i>	<i>Aglais urticae</i>
	<i>Apus apus</i>	<i>Sylvia communis</i>	<i>Vanessa atalanta</i>
	<i>Upupa epops</i>	<i>Sylvia melanocephala</i>	<i>Vanessa cardui</i>
	<i>Dendrocopos major</i>	<i>Erithacus rubecula</i>	<i>Pararge aegeria</i>
	<i>Dendrocopos medius</i>	<i>Luscinia megarhynchos</i>	<i>Coenonympha pamphilus</i>
	<i>Dryocopus martius</i>	<i>Phoenicurus ochrurus</i>	<i>Maniola jurtina</i>
	<i>Picus canus</i>	<i>Phoenicurus phoenicurus</i>	<i>Brintesia circe</i>
	<i>Picus viridis</i>	<i>Saxicola rubetra</i>	
	<i>Falco tinnunculus</i>	<i>Saxicola rubicola</i>	
	<i>Lanius collurio</i>	<i>Oenanthe oenanthe</i>	
	<i>Oriolus oriolus</i>	<i>Turdus merula</i>	
	<i>Garrulus glandarius</i>	<i>Turdus philomelos</i>	
	<i>Pica pica</i>	<i>Turdus viscivorus</i>	
	<i>Corvus corone</i>	<i>Prunella modularis</i>	
	<i>Corvus frugilegus</i>	<i>Motacilla flava</i>	
	<i>Corvus monedula</i>	<i>Anthus campestris</i>	
	<i>Lullula arborea</i>	<i>Anthus pratensis</i>	
	<i>Alauda arvensis</i>	<i>Emberiza calandra</i>	
	<i>Galerida cristata</i>	<i>Emberiza cirrus</i>	
	<i>Hirundo rustica</i>	<i>Emberiza citrinella</i>	
	<i>Delichon urbicum</i>	<i>Emberiza hortulana</i>	
	<i>Periparus ater</i>	<i>Fringilla coelebs</i>	
	<i>Lophophanes cristatus</i>	<i>Coccothraustes</i>	
	<i>Poecile palustris</i>	<i>coccothraustes</i>	
	<i>Cyanistes caeruleus</i>	<i>Pyrrhula pyrrhula</i>	
	<i>Parus major</i>	<i>Carduelis cannabina</i>	
	<i>Parus montanus</i>	<i>Carduelis carduelis</i>	
	<i>Sitta europaea</i>	<i>Carduelis chloris</i>	
	<i>Certhia familiaris</i>	<i>Serinus serinus</i>	
	<i>Certhia brachydactyla</i>	<i>Passer domesticus</i>	
	<i>Troglodytes troglodytes</i>	<i>Passer montanus</i>	

Supplementary Table 2. Strength of the different paths by which diversity and habitat degradation affect the stability of local communities of bats, using species richness observed or estimated by Chao index, for the three buffer sizes and the three data selections.

	Observed species richness			Estimated species richness		
	DATASET 1					
Effects on community stability	250m	500m	1000m	250m	500m	1000m
Diversity loss:						
Total effects	-0.436	-0.433	-0.415	-0.454	-0.452	-0.435
Richness effects	-0.201	-0.195	-0.175	-0.204	-0.200	-0.182
Phylogenetic diversity effects	-0.235	-0.238	-0.240	-0.249	-0.252	-0.253
Effects via population stability	NS	NS	NS	NS	NS	NS
Effects via population asynchrony	-0.436	-0.433	-0.415	-0.454	-0.452	-0.435
Habitat degradation:						
Total effects	-0.278	-0.320	-0.304	-0.277	-0.320	-0.190
Urbanization effects	-0.077	-0.078	-0.063	-0.077	-0.076	0.052
Agricultural intensification effects	-0.201	-0.243	-0.242	-0.201	-0.244	-0.242
Effects via diversity	0.053	0.016	0.015	0.048	0.010	0.009
Effects via population stability	-0.331	-0.336	-0.319	-0.326	-0.330	-0.200
Effects via population asynchrony	NS	NS	NS	NS	NS	NS
	DATASET 2					
Effects on community stability	250m	500m	1000m	250m	500m	1000m
Diversity loss:						
Total effects	-0.476	-0.466	-0.442	-0.466	-0.457	-0.434
Richness effects	-0.212	-0.201	-0.177	-0.187	-0.178	-0.156
Phylogenetic diversity effects	-0.263	-0.264	-0.265	-0.278	-0.279	-0.278
Effects via population stability	NS	NS	NS	NS	NS	NS
Effects via population asynchrony	-0.476	-0.466	-0.442	-0.466	-0.457	-0.434
Habitat degradation:						
Total effects	-0.336	-0.340	-0.215	-0.339	-0.230	-0.186
Urbanization effects	-0.066	-0.063	0.056	-0.071	0.045	0.053
Agricultural intensification effects	-0.270	-0.277	-0.271	-0.268	-0.275	-0.240
Effects via diversity	0.055	0.055	0.056	0.044	0.045	0.082
Effects via population stability	-0.391	-0.395	-0.271	-0.383	-0.275	-0.268
Effects via population asynchrony	NS	NS	NS	NS	NS	NS
	DATASET 3					
Effects on community stability	250m	500m	1000m	250m	500m	1000m
Diversity loss:						
Total effects	-0.260	-0.261	-0.260	-0.267	-0.267	-0.265
Richness effects	NS	NS	NS	NS	NS	NS
Phylogenetic diversity effects	-0.260	-0.261	-0.260	-0.267	-0.267	-0.265
Effects via population stability	NS	NS	NS	NS	NS	NS
Effects via population asynchrony	-0.260	-0.261	-0.260	-0.267	-0.267	-0.265
Habitat degradation:						
Total effects	-0.516	-0.551	-0.586	-0.51	-0.543	-0.573
Urbanization effects	-0.210	-0.224	-0.229	-0.204	-0.215	-0.218
Agricultural intensification effects	-0.305	-0.328	-0.357	-0.306	-0.328	-0.355
Effects via diversity	NS	NS	NS	NS	NS	NS
Effects via population stability	-0.516	-0.551	-0.586	-0.510	-0.543	-0.573
Effects via population asynchrony	NS	NS	NS	NS	NS	NS

Supplementary Table 3. Strength of the different paths by which diversity and habitat degradation affect the stability of local communities of birds, using species richness observed or estimated by Chao index, for the three buffer sizes and the three data selections.

	Observed species richness			Estimated species richness		
	DATASET 1					
Effects on community stability	1000m	1250m	1500m	1000m	1250m	1500m
Diversity loss:						
Total effects	-0.224	-0.226	-0.229	-0.224	-0.228	-0.231
Richness effects	-0.139	-0.140	-0.144	-0.133	-0.135	-0.139
Phylogenetic diversity effects	-0.085	-0.086	-0.085	-0.092	-0.092	-0.092
Effects via population stability	0.076	0.075	0.072	0.064	0.062	0.060
Effects via population asynchrony	-0.299	-0.300	-0.302	-0.289	-0.290	-0.292
Habitat degradation:						
Total effects	-0.246	-0.249	-0.244	-0.232	-0.213	-0.227
Urbanization effects	NS	NS	NS	NS	NS	-0.018
Agricultural intensification effects	-0.246	-0.249	-0.244	-0.232	-0.213	-0.209
Effects via diversity	-0.028	-0.028	-0.028	-0.021	NS	-0.018
Effects via population stability	-0.218	-0.221	-0.216	-0.211	-0.213	-0.209
Effects via population asynchrony	NS	NS	NS	NS	NS	NS
	DATASET 2					
Effects on community stability	1000m	1250m	1500m	1000m	1250m	1500m
Diversity loss:						
Total effects	-0.319	-0.320	-0.321	-0.316	-0.317	-0.318
Richness effects	-0.204	-0.203	-0.204	-0.189	-0.188	-0.188
Phylogenetic diversity effects	-0.115	-0.117	-0.117	-0.128	-0.130	-0.130
Effects via population stability	NS	NS	NS	NS	NS	NS
Effects via population asynchrony	-0.319	-0.320	-0.321	-0.316	-0.317	-0.318
Habitat degradation:						
Total effects	-0.243	-0.246	-0.241	-0.219	-0.223	-0.220
Urbanization effects	NS	NS	NS	NS	NS	NS
Agricultural intensification effects	-0.243	-0.246	-0.241	-0.219	-0.223	-0.220
Effects via diversity	-0.060	-0.059	-0.059	-0.042	-0.042	-0.043
Effects via population stability	-0.182	-0.186	-0.183	-0.176	-0.181	-0.177
Effects via population asynchrony	NS	NS	NS	NS	NS	NS
	DATASET 3					
Effects on community stability	1000m	1250m	1500m	1000m	1250m	1500m
Diversity loss:						
Total effects	-0.578	-0.584	-0.597	-0.568	-0.574	-0.587
Richness effects	-0.300	-0.300	-0.303	-0.281	-0.280	-0.282
Phylogenetic diversity effects	-0.277	-0.284	-0.294	-0.287	-0.294	-0.304
Effects via population stability	-0.119	-0.125	-0.132	-0.120	-0.125	-0.132
Effects via population asynchrony	-0.459	-0.459	-0.465	-0.448	-0.449	-0.454
Habitat degradation:						
Total effects	-0.252	-0.247	-0.241	-0.327	-0.324	-0.309
Urbanization effects	NS	NS	NS	NS	NS	NS
Agricultural intensification effects	-0.252	-0.247	-0.241	-0.327	-0.324	-0.309
Effects via diversity	-0.065	-0.066	-0.067	NS	NS	NS
Effects via population stability	-0.187	-0.181	-0.174	-0.187	-0.181	-0.175
Effects via population asynchrony	NS	NS	NS	-0.140	-0.143	-0.134

Supplementary Table 4. Strength of the different paths by which diversity and habitat degradation affect the stability of local communities of butterflies, using species richness observed or estimated by Chao index, for the three buffer sizes and the three data selections.

	Observed species richness			Estimated species richness		
DATASET 1						
Effects on community stability	250m	500m	1000m	250m	500m	1000m
Diversity loss:						
Total effects	-0.504	-0.513	-0.501	-0.349	-0.361	-0.363
Richness effects	-0.339	-0.347	-0.328	-0.176	-0.184	-0.182
Phylogenetic diversity effects	-0.165	-0.166	-0.173	-0.174	-0.177	-0.181
Effects via population stability	-0.182	-0.172	-0.148	NS	NS	NS
Effects via population asynchrony	-0.321	-0.341	-0.353	-0.349	-0.361	-0.363
Habitat degradation:						
Total effects	-0.317	-0.319	-0.411	-0.261	-0.246	-0.271
Urbanization effects	-0.317	-0.319	-0.355	-0.261	-0.246	-0.271
Agricultural intensification effects	NS	NS	-0.055	NS	NS	NS
Effects via diversity	-0.072	-0.092	-0.162	0.037	0.039	0.034
Effects via population stability	-0.245	-0.227	-0.249	-0.298	-0.285	-0.305
Effects via population asynchrony	NS	NS	NS	NS	NS	NS
DATASET 2						
Effects on community stability	250m	500m	1000m	250m	500m	1000m
Diversity loss:						
Total effects	-0.440	-0.453	-0.320	-0.336	-0.351	-0.351
Richness effects	-0.302	-0.314	-0.177	-0.185	-0.195	-0.193
Phylogenetic diversity effects	-0.138	-0.140	-0.144	-0.151	-0.156	-0.159
Effects via population stability	-0.139	-0.133	NS	NS	NS	NS
Effects via population asynchrony	-0.301	-0.320	-0.320	-0.336	-0.351	-0.351
Habitat degradation:						
Total effects	-0.274	-0.272	-0.251	-0.232	-0.221	-0.253
Urbanization effects	-0.274	-0.272	-0.251	-0.232	-0.221	-0.253
Agricultural intensification effects	NS	NS	NS	NS	NS	NS
Effects via diversity	-0.080	-0.100	-0.057	-0.010	-0.017	-0.030
Effects via population stability	-0.194	-0.172	-0.194	-0.222	-0.204	-0.223
Effects via population asynchrony	NS	NS	NS	NS	NS	NS
DATASET 3						
Effects on community stability	250m	500m	1000m	250m	500m	1000m
Diversity loss:						
Total effects	NS	-0.176	-0.216	-0.171	-0.363	-0.404
Richness effects	NS	NS	NS	-0.171	-0.191	-0.198
Phylogenetic diversity effects	NS	-0.176	-0.216	NS	-0.172	-0.207
Effects via population stability	NS	NS	NS	NS	NS	NS
Effects via population asynchrony	NS	-0.176	-0.216	-0.171	-0.363	-0.404
Habitat degradation:						
Total effects	-0.305	-0.271	-0.118	-0.355	-0.325	-0.165
Urbanization effects	-0.305	-0.271	-0.311	-0.355	-0.325	-0.364
Agricultural intensification effects	NS	NS	0.193	NS	NS	0.200
Effects via diversity	NS	0.056	0.066	NS	0.055	0.063
Effects via population stability	-0.305	-0.327	-0.377	-0.355	-0.380	-0.427
Effects via population asynchrony	NS	NS	0.193	NS	NS	0.200

Supplementary Table 5. Standardized coefficients from the Structural Equation Models on the stability of bat communities using observed richness for the three buffer sizes and the three data selections. Est. stands for estimates. SE for standard errors. P-val. for P-value.

		DATASET 1								
		250m buffer radius Fischer C= 9.17 p-value= 0.517 AIC= 65.17			500m buffer radius Fischer C= 5.47 p-value= 0.858 AIC= 61.47			1000m buffer radius Fischer C= 5.85 p-value= 0.828 AIC= 61.85		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.039	0.082	0.634	-0.034	0.081	0.677	0.010	0.081	0.900
	Urbanization gradient	0.263	0.082	0.002	0.284	0.081	0.001	0.317	0.081	<0.001
Phylogenetic diversity	Agricultural intensification gradient	-0.151	0.084	0.074	-0.166	0.083	0.049	-0.169	0.084	0.047
	Urbanization gradient	-0.037	0.084	0.660	-0.053	0.083	0.528	-0.032	0.084	0.706
Population stability	Agricultural intensification gradient	-0.292	0.082	<0.001	-0.296	0.082	<0.001	-0.293	0.083	0.001
	Urbanization gradient	-0.189	0.084	0.026	-0.194	0.084	0.022	-0.172	0.086	0.048
	Phylogenetic diversity	-0.124	0.079	0.119	-0.131	0.079	0.101	-0.127	0.080	0.111
	Species richness	0.084	0.081	0.301	0.091	0.082	0.269	0.095	0.083	0.250
Population asynchrony	Agricultural intensification gradient	0.098	0.076	0.201	0.128	0.076	0.093	0.143	0.077	0.064
	Urbanization gradient	-0.097	0.078	0.212	-0.048	0.078	0.536	0.048	0.080	0.545
	Phylogenetic diversity	0.371	0.073	<0.001	0.376	0.073	<0.001	0.379	0.074	<0.001
	Species richness	0.318	0.075	<0.001	0.308	0.076	<0.001	0.277	0.076	<0.001
Community stability	Population asynchrony	0.633			0.633			0.633		
	Population stability	0.687			0.687			0.687		
		DATASET 2								
		250m buffer radius Fischer C= 6.79 p-value= 0.745 AIC= 62.79			500m buffer radius Fischer C= 9.69 p-value= 0.468 AIC= 65.69			1000m buffer radius Fischer C= 7.7 p-value= 0.658 AIC= 63.7		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.132	0.117	0.260	-0.134	0.118	0.256	-0.030	0.119	0.799
	Urbanization gradient	0.259	0.083	0.002	0.275	0.081	0.001	0.319	0.081	<0.001
Phylogenetic diversity	Agricultural intensification gradient	-0.149	0.084	0.078	-0.141	0.084	0.095	-0.133	0.085	0.119
	Urbanization gradient	-0.010	0.084	0.904	-0.018	0.084	0.830	-0.012	0.085	0.888
Population stability	Agricultural intensification gradient	-0.391	0.080	<0.001	-0.401	0.080	<0.001	-0.392	0.082	<0.001
	Urbanization gradient	-0.174	0.084	0.038	-0.171	0.083	0.042	-0.140	0.085	0.102
	Phylogenetic diversity	-0.139	0.077	0.073	-0.139	0.077	0.072	-0.134	0.077	0.084
	Species richness	0.061	0.081	0.454	0.066	0.080	0.415	0.070	0.082	0.391
Population asynchrony	Agricultural intensification gradient	0.009	0.076	0.908	0.034	0.075	0.653	0.062	0.077	0.419
	Urbanization gradient	-0.089	0.078	0.261	-0.037	0.079	0.640	0.070	0.080	0.382
	Phylogenetic diversity	0.397	0.072	<0.001	0.398	0.072	<0.001	0.399	0.072	<0.001
	Species richness	0.320	0.076	<0.001	0.303	0.076	<0.001	0.266	0.077	0.001
Community stability	Population asynchrony	0.663			0.663			0.663		
	Population stability	0.692			0.692			0.692		
		DATASET 3								
		250m buffer radius Fischer C= 6.78 p-value= 0.746 AIC= 62.78			500m buffer radius Fischer C= 6.09 p-value= 0.808 AIC= 62.09			1000m buffer radius Fischer C= 7.34 p-value= 0.693 AIC= 63.34		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.030	0.104	0.772	-0.003	0.104	0.978	0.056	0.104	0.594
	Urbanization gradient	0.332	0.104	0.002	0.355	0.104	0.001	0.402	0.104	<0.001
Phylogenetic diversity	Agricultural intensification gradient	-0.072	0.110	0.519	-0.097	0.111	0.385	-0.113	0.113	0.316
	Urbanization gradient	0.035	0.110	0.754	0.027	0.111	0.808	0.020	0.113	0.859
Population stability	Agricultural intensification gradient	-0.388	0.101	<0.001	-0.416	0.101	<0.001	-0.454	0.103	<0.001
	Urbanization gradient	-0.267	0.107	0.015	-0.284	0.107	0.010	-0.291	0.110	0.010
	Phylogenetic diversity	-0.074	0.10	0.464	-0.087	0.099	0.384	-0.098	0.099	0.325
	Species richness	0.004	0.106	0.972	0.020	0.106	0.852	0.038	0.107	0.719
Population asynchrony	Agricultural intensification gradient	-0.015	0.095	0.874	0.002	0.096	0.984	0.007	0.097	0.940
	Urbanization gradient	0.038	0.101	0.711	0.066	0.102	0.519	0.156	0.104	0.138
	Phylogenetic diversity	0.478	0.094	<0.001	0.479	0.094	<0.001	0.478	0.093	<0.001
	Species richness	0.173	0.10	0.087	0.163	0.100	0.108	0.127	0.101	0.212
Community stability	Population asynchrony	0.544			0.544			0.544		
	Population stability	0.787			0.787			0.787		

Supplementary Table 6. Standardized coefficients from the Structural Equation Models on the stability of bat communities using richness estimated with Chao index for the three buffer sizes and the three data selections. Est. stands for estimates. SE for standard errors. P-val. for P-value.

		DATASET 1								
		250m buffer radius Fischer C= 11.19 p-value= 0.343 AIC= 67.19			500m buffer radius Fischer C= 7.46 p-value= 0.681 AIC= 63.46			1000m buffer radius Fischer C= 7.82 p-value= 0.646 AIC= 63.82		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.046	0.082	0.580	-0.043	0.081	0.599	-0.004	0.082	0.957
	Urbanization gradient	0.236	0.082	0.005	0.260	0.081	0.002	0.287	0.082	0.001
Phylogenetic diversity	Agricultural intensification gradient	-0.151	0.084	0.074	-0.166	0.083	0.049	-0.169	0.084	0.047
	Urbanization gradient	-0.037	0.084	0.660	-0.053	0.083	0.528	-0.032	0.084	0.706
Population stability	Agricultural intensification gradient	-0.292	0.082	<0.001	-0.295	0.082	<0.001	-0.290	0.083	0.001
	Urbanization gradient	-0.182	0.084	0.031	-0.186	0.083	0.028	-0.163	0.085	0.059
	Phylogenetic diversity	-0.120	0.079	0.134	-0.126	0.079	0.116	-0.122	0.080	0.128
	Species richness	0.065	0.081	0.423	0.070	0.082	0.392	0.074	0.082	0.373
Population asynchrony	Agricultural intensification gradient	0.104	0.076	0.175	0.135	0.076	0.076	0.151	0.076	0.051
	Urbanization gradient	-0.089	0.077	0.249	-0.042	0.077	0.589	0.054	0.079	0.492
	Phylogenetic diversity	0.394	0.073	<0.001	0.399	0.073	<0.001	0.400	0.074	<0.001
	Species richness	0.323	0.075	<0.001	0.316	0.075	<0.001	0.287	0.076	<0.001
Community stability	Population asynchrony	0.633			0.633			0.633		
	Population stability	0.687			0.687			0.687		
		DATASET 2								
		250m buffer radius Fischer C= 8.24 p-value= 0.605 AIC= 64.24			500m buffer radius Fischer C= 11.67 p-value= 0.308 AIC= 67.67			1000m buffer radius Fischer C= 9.33 p-value= 0.501 AIC= 65.33		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.057	0.115	0.618	-0.06	0.116	0.607	0.183	0.080	0.024
	Urbanization gradient	0.234	0.084	0.006	0.254	0.082	0.002	0.342	0.080	<0.001
Phylogenetic diversity	Agricultural intensification gradient	-0.149	0.084	0.078	-0.141	0.084	0.095	-0.133	0.085	0.119
	Urbanization gradient	-0.010	0.084	0.904	-0.018	0.084	0.830	-0.012	0.085	0.888
Population stability	Agricultural intensification gradient	-0.388	0.080	<0.001	-0.398	0.080	<0.001	-0.388	0.082	<0.001
	Urbanization gradient	-0.166	0.082	0.046	-0.162	0.082	0.050	-0.132	0.085	0.120
	Phylogenetic diversity	-0.136	0.077	0.081	-0.135	0.077	0.081	-0.130	0.077	0.096
	Species richness	0.041	0.080	0.607	0.046	0.080	0.565	0.052	0.081	0.522
Population asynchrony	Agricultural intensification gradient	0.014	0.076	0.850	0.040	0.076	0.601	0.069	0.077	0.371
	Urbanization gradient	-0.063	0.078	0.424	-0.014	0.078	0.862	0.088	0.080	0.272
	Phylogenetic diversity	0.420	0.073	<0.001	0.420	0.073	<0.001	0.419	0.073	<0.001
	Species richness	0.282	0.076	<0.001	0.268	0.076	0.001	0.235	0.077	0.003
Community stability	Population asynchrony	0.663			0.663			0.663		
	Population stability	0.692			0.692			0.692		
		DATASET 3								
		250m buffer radius Fischer C= 5.66 p-value= 0.843 AIC= 61.66			500m buffer radius Fischer C= 4.9 p-value= 0.897 AIC= 60.9			1000m buffer radius Fischer C= 6.31 p-value= 0.788 AIC= 62.31		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.024	0.105	0.822	-0.007	0.105	0.947	0.047	0.105	0.659
	Urbanization gradient	0.318	0.105	0.003	0.343	0.105	0.002	0.381	0.105	<0.001
Phylogenetic diversity	Agricultural intensification gradient	-0.072	0.110	0.519	-0.097	0.111	0.385	-0.113	0.113	0.316
	Urbanization gradient	0.035	0.110	0.754	0.027	0.111	0.808	0.020	0.113	0.859
Population stability	Agricultural intensification gradient	-0.388	0.101	<0.001	-0.416	0.101	<0.001	-0.451	0.103	<0.001
	Urbanization gradient	-0.259	0.107	0.017	-0.274	0.107	0.012	-0.277	0.110	0.013
	Phylogenetic diversity	-0.074	0.100	0.463	-0.086	0.099	0.390	-0.095	0.099	0.336
	Species richness	-0.021	0.105	0.845	-0.010	0.105	0.924	0.003	0.106	0.975
Population asynchrony	Agricultural intensification gradient	-0.016	0.096	0.868	0.004	0.096	0.970	0.011	0.097	0.914
	Urbanization gradient	0.046	0.101	0.648	0.075	0.102	0.464	0.166	0.104	0.113
	Phylogenetic diversity	0.491	0.094	<0.001	0.491	0.094	<0.001	0.487	0.093	<0.001
	Species richness	0.151	0.099	0.132	0.142	0.100	0.160	0.107	0.100	0.288
Community stability	Population asynchrony	0.544			0.544			0.544		
	Population stability	0.787			0.787			0.787		

Supplementary Table 7. Standardized coefficients from the Structural Equation Models on the stability of birds communities using observed richness for the three buffer sizes and the three data selections. Est. stands for estimates. SE for standard errors. P-val. for P-value.

		DATASET 1								
		1000m buffer radius Fischer C= 7.46 p-value= 0.682 AIC= 67.46			1250m buffer radius Fischer C= 8.73 p-value= 0.558 AIC= 68.73			1500m buffer radius Fischer C= 7.46 p-value= 0.682 AIC= 67.46		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.205	0.076	0.007	-0.201	0.076	0.009	-0.196	0.077	0.012
	Urbanization gradient	-0.071	0.056	0.202	-0.071	0.056	0.209	-0.082	0.057	0.151
Phylogenetic diversity	Agricultural intensification gradient	0.033	0.078	0.677	0.070	0.078	0.370	0.102	0.079	0.199
	Urbanization gradient	-0.072	0.062	0.247	-0.072	0.062	0.244	-0.077	0.063	0.221
Population stability	Agricultural intensification gradient	-0.436	0.076	<0.001	-0.442	0.077	<0.001	-0.433	0.079	<0.001
	Urbanization gradient	0.028	0.056	0.617	0.034	0.057	0.556	0.035	0.058	0.547
	Phylogenetic diversity	0.028	0.056	0.619	0.037	0.056	0.509	0.045	0.056	0.420
	Species richness	-0.151	0.062	0.015	-0.149	0.062	0.016	-0.145	0.062	0.020
Population asynchrony	Agricultural intensification gradient	-0.003	0.061	0.961	-0.005	0.061	0.930	0.001	0.061	0.993
	Urbanization gradient	-0.015	0.059	0.804	-0.003	0.059	0.953	0.004	0.059	0.946
	Phylogenetic diversity	0.118	0.059	0.045	0.119	0.059	0.044	0.118	0.059	0.046
	Species richness	0.297	0.061	<0.001	0.298	0.061	<0.001	0.300	0.061	<0.001
Community stability	Population asynchrony	0.722			0.722			0.722		
	Population stability	0.500			0.500			0.500		
		DATASET 2								
		1000m buffer radius Fischer C= 8.76 p-value= 0.555 AIC= 68.76			1250m buffer radius Fischer C= 9.04 p-value= 0.528 AIC= 69.04			1500m buffer radius Fischer C= 10.3 p-value= 0.414 AIC= 70.3		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.296	0.075	<0.001	-0.292	0.076	<0.001	-0.289	0.077	<0.001
	Urbanization gradient	-0.061	0.056	0.273	-0.066	0.056	0.244	-0.081	0.057	0.158
Phylogenetic diversity	Agricultural intensification gradient	0.046	0.078	0.554	0.085	0.078	0.277	0.116	0.078	0.138
	Urbanization gradient	-0.086	0.062	0.168	-0.090	0.063	0.154	-0.096	0.063	0.131
Population stability	Agricultural intensification gradient	-0.423	0.078	<0.001	-0.433	0.079	<0.001	-0.424	0.080	<0.001
	Urbanization gradient	0.056	0.058	0.339	0.060	0.059	0.308	0.058	0.059	0.331
	Phylogenetic diversity	0.062	0.057	0.278	0.070	0.057	0.222	0.078	0.058	0.177
	Species richness	-0.084	0.063	0.189	-0.083	0.063	0.192	-0.077	0.064	0.226
Population asynchrony	Agricultural intensification gradient	-0.045	0.062	0.472	-0.055	0.062	0.379	-0.052	0.062	0.401
	Urbanization gradient	-0.021	0.059	0.723	-0.012	0.059	0.840	-0.010	0.059	0.870
	Phylogenetic diversity	0.154	0.059	0.009	0.156	0.059	0.008	0.157	0.059	0.008
	Species richness	0.274	0.062	<0.001	0.272	0.062	<0.001	0.273	0.062	<0.001
Community stability	Population asynchrony	0.747			0.747			0.747		
	Population stability	0.431			0.431			0.431		
		DATASET 3								
		1000m buffer radius Fischer C= 12.72 p-value= 0.24 AIC= 72.72			1250m buffer radius Fischer C= 11.49 p-value= 0.32 AIC= 71.49			1500m buffer radius Fischer C= 12.97 p-value= 0.225 AIC= 72.97		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.217	0.098	0.029	-0.220	0.099	0.028	-0.223	0.100	0.028
	Urbanization gradient	0.063	0.089	0.484	0.046	0.093	0.623	0.027	0.095	0.780
Phylogenetic diversity	Agricultural intensification gradient	-0.064	0.122	0.601	-0.024	0.121	0.842	0.028	0.121	0.819
	Urbanization gradient	0.069	0.090	0.445	0.080	0.092	0.387	0.076	0.094	0.420
Population stability	Agricultural intensification gradient	-0.389	0.102	<0.001	-0.378	0.103	<0.001	-0.363	0.104	0.001
	Urbanization gradient	0.083	0.084	0.325	0.058	0.088	0.515	0.029	0.091	0.754
	Phylogenetic diversity	0.249	0.090	0.007	0.261	0.091	0.005	0.276	0.092	0.003
	Species richness	0.008	0.095	0.932	0.015	0.096	0.876	0.021	0.097	0.832
Population asynchrony	Agricultural intensification gradient	-0.155	0.089	0.084	-0.159	0.089	0.079	-0.148	0.090	0.103
	Urbanization gradient	0.046	0.087	0.597	0.060	0.087	0.486	0.057	0.087	0.508
	Phylogenetic diversity	0.216	0.087	0.014	0.218	0.087	0.014	0.221	0.087	0.013
	Species richness	0.411	0.090	<0.001	0.410	0.090	<0.001	0.415	0.090	<0.001
Community stability	Population asynchrony	0.731			0.731			0.731		
	Population stability	0.479			0.479			0.479		

Supplementary Table 8. Standardized coefficients from the Structural Equation Models on the stability of bird communities using richness estimated with Chao index for the three buffer sizes and the three data selections. Est. stands for estimates. SE for standard errors. P-val. for P-value.

		DATASET 1								
		1000m buffer radius Fischer C= 8.52 p-value= 0.578 AIC= 68.52			1250m buffer radius Fischer C= 8.84 p-value= 0.548 AIC= 68.84			1500m buffer radius Fischer C= 8.5 p-value= 0.58 AIC= 68.5		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.161	0.077	0.037	-0.150	0.077	0.053	-0.145	0.078	0.063
	Urbanization gradient	-0.114	0.059	0.054	-0.115	0.059	0.054	-0.131	0.060	0.030
Phylogenetic diversity	Agricultural intensification gradient	0.033	0.078	0.677	0.070	0.078	0.370	0.102	0.079	0.199
	Urbanization gradient	-0.072	0.062	0.247	-0.072	0.062	0.244	-0.077	0.063	0.221
Population stability	Agricultural intensification gradient	-0.423	0.076	<0.001	-0.427	0.077	<0.001	-0.418	0.078	<0.001
	Urbanization gradient	0.026	0.057	0.646	0.031	0.057	0.584	0.033	0.059	0.578
	Phylogenetic diversity	0.029	0.056	0.609	0.038	0.056	0.502	0.046	0.056	0.420
	Species richness	-0.128	0.059	0.031	-0.125	0.059	0.036	-0.121	0.059	0.043
Population asynchrony	Agricultural intensification gradient	-0.025	0.061	0.685	-0.027	0.060	0.654	-0.021	0.060	0.730
	Urbanization gradient	-0.013	0.060	0.829	-0.002	0.060	0.967	0.005	0.060	0.934
	Phylogenetic diversity	0.127	0.059	0.032	0.128	0.059	0.031	0.128	0.059	0.032
	Species richness	0.273	0.060	<0.001	0.274	0.060	<0.001	0.276	0.060	<0.001
Community stability	Population asynchrony	0.722			0.722			0.722		
	Population stability	0.500			0.500			0.500		

		DATASET 2								
		1000m buffer radius Fischer C= 9.59 p-value= 0.478 AIC= 69.59			1250m buffer radius Fischer C= 10.29 p-value= 0.416 AIC= 70.29			1500m buffer radius Fischer C= 11.26 p-value= 0.338 AIC= 71.26		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.225	0.075	0.003	-0.226	0.075	0.003	-0.227	0.076	0.003
	Urbanization gradient	-0.084	0.059	0.154	-0.082	0.059	0.167	-0.090	0.059	0.130
Phylogenetic diversity	Agricultural intensification gradient	0.046	0.078	0.554	0.085	0.078	0.277	0.116	0.078	0.138
	Urbanization gradient	-0.086	0.062	0.168	-0.090	0.063	0.154	-0.096	0.063	0.131
Population stability	Agricultural intensification gradient	-0.410	0.077	<0.001	-0.420	0.078	<0.001	-0.412	0.079	<0.001
	Urbanization gradient	0.056	0.058	0.340	0.060	0.059	0.305	0.059	0.060	0.322
	Phylogenetic diversity	0.060	0.057	0.294	0.068	0.057	0.238	0.076	0.058	0.192
	Species richness	-0.056	0.061	0.356	-0.056	0.061	0.359	-0.053	0.061	0.387
Population asynchrony	Agricultural intensification gradient	-0.069	0.061	0.261	-0.078	0.061	0.201	-0.075	0.061	0.219
	Urbanization gradient	-0.022	0.060	0.708	-0.015	0.059	0.802	-0.014	0.060	0.808
	Phylogenetic diversity	0.171	0.059	0.004	0.174	0.059	0.004	0.174	0.059	0.003
	Species richness	0.252	0.061	<0.001	0.251	0.061	<0.001	0.252	0.061	<0.001
Community stability	Population asynchrony	0.747			0.747			0.747		
	Population stability	0.431			0.431			0.431		

		DATASET 3								
		1000m buffer radius Fischer C= 12.66 p-value= 0.243 AIC= 72.66			1250m buffer radius Fischer C= 11.47 p-value= 0.322 AIC= 71.47			1500m buffer radius Fischer C= 13.34 p-value= 0.205 AIC= 73.34		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.112	0.106	0.296	-0.116	0.107	0.281	-0.128	0.108	0.237
	Urbanization gradient	0.061	0.090	0.498	0.056	0.093	0.550	0.048	0.095	0.616
Phylogenetic diversity	Agricultural intensification gradient	-0.064	0.122	0.601	-0.024	0.121	0.842	0.028	0.121	0.819
	Urbanization gradient	0.069	0.090	0.445	0.080	0.092	0.387	0.076	0.094	0.420
Population stability	Agricultural intensification gradient	-0.389	0.101	<0.001	-0.378	0.102	<0.001	-0.364	0.103	0.001
	Urbanization gradient	0.083	0.084	0.325	0.058	0.088	0.515	0.029	0.091	0.754
	Phylogenetic diversity	0.250	0.090	0.007	0.262	0.091	0.005	0.276	0.092	0.003
	Species richness	0.014	0.093	0.885	0.019	0.094	0.840	0.022	0.095	0.818
Population asynchrony	Agricultural intensification gradient	-0.192	0.088	0.032	-0.195	0.089	0.030	-0.184	0.089	0.042
	Urbanization gradient	0.048	0.088	0.588	0.057	0.088	0.514	0.051	0.088	0.562
	Phylogenetic diversity	0.228	0.088	0.011	0.231	0.088	0.010	0.235	0.088	0.009
	Species richness	0.384	0.090	<0.001	0.383	0.090	<0.001	0.386	0.090	<0.001
Community stability	Population asynchrony	0.731			0.731			0.731		
	Population stability	0.479			0.479			0.479		

Supplementary Table 9. Standardized coefficients from the Structural Equation Models on the stability of butterflies communities using observed richness for the three buffer sizes and for the three data selections. Est. stands for estimates. SE for standard errors. P-val. for P-value.

		DATASET 1								
		250m buffer radius Fischer C= 25.51 p-value= 0.004 AIC= 77.51			500m buffer radius Fischer C= 20.48 p-value= 0.025 AIC= 72.48			1000m buffer radius Fischer C= 22.28 p-value= 0.014 AIC= 74.28		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.104	0.084	0.218	-0.135	0.081	0.100	-0.168	0.079	0.035
	Urbanization gradient	-0.318	0.084	<0.001	-0.370	0.081	<0.001	-0.423	0.079	<0.001
Phylogenetic diversity	Agricultural intensification gradient	-0.043	0.074	0.569	-0.054	0.077	0.488	-0.048	0.082	0.555
	Urbanization gradient	0.215	0.069	0.002	0.221	0.068	0.002	0.188	0.069	0.007
Population stability	Agricultural intensification gradient	0.063	0.083	0.446	0.013	0.085	0.879	-0.034	0.085	0.689
	Urbanization gradient	-0.345	0.085	<0.001	-0.320	0.088	<0.001	-0.350	0.088	<0.001
	Phylogenetic diversity	0.132	0.083	0.113	0.119	0.085	0.162	0.097	0.084	0.252
	Species richness	0.257	0.084	0.003	0.242	0.087	0.006	0.209	0.088	0.019
Population asynchrony	Agricultural intensification gradient	0.099	0.089	0.266	0.121	0.089	0.177	0.129	0.090	0.155
	Urbanization gradient	0.053	0.092	0.563	0.109	0.093	0.243	0.115	0.093	0.220
	Phylogenetic diversity	0.259	0.089	0.004	0.260	0.090	0.004	0.271	0.090	0.003
	Species richness	0.245	0.090	0.007	0.275	0.091	0.003	0.283	0.094	0.003
Community stability	Population asynchrony	0.637			0.637			0.637		
	Population stability	0.710			0.710			0.710		
		DATASET 2								
		250m buffer radius Fischer C= 16.83 p-value= 0.078 AIC= 68.83			500m buffer radius Fischer C= 18.04 p-value= 0.054 AIC= 70.04			1000m buffer radius Fischer C= 13.5 p-value= 0.197 AIC= 65.5		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.062	0.083	0.456	-0.090	0.080	0.266	-0.130	0.078	0.096
	Urbanization gradient	-0.364	0.083	<0.001	-0.415	0.080	<0.001	-0.466	0.078	<0.001
Phylogenetic diversity	Agricultural intensification gradient	-0.104	0.072	0.151	-0.121	0.075	0.110	-0.121	0.080	0.132
	Urbanization gradient	0.214	0.067	0.002	0.215	0.066	0.001	0.177	0.067	0.009
Population stability	Agricultural intensification gradient	0.031	0.088	0.726	-0.030	0.090	0.738	-0.064	0.090	0.478
	Urbanization gradient	-0.283	0.091	0.002	-0.252	0.094	0.008	-0.284	0.094	0.003
	Phylogenetic diversity	0.065	0.088	0.464	0.042	0.091	0.643	0.024	0.091	0.795
	Species richness	0.203	0.089	0.024	0.194	0.092	0.036	0.165	0.094	0.082
Population asynchrony	Agricultural intensification gradient	0.084	0.091	0.359	0.104	0.092	0.260	0.099	0.094	0.293
	Urbanization gradient	0.005	0.094	0.954	0.057	0.096	0.551	0.041	0.097	0.675
	Phylogenetic diversity	0.210	0.092	0.023	0.213	0.093	0.024	0.219	0.094	0.021
	Species richness	0.249	0.092	0.008	0.276	0.094	0.004	0.269	0.097	0.006
Community stability	Population asynchrony	0.655			0.655			0.655		
	Population stability	0.684			0.684			0.684		
		DATASET 3								
		250m buffer radius Fischer C= 16.17 p-value= 0.095 AIC= 68.17			500m buffer radius Fischer C= 14.66 p-value= 0.145 AIC= 66.66			1000m buffer radius Fischer C= 14.53 p-value= 0.15 AIC= 66.53		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.011	0.127	0.930	-0.073	0.123	0.558	-0.140	0.119	0.244
	Urbanization gradient	-0.367	0.127	0.006	-0.422	0.123	0.001	-0.472	0.119	<0.001
Phylogenetic diversity	Agricultural intensification gradient	-0.147	0.104	0.163	-0.092	0.110	0.406	-0.080	0.114	0.485
	Urbanization gradient	0.299	0.102	0.005	0.319	0.101	0.003	0.306	0.101	0.004
Population stability	Agricultural intensification gradient	0.105	0.129	0.418	0.099	0.129	0.447	0.087	0.127	0.498
	Urbanization gradient	-0.399	0.132	0.004	-0.429	0.135	0.002	-0.494	0.134	0.001
	Phylogenetic diversity	0.240	0.134	0.080	0.256	0.134	0.063	0.260	0.131	0.053
	Species richness	0.191	0.133	0.156	0.165	0.135	0.228	0.120	0.136	0.381
Population asynchrony	Agricultural intensification gradient	0.096	0.141	0.496	0.210	0.139	0.137	0.349	0.137	0.014
	Urbanization gradient	0.033	0.144	0.822	0.077	0.146	0.600	0.019	0.144	0.894
	Phylogenetic diversity	0.284	0.146	0.058	0.318	0.145	0.033	0.390	0.141	0.008
	Species richness	0.224	0.145	0.127	0.265	0.146	0.075	0.284	0.146	0.058
Community stability	Population asynchrony	0.553			0.553			0.553		
	Population stability	0.763			0.763			0.763		

Supplementary Table 10. Standardized coefficients from the Structural Equation Models on the stability of butterflies communities using richness estimated with Chao index for the three buffer sizes and for the three data selections. Est. stands for estimates. SE for standard errors. P-val. for P-value.

		DATASET 1								
		250m buffer radius Fischer C= 22.25 p-value= 0.014 AIC= 74.25			500m buffer radius Fischer C= 19.97 p-value= 0.03 AIC= 71.97			1000m buffer radius Fischer C= 20.78 p-value= 0.023 AIC= 72.78		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.110	0.089	0.217	-0.145	0.087	0.100	-0.142	0.087	0.105
	Urbanization gradient	-0.100	0.089	0.259	-0.120	0.087	0.172	-0.154	0.087	0.078
Phylogenetic diversity	Agricultural intensification gradient	-0.043	0.074	0.569	-0.054	0.077	0.488	-0.048	0.082	0.555
	Urbanization gradient	0.215	0.069	0.002	0.221	0.068	0.002	0.188	0.069	0.007
Population stability	Agricultural intensification gradient	0.049	0.085	0.565	-0.005	0.087	0.954	-0.059	0.086	0.490
	Urbanization gradient	-0.420	0.084	<0.001	-0.402	0.084	<0.001	-0.430	0.082	<0.001
	Phylogenetic diversity	0.142	0.085	0.098	0.130	0.087	0.139	0.101	0.086	0.244
Population asynchrony	Species richness	0.092	0.082	0.263	0.080	0.083	0.337	0.060	0.082	0.466
	Agricultural intensification gradient	0.108	0.088	0.222	0.131	0.089	0.140	0.126	0.089	0.159
	Urbanization gradient	0	0.086	1	0.038	0.086	0.662	0.038	0.085	0.658
	Phylogenetic diversity	0.273	0.088	0.002	0.278	0.089	0.002	0.284	0.089	0.002
Community stability	Species richness	0.276	0.084	0.001	0.288	0.084	0.001	0.286	0.085	0.001
	Population asynchrony	0.637			0.637			0.637		
	Population stability	0.710			0.710			0.710		
		DATASET 2								
		250m buffer radius Fischer C= 19.79 p-value= 0.031 AIC= 71.79			500m buffer radius Fischer C= 19.61 p-value= 0.033 AIC= 71.61			1000m buffer radius Fischer C= 15.87 p-value= 0.103 AIC= 67.87		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.072	0.087	0.412	-0.104	0.085	0.225	-0.136	0.084	0.108
	Urbanization gradient	-0.227	0.087	0.010	-0.259	0.085	0.003	-0.304	0.084	<0.001
Phylogenetic diversity	Agricultural intensification gradient	-0.104	0.072	0.151	-0.121	0.075	0.110	-0.121	0.080	0.132
	Urbanization gradient	0.214	0.067	0.002	0.215	0.066	0.001	0.177	0.067	0.009
Population stability	Agricultural intensification gradient	0.034	0.089	0.702	-0.027	0.091	0.766	-0.066	0.091	0.473
	Urbanization gradient	-0.325	0.088	<0.001	-0.299	0.088	0.001	-0.326	0.087	<0.001
	Phylogenetic diversity	0.079	0.089	0.378	0.057	0.091	0.534	0.034	0.091	0.714
Population asynchrony	Species richness	0.154	0.085	0.073	0.143	0.087	0.103	0.118	0.088	0.179
	Agricultural intensification gradient	0.095	0.090	0.293	0.120	0.092	0.193	0.113	0.093	0.227
	Urbanization gradient	-0.025	0.089	0.776	0.015	0.089	0.866	0.001	0.089	0.988
	Phylogenetic diversity	0.230	0.090	0.012	0.238	0.092	0.011	0.242	0.093	0.010
Community stability	Species richness	0.282	0.087	0.002	0.298	0.088	0.001	0.294	0.089	0.001
	Population asynchrony	0.655			0.655			0.655		
	Population stability	0.684			0.684			0.684		
		DATASET 3								
		250m buffer radius Fischer C= 13.73 p-value= 0.186 AIC= 65.73			500m buffer radius Fischer C= 14.56 p-value= 0.149 AIC= 66.56			1000m buffer radius Fischer C= 8.81 p-value= 0.55 AIC= 60.81		
Response	Predictor	Est.	SE	P-val.	Est.	SE	P-val.	Est.	SE	P-val.
Species Richness	Agricultural intensification gradient	-0.064	0.135	0.636	-0.154	0.133	0.252	-0.160	0.133	0.232
	Urbanization gradient	-0.109	0.135	0.423	-0.139	0.133	0.300	-0.180	0.133	0.180
Phylogenetic diversity	Agricultural intensification gradient	-0.147	0.104	0.163	-0.092	0.110	0.406	-0.080	0.114	0.485
	Urbanization gradient	0.299	0.102	0.005	0.319	0.101	0.003	0.306	0.101	0.004
Population stability	Agricultural intensification gradient	0.086	0.131	0.514	0.064	0.131	0.629	0.043	0.127	0.737
	Urbanization gradient	-0.466	0.128	0.001	-0.498	0.127	<0.001	-0.560	0.123	<0.001
	Phylogenetic diversity	0.199	0.135	0.146	0.218	0.134	0.111	0.226	0.130	0.087
Population asynchrony	Species richness	-0.058	0.125	0.642	-0.070	0.125	0.579	-0.100	0.121	0.413
	Agricultural intensification gradient	0.109	0.137	0.427	0.241	0.135	0.080	0.361	0.131	0.008
	Urbanization gradient	-0.013	0.133	0.924	0.015	0.131	0.908	-0.046	0.127	0.716
	Phylogenetic diversity	0.271	0.140	0.059	0.311	0.139	0.029	0.374	0.134	0.007
Community stability	Species richness	0.309	0.130	0.021	0.345	0.129	0.010	0.358	0.125	0.006
	Population asynchrony	0.553			0.553			0.553		
	Population stability	0.763			0.763			0.763		

Supplementary Table 11. GeneBank accession numbers of genes used to generate the phylogeny of butterflies

Species	COI	Gene			
		wingless	EF-1 α	GAPDH	RpS5
<i>Aglais urticae</i>	HQ003951	AF412777	AY248811	FJ639522	FJ639577
<i>Aporia crataegi</i>	HM393180	EU141242	AY870529	EU141496	EU141394
<i>Argynnis paphia</i>	FJ663298	AY090133	GU372616	EU141519	EU141421
<i>Brintesia circe</i>	HQ004137	DQ338729	DQ339020	EU141474	EU141370
<i>Cacyreus marshalli</i>	AY556966	GQ128914	GQ128703		
<i>Coenonympha pamphilus</i>	GU707174	DQ338637	DQ338920	EU528385	EU528428
<i>Inachis io</i>	FJ663678	AF412766	AY248810	FJ639521	FJ639576
<i>Iphiclides podalirius</i>	GU559736	DQ351129	AF173413		
<i>Macroglossum stellatarum</i>	JF415393	EU479508	EU479296		
<i>Maniola jurtina</i>	FJ663756	AY090147	AY090180	EU141481	EU141376
<i>Papilio machaon</i>	HQ004884	AY569124	AF044828		
<i>Pararge aegeria</i>	GU655008	DQ176340	DQ338913	EU141476	EU141372
<i>Vanessa atalanta</i>	FJ664079	HQ734826	AY090187	HQ734959	HQ735034
<i>Vanessa cardui</i>	HQ990383	HQ734828	HQ734947	HQ734971	HQ735047

Supplementary Table 12. Variables used to describe the urbanization and the agricultural intensification. The urban, cropland, heterogenous agricultural, woodland and semi-natural open areas. CLC is for Corine Land Cover.

Data	Description	CLC Code	Units
Soil sealing	Sealed soil		m ²
Agricultural inputs	Fertilizers		k€
	Pesticides		k€
	Livestock food		k€
	Veterinarian medics		k€
Landscape complexity	Shannon index based on CLC land-uses	111-524	
Urban area	Artificial surfaces	111-142	m ²
Cropland area	Arable land	211-213	m ²
	Permanent crops	221-223	m ²
Heterogeneous agricultural areas	Pastures	231	m ²
	Heterogeneous agricultural areas	241-244	m ²
Woodland area	Forests	311-313	m ²
Semi-natural open area	Scrub and/or herbaceous vegetation associations	321-324	m ²

Préambule aux chapitres 2 et 3 : Estimation d'abondances annuelles à partir de données de comptages

Contexte

Dans les chapitres 2 et 3, j'ai utilisé les données du programme de suivi Butterfly Monitoring Scheme de Grande Bretagne. Ce jeu de données consiste en des comptages d'individus le long de transects. D'avril à octobre, les observateurs réalisent un comptage par semaine selon les conditions météo. Cependant, du fait des conditions météorologiques et de la disponibilité des observateurs, les comptages ne sont pas tous réalisés les mêmes jours, et chaque transect ne contient pas le même nombre de sorties par an. De plus, la longueur des transects varie également et l'abondance des papillons au cours d'une année varie selon des cycles pouvant différer d'une espèce à l'autre et d'une année sur l'autre. Afin de pouvoir comparer les transects, une méthode a récemment été développée pour estimer une abondance annuelle relative par espèce et transect, avec notamment l'utilisation d'une distribution de Poisson. Cependant, ce genre de données de comptage est susceptible de présenter de la surdispersion, rendant la distribution de Poisson non pertinente. Dans ce préambule, j'ai testé la pertinence de la distribution de Poisson pour estimer l'abondance annuelle des populations de papillons sur les transects suivis, et je l'ai comparé à la distribution Négative Binomiale, qui permet de prendre en compte la surdispersion des données.

Résultats

Mes résultats montrent une meilleure adéquation des modèles réalisés avec une distribution Négative Binomiale, et que l'indice de surdispersion estimé dans le cas de l'utilisation d'une distribution Négative Binomiale suggère de la surdispersion dans les données. Dans les chapitres 2 et 3, l'estimation de l'abondance annuelle des populations pour l'étude de la synchronie locale ou régionale entre espèces a été réalisée en utilisant une distribution Négative Binomiale.

Introduction

The increase of biodiversity monitoring programs with long time series enables finer studies, over multiple species, of the environmental drivers of year-to-year population fluctuations (Chandler et al., 2017; Magurran et al., 2010). However, most such monitoring programs have methodological limitations that constrain statistical analyses. For example, populations or communities are not surveyed every day and/or all monitored sites are not surveyed on the same days. Therefore, for populations with seasonal abundance fluctuations, there is a need to account for species phenologies for an accurate estimation of annual population relative abundance. The phenology of plant or animal species refers to periodic life cycle events influenced by seasonal variations of environmental conditions, and is often characterized by variations in population abundance through the year. Because species have different ecological requirements, phenologies vary across species (Stålhandske, 2016; Thackeray et al., 2016). Moreover, the variations of environmental conditions can lead to intra-specific variations of phenologies across years (Thackeray et al., 2016).

Recently, a method has been developed to estimate both species phenology and annual population relative abundances with large datasets such as the UK Butterfly Monitoring Scheme (UKBMS) (Schmucki et al., 2016). Butterfly phenology is defined as the temporal sequence of adult emergence along the year. The principle of this method is to aggregate data from multiple sites with similar phenology to maximise the number of surveyed days along a year. This method estimates first the shape of the annual phenology of a given species using the aggregated count data from multiple sites throughout a region. Then the standardized estimated phenology is used as an offset to predict missing counts site by site in a loglinear model. An annual abundance index for each site is finally computed from the area under the curve obtained with observed and imputed counts. In (Schmucki et al., 2016) the number N_{sd} of individuals counted on day d at site s for a given year is modelled according to a semi-parametric generalized linear model with log link and Poisson distribution:

$$E[N_{sd}] = e^{(\gamma_s + f(d))} \quad (1)$$

with γ_s the effect of site s and $f(d)$ the phenology across all days d within a year. The parameters γ_s and the phenology $f(d)$ are fitted by maximising the likelihood under the constraint that f is a cubic spline fulfilling $\sum_d e^{f(d)} = 1$.

The choice of a Poisson distribution for count data is a classical one. It is important yet, to investigate the goodness of fit of the Poisson distribution, since overdispersion has been frequently reported in ecological count data. Here, we investigated the goodness of fit of the model (1) with Poisson distribution on the same dataset as Schmucki *et al.* (2016) using a data splitting approach. On part of the data, we estimated the annual flight period (=phenology) of 49 butterfly species occurring in Great Britain, including abundant and rare species but also species with one or more peaks in their phenology. On a second part of the data, we tested the adequacy of the Poisson distribution after correction with the estimated phenology. Finally, we compared the goodness of fit of the Poisson versus Negative Binomial distributions on the basis of AIC. We show that the Negative Binomial provides better fit than the Poisson distribution across species and across different phenologies.

Materials and methods

Dataset

The UK Butterfly Monitoring Scheme (UKBMS, <http://www.ukbms.org/>) consists in butterfly counts in sites located all over the UK. Each site is divided into transects located in different local habitat or management units, for a total length of about 2-4km. The spatial position of transects is fixed across years. Butterflies are recorded on a weekly basis every year from the beginning of April until the end of September in a fixed-width band (5m wide) along transects. Transects walks are undertaken between 10.45am and 3.45pm with the following requirements for weather conditions: (1) temperature above 13°C (in northern upland areas this may be reduced to 11°C); (2) between 13-17°C, a transect may be walked providing there is at least 60% sun and (3) wind speed below 5 on the Beaufort scale. We performed our analyses on 49 species, and a time period between 2006 and 2015. Species were selected on the following basis: each species has been recorded in at least two sites every year between 2006 and 2015, and for each species, at least one site has made records every year from 2006 to 2015.

Adequacy of Poisson distribution

When a species is not observed at a given site and day, but is observed at least once in this site within the year, the count of the species is set to 0 at this day and site (i.e. pseudo-absence). Due to the variation in individual detectability and in relative abundance across sites, the dataset can contain 0 together with high abundance values for the same day and the same species in different sites. Moreover, the phenology length combined with the weekly basis survey can generate an important number of 0, especially for species with a short phenology. These two situations can lead to overdispersion in the data, and make the use of Poisson distribution irrelevant.

We tested the adequacy of the Poisson distribution for each species and year using a data splitting approach:

1. We randomly selected 80% of the sites, and we fitted the model developed by Schmucki et al. (2006), with a Poisson distribution and a log link.
2. For each of the 20% remaining sites, we estimated the expected mean λ_{sd} :

$$\lambda_{sd} = e^{f(d)} \frac{\sum_d N_{sd}}{\sum_d e^{f(d)}}$$

with d the days with counts at site s , and $f(d)$ the phenology previously estimated using 80% randomly selected sites.

3. Then we compared the estimated λ_{sd} to observed N_{sd} with the following standardization:

$$X_{sd} = \frac{(N_{sd} - \lambda_{sd})}{\sqrt{\lambda_{sd}}}.$$

If the Poisson distribution is relevant, X_{sd} would approximate a normal distribution, based on the central limit theorem, at least for λ_{sd} values larger than 10 (Berry, 1941). To test this hypothesis, we tested the deviation of X_{sd} to the Gaussian distribution with normal quantiles – quantiles plots. A distribution of points on the first bisector would indicate a good relevance of the Poisson distribution.

Comparison of the Poisson model to the negative binomial model with AIC criterion

To compare the two distributions, we performed the same models as above but assuming a negative binomial distribution of count data. We compared the fits of each pair of models using AIC criterion. This index assesses the fit of a model, based on the number of parameters and the likelihood. The AIC criterion increases with the number of parameters estimated by the model. Between two models, the model with the lowest AIC has a better fit on the data. The standard threshold to conclude for a better model is $\Delta AIC > 2$.

The Negative binomial distribution contains an overdispersal parameter r , strictly superior to 0. This parameter allows to adjust the variance independently of the mean. In a Negative binomial distribution, the variance is equal to

$$\sigma^2 = \lambda + \frac{\lambda}{r}$$

with r the coefficient of overdispersion, and λ the mean of the distribution. The Negative binomial distribution converges to a Poisson distribution as r goes to infinity. We examined the r coefficients estimated with the negative binomial distribution to check for overdispersion in the data.

Results

Adequacy of Poisson distribution

Instead of a distribution along the $x=y$, our adequacy tests show distributions combining two straight lines with a knee around 1, and with variations across species and year (Figure 1). The left part of the distribution is on the $x=y$ line and indicates a good fit of the model to the data. In contrast, the right part has a larger slope and suggests an underestimation of λ_{sd} for high values of N_{sd} , because of data overdispersion. Moreover, λ_{sd} larger than ten are not only on the $x=y$ line, but distributed on the two segments.

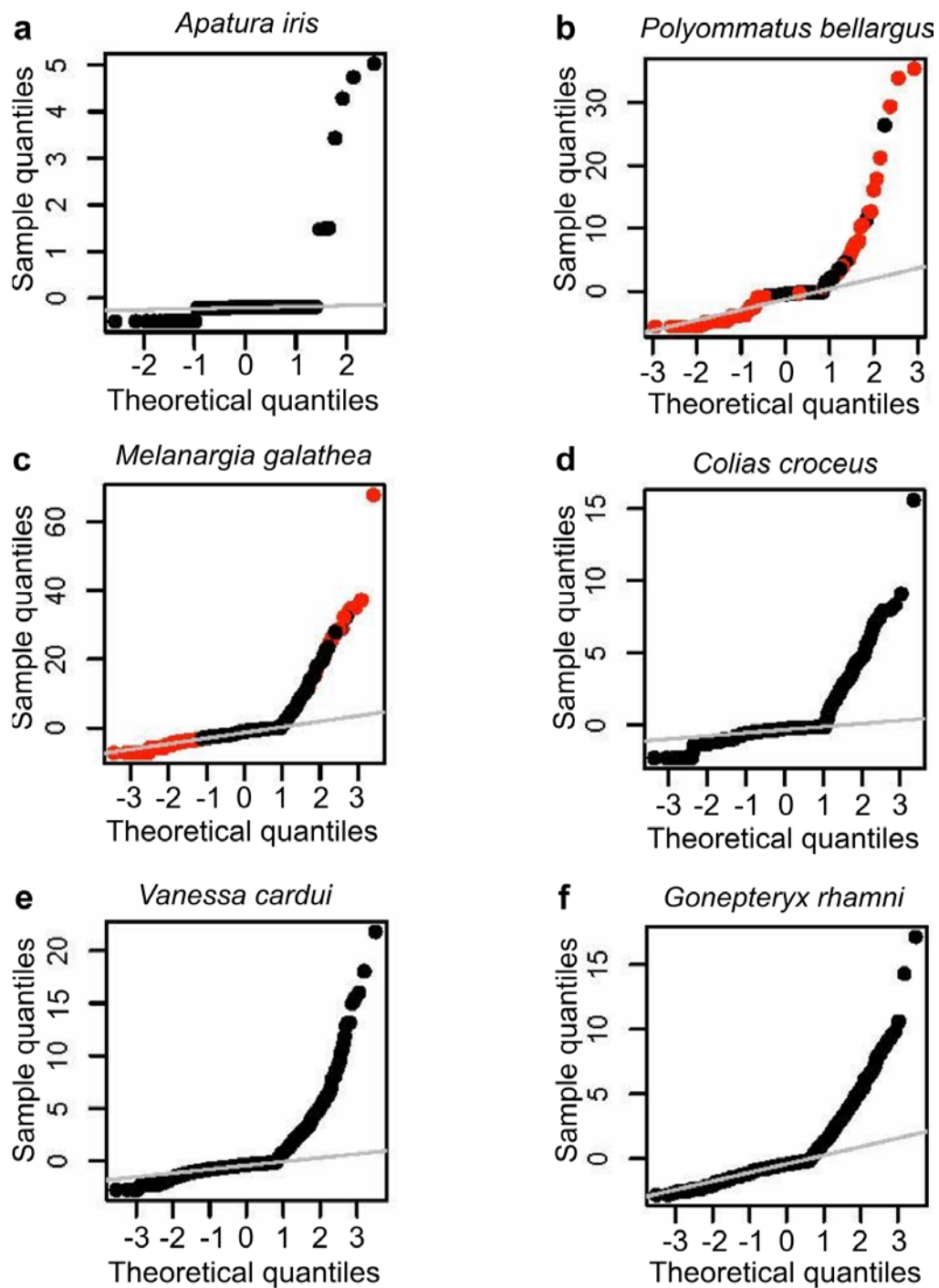


Figure 1. Examples of quantiles – quantiles plots for 6 of the 49 species and for the year 2006. The grey line is the $y = x$ line. Red dots are for $\lambda_{sd} > 10$. Species on the left have one peak in their phenology, and species on the right have more than one peak. *Apatura iris* (a) and *Polyommatus bellargus* (b) were present in less than 100 sites to estimate the phenology, *Melanargia galathea* (c) and *Colias croceus* (d) between 250 and 350 sites and *Vanessa cardui* (e) and *Gonepteryx rhamni* (f) more than 450 sites.

Comparison of the Poisson model to the negative binomial model with AIC criterion

Across the 490 species/year couples, AIC criterion was significantly lower ($\Delta AIC > 2$) with the negative binomial for 459 models, with the Poisson for 20 models and was not significantly different between the two distributions for 11 models (Figure 2). These results are consistent with low r coefficients estimated by the negative binomial models indicating overdispersion (Figure 3). We observe that the four models with r coefficient superior to ten did not show differences in AIC between Poisson and Negative Binomial distributions.

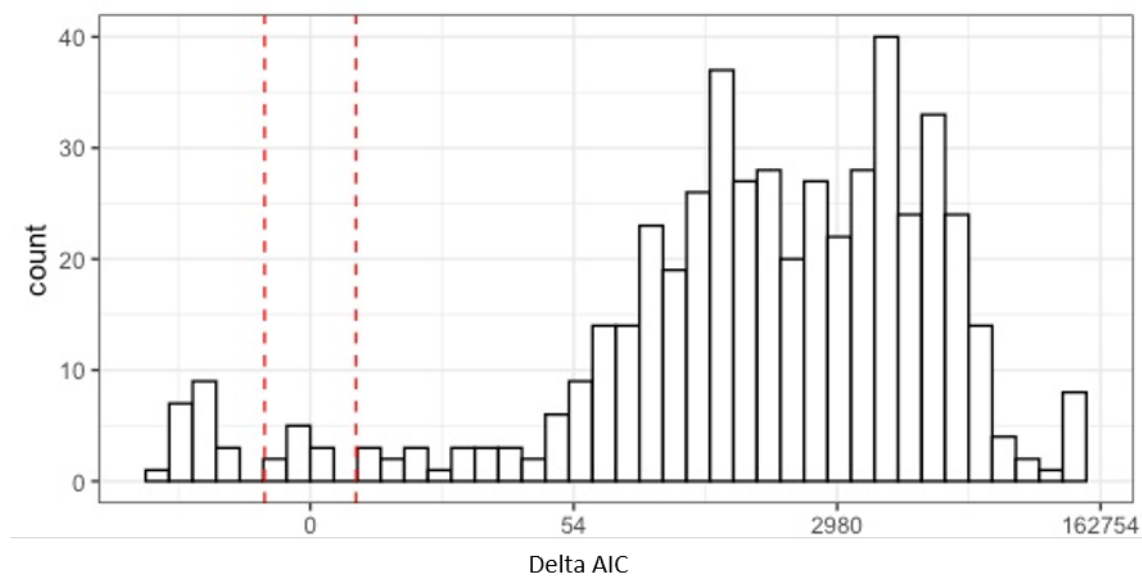


Figure 2. AIC comparison between the negative binomial and the Poisson distribution models. The x scale is on a log scale. Red lines are the significant thresholds ($\Delta AIC > 2$). Values below the red line on the left (respectively above the red line on the right) indicate that the Poisson (respectively the Negative Binomial) model provides the best fit; values between the two red lines indicate no significant difference between the fit of the two distributions.

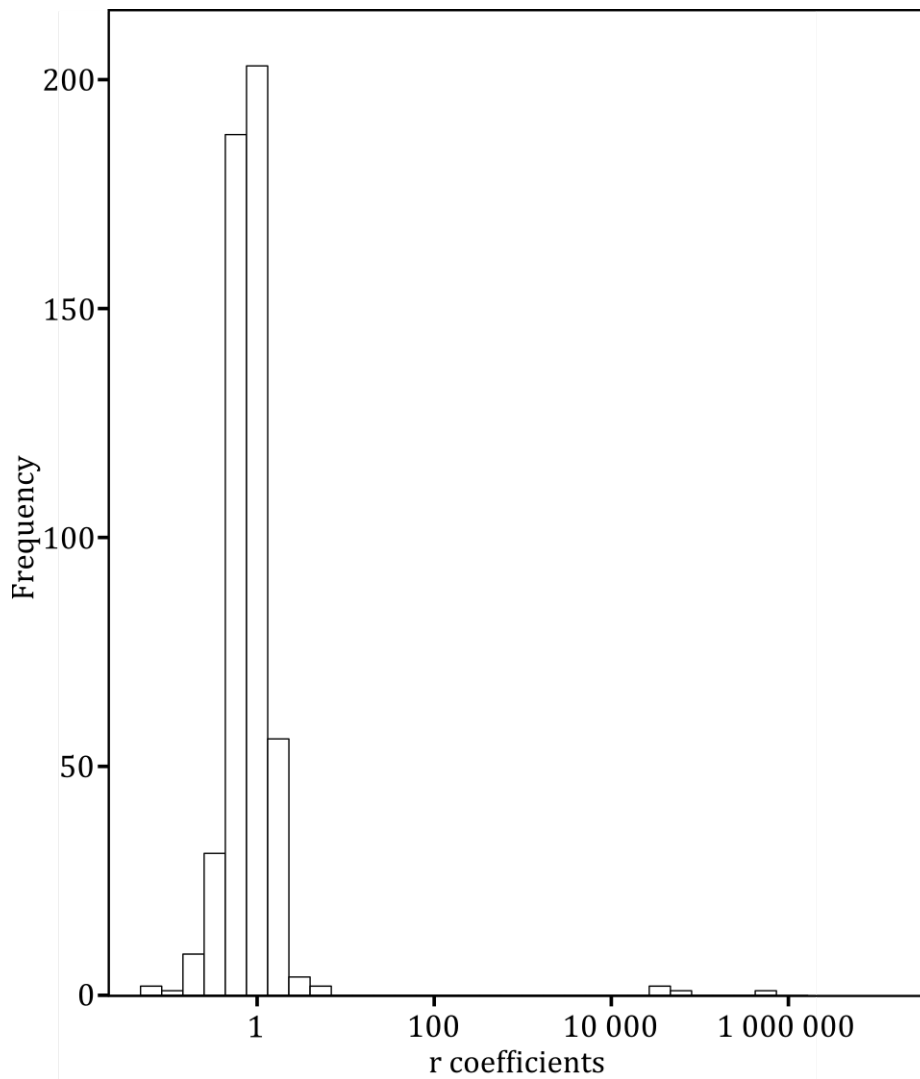


Figure 3. Histogram of r coefficients estimated by models with negative binomial distributions. The x-axis is on a log scale.

Conclusion

Our results showed a higher relevance of models using a negative binomial. In the second and third chapter of this manuscript, phenology and annual abundances have been estimated using a Negative Binomial distribution rather than a Poisson distribution.

However, the amount of 0 and the potential overdispersion in our data can vary across species and year, in relation with phenology length and commonness of species that affect the detection probability along the years. Better ΔAIC for Poisson models could reflect species/year couples with low overdispersion, leading to a stronger negative contribution of

the overdispersion coefficient to the AIC of Negative binomial models than for species/year couples with high overdispersion.

Finally, zero-inflation could also occur in count datasets like UKBMS dataset, for the same reasons as for overdispersion. To maximise the relevance of the model choose to estimate yearly phenologies and annual abundance indices, an exploration of the zero-inflation in data should be made.

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Chapitre 2. Le rôle de la similarité des traits des espèces et des conditions environnementales dans la synchronie locale entre espèces de papillons

Contexte

Dans le 1^{er} chapitre, j'ai mis en évidence un rôle principal de la synchronie entre espèces dans la relation entre la diversité et la stabilité de l'abondance des communautés naturelles de chauves-souris, de papillons et d'oiseaux. Cette synchronie entre espèces diminue lorsque la richesse spécifique et la diversité phylogénétique augmentent, reflétant des réponses différentes aux conditions environnementales. Plus une communauté est riche, plus la probabilité qu'elle contienne des espèces qui réagiront différemment aux conditions environnementales est grande. De même, plus la diversité phylogénétique au sein d'une communauté est grande, plus les espèces de cette communauté peuvent avoir des traits de réponses aux conditions environnementales différents. Afin de mieux appréhender cette relation diversité – synchronie au niveau des communautés locales, dans le but d'orienter des politiques de décisions qui permettront de maintenir une diversité locale assurant la stabilité des communautés, il est nécessaire de comprendre quels traits des espèces affecte leur synchronie. Dans ce second chapitre, je me suis intéressé à la synchronie locale entre espèces de papillons. J'ai cherché à expliquer cette synchronie avec des indices de similarité de traits, liés aux ressources utilisées par les chenilles et adultes, et aux conditions environnementales subies par les adultes. J'ai également intégré à mon modèle les conditions environnementales comme le contexte paysager, le climat et la variabilité climatique, facteurs qui peuvent affecter localement la synchronie entre espèces et qui sont directement concernés par les changements globaux.

Résultats

Dans cette étude je montre le rôle principal de la similarité des ressources utilisées au stade chenille comme au stade adulte, et du chevauchement de phénologie des adultes qui reflète de la similarité des conditions environnementales subies par les individus adultes, dans la synchronie locale entre espèces de papillons. Je montre également que le climat et la variabilité climatique affectent la synchronie, et que le contexte paysager (notamment la quantité et la diversité d'habitat) peut tamponner les effets synchronisant du climat. Ces résultats suggèrent que favoriser des communautés de papillons avec des espèces qui se nourrissent sur des plantes différentes et dont les adultes volent à des moments différents de l'année peut diminuer la synchronie locale entre espèces, et stabiliser les communautés. De plus, favoriser la diversité d'habitat peut fournir aux espèces une plus grande diversité de refuges aux variations des conditions climatiques et ainsi diminuer l'effet synchronisant des conditions environnementales comme la variabilité climatique.

Combined effects of traits, habitat context and weather variability on interspecific synchrony in common butterflies of Great Britain

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Abstract

The long standing interest for synchrony across populations within a species is related to the increased risks of regional extinction when population dynamics are synchronized. Synchrony among species within local communities has received less attention, although it can lead to instability of ecosystem functions in case of high synchrony among species in the same functional group. The factors influencing interspecific synchrony, such as similarities in species traits and local environmental conditions, remain poorly known. Here we show that for butterfly communities, local interspecific synchrony increases with species trait similarity related to shared food sources and with adult phenology overlap. These results reflect shared trophic interactions and resource availability effects, as well as responses to shared environmental conditions on synchrony among species. We also show a positive correlation between synchrony among species and the increase in detrimental climatic conditions, weather variability, modulated by landscape context. The effects of species trait similarity on synchrony among species depended on environmental conditions. For example, synchrony among species increased more with hostplant similarity in sites with low grassland area, suggesting a stronger shared resource availability than in sites with high grassland area. Our results suggest that the diversity of both biotic and abiotic interactions is an important driver of the synchrony among species inside local communities. Synchrony among species has been highlighted as a major driver of the diversity – stability relationship. Our findings strengthen the hypothesis of a negative effect of global changes on community stability and on ecosystem functions, through the increase of environmental forcing and the decrease of functional diversity.

Keywords

Local interspecific synchrony, Species traits, Butterflies, Food sources, Phenology overlap, Weather, Habitat

Introduction

Synchrony has mainly been studied in space and across population dynamics of a given species (Liebhold et al., 2004), particularly to understand the increased risk of regional or global extinction associated with highly synchronous populations (Allen et al., 1993; Black et al., 2018; Mikko et al., 1997; Palmqvist and Lundberg, 1998). Three main mechanisms are thought to influence spatial population synchrony: (i) individual dispersal, with a synchrony at broader spatial scale for species with high vs. low dispersal ability (Anderson et al., 2018; Hopson and Fox, 2019; Paradis et al., 1999; Pardikes et al., 2017; Sutcliffe et al., 1996), (ii) species interactions such as predation or competition can synchronize populations of either interacting species (e.g. Ims and Andreassen (2000) for preys, Jarillo et al. (2018) for competing species, Liebhold et al. (2004)) and (iii) environmental conditions, which seem to have the strongest effect on population synchrony (Lande et al. 1999, Pardikes et al. 2017). Environmental variability such as rainfall or temperature affect population abundance and dynamics, such that populations of sites with similar and synchronous variations in environmental conditions are expected to be synchronous (Hudson and Cattadori, 1999; Koenig, 2002), a phenomenon called Moran's effect (Moran, 1953). The positive correlation between synchrony of population fluctuation and environmental conditions has been shown for a large variety of taxa including trees (Shestakova et al., 2016), birds (Bellamy et al., 2003; Black et al., 2018), insects (Allstadt et al., 2015; Powney et al., 2010; Sheppard et al., 2016), large vertebrates (Grenfell et al., 1998; Post and Forchhammer, 2002) and plankton (Defriez et al., 2016).

Besides their effects on temporal fluctuations among population of the same species across space, environmental conditions may also influence the temporal synchrony among species within local communities, depending on their ecological traits. Local synchrony among species, hereafter interspecific synchrony, has received less attention although it is one of the main drivers of the temporal stability of communities (Blüthgen et al., 2016; Thibaut and Connolly, 2013). For example, Hansen et al. (2013) showed a synchronizing effect of extreme weather events on a rodent community in Svalbard islands. Moran's effect on spatial

population synchrony can differ among species because of contrasting sensitivities to environmental variations, related to different ecological traits (Tedesco et al. 2006, Franzén et al. 2013). Therefore, local interspecific synchrony may also increase with ecological trait similarity, due to similar responses to environmental conditions. For example, Raimondo et al. (2004a, b) showed that butterfly species are more synchronous when sharing similar larval feeding strategy or larval phenology, related to shared predators and meteorological conditions. More generally, Rocha et al., (2011) found that plankton interspecific synchrony increases with functional similarity. However, in general we know little about the identity of traits affecting interspecific synchrony.

Local habitat characteristics are a much less studied but potentially important modifier of interspecific synchrony, in interaction with species ecological traits. For example, Oliver et al. (2010) suggested that habitat heterogeneity increases the diversity of contrasting environmental conditions such as food sources, or microclimatic conditions used by butterflies as refuges to face adverse meteorological conditions. Species inhabiting locally different habitats could face weather and climatic conditions differently, leading to more asynchronous dynamics at the local scale. Oliver et al. (2010) predicted a decrease of interspecific synchrony when increasing local habitat diversity. Different environmental conditions such as habitat context, weather variability or climatic conditions could interact with each other and affect interspecific synchrony, as it is suggested for habitat diversity. These combined effects could vary according to trait similarity among species, but we still know little about the potential interactions between factors that influence interspecific synchrony. There is thus a need for studies integrating both environmental and species trait components to better understand the drivers of interspecific synchrony within local communities. Such knowledge is crucial in the current context of global changes, resulting in increased habitat degradation, a potential increase in climate variability (Huntingford et al., 2013; Pendergrass et al., 2017) and population declines (Fox et al., 2015; Wenzel et al., 2006), if we are to maintain stable ecosystem functions.

In this study we tested how climatic conditions, habitat context and species trait similarity and their interactions are related to interspecific synchrony, focusing on 52 butterfly species surveyed each year in 393 sites across the UK between 2006 and 2015. We specifically tested the following hypotheses.

First, butterflies are known to be highly sensitive to both habitat and climate conditions (Botham et al., 2015; Crozier, 2004; Fourcade et al., 2017; Krauss et al., 2003; Oliver et al., 2010; Olivier et al., 2016; Pollard, 1988; Roy et al., 2001; Tack et al., 2015; Wenzel et al., 2006). Hence, we hypothesized that more variable climate conditions, e.g. in terms of temperature and rainfall, could increase interspecific synchrony, because of more variable resource availability and lower survival rates affecting all species similarly. These synchronizing effects of climate conditions may increase along a latitudinal gradient, as butterflies tend to be more sensitive to temperature or rainfall towards their range edges, and especially towards north, because of less suitable climate conditions compared to the core of their range (Mills et al., 2017; Oliver et al., 2014; Thomas et al., 1994). Second, following Oliver et al. (2010), we hypothesize that a decrease in habitat amount and diversity could increase interspecific synchrony through more homogeneous microclimatic conditions. However, a decrease in habitat amount and diversity could also decrease interspecific synchrony through increased competition for resources. In addition to simple effects, we tested first order interactions based on the following hypotheses: by providing more climatic refuges and food sources, an increase in habitat amount and diversity can buffer the predicted increase in interspecific synchrony with the increase in detrimental climate conditions and their variability.

Third, we hypothesized that interspecific synchrony increases with food source similarity, for both adults and caterpillars, because of more similar food resource availability or more shared predators. We also hypothesized that interspecific synchrony increases with the level of phenology overlap because of more shared environmental conditions. In addition to simple effects, we tested first order interactions based on the following hypotheses:

- (i) The increase in amount and diversity of habitat could increase the amount and diversity of food sources, and exacerbate the correlation between interspecific synchrony and food source similarity due to competition or food source availability
- (ii) The correlation between interspecific synchrony and climate and habitat conditions can increase with adult phenology overlap because of environmental conditions that are more likely to be shared when adults fly concomitantly.

Materials and method

We first estimated annual local species abundances using data collected by the UK Butterfly Monitoring Scheme. These annual local abundances were then used to compute an index of synchrony across years and between species, for each pair of species at each site. We then correlated local interspecific synchrony with local landscape context, climate conditions and their inter-annual variations, resource similarity between species, and their first order interactions.

Butterfly variables

Dataset

We used data from the UK Butterfly Monitoring Scheme (UKBMS, <http://www.ukbms.org/>), which consists in butterfly counts in sites located all over the UK. Each site is divided into transects corresponding to different local land cover types or management units, for a total length of about 2-4km. Transects are fixed across years. Butterflies are recorded on a weekly basis every year from the beginning of April until the end of September, following weather and time restrictions (Pollard, 1977). We used counts of 52 species in 1,859 sites surveyed during the 2006-2015 period (Appendix 1).

Phenology and annual abundance estimation

The estimation of local required comparable time series of annual abundance across species. The strong seasonal patterns – i.e. phenology – of butterfly species abundance and the

absence of daily counts constrained us to estimate the phenology of each species in order to compute a representative index of annual abundance. Recently, a method has been developed to estimate both species phenology and annual population abundances with large datasets such as the UK Butterfly Monitoring Scheme (UKBMS) (Schmucki et al., 2016). The principle of this method is to aggregate data from multiple sites with similar phenology to maximise the number of surveyed days along a year. This method estimates first the shape of the annual phenology of a given species using the aggregated count data from multiple sites throughout a region. Counts are modelled according to a semi-parametric generalized linear model with log link and Poisson distribution:

$$E[N_{sd}] = \lambda_{sd} = e^{(\gamma_s + f(d))}$$

with $E[N_{sd}]$ the expected number of individuals counted on day d at site s , corresponding to the estimated mean of the Poisson distribution λ_{sd} , γ_s the effect of site s on the number of individuals, and $f(d)$ the phenology across all days d within a year. To obtain $f(d)$, a cubic spline is applied on d , where the sum of $f(d)$ over all days within a year is set to 0.

We modified the method of Schmucki et al. (2016), which uses Generalized Additive Models (GAM) with Poisson distribution, by using a Negative Binomial to fit our models and take account of potential overdispersion. We grouped sites into bioclimatic regions (Appendix 2) as defined by the UK Meteorological Office [www.metoffice.gov.uk], because of the known effect of climatic conditions on phenology (Davies, 2019; Parmesan, 2007; Roy and Sparks, 2000; Sparks and Yates, 1997; Stålhandske et al., 2015; Walther et al., 2002). We therefore estimated one phenology per species, region and year. When a species was not observed during a monitoring event at a given site and day, but was observed at least once in this site within the year, the abundance of the species was set to 0 at this day and site (i.e. pseudo-absence).

From each model we extracted two estimates:

- (i) The annual phenology of species i $\hat{f}_y^i(d)$, shared by all populations of the species within a climatic region and year. Each $\hat{f}_y^i(d)$ corresponds to daily normalized abundances, such that the sum over d is 1.

- (ii) The site effect $\hat{\gamma}_{sy}^i$, which we used as an index of the annual abundance of species i at site s on year y .

Butterfly abundance time series

To characterize interspecific synchrony, we first split the yearly site effect γ_{sy}^i into two components:

$$\gamma_{sy}^i = \alpha_s^i + \beta_{sy}^i$$

with α_s^i an overall site effect, constant through time, computed as the mean γ_{sy}^i over years, and β_{sy}^i the yearly variation of the site effect around its mean. Because we wanted to compute the synchrony between species inter-annual variations independently of the site effect, we retained only the time series of $\beta_{sy}^i = \gamma_{sy}^i - \alpha_s^i$ for all species and sites.

Temporal Trend

Significant temporal trends could occur at a local scale, as already known at the UK scale (Fox et al., 2015). Such temporal trends could influence our synchrony measures of inter-annual variations. For example, two species could be synchronous because of a similar decline across time and not because of non-systematic inter-annual variations (Figure 1). To avoid the potential confounding effect of temporal trends, we also used corrected β_{sy}^i to estimate local interspecific synchrony. To correct β_{sy}^i times series, we regressed β_{sy}^i linearly on year for each species at each site, and we retrieved the residuals of β_{sy}^i for each species, site and year. This yielded two time series, the raw and the corrected β_{sy}^i , for each species/site couple.

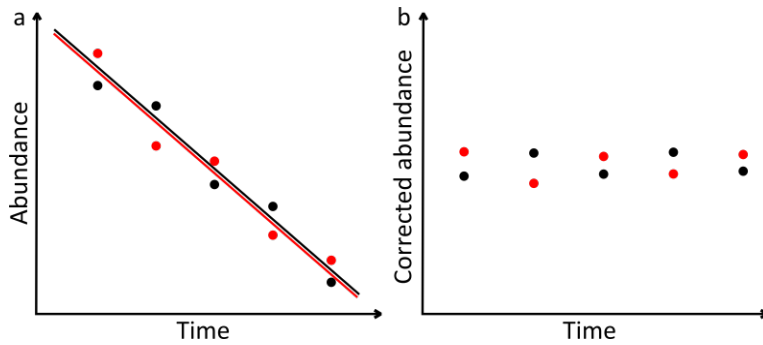


Figure 1. Example of time series of two species (red and black) exhibiting highly synchronous fluctuations due to a similar temporal trend (decline) (a), but highly asynchronous fluctuations after correcting for the temporal trends (b). Circles represent abundance values, and lines the temporal trends.

Synchrony index

We measured synchrony between two species as the correlation between their β_{sy}^i time series across years. To only account for the year-to-year fluctuations without the differences in relative abundance between species, we used Spearman's rank correlation coefficient. To compute synchrony on sufficiently long time series, we only kept species/site couples with survey events every year and at least one observation per year for at least 9 out of the 10 years of the study period. For species that were recorded only 9 years despite survey events the 10 years in a given site, we considered the missing year as the year with the lowest abundance in the time series. Interspecific synchrony was computed with both raw and corrected β_{sy}^i time series.

Climate conditions

To characterize temperature and rainfall conditions, we first extracted daily temperature and rainfall at each site from October 2005 to October 2015 from the ENSEMBLES dataset (Haylock et al., 2008), using data from the nearest E-OBS station in the UK on a 0.25-degree grid. Climate data were extracted using the R package `climateExtract` (Schmucki, 2018), and `devtools` (Wickham et al., 2018). As butterfly species abundance and survival can be influenced by temperature and rainfall during both summer and winter (Crozier, 2004; Fourcade et al., 2017; Klockmann and Fischer, 2019; Roy et al., 2001; Tack et al., 2015;

Thomas et al., 1994), each year was split into winter – from October to March - and summer – from April to September – seasons, with the latter matching the UKBMS survey period. At each site, we computed the seasonal mean temperature and rainfall across 2006-2015 for summer and winter. Then, for each season and at each site we computed the mean and the standard deviation of temperature and rainfall across years. To reduce the number of variables and avoid correlations among temperature and rainfall variables, we performed a PCA on all variables plus the latitude of each site. This allowed us to extract two gradients explaining 51.9% and 23.8% of the variance. The first gradient, hereafter latitudinal gradient, reflected the distribution of sites from south to north. Correlated to latitude, there was a decrease of mean temperature and an increase of summer rainfall mean and variability along this gradient. The second gradient, hereafter climate variability gradient, opposed sites with high winter rainfall mean and inter-annual mean variability to sites with high temperature inter-annual mean variability (Appendix 3).

Landscape context

Using Land Cover Map 2015 [<https://www.ceh.ac.uk/services/land-cover-map-2015>], we extracted landscape variables in buffers of 1,000, 2,000 and 5,000m around the centroid of each site; this range of distances is considered appropriate to study the relationships of butterflies with their surrounding landscape (Oliver et al. 2010).

The area of favourable land cover types is known to affect species abundances (Botham et al., 2015; Krauss et al., 2003; Olivier et al., 2016) because of increased resource availability. To estimate the area of favourable land cover types, we computed the total area of open land covered by different types of grasslands (Appendix 4). Because woodland edges may provide large amounts and diversity of resources for both caterpillars and adults, but also refuges against rain and high temperatures (Fry and Sarlöv-Herlin, 1997), we also computed the total length of woodland edges in each buffer.

Oliver et al. (2010) suggested that different species using locally different land cover types could have different population dynamics because of different survival rates, resource availability and microclimatic conditions. Landscapes that are more diverse would then host

more asynchronous populations than landscapes with less diverse land cover (Oliver et al. 2010). To reflect habitat diversity, we computed a Shannon diversity index on the basis of two land cover types: grassland and woodland.

A PCA on these three landscape variables indicated that the total length of woodland edges was highly correlated with Shannon diversity and not with grassland area; we thus retained total area of grassland and total length of woodland edges to characterize the landscape context (Appendix 5).

Species trait similarity

Similarity of species resources

The similarity in food source availability between two species could affect their individual survival and reproduction similarly, so the synchrony between their population fluctuations. To test this hypothesis, we computed food sources similarity between each pair of species. Raimondo et al. (2004a) used a categorical index to assess caterpillar feeding strategy similarity. Here we computed quantitative indices about food source similarity to highlight a potential linear increase of interspecific synchrony along trait similarity indices. Moreover, butterflies are characterized by contrasting life stages with different ecological traits. We computed two food source similarity indices, one based on hostplants used caterpillar, and one based on nectar plants used by adults. We used the larval hostplant and key nectar plant species list compiled for UK butterfly species in Dennis (2012). For each pair of species, we computed the Jaccard similarity index of hostplants used by larvae, and the Jaccard similarity index of nectar plants used by adults.

Adult phenology overlap

Each butterfly species has an adult flight period, called adult phenology and related to environmental conditions and species traits. Variations of adult flight period among species can reflect variations in shared experience environmental conditions such as daily temperature and rainfall. These environmental conditions could affect individual survival

and reproduction, and adults experiencing the same environmental conditions could have similar population fluctuations. To test this hypothesis, we computed an index of adult phenology overlap for each species pair from the yearly adult phenology, in each bioclimatic region. This index reflected the proportion of adults of each species of a pair that experienced the same environmental conditions (Figure 2), and extends the previous study of (Raimondo et al., 2004b), based on caterpillar phenology. We computed this overlap as the sum, over all days, of the minimum estimated phenology $f(d)$ between the two species. This yielded one overlap index per species pair, year and region between 2006 and 2015. To obtain a single overlap index per pair and bioclimatic region, we computed for each region and pair the mean index across years. This index can vary from 0 for species that do not overlap to 1 for species that have a perfect phenology overlap; across the 52 species studied here, the average phenology overlap varied between 0.0001 and 0.91 (Figure 2).

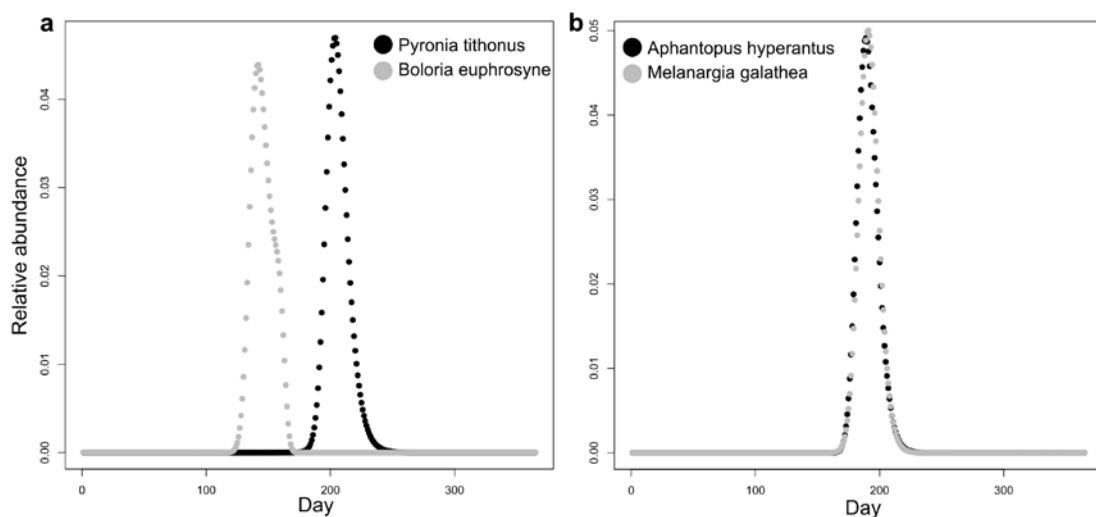


Figure 2. Examples of adult phenology overlap for the year 2006 in the south-east region of the UK, with overlap < 0.001 (a), and overlap = 0.94 (b).

Hostplant similarity was weakly correlated with both nectar plant similarity and adult phenology overlap (Pearson's $r^2 = 0.33$, p -value <0.001 and $r^2=0.12$, p -value <0.001 respectively), while nectar plant similarity and adult phenology overlap were more strongly correlated (Pearson's $r^2 = 0.49$, p -value <0.001). These three trait similarity indices reflected different aspects of the shared environmental conditions between butterfly species. Hostplant and nectar plant similarity reflect food sources availability at two different life

stages, and adult phenology overlap reflect the environmental conditions shared by adults. We thus retained these three between-species similarity indices to correlate interspecific synchrony with trait similarity.

Statistical analyses

We used Bayesian models to correlate local interspecific synchrony with temperature and rainfall gradients, landscape, diet similarity and phenology overlap variables. We included different interactions between our explanatory variables in our model:

$$\begin{aligned}
 Synchrony_{(a,b)i} = & \mu + \alpha_1 GrassArea_i + \alpha_2 WoodEdge_i + \alpha_3 HostSim_{(a,b)} \\
 & + \alpha_4 NectarSim_{(a,b)} + \alpha_5 ClimVarGrad_i + \alpha_6 LatGrad_i \\
 & + \alpha_7 PhenOverlap_{(a,b)i} + \alpha_8 GrassArea_i * NectarSim_{(a,b)} \\
 & + \alpha_9 GrassArea_i * HostSim_{(a,b)} + \alpha_{10} GrassArea_i * ClimVarGrad_i \\
 & + \alpha_{11} GrassArea_i * LatGrad_i + \alpha_{12} WoodEdge_i * NectarSim_{(a,b)} \\
 & + \alpha_{13} WoodEdge_i * HostSim_{(a,b)} + \alpha_{14} WoodEdge_i * ClimVarGrad_i \\
 & + \alpha_{15} WoodEdge_i * LatGrad_i + \alpha_{16} PhenOverlap_{(a,b)i} * ClimVarGrad_i \\
 & + \alpha_{17} PhenOverlap_{(a,b)i} * LatGrad_i + Site_i + a + b
 \end{aligned}$$

with $Synchrony_{(a,b)i}$ the Spearman coefficient of species pair (a,b) at site i (i.e. synchrony), μ the mean of $Synchrony_{(a,b)i}$, $GrassArea$ the grassland area, $WoodEdge$ the total length of woodland edges, $HostSim$ the hostplant similarity index, $NectarSim$ the nectar plant similarity index, $ClimVarGrad$ the climate variability gradient, $LatGrad$ the latitudinal gradient, $PhenOverlap$ the mean adult phenology overlap index, $Site$ the site of the species pair, a and b the two species in the pair. Site and species were considered random effects, to control for pseudo-replication across sites and species, and with a Gaussian distribution centred on zero. Because a given species can appear indiscriminately as a or b depending on the species pair, we assumed that the two random species effects were sampled from the same distribution (same variance). We performed models at the three spatial scales of landscape context, and for synchrony calculated with and without correction for temporal trends. Four chains were run using uninformative priors to draw 10,000 MCMC iterations,

discarding the first 5,000 iterations. Samples were thinned by 1 in 10 to reduce autocorrelation.

We present results of models with landscape context extracted at the best spatial scale based on DIC for models with raw and corrected β_{sy}^i (Appendix 6).

Results

Interspecific synchrony was higher between species with more similar hostplants, nectar plants or adult phenology overlap, regardless of whether raw or corrected β_{sy}^i time series were considered (Table 1 and Figures 3 and 4). In addition, some of the effects of trait similarity were modulated by environmental variables. Associated with adult phenology overlap, interspecific synchrony increased steeper in sites with low inter-annual temperature variability and high mean and inter-annual variability winter rainfall than in sites with high inter-annual temperature variability and low mean and inter-annual variability winter rainfall (Table 1 and Figures 3d). Interspecific synchrony tended to increase along the latitudinal gradient in sites with high grassland area, while it tended to decrease in sites with low grassland area (Table 1 and Figure 3c and 4c). In general, the significant interactions were much weaker than simple effects.

Interspecific synchrony was also influenced by environmental variables. The climate variability gradient showed a positive correlation with interspecific synchrony, with strength similar to the correlation with the three species traits variables. Interspecific synchrony was higher in sites with high inter-annual mean temperature variability and low mean an inter-annual variability rainfall than in sites with low inter-annual mean temperature variability and high mean an inter-annual variability rainfall.

Finally, the patterns for corrected β_{sy}^i were generally identical to those for raw betas, with a few exceptions. With corrected β_{sy}^i , we found no significant interaction between adult phenology overlap and the climate variability gradient compared to raw β_{sy}^i . With corrected β_{sy}^i , interspecific synchrony was negatively correlated with the climate variability gradient in sites associated with high woodland edge length, and positively correlated in sites associated

with low woodland edge length (Table 1 and Figure 4e). With corrected β_{sy}^i the strength of the positive correlation between hostplant similarity and interspecific synchrony increased while the grassland area decreased (Table 1 and Figure 4b).

Table 1. Parameter estimates of models performed with synchrony computed with raw β_{sy}^i time series or corrected β_{sy}^i time series. *Nectar* is the nectar plant similarity, *Hostplants* the hostplant similarity, *Overlap* the mean adult phenology overlap, *LatGrad* the latitudinal gradient, *ClimVarGrad* the climate variability gradient, *Grass* the grassland area and *Edge* the total length of woodland edges. Two variables with “x” indicate the interaction effect between the two variables. Variables for which zero is not included in the 95% credibility interval of their mean are in bold.

Variable	Raw time series			Corrected time series		
	Mean	2.5%	97.5%	Mean	2.5%	97.5%
NectarSim	0.016	0.012	0.021	0.010	0.005	0.015
HostSim	0.010	0.007	0.014	0.015	0.011	0.019
PhenOverlap	0.030	0.026	0.034	0.030	0.026	0.035
LatGrad	0	-0.008	0.007	0.004	-0.003	0.012
ClimVarGrad	0.013	0.005	0.022	0.010	0.001	0.019
GrassArea	-0.007	-0.016	0.003	-0.007	-0.016	0.001
WoodEdge	0.006	-0.003	0.014	0.006	-0.002	0.014
NectarSim x GrassArea	-0.001	-0.005	0.002	-0.002	-0.005	0.002
NectarSim x WoodEdge	-0.002	-0.006	0.001	-0.002	-0.005	0.002
HostSim x GrassArea	-0.003	0.006	0	-0.006	-0.009	-0.003
HostSim x WoodEdge	0.003	0	0.006	0.001	-0.002	0.004
PhenOverlap x LatGrad	0.001	-0.002	0.004	0.003	0	0.006
PhenOverlap x ClimVarGrad	0.004	0.001	0.007	0.002	-0.001	0.005
PhenOverlap x GrassArea	0.001	-0.002	0.004	0.002	-0.001	0.006
PhenOverlap x WoodEdge	-0.002	-0.006	0.001	-0.003	-0.006	0
GrassArea x LatGrad	0.007	0.001	0.013	0.007	0.002	0.013
GrassArea x ClimVarGrad	-0.003	-0.013	0.006	0.004	-0.005	0.013
WoodEdge x LatGrad	-0.001	-0.008	0.006	0.002	-0.004	0.008
WoodEdge x ClimVarGrad	-0.007	-0.017	0.003	-0.011	-0.020	-0.004

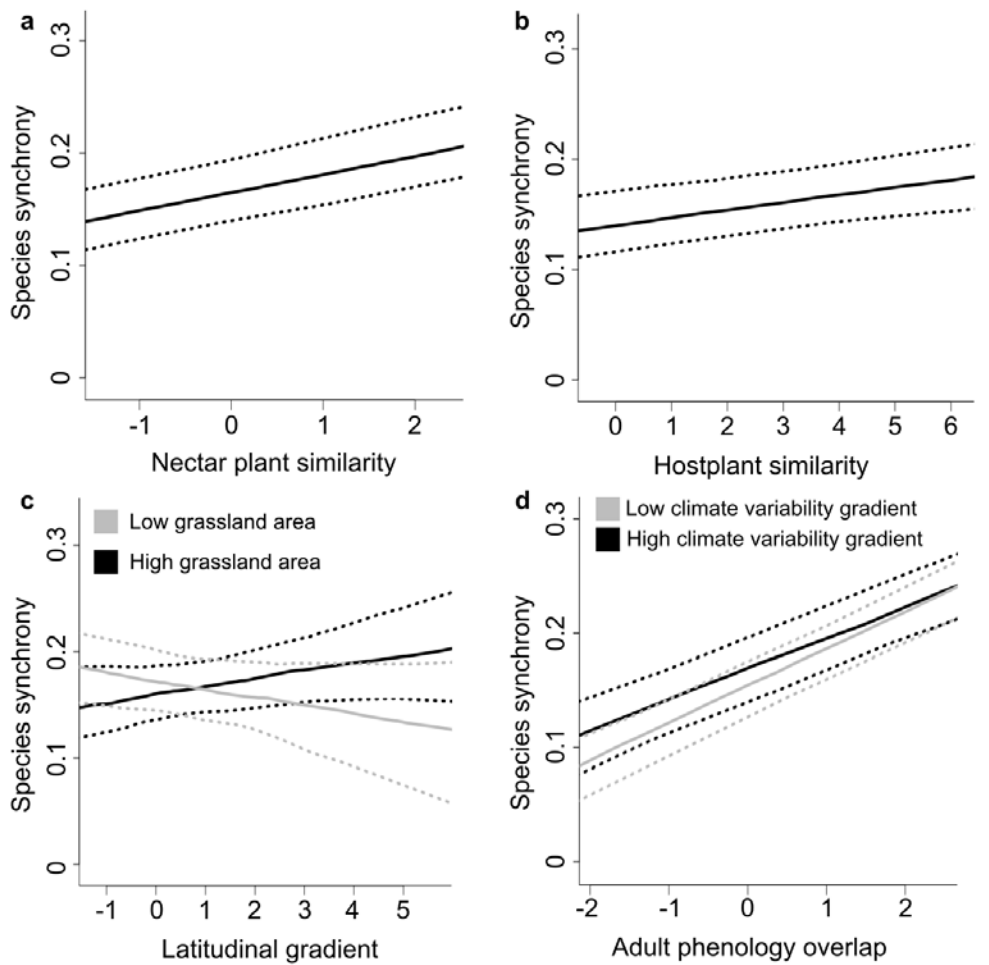


Figure 3. Correlations between environmental variables, species traits similarity and interspecific synchrony computed with raw β_{sy}^i time series. Dashed lines are the 95% confidence interval. When present, significant interactions are illustrated by plotting the predicted linear relationship with two contrasting values for the interacting variable: mean value minus (grey lines) or plus (black lines) one standard deviation.

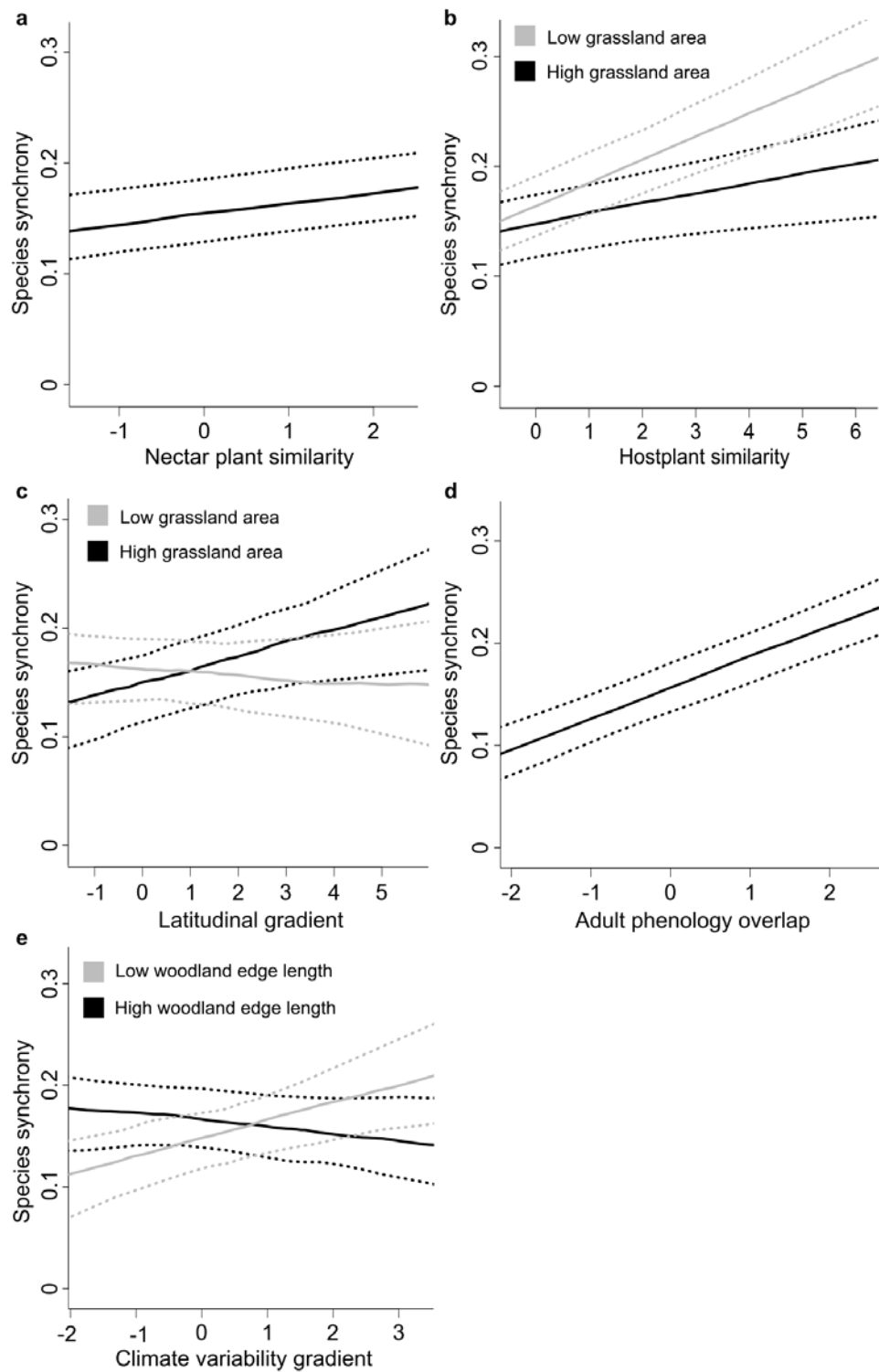


Figure 4. Correlations between environmental variables, species traits similarity and interspecific synchrony computed with corrected β_{Sy}^i time series. Dashed lines are the 95% confidence interval. When present, significant interactions are illustrated by plotting the

predicted linear relationship with two contrasting values for the interacting variable: mean value minus (grey lines) or plus (black lines) one standard deviation.

Discussion

In this study, we first showed that local interspecific synchrony increase with adult phenology overlap, as well as nectar and hostplant plant similarity. These species trait similarities had the main effect on interspecific synchrony. Second, our results suggest that variations in temperature and rainfall mean and inter-annual variability can increase interspecific synchrony, with different mitigating effects of grassland area and woodland edge length.

The role of species trait similarity in interspecific synchrony

Our results suggest a strong correlation between interspecific synchrony and shared environmental conditions such as weather conditions, species interactions and food resource availability.

The adult phenology overlap was positively related with interspecific synchrony, extending the results of Raimondo et al. (2004b), who found that species with larvae present during the same season were more synchronous than those with larvae present in different seasons. This result suggests that interspecific synchrony is related to adult responses to environmental conditions that vary along the years, with more similar responses when adult individuals are active during the same period and thus share same environmental conditions. However, our results did not disentangle the role of different environmental conditions such as climate or species interactions that can underlie shared adult phenology.

We found a positive correlation between food source similarity and interspecific synchrony for both butterfly caterpillars and adults. This could suggest that diet similarity at different life-stages affects the fluctuation of species local adult abundances, through a bottom-up effect. The amount of food sources for caterpillars affects both larval and adult survival, hence the number of flying adults in the same year (Boggs and Freeman, 2005). The amount

of food sources for adults affects adult reproduction, hence the number of larvae of the following year, as it has been shown that adult resources affect their reproductive success (Boggs and Ross, 1993; Murphy et al., 1983). Consequently, interspecific synchrony could increase with hostplant similarity because of similar hostplants availability, leading to similar caterpillar and adult survival, hence similar number of adults in the same year. Similarly, interspecific synchrony could increase with nectar plants similarity because of similar nectar plants availability, leading to similar variations of adult reproductive success, hence similar number of adults the following year. Bottom-up effects of resource availability on interspecific synchrony have already been hypothesized, and Mysterud et al. (2007) suggested that the synchrony of mass variation between roe deer and boar is driven by the temporal variation of crop availability used by both species.

The positive correlation between interspecific synchrony and the similarity of hostplants or nectar plants follow the results of Raimondo et al. (2004a) and highlight a primary role of trophic interactions on the interspecific synchrony. Because all the species they studied were feeding on oaks, Raimondo et al. suggested a top-down effect of predators caused by similar exposure to generalist predators of species with similar larval feeding behaviour, rather than a bottom-up effect due to similar resource availability. Here we assessed diet similarity as a quantitative measure of hostplants and nectar plants similarity, but our results cannot exclude a top-down effect on butterfly interspecific synchrony as suggested by Raimondo et al. (2004a).

The significant interaction between hostplant similarity and grassland area observed with corrected β_{sy}^i , where the correlation between hostplant similarity and interspecific synchrony increases when grassland area decreases, can also be the result of bottom-up effects. Plant richness has been shown to be positively correlated with grassland area (Krauss et al., 2004). Food limitation for species with similar hostplants could thus increase in sites with low vs. high grassland area, and increase the synchrony among species sharing hostplants (Figure 4b).

Abundance time series of butterfly hostplants, nectar plants and predators would make it possible to disentangle between bottom-up vs. top-down effects, by assessing butterfly

interspecific synchrony and their resources or predators. Bottom-up and top-down effects would depend on the synchrony between butterfly species and their resources or predator fluctuations, but also on potential time lag in these synchrony (Stenseth et al., 1999). Koenig (2001) suggested that a high synchrony of seed productions among tree species could explain a weak relationship between synchrony among boreal birds in North-America and diet similarity. Assess the synchrony among butterfly food resources could also argue for a top-down or a bottom-up effect.

Environmental conditions

The climate variability gradient was the only environmental variable that showed a significant simple effect on interspecific synchrony, with strength similar to species trait similarity variables. This climate variability conditions – synchrony correlation is consistent with previous studies showing a synchronizing effect of weather conditions on plankton (Buttay et al., 2017) and of rainfall variability on mammal species (Hansen et al., 2013; Stien Audun et al., 2012). In our study, interspecific synchrony was higher in sites with high inter-annual variations of temperature and low winter rainfall mean and standard deviation (Appendix 3). This suggests that temperature inter-annual variations have synchronizing effect through individual survival, regardless species characteristics.

Moreover, interspecific synchrony with raw β_{sy}^i was also higher in sites with high inter-annual mean temperature variability and low rainfall mean for species pairs with low adult phenology overlap only (Figure 3d). This suggests that inter-annual variations in mean temperature and rainfall are similar along the year in a site, and can affect species that do not fly at the same time.

Grassland area and woodland edge length showed significant effects on interspecific synchrony only in interactions with other variables. For both raw and corrected β_{sy}^i interspecific synchrony increased along the latitudinal gradient in sites with high grassland area and decreased in sites with low grassland area. Species are predicted to be more sensitive to climate conditions closer to the edge of their distribution, as shown for the

sensitivity of European butterfly populations to climate (Thomas et al. 1994, Mills et al. 2017). We expected an increase in interspecific synchrony along the latitudinal gradient, reflecting synchronizing climatic factors in sites located close to the northern edge of species distribution, and with lower mean temperatures and higher mean summer rainfall. The positive correlation between the latitudinal gradient and the interspecific synchrony in sites with high grassland area is then consistent with our expectations. The contrasted results in sites with low grassland area is more difficult to interpret. Nevertheless, it could reflect differences in community composition related to grassland area and species habitat preferences (Kuussaari et al., 2007). Sites with less grassland could contain more species affiliated to other habitats than sites with high grassland area. As Shreeve et al. (2001) showed that species habitat preference is related to species traits, communities in sites with low grassland area could contain species with more different traits relative to the sensitivity to climate conditions, leading to more contrasting interspecific synchrony values.

Habitat amount and diversity may mitigate the role of climate variability on interspecific synchrony. In our study, woodland edge length was positively correlated with habitat diversity, and interacted with the climate variability gradient to mitigate its influence on interspecific synchrony with corrected β_{sy}^i (Figure 4e). Beyond a mere proxy for habitat diversity, woodland edges are known to provide micro-climatic conditions, refuges, and specific habitats (Fry and Sarlöv-Herlin 1997). Our result follows Oliver et al. (2010) predictions that the increase in habitat diversity decreases interspecific synchrony, because of more plants diversity and more microclimates that can be used as refuges against climate variations.

Conclusion

This study brings to light mechanisms involved in local interspecific synchrony and related to community trait diversity. The decrease in biodiversity and homogenization of communities (Devictor et al., 2008; Ekroos et al., 2010; Gámez-Virués et al., 2015) can lead to an increase in diet similarity and phenology overlap, increasing interspecific synchrony and destabilizing local communities. Increasing climate variability (Huntingford et al., 2013; Pendergrass et al.,

2017) could also destabilize local communities through the increase of interspecific synchrony, with less mitigating effects of landscape in the context of habitat degradation. Climate warming could lead to lower interspecific synchrony in high latitudes where mean temperature increases. Nevertheless, climate warming could also lead to detrimental climatic conditions in southern latitudes, and increase inter-annual climate variability in both south and north (Huntingford et al., 2013; Pendergrass et al., 2017).

By reducing the compensatory dynamics related to various level of interspecific synchrony, these factors could lead to a strong decrease in the temporal stability of local community abundance, with potential consequences for ecosystem functions such as pollination. Our results showed significant interactions between species traits similarity and environmental conditions in their role on interspecific synchrony. This suggests the need to integrate both environmental and species components when assessing the factors that drive interspecific synchrony. For butterflies, management strategies that maximise diversity traits related to food resources and top adult phenology are required to increase the stability of natural butterfly communities and the pollination service they provide.

Declaration

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Author contributions – All authors designed the study and analysed the results, T.O. managed the datasets and performed the statistical analyses; all authors participated in writing.

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Appendices

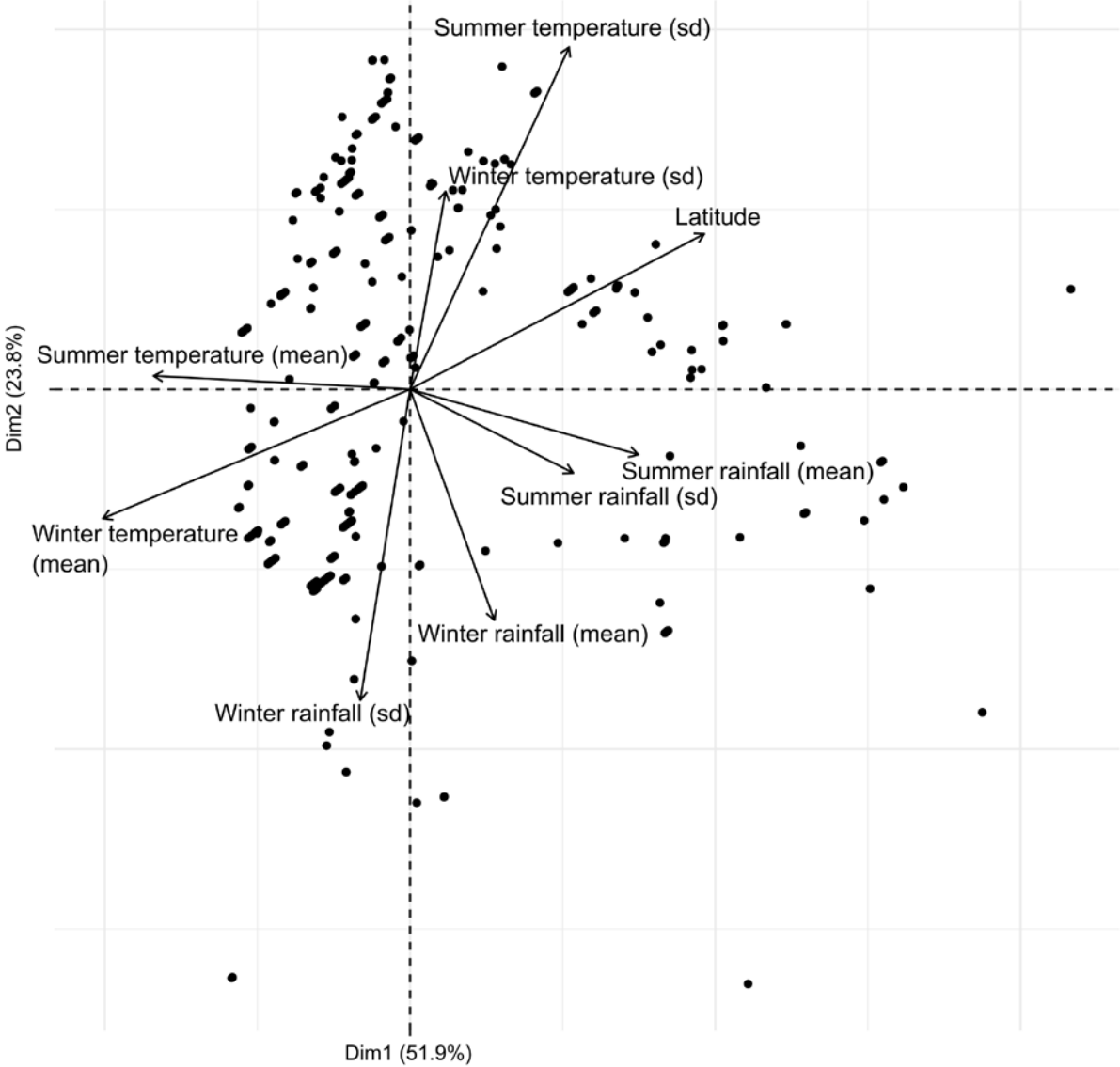
Appendix 1. List of butterfly species

Species	
<i>Aglais io</i>	<i>Limenitis camilla</i>
<i>Aglais urticae</i>	<i>Lycaena phlaeas</i>
<i>Anthocharis cardamines</i>	<i>Erebia aethiops</i>
<i>Aphantopus hyperantus</i>	<i>Maniola jurtina</i>
<i>Argynnis adippe</i>	<i>Melanargia galathea</i>
<i>Argynnis aglaja</i>	<i>Melitaea athalia</i>
<i>Argynnis paphia</i>	<i>Ochlodes sylvanus</i>
<i>Aricia artaxerxes</i>	<i>Pararge aegeria</i>
<i>Aricia agestis</i>	<i>Pieris brassicae</i>
<i>Boloria euphrosyne</i>	<i>Pieris napi</i>
<i>Boloria selene</i>	<i>Pieris rapae</i>
<i>Callophrys rubi</i>	<i>Plebejus argus</i>
<i>Celastrina argiolus</i>	<i>Polygonia c-album</i>
<i>Coenonympha pamphilus</i>	<i>Polyommatus bellargus</i>
<i>Colias croceus</i>	<i>Polyommatus coridon</i>
<i>Coenonympha tullia</i>	<i>Polyommatus icarus</i>
<i>Cupido minimus</i>	<i>Pyrgus malvae</i>
<i>Erynnis tages</i>	<i>Pyronia tithonus</i>
<i>Euphydryas aurinia</i>	<i>Stayirium pruni</i>
<i>Favonius quercus</i>	<i>Satyrium w-album</i>
<i>Gonepteryx rhamni</i>	<i>Thymelicus lineola</i>
<i>Hesperia coma</i>	<i>Thecla betulae</i>
<i>Hipparchia semele</i>	<i>Thymelicus acteon</i>
<i>Hamearis lucina</i>	<i>Thymelicus sylvestris</i>
<i>Lasiommata megera</i>	<i>Vanessa atalanta</i>
<i>Leptidea sinapis</i>	<i>Vanessa cardui</i>

Appendix 2. Map of the 393 sites with at least two species observed every year between 2006 and 2015 and used to compute local interspecific synchrony, with the different climatic regions used to estimate annual species abundances and yearly phenology.



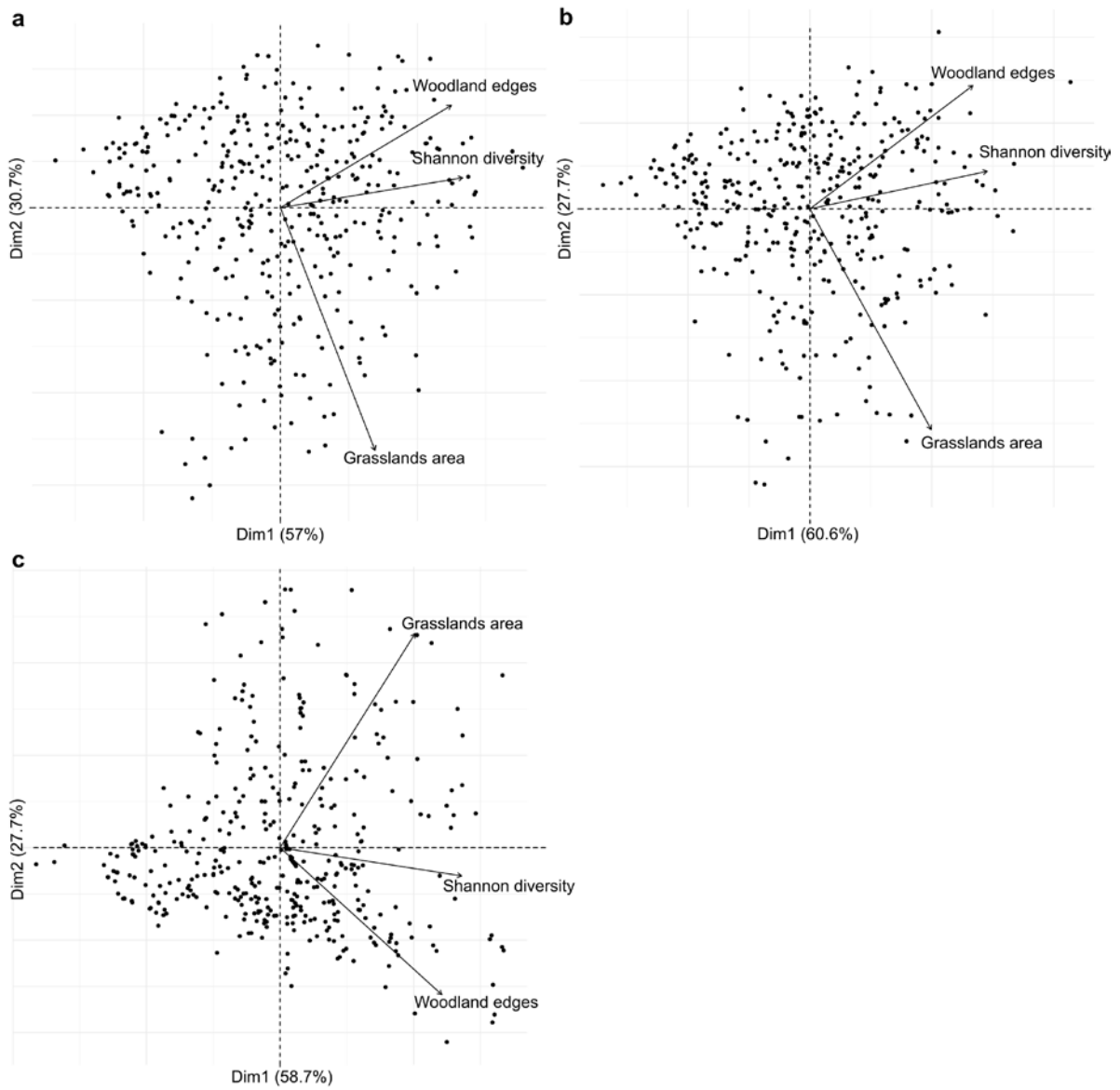
Appendix 3. PCA of weather variables.



Appendix 4. Land Cover Map categories retained for grassland area, woodland edges and Shannon diversity.

Aggregate class	Broad Habitat	Variable
Broadleaf woodland	Broadleaved, Mixed and Yew Woodland	Woodland edges Shannon diversity
Coniferous woodland	Coniferous Woodland	Woodland edges Shannon diversity
Improved grassland	Improved Grassland	Grasslands area Shannon diversity
Semi-natural grassland	Neutral Grassland Calcareous Grassland Acid Grassland Fen, Marsh and Swamp	Grasslands area Shannon diversity
Heath	Heather Heather grassland	Grasslands area Shannon diversity

Appendix 5. PCA of landscape variables at 1000m (a), 2000m (b) and 5000m (c) scales.



Appendix 6. DIC of Bayesian models at each spatial scale.

Spatial scale	1000m	2000m	5000m
Corrected time-series	37517	37521	37531
Non corrected time-series	34250	34213	34226

Chapitre 3. L'impact des tendances temporelles d'abondance sur les dynamiques compensatoires entre espèces de papillons à l'échelle régionale

Contexte

Dans les deux premiers chapitres, je me suis intéressé à la stabilité des communautés et à la synchronie entre espèces à une échelle locale. Cette échelle spatiale est la plus communément utilisée dans l'étude et la compréhension de la stabilité des systèmes écologiques. Récemment, la stabilité à l'échelle régionale a commencé à être étudiée, notamment dans le cadre des changements globaux pour comprendre l'impact d'extinctions régionales sur la stabilité des écosystèmes et de leur fonctionnement. Cette approche à plus large échelle permet aussi de faciliter l'utilisation des résultats pour prendre des décisions de management et de conservation des écosystèmes.

A l'échelle régionale, on retrouve les mêmes types de mécanismes qui vont agir sur la stabilité, comme la stabilité des composantes du système étudié, et la synchronie entre les fluctuations de ces composantes. A l'échelle régionale également, on observe des tendances temporelles dans l'évolution de l'abondance des espèces. Ces tendances, lorsqu'elles sont négatives, peuvent mener à l'extinction d'espèces, et donc à l'extinction de la part qu'elles prenaient dans le fonctionnement des écosystèmes.

Dans ce 3^{ème} chapitre, je me suis intéressé au lien entre synchronie entre espèces à l'échelle régionale et tendances temporelles de l'abondance de ces mêmes espèces. J'ai travaillé sur des espèces de papillons à l'échelle du Royaume-Uni. J'ai ainsi regroupé les espèces selon leur degré de synchronie, et j'ai confronté ces groupes d'espèces à leurs tendances temporelles. L'hypothèse de cette étude est que si les espèces en déclin et les espèces en augmentation sont dans des groupes de synchronie distincts, on peut s'attendre à ce que l'extinction des espèces en déclin entraîne la disparition de groupes d'espèces synchrones, affectant ainsi le potentiel de dynamiques compensatoires et la stabilité des communautés à l'échelle régionale.

Résultats

Dans ce troisième chapitre, je montre ainsi qu'il existe une variation des valeurs de synchronie entre espèces de papillons à l'échelle régionale, suggérant un potentiel de dynamiques compensatoires pouvant stabiliser les communautés à l'échelle régionale. Après avoir regroupé les espèces en groupes d'espèces synchrones, je n'ai pas montré de répartition des tendances temporelles différente de celle aléatoirement attendue.

Ces résultats suggèrent que le déclin des espèces du fait des changements globaux n'est pas susceptible d'affecter le potentiel de dynamiques compensatoires de la communauté de papillons au Royaume-Uni à l'échelle régionale de façon plus importante qu'aléatoirement attendue.

Une approche basée sur les traits des espèces pourrait permettre d'identifier quels traits des espèces expliquent les tendances temporelles ou les groupes d'espèces synchrones, pour identifier des mécanismes différents entre ceux liés aux tendances temporelles et ceux liés à la synchronie entre espèces. De plus, le déclin des espèces peut aussi déstabiliser les populations à l'échelle régionale. Étudier le lien entre stabilité des populations à l'échelle régionale et tendances temporelles des espèces pourrait aider à la compréhension de l'impact des changements globaux sur la stabilité des communautés à l'échelle régionale.

What are the links between long-term temporal trends and regional-scale species synchrony in butterfly communities of Great Britain?

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Abstract

Because of biodiversity loss and ecosystem homogenization, global changes are expected to decrease the temporal stability of ecological properties such as community abundance or biomass. This in turn could destabilize ecosystem functions and services provided by animal and plant communities, at both local and regional scale. Recently, studies focusing on community and population stability have switched from the local to the regional scale, in order to fit better with management and conservation policies. At the regional scale, species abundances can show increasing or decreasing temporal trends in response to global changes. In the case of a decline of abundance or biomass, species can go extinct at some point. Synchrony among species at the regional scale is predicted to be one of the main mechanism controlling regional stability. If all synchronous species show similar temporal trends, the potential extinction of declining species could affect the potential for compensatory dynamics at the regional scale. This in turn would destabilize ecosystem functions and services at the regional scale. To assess the effect of temporal trends on regional stability through interspecific synchrony, we first grouped species according to their synchrony on the 2006-2015 period at the UK scale. Second, we analysed the distribution of long-term temporal trends across groups of synchrony. Our results do not support a negative effect of long-term temporal trends on the compensatory dynamics at the regional scale. In all groups of synchrony temporal trends were not distributed differently than randomly expected. Further analyses with species traits could help to understand differences in global change impact on synchrony among species and temporal trends at the regional scale. However, in our study all groups of synchrony contained both declining and increasing species, suggesting that in each group the decline of some species might be partly compensated by the increase of other species.

Keywords

Butterfly, Regional synchrony, Temporal trends, Hierarchical clustering

Introduction

In a local community, synchrony reflects the similarity across species of local temporal fluctuations in a given property such as biomass or abundance, and is negatively correlated with stability (Thibaut and Connolly, 2013). A decrease in the compensatory dynamics increases synchrony among species, leading to an increase of the stability of the whole community (Loreau and de Mazancourt, 2008, 2013; Thibaut and Connolly, 2013). Synchrony among species is one of the main drivers of the stability of local community (Hector et al., 2010; Loreau and de Mazancourt, 2013; Sasaki et al., 2019; Thibaut and Connolly, 2013).

Recently, theoretical studies have extended our understanding of stability to larger spatial scales (Wang and Loreau, 2014, 2016; Wang et al., 2019), to better fit with the spatial scale of management and conservation policies. At the regional scale, the stability of metacommunities can be decomposed into two components (Wang et al. 2019). First, the average metapopulation stability, that reflects the stability of aggregated local populations of a species. The contribution of each metapopulation stability to the average metapopulation stability is weighted by its relative abundance in the metacommunity. The stability of the metacommunity increases with the average metapopulation stability, and depends more on the abundant than rare metapopulations. Second, the regional-scale species synchrony. Synchrony reflects the correlation between regional-scale species fluctuations. Metapopulations with low synchrony (high asynchrony) will stabilize the metacommunity because of compensatory dynamics. Wang et al. (2019) showed that at both local and regional scale, species synchrony decreased when species richness increased. They also showed that species synchrony decreased from local to regional scale, and suggested a potential effect of an increase of species richness from local to regional scale.

In local communities, variations in synchrony among species are related to species responses to variations of environmental conditions (Tredennick et al., 2017). Variations of environmental conditions could also explain synchrony among species at a regional scale. Environmental changes such as landscape degradation or climate change affect environmental conditions but also temporal trends of species abundance, for example butterflies (Fox et al., 2015). Species that are synchronous because of similar responses to

environmental condition variations could also have similar temporal trends because of similar sensitivity to environmental changes. Species groups according to regional species synchrony could be correlated with species group according to temporal trends. In the case of decline, temporal trends can lead to the extinction of a species. If declining species are in the same groups of synchronous species, the potential extinction of these groups would decrease the potential of compensatory dynamics at the regional scale, decreasing the regional metacommunity stability.

In this study, we aimed to assess if long-term temporal trends of butterfly species computed on the 1976-2004 period are specifically distributed in groups of synchronous species, and if potential species extinction could affect compensatory dynamics at the regional scale. We worked on 53 butterfly species located in the UK and surveyed in more than 1865 sites between 2006 and 2015. We first grouped species according to their temporal synchrony. Second, we analysed the distribution of long-term temporal trends across groups of synchrony.

Material and methods

We first estimated annual local species abundances using data generated by the UK Butterfly Monitoring Scheme. To get one annual abundance per species and year that reflect the regional annual abundance we retained for each species and year the median local abundance across populations. Median values allow us to mitigate the impact of potential outliers to reflect of the regional abundance index of species. With median abundance time series, we computed a synchrony index across years for each pair of species, and clustered species in synchronous groups. We then investigated the distribution of temporal trends across synchronous groups.

Clustering of butterfly species in groups of synchrony

Dataset

We used data from the UK Butterfly Monitoring Scheme (UKBMS, <http://www.ukbms.org/>), which consist in butterfly counts in sites located all over the UK. Each site is divided into transects corresponding to different local land cover types or management units, for a total

length of about 2-4km long. Transects are fixed across years. Butterflies are recorded on a weekly basis every year from the beginning of April until the end of September, following weather and time restrictions (Pollard, 1977). We used counts of 53 species in 1,859 sites surveyed during the 2006-2015 period (Appendix 1).

Annual abundance estimation

The estimation of local species synchrony required comparable time series of annual abundance across species. The strong seasonal patterns – i.e. phenology – of butterfly species abundance and the absence of daily counts constrained us to estimate the phenology of each species in order to compute a representative annual abundance index. We modified the method of Schmucki et al. (2016), which uses semi-parametric generalized linear models with Poisson distribution on repeated counts within sites to fit the phenology of a species, by using a Negative Binomial to fit our models and take account of potential overdispersion. We grouped sites into bioclimatic regions (Appendix 2) as defined by the UK Meteorological Office [www.metoffice.gov.uk], because of the known effect of meteorological conditions on phenology (Davies, 2019; Parmesan, 2007; Roy and Sparks, 2000; Sparks and Yates, 1997; Stålhandske et al., 2015; Walther et al., 2002). We therefore estimated one phenology per species, region and year by fitting a semi-parametric generalized linear model with negative binomial distribution and mean modelling:

$$E[N_{sdy}^i] = e^{(\gamma_{sy}^i + f_y^i(d))}$$

with N_{sdy}^i the expected mean number of individuals of species i counted on day d of year y at site s , γ_{sy}^i the effect of site s on the abundance of species i on year y , and $f_y^i(d)$ the phenology of species i on year y , across all days d . Note that we assumed identical phenologies for a given species and year across all sites in a region. When a species was not observed during a monitoring event at a given site and day, but was observed at least once in this site within the year, the count of the species was set to 0 at this day and site (i.e. pseudo-absence). From each model we extracted the site effect $\hat{\gamma}_{sy}^i$, which we used as an index of the annual abundance of species i at site s on year y .

Butterfly median abundance time series

To characterize species synchrony, we first split the yearly site effect γ_{sy}^i into two components:

$$\gamma_{sy}^i = \alpha_s^i + \beta_{sy}^i$$

With α_s^i an overall site effect, constant through time, computed as the mean γ_{sy}^i over years, and β_{sy}^i the yearly variation of the site effect around its mean. To consider only abundance interannual variations among species, we retained the time series of $\beta_{sy}^i = \gamma_{sy}^i - \alpha_s^i$ for all species and sites. We then retained for each species and year the median β_y^i across all sites s of β_{sy}^i , to characterize the interannual variations of species abundance at the regional scale. Retain the median rather than the mean allowed us to mitigate the impact of outliers.

Correction for temporal trends

Significant temporal trends could occur at a local scale, as already known at the UK scale (Fox et al., 2015). Such temporal trends could influence synchrony measured on the basis of inter-annual variations. For example, two species could be synchronous because of a similar decline across time and not because of non-systematic inter-annual variations. To avoid the potential confounding effect of temporal trends, we used corrected β_y^i to estimate synchrony among species. To correct β_{sy}^i times series, we regressed median β_{sy}^i linearly on year for each species, and we retrieved the residuals for each species and year, referred as the corrected median below.

Synchrony index

We measured synchrony between two species as the correlation between their corrected median β_{sy}^i time series across years. To take only account of the year-to-year fluctuations without the differences in relative abundance between species populations, we used Spearman's rank coefficient of correlation.

Hierarchical clustering

To separate species in groups of synchrony, we used the hierarchical clustering method. A hierarchical clustering use a dissimilarity matrix to build a dendrogram and differentiate groups. In a dendrogram, each observation is a "leaf", and each node is a group of leaves.

The height of a node gives the dissimilarity at which leaves in the node have been grouped. The root of the dendrogram is the node that contains all observations. To build the dendrogram, we used an agglomerative method.

An agglomerative clustering is a bottom-up method, and starts at the leaf level. At the first step, each leaf is a group. At each step the agglomerative clustering groups leaf according to the dissimilarity matrix, until there is only one group left with all the observations inside. Our agglomerative method was based on Ward method (Ward, 1963). The algorithm computes the sum of distances between each leaf outside a group and the centre of gravity of the group. Then the Ward method groups leaf in the way to maximise this sum of distances. We grouped species according to three, five and seven groups of synchronous species. We used the “hclust” function from the R package “stats” (R Core Team, 2013).

Link with long-term temporal trends

1976 – 2014 UK butterfly temporal trends

To investigate the link between regional interspecific synchrony and temporal trends, we used data from The State of the UK’s Butterflies 2015 (Fox et al. 2015) (Appendix 1). This report estimated the temporal trend of butterfly species in the UK, based on the UKBMS counts from 1976 to 2014. For each species, we extracted the percentage of abundance change over the 1976-2014 period as well as the significance of estimated temporal trends. We only used significant trends to analyse the distribution of temporal trends among groups of synchrony.

Null models

To investigate if some groups of synchrony showed particular global temporal trend, we performed null models. For each group, we computed the mean temporal trend for species with significant temporal trend. We then sampled 1,000 times in the full set of species the same number of species as in the group, and computed the mean temporal trend of species with significant trend. We compared the mean temporal trends of the group to the distributions of mean temporal trend of random samples. If the group mean temporal trend

is outside the 95% confidence interval of the distribution, the mean temporal trend is different from randomly expected.

Results

We observed contrasting Spearman's correlation values across species pairs, with both highly synchronous and highly asynchronous species pairs (Figure 1). We chose arbitrarily three different distance thresholds to separate species into groups of synchrony, resulting in three, five or seven groups (Figure 2). These three clusters allowed us to analyse the distribution of temporal trends inside groups of synchrony according to different level of synchrony among species.

Of the 53 species used in this study, eleven showed a significant and positive temporal trend, twenty a significant and negative temporal trend, and twenty-two a non-significant temporal trend on the 1976-2004 period in the UK. There were both declining and increasing species in all groups of synchrony, except in group B.2, which contained only decreasing species and one stable species. In all groups but two, the number of species with significant declining temporal trend was greater than the number of species with significant increasing temporal trend (Figure 2). For group A.2, there was more species with significant increase, and for group C.3 there is an equal number of declining and increasing species. However, mean temporal trends inside groups were not different than randomly expected. Null models did not show any mean temporal trend outside the 95% confidence interval (Figure 3).

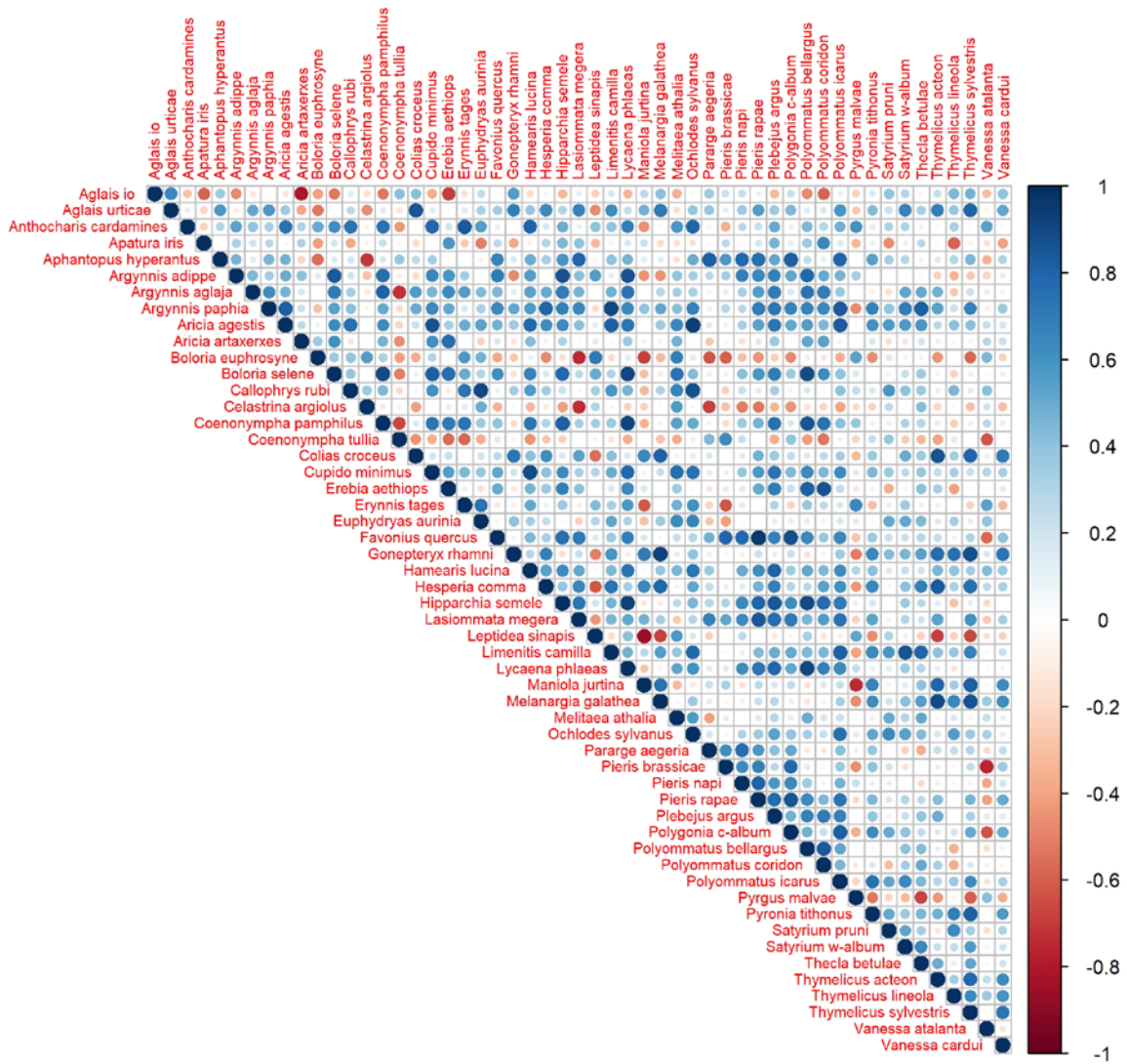


Figure 1. Correlation matrix of median β_{sy}^i computed with Spearman's rank coefficient of correlation. A value of 1 (dark blue) corresponds to perfectly synchronous species, and -1 (dark red) to perfectly asynchronous species. Species are ordered by alphabetical order.

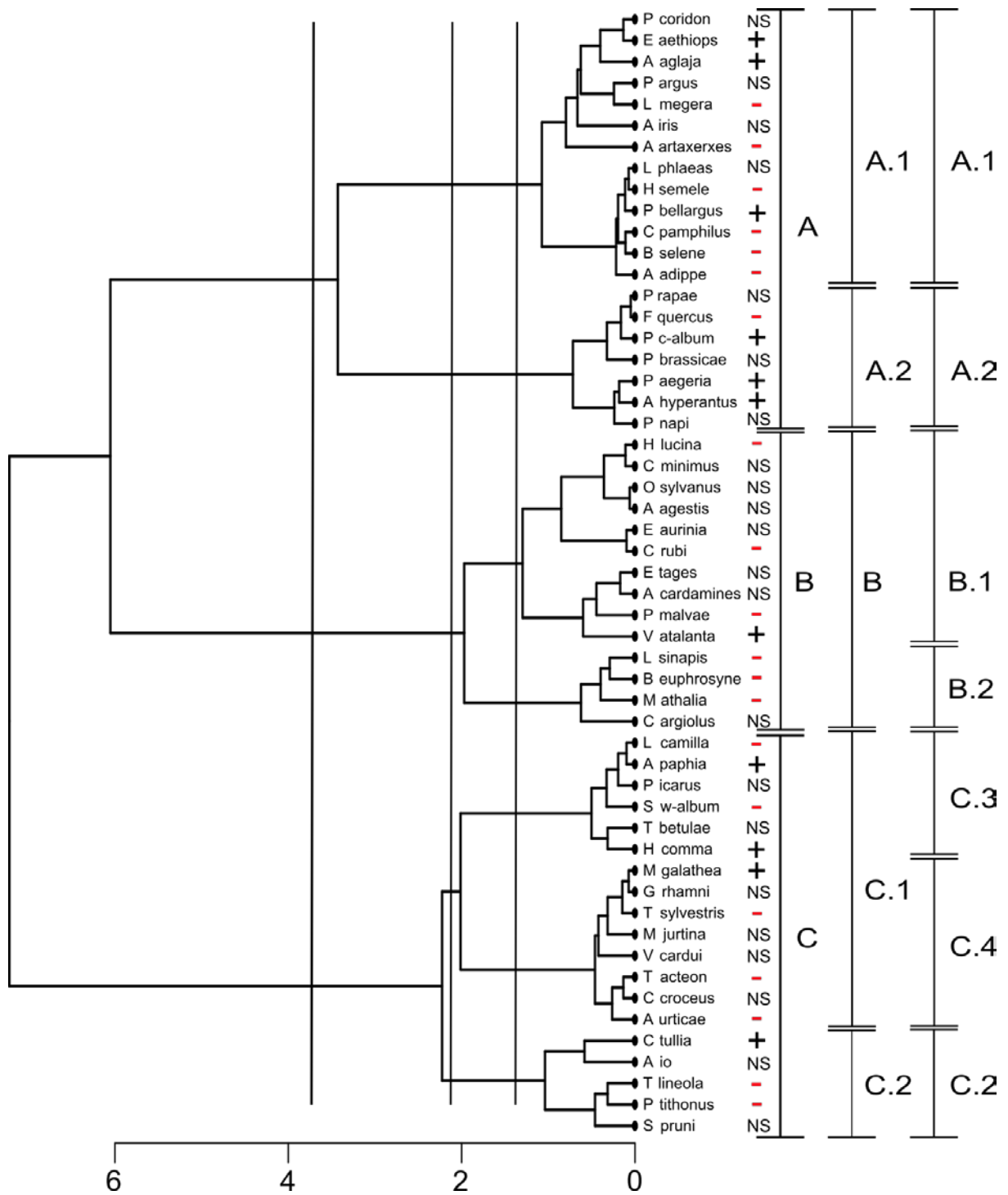


Figure 2. Dendrogram of the hierarchical clustering performed for three thresholds of synchrony. Vertical black lines are the different thresholds to separate species into groups of synchrony.

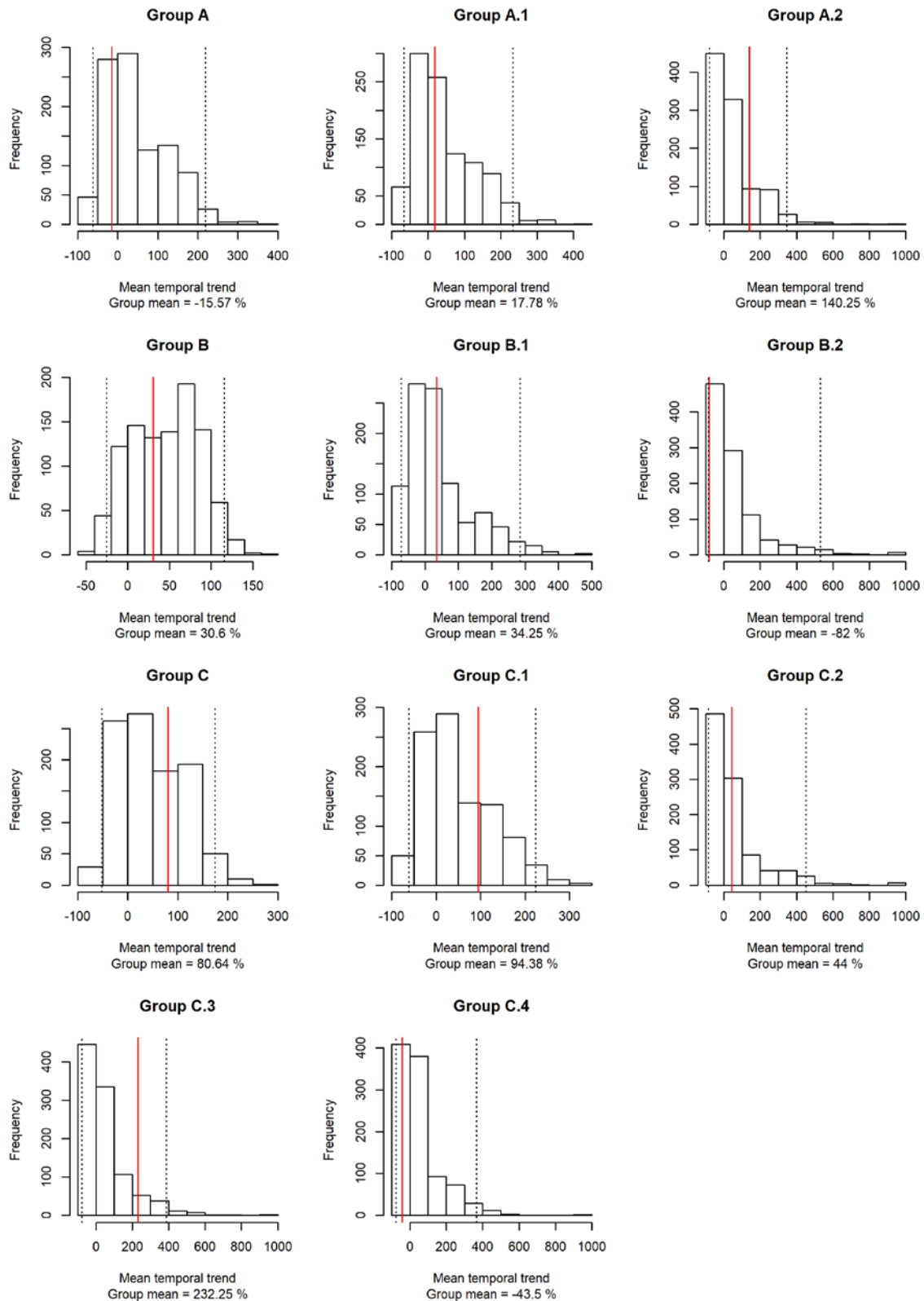


Figure 3. Histograms of the null models by groups of synchrony, with only species with significant trends, for hierarchical clustering based on three, five and seven groups. Dashed black lines are the 95% confidence interval, and red lines are the mean temporal trend of groups.

Discussion

In this study, we highlighted variations in regional interspecific synchrony values across species pairs, suggesting that compensatory dynamics can occur to stabilize the abundance of regional butterfly communities. Variations in regional synchrony among species could be related to similarity in species traits as it has been found on local synchrony among species (Olivier et al. *in prep*; Raimondo et al., 2004). The regional synchrony among species could also increase with the similarity in latitudinal range edges because of similar sensitivity to the variations of environmental conditions (Thomas et al., 1994).

When analysing the distribution of significant temporal trends across groups of synchrony, we did not highlight groups with significant temporal trends lower or higher than randomly expected (Figures 2 and 3). The absence of particular distribution of temporal trends among groups of synchronous species suggests that different environmental factors drive temporal trends and synchrony. Temporal trends of butterfly abundance seems to be mainly affected by habitat loss and fragmentation (Fox et al., 2015, Potts et al., 2010). At the local scale, synchrony among species increases primarily with species trait similarity and climate variability (Olivier et al., *in prep*). Species trait based approaches could allow to describe precisely which species traits explain temporal trends or regional interspecific synchrony and help conservation decisions.

Our results suggests that global changes responsible for temporal trends are not likely to affect regional compensatory dynamics more than if declining species were randomly distributed among groups of synchrony. However, temporal trends may affect average metapopulation stability. In addition to the correlation between temporal trends and regional-scale species synchrony, there is the need to investigate the potential correlation between temporal trends and average metapopulation stability.

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Appendix 1. Species list and long-term temporal trends (Fox et al., 2015)

Species	% Abundance change (1976-2014)	P-value
<i>Aglais io</i>	17	>0.05
<i>Aglais urticae</i>	-73	<0.05
<i>Anthocharis cardamines</i>	10	>0.05
<i>Apatura iris</i>	69	>0.05
<i>Aphantopus hyperantus</i>	381	<0.001
<i>Argynnis adippe</i>	-62	<0.05
<i>Argynnis aglaja</i>	186	<0.001
<i>Argynnis paphia</i>	141	<0.001
<i>Aricia agestis</i>	-25	>0.05
<i>Aricia artaxerxes</i>	-52	<0.05
<i>Boloria euphrosyne</i>	-71	<0.001
<i>Boloria selene</i>	-58	<0.001
<i>Callophrys rubi</i>	-41	<0.01
<i>Celastrina argiolus</i>	37	>0.05
<i>Coenonympha pamphilus</i>	-54	<0.001
<i>Coenonympha tullia</i>	261	<0.01
<i>Colias croceus</i>	734	>0.05
<i>Cupido minimus</i>	9	>0.05
<i>Erebia aethiops</i>	170	<0.01
<i>Erynnis tages</i>	-19	>0.05
<i>Euphydryas aurinia</i>	-10	>0.05
<i>Favonius quercus</i>	-54	<0.05
<i>Gonepteryx rhamni</i>	1	>0.05
<i>Hamearis lucina</i>	-42	<0.01
<i>Hesperia comma</i>	943	<0.001
<i>Hipparchia semele</i>	-58	<0.001
<i>Lasiommata megera</i>	-87	<0.001
<i>Leptidea sinapis</i>	-88	<0.001
<i>Limenitis camilla</i>	-59	<0.01
<i>Lycaena phlaeas</i>	-37	>0.05
<i>Maniola jurtina</i>	1	>0.05
<i>Melanargia galathea</i>	50	<0.05
<i>Melitaea athalia</i>	-87	<0.001
<i>Ochlodes sylvanus</i>	-17	>0.05
<i>Pararge aegeria</i>	84	<0.01
<i>Pieris brassicae</i>	-30	>0.05
<i>Pieris napi</i>	-7	>0.05
<i>Pieris rapae</i>	-25	>0.05
<i>Plebejus argus</i>	19	>0.05
<i>Polygonia c-album</i>	150	<0.001
<i>Polyommatus bellargus</i>	175	<0.01
<i>Polyommatus coridon</i>	20	>0.05
<i>Polyommatus icarus</i>	-17	>0.05
<i>Pyrgus malvae</i>	-37	<0.05
<i>Pyronia tithonus</i>	-41	<0.05
<i>Satyrium pruni</i>	-54	>0.05
<i>Satyrium w-album</i>	-96	<0.001
<i>Thecla betulae</i>	-15	>0.05
<i>Thymelicus acteon</i>	-76	<0.01
<i>Thymelicus lineola</i>	-88	<0.001
<i>Thymelicus sylvestris</i>	-75	<0.001
<i>Vanessa atalanta</i>	257	<0.01
<i>Vanessa cardui</i>	133	>0.05

Discussion

Comprendre comment les écosystèmes et leur fonctionnement font face aux changements globaux est primordial, particulièrement dans un contexte où l'intensité des activités humaines ne fait qu'augmenter. Les derniers rapports concernant le déclin de la biodiversité, notamment le déclin de 80% des insectes en Europe en 30 ans (Hallmann et al., 2017) et de 60% des vertébrés à l'échelle mondiale depuis 1970 (WWF, 2018) ne laissent plus de doute quant au fait que les écosystèmes et leur fonctionnement sont gravement altérés. L'importance de comprendre les causes et les effets de ces modifications réside dans la responsabilité que l'être humain a de ses actes sur l'ensemble de la planète, mais également du fait des bénéfices qu'il tire de cette planète pour son bien-être et son développement (Díaz et al., 2018). Afin de proposer des solutions pour limiter les dégâts, il faut comprendre précisément comment les perturbations issues des changements globaux affectent le fonctionnement des écosystèmes. Ces effets négatifs peuvent passer par le déclin d'abondance ou de biomasse des espèces, les extinctions, mais aussi des effets directs sur la stabilité des communautés, et ce à différentes échelles spatiales.

Mon travail de thèse contribue à une meilleure compréhension de la stabilité temporelle des communautés animales en conditions naturelles, et notamment des mécanismes qui lient diversité, perturbations environnementales et stabilité temporelle. Dans cette discussion, je vais rappeler les principaux résultats développés dans les chapitres, afin de les relier et de discuter des éventuelles limites et des perspectives dans lesquelles ces résultats pourraient suggérer de s'engager.

Une relation diversité - asynchronie positive commune à travers les taxons versus une relation diversité – stabilité des populations dépendant des taxons

Dans cette première partie, je discute des résultats du chapitre 1 afin de confronter les relations entre diversité des communautés et stabilité des populations versus diversité des communautés et asynchronie entre fluctuations des populations, puis je compare les différents taxons que j'ai étudié. Je lierai ensuite ces résultats à ceux du chapitre 2 sur la corrélation entre similarité de traits et synchronie, afin de préciser les mécanismes sous-jacents à la relation entre diversité et asynchronie.

Le premier apport de cette thèse concerne le rôle des dynamiques compensatoires dans la stabilité des communautés naturelles, et sa relation avec la diversité. Dans le 1^{er} chapitre, j'ai montré le rôle stabilisateur de la diversité des communautés naturelles en termes de richesse spécifique et de diversité phylogénétique via l'asynchronie entre les fluctuations des populations. Les mécanismes associés à la relation entre diversité et stabilité temporelle de l'abondance des communautés sont les interactions entre les espèces et leur environnement qui affectent la stabilité de leurs populations et l'asynchronie entre leurs fluctuations. La relation positive entre diversité et asynchronie, mise en avant par les travaux théoriques (Loreau and de Mazancourt, 2013) et retrouvée dans des études expérimentales (Downing et al., 2014; Hector et al., 2010) et empiriques (Zhang et al., 2018), est un des principaux mécanismes de la relation diversité - stabilité et reflète notamment les réponses différences des espèces aux variations des conditions environnementales. Dans ma thèse, je montre une corrélation positive entre diversité et asynchronie chez trois taxons animaux différents, les chauves-souris, les oiseaux et les papillons. Ces taxons représentent des groupes d'espèces très différentes, que ce soit en termes de position dans les réseaux trophiques, de longévité, de diversité au sein de ces taxons mais aussi en termes de groupes fonctionnels (pollinisation, contrôle des ravageurs, dispersion de graines). Ce qui est intéressant est l'existence de cette relation positive entre diversité et asynchronie à travers différents organismes d'un côté, et de l'autre l'absence de relation générale entre diversité et stabilité des populations.

En effet, dans mon étude, comme dans la littérature (Hooper et al., 2005; Jiang and Pu, 2009), je retrouve des relations entre diversité et stabilité des populations différentes selon les taxons. Contrairement à Jiang and Pu (2009) qui montrent des variations dans cette relation selon le contexte empirique / expérimental, terrestre / aquatique, ici il ne s'agit que de communautés terrestres et de conditions naturelles. Ainsi, lorsque Jiang and Pu (2009) mettent en avant l'effet du contexte de l'étude, mon premier chapitre suggère également un effet du type d'organisme considéré. Comme mentionné dans l'introduction générale, selon la force des interactions entre espèces, comme la compétition ou des relations trophiques au sein d'une communauté, des changements de diversité peuvent affecter positivement ou négativement la stabilité des populations. Ainsi, chez les oiseaux la relation négative entre diversité et stabilité des populations pourrait suggérer une forte compétition pour les ressources, tandis que chez les papillons une augmentation de la diversité pourrait diminuer la pression moyenne exercée par les prédateurs de papillons et stabiliser les populations, d'où la relation positive observée entre diversité et stabilité des populations.

Le degré d'asynchronie entre espèces semble plus relever de réponses aux conditions environnementales que d'interactions entre espèces (Loreau and de Mazancourt, 2013; Sasaki et al., 2019; Tredennick et al., 2017). La diversité phylogénétique reflète des différences entre espèces, différences pouvant générer des réponses différentes aux conditions environnementales. Ainsi, la corrélation positive entre diversité phylogénétique et asynchronie mise en évidence chez les trois taxons dans mon premier chapitre va dans le sens de Tredennick et al. (2017), Loreau et de Mazancourt (2013) et Sasaki et al. (2019). Cependant, l'augmentation de la diversité phylogénétique peut aussi affecter les interactions entre espèces. Cadotte et al. (2012) montrent une corrélation positive entre diversité phylogénétique et stabilité des communautés. Dans leur cas la diversité phylogénétique est corrélée à une plus grande stabilité des populations de plantes du fait de l'utilisation de ressources différentes qui diminue la compétition. On voit donc la nécessité de préciser dans chaque étude les mécanismes sous-jacents aux relations entre diversité, stabilité des populations et asynchronie, afin d'éviter de dégager des patrons généraux qui reflètent en fait des mécanismes très différents, pouvant mener à des politiques de gestion ou de

conservations mal adaptées. Le second chapitre m'a permis de préciser les mécanismes derrière la relation entre la diversité et l'asynchronie chez les papillons.

Les résultats du second chapitre suivent l'hypothèse de réponses différentes aux conditions environnementales pour expliquer l'asynchronie, suggérée dans le premier chapitre et par Tredennick et al. (2017). En effet, je mets en évidence une corrélation positive entre synchronie entre espèces et similarité de traits, notamment la similarité des ressources utilisées par les chenilles et adultes. Mes résultats concordent avec ceux de précédentes études sur le lien entre traits et synchronie entre espèces chez les papillons (Raimondo et al., 2004a, 2004b). Cette corrélation positive va dans le sens de réponses similaires aux conditions environnementales plus que de compétition entre espèces similaires, qui aurait potentiellement diminué la synchronie. Ce mécanisme est de plus cohérent avec la relation positive entre la richesse spécifique et la stabilité des populations du premier chapitre, qui ne suggère pas de la compétition. Il serait intéressant de regarder la relation entre similarité des traits comme l'utilisation des ressources et l'asynchronie chez les oiseaux. En effet, la relation négative entre richesse et stabilité des populations d'oiseaux peut refléter une augmentation de la compétition. S'il s'agit de compétition pour les ressources, la similarité dans les ressources utilisées par les oiseaux pourrait augmenter l'asynchronie.

Un impact des perturbations dépendant du contexte et du taxon

Dans cette seconde partie, je discute et compare les résultats concernant l'impact des perturbations environnementales sur la stabilité temporelle de l'abondance des communautés, et leur rôle dans la relation entre diversité et stabilité.

Le second point central de cette thèse, commun aux trois chapitres, est l'intégration des perturbations environnementales, résultat des activités humaines, dans l'étude de la stabilité des communautés. Dans le cadre de ces études, j'ai notamment pris en compte des perturbations permanentes du paysage, comme l'urbanisation et l'imperméabilisation des sols, ou l'intensification agricole. Ces perturbations dégradent les habitats et simplifient les

paysages. Elles sont responsables d'une diminution de la diversité et de l'abondance des espèces, mais également de filtres qui modifient les assemblages, pouvant ainsi simplifier la diversité de traits ou de fonctions au sein des communautés (Ekroos et al., 2010; Gámez-Virués et al., 2015; McKinney, 2006; Olivier et al., 2016; Potts et al., 2010). Enfin, la diminution de la diversité et de la quantité d'habitats offre moins de possibilités aux espèces pour affronter des événements et des conditions météorologiques délétères (Oliver et al., 2010).

Dans le premier chapitre, j'ai mis en évidence pour les trois taxons un effet négatif de la dégradation des habitats sur la stabilité des communautés, principalement via la déstabilisation des populations. Comme pour la corrélation positive entre diversité et asynchronie, cet effet va dans le même sens pour les trois taxons. Cependant, le type de dégradation des habitats qui déstabilise les populations n'est pas le même pour tous les taxons. La sensibilité aux perturbations environnementales pourrait ainsi dépendre des traits des espèces, soulignant la nécessité d'étudier le rôle des perturbations sur différents types d'organismes pour avoir une vision globale de l'impact des changements globaux sur la stabilité des communautés et écosystèmes. La complexité et la spécificité des relations entre les espèces et leur habitat demande une prise en compte adaptée des perturbations telles que la dégradation des habitats en fonction du taxon étudié (Jeanmougin, 2017). Un autre point important de cette étude réside dans le fait que la dégradation des habitats affecte la stabilité des populations principalement de façon directe, plus qu'à travers des diminutions de richesse spécifique et de diversité phylogénétique, pour les trois taxons.

Dans le premier chapitre, je ne montre pas de lien direct entre dégradation de l'habitat et synchronie entre populations, en contradiction avec de précédentes études (Blüthgen et al., 2016; Xu et al., 2015). Dans le chapitre 2, je montre des corrélations significatives entre synchronie et perturbations environnementales. Ces différences observées entre mes deux chapitres, et avec d'autres études, pointe le rôle contrasté de perturbations environnementales différentes sur la stabilité des communautés. Les perturbations environnementales qui affectent la synchronie entre espèces dans le chapitre 2 correspondent à des variations interannuelles de conditions météorologiques. Comme nos

mesures de stabilité et de synchronie sont également basées sur des variations interannuelles, il est cohérent que ces perturbations basées sur des variations interannuelles influent la synchronie, via un effet sur la survie et la reproduction d'année en année. Les perturbations intégrées dans le chapitre 1 sont des perturbations de type permanentes, reflétant la quantité et la qualité de l'habitat. Ces perturbations ne sont pas susceptibles de présenter de fortes variations interannuelles et sont donc moins à même d'affecter la synchronie entre espèces. Cependant, elles peuvent avoir un effet sur la capacité des espèces à répondre à des variations de conditions environnementales de type météorologiques.

En effet, dans le chapitre 2, le contexte paysager semble jouer le rôle de modulateur des effets synchronisant des conditions météorologiques. En offrant plus d'habitats ou de refuges, le paysage permettrait ainsi aux espèces de moins subir des conditions délétères. Cet effet peut être perçu de la même façon avec la stabilité des populations. Ainsi, on peut imaginer que dans des habitats très dégradés, les populations sont plus exposées aux conditions météorologiques, et donc potentiellement moins stables. L'absence de corrélation entre dégradation des habitats et synchronie dans le chapitre 1 pourrait être due à une répartition homogène des sites dégradés et non dégradés au sein du gradient de variabilité météorologique et climatique. Ces résultats suggèrent d'intégrer dans les analyses sur l'impact des perturbations sur la stabilité temporelle plusieurs types de perturbations, notamment lorsqu'elles sont de types différents (ponctuelles, permanentes).

L'impact des déclin d'abondances et des risques d'extinctions sur la stabilité temporelle des communautés à l'échelle régionale

Dans cette troisième partie, je vais discuter des résultats du chapitre 3, dans lequel j'ai étudié la synchronie à l'échelle régionale. Les résultats présentés dans ce manuscrit nécessitent encore d'être développés afin d'apporter plus d'informations sur l'impact des déclin d'espèces sur la stabilité à l'échelle régionale et de préciser les mécanismes associés, notamment liés aux traits des espèces étudiées.

Ce troisième chapitre n'intègre pas de perturbation environnementale explicite, mais analyse l'impact d'extinctions potentielles dues aux déclin d'abondance sur la stabilité à l'échelle régionale. Comme mentionné au début de cette discussion, le déclin de la biodiversité est considérée comme l'une des conséquences principales des changements globaux, qui se traduit par une diminution de l'abondance des espèces, pouvant mener à leur extinction (Ceballos and Ehrlich, 2002; Manne et al., 1999; Pimm et al., 2014). Ce déclin fait l'objet de suivis temporels pour comprendre quelles espèces déclinent et dans quelle mesure, résultant en l'estimation de tendances temporelles. Si les espèces en déclin sont également synchrones, on pourrait s'attendre à des extinctions de groupes d'espèces synchrones, réduisant par conséquent le potentiel de dynamiques compensatoires, en plus de diminuer la diversité des communautés. Dans cette étude j'ai mis en évidence des groupes d'espèces synchrones à l'échelle régionale, sans toutefois trouver de répartition particulière des tendances temporelles à travers les groupes d'espèces synchrones. Dans mon troisième chapitre, la tendance moyenne au sein des groupes d'espèces synchrones ne suggère pas d'extinctions de certains groupes d'espèces synchrones, qui affecteraient le potentiel de dynamiques compensatoires à l'échelle régionale. Ceci est dû aux espèces montrant des tendances temporelles d'abondance positive (Fox et al., 2015). Chez les papillons, des changements globaux comme le réchauffement climatique peuvent en effet améliorer les conditions environnementales dans certaines régions et permettre l'expansion de certaines espèces (Hill et al., 2002; Roy et al., 2001). Comme observé à l'échelle locale dans les chapitres 1 et 2, les différents types de perturbations tels que le réchauffement climatique ou la dégradation des habitats peuvent affecter différemment les papillons et donc leurs réponses à ces changements (Warren et al., 2001). De plus, comme pour la synchronie à l'échelle locale, la synchronie à l'échelle régionale pourrait être expliquée par des traits. Les résultats préliminaires de ce troisième chapitre suggèrent d'explicitier les perturbations qui peuvent intervenir à l'échelle régionale, mais également d'intégrer les traits des espèces. De plus, conduire ces analyses sur des données provenant de régions situées dans différentes gammes de latitudes pourrait montrer d'autres résultats du fait de tendances temporelles différentes selon les latitudes des sites et donc de modifications différentes des conditions environnementales dues au réchauffement climatique.

Perspectives générales

Ce travail s'inscrit dans la volonté de comprendre l'impact des changements globaux sur le fonctionnement des écosystèmes et donc potentiellement sur les services écosystémiques. Le déclin de la biodiversité dû aux changements globaux entraîne le déclin des fonctions et des services (Potts et al., 2010). De même, les changements globaux affectent la stabilité temporelle des communautés, affectant possiblement la stabilité temporelle des fonctions et services. L'ensemble des impacts des changements globaux peut ainsi conduire à l'effondrement de nombreux écosystèmes et de leurs fonctions et services associés.

Comprendre et identifier la complexité des facteurs influençant la stabilité temporelle des communautés requiert de multiplier des études en conditions naturelles, en prenant soin de décrire avec précision les perturbations présentes. Ainsi dans mon premier chapitre la relation diversité – stabilité et l'impact des perturbations environnementales a été étudiée dans trois taxons très différents, les chauves-souris, les oiseaux et les papillons. Ces taxons représentent des organismes avec par exemple des espérances de vies ou des positions dans les réseaux trophiques différentes. Cette approche multi-taxons m'a permis de montrer des relations similaires, comme la relation positive entre diversité et asynchronie, et des relations différentes, notamment la relation entre diversité et stabilité des populations. Une des limites de mon premier chapitre, que l'on retrouve également dans la majorité des études expérimentales et empiriques, est cependant l'analyse de la stabilité d'une seule communauté par site. Dans mon premier chapitre, les taxons n'ont pas été relevés au même endroit et leurs dynamiques ne reflètent pas leurs potentielles interactions. En plus des conditions météorologiques et climatiques, qui peuvent affecter la survie et la reproduction, la disponibilité en ressources et la pression exercée par les prédateurs peuvent faire varier le nombre d'individus au cours du temps. Analyser des données de plusieurs communautés relevées au même endroit et au même moment pourrait par exemple permettre de distinguer des effets top-down et bottom-up dans la synchronie et donc la stabilité des communautés, si par exemple on observe de la synchronie entre populations de papillons et populations de plantes hôtes et nectarifères. Certaines études ont intégré plusieurs niveaux trophiques pour

comprendre la relation diversité – stabilité des écosystèmes (Jiang et al., 2009; Proulx et al., 2010). Les programmes de suivis de biodiversité avec des relevés de plantes et d’insectes au même endroit pourraient permettre par exemple d’analyser la relation diversité – stabilité dans le cadre des interactions plantes – pollinisateurs. Dans cet optique, les sciences participatives semblent constituer un outil prometteur permettant de récolter simultanément un grand nombre de données, en terme de nombre de sites, d’années de suivis, de conditions environnementales différentes et de taxons relevés.

L’approche basée sur les traits a permis de suggérer de potentiels mécanismes pouvant expliquer les relations entre perturbations, diversité et stabilité via la synchronie. Cette approche doit être plus souvent intégrée aux études sur la stabilité des communautés, notamment car ces mécanismes peuvent varier selon le taxon étudié et les perturbations prises en compte. Intégrer les traits pourrait par exemple expliquer pourquoi on ne retrouve pas de répartition particulière des tendances temporelles à travers les groupes d’espèces synchrones, si les traits qui expliquent la synchronie régionale ne sont pas les mêmes que ceux qui expliquent les tendances. Cet objectif est une des perspectives de ma thèse, mais la méthode pour expliquer des groupes à partir de traits est encore en développement (Figure 7). Expliquer la stabilité des populations par les traits pourrait également permettre d’éclaircir les raisons des résultats contrastés sur la relation entre la diversité et la stabilité des populations. La mobilité des papillons a déjà été mise en évidence comme affectant la stabilité (Oliver et al., 2010), mais d’autres traits comme le spécialisme alimentaire pourrait intervenir également.

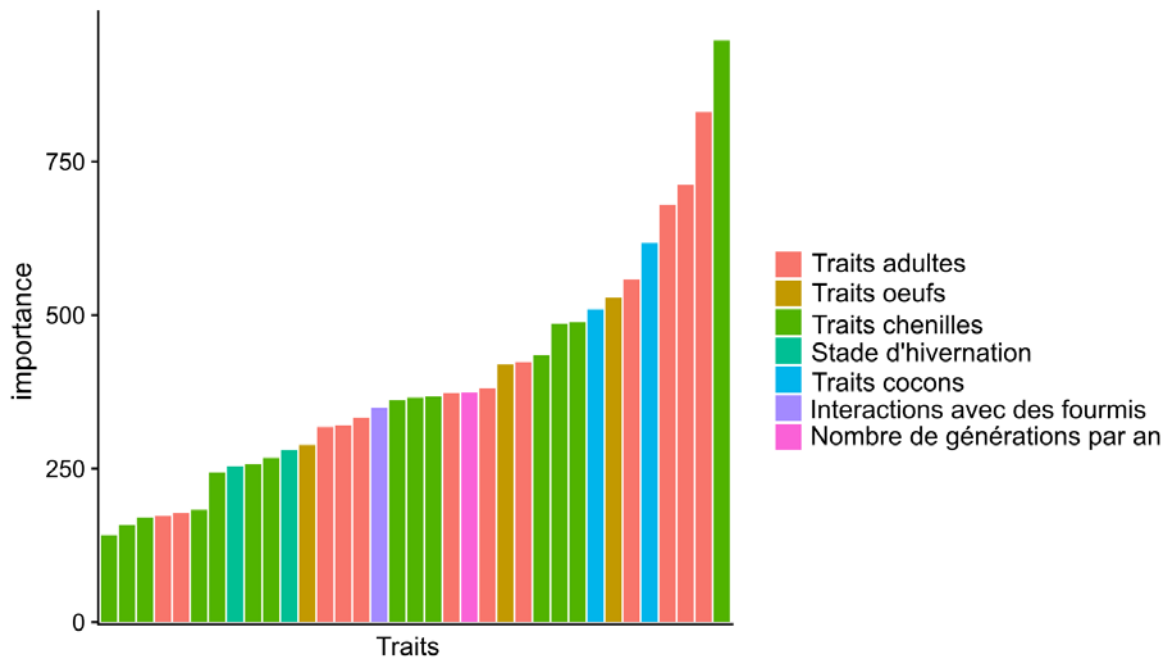


Figure 7. Importance de différents traits des papillons pour expliquer les trois groupes de synchronie A, B et C dans le chapitre 3, à partir de réseaux de neurones. Chaque barre correspond à un trait. Cette méthode pourrait permettre de mettre en évidence l'importance relative des traits pour expliquer la synchronie ou la stabilité des populations mais aussi l'importance des stades de vie dans la synchronie ou la stabilité des populations. Enfin, cela pourrait permettre d'analyser la variation de l'importance des traits selon que l'on s'intéresse à la synchronie, la stabilité des populations, ou bien l'impact des perturbations sur les tendances temporelles des espèces par exemple.

Finalement il ne faut pas oublier que dans cette thèse, les mécanismes sont proposés à partir d'analyses corrélatives. Montrer l'effet causal des traits sur la stabilité pourrait permettre de confirmer des mécanismes prédits par les corrélations observées. Utiliser des variables qui permettent de prendre en compte de façon explicite les traits des espèces dans les communautés à la place de la richesse spécifique ou de la diversité phylogénétique pourrait-il permettre de montrer des liens de causalité entre traits et synchronie, stabilité des populations et stabilité des communautés ?

Intégrer l'aspect spatial pourrait également apporter de nouvelles informations sur la stabilité des communautés en milieu naturel en lien avec la diversité. En effet, dans notre étude nous ne prenons pas en compte la distance spatiale entre communautés et les potentiels flux d'individus qui pourraient avoir lieu. Ces échanges d'individus entre populations pourraient contribuer à la stabilité d'une communauté, en compensant des diminutions d'abondances dues aux conditions et perturbations environnementales locales, et ainsi expliquer une partie de la variabilité de la stabilité observée. Ce mécanisme est lié à l'hypothèse spatiale de l'assurance, principalement étudiée théoriquement (Loreau et al., 2003; Naeem et al., 2009; Shanafelt et al., 2015; Thompson et al., 2017). Cette hypothèse se base sur l'asynchronie entre populations ou communautés, mécanisme stabilisant à l'échelle des méta-populations et méta-communautés. Comme pour les réponses aux conditions environnementales et les interactions entre espèces, le rôle de la connexion entre populations et communautés dépendrait également des taxons et de leurs capacités de dispersion (Loreau et al., 2003). Après plusieurs décennies d'étude de la stabilité à l'échelle locale, l'intérêt d'élargir à des échelles plus grandes a récemment fait l'objet d'études théoriques et expérimentales (Howeth and Leibold, 2010; Wang and Loreau, 2014, 2016; Wang et al., 2019; Wilcox et al., 2017) Cette approche pourrait contribuer à une meilleure compréhension de la stabilité dans des environnements altérés par les changements globaux. Ici encore, les sciences participatives pourraient être un outil adapté à ce genre d'approche. En effet, la grande quantité de sites échantillonnés rend possible l'analyse de la relation diversité – stabilité à travers plusieurs méta-communautés situées dans des milieux aux conditions et perturbations environnementales variées.

Conclusion

Cette thèse a permis de préciser le rôle de la diversité et des perturbations sur la stabilité de l'abondance de communautés animales naturelles. Ces études permettent d'éclairer l'impact des changements globaux sur les fonctions réalisées au sein des écosystèmes, notamment la pollinisation, le contrôle des ravageurs ou encore la dispersion des graines. De plus, pour reprendre Hill (1987), il semble compliqué de dégager des relations générales sur la stabilité

des populations, communautés et écosystèmes, du fait de la multiplicité des modes de vie et des interactions à travers les taxons constituant les écosystèmes. Une approche basée sur des communautés naturelles, avec des conditions naturelles variées et en reliant les mécanismes aux traits des espèces, est nécessaire afin d'appréhender l'impact des changements globaux sur la stabilité des écosystèmes, et de dégager des actions de conservation efficaces.

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