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# CONSÉQUENCES DES INTERACTIONS ENTRE VOIES VERTES ET BRUNES SUR LA STABILITÉ DES RÉSEAUX TROPHIQUES

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Thèse de doctorat d'Écologie

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# Résumé - Abstract

## Mots clés

Réseau trophique - Recyclage des nutriments - Stabilité - Réseau vert - Réseau brun - Contrôle bottom-up - Contrôle top-down - Mesocosme - Métabolisme - Allométrie

## Résumé

Cette thèse a pour but de comprendre les implications des relations entre réseau trophique vert et réseau trophique brun sur la stabilité et le fonctionnement des réseaux trophiques. Les interactions entre ces deux réseaux, respectivement fondés sur la photosynthèse et la consommation de la matière organique morte, sont essentielles au fonctionnement des écosystèmes : l'un produit de la matière organique à partir de nutriments minéraux et l'autre recycle les nutriments contenus dans la matière organique morte. Cette question est abordée à l'aide de deux modèles théoriques et d'une étude expérimentale. Mon premier modèle montre que la boucle de rétroaction induite par le recyclage des nutriments dans un réseau trophique exclusivement vert a un effet stabilisant sur les dynamiques d'une chaîne trophique et un effet enrichissement à cause de la remise à disposition pour les producteurs primaires des nutriments excrétés par l'ensemble des organismes du réseau trophique. Cependant seul l'effet enrichissement, qui est déstabilisant, persiste dans un modèle de réseau trophique. Mon second modèle intègre le réseau brun de manière explicite et montre que ce réseau est davantage déstabilisé que le réseau vert lorsque la disponibilité en nutriments augmente. Cette effet est amplifié si la majeure partie de l'excrétion se fait sous forme de détritiques qui déstabilisent le réseau brun par un effet d'enrichissement. Ce modèle montre également que la survie des consommateurs est améliorée lorsqu'ils peuvent consommer des proies provenant des deux réseaux. Mon expérience en mésocosmes aquatiques a permis d'étudier les effets en cascades entre réseaux vert et brun via une filtration de la lumière (manipulation directe du réseau vert), l'ajout de carbone organique dissous (manipulation directe du réseau brun) et l'ajout de poissons (manipulation de la structure du réseau trophique). Nous n'avons pas observé d'effets en cascade du réseau vert sur le réseau brun et inversement, notamment à cause d'un ajout probablement trop faible de carbone dissout. Les poissons ont eux eu un fort effet sur les deux réseaux avec des effets positifs sur le phytoplancton lorsque la lumière est réduite à cause de la diminution de la limitation par les nutriments grâce à l'excrétion des poissons, une augmentation de la concentration en carbone organique dissout et une modification du profil métabolique de la communauté bactérienne benthique. Un modèle annexe montre quant à lui que la plasticité du métabolisme chez les organismes, c'est-à-dire leur capacité à réduire ou à augmenter leur métabolisme en fonction de la disponibilité en ressources afin de maximiser leur bilan énergétique permet de stabiliser les dynamiques d'une chaîne trophique en diminuant la variabilité temporelle des biomasses des espèces. Dans un réseau trophique, cette stabilisation se traduit par une augmentation de la persistance des espèces. Cette thèse a permis de mieux relier l'écologie des communautés à l'écologie fonctionnelle, améliorant ainsi notre compréhension des conséquences de grands processus écosystémiques comme le recyclage des nutriments sur la stabilité des réseaux trophiques et des effets de la structure de ces réseaux sur le fonctionnement des écosystèmes.

## Key words

Food web - Nutrient cycling - Stability - Green food web - Brown food web - Bottom-up control - Top-down control - Mesocosm - Metabolism - Allometry

## Abstract

The aim of this thesis is to understand the implications of the relationships between green and brown food webs on the stability and functioning of food webs. The interactions between these two food webs, based respectively on photosynthesis and the consumption of dead organic matter, are essential for the functioning of ecosystems: one produces organic matter from mineral nutrients and the other one recycles the nutrients contained in dead organic matter. I address this by using two theoretical models and an experimental study. My first model shows that the feedback loop induced by nutrient cycling in an exclusively green food web has a stabilising effect on species dynamics in a food chain and an enrichment effect due to the excretion of nutrients that are available again for primary producers. However, only the enrichment effect, which is destabilising, persists in a food web model. My second model integrates a true brown food web and shows that this food web is more destabilised than the green food web when nutrient availability increases. This effect is amplified if most of nutrients are excreted as detritus that destabilises the brown food web through an enrichment effect. This model also shows that consumer survival is improved when they can consume prey from both green and brown food webs. My experiment in aquatic mesocosms enabled me to study the cascading effects between green and brown food webs thanks to light filtration (direct manipulation of the green food web), the addition of dissolved organic carbon (direct manipulation of the brown food web) and the addition of fish (manipulation of food web structure). We did not observe any cascading effects of the green food web on the brown food web and vice versa, probably because of a too low addition of dissolved carbon. The fish had a strong effect on both green and brown food webs with positive effects on phytoplankton when light is filtered because of the decreased nutrient limitation thanks to fish excretion, an increased concentration of dissolved organic carbon and a change in the metabolic profile of the benthic bacterial community. An additional model shows that the plasticity of metabolic rate, that is the ability of organisms to increase or decrease their metabolic rate depending on resource availability in order to optimise their energy budget, stabilises species dynamics in a food chain model by decreasing biomass time variability. Such a stabilising effect results in increase of species persistence in a complex food web model. This thesis is an additional step to better link community ecology to functional ecology, thus improving our understanding of the consequences on food web stability of major ecosystem processes such as the nutrient cycling and the effects of food web structure on ecosystem functioning.

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# Introduction générale

Cette thèse a pour but d'étudier les conséquences des interactions entre réseaux vert et brun sur la stabilité et le fonctionnement des écosystèmes. Elle combine ainsi deux champs de l'écologie qui ont été la plupart du temps traités séparément : l'écologie fonctionnelle et l'écologie des communautés. Cette introduction vise à définir les concepts clés et le cadre général de cette thèse. Je présente donc dans un premier temps le fonctionnement général des écosystèmes ainsi que les réseaux trophiques décrivant des communautés d'organismes liés entre eux par des interactions alimentaires. Je présente ensuite comment les réseaux trophiques sont modélisés mathématiquement et je définis les mesures de stabilité utilisées pour décrire le comportement de ces modèles. Je présente par la suite deux des piliers des modèles de réseaux trophiques complexes que j'ai utilisés : la structuration du réseau suivant la taille des organismes et la Théorie Métabolique de l'Écologie permettant de paramétrer les divers taux biologiques suivant des relations d'allométrie. Je définie ensuite les notions de contrôles top-down et bottom-up qui décrivent la régulation des populations d'organismes par la prédation ou par la limitation en ressources. Ces notions sont remises en question dans les modèles de réseaux trophiques par l'inclusion du recyclage des nutriments qui relie chaque organisme aux ressources tout en bas du réseau. Je présente enfin comment la prise en compte d'un réseau trophique brun, assurant le recyclage des nutriments par consommation de la matière organique morte, peut modifier la stabilité des réseaux trophiques par son couplage au réseau vert qui assure la production de biomasse à partir de nutriments minéraux.

## La représentation des écosystèmes

Un écosystème est un ensemble composé d'un milieu et d'une communauté d'organismes qui y vivent. C'est un système vivant qui est caractérisé par des flux de matière et d'énergie entre le milieu et les organismes et entre organismes (Fig.1). En effet, les êtres vivants ont besoin de matière pour grandir et se reproduire, mais aussi d'énergie pour faire fonctionner leur métabolisme. La biomasse est originellement produite par les producteurs primaires qui utilisent l'énergie du Soleil pour réduire de la matière minérale (dioxyde de carbone, eau, nitrates...) en matière organique. Cette biomasse va ensuite être consommée par une succession de consommateurs (herbivores, carnivores...) qui vont alors en minéraliser (*i.e.* oxyder) une partie pour produire de l'énergie et alimenter leur métabolisme, et intégrer l'autre partie à leur propre biomasse. Tous ces organismes forment alors un réseau régi par des interactions alimentaires que l'on appelle réseau trophique. A chaque fois que de la biomasse est consommée par un des organismes du réseau, il y a donc une perte de biomasse par dissipation de l'énergie utilisée par le métabolisme de chaque organisme. Alors que l'énergie dissipée est perdue par le système, la matière minéralisée retourne dans le milieu (dioxyde de carbone, nitrates...). Un écosystème est donc un grand système thermodynamique alimenté par l'énergie solaire (on ne considérera que les écosystèmes fondés sur la photosynthèse) qui dissipe de l'énergie à chaque niveau trophique (Lindeman, 1942).



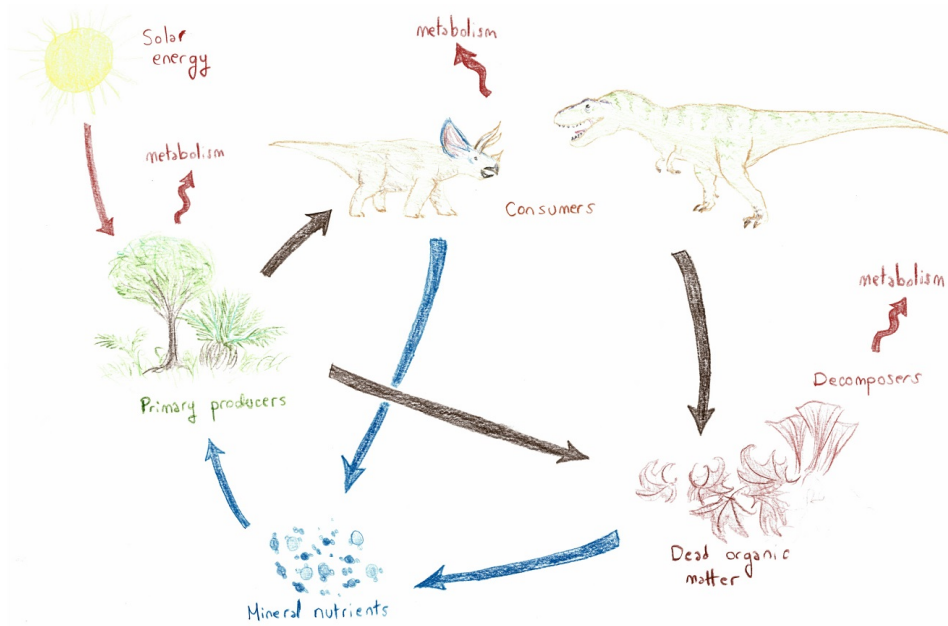


Figure 1: Représentation schématique du fonctionnement d'un écosystème. Le Soleil fournit l'énergie permettant aux producteurs primaires de synthétiser de la matière organiques à partir de matière minérale. La biomasse produite est ensuite consommée par les consommateurs pour produire leur propre biomasse et pour l'oxyder afin de faire fonctionner leur métabolisme. Les nutriments minéralisés sont réutilisés par les producteurs primaires et de l'énergie est dissipée par le métabolisme.

## Les réseaux trophiques

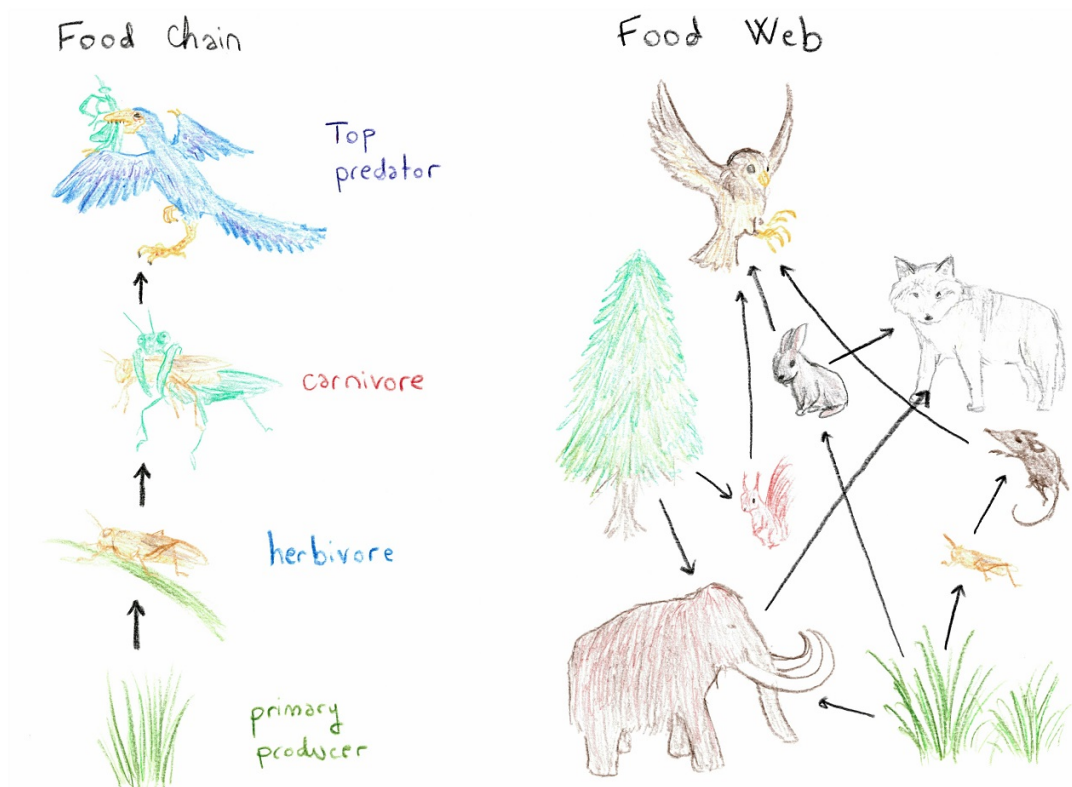


Figure 2: Chaîne trophique et réseau trophique. Dans une chaîne, l'énergie circule de façon linéaire de bas en haut et les niveaux trophiques sont bien distincts. Dans un réseau trophique, la multitude d'espèces interconnectées crée de nombreux chemins possibles pour la circulation de la matière et de l'énergie.

Les réseaux trophiques sont une représentation des interactions entre espèces où l'on se focalise sur les relations de type alimentaire. Dans un réseau trophique, chaque nœud du réseau représente une population (équivalent à une espèce, mais on peut également distinguer dans une même espèce une population de juvéniles et une population d'adultes par exemple) et chaque connexion une interaction de type alimentaire. Là où une chaîne alimentaire est purement verticale (producteur primaire, herbivore, carnivore et super prédateur), un réseau trophique comporte aussi une dimension horizontale puisque plusieurs espèces ont le même niveau trophique (même position dans la chaîne alimentaire) (Fig.2).

## Le modèle proie-prédateur

Le module de base de tout réseau trophique est le système proie-prédateur décrit de façon mathématique pour la première fois par Lotka et Volterra (Volterra, 1926) :

$$\frac{dN}{dt} = bN - aNP \quad (1a)$$

$$\frac{dP}{dt} = eaNP - dP \quad (1b)$$

Avec  $N$  la densité de proies,  $P$  la densité de prédateurs,  $b$  le taux net de croissance de la population de proies,  $a$  le taux d'attaque du prédateur,  $e$  le taux d'assimilation de la proie par le prédateur (fraction de la biomasse ingérée qui est absorbée) et  $d$  le taux de mort des prédateurs. Ce type de système peut être étudié de façon analytique avec un calcul des points d'équilibre (densité des organismes à l'équilibre) et une évaluation de leur stabilité (voir section suivante), ou de façon numérique avec une résolution par ordinateur des équations à chaque pas de temps, ce qui permet de visualiser les dynamiques temporelles du système. Il est alors possible d'étudier de façon théorique l'impact des différents paramètres cités précédemment sur le système. L'un des résultats emblématiques de ce modèle est la reproduction de dynamiques oscillatoires entre proies et prédateurs (Fig.3) qui a également été retrouvée dans des systèmes naturels (MacLulich, 1937) ou expérimentaux (Fussmann et al., 2014). Le modèle de Lotka-Volterra est très simple, ce qui facilite énormément les calculs, mais il repose sur une hypothèse très forte : la linéarité de tous les processus biologiques. En effet, le taux net de croissance des proies augmente de façon linéaire avec la densité de proie, ce qui fait que la population peut augmenter de façon exponentielle. De même, la quantité de proies mangée par les prédateurs augmente indéfiniment proportionnellement à la densité de proies, ce qui est parfaitement impossible.

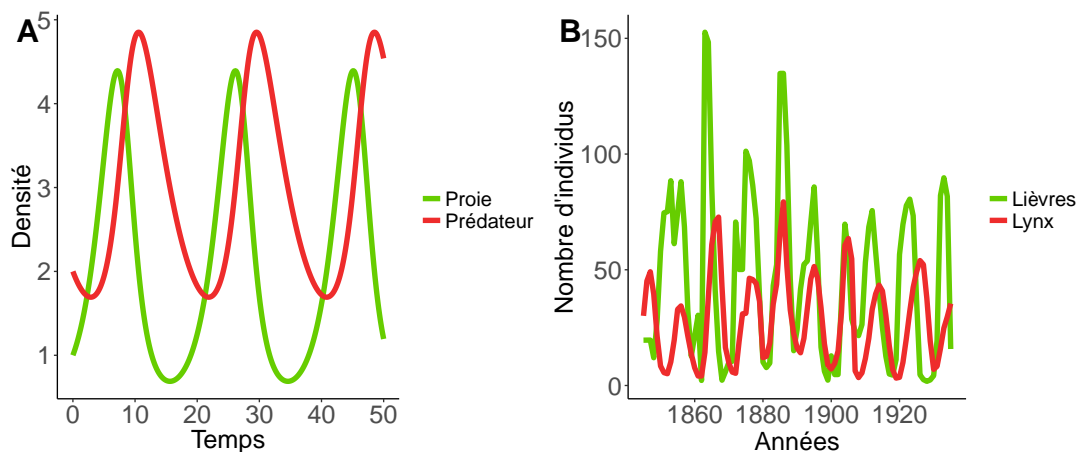


Figure 3: **A)** Dynamiques proie-prédateur simulées avec le modèle de Lotka-Volterra ( $b = 0.6$ ,  $a = 0.2$ ,  $e = 0.5$ ,  $d = 0.2$ ). **B)** Dynamiques des populations de lièvres et de lynx du Canada enregistrées par les captures des trappeurs (MacLulich, 1937) (données disponibles sur <http://pbil.univ-lyon1.fr/R/donnees/lynxhare.txt>). Des oscillations similaires à celles simulées par le modèle de Lotka-Volterra sont visibles, les irrégularités étant dues à de la variabilité environnementale non prise en compte dans le modèle.

## Tenir compte des limitations biologiques

Un autre modèle tenant compte de la finitude de l'Univers a été mis au point par [Rosenzweig and MacArthur \(1963\)](#) :

$$\frac{dN}{dt} = bN\left(\frac{K-N}{K}\right) - \frac{aN P}{1+ahN} \quad (2a)$$

$$\frac{dP}{dt} = \frac{eaNP}{1+ahN} - dP \quad (2b)$$

Avec  $N$  la densité de proies,  $P$  la densité de prédateurs.  $b$  est le taux net de croissance de la population de proies et  $K$  est la capacité de charge qui exprime la finitude du milieu et impose une densité maximale de proies égale à  $K$  (pour  $N = K$ , la population cesse de croître et pour  $N > K$ , la population décroît).  $a$  est le taux d'attaque du prédateur,  $e$  le taux d'assimilation de la proie par le prédateur (fraction de la biomasse de proie convertie en biomasse de prédateur),  $h$  le temps de manipulation qui limite le nombre de proies que peut consommer un prédateur et  $d$  le taux de mort des prédateurs. La croissance des producteurs primaires et la réponse fonctionnelle des prédateurs (fonction de consommation de proies en fonction de leur densité) sont donc saturantes (Fig.4).

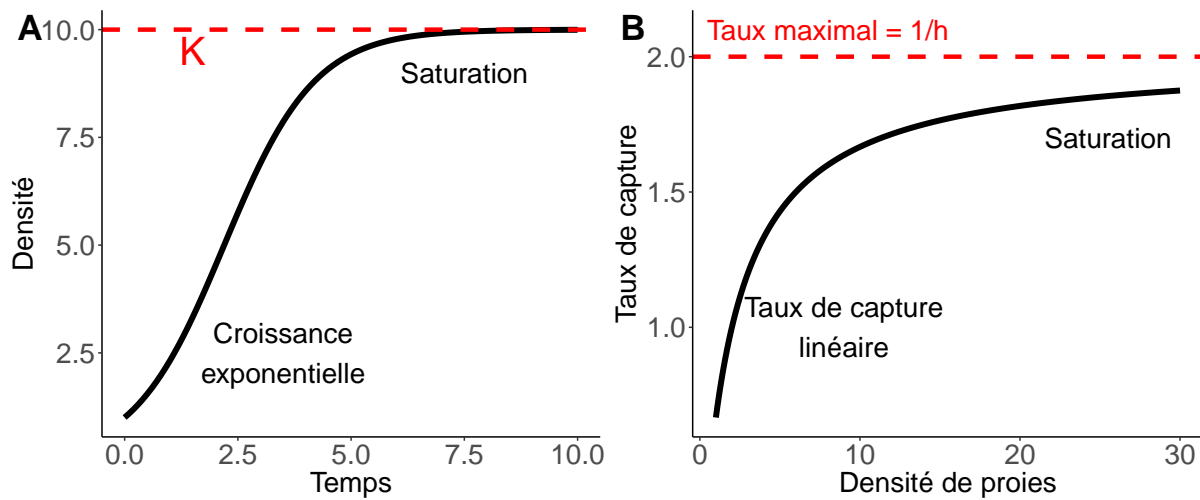


Figure 4: **A)** Croissance logistique des proies en absence de prédateurs. Après une phase de croissance exponentielle, le taux de croissance tend vers zéro et la population stagne à une densité égale à la capacité de charge  $K$ . **B)** Taux de capture des proies par le prédateur en fonction de la densité de proies. Pour une faible densité de proies, le taux de capture augmente linéairement avec la densité de proies comme dans le modèle de Lotka-Volterra. Pour une forte densité de proies, le taux de capture sature à une valeur égale à l'inverse du temps de manipulation  $h$ .

Ce modèle a eu des résultats très inattendus: l'augmentation de la capacité de charge du milieu (ce qui peut être grossièrement assimilée à une fertilisation du milieu par exemple) conduit à l'augmentation de l'amplitude des oscillations des densités de proies et de prédateurs jusqu'à l'effondrement du système (Fig.5). Cette effet négatif de l'enrichissement du milieu était complètement contre intuitif et a été nommé paradoxe de l'enrichissement ([Rosenzweig, 1971](#); [Rip and McCann, 2011](#)). Le paradoxe de l'enrichissement a donné lieu à de nombreuses études théoriques cherchant à trouver des mécanismes interagissant avec cet effet négatif ([Mougi and Nishimura, 2007, 2008, 2009](#); [Binzer et al., 2012, 2016](#); [Hauzy et al., 2013](#); [Gounand et al., 2014](#)). Cependant la plupart des systèmes réels où le paradoxe de l'enrichissement a été observé étaient des systèmes expérimentaux simples avec peu d'espèces en interactions ([Roy and Chattopadhyay, 2007](#)).

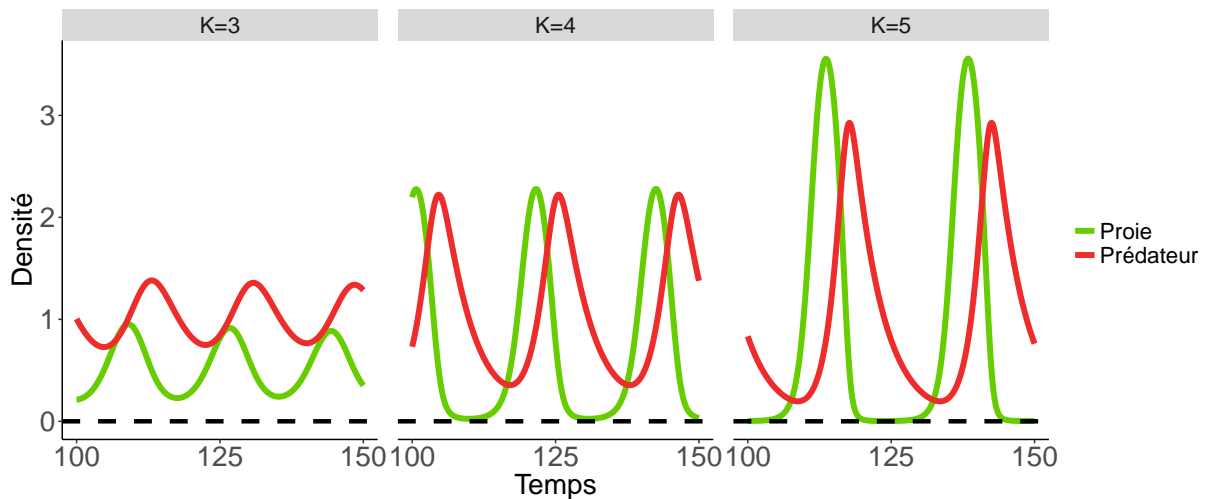


Figure 5: Système proie-prédateur simulé avec les équations de Rosenzweig-MacArthur. L'augmentation de la capacité de charge  $K$  augmente l'amplitude des oscillations et rapproche les densités des espèces de zéro, augmentant ainsi leur chance d'extinction.

Ces modèles ont été largement utilisés et adaptés (DeAngelis et al., 1975; Yodzis and Innes, 1992) pour décrire des systèmes simples avec quelques espèces en interactions. Cependant, leur extension à des modèles complexes avec un très grand nombre d'espèces en interactions est un réel défi car d'une part leur étude analytique devient très difficile et d'autre part leur étude numérique pose un énorme problème de paramétrisation (Hudson and Reuman, 2013).

## La stabilité

Une des questions majeures de l'écologie est l'évaluation de la stabilité des écosystèmes et des communautés dans le temps et face aux perturbations, en particulier dans le contexte actuel de dégradation des écosystèmes, de changements globaux et d'extinction des espèces. La stabilité n'est cependant pas une notion triviale puisqu'elle peut être mesurée de plusieurs façons (DeAngelis, 1992; McCann, 2000, 2011). La résistance, par exemple, est l'amplitude du changement d'une variable après perturbation du système. Plus cette amplitude est faible, plus le système est résistant aux perturbations et donc stable. La résilience, c'est-à-dire la capacité d'un système à retourner vers un point d'équilibre après perturbation, a quant à elle été très largement utilisée puisqu'elle peut être calculée à partir des équations des systèmes dynamiques modélisant les écosystèmes et les communautés. La variabilité temporelle des populations et la survie des espèces sont elles plus proches des approches empiriques (McCann, 2000, 2011). La résilience est une définition très restrictive puisqu'elle n'étudie que le potentiel retour du système linéarisé autour de son point d'équilibre. Elle ne prend donc en compte que des systèmes à l'équilibre et ayant reçu une très faible perturbation, on parle alors de stabilité locale. Elle a cependant été très largement utilisée dans les études théoriques (May, 1972; DeAngelis, 1980; DeAngelis et al., 1989a; DeAngelis, 1992; Moore et al., 1993; Loreau, 1994, 2010; de Ruiter et al., 1998; Neutel and Thorne, 2014) car elle ne nécessite pas de résolution complète du système d'équations différentielles qui est généralement impossible de façon analytique (Dunne et al., 2005; McCann, 2011). La variabilité temporelle et la survie des espèces sont elles utilisées dans les études faisant appel à la résolution numérique des équations et qui fournissent des données proches des données expérimentales (séries temporelles de biomasses de populations par exemple)(McCann, 2000).

En plus de ses multiples définitions, la stabilité en tant que propriété inhérente aux systèmes écologiques a été fortement débattue depuis les années 70. En effet, il était admis que la complexité des systèmes écologiques, c'est-à-dire la quantité et la diversité des espèces et des interactions qui les relient, était

une de leurs caractéristiques assurant leur stabilité (Odum, 1953; Elton, 1958; McCann, 2000; Dunne et al., 2005). Cependant, May (1972) montra qu'un réseau complexe d'interactions aléatoires perdait en stabilité si on augmentait le nombre d'interactions et/ou la force des interactions. Comme ce modèle n'a aucun a priori sur la structure du réseau trophique ou sur les caractéristiques des espèces (c'est un modèle nul de réseau d'interaction en somme), il présente l'effet de la complexité sur la stabilité de la façon la plus indépendante possible du reste des propriétés particulières de chaque type de réseaux d'interactions. Les écologues n'ont ensuite eu de cesse d'identifier des mécanismes assurant la stabilité des réseaux trophiques complexes (Kondoh, 2003; Brose et al., 2006b; Otto et al., 2007).

## Règles allométriques et structuration en taille des réseaux trophiques

Pour décrire de façon efficace un réseau trophique et son fonctionnement, il faut être en mesure de décrire des interactions entre chacune des espèces du réseau. Un problème important apparaît alors car il faudrait soit quantifier chacune de ces interactions possibles expérimentalement, ce qui est bien sûr irréalisable, ou trouver des descripteurs des espèces permettant de prédire ces interactions. Or trouver des descripteurs s'appliquant autant à un cachalot, un géranium, une cyanobactérie ou une paramécie est loin d'être trivial. Cependant, il s'est avéré que la taille corporelle était à elle seule capable de décrire de façon très efficace l'architecture du réseau d'interactions d'une part, et les flux de matière et d'énergie au niveau de chaque espèce d'autre part.

### Structuration en taille des réseaux trophiques

La taille corporelle décrit les réseaux trophique de façon très pertinente, car de façon générale, les petites bêtes se font dévorer par les grosses. La différence de taille permet en effet aux prédateurs de capturer efficacement leur proie (capacité d'ingestion avec la phagocytose des unicellulaires eucaryotes ou supériorité musculaire pour les animaux). De manière générale, un prédateur ne consomme que des proies qui lui sont de 10 à 100 fois plus petites en moyenne (Woodward et al., 2005; Brose et al., 2006a; Brose, 2010; Petchey et al., 2008), les variations étant dues à des stratégies de capture différentes (filtreurs préférant des proies très petites et chasseurs à vue des proies plus grosses). Cette façon de décrire les réseaux trophiques est particulièrement efficace pour les milieux aquatiques pélagiques où le phytoplancton et le bactérioplancton sont à la base du réseau trophique tandis que les grands vertébrés en sont au sommet (Fig.6) (Boit et al., 2012). Comme l'a montré Petchey et al. (2008), un réseau trophique théorique où les prédateurs mangent des proies dans une gamme déterminée par le ratio entre la taille de la proie et celle du prédateur donne une structure de réseau proche de celle observée dans la nature. Enfin, dans le modèle de réseau trophique complexe de Heckmann et al. (2012), où les consommateurs sont capables de sélectionner les proies les plus profitables en terme d'acquisition de biomasse, on observe que les réseaux originellement aléatoires (comme ceux de May (1972)) se réorganisent spontanément vers des réseaux structurés en taille où les prédateurs sont plus gros que leurs proies.

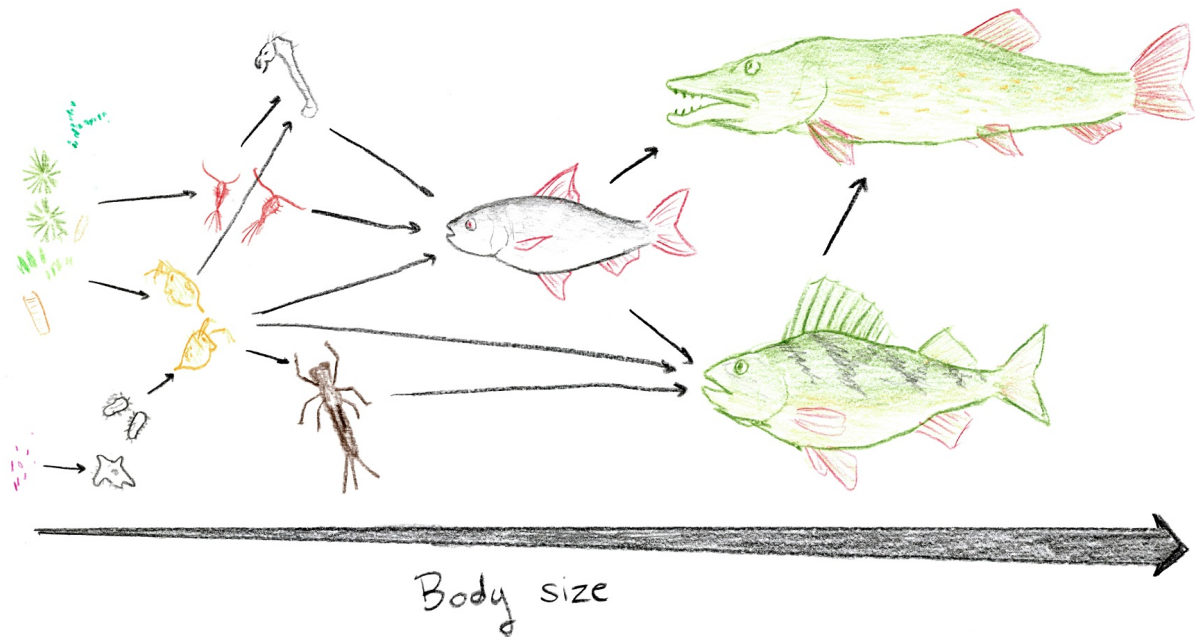


Figure 6: Réseau trophique typique d'une écosystème aquatique d'eau douce dans le compartiment pélagique. La production primaire est assurée par des organismes photosynthétiques unicellulaires (phytoplancton), qui sont consommés par des animaux du zooplancton eux même consommés par des poissons. Les poissons piscivores étant au sommet du réseau trophique.

## Théorie Métabolique de l'Écologie

Pour décrire les interactions entre organismes dans un réseau trophique, il faut quantifier les flux de matière et d'énergie entre les différentes espèces. Ces flux vont dépendre des grandes fonctions biologiques comme la nutrition, la croissance, la reproduction... (Yodzis and Innes, 1992). Or toutes ces fonctions biologiques nécessitent de l'énergie (division cellulaire, action musculaire...) qui est fournie par le métabolisme. Le taux métabolique d'un organisme peut être exprimé comme une fonction de sa masse corporelle (Kleiber, 1932) qui est une bonne approximation de la quantité totale de structures produisant de l'énergie (comme les mitochondries), ce qui est la base de la Théorie Métabolique de l'Écologie (West, 1997, 1999; West et al., 1999; Gillooly, 2001; Brown et al., 2004b; Savage et al., 2004b). Le taux métabolique est donc représenté par une fonction de puissance de la masse corporelle :

$$x_i = a_x M_i^q \quad (3)$$

Avec  $x_i$  le taux métabolique de l'espèce  $i$ ,  $a_x$  un coefficient allométrique,  $M_i$  la masse corporelle de l'espèce  $i$  et  $q$  un exposant allométrique. Cette relation a été obtenue par régression linéaire sur des données de taux métabolique collectées chez un grand nombre de taxons (animaux, végétaux...) (Fig.7A). Un organisme vivant peut être donc considéré comme une machine thermique avec des entrées de matière et d'énergies (création de biomasse par nutrition) et des sorties (dissipation d'énergie par le métabolisme) (Fig.7AB). Cette modélisation des processus biologiques à l'échelle de l'organisme a été très largement débattue au cours des deux dernières décennies avec notamment des études cherchant à affiner l'équation en fonction de la température qui est capitale pour les organismes ectothermes (Vucic-Pestic et al., 2010; Rall et al., 2010, 2012; Hirt et al., 2017), du ratio de taille entre prédateur et proie pour le taux maximal d'ingestion d'une proie (Hjelm and Persson, 2001; Aljetlawi et al., 2004; Kalinkat et al., 2013) ou encore de la dimension du milieu (2D au sol, 3D dans l'eau ou dans l'air) (Pawar et al., 2012).

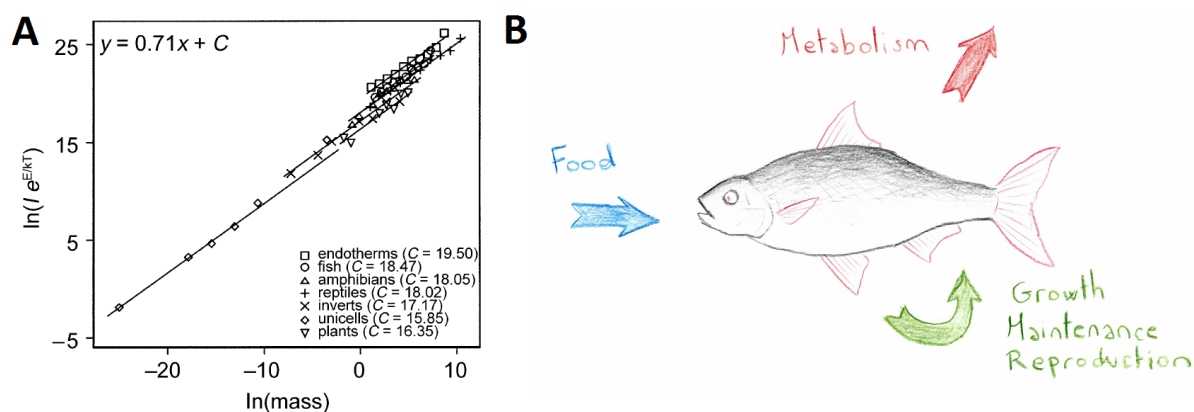


Figure 7: **A**) Relation entre le taux métabolique et la masse corporelle d'organismes appartenant à des phylums représentatif de l'ensemble du monde vivant (Gillooly, 2001; Brown et al., 2004b). **B**) Budget énergétique d'un organisme.

Malgré la simplicité de cette modélisation, la Théorie Métabolique de l'Écologie a permis de paramétrer des modèles de réseaux trophiques avec des dizaines d'espèces et des centaines d'interactions avec seulement la connaissance de quelques constantes et de la masse corporelle des espèces du réseau. Les réseaux trophiques ainsi paramétrés se sont révélés plus stables (meilleure persistance) qu'avec une paramétrisation aléatoire (Brose et al., 2006b; Otto et al., 2007; Kartascheff et al., 2010) mais également capables de reproduire des dynamiques de réseaux trophiques empiriques (Boit et al., 2012; Hudson and Reuman, 2013).

## Contrôles top-down et bottom-up

Une population donnée ne peut croître indéfiniment. Par exemple, les daphnies du zooplancton cesseront de croître lorsqu'elles auront consommé la majeure partie du phytoplancton et la population sera alors conditionnée par la multiplication du phytoplancton, c'est le contrôle bottom-up. Ces mêmes daphnies pourront également être limitées par l'introduction de prédateurs, comme des poissons planctonophages, qui augmenteront la mortalité des daphnies, c'est le contrôle top-down (Hunter and Price, 1992). Le contrôle top-down a été largement reconnu depuis Hairston et al. (1960) et Oksanen et al. (1981) avec la Green World Hypothesis expliquant l'abondance de la biomasse végétale par la forte régulation qu'exercent les prédateurs sur les herbivores. L'importance du contrôle top-down a également été relayée avec le concept de cascade trophique (Carpenter et al., 1985, 2001; Shurin et al., 2002; Ripple et al., 2016) où, par exemple, la présence de poissons planctonophages diminue la densité du zooplancton et augmente la densité du phytoplancton (Fig.8). Cependant, les contrôles top-down et bottom-up sont couplés à cause de nombreuses rétroactions et peuvent donner lieu à des réponses complexes des écosystèmes (Hunter and Price, 1992; Power, 1992; Hulot et al., 2014) en grande partie à cause de la structure du réseau trophiques et de l'existence de plusieurs sous-réseaux (Wollrab et al., 2012).



Figure 8: Long Lake (Michigan) a été séparé en deux. Dans la partie de gauche, les poissons piscivores (black bass) ont été enlevés, ce qui a conduit à la multiplication des poissons planctonophages qui ont fortement réduit la population de zooplancton et a conduit à la prolifération du phytoplancton, d'où la différence de couleur de l'eau (Carpenter et al., 2001).

## Recyclage des nutriments

Les modèles de réseaux trophiques se sont concentrés sur l'écologie des communautés sans vraiment tenir compte de l'environnement abiotique (Loreau, 2010) mis à part la disponibilité en ressources (Rosenzweig, 1971; Brose, 2008; Binzer et al., 2016). Nous avons vu précédemment que les écosystèmes pouvaient être vus comme de grands systèmes thermodynamiques alimentés par le Soleil et dissipant de l'énergie à chaque interaction trophique. Comme la matière passe d'un état oxydé minéral à un état réduit organique puis à nouveau à un état oxydé minéral, il y a formation d'un cycle. Or ces cycles sont très différents d'un élément chimique à l'autre. Alors que le carbone, l'oxygène et l'hydrogène sont présents en grandes quantités dans l'air et dans l'eau et circulent facilement, rendant ainsi leur stocks quasi-illimités au cours du temps dans un grand nombre d'écosystèmes, la disponibilité en nutriments comme l'azote ou le phosphore par exemple est beaucoup plus critique. Les cycles de l'azote ou du phosphore sont donc des processus écosystémiques de première importance (DeAngelis, 1992).

Alors que les modèles de chaînes trophiques fondés sur la production primaire ne considèrent qu'un flux vertical de matière et d'énergie, l'ajout d'un cycle des nutriments relie chaque organisme à la ressource basale que sont les nutriments minéraux et change ainsi profondément la structure du réseau d'interactions et ses propriétés (Fath and Hynes, 2007; Hynes et al., 2007). Par exemple, le recyclage des nutriments diminue la résilience des chaînes trophiques (DeAngelis, 1980, 1992; Loreau, 1994, 2010) car plus un système est fermé, moins les perturbations seront résorbées par les flux entrants et sortants (DeAngelis, 1992). Le cycle des nutriments induit également un couplage entre les contrôles top-down et bottom-up car les consommateurs influent aussi sur la disponibilité (en générale en l'augmentant) des ressources en raison de leur excrétion (Vanni and Layne, 1997; Vanni et al., 1997; Vanni, 2002; de Mazancourt et al., 1999; Belovsky and Slade, 2000; Attayde and Hansson, 2001; Harrault et al., 2014). Ce type de couplage peut alors donner lieu à une stabilisation du système (si on regarde la stabilité temporelle au lieu de la résilience) car l'excrétion de nutriments augmente la productivité des organismes qui subissent le contrôle top-down (Brown et al., 2004a). L'effet du recyclage des nutriments sur la stabilité des réseaux trophiques n'a été abordé que via des modèles de chaînes trophiques mais jamais via des modèles de réseaux trophiques complexes (DeAngelis, 1980, 1992; Loreau, 1994, 2010; Leroux and Loreau, 2010; Gounand et al., 2014).



## Réseau vert et réseau brun

Le recyclage des nutriments n'est pas une grande chaîne circulaire où la biomasse est entièrement minéralisée pour redonner des nutriments minéraux qui sont ensuite réabsorbés par les producteurs primaires. En effet, les organismes excrètent à la fois des nutriments sous forme minérale, mais aussi de la matière organique morte, contenant à la fois du carbone et des nutriments comme l'azote ou le phosphore, qui forme le compartiment détritus (Moore et al., 2004). Le compartiment détritus représente alors un formidable réservoir nutritif rempli de molécules organiques et de nutriments. Le réseau trophique se divise alors en deux : le réseau trophique vert et le réseau trophique brun (Fig.9). Le réseau trophique vert est fondé sur les producteurs primaires qui produisent de la biomasse à partir d'éléments chimiques minéraux alors que le réseau trophique brun est fondé sur les décomposeurs qui produisent de la biomasse à partir des détritus qu'ils consomment. Ces deux réseaux trophiques ont des fonctions écosystémiques complémentaires puisque le réseau vert produit de la biomasse *de novo* alors que le réseau brun remobilise la matière organique morte et permet de minéraliser les nutriments qui y sont contenus, les rendant alors à nouveau disponibles pour les producteurs primaires. Cependant, les interactions entre ces deux réseaux ne sont pas aussi simples et peuvent donner lieu à des couplages bottom-up et top-down avec des effets très contrastés.

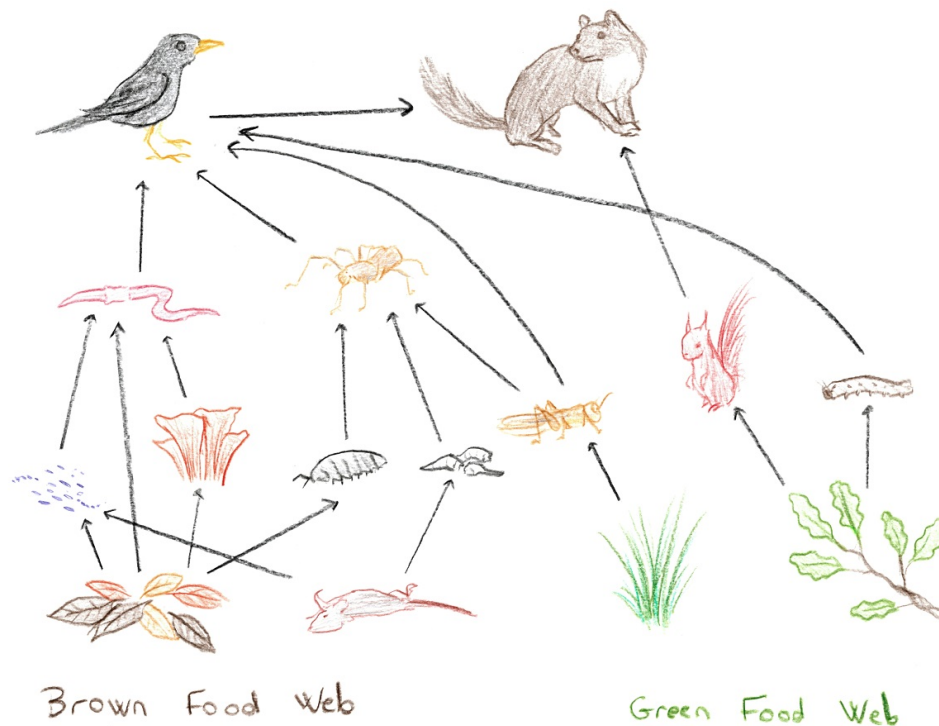


Figure 9: Réseau trophique sous-divisé en un réseau trophique vert et un réseau trophique brun. Les producteurs primaires produisent de la biomasse à partir de nutriments minéraux alors que les décomposeurs consomment la matière organique morte des détritus. Les différents consommateurs peuvent ensuite manger des proies appartenant aux deux réseaux.

### Couplage bottom-up

Le couplage bottom-up entre le réseau vert et le réseau brun peut donner lieu à des interactions mutualistes car les producteurs primaires produisent la matière organique qui deviendra détritus et les décomposeurs participent à la minéralisation des nutriments séquestrés dans ces détritus. Mais cette relation peut être altérée par la composition chimique des détritus. En effet, les producteurs primaires, terrestres en particulier, ont tendance à avoir un ratio carbone sur nutriments plus élevé que les producteurs secondaires (paroi pecto-cellulosique, bois...), ce qui conduit à la production de détritus avec un ratio C:nutriments

plus élevé que celui des décomposeurs. Les décomposeurs, et en particulier les bactéries, sont capables d'absorber les nutriments minéraux (Rhee, 1972; Kirchman, 1994) pour combler ce manque et entrent alors en compétition avec les producteurs primaires (Danger et al., 2007a,b)(Fig.10). Daufresne and Loreau (2001) ont montré théoriquement qu'un système phytoplancton-bactérie ne peut se maintenir que si les bactéries sont limitées par le carbone (donc mutualisme) et ont montré expérimentalement (Daufresne et al., 2008) qu'un tel système converge spontanément vers une co-limitation par le carbone et l'azote. Dans des milieux naturels et des expériences en mésocosmes, l'apport de matière organique allochtone augmente la limitation par les nutriments qui conduit à une augmentation de la biomasses de bactéries par rapport au phytoplancton car ce dernier est moins compétitif pour l'absorption des nutriments minéraux (Joint et al., 2002; Stets and Cotner, 2008; Faithfull et al., 2011; Degerman et al., 2018). Le réseau brun qui domine alors le réseau trophique en terme de productivité a une longueur de chaîne plus importante qui diminue l'efficacité du transfert d'énergie vers les poissons qui sont alors impactés négativement (Berghlund et al., 2007; Degerman et al., 2018). Ainsi, la modification des interactions entre les espèces basales de ces deux réseaux peut avoir des conséquences importantes sur les espèces au sommet du réseau.

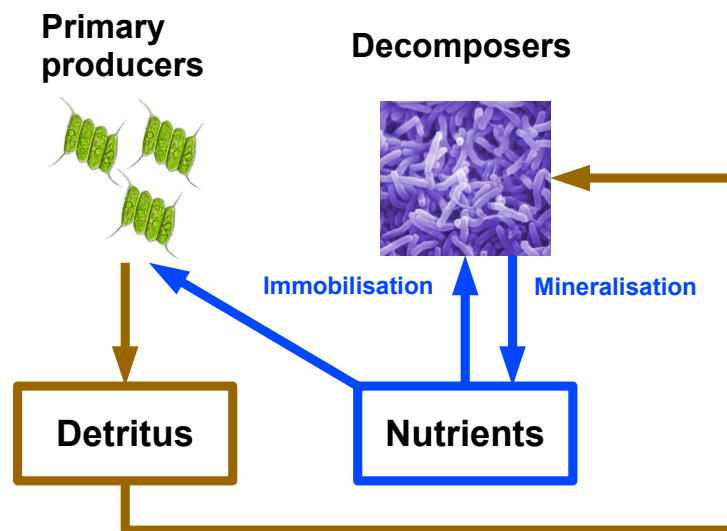


Figure 10: Couplage bottom-up entre producteurs primaires et décomposeurs. Les producteurs primaires absorbent les nutriments minéraux, produisent de la biomasse qui devient des détritits qui sont alors consommés par les décomposeurs qui minéralisent les nutriments qui y sont contenus. Il y a alors mutualisme. Si les détritits sont trop pauvres en nutriments par rapport aux besoins des décomposeurs, alors ces derniers prélèvent également des nutriments minéraux, les immobilisent dans leur biomasse et entrent en compétition avec les producteurs primaires.

### Couplage top-down

Le couplage top-down entre réseaux verts et bruns passe par la présence de consommateurs généralistes consommant des organismes appartenant aux deux réseaux. En effet, les réseaux verts et bruns sont souvent séparés dans l'espace avec par exemple le compartiment pélagique très largement vert car exposé à la lumière et le compartiment benthique principalement brun car accumulant les détritits par sédimentation (mais aussi les compartiments above-ground et below-ground pour les systèmes terrestres). Des consommateurs mobiles comme les poissons font alors le lien entre ces deux compartiments et ainsi entre les deux réseaux (Shimazaki and Miyashita, 2005; Vadeboncoeur et al., 2005; Oelbermann et al., 2008; Wolkovich et al., 2014). Or l'existence de consommateurs généralistes tirant leurs ressources de deux voies énergétiques distinctes (même autres que vertes et brunes) a de profondes conséquences sur la stabilité et le fonctionnement du réseau trophique. Par exemple, Post et al. (2000) ont montré que la présence de prédateurs de sommet de chaîne ayant une préférence asymétrique pour l'une des deux chaînes avait un effet stabilisant (élimination du chaos, conversion des dynamiques oscillatoires en points fixes). Rooney et al. (2006) ont mis en avant l'effet stabilisant (en terme de résilience) du couplage de

voies énergétiques avec des productivités différentes : la voie lente tamponne les perturbations par sa faible réactivité alors que la voie rapide permet de résorber une perturbation par une production ou une perte rapide de biomasse. Cependant, l'effet de ces prédateur de sommet de chaîne est fortement affecté par la structure du réseau et la longueur de chacune des chaînes (Wollrab et al., 2012).

## **Interactions entre couplages top-down et bottom-up**

Le couplage top-down des réseaux verts et bruns a également des interactions avec le couplage bottom-up via le recyclage des nutriments. Attayde and Ripa (2008) ont montré dans leur modèle, et Ward et al. (2015) avec l'analyse de réseaux trophiques marins, que les carnivores favorisent les producteurs primaires en consommant les herbivores, ce qui augmente la production de biomasse et donc de détritus. La biomasse de décomposeurs également consommés par les carnivores augmente par effet bottom-up, ce qui renforce alors la cascade trophique sur les herbivores. Cependant, les effets top-down des consommateurs dépendent aussi du couplage bottom-up entre réseaux verts et brun. Zou et al. (2016) ont montré que les effets en cascade à l'intérieur du réseau vert ou brun ont des effets positifs ou négatifs sur l'autre réseau suivant les cas où les interactions entre producteurs primaires et décomposeurs sont compétitives ou mutualistes. Par exemple, l'augmentation de la consommation de producteurs primaires dans le réseau vert a un effet positif sur le réseau brun si les décomposeurs sont limités par les nutriments. Cependant les modèles étudiant les effets en cascades d'un réseau sur l'autre (Attayde and Ripa, 2008; Ward et al., 2015; Wollrab et al., 2012; Zou et al., 2016) n'ont jusqu'à présent que considéré des chaînes trophiques et non des réseaux comportant des dizaines d'espèces. Les expériences en mésocosmes contenant des réseaux allant jusqu'aux poissons n'ont de leur côté exploré les effets de ce couplage bottom-up et top-down que de façon très parcellaire.

## **Structure de la thèse**

Ce manuscrit de thèse regroupe le travail fait à partir de janvier 2014, date du début de mon stage de master 2. Il comporte trois chapitres principaux : deux portant sur des modèles développés sous la direction de Sébastien Barot et Élisabeth Thébault et un portant sur une expérience en mésocosme faite en 2015 à la station de recherche du CEREEP Ecotron IleDeFrance sous la direction de Gérard Lacroix, Sébastien Barot et Élisabeth Thébault, en collaboration avec Ludwig Jardillier, Emma Rochelle-Newall, Éric Edeline et Kejun Zou. Ce manuscrit comporte également un chapitre annexe comportant le travail que j'ai fait avec Ulrich Brose entre mon stage de M2 et le début des expériences en mésocosme, mais qui a été poursuivi pendant la thèse. Ce travail ne porte pas directement sur le sujet de la thèse mais traite aussi de questions de stabilité dans les réseaux trophiques.

### **Chapitre 1 : Impact of nutrient cycling on food web stability**

Ce premier chapitre étudie l'effet du recyclage des nutriments, dans sa version la plus simple, sur la stabilité d'un réseau trophique complexe. Ici, le recyclage consiste en un retour sous forme minérale (recyclage direct) ou sous forme de détritus (recyclage indirect) des nutriments excrétés par les organismes. Comme présenté précédemment, nous nous attendons à un effet enrichissement du recyclage des nutriments mais également à un effet de la présence d'une boucle de rétroaction couplant les contrôles top-down et bottom-up au sein du réseau trophique. Dans ce chapitre, nous étudions les questions suivantes :

Comment l'effet enrichissement du recyclage de nutriments interagit avec un gradient d'apports externes en nutriments minéraux sur la stabilité du réseau trophique ?

La boucle de rétroaction générée par le recyclage des nutriments a-t-elle un effet stabilisant dans une chaîne trophique autant que dans un réseau trophique ?

La proportion entre recyclage direct et recyclage indirect influe-t-elle sur la stabilité ?

## **Chapitre 2 : Linking green and brown food webs: does this wedding bring stability to both partners?**

Ce chapitre présente l'extension du modèle précédent : cette fois-ci le recyclage des nutriments est assuré par un réseau brun. Ce réseau brun est couplé au réseau vert de façon bottom-up via les nutriments minéraux mais aussi de façon top-down via des consommateurs généralistes. Comme dans le chapitre précédent, nous considérons les effets d'apports externes en nutriments minéraux via les questions suivantes :

Les réseaux trophiques vert et brun réagissent-ils de la même façon à l'enrichissement en nutriments et à la fraction de recyclage direct ?

Ces différences potentielles entre les réponses des réseaux vert et brun affectent-elles la stabilité du réseau trophique en général ?

Le couplage top-down entre les deux réseaux exercé par des consommateurs généralistes modifie-t-il la réponse à l'enrichissement en nutriments ?

## **Chapitre 3 : Interactions between green and brown food webs in freshwater ecosystems: a mesocosm experiment**

Ce chapitre rapporte les résultats d'une expérience en mésocosmes aquatiques. Cette expérience tente de mettre en évidence les couplages bottom-up et top-down entre réseaux trophiques vert et brun via trois traitements croisés : la filtration de la lumière qui est susceptible d'affecter de façon bottom-up et négative le réseau vert, l'ajout de carbone organique dissout qui est susceptible d'affecter de façon bottom-up et positive le réseau brun et la présence ou non de poissons qui couplent les deux réseaux de façon top-down. Nous étudions dans ce chapitre les questions suivantes :

Le couplage bottom-up entre réseaux vert et brun est-il mutualiste ou compétitif, c'est-à-dire est-ce qu'un traitement avec un effet positif sur un des deux réseaux à un effet en cascade positif (mutualisme) ou négatif (compétition) sur l'autre réseau ?

Comment le couplage top-down exercé par les poissons interagit avec le couplage bottom-up entre les réseaux vert et brun via les traitement lumière et ajout de carbone organique dissout ?

## **Chapitre 4 annexe : Metabolic adjustment enhances food web stability**

Ce chapitre annexe remet en question l'un des piliers de la modélisation des réseaux trophiques complexes : la paramétrisation des taux biologiques en fonction du taux métabolique qui est un paramètre fixe calculé par des relations d'allométrie. Or le taux métabolique peut être considéré comme une variable du système que chaque organisme va ajuster en fonction de la disponibilité en ressources afin de maximiser son taux de croissance net. Le contrôle top-down sur les ressources sera donc d'autant plus fort qu'elles sont abondantes par augmentation du métabolisme des consommateurs et le contrôle bottom-up sur les ressources sera d'autant plus faible qu'elles sont rares par une diminution du métabolisme des consom-

mateurs.

L'ajustement métabolique a-t-il un effet stabilisant sur les dynamiques des espèces, c'est-à-dire une réduction de la variabilité temporelle de leur biomasse ?

Si une telle stabilisation existe, se traduit-elle pas une augmentation de la persistance des espèces dans un réseau trophique complexe ?

# Chapter 1

## Impact of nutrient cycling on food web stability

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### Abstract

1. Nutrient cycling is fundamental to ecosystem functioning. Despite recent major advances in the understanding of complex food web dynamics, food web models have so far generally ignored nutrient cycling. However, nutrient cycling is expected to strongly impact food web stability and functioning.
2. To make up for this gap, we built an allometric and size structured food web model including nutrient cycling. By releasing mineral nutrients, recycling increases the availability of limiting resources for primary producers and links each trophic level to the bottom of food webs.
3. We found that nutrient cycling can provide more than 50% of the total nutrient supply of the food web, leading to a strong enrichment effect that promotes species persistence in nutrient poor ecosystems but leads to a paradox of enrichment at high nutrient inputs, *i.e.* to destabilisation.
4. In addition to this enrichment effect, the presence of recycling loops linking each trophic level to the basal resources stabilises species biomass dynamics in food chains but has only weak effects in complex food webs.
5. This new model opens perspectives for better linking studies on food web dynamics to ecosystem processes.

### Key words

detritus, diversity, enrichment, mineral nutrients, paradox of enrichment, size structured

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## Introduction

Food web dynamics and functioning have been studied thoroughly through empirical and modelling approaches because food webs are essential to ecosystem functioning. A key issue is to determine the characteristics of food webs that stabilise their key properties, *e.g.* the number of species composing them, primary production or secondary production. In particular, dynamical models of complex food webs (*i.e.* food webs including numerous interacting species) reveal that size structured food webs (Brose et al., 2006b; Heckmann et al., 2012), allometric scaling of biological rates (Brose et al., 2006b) and adaptive foraging (Kondoh, 2003; Heckmann et al., 2012) promote species coexistence and population stability. However, these models focus on population dynamics and carbon fluxes, forgetting non-living compartments (mineral nutrients and dead organic matter) and nutrient cycling. Some studies include mineral nutrients as basal resources for primary producers (Schneider et al., 2016; Wang and Brose, 2017) or detritus as basal resources for bacteria (Boit et al., 2012) or for species higher in the food web (Legagneux et al., 2012), but they never include a complete nutrient cycling.

Nevertheless, the cycling of mineral nutrients such as nitrogen and phosphorus likely tightly interacts with food web dynamics and stability. Several studies indeed highlighted the importance of nutrient cycling processes for ecosystem stability, but with contrasting results (O'Neill, 1976; DeAngelis, 1980; DeAngelis et al., 1989b; DeAngelis, 1992; Loreau, 1994; McCann, 2011; Neutel and Thorne, 2014). DeAngelis (1980, 1992) showed that recycling affects food chain resilience, systems with tighter recycling being less resilient. On the other hand, Loreau (1994) suggested that tighter recycling was associated with greater food chain resistance to perturbations, and McCann (2011) found that food chains with recycling through a detritus pool were less destabilised by nutrient enrichment than food chains without recycling. Meanwhile, Neutel and Thorne (2014) did not find clear effects of the presence of recycling loops on the resilience of complex soil food webs, some food webs being unaffected by recycling and others being either destabilised or stabilised. While the study of consequences of recycling processes on stability has largely been restricted to resilience of small food web motifs or food chains (but see Neutel and Thorne (2014)), understanding the consequences of nutrient cycling on the stability of complex food webs becomes crucial to predict ecosystem stability in response to perturbations. Observed contradictory results on the impact of nutrient cycling on stability might arise from the fact that nutrient cycling can affect food web stability through different mechanisms, whose importance could also differ between food chain and food web models.

First, the recycled nutrients add up to the external inputs of mineral nutrients and could lead to an enrichment effect (Loreau, 2010). Recent studies have emphasized that nutrient fluxes between ecosystems can strongly determine ecosystem functioning and stability (Leroux and Loreau, 2008; Gounand et al., 2014). Effects on nutrient availability thus clearly need to be accounted for when studying recycling effects on food web stability (McCann, 2011). Nutrient cycling increases primary production (Loreau, 2010), which increases the energy transfer to consumers. This could increase species persistence and sustain higher trophic levels (Abrams, 1993; Binzer et al., 2011). On the contrary, nutrient cycling could lead the destabilisation of food web dynamics through the increase of basal resources availability. Indeed, increasing this availability tends to increase the amplitude of population oscillations, which increases the risk of extinction. This characterises the paradox of enrichment (Rosenzweig, 1971; Rip and McCann, 2011) predicted by several food chain and food web models (Roy and Chattopadhyay, 2007; Rall et al., 2008; Hauzy et al., 2013; Gounand et al., 2014; Binzer et al., 2016) and some experiments (Fussmann et al., 2000; Persson et al., 2001). Taken together, this leads to the hypothesis that in nutrient poor ecosystems, nutrient cycling would increase food web stability, *i.e.* species persistence and the persistence of higher trophic levels while, in nutrient rich ecosystems, nutrient cycling would destabilise food webs. Testing this hypothesis is particularly meaningful in a context of global nutrient enrichment due

to human activities (Vitousek and Reiners, 1975; Smith et al., 1999).

Second, nutrient cycling adds direct feedback loops from all trophic levels to the bottom of food webs. Besides the consequent enrichment effect, these feedback loops may affect stability (McCann, 2011; Neutel and Thorne, 2014). Because these feedback loops are positive (Fath and Hynes, 2007; Hynes et al., 2007) they may have a destabilising effect causing an increase in oscillation amplitude. However, they could have the opposite effect if nutrient cycling leads to asynchronous dynamics of mineral nutrients and primary producers, as found in a food chain model (McCann, 2011). In such case, a decrease in primary producers could be dampened by a simultaneous increase in mineral nutrients availability, thus reducing population oscillations in the food chain (Brown et al., 2004a). Such effects of recycling feedback loops on stability might however be weaker in complex food webs. In complex food webs, recycled nutrient inputs to detritus and mineral nutrient pools results from many feedback loops, which might attenuate the fluctuations of mineral nutrient dynamics and thus limit the stabilising (resp. destabilising) effect of asynchronous (resp. synchronous) fluctuations of mineral nutrients and primary producers.

Third, the effects of nutrient cycling on stability might be modulated by the ways nutrient are recycled. Consumers in food webs directly affect nutrient cycling both through immobilisation of nutrients in their biomass and through egestion and excretion of non-assimilated food (Vanni, 2002). Furthermore, nutrients are excreted as mineral nutrients (direct recycling) or as detritus releasing mineral nutrients during decomposition (indirect recycling) (Vanni, 2002; Zou et al., 2016). Direct recycling is faster than indirect recycling because decomposition is required before the return of nutrients to the mineral pool, leading to increased primary production (Zou et al., 2016). Increasing the fraction of direct recycling should amplify the enrichment effect by accelerating the recycling. Increasing the decomposition rate of detritus should have a similar effect, especially if direct recycling does not prevail.

To study the consequences of nutrient cycling on food web stability, we extended the recent food web modelling approach based on allometric relations with species body mass (*e.g.* Brose et al. (2006b); Heckmann et al. (2012); Schneider et al. (2016); Wang and Brose (2017)) by integrating basic aspects of nutrient cycling in this framework. Species body mass relates with fundamental species traits such as metabolic or growth rates (Yodzis and Innes, 1992; Brown et al., 2004b) and it is also a good predictor of trophic interactions in ecosystems (Williams and Martinez, 2000; Petchey et al., 2008). Models parametrised with such allometric relations have been increasingly used to study food web dynamics and stability, especially because they allow recreating observed patterns and dynamics of complex food webs (Boit et al., 2012; Hudson and Reuman, 2013). This framework thus offers a good opportunity to include nutrient cycling to food web models. To disentangle the mechanisms by which nutrient cycling affects food web stability (defined by species persistence and time variability of biomass dynamics), we assessed and compared the respective impact of nutrient cycling through the addition of mineral resources and the addition of feedback loops in both a complex food web and a food chain. These aspects were critical to answer the following questions: Can nutrient cycling lead to a paradox of enrichment and how does it interact with the overall nutrient richness of the ecosystem? Can the addition of feedback loops by nutrient cycling stabilise food chains as well as complex food webs? Do the relative importance of direct and indirect nutrient cycling and the decomposition rate influence food web stability?

## Material and methods

### General description of the model

We developed a food web model including basic aspects of nutrient cycling by combining food web, allometry and stoichiometric theories (Fig.1.1). Following classical allometric food web models (Brose, 2008;



Heckmann et al., 2012), that are based on carbon flows, species biological parameters and trophic interactions scale with their body mass. Our model adds two major abiotic compartments, mineral nutrients (*e.g.* mineral nitrogen pool) and detritus (dead organic matter), to food web dynamics. Since detritus and mineral nutrient compartments are expressed in mass of nutrient whereas species compartments are expressed in mass of carbon, stoichiometry rules ensure the conversion between carbon flows and nutrient flows between the biotic and abiotic compartments and account for species stoichiometric homeostasis in the food web. Nutrients are either directly recycled (species excretion of mineral nutrients directly available for primary producers) or indirectly recycled (species excretion of detritus releasing mineral nutrients through decomposition). All stocks are expressed for an arbitrary unit of habitat either a surface or a volume. The model is parametrised for nitrogen, but could be applied to other limiting nutrients such as phosphorus. The studied food chain model is a simplified version of the food web model, with only three species, a plant, a herbivore and a carnivore. It is thus built with the same equations and the same parameters than the food web model.

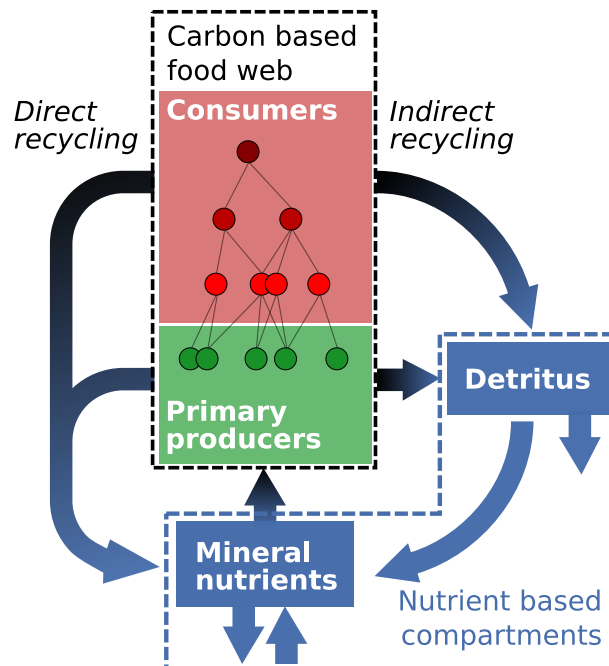


Figure 1.1: Schematic diagram of the modelled food web. The food web contains several primary producers and consumers forming a complex interaction network. It also includes two non-living compartments: mineral nutrients and detritus. Each organism excretes nutrients either directly as mineral nutrients (arrows on the left), or indirectly through the production of degradable detritus (arrows on the right). Stoichiometric rules ensure the conversions between the carbon based food web and the nutrient based compartments.

## Predator-prey interactions in the allometric food web model

For modelling food web dynamics, one needs to model both the structure of the food web (*i.e.* who eats whom) and the population dynamics within the food web. To define trophic interactions between species (*i.e.* food web structure), we took inspiration from the approach of the allometric diet breath model (ADBM, Petchey et al. (2008); Thierry et al. (2011)) because it predicts well trophic interactions in real food webs from species body mass and does not require additional assumptions on food web connectance (Petchey et al., 2008). To each of the 50 initial species is attributed a value  $c$  drawn uniformly in the interval  $[-5; 1]$ . Then, their body mass  $M$  is calculated as follow:

$$M = 10^c \quad (1.1)$$

The five smallest species are defined as primary producers, the other as consumers. The diet of consumers

depends on the profitability of each prey based on prey handling (*i.e.* the lower is the handling time, the more profitable is the prey). Following [Petchey et al. \(2008\)](#) and [Thierry et al. \(2011\)](#), mass specific handling time  $h_{ij}$  of species  $j$  by the consumer  $i$  is defined by:

$$h_{ij} = \begin{cases} \frac{h_i}{b - \frac{M_j}{M_i}} \frac{1}{M_j} & \text{if } \frac{M_j}{M_i} < b \\ \infty & \text{if } \frac{M_j}{M_i} > b \end{cases} \quad (1.2)$$

With  $h_i$  a time constant (calculation detailed in the section A1 of the supporting informations),  $M_j$  the body mass of the prey,  $M_i$  the body mass of the consumer and  $b$  the maximum prey-predator body mass ratio above which the prey cannot be eaten. The handling time function against prey body mass is U-shaped, handling time being minimal when prey body mass is equal to  $b/2 \times M_j$ . We consider that predators can only interact with preys within the body-mass interval  $[0.1bM_i, bM_i]$  with  $b < 1$  (*i.e.* predators are always larger than their prey) as the handling time increases exponentially out of this interval.

The predator-prey dynamics follow previous allometric food web models ([Brose, 2008](#); [Heckmann et al., 2012](#)). The respective equations for primary producers (equation 1.3a) and consumers (equation 1.3b) are:

$$\frac{dB_i}{dt} = r_i G_i B_i - x_i B_i - \beta_i B_i^2 - \sum_{j=\text{consumers}} B_j F_{ji} \quad (1.3a)$$

$$\frac{dB_i}{dt} = -x_i B_i - \beta_i B_i^2 + \sum_{j=\text{prey}} e_{ij} B_i F_{ij} - \sum_{j=\text{consumers}} B_j F_{ji} \quad (1.3b)$$

In these equations,  $B_i$  is the biomass of population  $i$ ,  $G_i$  is the nutrient-dependant growth rate of primary producers,  $r_i$  is the mass-specific maximum growth rate of primary producers,  $x_i$  is the mass-specific metabolic rate,  $\beta_i$  is the intraspecific competition coefficient and  $e_{ij}$  the assimilation efficiency of species  $j$  by species  $i$ . Primary producer growth rates  $r_i$  as well as species metabolic rates  $x_i$  are defined as functions of species body masses, according to the allometric quarter-power laws as described by [Yodzis and Innes \(1992\)](#) and [Brown et al. \(2004b\)](#):

$$r_i = r M_i^{-1/4} \quad (1.4a)$$

$$x_i = x M_i^{-1/4} \quad (1.4b)$$

With  $M_i$  the body mass of species  $i$  and  $r$  and  $x$  allometric constants (Table 1.1) (See the section A1 in the supporting informations).

$F_{ij}$  represents the fraction of species  $j$  consumed by  $i$  and follows a Holling functional response:

$$F_{ij} = \frac{\omega_{ij} a_i B_j^q}{1 + \sum_{k=\text{prey}} \omega_{ik} a_i h_{ik} B_k^q} \quad (1.5)$$

Here  $B_j$  represents the biomass of the prey  $j$ ,  $q$  is the Hill exponent (the functional response is of type II if  $q = 1$  or type III if  $q = 2$ ),  $a_i$  is the attack rate of consumer  $i$  and  $h_{ik}$  is the handling time of  $k$  by consumer  $i$ .  $\omega_{ij}$  is the preference of  $i$  for the prey  $j$ . We chose here to model preferences as time variables and not as fixed parameters according to the adaptive foraging theoretical framework (results with preferences as fixed parameters are available in section A3 in the supporting informations). Adaptive foraging is indeed an important aspect of predator-prey interactions (*e.g.* predator foraging efforts depend on prey availability) and it strongly affects food web dynamics ([Kondoh, 2003](#); [Uchida and Drossel, 2007](#);

Heckmann et al., 2012). The dynamics of foraging efforts were modelled through changes over time of the consumer preferences  $\omega_{ij}$  according to the following equation:

$$\frac{d\omega_{ij}}{dt} = A\omega_{ij} \left( \frac{\partial g_i}{\partial \omega_{ij}} - \sum_{k=prey} \omega_{ik} \frac{\partial g_i}{\partial \omega_{ik}} \right) \quad (1.6)$$

Here,  $A$  represents the adaptive rate of the diet preference and  $g_i$  the total growth rate of species  $i$  defined such as  $\frac{dB_i}{dt} = g_i B_i$ . The initial value of  $\omega_{ij}$  is set assuming a uniform distribution among preys and during the simulation, the  $\omega_{ij}$  are rescaled after the resolution of equation 1.6 to keep the relation  $\sum_{k=prey} \omega_{ik} = 1$  true at each time step.

## From a carbon-based food web model to an ecosystem model including nutrient cycling

To expand the classical food web model to take fundamental aspect of nutrient cycling into account, we model the dynamics of two abiotic compartments, mineral nutrients  $N$  and detritus  $D$ . These compartments are described as masses of nutrient while species biomass is based on carbon in the food web model. We use species carbon to nutrient ratios (C:N)  $\alpha_i$  to convert carbon flows into nutrient flows (and vice versa).

The dynamics of nutrients in the mineral and detritus compartment are described by:

$$\frac{dN}{dt} = I - \ell N + dD + \delta \underbrace{\sum_{i=diversity} \frac{x_i B_i + \beta_i B_i^2}{\alpha_i}}_{\text{direct recycling}} - \underbrace{\sum_{i=primary\ producer} \frac{r_i G_i B_i}{\alpha_i}}_{\text{primary producers uptake}} \quad (1.7a)$$

$$\frac{dD}{dt} = -\ell N - dD + \underbrace{\sum_{i=consumer} \sum_{j=prey} \frac{(1 - e_{ij}) B_i F_{ij}}{\alpha_{Dij}}}_{\text{non assimilated biomass}} + (1 - \delta) \underbrace{\sum_{i=diversity} \frac{x_i B_i + \beta_i B_i^2}{\alpha_i}}_{\text{indirect recycling}} \quad (1.7b)$$

We consider an open ecosystem where  $I$  is the constant input of nutrients (*e.g.* through erosion or atmospheric deposition) and  $\ell$  is the rate of loss of mineral nutrients and detritus (*e.g.* through leaching, sedimentation).

The nutrient-dependant growth rate of primary producers is expressed as (DeAngelis, 1980; DeAngelis et al., 1989b):

$$G_i = \frac{N}{K_i + N} \quad (1.8)$$

where  $K_i$  is the half saturation constant of nutrient up-take of primary producer  $i$ . The nutrient uptake by primary producer (expressed as a nutrient flow) is calculated by dividing the growth rate of primary producers (expressed as a carbon flow) by their C:N ratio.

Detritus are decomposed at a constant rate  $d$ . Organisms release nutrients through excretion and mortality to the detritus and mineral nutrient pools. A fraction  $\delta$  of these nutrients is released in their mineral form (urine for instance) while the remaining fraction is released as dead organic matter (detritus like feces, dead bodies, litter fall...) (Fig.1.2A)(Zou et al., 2016). We assume that the nutrients contained in the non-assimilated biomass ( $e_{ij}$  fraction of the eaten biomass) go in the detritus.

The amount of nutrients released by species in the food web depends on their C:N ratio  $\alpha_i$ . The carbon to nutrient ratio of non-assimilated biomass  $\alpha_{Dij}$  depends on both the C:N ratio of the prey  $j$  and of the consumer  $i$  (calculation detailed in the section A1 of the supporting informations):

$$\alpha_{Dij} = \frac{\alpha_j \alpha_i (1 - e_{ij})}{\alpha_i - \alpha_j e_{ij}} \quad (1.9)$$

## Assessing nutrient cycling effects on stability

Stability was assessed by two complementary measures: species persistence and average coefficient of variation of species biomass (CV). To investigate the effects of nutrient cycling on food web dynamics and disentangle effects due to enrichment from effects due to presence of additional loops, each food web is studied for three configurations of nutrient cycling (Fig.1.2). (1) No nutrient cycling with the fraction of direct recycling  $\delta$  and the decomposition rate  $d$  set to zero. This corresponds to the dynamics obtained with classic allometric food web models and will be referred as the NC model (No Cycling) (Fig.1.2A). (2) With nutrient cycling with the fraction of direct recycling  $\delta$  and the decomposition rate  $d$  strictly positive (Fig.1.2B). This food web is referred as the C model (Cycling). (3) No nutrient cycling but the enrichment effect of nutrient cycling is simulated (Fig.1.2C). This food web is referred as the SC model (Simulated Cycling). In this last case, we remove the potential effect of the coupling between higher trophic levels and the basal resource due to the presence of recycling loops while keeping the additional inputs of nutrients associated with nutrient cycling. To simulate the enrichment effect of nutrient cycling, we replaced the basal nutrient input by the total nutrient input  $I_{tot}$ :

$$I_{tot} = I + I_{recy} \quad (1.10)$$

With  $I$  the external nutrient input and  $I_{recy}$  the average quantity of recycled nutrients.

In addition to the complex food web, a tri-trophic food chain (*i.e.* with three species) is build to track the effects of nutrient cycling in a simpler system. The tri-trophic food chain is ruled by the same equations than the complex food web except for the adaptive foraging that is not relevant in such a model.

	Value and units	Description	Reference
$B_i$	$kg.v^{-1}$	Biomass (carbon) of species $i$	Variable (equation 1.3a, 1.3b)
$N$	$kg.v^{-1}$	Mineral nutrient (nitrogen)	Variable (equation 1.7a)
$D$	$kg.v^{-1}$	Detritus (nitrogen)	Variable (equation 1.7b)
$\omega_{ij}$	Dimensionless	Preference of predator $j$ for prey $i$	Variable (equation 1.6)
$r$	$0.87 kg^{1/4}.year^{-1}$	Growth rate allometric constant	Binzer et al. (2012)
$x$	$0.12 kg^{1/4}.year^{-1}$	(primary prod.) Metabolic rate	Brose (2008)
	$0.27 kg^{1/4}.year^{-1}$	(consumer) allometric constant	
$h_j$	$year.kg^{-1}$	Handling time	Section A1 supp. inf.
$a_i$	$0.1 v.year^{-1}$	Attack rate	Arbitrary
$\beta_i$	$0.001 v.kg^{-1}.year^{-1}$	Intraspecific competition coefficient	Arbitrary
$e_{ij}$	0.45 (herbivore)	Assimilation efficiency of species $j$	Yodzis and Innes (1992)
	0.85 (carnivore)	eaten by species $i$	
$q$	1	Hill exponent	Brose et al. (2006b)
$A$	0.01	Adaptive rate	Arbitrary
$b$	0.05	Max prey-predator body mass ratio	Brose et al. (2006a)
$\alpha_i$	6.6 (primary prod.)	Carbon to nutrient ratio	Anderson (1992)
	5 (consumer)		
$K_i$	$10 kg.v^{-1}$	Half saturation of nitrogen uptake	Arbitrary
$\ell$	$0.2 year^{-1}$	Leaching rate	Arbitrary
$M_i$	$kg$ (of C)	Body mass of species $i$	Log uniform in $[10^{-5}, 10]$
$I$	$kg.v^{-1}.year^{-1}$	External nutrient input	$[0, 400]$
$d$	Dimensionless	Decomposition rate of detritus	$[0, 1]$
$\delta$	Dimensionless	Fraction of direct recycling	$[0, 1]$

Table 1.1: Table of parameters and variables.  $v$  represents a generic metric of space (*e.g.* that could represent liters or square meters). Indeed all the parameters depending on space are set arbitrarily and thus we do not need to specify a particular unit of space.

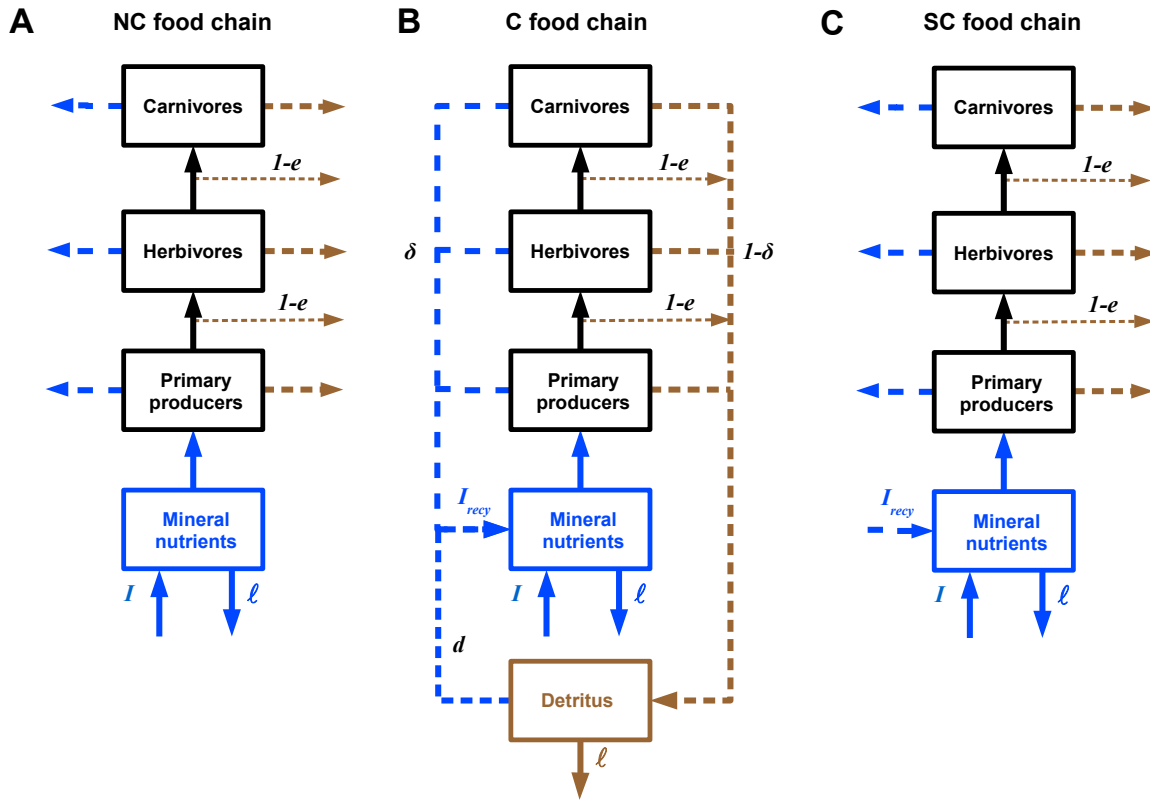


Figure 1.2: Diagram of the general structure of our models with and without nutrient cycling feedback loops. The dotted arrows represent nutrient cycling (nutrient flux in blue, detritus in brown). **A)** NC model. Food chain without nutrient cycling. **B)** C model. Food chain with nutrient cycling. A fraction  $\delta$  of nutrients is excreted as mineral nutrients (direct recycling on the left) and a fraction  $1 - \delta$  plus the fraction  $1 - e$  of non ingested biomass are excreted as detritus (indirect recycling on the right). The total nutrient input  $I_{tot}$  in the pool of mineral nutrients is the sum of the external nutrient input  $I$  and the recycled nutrient  $I_{recy}$ . **C)** SC model. Food web without nutrient recycling but with corrected nutrient input that is equal to  $I_{recy}$ . The resulting food web does not have the feedback loop induced by nutrient cycling but has an equivalent nutrient availability than in the food web with nutrient recycling. Note that the first version of our model (NC) is based on the C model where  $I_{recy}$  is set to 0.

## Simulations

All the parameters, their units and their values as used in the simulations are given in the table 1.1. The sensitivity of the results to arbitrarily set parameters is in the section A3 in the supporting informations. The simulations are performed with *C++* and the *GSL* ode solver using the Runge-Kutta-Fehlberg (4, 5) method with an adaptive time step and an absolute accuracy of  $10^{-6}$ . Simulations are run for 10,000 years and the outputs recorded for the last 1000 years. Species persistence is measured as the ratio of the final number of species at  $t = 10,000$  to the initial number of species at  $t = 0$ . The CV is the ratio of the standard deviation to the mean of species biomass or recycled quantity of nutrients over time, calculated for the 1000 last years of each simulation. Each combination of parameters is tested for 100 different food webs (*i.e.* different randomly drawn sets of species body mass), each of these food webs being simulated in the three configurations of nutrient cycling (*i.e.* for the NC, C and SC models). To implement the SC model, we recorded the density of each compartment in the simulation of the C model at  $t = 9,000$  and the averaged quantity of recycled nutrient  $I_{recy}$  recorded for the last 1,000 years. We then ran corresponding food web simulations for the SC model (*i.e.* with  $\delta = d = 0$  and  $D = 0$ ) for 1000 years with initial densities and a nutrient input  $I$  respectively set equal to the densities and  $I_{tot}$  recorded in the C model.

In each simulation for complex food webs, there are initially 50 species and their initial biomass is set at  $10 \text{ kg.v}^{-1}$  for primary producers and at  $5 \text{ kg.v}^{-1}$  for consumers ( $v$  is an arbitrary metric of space, see

table 1.1). Initial quantities of nutrients in the mineral nutrients and detritus pools are set at  $10 \text{ kg.v}^{-1}$ . In the simulations for the food chain model, the body masses of the primary producer, the herbivore and the carnivore are respectively 1, 10 and 100 kg, and their initial biomass are respectively 1, 0.5 and 0.1  $\text{kg.v}^{-1}$ .

## Results

### Overall effects of nutrient cycling on food web dynamics

Nutrient cycling contributes to an important part of the total mineral inputs of nutrients in the food web, and its contribution varies with the levels of external inputs of nutrients (Fig.1.3A), in parallel with variations of total biomass in the food web and primary production (see Fig.A2-3 in the supporting informations). Nutrient cycling always represents larger inputs of nutrients to the food web than external inputs. At low nutrient enrichment levels, consumers are responsible for most of the recycling. However, at high nutrient enrichment levels, the quantity of nutrient recycled by consumers stops increasing while the total quantity of nutrient recycled still increases linearly with the external nutrient input  $I$  due to a large increase in the quantity of nutrient cycled by primary producers. A similar relation is observed for the primary and the secondary productions (see Fig.A2-4C in the supporting informations).

Nutrient cycling affects the relationship between nutrient enrichment (*i.e.* external nutrient inputs) and food web stability (Fig.1.3). First, it affects the relationship between species persistence and nutrient enrichment (Fig.1.3B). In either food webs with and without nutrient cycling, persistence follows a hump-shaped relationship with external nutrient input  $I$ : first there is a sharp increase of the persistence for low nutrient inputs, then a plateau with maximum persistence (area outlined in dark grey for the C food webs) and finally a decrease of the persistence for high nutrient inputs. However, maximum persistence is reached for lower input values and effects of enrichment are sharper for the case with nutrient cycling than for the case without nutrient cycling. These sharp changes in species persistence along the gradient of nutrient enrichment are paralleled by strong changes in food web maximum trophic level with an increase and then a decrease of the maximum trophic level with increasing external nutrient input  $I$  (See Fig.A2-2C in the supporting informations).

Second, nutrient cycling affects the relation between the average coefficient of variation (CV) of the species biomass and nutrient enrichment (Fig.1.3C). While the average CV of species biomass increases monotonically with nutrient enrichment when there is no nutrient cycling, it shows a saturating relationship in food webs with nutrient cycling. In this case, the CV of species biomass increases at low input values but it stop increasing at high nutrient enrichment. However, high CVs only occur in food webs with surviving consumers (Fig.A2-2B and A2-2D in the supporting informations). The CV of the quantity of recycled nutrients follows a hump-shaped relation with external nutrient input  $I$  but the temporal variability of the quantity of recycled nutrients is about 25 times smaller than the CV of species biomass (see also Fig.A2-1 in the supporting informations).

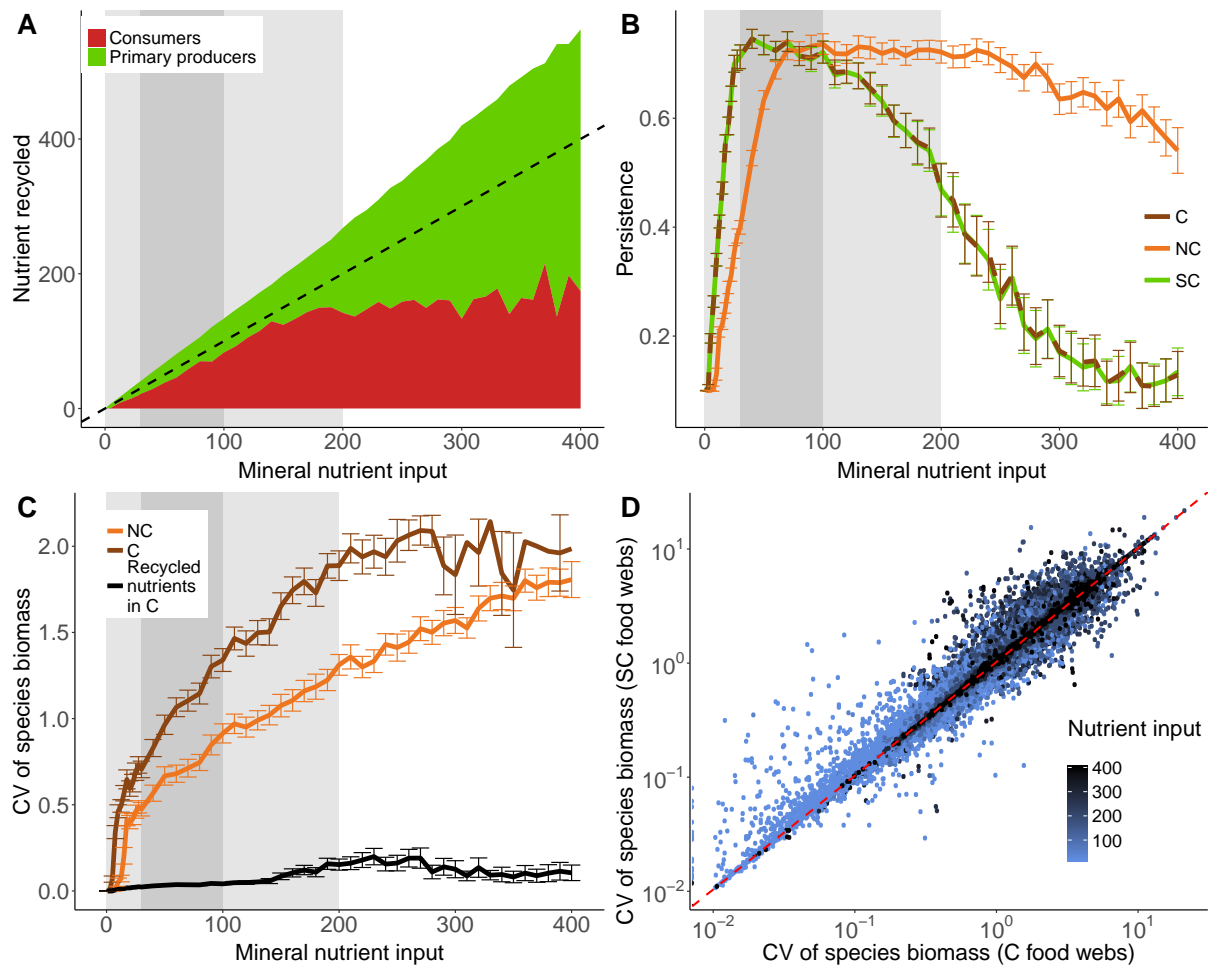


Figure 1.3: Overall effects of nutrient cycling on nutrient supply and food web dynamics in the complex food web model. **A)** Quantity of recycled nutrients by primary producers (green) and consumers (red) along a nutrient enrichment gradient (average of simulated food webs where at least one species persists). The dashed line is the bisector symbolising the case where the quantity of recycled nutrient is equal to the external nutrient input  $I$ . The light grey domain (for  $I$  in  $[0, 200]$ ) emphasises the mineral nutrient input range where the quantity of nutrients recycled by consumers increases. **B)** Effects of nutrient cycling on species persistence (proportion of species surviving at the end of simulations) along a nutrient enrichment gradient. Each point represents the average persistence of 100 simulated food webs. The brown dashed curve represents the C food webs with nutrient cycling ( $\delta = 0.2$ ,  $d = 0.2$ ), the orange curve represents the NC food webs without nutrient cycling and the green curve represents the SC food webs without nutrient recycling but with a mineral nutrient input simulating the enrichment effect of nutrient cycling in the C food web. The dark grey domain emphasises the plateau of maximal species persistence in the C food webs. **C)** Effect of the external nutrient input  $I$  on the average coefficient of variation (CV) of species biomass (error bars represent the confidence interval of the mean) in C food web (brown) and in NC food webs (orange). Each point represents the average of simulated food webs where at least one species persists. The black curve represents the average CV of the quantity of recycled nutrients in C food webs. **D)** CV of the species biomass in C food webs versus in the SC food webs. Each dot represents the average CV of one species of one food web in its C and SC versions. The dashed red line is the bisector and the color scale represents the external nutrient input  $I$ .

## Influence of the recycling parameters

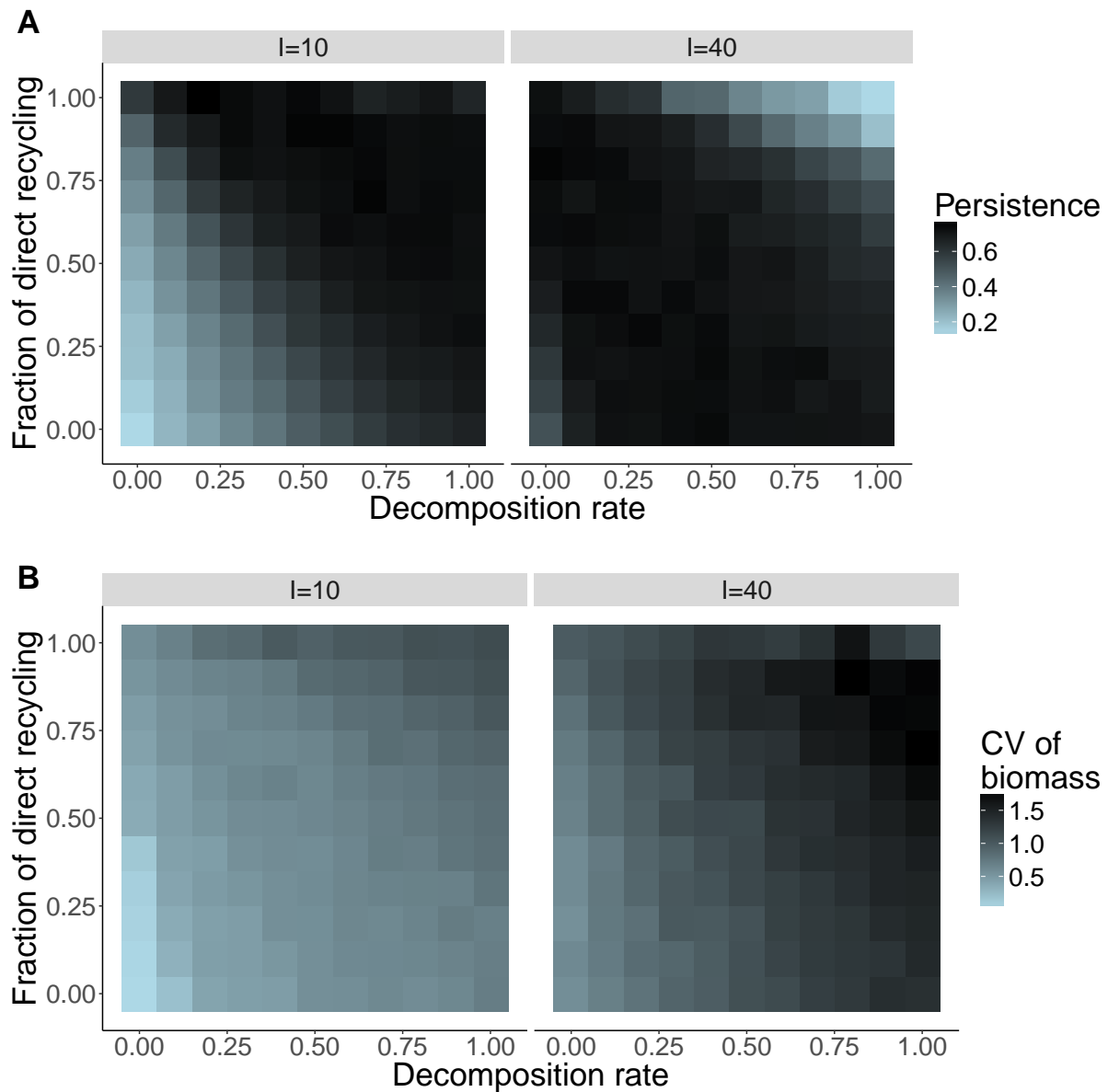


Figure 1.4: Effect of the recycling parameters  $d$  (detritus decomposition rate) and  $\delta$  (fraction of direct recycling) in the complex food web model **A**) on species persistence and **B**) on the average coefficient of variation of the biomass of species for  $I = 10$  and  $I = 40$ . In **A**), each square represents the average value for 100 replicates while in **B**) it represents the average value for persistent food webs only (*i.e.* food webs where at least one species persists).

Both the decomposition rate and the fraction of directly recycled nutrients affect species persistence and the coefficient of variation of species biomass (Fig.1.4). When  $I = 10$ , increasing the decomposition rate  $d$  and the fraction of directly recycled nutrients  $\delta$ , increases the persistence (Fig.1.4A) and the average CV of species biomass (Fig.1.4B). When  $I = 40$ , increasing  $d$  and  $\delta$  first increases and then decrease persistence while the average CV of species biomass increases and stays at its maximum value. Increasing  $d$  and  $\delta$  always increases the quantity of recycled nutrients in the food web (Fig.A2-5 in the supporting informations) and it further affects food web maximum trophic level in the same way than species persistence.



## Effects of nutrient cycling: enrichment vs feedback loop

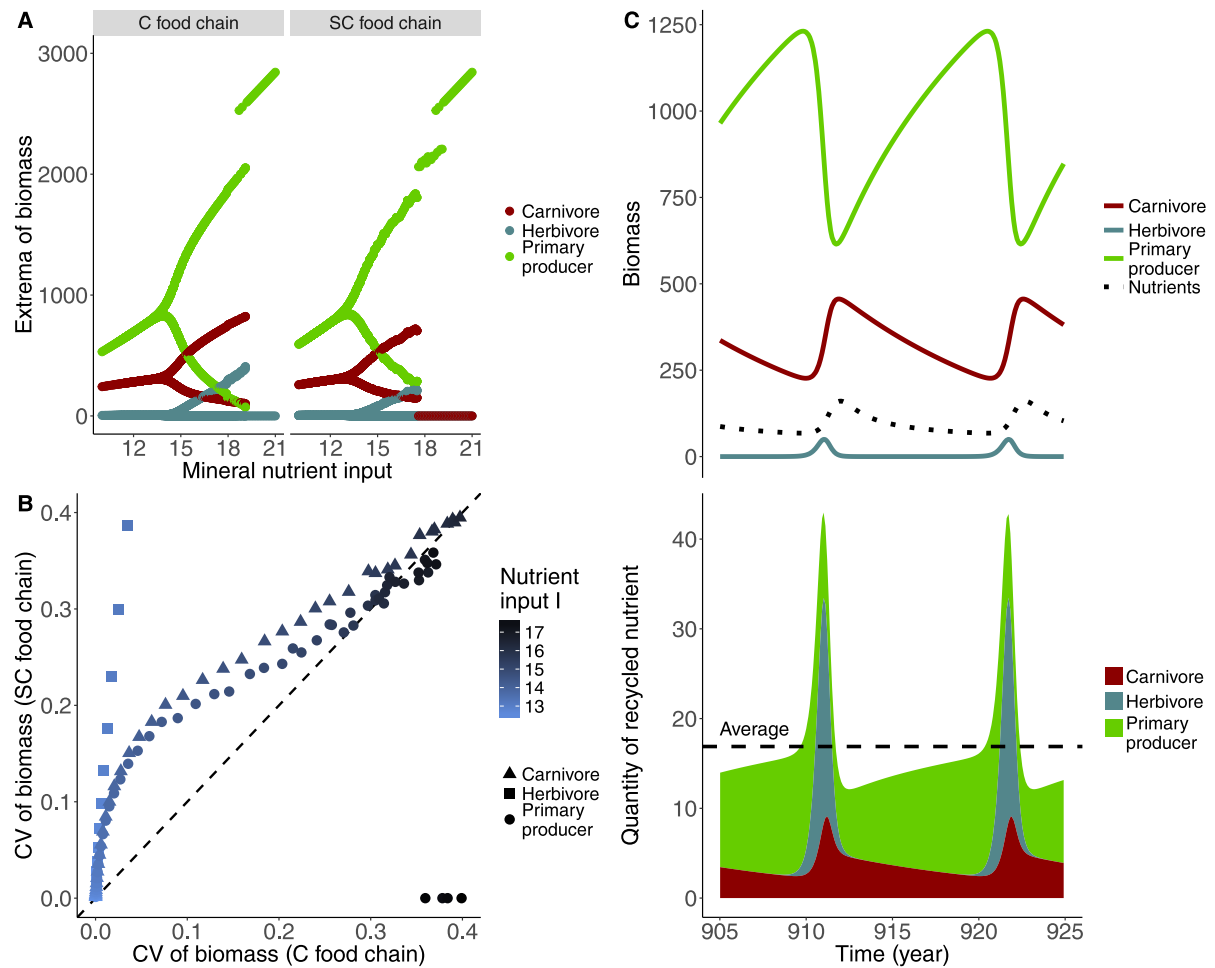


Figure 1.5: Effect of the feedback loop in a tri-trophic food chain. **A)** Diagram of bifurcation of species biomass (minima and maxima of biomass in dynamics) in a tri-trophic food chain (plant, herbivore and carnivore) along a nutrient enrichment gradient. Two cases are represented: a case with nutrient cycling (C food chain) and a case without nutrient cycling but with a simulated enrichment due to nutrient cycling (SC food chain). **B)** CV of the species biomass in the C food chain versus the SC food chain. The dashed line represents the bisector and the color scale represents the nutrient input  $I$ . In order to improve the readability, values on the y axis above 0.4 (corresponding to herbivore CV) are not shown but herbivore CV response to enrichment is qualitatively similar to plant's and carnivore's one. **C)** Dynamics of the biomass of species and the mineral nutrients compartment (values of the mineral compartment have been magnified by 30 for more readability) and of the quantity of nutrients recycled by each trophic level in the C food chain ( $I = 15$ ,  $\delta = 0.2$ ,  $d = 0.2$ ). The dashed line represents the average quantity of recycled nutrients.

The comparison between the case with nutrient cycling (case C) and the case without nutrient cycling but with a nutrient input simulating the enrichment effect of nutrient cycling (case SC) allows to separate the effects of nutrient cycling due to enrichment from those due to the creation of additional feedback loops from each trophic levels to the bottom of the food web. When we model food web dynamics without nutrient cycling but including the enrichment effect of nutrient cycling (*i.e.* SC case), the relationships between external nutrient inputs and species persistence or biomass CV are the same than in presence of nutrient cycling (Fig.1.3B and A2-2A in the supporting informations). Indeed, the curves corresponding to C and SC strongly overlap. Most of the effects of nutrient cycling on food web stability are thus due to an enrichment effect caused by recycled nutrients. Weak effects of the addition of recycling loops appear when we compare more closely the CV of species in individual food webs with or without these loops (Fig.1.3D). Although the CVs of species are strongly correlated between the C and SC simulations, at

low nutrient inputs species biomasses are generally less variable over time in food webs when recycling adds feedback loops (see Fig.A2-6 in the supporting informations).

In simple food chain models, as in complex food webs, effects of nutrient cycling on stability are mainly due to an enrichment effect (Fig.1.3A and Fig.A2-7A in supporting informations). The variability of species biomasses increases with nutrient inputs and with comparable CV values in both the C and SC cases (see Fig.A2-7B in the supporting informations). However, a stabilising effect of the recycling loops, already observed in the food webs, appears more clearly in the food chain model (Fig.1.5B and Fig.A2-7C in supporting informations). For low nutrient inputs, the CV of biomass is higher in the SC food chain, especially for herbivores. In addition, the herbivore and carnivore go extinct at lower threshold value of increased inputs in the SC case than in the C case (Fig.1.5A). Contrary to what we found in the complex food web model (Fig.1.3C), the temporal variabilities of the quantity of recycled nutrients and of species biomasses are of similar magnitude in the food chains (Fig.1.5C and A2-7B in the supporting informations). While the total quantity of recycled nutrient is below the average recycled quantity during most of the dynamic, it picks for a short time when primary producer biomass and primary production (see Fig.A2-7D in supporting informations) decrease while herbivore and carnivore biomasses increases.

## Discussion

By integrating nutrient cycling, our food web model allows to better link population dynamics and ecosystem functioning. Results of this model highlight that nutrient cycling strongly affects food web dynamics and its response to nutrient enrichment. We show that the effects of nutrient cycling on food web stability are mostly due to the increased nutrient availability (*i.e.* enrichment effect due to efficient recycling) that promotes species persistence at low nutrient inputs but leads to a paradox of enrichment at high level of nutrient inputs. The addition by nutrient cycling of feedback loops from each species to the bottom resource has a clear stabilising effect in food chains but only weakly affects the stability of complex food webs. These results are thoroughly discussed below and their sensitivity to the parameters (Table 1.1) is tested in section A3 in the supporting information.

### Nutrient cycling and enrichment effects

Our results show that nutrient cycling mainly affects food web stability through its impacts on nutrient availability in ecosystems. Indeed, effects of increased inputs of nutrients on food web stability are qualitatively similar with and without nutrient cycling but they occur for lower inputs when nutrient cycling is present. Similarly, factors increasing recycling speed and the effectively recycled nutrient quantity (*i.e.* higher decomposition rate and fraction of direct recycling) lead to stability values that are obtained for increased levels of nutrient inputs in food webs with a slower nutrient cycling.

In agreement with previous food web studies (Rall et al., 2008; Binzer et al., 2016), we observe two contrasting responses of species diversity and food web stability to increased nutrient availability. While higher nutrient availability consistently increases the temporal variability of species biomasses, it also increases species persistence in nutrient poor ecosystems (*i.e.* low external nutrient inputs) but leads to decreased persistence at high inputs of nutrients. The increase in persistence at low nutrient inputs is likely due to the increased persistence of species at higher trophic levels (Fig.A2-2C). Higher trophic levels are known to require a sufficient ecosystem productivity (limited by nutrient availability) to meet their energetic requirement and persist (*e.g.* Oksanen et al. (1981); Abrams (1993); Leibold (1996)), which can explain why increased persistence is only found in our case for nutrient poor ecosystems. The observed increase in the amplitude of species biomass oscillations (*i.e.* increase of species CVs) with increasing nutrient inputs is typical of the well-known paradox of enrichment (Rosenzweig, 1971; DeAngelis, 1992; Roy and Chattopadhyay, 2007; Rip and McCann, 2011). In accordance with our model results, the para-

dox of enrichment has been found in complex food web models with type II functional responses (Rall et al., 2008; Binzer et al., 2016). While the use of type III functional responses removes in our model the destabilising effect of nutrient enrichment (Fig.A3-3, see also Rall et al. (2008)), adaptive foraging as included in our study does not prevent the occurrence of the paradox of enrichment (Fig.A3-2) as already observed by Mougi and Nishimura (2008) in a one predator-two prey model. Such destabilising effects of nutrient availability on species dynamics might explain the decrease in species persistence we observe at high levels of nutrient inputs. In case of type III functional responses where no such destabilising effects occur, persistence does not decline at high levels of nutrient availability (Fig.A3-3). Large oscillations of species biomass caused by nutrient enrichment likely trigger species extinctions as their biomass might reach the extinction threshold value, thus counteracting the positive effect of nutrient enrichment on persistence at low nutrient levels and resulting in an hump-shaped relationship between species persistence and nutrient enrichment.

Our results highlight that effects of nutrient cycling on nutrient availability are key to understand consequences of nutrient cycling on food web dynamics in ecosystems. Several mechanisms can determine how nutrient cycling affect nutrient availability in our model. First, the efficiency of nutrient cycling, as defined by the proportion of nutrient that is recycled without being leached out of the ecosystem, has been shown to increase the total amount of mineral nutrient circulating in the ecosystem and primary production (DeAngelis, 1980; de Mazancourt et al., 1998; Barot et al., 2007; Loreau, 2010). In our model, detritus just represent a pool of nutrient unavailable for primary producers and increase the probability of a nutrient to be lost by the ecosystem as the loss rate is the same as in the mineral nutrient pool. Increasing the direct recycling and the decomposition rate respectively decreases the proportion of nutrient passing through the detritus pool and the residence time of nutrient contained in detritus, leading to increased nutrient availability. This suggests that the impact of nutrient cycling partly arises in our models from complex interactions between the speed of recycling and nutrient losses (Fig.A3-1C,D). These interactions should be further disentangled through new simulations manipulating independently rates of mineral nutrient and detritus loss that are set equal in our model while higher losses for mineral nutrients than for detritus would be more realistic, at least in terrestrial ecosystems.

Second, the amount of recycled nutrients depends on food web species biomass and on primary production, which increases linearly with nutrient inputs (Loreau, 2010). In fact, nutrient uptake by producers necessarily balances nutrient losses from all trophic levels at equilibrium (Fig.A2-4C and D). At low nutrient inputs, consumers are the main contributors to nutrient cycling, in agreement with experimental and empirical studies (Vanni, 2002; Schmitz et al., 2010). While nutrient losses per unit of biomass due to species metabolism are lower for consumers because of their larger body mass, consumers also strongly contribute to recycling through nutrient losses associated to feeding inefficiency, This is particularly true for herbivores whose assimilation efficiency is low ( $e_{ij} = 0.45$ ) so that they produce a lot of detritus by consuming primary producers, as also emphasised by previous ecosystem models (Leroux and Loreau, 2010; Krumins et al., 2015). However, at high nutrient input, food webs are dominated by primary producers, which become the main contributors to nutrient cycling. In such case, primary producers release large amounts of detritus and nutrients due to high metabolism rates and large density dependant mortalities (Fig.A2-4). At high external nutrient inputs, the total quantity of recycled nutrients is lower for food webs with higher trophic levels (Fig.A2-3 A). This seems contradictory to the results of Wang and Brose (2017) who found that higher vertical diversity (*i.e.* presence of species at higher trophic levels) increases the nutrient flow in food webs. However, results are not fully comparable between the two studies as we do not directly manipulate species richness and vertical diversity while Wang and Brose (2017) did not include nutrient recycling in their model.

Food web structure influences nutrient cycling through other already identified mechanisms pertaining to the quality of the produced detritus that are not included in our model. In nature, the fraction of direct

recycling and the degradability of detritus can be controlled by the trophic structure of the food web. In aquatic ecosystems, top predators such as fishes produce large quantities of highly degradable detritus (Harrault et al., 2012) that sustain a higher biomass of phytoplankton and zooplankton (Vanni and Layne, 1997; Harrault et al., 2014). In terrestrial ecosystems, herbivores also produce excrements that are easily degraded by the soil community and lead to an increase of the primary production (McNaughton, 1984; Belovsky and Slade, 2000). Primary producers can also strongly influence decomposition. In terrestrial ecosystems, plant leaf traits affect the composition and the quality of the litter (Cornwell et al., 2008). These mechanisms might strongly influence food web stability through their impact on nutrient availability. Including further the links between food web structure and the degradability of detritus would thus need to be tested in new versions of our model.

### Nutrient cycling and effects of feedback loops

Though we found that nutrient cycling mostly destabilises food web through an enrichment effect, we also find stabilising effects of nutrient cycling through feedback loops from all trophic levels to primary producers and these effects were much stronger in our food chain model than in our food web model. These stabilising effects were visible through the decrease of the temporal variability of species biomasses between the SC and C models (Fig.A2-7 A,C) that compare the effects of the addition of nutrients by nutrient cycling with and without the feedback loops. Rip and McCann (2011) showed that the destabilising effect of enrichment may occur due to an unbalance between species growth rates and loss rates. In our food chain model, such unbalance is decreased for primary producers in presence of feedback loops (see Fig.A2-8 in supporting information) thanks to out-of-phase dynamics of recycled nutrients and primary producers, which stabilizes population dynamics in the food chain. Indeed, when herbivore and carnivore biomasses increase a large quantity of nutrient becomes available through recycling due to relatively low efficiency of herbivore consumption especially (Fig.A2-7C). This increased nutrient availability boosts primary production and compensates for the increased mortality due to grazing. On the contrary, when the herbivore and the predator biomasses decrease, the quantity of recycled nutrients is lower which limits the increase of primary producers due to a reduced mortality (Fig.A2-7D and Fig.A2-8). Similar results have been described by Brown et al. (2004a) who showed that a positive feedback loop in a food chain stabilises species densities dynamics. Although Brown et al. (2004a) did not consider nutrient cycling but a positive effect of predators on resource uptake by prey, our results can be understood through the same kind of mechanisms. Our results contradict previous studies on food chains suggesting that feedback loops generated by nutrient cycling are destabilising (DeAngelis, 1980). This discrepancy likely arises from these latter results being based on a different stability measure (*i.e.* resilience instead of temporal variability) and because previous studies did not separate enrichment effects from feedback loop effects of recycling.

Our results show that the stabilising effects of recycling loops are weaker in food webs than in food chains. By considering a different stability measure (*i.e.* resilience), Neutel and Thorne (2014) also suggested that the presence of recycling feedback loops have significant effects on food web stability only in food webs with low diversities and simple structures. In our case, such weaker effects in complex food webs might be explained by the low temporal variability of the total quantity of recycled nutrients observed in the food web model, which does not allow strong asynchrony between the dynamics of mineral nutrients and primary producers as found in the food chain model (Fig.A2-1, Fig.A2-7B,C). While the CV of recycled nutrients is in the same order of magnitude as the CV of species biomass in the food chain model, it is smaller by one order of magnitude in the food web model. Nutrient cycling is the outcome of the aggregated nutrient loss from numerous species whose dynamics are not synchronous and lead to compensation effects: when the biomasses of some species decrease, the biomasses of other species likely increase, thus keeping the total biomass and the total quantity of recycled nutrients less variable

(Fig.A2-1C). Theory predicts that species diversity stabilises aggregated ecosystem properties through asynchronous species dynamics (Doak et al., 1998; Gonzalez and Loreau, 2008; Loreau and de Mazancourt, 2013). This rationale is supported by numerous experimental studies showing that aggregated ecosystem processes, such as primary production (Tilman, 1996; Tilman et al., 2006; Schläpfer and Schmid, 1999; Loreau, 2000; Hooper et al., 2005) or dead biomass decomposition (Knops et al., 2001; Keith et al., 2008; Gessner et al., 2010; Nielsen et al., 2011) are more stable over time than individual species dynamics. Interestingly, our results also suggest that positive effects of biodiversity on ecosystem stability might also occur for nutrient cycling. Up to our knowledge, this hypothesis has never been fully tested in biodiversity experiments and could lead to a new research avenue.

## Conclusion and perspectives

In an ecosystem model linking population dynamics in a food web to ecosystem functioning, we found strong effects of nutrient cycling on food web stability. Thus, ecologists need to incorporate nutrient cycling in theoretical and empirical work to better predict food web stability. We identified two distinct effects of nutrient cycling. First, an enrichment effect due to the recycled nutrients that increase species persistence at low nutrient input by increasing resource availability but leads to a decrease in species persistence through a paradox of enrichment at higher nutrient input. Second, a stabilising effect of the feedback loops that links each trophic level to the mineral resource through nutrient cycling. However, this stabilising effect is stronger in food chains than in complex food webs where nutrient cycling can be reduced to its enrichment effect.

Real ecosystems are known to differ by their dependence on external inputs of mineral nutrients (Polis et al., 1997; Vadeboncoeur et al., 2003; Jickells, 2005; Bokhorst et al., 2007), and ecosystems relying less on such inputs likely depend more on nutrient cycling than ecosystems depending more on external inputs. Therefore, nutrient cycling, as suggested by our results, could influence the food webs of these ecosystems in contrasted ways. For example, in ecosystems such as eutrophic lakes (Vadeboncoeur et al., 2003) with high inputs of nutrients, nutrient cycling could mostly have a destabilising effect while in ecosystems with low inputs of nutrients such as Antarctic terrestrial ecosystems (Bokhorst et al., 2007) or infertile landscapes (Hopper, 2009) nutrient cycling could have a stabilising effect. In the same vein, in ecosystems with efficient nutrient cycling, nutrient losses are low so that nutrient cycling represent a very important source of nutrient and more likely might lead to destabilising effects.

The predictions of our model should be tested experimentally. For example, it would be possible in mesocosms to manipulate both inputs of mineral nutrients and the efficiency of nutrient cycling (Harrault et al., 2014), *e.g.* exporting an increasing proportion of detritus, and to measure the response in terms of food web functioning and stability. It would also be interesting to compare food webs of different types of natural ecosystem with contrasting nutrient cycling and mineralisation rates. Typically, our model probably better corresponds to an aquatic food web (*i.e.* fully size-structured web) and aquatic and terrestrial food webs should be compared.

It should be noted that the role of detritus cannot be fully appreciated in our model because there are no decomposers and no brown food web. In fact, detritus are more than a transient pool for nutrients since, in real food webs, they are resources for decomposers and are recycled through the whole brown food web (Moore et al., 2004). Another important step will be to include in models a true brown food web containing decomposers feeding on detritus in parallel to the green food webs relying on photosynthesis (Moore et al., 2004; Zou et al., 2016). The interactions between green and brown food webs can deeply change the functioning and the stability of ecosystems (Daufresne and Loreau, 2001; Moore et al., 2005; Attayde and Ripa, 2008; Zou et al., 2016) but these results have so far not been tested in complex realistic food webs.

## Acknowledgement

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## Data accessibility

All data are included in the manuscript and its supporting information. The codes are available on Zenodo and GitHub (doi:[10.5281/zenodo.1143996](https://doi.org/10.5281/zenodo.1143996)).

## A1 Appendix - Parameter calculation

### Allometric parameter calculation

The value of the primary producers growth rate was taken from [Savage et al. \(2004a\)](#) and [Binzer et al. \(2012\)](#):

$$r_i = e^{I_r} M_i^{-1/4} e^{E a_r (T_0 - T / k T T_0)} \quad (1.11)$$

$e^{I_r}$	allometric scaling constant at 20°C ( $g^{1/4} \cdot s^{-1}$ )
$M_i$	body mass ( $g$ )
$e^{E a_r (T_0 - T / k T T_0)}$	temperature dependency term

We considered temperature was constant at 20°C and with  $I_r = -15.68$  ([Binzer et al., 2012](#)) we have:

$$r_i = r M_i^{-1/4} \quad (1.12)$$

With  $r = 0.87 \text{ kg}^{1/4} \cdot \text{year}^{-1}$ . Metabolic rates were taken from [Brose et al. \(2006b\)](#); [Brose \(2008\)](#) with  $x/r = 0.138$  for primary producers,  $x/r = 0.314$  for invertebrates and  $x/r = 0.88$  for ectotherm vertebrates. Since we did not apply the time scale normalisation by the growth rate of primary producers as done in [Brose et al. \(2006b\)](#), we have  $x = 0.12$  for primary producers,  $x = 0.27$  for invertebrates and  $x = 0.78$  for ectotherm vertebrates. For the simulation we used the values for invertebrates for consumers.

### Handling time

In this model, the handling time  $h_{ij}$  also follows an allometric scaling. We used the expression defined by [Petchey et al. \(2008\)](#) and also used by [Thierry et al. \(2011\)](#). The original expression has been divided by the prey body mass to have a mass specific allometric parameter:

$$h_{ij} = \begin{cases} \frac{h_i}{b - \frac{M_j}{M_i}} \frac{1}{M_j} & \text{si } \frac{M_j}{M_i} < b \\ \infty & \text{si } \frac{M_j}{M_i} > b \end{cases} \quad (1.13)$$

$h_i$	allometric scaling constant ( $\text{year} \cdot \text{kg}^{-1}$ )
$b$	maximum prey-predator body mass ratio (0.05)
$M_i$	body mass of the predator ( $\text{kg}$ )
$M_j$	body mass of the prey ( $\text{kg}$ )

The maximum prey-predator body mass ratio  $b$  delimits the diet breadth. If the prey-predator body mass ratio is below  $b$ , the handling time function has a U-shape as shown in Fig.A1-1, otherwise the handling time tends to infinity and the prey is not consumed by the predator. Unfortunately, no value of the allometric scaling constant  $h_i$  could be found in the literature. However, the maximum ingestion rate  $y_i$  is well quantified ([Yodzis and Innes, 1992](#); [Brose et al., 2006b](#); [Vucic-Pestic et al., 2010](#)) and corresponds to the reverse of the handling time. Following [Brose et al. \(2006b\)](#), the ingestion rate is set proportional to the metabolic rate:

$$y_i = y x_i \quad (1.14)$$

With  $y = 8$  for invertebrates and  $y = 4$  for ectotherm vertebrates. Then, we assumed that the values from [Brose et al. \(2006b\)](#), that do not depend on the body mass of the prey, are the average over all possible prey body masses (interval  $[0, bM_i]$  defined in equation 1.13). Thus, we can state that:

$$y_i = \frac{1}{bM_i} \int_0^{bM_i} \frac{1}{h_{ij}} dM_j \quad (1.15)$$

Thus, by replacing  $h_{ij}$  by the expression from equation 1.13:

$$\begin{aligned}
 y_i &= \frac{1}{bM_i} \int_0^{bM_i} \frac{1}{\frac{h_i}{b - \frac{M_j}{M_i}} \frac{1}{M_j}} dM_j \\
 &= \frac{1}{h_i b M_i} \int_0^{bM_i} (b - \frac{M_j}{M_i}) M_j dM_j \\
 &= \frac{1}{h_i b M_i} \left[ \frac{bM_j^2}{2} - \frac{M_j^3}{3M_i} \right]_0^{bM_i} \\
 &= \frac{b^2 M_i}{6h_i}
 \end{aligned} \tag{1.16}$$

Thus:

$$h_i = b^2 M_i / 6y_i \tag{1.17}$$

And by replacing  $h_i$  in equation 1.13 by the expression found in equation 1.17:

$$h_{ij} = \frac{b^2}{6y_i} \frac{M_i}{(b - \frac{M_j}{M_i}) M_j} \tag{1.18}$$

$y_i$  is defined as in equation 1.4a:

$$y_i = y M_i^{-0.25} \tag{1.19}$$

$y$  | allometric scaling constant ( $year.kg^{0.25}$ ) expressed as  $8.x$  (Brose et al., 2006b)  
 $M_i$  | body mass of the organism ( $kg$ )

Handling time is minimum for  $M_j = \frac{b}{2} M_i$ . The value of the maximum prey-predator body mass ratio  $b$  is set to 0.05 so that we have minimum handling time for prey 40 times smaller than predators. This value is consistent with the prey-predator body mass ratio found by Brose et al. (2006a). To limit the number of equations, the interactions involving prey out of the interval  $[0.1bM_i, bM_i]$  were neglected.

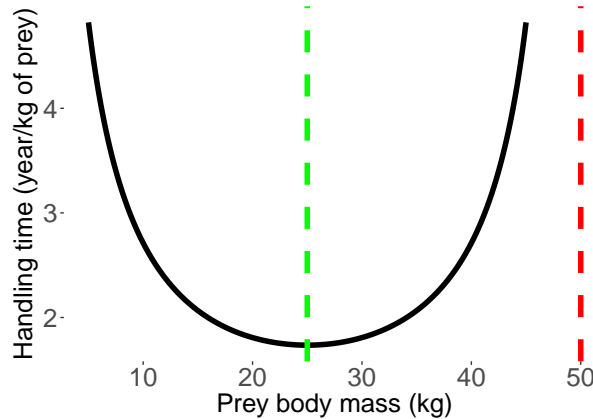


Figure A1-1: Handling time as a function of prey body mass ( $b = 0.05$ ,  $M_i = 1000kg$ ). The red dashed line represents the upper limit of body mass of prey that the predator can handle ( $M_i/M_j < b$ ) and the green dashed line represents the optimal prey body mass minimising the handling time ( $M_j = \frac{b}{2} M_i$ ).

## Stoichiometry and C:N ratios

The limiting nutrients taken into account in our model could be any mineral nutrient but we chose nitrogen to parametrise the carbon to nutrient ratio. The C:N ratio was taken from data of pelagic communities (Anderson, 1992). We took phytoplankton C:N ratio as the C:N ratio of primary producers (6.6) and



for consumers the C:N ratio was set to 5 as the average of C:N ratios of bacteria (5.1), protozoa (5.5) and copepods (4.67). The amount of nutrients released by consumers from non-assimilated prey biomass depends on both the C:N ratio of prey and consumers. The C:N ratio of non-assimilated biomass  $\alpha_{Dij}$  can be calculated by using the constraints on mass conservation and maintenance of species homeostasis (equation 1.9). The ingested biomass by consumer species  $i$  of prey species  $j$  contains a mass  $C_j$  of C and  $N_j$  of nutrient ( $\alpha_j = C_j/N_j$ ). A fraction  $e_{ij}$  of  $C_j$  is converted into a mass  $C_i$  of C of the consumer while the remaining fraction  $1 - e_{ij}$  is converted into a mass  $C_{Dij}$  of detritus. We define  $N_i$  as the assimilated mass of nutrient by the consumer ( $\alpha_i = C_i/N_i$ ), and  $N_{Dij}$  as the non assimilated mass of nutrient excreted to the detritus pool (with  $\alpha_{Dij} = C_{Dij}/N_{Dij}$ ). By law of conservation of mass, we have the two following relations:

$$N_j = N_i + N_{Dij} \quad (1.20a)$$

$$C_j = C_i + C_{Dij} = e_{ij}C_j + (1 - e_{ij})C_j \quad (1.20b)$$

By adding conditions on the maintenance of species homeostasis ( $\alpha_i$  and  $\alpha_j$  are constant), we can then derive the expression of  $\alpha_{Dij}$  as a function of  $e_{ij}$ ,  $\alpha_i$  and  $\alpha_j$ :

$$\begin{aligned} \frac{C_j}{\alpha_j} &= \frac{C_i}{\alpha_i} + \frac{C_{Dij}}{\alpha_{Dij}} \\ \frac{C_j}{\alpha_j} &= \frac{e_{ij}C_j}{\alpha_i} + \frac{(1 - e_{ij})C_j}{\alpha_{Dij}} \\ \frac{1}{\alpha_j} &= \frac{e_{ij}}{\alpha_i} + \frac{1 - e_{ij}}{\alpha_{Dij}} \\ \alpha_{Dij} &= \frac{\alpha_j\alpha_i(1 - e_{ij})}{\alpha_i - \alpha_j e_{ij}} \end{aligned} \quad (1.21)$$

## A2 Appendix - Complementary results

### Complex food webs

#### Overview of the dynamics of the food web

Our complex food web model generates highly variable dynamics at the species level (Fig.A2-1A) while aggregated biomasses are more stable (Fig.A2-1B). The quantity of recycled nutrient by each species is also highly variable while the total quantity of recycled nutrients is less variable (Fig.A2-1C). The total quantity of recycled nutrients is calculated as the sum of the direct recycling and the quantity of nutrients released through decomposition (equation 1.7a) while the quantity of nutrient recycled by each species is estimated by the sum of the direct recycling and the fraction of excreted detritus that will be decomposed ( $d/(d + \ell)$ ). That is why these two measures are not perfectly equal. Nevertheless, we can see that the aggregated quantities of nutrient recycled is more stable than the dynamics at the species level. We also observe that the primary producers and the herbivores are the main contributors to nutrient cycling (Fig.A2-1D) respectively because of their high biomass and their low assimilation efficiency ( $e_{ij} = 0.45$ ). The low contribution of the carnivores can be attributed to their high assimilation efficiency ( $e_{ij} = 0.85$ ) and their low metabolic rate due to their large body mass.

#### Complementary results on species dynamics

As for species persistence in Fig.1.3A, the curves of the CV of species biomass of the C food webs and the SC food webs strongly overlap. Thus, the enrichment effect explains most of the difference between the C food webs and the NC food webs. Average CV of species biomass is either high when food webs have at least two trophic levels, or it is null when the food webs contain only primary producers (Fig.A2-2B and D).

In food webs with nutrient cycling, maximum trophic level follows a hump-shaped relationship with external nutrient input: first there is a sharp increase in food web maximum trophic levels for low nutrient inputs, then a plateau and finally a decrease in food web maximum trophic levels for high nutrient inputs (Fig.A2-2C). However, food webs reach highest values of maximum trophic levels for lower inputs and effects of enrichment are sharper on food web structure for the cases SC and C than for the case NC. In spite of the decrease of persistence with increasing external nutrient inputs, the maximum trophic level remains high (between 3 and 4) in most of the persisting food webs.

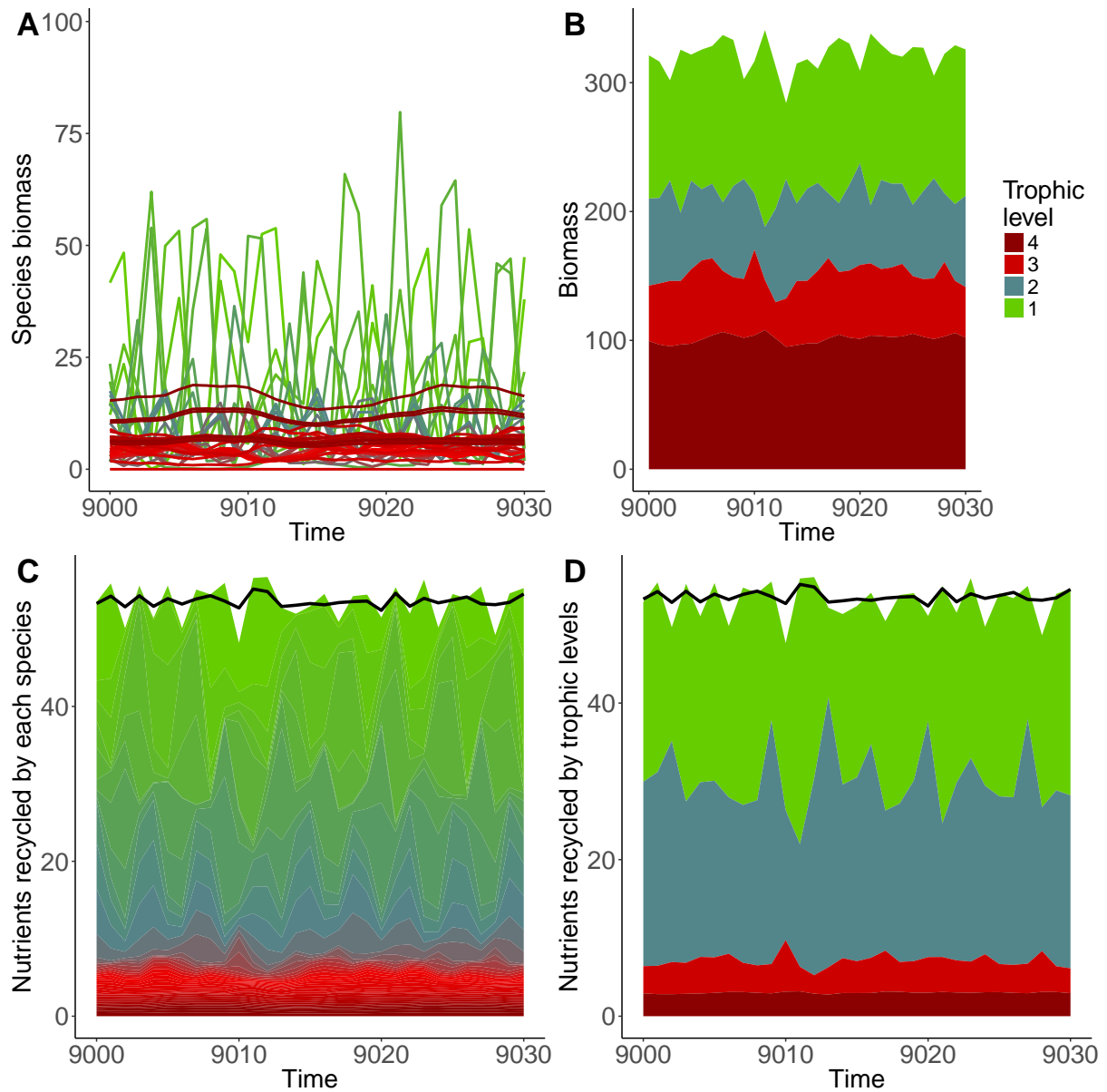


Figure A2-1: Dynamics of species biomasses and nutrients recycled by species in a complex food web ( $I = 40, \delta = 0.2$  and  $d = 0.2$ ). **A)** Species biomasses. Lower trophic levels are in green and higher trophic levels are in red. **B)** Species biomasses aggregated by trophic levels. **C)** Nutrients recycled by each species (coloured areas) and dynamics of the total quantity of recycled nutrients (black line). The difference between the total quantity of recycled nutrients and the sum of the quantities of recycled nutrient by each species is due to the estimation of indirect recycling when detritus are excreted (a proportion  $d/(d + \ell)$  of excreted detritus are expected to be mineralised). **D)** Nutrient recycled by species aggregated by trophic levels and dynamics of the total quantity of recycled nutrients (black line).

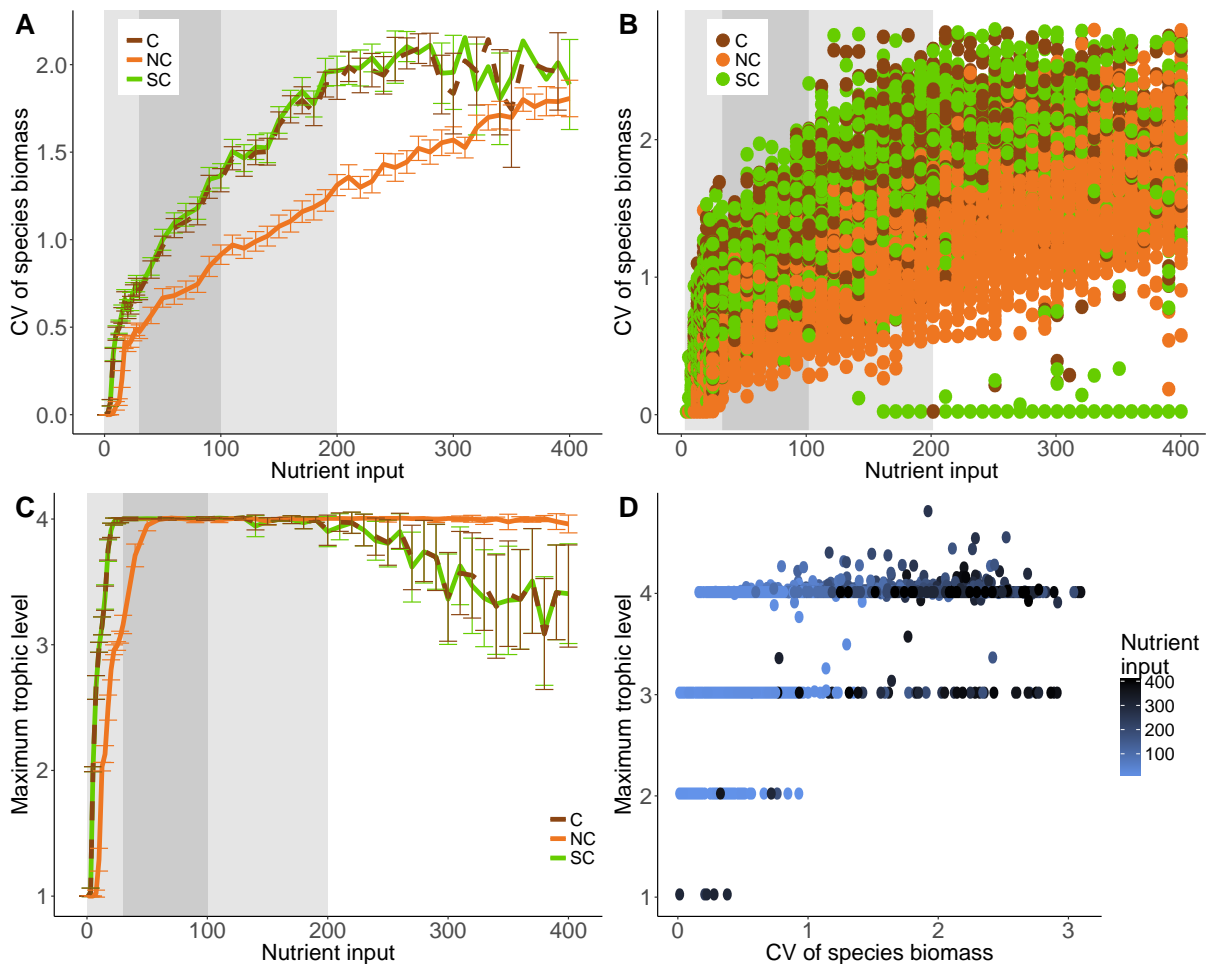


Figure A2-2: **A)** Coefficient of variation of species biomass along an enrichment gradient ( $d = 0.2$  and  $\delta = 0.2$ ). Each point represents the average value of all the species of persistent food webs. The C food webs (brown) are the food webs with nutrient cycling, the NC food webs (orange) are the food webs without nutrient cycling and the SC food webs (green) are the food webs without nutrient cycling but with a simulated enrichment due to nutrient recycling. The lines are the same than in the Fig.1.3C but here, the data from the SC food webs are also represented. **B)** Same data represented at the scale of each food web. Each point represents the average value of all the species of one food webs. **C)** Average maximum trophic level. The trophic level 1 corresponds to primary producers. **D)** Maximum trophic level of each food web as a function of the average coefficient of variation of biomasses. The colour scale represents the nutrient enrichment gradient.

### Response of nutrient stocks and flows to nutrient enrichment

The quantity of recycled nutrients increases linearly with increasing external nutrient input  $I$  (Fig.1.3A and Fig.A2-3A). This increase is higher in food webs with a low maximal trophic level, resulting in higher quantity of recycled nutrients in food webs with only primary producers at high nutrient inputs. Such larger increase of nutrient cycling for primary producers dominated food webs might be related to the fact that the biomass of primary producers is negatively correlated with the biomass of consumers (Fig.A2-3B). While primary production and detritus pool both follow the same trend than the quantity of recycled nutrients and increase linearly with increasing external nutrient input, total biomass and secondary production saturate at high input levels (Fig.A2-3 and A2-4). The increase of quantity of recycled nutrients is thus correlated to the increase of the total biomass at low external nutrient input, while it is not at high external input (Fig.A2-3D). The mineral nutrient stock remains very low and its response to nutrient enrichment is similar to the response of the total biomass (Fig.A2-4B). The density dependant mortality rate (that is quadratic function of the biomass) of primary producers strongly increases (Fig.A2-4D) with the increasing nutrient input which might at least partly explains the linear

increase of production of detritus while the total biomass weakly increases.

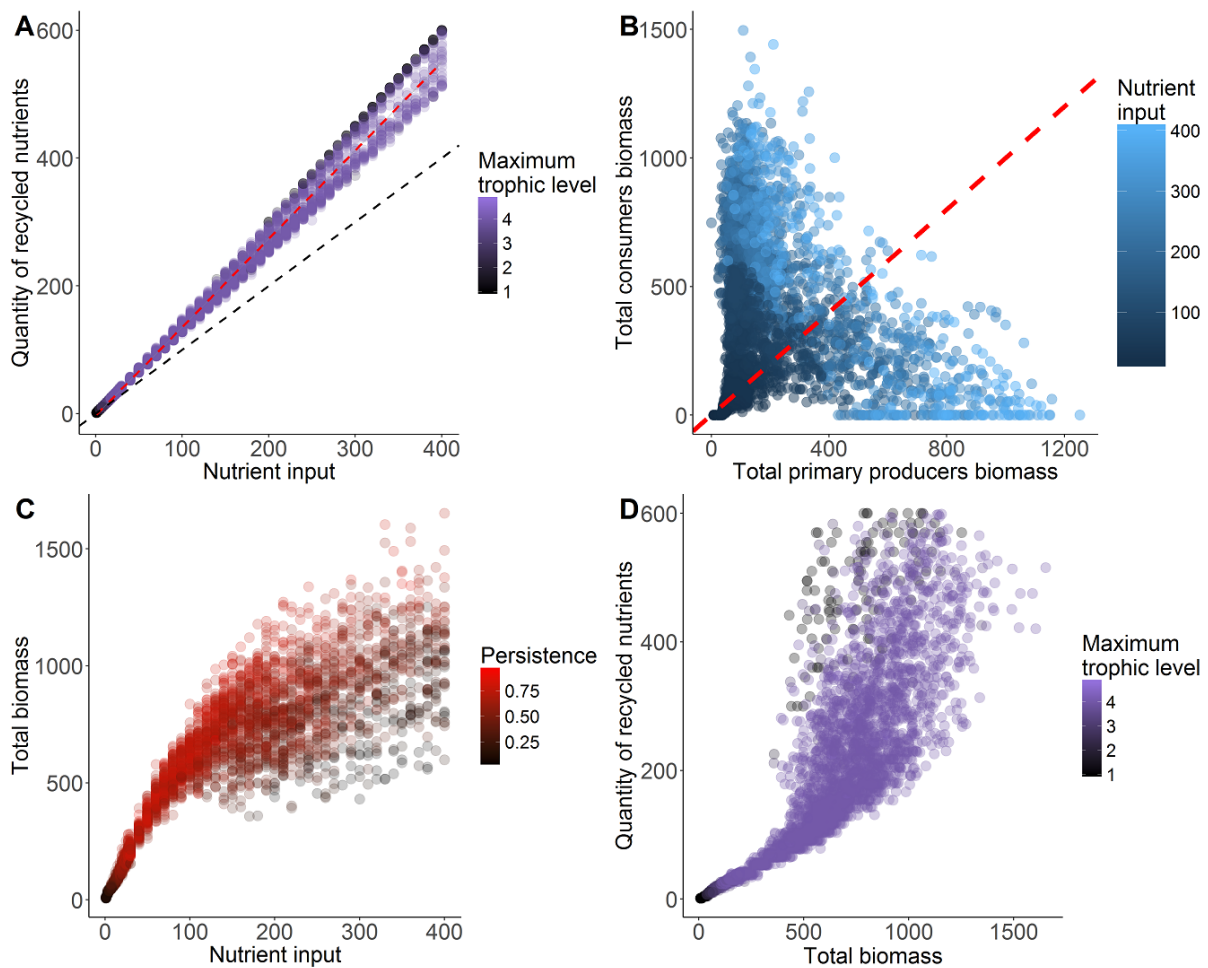


Figure A2-3: Response of the quantity recycled nutrients and of the total biomass to nutrient enrichment. **A)** Response of the total quantity of recycled nutrients to the external nutrient input  $I$ . The red dashed line represents the average and the black dashed line the bisector (quantity of recycled nutrients equal to the external input). The colour scale represents the maximum trophic level. **B)** Total consumers biomass versus the total primary producers biomass for different nutrient inputs (colour scale). The red dashed line is the bisector separating the food webs dominated by consumers from the food web dominated by primary producers. **C)** Response of the total biomass to the external nutrient input  $I$ . The colour scale represents the species persistence. **D)** Total quantity of recycled nutrients versus the total biomass. The colour scale represents the maximum trophic level.

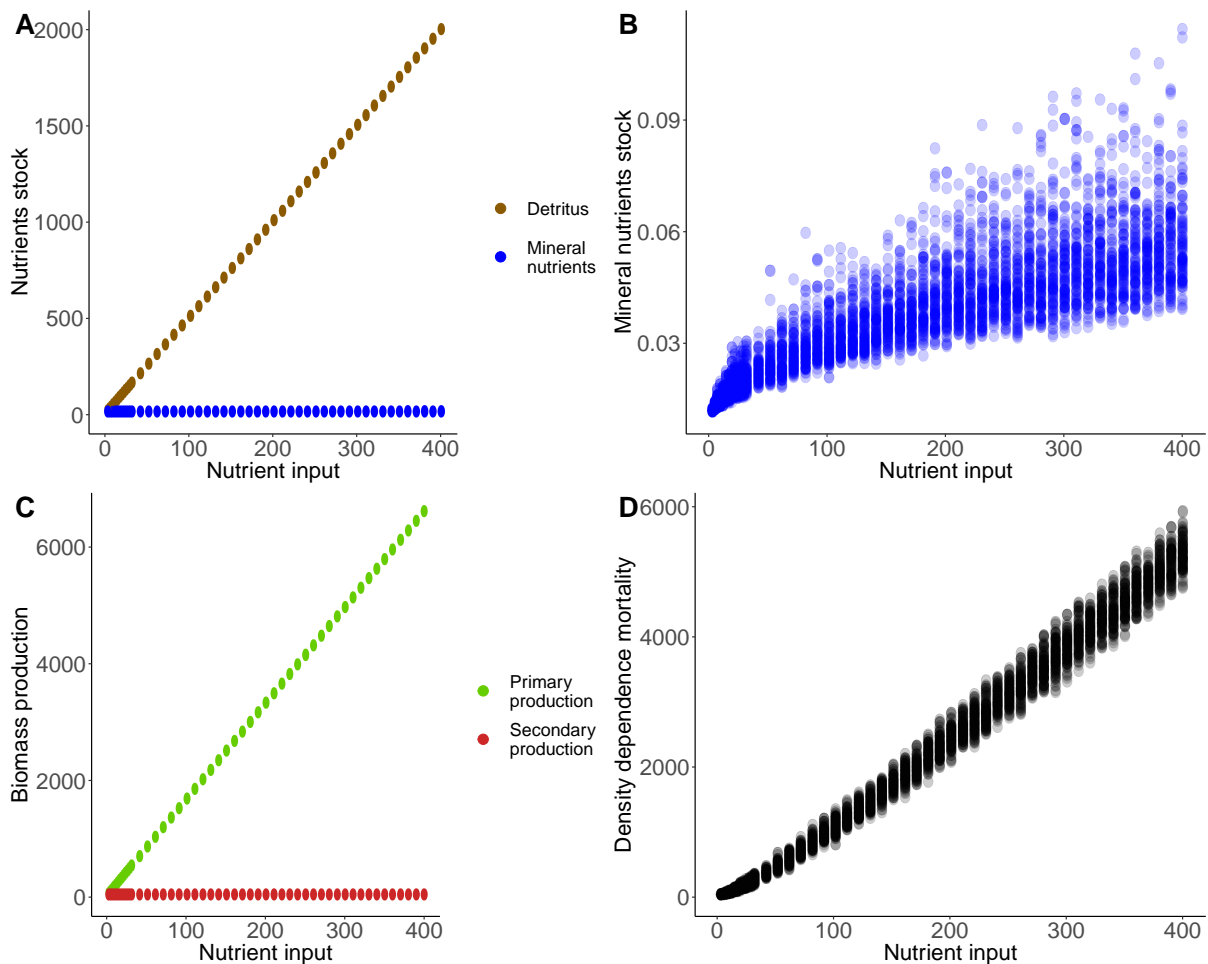


Figure A2-4: Response of nutrient stocks and nutrient flows to nutrient enrichment. **A)** Detritus and mineral nutrient stocks along a nutrient enrichment gradient. Data from 96 food webs containing only five primary producers. **B)** Mineral nutrient stock along a nutrient enrichment gradient. Data from 96 food webs containing only five primary producers. **C)** Primary and secondary productions along a nutrient enrichment gradient. **D)** Density dependent mortality rate of primary producers along a nutrient enrichment gradient. Data from 96 food webs containing only five primary producers.

#### Additional effects of the decomposition rate and of the fraction of direct recycling

The effects of the decomposition rate  $d$  and the fraction of directly recycled nutrients  $\delta$  on maximum trophic level are also similar to the effects on persistence (Fig.1.4A): at  $I = 10$ , increasing  $d$  and  $\delta$  increases the maximum trophic level (Fig.A2-5A). At  $I = 40$ , the two decomposition parameters first increase and then weakly decrease maximum trophic level.

Increasing  $d$  and  $\delta$  always increases the quantity of recycled nutrients by accelerating nutrient recycling and thus reducing the residence time of nutrients in the detritus compartment where they can be lost (A2-5B) (a fraction  $d/(d + \ell)$  of nutrients in the detritus pool is recycled). The decrease of the quantity of recycled nutrients for  $d$  and  $\delta$  close to 1 is due to the drop of species persistence seen in Fig.1.4A. Increasing  $d$  and  $\delta$  increases the CV of the quantity of recycled nutrients (Fig.A2-5C). This response is similar to the response of the CV of species biomasses (Fig.1.4B) as nutrient cycling directly depends on species biomass. The reduced CV of the quantity of recycled nutrients compared to the CV of species biomasses observed in Fig.1.3C is also verified for each combination of  $d$  and  $\delta$ .

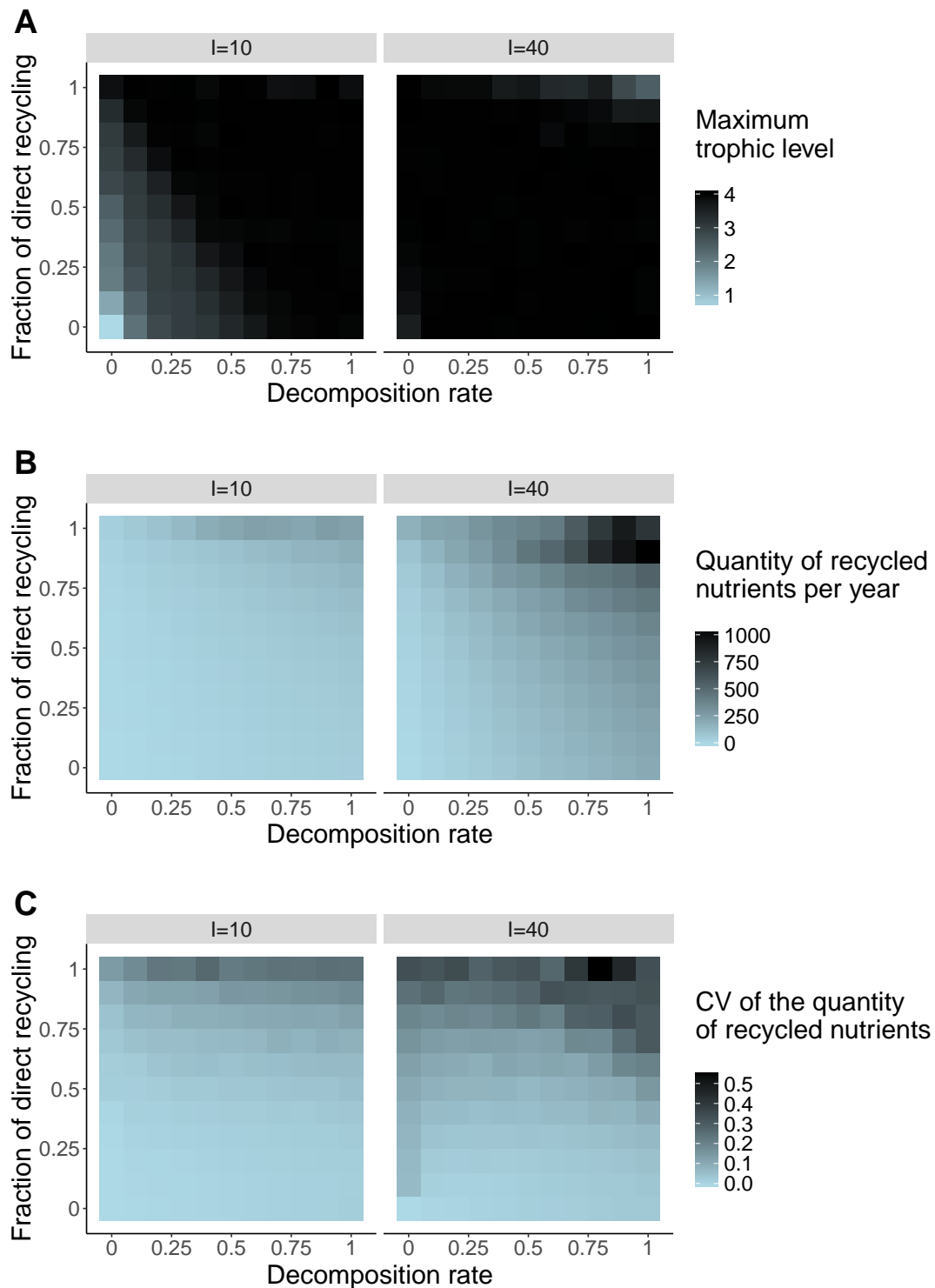


Figure A2-5: Effect of the recycling parameters  $d$  (detritus decomposition rate) and  $\delta$  (fraction of direct recycling) on **A**) maximum trophic level, **B**) quantity of recycled nutrients and **C**) CV of the quantity of recycled nutrients for  $I = 10$  and  $I = 40$ . Each square represents the average value for persistent food webs only (*i.e.* food webs where at least one species persists). A few points for  $\delta = 1$  have been removed in **B**) because the quantity of recycled nutrients was 100 times higher in a few simulations where primary producers dominate the ecosystem and recycle most of the nutrients.

### Comparison between species biomass CV in C and SC models

When external nutrient input  $I$  is lower than  $300 \text{ kg.v}^{-1}.\text{year}^{-1}$ , nearly half of the species have a lower biomass CV in the C food web than in the SC food web (Fig.A2-6A). A quarter of species have a higher

CV and another quarter of species have a CV that does not change slightly between the C and the SC food webs. Nutrient cycling changes the survival of very few species (lethal and vital classes). Thus, the feedback loop is mostly stabilising but has a negligible effect for high external nutrient inputs. Effects of the presence of recycling loops also depend on the trophic level considered (Fig.A2-6B). Primary producers are mostly unaffected by recycling feedback loops and the proportions of stabilised or destabilised species are similar. The other trophic levels respond as described in the Fig.A2-6A. In addition, the proportion of unaffected species decreases when the trophic level increases. The highest trophic levels are the most affected by recycling loops while primary producers remain mostly unaffected.

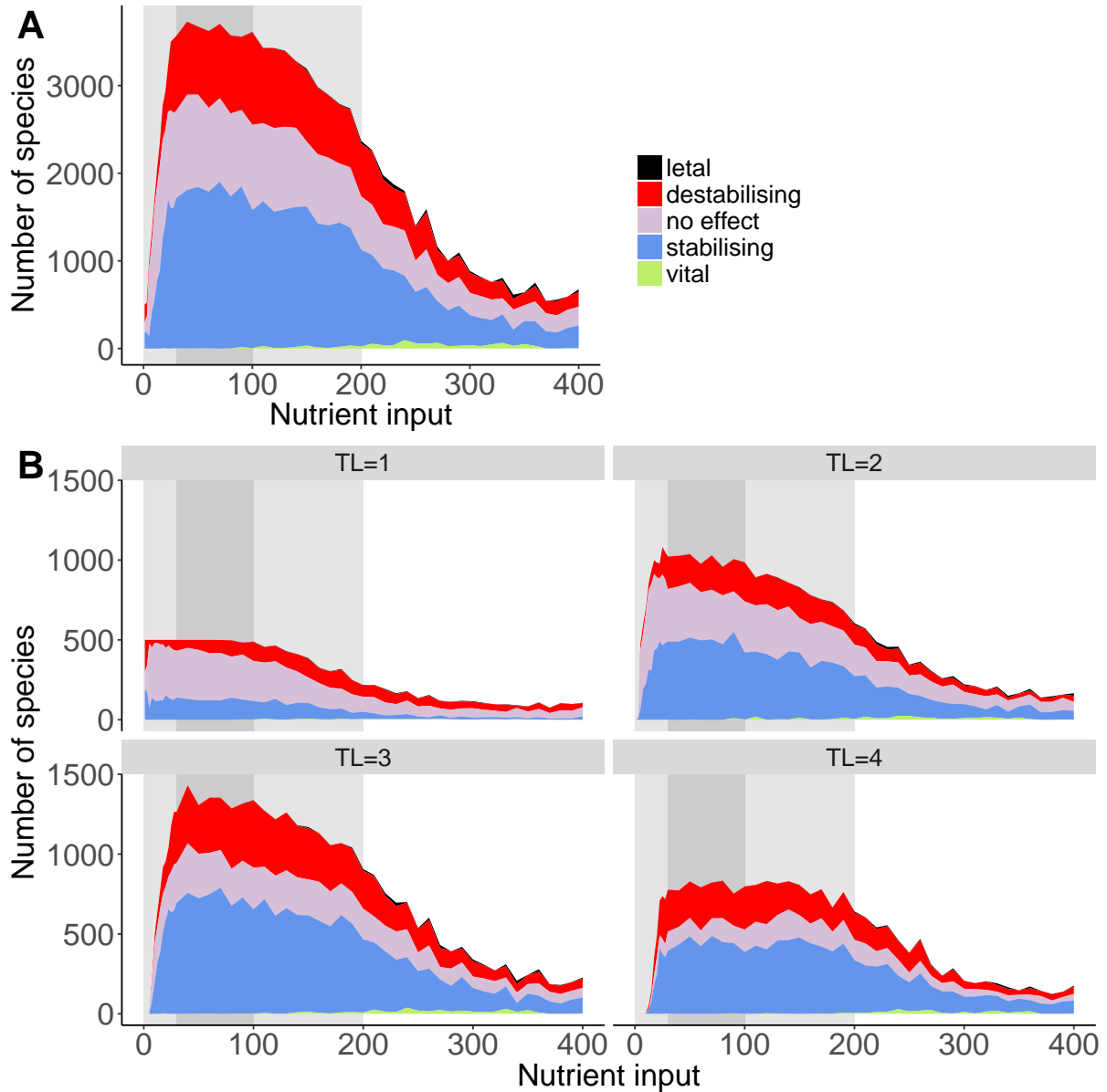


Figure A2-6: Effects of recycling feedback loops on the individual CV of biomasses of each species. These effects are assessed through the comparison of the C and SC models over the 1000 last years of the simulations. **A**) Number of species (among the 100 replicated food webs) whose CV of biomass increases (*i.e.* experiencing a destabilisation, red area) or decreases (*i.e.* experiencing a stabilisation, blue area) when the food web has recycling feedback loops. The no effect area (in purple) represents the species whose log linearised CV does not varies more than  $\pm 0.01$ . The lethal area (black) represents the species going extinct in the C food web but surviving in the SC food web. The vital area (green) is the opposite. **B**) Same data separated for each trophic level (TL=1 for the primary producer and TL=4 for the top predator). The species with a trophic level in the interval  $[n, n + 1[$  are assigned to the "TL= $n$ " category.



### Tri-trophic food chain

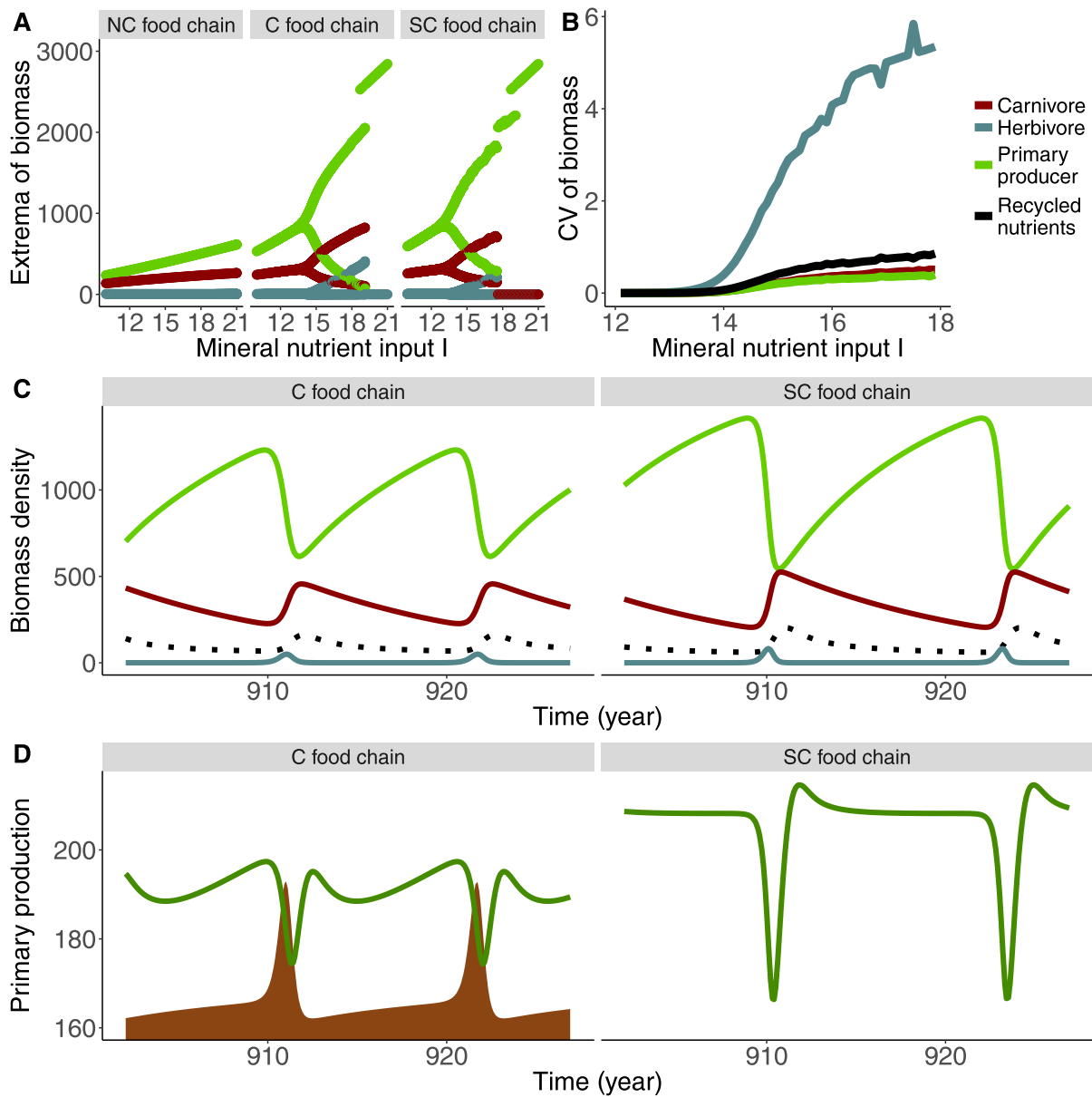


Figure A2-7: Effect of nutrient cycling in a tri-trophic food chain. **A**) Diagram of bifurcation of species biomasses (minima and maxima of biomass in dynamics) along a nutrient enrichment gradient. Three cases are represented: a case without nutrient cycling (NC food chain), a case with nutrient cycling (C food chain) and a case without nutrient cycling but with a simulated enrichment effect (SC food chain). **B**) CV of biomass of the three species and of the quantity of recycled nutrients along the enrichment gradient. **C**) Dynamics of the biomass of each trophic level and of mineral nutrients (multiplied by 30 for more readability) in the C food chain and the SC food chain. **D**) Dynamics of the primary production (green line) and of the total quantity of recycled nutrients (brown area) in the C food chain and the SC food chain. The parameters are:  $I = 15$ ,  $\delta = 0.2$  and  $d = 0.2$ .

Fig.A2-7A highlights the enrichment effect of nutrient cycling in the food chain model (comparison between the dynamics in the cases NC and C). CV of the quantity of recycled nutrients is in the same order of magnitude than the CVs of species biomasses (Fig.A2-7B). The dynamics of species biomass and nutrient stock are qualitatively similar in both C and SC food chains (Fig.A2-7C) but the amplitude of the oscillations is larger in the SC food web and variations of biomass are also sharper. This confirms the higher CV of species biomass in the SC food web observed in Fig.1.5B. The outbreak of herbivores strongly decreases primary producers biomass but it also creates a burst of recycled nutrients due to the

low assimilation efficiency of biomass by herbivores (Fig.A2-7D). This burst of recycled nutrients limits the loss of productivity compared to the SC food chain and thus dampens the negative top down effect of herbivores on primary producers. Otherwise, the quantity of recycled nutrient is low and limits primary production when primary producers thrive. These effects lead to a decrease of the growth to death ratio of each species (Fig.A2-8) and thus stabilise their dynamics.

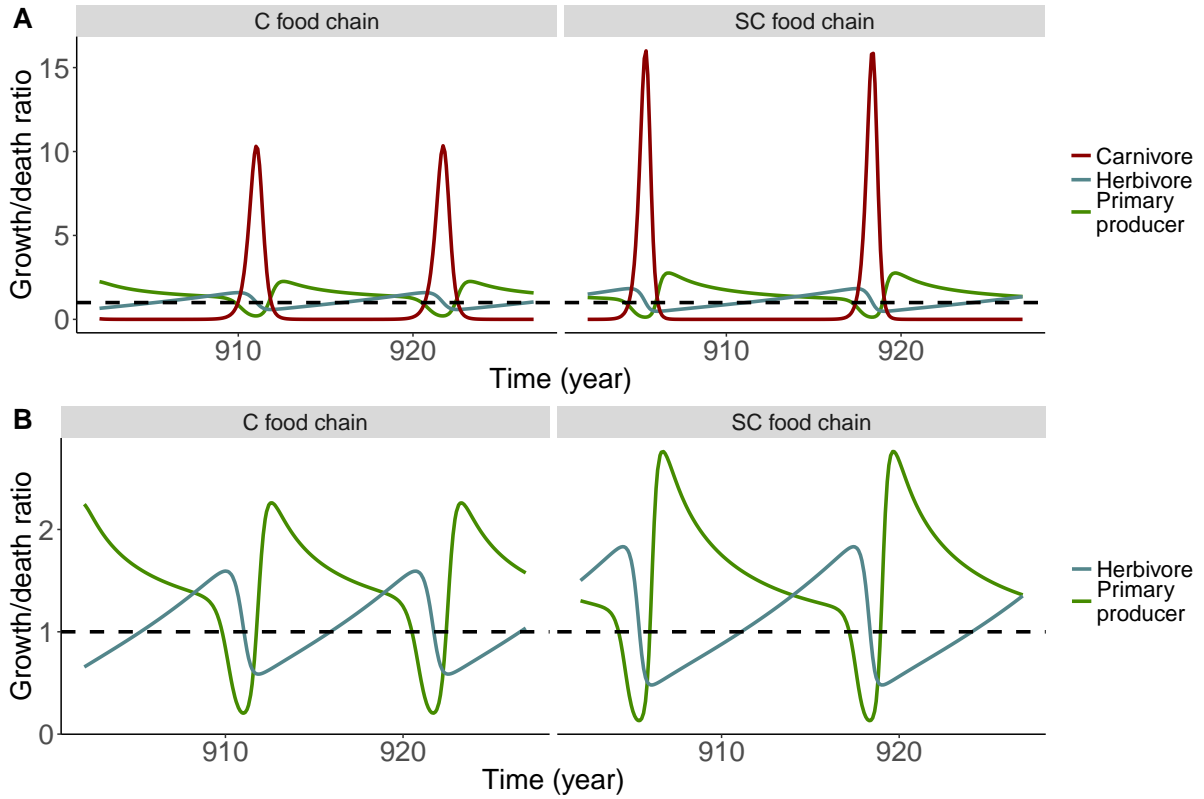


Figure A2-8: Effect of nutrient cycling on the dynamics of growth/death ratios of species in the C food chain and the SC food chain. The dashed black line corresponds to a ratio equal to 1 and thus to balanced growth and death rates. **A)** Representation for all trophic levels. **B)** Representation for the primary producer and the herbivore only. The parameters are:  $I = 15$ ,  $\delta = 0.2$  and  $d = 0.2$ .

### A3 Appendix - Sensitivity analysis

#### Effects of values of attack rate, intraspecific competition, nutrient loss rate and half saturation of nutrient uptake on persistence and stability

The species persistence in the food web is maximised only for a restricted combinations of values of the attack rate  $a$  and the intraspecific competition coefficient  $\beta$  (Fig.A3-1A). In fact, if  $a$  is high and  $\beta$  low, the consumers strongly exploit their prey and weakly self regulate, leading to the extinction of their prey. The reverse case leads to the extinction of consumers that cannot eat enough to compensate the loss of biomass due to a strong self regulation. The response of the CV of species biomasses to  $a$  and  $\beta$  is qualitatively similar to the response of species persistence (Fig.A3-1B) but occurs for smaller values of  $\beta$ .  $\beta$  strongly dampens species biomass oscillations and a large part of the parameter space leads to food webs with very low average CV of species biomass. Therefore, we chose  $a$  and  $\beta$  to maximise species persistence but with a minimal  $\beta$ . Indeed, a high  $\beta$  strongly stabilise species dynamics and might obscure potential effects of nutrient cycling on stability.

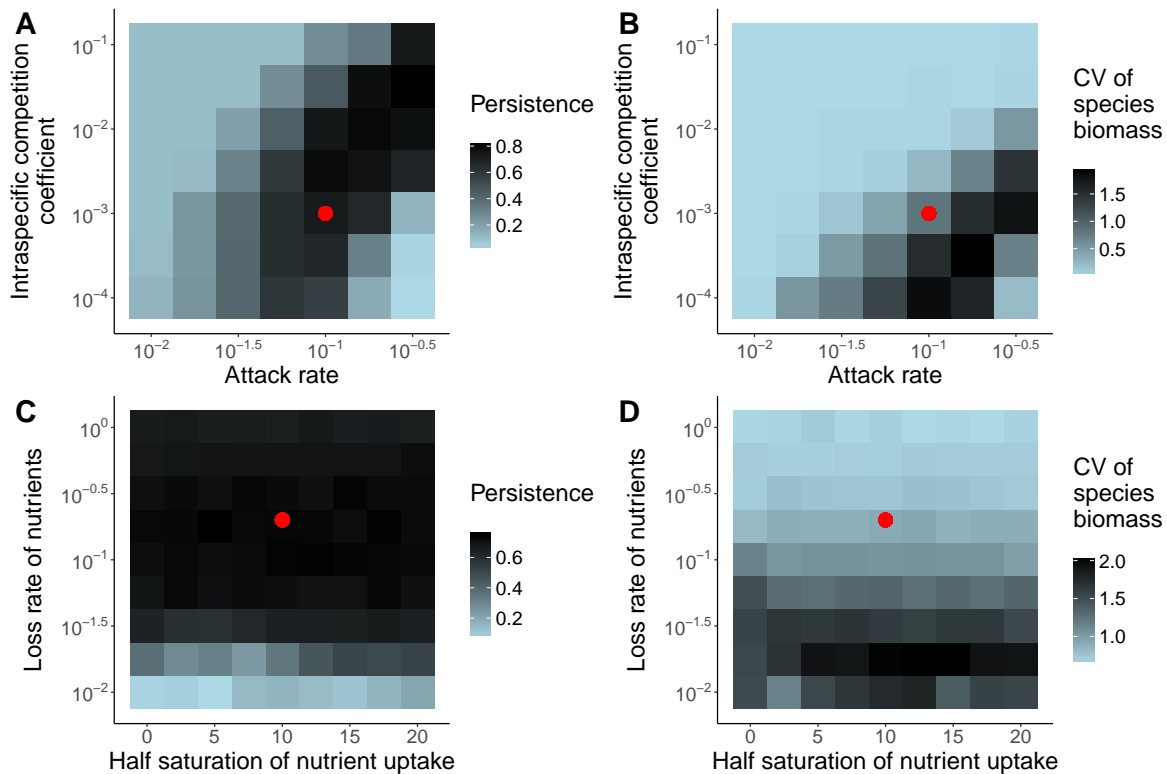


Figure A3-1: Effects of the attack rate  $a$  and the intraspecific competition coefficient  $\beta$  on **A**) persistence and **B**) CV of species biomass. Effects of the half saturation of nutrient uptake  $K$  and the loss rate of mineral nutrients and detritus  $\ell$  on **C**) persistence and **D**) CV of species biomass. Each square is the average of 100 simulated food webs (except for **B**) and **D**) where only data from persistent food webs are represented). The mineral nutrient input is  $I = 40$ , the fraction of direct recycling is  $\delta = 0.2$  and the decomposition rate of detritus  $d = 0.2$ . The red dots represent the combinations of parameters used in the simulations ( $a = 0.1$  and  $\beta = 0.001$  in A and B,  $K = 10$  and  $\ell = 0.2$  in C and D).

The decrease of species persistence with the decrease of the loss rate  $\ell$  in Fig.A3-1C is due to the enrichment caused by the accumulation of nutrients. In fact, decreasing  $\ell$  for a constant nutrient input  $I$  increases the availability of mineral nutrients and is equivalent to an increase of nutrients inputs. The CV of species biomasses (Fig.A3-1D) first increases with  $\ell$  and then decreases. On the contrary, the half saturation of nutrient uptake  $K$  only slightly affects the persistence and the CV of species biomasses when compared to  $\ell$ . For  $\ell$  higher than  $10^{-1.25}$  ( $\sim 0.05$ , corresponding to a loss of 5% of the nutrient

stock), changing  $\ell$  and  $K$  do not change species persistence and the CV of species biomasses. Then, we arbitrary set  $\ell$  and  $K$  to have a maximum species persistence for  $I \simeq 50$ .

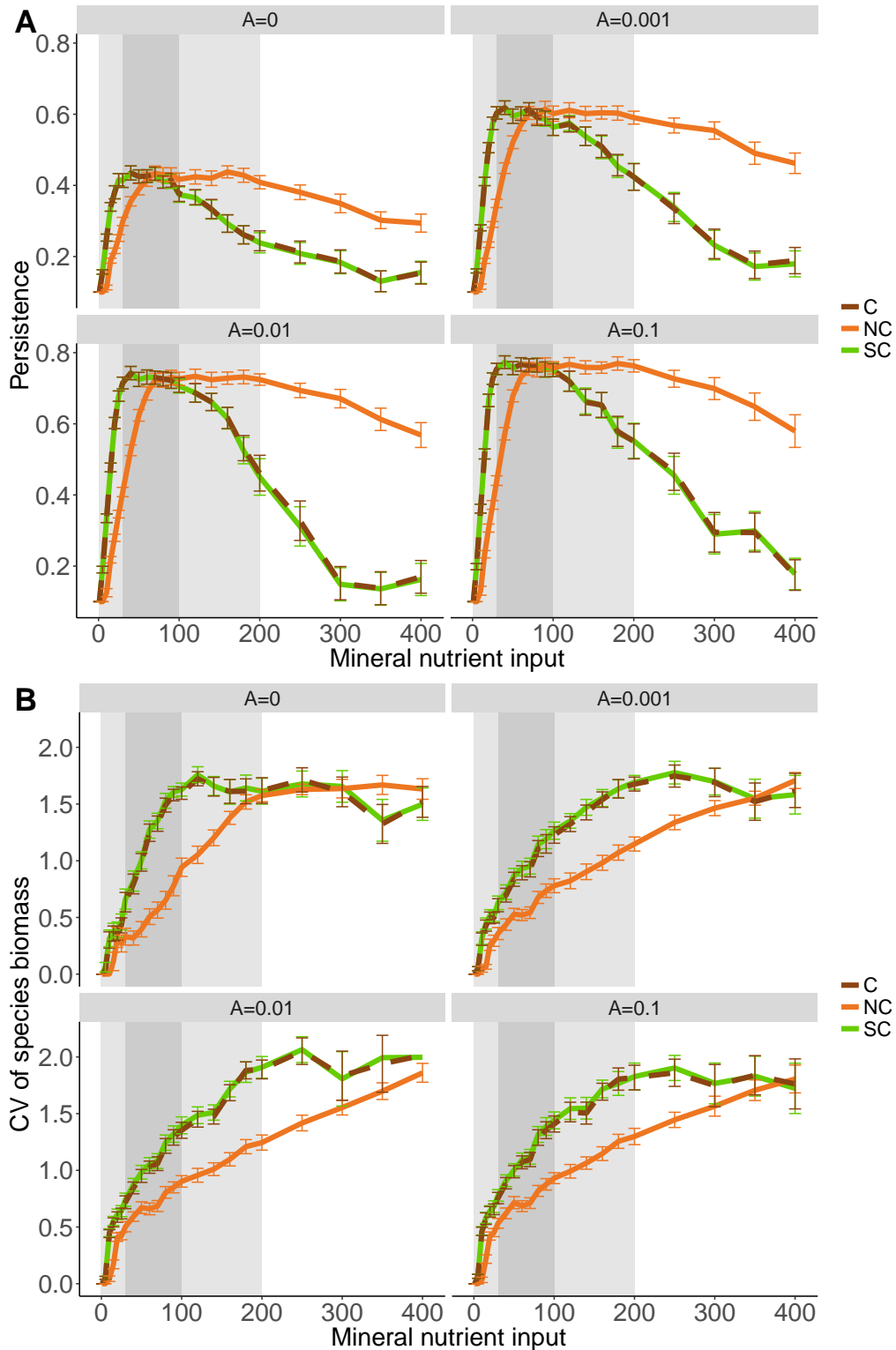


Figure A3-2: Effects of the adaptive rate  $A$  of the adaptive foraging on **A)** species persistence and on **B)** the coefficient of variation of species biomasses along a nutrient enrichment gradient. The brown curve represents the C food webs with nutrient cycling ( $\delta = 0.2$ ,  $d = 0.2$ ), the orange curve represents the NC food webs without nutrient cycling and the green curve represents the SC food webs without nutrient cycling but with a mineral nutrient input simulating the enrichment effect of nutrient cycling assessed in the C food web. The graph with  $A = 0.01$  corresponds to the graph in Fig.1.3A.

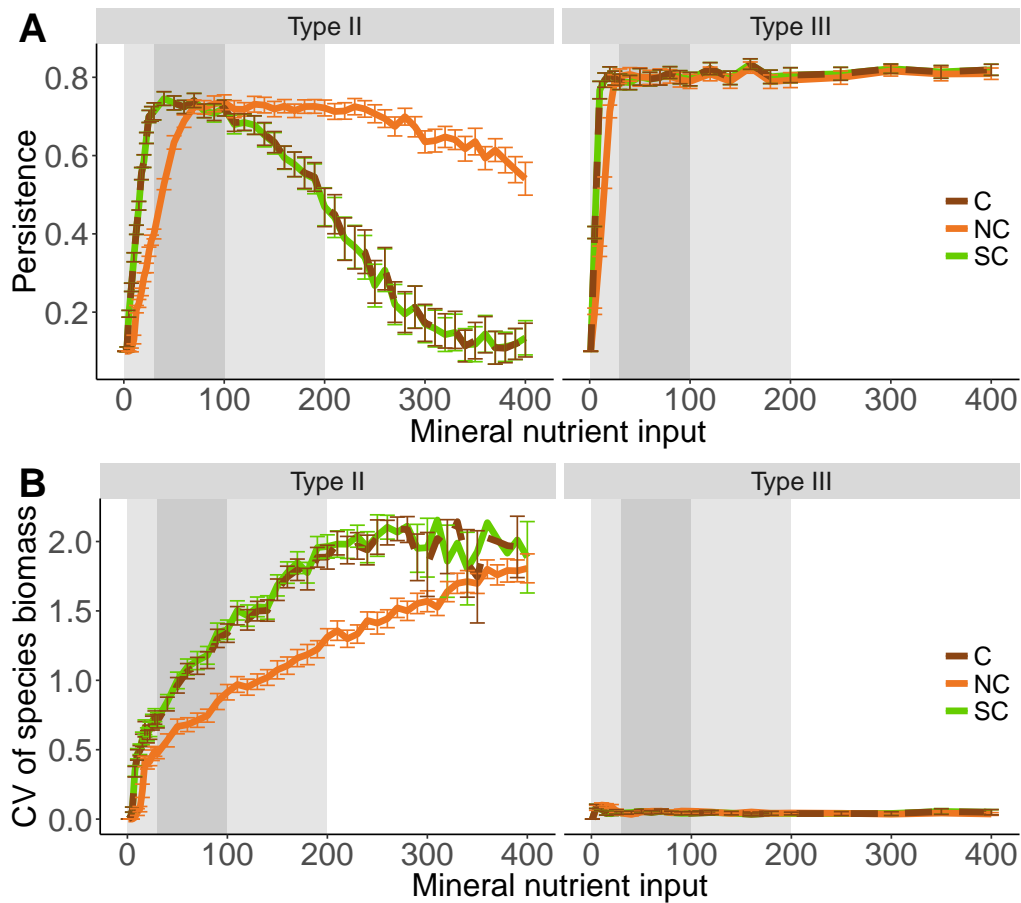


Figure A3-3: Effects of the functional response on **A**) species persistence and on **B**) the coefficient of variation of species biomasses along a nutrient enrichment gradient. The brown curve represents the C food webs with nutrient cycling ( $\delta = 0.2$ ,  $d = 0.2$ ), the orange curve represents the NC food webs without nutrient cycling and the green curve represents the SC food webs without nutrient recycling but with a mineral nutrient input simulating the enrichment effect of nutrient cycling of the C food web. The type II functional response was used in the study.

### Sensitivity of the results to the value of adaptive foraging rate

We included adaptive foraging in our model as a mechanism promoting species persistence. Increasing the adaptive rate  $A$  increases species persistence in Fig.A3-2A, as demonstrated by Kondoh (2003); Heckmann et al. (2012), while the qualitative response of food web persistence to increased nutrient input remains unchanged (*i.e.* maximum of persistence occurring for the same values of nutrient input  $I$ ). The CV of species biomasses (Fig.A3-2B) increases more sharply without adaptive foraging but the general response to nutrient enrichment remains also qualitatively very similar for varying value of adaptive rate. In conclusion, our main results remain virtually unchanged when the rate of adaptive foraging is changed and we chose  $A = 0.01$  as it promotes a high species persistence (higher values of adaptive rate only slightly increase species persistence).

### Sensitivity of the results to the type of functional response

The type II functional response leads to a decrease of species persistence at high nutrient inputs while species persistence stays maximum in food webs with a type III functional response (Fig.A3-3A). In addition, the CV of species biomasses is much lower in food webs with a type III functional response compared to food webs with a type II functional response. Thus, we do not observe a paradox of enrichment with a type III functional response in our model. This is consistent with Rall et al. (2008). However, we still observe a sharper increase of species persistence in the food webs with a type II

functional response and a maximum of persistence reached for lower mineral nutrient input  $I$ , as found for food webs with a type II functional response. We also still observe that the curves of the C and SC food webs strongly overlap. The major enrichment effect of nutrient cycling and its preponderance compared to the weak stabilising effect of the positive feedback loop is thus robust to the type of functional response.

## Chapter 2

# Linking green and brown food webs: does this wedding bring stability to both partners?

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### Key words

Detritus, mineral nutrients, generalist predator, nutrient enrichment, stoichiometry, decomposer

### Abstract

Ecosystems rely on the green food web to produce biomass from mineral nutrients and on the brown food web to recycle these nutrients contained in dead organic matter. However, complex food web models have mainly focused on green food webs and largely ignored the brown food web. The interactions between green and brown food webs can be mutualistic because of their synergistic functions in the ecosystem. However, these can have competitive interactions because decomposers also take up mineral nutrients depending on the stoichiometry of detritus to keep a constant carbon to nutrient ratio. In addition, interweb generalist consumers can eat species from both green and brown food webs and create a top-down coupling between the two food webs. Here, we assess the stability of an allometric and size structured model coupling both green and brown food webs along a nutrient enrichment gradient. We found that the brown food web is responsible of most of the biomass production at low nutrient inputs, promoting consumer persistence whereas, at higher nutrient inputs, primary production increases more than decomposers production and the food web mainly relies on green production. Decomposers are generally more destabilised than primary producers by nutrient enrichment, which might be related to the large increase of the detritus stock along the nutrient enrichment gradient. Interweb generalism, the

ability of consumers to eat prey from both green and brown food webs, promotes consumer persistence probably because of the increased number of available prey, but it also has a destabilising effect on decomposers. Our model merging population dynamics models and ecosystem functioning provides a promising framework to better understand the response of ecosystems to environmental changes such as nutrient enrichment.

## Introduction

Food webs are not just networks linking species through trophic interaction, they also link species to abiotic compartments through interactions that are critical in ecosystem functioning [Lindeman \(1942\)](#). Mineral nutrients such as nitrogen or phosphorus are taken up by primary producers that produce biomass by photosynthesis and sustain the green food web. A fraction of the primary production returns to the environment as dead organic matter and forms the detritus compartment. Decomposers consume detritus and sustain the brown food web that recycles the nutrients contained in the dead organic matter ([Polis and Strong, 1996](#); [Moore et al., 2004](#); [Olf et al., 2009](#)). In spite of its critical role in ecosystem functioning, the brown food web has been largely ignored by complex food web models that focused on green food webs.

Complex food web models are now extensively used to study dynamics and stability of species communities ([Brose et al., 2006b](#); [Brose, 2008](#); [Heckmann et al., 2012](#)). These models based on the allometric scaling of biological rates ([Yodzis and Innes, 1992](#); [Brown et al., 2004b](#)) have been successful in reproducing the dynamics of natural communities ([Boit et al., 2012](#); [Hudson and Reuman, 2013](#)). However, these studies largely focused on population dynamics and forgot abiotic compartments such as mineral nutrients or detritus that are central in ecosystem functioning ([Moore et al., 2004](#)). A few recent studies have started to integrate the dynamics of abiotic compartments into allometric food web modelling. [Wang and Brose \(2017\)](#) showed that food web vertical diversity increases nutrient uptake by primary producers and [Quévreux et al. \(2018\)](#) highlighted the consequences of nutrient cycling on food web stability. In spite of these efforts to integrate ecosystem functioning to food web models, considering the brown food web is critical to fully understand nutrient cycling and the dynamics of abiotic compartments.

Green and brown food webs are coupled by bottom-up and top-down interactions. Since primary producers produce detritus consumed by decomposers and decomposers recycle nutrients that become available for primary producers are involved in a mutualistic interactions ([Harte and Kinzig, 1993](#)). For instance, [Danger et al. \(2007b\)](#) observed that axenic algae cultures were nitrogen limited because of the absence of bacteria recycling the nitrogen contained in detritus. However, decomposers can also take up mineral nutrients ([Kirchman, 1994](#)) if the carbon to nutrient ratio (C:N) of detritus is too high compared to the C:N of decomposers, leading to competitive interactions ([Rhee, 1972](#); [Daufresne and Loreau, 2001](#); [Joint et al., 2002](#); [Danger et al., 2007b](#); [Daufresne et al., 2008](#)). Generalist consumers eating prey from both green and brown food webs, defined here as interweb generalists, generate a top-down coupling between green and brown food web affecting the propagation of cascading effects ([Attayde and Ripa, 2008](#); [Wollrab et al., 2012](#)).

The bottom-up coupling of green and brown food webs has been extensively studied in simple phytoplankton-bacteria systems. In these systems, the stoichiometry of primary producers and detritus is critical as it determines the limitation of decomposers by carbon or mineral nutrients and therefore competition between primary producers and decomposers. [Daufresne and Loreau \(2001\)](#) showed in their model that primary producers and decomposers can only coexist if decomposers are limited by carbon. Experimentally, [Daufresne et al. \(2008\)](#) proved that in simple algae-bacteria systems in microcosms, microbial communities always become co-limited by carbon and nutrients. Nutrient enrichment and nutrient recy-



cling efficiency can also affect this bottom-up coupling by modifying mineral nutrient availability (Danger et al., 2007a). The impact of nutrient cycling on nutrient availability strongly affects food web stability and ecosystem functioning (Loreau, 2010; McCann, 2011). Nutrient cycling decreases the resilience (*i.e.* destabilisation) of simple food chain models (DeAngelis, 1980, 1992) while it decreases the coefficient of variation (*i.e.* stabilisation) of species biomass in a tri-trophic food chain (Quévrex et al., 2018). Nutrient cycling affects the stability of complex food web models mostly through an increased mineral nutrient availability that promotes the paradox of enrichment (Quévrex et al., 2018). In a complex food web model with a green and a brown food web, we could expect contrasting effects of mineral nutrient availability as organism excretion is partitioned among the mineral pool and the detritus pool. Because detritus must be mineralised by decomposers before their mineral nutrients become available to primary producers, these two recycling paths are respectively called direct and indirect recycling (Zou et al., 2016). Thus, increasing indirect recycling would increase resource availability for decomposers and reduce nutrient availability for primary producers as nutrient would be sequestered in detritus. Depending on the fraction of direct recycling, increasing nutrient inputs are expected to affect more the green or the brown food web stability, with overall similar effects on species persistence and species biomass CV as found by Quévrex et al. (2018).

Interweb generalism is ubiquitous among ecosystems (Vadeboncoeur et al., 2005; Wolkovich et al., 2014; Koltz et al., 2017). Many studies focused on the effect of generalist top predators on simple parallel food chain (Post et al., 2000; McCann et al., 2005; Rooney et al., 2006) or coupled green and brown food chains (Attayde and Ripa, 2008; Blanchard et al., 2011). They mainly found that interweb generalism has a positive effect on predator survival and biomass as they have access to a large variety of prey. They also found stabilising effects (increase of resilience) of interweb generalism as generalist consumers couple food chains with different biomass turnover. However, consumers have contrasting cascading effects depending on food chain length in each food chain (Wollrab et al., 2012) but so far their impacts on complex food webs is not clear. Interweb generalism is also likely to interact with nutrient enrichment. Attayde and Ripa (2008) showed that in green and brown food chains coupled by a generalist carnivore, nutrient enrichment has a positive effect on primary producer biomass and increases the size of the detritus stock. Wollrab et al. (2012) also showed that depending on the food chain length of green and brown chains coupled by a generalist top predator, nutrient enrichment could have similar or opposite effects on primary producers and detritus stocks. As nutrient enrichment has a negative effect on top-predators (Binzer et al., 2011; Quévrex et al., 2018), generalist consumer must benefit from the differential response of green and brown food webs to enrichment if one of them is less sensitive to enrichment.

To explore these aspects of the interactions between green and brown food webs, we modified our previous size structured food web model based on allometric parametrisation (Quévrex et al., 2018) by adding decomposers consuming detritus. Interweb generalism was tested by considering either food webs with totally separated green and brown food webs (*i.e.* consumers only eating prey from their own food web) or food webs where consumers were generalist (*i.e.* consumers eating prey from the green or the brown food web without distinction). We tested the response of these food webs along an enrichment gradient for two contrasting fraction of direct recycling to study the response of the green and the brown food webs to resource availability. We ask the following questions: does nutrient enrichment and the fraction of direct recycling affect in the same way the stability of the green and the brown food web? How the potential differences in their response affects the stability of the whole food web? How interweb generalism alters the response of the green and the brown food webs to nutrient enrichment?

## Material and methods

### General description of the model

Our ecosystem model extends the model of [Quévreur et al. \(2018\)](#) as it integrates a green food web based on primary producers and a brown food web ensuring detritus decomposition (Fig.2.1). As in [Quévreur et al. \(2018\)](#), the abiotic part consists in two major compartments, mineral nutrients (*e.g.* mineral nitrogen pool) and detritus (dead organic matter). The biotic part of the ecosystem is an allometric food web model ([Brose, 2008](#); [Heckmann et al., 2012](#)) based on carbon flows and species biological parameters and trophic interactions scale with their body mass. Here, the food web is split into a green food web based on primary producers taking up mineral nutrients and a brown food web based on decomposers decomposing detritus and taking up or releasing mineral nutrients. Nutrients are either directly recycled (species excretion of mineral nutrients) or indirectly recycled (species excretion of detritus containing both nutrients and carbon). As our model combines a carbon based food web and carbon and nutrient based abiotic compartments, stoichiometry rules ensure the conversion between carbon flows and nutrient flows between the biotic and abiotic compartments and account for species stoichiometric homeostasis in the food web. The green and the brown food webs are bottom-up coupled by detritus and mineral nutrients. They can also be top-down coupled by consumers eating prey in both green and brown food webs. All stocks are expressed for an arbitrary unit of habitat either a surface or a volume. The model is parametrised for nitrogen, but could be applied to other limiting nutrients such as phosphorus.

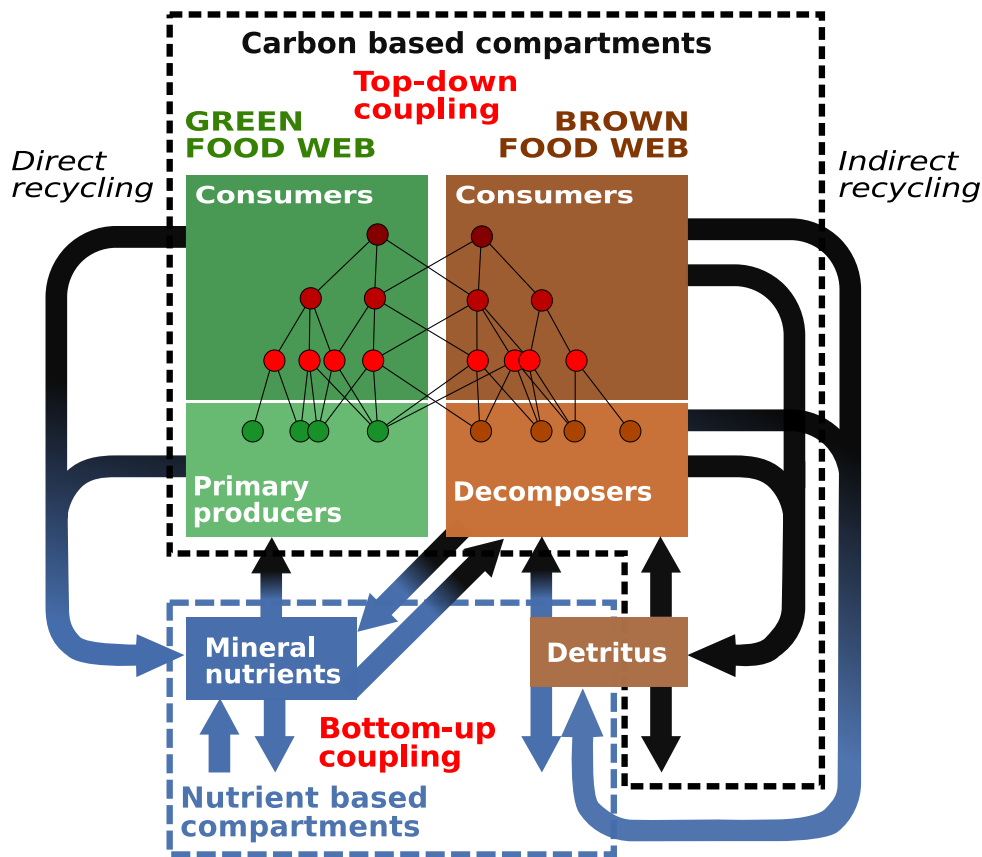


Figure 2.1: Schema of the ecosystem model. The food web is split into a green food web containing several primary producers and consumers, and a brown food web containing several decomposers and consumers. The resulting food webs can be connected through interweb generalist consumers eating prey from both green and brown food webs and this leads to a top-down coupling. Each organism from both green and brown food webs excretes nutrients either directly as mineral nutrients (arrows on the left), or indirectly through the production of degradable detritus (arrows on the right). Primary producers take up nutrients for their photosynthesis and decomposers consume detritus and take up or release mineral nutrients to maintain their stoichiometry. These shared basal resources lead to a bottom-up coupling.

## Predator-prey interactions in the allometric food web model

For modelling food web dynamics, both the structure of the food web (*i.e.* who eats whom) and the population dynamics within the food web have to be described. To define trophic interactions between species (*i.e.* food web structure), we used the approach of the allometric diet breath model (ADBM, [Petchey et al. \(2008\)](#); [Thierry et al. \(2011\)](#)) that predicts well trophic interactions in real food webs from species body mass and does not require additional assumptions on food web connectance ([Petchey et al., 2008](#)). To each of the 60 initial species is attributed a value  $c$  drawn uniformly in the interval  $[-5; 1]$ . Then, their body mass  $M$  is calculated as follow:

$$M = 10^c \quad (2.1)$$

Half of the species are attributed to the green food web and the other half to the brown food web. The five smallest species of these two food webs are defined as basal species (*i.e.* primary producers for the green food web and decomposers for the brown food web), the other as consumers. The diet of consumers depends on the profitability of each prey based on prey handling (*i.e.* the lower is the handling time, the more profitable is the prey). Following [Petchey et al. \(2008\)](#) and [Thierry et al. \(2011\)](#), mass specific handling time  $h_{ij}$  of species  $j$  by the consumer  $i$  is defined by:

$$h_{ij} = \begin{cases} \frac{h_i}{b - \frac{M_j}{M_i}} \frac{1}{M_j} & \text{if } \frac{M_j}{M_i} < b \\ \infty & \text{if } \frac{M_j}{M_i} > b \end{cases} \quad (2.2)$$

With  $h_i$  a time constant (calculation detailed in the section A1 of the supporting informations),  $M_j$  the body mass of the prey,  $M_i$  the body mass of the consumer and  $b$  the maximum prey-predator body mass ratio above which the prey cannot be eaten. The handling time function against prey body mass is U-shaped, handling time being minimal when prey body mass is equal to  $b/2 \times M_j$ . We consider that predators can only interact with preys within the body-mass interval  $[0.1bM_i, bM_i]$  with  $b < 1$  (*i.e.* predators are always larger than their prey) as the handling time increases exponentially out of this interval. Here, interweb generalism is defined as the ability of consumers to feed on prey from their own food web (*e.g.* green) and on food web on the other food web (*e.g.* brown). We study two contrasted cases where consumer are either fully interweb generalist (*i.e.* they consume green and brown prey without distinction) or not interweb generalist at all (*i.e.* they only consume prey from their own food web).

The predator-prey dynamics follow previous allometric food web models ([Brose, 2008](#); [Heckmann et al., 2012](#)). The respective equations for primary producers (equation 2.3a), decomposers (equation 2.3b) and consumers (equation 2.3c) are:

$$\frac{dB_i}{dt} = r_i G_{PPi}(N) B_i - x_i B_i - \beta_i B_i^2 - \sum_{j=consumer} B_j F_{ji} \quad (2.3a)$$

$$\frac{dB_i}{dt} = r_i G_{Di}(N, D) B_i - x_i B_i - \beta_i B_i^2 - \sum_{j=consumer} B_j F_{ij} \quad (2.3b)$$

$$\frac{dB_i}{dt} = -x_i B_i - \beta_i B_i^2 + \sum_{j=prey} e_{ij} B_j F_{ij} - \sum_{j=consumer} B_j F_{ji} \quad (2.3c)$$

In these equations,  $B_i$  is the biomass of population  $i$ ,  $G_{PPi}(N)$  is the nutrient-dependant growth rate of primary producers,  $G_{Di}(N, D)$  is the detritus and nutrient-dependant growth rate of decomposers (depending on the limitation of decomposers),  $r_i$  is the mass-specific maximum growth rate of primary producers and decomposers,  $x_i$  is the mass-specific metabolic rate,  $\beta_i$  is the intraspecific competition coefficient and  $e_{ij}$  the assimilation efficiency of species  $j$  by species  $i$ . Primary producer growth rates  $r_i$

as well as species metabolic rates  $x_i$  are defined as functions of species body masses, according to the allometric quarter-power laws as described by [Yodzis and Innes \(1992\)](#) and [Brown et al. \(2004b\)](#):

$$r_i = rM_i^{-1/4} \quad (2.4a)$$

$$x_i = xM_i^{-1/4} \quad (2.4b)$$

With  $M_i$  the body mass of species  $i$  and  $r$  and  $x$  allometric constants (Table 2.1) (See the section A1 in the supporting informations).

$F_{ij}$  represents the fraction of species  $j$  consumed by  $i$  and follows a Holling functional response:

$$F_{ij} = \frac{\omega_{ij}a_iB_j^q}{1 + \sum_{k=prey} \omega_{ik}a_ih_{ik}B_k^q} \quad (2.5)$$

Here  $B_j$  represents the biomass of the prey  $j$ ,  $q$  is the Hill exponent (the functional response is of type II if  $q = 1$  or type III if  $q = 2$ ),  $a_i$  is the attack rate of consumer  $i$  and  $h_{ik}$  is the handling time of  $k$  by consumer  $i$ .  $\omega_{ij}$  is the preference of  $i$  for the prey  $j$ . We chose here to model preferences as time variables and not as fixed parameters according to the adaptive foraging theoretical framework. Adaptive foraging is indeed an important aspect of predator-prey interactions (*e.g.* predator foraging efforts depend on prey availability) and it strongly affects food web dynamics ([Kondoh, 2003](#); [Uchida and Drossel, 2007](#); [Heckmann et al., 2012](#)). The dynamics of foraging efforts were modelled through changes over time of the consumer preferences  $\omega_{ij}$  according to the following equation:

$$\frac{d\omega_{ij}}{dt} = A\omega_{ij}\left(\frac{\partial g_i}{\partial \omega_{ij}} - \sum_{k=prey} \omega_{ik}\frac{\partial g_i}{\partial \omega_{ik}}\right) \quad (2.6)$$

Here,  $A$  represents the adaptive rate of the diet preference and  $g_i$  the total growth rate of species  $i$  defined such as  $\frac{dB_i}{dt} = g_iB_i$ . The initial value of  $\omega_{ij}$  is set assuming a uniform distribution among preys and during the simulation, the  $\omega_{ij}$  are rescaled after the resolution of equation 2.6 to keep the relation  $\sum_{k=prey} \omega_{ik} = 1$  true at each time step.

## Integrating nutrient cycling through a brown food web

In addition to the carbon based food web model, our ecosystem model contains two abiotic compartments, mineral nutrients  $N$  and detritus  $D$ . The pool of nutrients contained in detritus  $N_D$  is modelled separately from the pool of carbon of detritus. Thus,  $N$  and  $N_D$  are masses of nutrient while species biomass and  $D$  are masses of carbon. We use species carbon to nutrient ratios (C:N)  $\alpha_i$  and detritus C:N  $\alpha_D$  ( $\alpha_D = D/N_D$ ) to convert flows between species and abiotic compartment from carbon to nutrient (and vice versa).

The dynamics of nutrients in the mineral and detritus compartments are described by:

$$\frac{dN}{dt} = -\ell N - \underbrace{\sum_{i=\text{primary producer}} \frac{r_i G_{PPi}(N) B_i}{\alpha_i}}_{\text{primary producers uptake}} - \underbrace{\sum_{i=\text{decomposer}} \frac{r_i G_{Ni}(N, D) B_i}{\alpha_i}}_{\text{decomposers uptake}} \quad (2.7a)$$

$$+ I + \delta \underbrace{\sum_{i=\text{diversity}} \frac{x_i B_i + \beta_i B_i^2}{\alpha_i}}_{\text{direct recycling}}$$

$$\frac{dD}{dt} = -\ell D - \underbrace{\sum_{i=\text{decomposer}} r_i G_{Di}(N, D) B_i}_{\text{decomposers uptake}} \quad (2.7b)$$

$$+ \underbrace{\sum_{i=\text{consumer}} \sum_{j=\text{prey}} (1 - e_{ij}) B_i F_{ij}}_{\text{non assimilated biomass}} + (1 - \delta) \underbrace{\sum_{i=\text{diversity}} x_i B_i + \beta_i B_i^2}_{\text{indirect recycling}}$$

$$\frac{dN_D}{dt} = -\ell N_D - \underbrace{\sum_{i=\text{decomposer}} \frac{r_i G_{Di}(N, D) B_i}{\alpha_D}}_{\text{decomposers uptake}} \quad (2.7c)$$

$$+ \underbrace{\sum_{i=\text{consumer}} \sum_{j=\text{prey}} \frac{(1 - e_{ij}) B_i F_{ij}}{\alpha_{ij}}}_{\text{non assimilated biomass}} + (1 - \delta) \underbrace{\sum_{i=\text{diversity}} \frac{x_i B_i + \beta_i B_i^2}{\alpha_i}}_{\text{indirect recycling}}$$

We consider an open ecosystem where  $I$  is the constant input of nutrients (*e.g.* through erosion or atmospheric deposition) and  $\ell$  is the rate of loss of mineral nutrients and detritus (*e.g.* through leaching, sedimentation).

The nutrient-dependant growth rate of primary producers is expressed as (DeAngelis, 1980; DeAngelis et al., 1989b):

$$G_{PPi}(N) = \frac{N}{K_{PPi} + N} \quad (2.8)$$

where  $K_{PPi}$  is the half saturation constant of nutrient uptake of primary producer  $i$ . The nutrient uptake by primary producers (expressed as a nutrient flow) is calculated by dividing the growth rate of primary producers (expressed as a carbon flow) by their C:N ratio  $\alpha_i$ .

Organisms from green and brown food webs release nutrients through excretion and mortality to the detritus and mineral nutrient pools. A fraction  $\delta$  of these nutrients is released in their mineral form (urine for instance) while the remaining fraction is released as dead organic matter (detritus like feces, dead bodies, litter fall...) (Fig.2.1A)(Zou et al., 2016). We assume that the nutrients contained in the non-assimilated biomass ( $e_{ij}$  fraction of the eaten biomass) go in the detritus. The amount of nutrients released by species in the food web depends on their C:N ratio  $\alpha_i$ . We assume that the C:N of the non-assimilated biomass is adjusted for each species to keep its fixed stoichiometric ratio: the C:N of the non-assimilated biomass  $\alpha_{ij}$  depends on both the C:N ratio of the prey  $j$  and of the consumer  $i$  (calculation detailed in the section A1 of the supporting informations and see also Quévreur et al. (2018)):

$$\alpha_{ij} = \frac{\alpha_j \alpha_i (1 - e_{ij})}{\alpha_i - \alpha_j e_{ij}} \quad (2.9)$$

This relation is possible only if  $\alpha_i - \alpha_j e_{ij} > 0$ , thus the maximum possible C:N ratio of primary producers must be smaller than 11.1 in order to keep a constant fraction of assimilated biomass  $e_{ij}$ .

Decomposers consume carbon and nutrients from detritus but can also take up nutrient from the mineral pool. Thus, their growth rate  $G_{Di}(N, D)$  is based on the consumption of detritus that is also conditioned by the mineral nutrient uptake because the stoichiometric requirement of decomposers must be fulfilled

[Daufresne and Loreau \(2001\)](#). We define  $G_{D_{i_{max}}}$  and  $G_{N_{i_{max}}}$  the detritus and nutrient-dependant growth rates that only depends on the detritus and nutrient availability and not on stoichiometry:

$$G_{D_{i_{max}}}(D) = \frac{D}{K_{D_i} + D} \quad (2.10a)$$

$$G_{N_{i_{max}}}(N) = \frac{N}{K_{B_i} + N} \quad (2.10b)$$

Thus, the hypothetical C:N  $\alpha_{max}$  of the ingested matter by decomposers is defined by:

$$\alpha_{max} = \frac{G_{D_{i_{max}}}}{\underbrace{\frac{G_{D_{i_{max}}}}{\alpha_D}}_{\substack{\text{nutrients} \\ \text{in detritus}}} + \frac{G_{N_{i_{max}}}}{\alpha_i}} \quad (2.11)$$

Then we define  $L$  the limitation index of decomposers as:

$$L = \alpha_{max} - \alpha_i \quad (2.12)$$

If  $L > 0$ , decomposers are limited by nutrients, else they are limited by carbon. If  $L=0$ , decomposers are co-limited by carbon and nutrients. In order to have an ingested matter that has a C:N equal to  $\alpha_i$ , decomposers decrease  $G_{N_i}$  if they are limited by carbon or  $G_{D_i}$  if they are limited by nutrients.

### Decomposer limitation by carbon

If decomposers are limited by carbon, they take up too much mineral nutrients (Figure 2.2A). Thus,  $G_{D_i} = G_{D_{i_{max}}}$  and  $G_{N_i} < G_{N_{i_{max}}}$  to have the C:N of the ingested matter equal to the C:N of the decomposers  $\alpha_i$ :

$$\frac{\frac{G_{D_{i_{max}}}}{\alpha_D} + \frac{G_{N_i}(N, D)}{\alpha_i}}{\alpha_D} = \alpha_i \quad (2.13a)$$

$$G_{N_i}(N, D) = G_{D_{i_{max}}} \left( \frac{\alpha_D - \alpha_i}{\alpha_D} \right) \quad (2.13b)$$

If  $\alpha_D - \alpha_i < 0$ ,  $G_{N_i}(N, D) < 0$  and decomposers release mineral nutrients while consuming detritus.

### Decomposer limitation by nutrients

If decomposers are limited by nutrients, they take up too much carbon (Figure 2.2B). Thus,  $G_{D_i}(N, D) < G_{D_{i_{max}}}$  and  $G_{N_i}(N, D) = G_{N_{i_{max}}}$  to have the C:N of the ingested matter equal to the C:N of the decomposers  $\alpha_i$ :

$$\frac{\frac{G_{D_i}(N, D)}{\alpha_D} + \frac{G_{N_{i_{max}}}}{\alpha_i}}{\alpha_D} = \alpha_i \quad (2.14a)$$

$$G_{D_i}(N, D) = G_{N_{i_{max}}} \left( \frac{\alpha_D}{\alpha_D - \alpha_i} \right) \quad (2.14b)$$

When decomposers are limited by nutrients,  $\alpha_D - \alpha_i > 0$  is always true and  $G_{D_i}(N, D)$  can always be calculated.

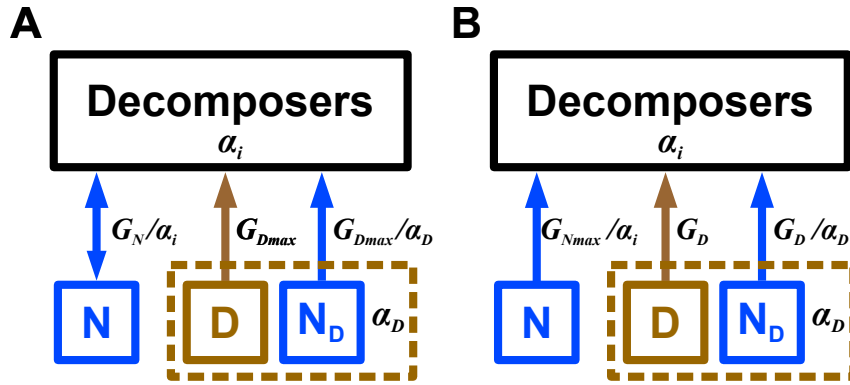


Figure 2.2: Limitation of decomposers and stoichiometric constraints. **A)** Limitation by carbon. Decomposers take up as much detritus as possible and reduce their nutrient uptake to have an ingested matter C:N equal to  $\alpha_i$ . If  $\alpha_D - \alpha_i < 0$ , detritus contain too much nutrients and decomposers release mineral nutrients ( $G_{N_i}(N, D) < 0$ ). **B)** Limitation by nutrients. Decomposers take up as much nutrients as possible and reduce their detritus uptake to have an ingested matter C:N equal to  $\alpha_i$ .

	Value and units	Description	Reference
$B_i$	$kg.v^{-1}$	Biomass (carbon) of species $i$	Variable (equation 2.3a, 2.3c)
$N$	$kg.v^{-1}$	Mineral nutrient (nitrogen)	Variable (equation 2.7a)
$D$	$kg.v^{-1}$	Detritus (carbon)	Variable (equation 2.7b)
$N_D$	$kg.v^{-1}$	Nutrients in detritus (nitrogen)	Variable (equation 2.7c)
$\omega_{ij}$	Dimensionless	Preference of predator $j$ for prey $i$	Variable (equation 2.6)
$r$	$0.87 kg^{1/4}.year^{-1}$	Growth rate allometric constant	Binzer et al. (2012)
$x$	$0.12 kg^{1/4}.year^{-1}$	(primary prod.) Metabolic rate	Brose (2008)
	$0.27 kg^{1/4}.year^{-1}$	(consumer) allometric constant	
$h_j$	$year.kg^{-1}$	Handling time	Section A1 supp. inf.
$a_i$	$0.1 v.year^{-1}$	Attack rate	Arbitrary
$\beta_i$	$0.001 v.kg^{-1}.year^{-1}$	Intraspecific competition coefficient	Arbitrary
$e_{ij}$	0.45 (herbivore)	Assimilation efficiency of species $j$	Yodzis and Innes (1992)
	0.85 (carnivore)	eaten by species $i$	
$q$	1	Hill exponent	Brose et al. (2006b)
$A$	0.01	Adaptive rate	Arbitrary
$b$	0.05	Max prey-predator body mass ratio	Brose et al. (2006a)
$\alpha_i$	Dimensionless	C:N of primary producers	(6.6, 11)
	5	C:N of decomposers	Anderson (1992)
	5	C:N of consumers	
$\alpha_{ij}$	Dimensionless	C:N of non assimilated matter	Variable (equation 2.9)
$\alpha_D$	$D/N_D$	C:N of detritus	Variable
$K_{PPi}$	$10 kg.v^{-1}$	N uptake constant of primary prod.	Arbitrary
$K_{Di}$	$100 kg.v^{-1}$	D uptake constant of decomposers	Arbitrary
$K_{Ni}$	$10 kg.v^{-1}$	N uptake constant of decomposers	Arbitrary
$\ell$	$0.2 year^{-1}$	Leaching rate	Arbitrary
$M_i$	$kg$ (of C)	Body mass of species $i$	Log uniform in $[10^{-5}, 10]$
$I$	$kg.v^{-1}.year^{-1}$	External nutrient input	$[0, 100]$
$\delta$	Dimensionless	Fraction of direct recycling	$(0.2, 0.8)$

Table 2.1: Table of parameters and variables.  $v$  represents a generic metric of space (*e.g.* that could represent liters or square meters). Indeed all the parameters depending on space are set arbitrarily and thus we do not need to specify a particular unit of space.

## Simulations

All the parameters, their units and their values as used in the simulations are given in the table 2.1. The simulations are performed with *C++* and the *GSL* ode solver using the Runge-Kutta-Fehlberg (4, 5) method with an adaptive time step and an absolute accuracy of  $10^{-6}$ . Simulations are run for 10,000 years and the outputs recorded for the last 1000 years. Species persistence is measured as the ratio of the

final number of species at  $t = 10,000$  to the initial number of species at  $t = 0$ . The CV is the ratio of the standard deviation to the mean of species biomass or recycled quantity of nutrients over time, calculated for the 1000 last years of each simulation. We measure the CV of the biomass of each species and the CV of ecosystem processes such as primary production or the quantity of recycled mineral nutrients. Each combination of parameters is tested for 100 different food webs (*i.e.* different randomly drawn sets of species body mass).

In each simulation, there are initially 60 species and their initial biomass is set at  $10 \text{ kg.v}^{-1}$  for primary producers and decomposers, and at  $5 \text{ kg.v}^{-1}$  for consumers ( $v$  is an arbitrary metric of space, see table 2.1). Initial quantities of nutrients in the mineral nutrients and detritus pools are set at  $10 \text{ kg.v}^{-1}$ .

## Results

### Food web stability

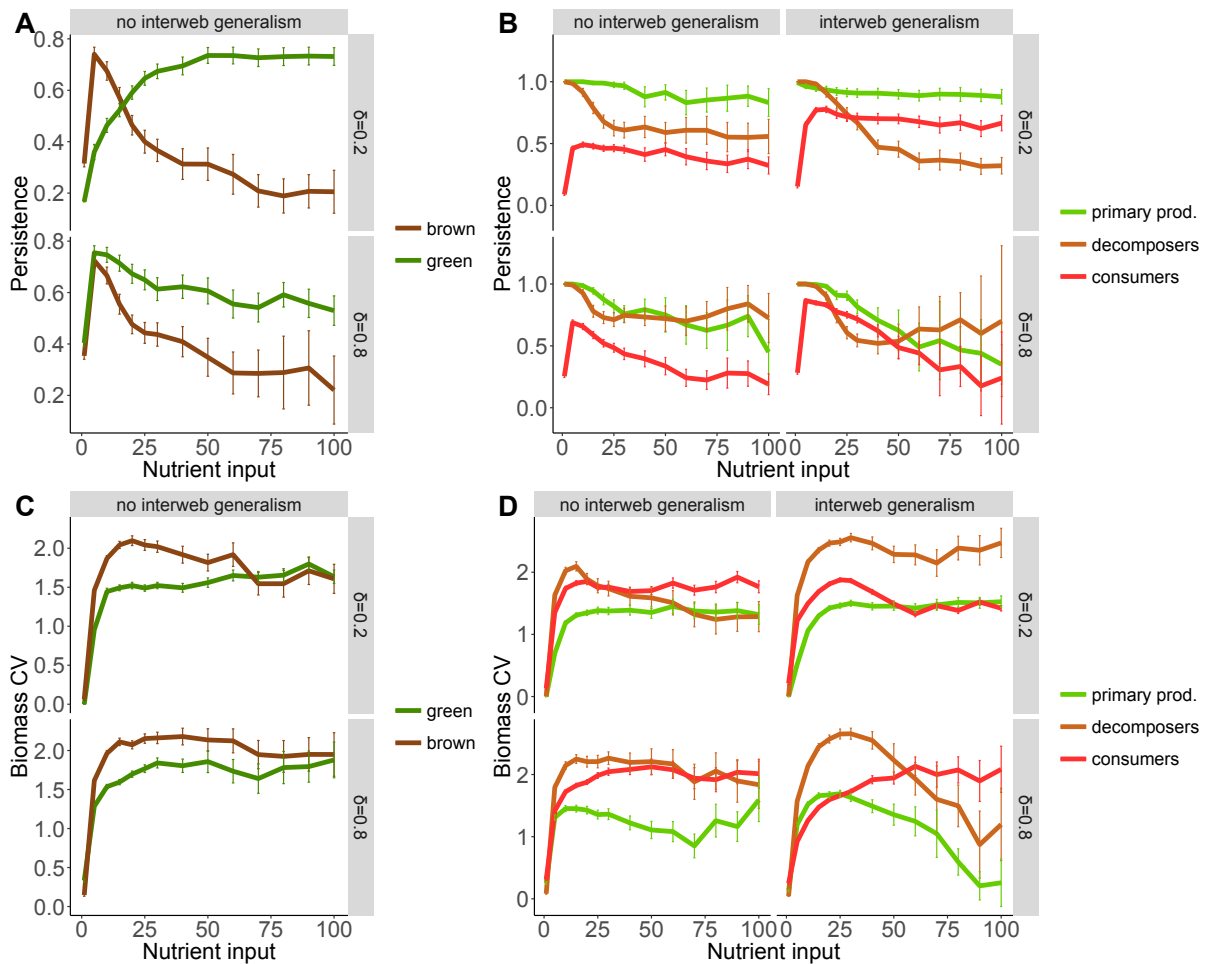


Figure 2.3: Average species persistence and biomass CV along a nutrient input gradient for two conditions of interweb generalism and fraction of direct recycling ( $CN_{PP} = 11$ ). Only food webs with at least one surviving decomposer are displayed. Error bars represent confidence intervals of the mean. **A)** Species persistence in the green food web (green) and in the brown food web (brown). **B)** Persistence of primary producers (green), decomposers (brown) and consumers (red). **C)** Average biomass CV of species from the green food web (green) and the brown food web (brown) among simulated food webs without interweb generalism. **D)** Average biomass CV of primary producers (green), decomposers (brown) and consumers (red) at the species level in food webs without and with interweb generalism.

In food webs without interweb generalism, we observe a sharp increase of species persistence at low nutrient input in the brown food web followed by a sharp decrease with increasing nutrient inputs (Fig.2.3A).



Species persistence in the green food web displays a slow increase with increasing nutrient input to reach a plateau if the fraction of direct recycling is low ( $\delta = 0.2$ ) while, with a high fraction of direct recycling ( $\delta = 0.8$ ), it sharply increases as in the brown food webs and then slowly decreases but remains higher than in the brown food web. In addition, we see that primary producer persistence is always higher than decomposer persistence at low fraction of direct recycling while they are similar for a high fraction of direct recycling (Fig.2.3B). Primary producer persistence is higher at low fraction of direct recycling while decomposer persistence is higher at high fraction of direct recycling. Consumer persistence displays a more contrasted response to nutrient input at high fraction of direct recycling with a sharper increase at low nutrient inputs and a stronger decrease with increasing nutrient inputs.

Primary producer persistence at  $\delta = 0.2$  is similar in food webs with and without interweb generalism (Fig.2.3B) while it decreases more at  $\delta = 0.8$  in food webs with interweb generalism. Decomposer persistence is lower at high nutrient inputs at  $\delta = 0.2$  and at intermediate nutrient inputs at  $\delta = 0.8$ . Consumer persistence is higher than in food webs without interweb generalism but has qualitatively similar variations.

The coefficient of variation (CV) of species biomass sharply increases at low nutrient inputs in both green and brown food webs in food webs without interweb generalism (Fig.2.3C). Species from the brown food web have a higher CV than species from the green food web except for high nutrient inputs where species from both food webs have similar biomass CV. Average species CV is also always higher for  $\delta = 0.8$  than for  $\delta = 0.2$  at all nutrient inputs for both green and brown food webs (Fig.A1-2B). This destabilising effect of  $\delta$  is also observed at high nutrient input for decomposers and consumers while it is observed at low nutrient input for primary producers (Fig.A1-2A). In addition, we notice that biomass CV is much lower for primary producers than for decomposers at  $\delta = 0.8$ .

In food webs with interweb generalism, decomposers have a much higher biomass CV than in food webs without interweb generalism at  $\delta = 0.2$  while primary producer biomass CV remains similar (Fig.2.3D). We also observe that consumer biomass CV is lower at high nutrient input to reach values similar to primary producer biomass CV. At  $\delta = 0.8$ , primary producer and decomposer biomass CV is higher at low and intermediate nutrient inputs than in food webs with interweb generalism and  $\delta = 0.2$  (Fig.A1-2A) and food webs without interweb generalism and  $\delta = 0.8$  (Fig.2.3D). However, it is lower at high nutrient inputs. Consumer biomass CV has a slower increase with nutrient input with than without interweb generalism at  $\delta = 0.8$  and is higher at high nutrient inputs than in food web with interweb generalism at  $\delta = 0.2$  (Fig.A1-2A).

## Ecosystem functioning

The mineral nutrient stock increases with nutrient input for all combination of parameters (Fig.2.4A). The nutrient stock is also higher in food webs with a high fraction of direct recycling ( $\delta = 0.8$ ). Such food webs are also characterised by a low primary producer persistence. Interweb generalism has no effect on the nutrient stock in food webs where  $\delta = 0.8$  while the mineral nutrient stock is lower in food webs with interweb generalism and  $\delta = 0.2$ .

The proportion of direct recycling and interweb generalism impact differently the effect of nutrient inputs on mineral nutrient stocks and detritus stocks (Fig.2.4B). The detritus stock is lower in food webs with  $\delta = 0.8$  and these food webs are also characterised by a lower primary producer persistence. We also only see an effect of interweb generalism in food webs with  $\delta = 0.2$  where the detritus stock is generally higher than in food webs without interweb generalism.

The total quantity of recycled nutrients is higher in food webs with a high fraction of direct recycling ( $\delta = 0.8$ ) and is always higher than the nutrient input (Fig.2.4C). In food webs with  $\delta = 0.2$ , the quantity of recycled nutrient is lower in food webs with interweb generalism and is even inferior or equal to nutrient

inputs.

Decomposer are always limited by carbon at low nutrient input (Fig.2.4D). The average limitation tends towards the co-limitation for  $\delta = 0.2$  but at high nutrient input, decomposers become more carbon limited for  $\delta = 0.8$ . Interweb generalism reduces the variability in limitation coefficient of decomposers among simulated food webs and keeps this coefficient close to co-limitation for  $\delta = 0.2$ . We also notice that for the same value of nutrient input, food webs with carbon limited decomposers are characterised by a high mineral nutrient stock and a low detritus stock (Fig.A1-3A).

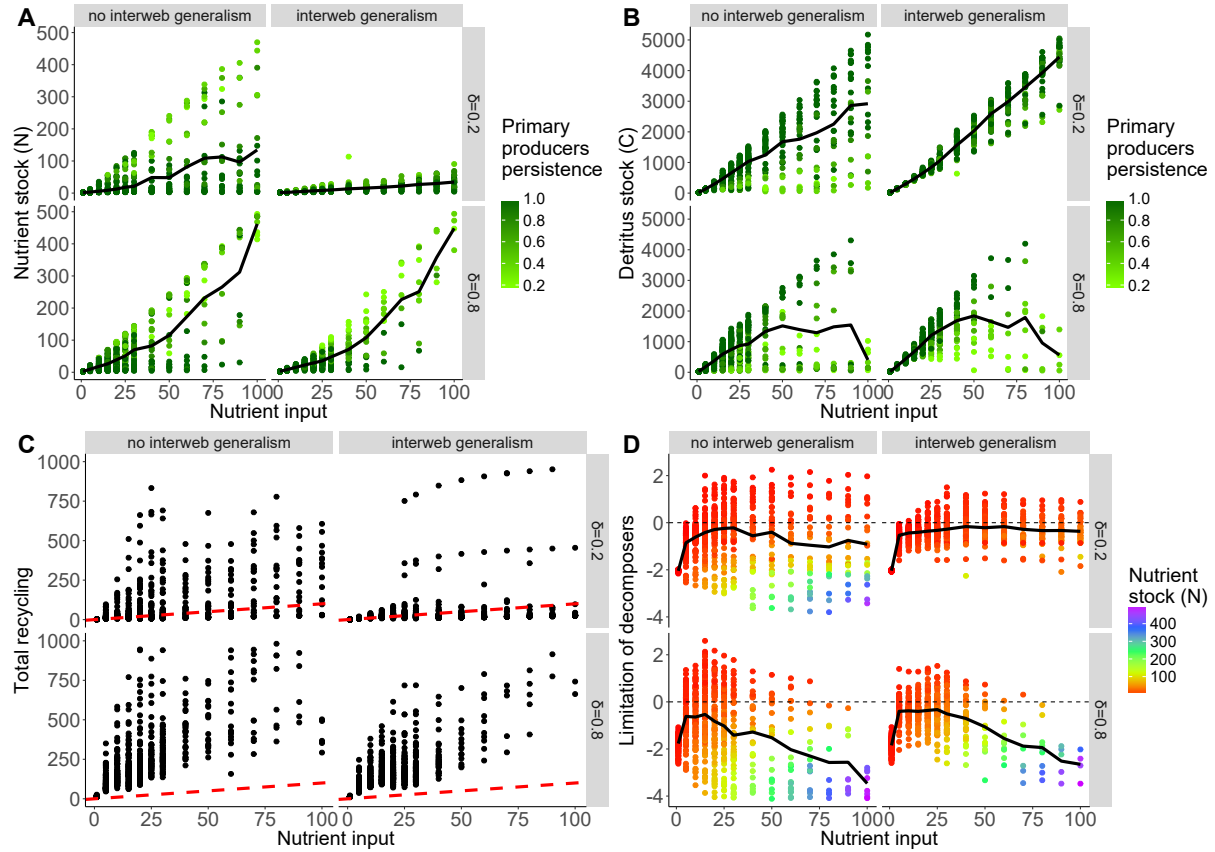


Figure 2.4: Response of abiotic compartments in each simulated food web (with at least one surviving decomposer) along a nutrient input gradient for two modalities of interweb generalism and fraction of direct recycling ( $CN_{PP} = 11$ ). **A)** Average mineral nutrient stock in each simulated food web. The colour scale represents primary producer persistence. **B)** Average detritus stock (in carbon) in each simulated food web. The colour scale represents primary producer persistence. **C)** Average total quantity of mineral nutrients recycled by all organisms in each simulated food web. The dashed line is the bisector that represents food webs where the quantity of recycled nutrients is equal to nutrient inputs. **D)** Average limitation of decomposers in each simulated food web. Positive values represent nutrient limitation while negative values represent carbon limitation. The dotted line representing the co-limitation. Solid lines represent the average among simulated food webs.

## Discussion

In our model, the response of the green and the brown food webs to nutrient enrichment depends both on the fraction of direct recycling that partitions nutrient excretion into mineral nutrients or detritus and on interweb generalism. For a low fraction of direct recycling, brown food web persistence is higher at low nutrient inputs while green food web persistence is higher at high nutrient inputs. For a high fraction of direct recycling, persistence in the green food web is always larger. Interweb generalism has a strong positive effect on consumer persistence and has a destabilising effect on decomposer, especially for a low fraction of direct recycling.

## Response of the food web to nutrient enrichment

We find a similar response of species persistence than in our previous model (Quévrex et al., 2018) (Fig.A1-1D): increasing nutrient inputs in a nutrient poor environment strongly enhances species persistence by increasing the energy flow sustaining higher trophic levels (Fig.A1-3B). Then, a large nutrient input leads to an increase of species biomass CV (*i.e.* larger amplitude of biomass oscillations) that drives some species to extinctions by lowering their biomass under a critical threshold. Such a response to nutrient enrichment is characteristic of the paradox of enrichment (Rosenzweig, 1971; DeAngelis, 1992; Roy and Chattopadhyay, 2007; McCann, 2011). However, we observe a contrasting response of species depending on their ecological function (*i.e.* primary producers, decomposer or consumer). Decomposers are less persistent and have a higher biomass CV than primary producers and thus seem to be more prone to the paradox of enrichment. The asymmetry between decomposers and primary producers in term of nutrition could be a mechanism responsible of such a difference of response to nutrient enrichment. Contrary to the nutrient-limited primary producers, decomposers can be limited by carbon from detritus and/or by the nutrients from both the detritus and the mineral compartments. As the C:N of detritus is always higher or equal to the C:N of decomposers (Fig.A1-3C), decomposers must immobilise nutrients most of the time. This particular nutritional function of decomposers might explain why the detritus stock is always much larger than the mineral nutrient stock, in our results (Fig.A1-4D), suggesting that while primary producers control the stock of mineral nutrients, decomposers do not control the stock of detritus. The larger accumulation of detritus than of mineral nutrients with nutrient enrichment can explain why decomposers are more destabilised than primary producers. More attention should be paid to this a mechanism that has not been investigated in previous studies focussing on primary producers and decomposers coexistence (Daufresne and Loreau, 2001) or on the consequence of decomposer limitation on ecosystem functioning (Zou et al., 2016). A promising direction would be to compare parallel food webs based on primary producers (Rooney et al., 2006) and parallel green and brown food webs (Attayde and Ripa, 2008; Zou et al., 2016) by modifying the ability of decomposers to take up mineral nutrients through the half saturation constant  $K$  (nutrition asymmetry) and by modifying the C:N ratio of species from 1 to higher values (asymmetry between C and N stocks).

This different effects of nutrient enrichment on species persistence in the green and brown food webs is modulated by the fraction of direct recycling  $\delta$ . In fact, nutrients can cycle in the ecosystem through the mineral pool or the detritus pool. A low  $\delta$  increases the proportion of cycles through detritus while a high  $\delta$  increases the number of cycles through the mineral pool (Similarly, Loreau (2010) showed that increasing the fraction of recycled nutrients without being leached out of the ecosystem increases the number of cycles of nutrients within the ecosystem). Increasing  $\delta$  increases the quantity of recycled nutrients as well as mineral nutrient availability, which enhances primary production (Fig.A1-2B and Fig.A1-4A) (Zou et al., 2016), leading to a destabilisation of primary producers. On the contrary, decreasing  $\delta$  increases the sequestration of nutrients in detritus and enhances decomposer production and biomass (Fig.A1-2B, Fig.A1-4B and E and Fig.A1-5A).

This differential response of primary producers and decomposers to enrichment has a strong impact on consumer persistence. In food webs without interweb generalism, consumers from the green and brown food webs only depend on primary producers or decomposers, respectively, to sustain their growth. For  $\delta = 0.2$ , persistence is mostly due to the brown food web at low nutrient input while it is mostly due to the green food web at high nutrient input. As a consequence, the general consumer persistence does not vary a lot along the enrichment gradient because the biomass production is mostly ensured by the brown food web at low nutrient inputs and by the green food web at high nutrient inputs (Fig.A1-4E) as shown by the ratio of green production to brown production (Fig.A1-4D). However, at  $\delta = 0.8$ , this alternation between high persistence in the brown and green food webs does not hold and green and brown food

webs have a similar response to nutrient enrichment. As a consequence, consumers persistence in the whole food web decreases with nutrient inputs. Thus, the complementarity of the green and the brown food webs in the maintenance of biodiversity strongly depends on the partitioning of nutrients between these two food webs due to the fraction of direct recycling. While [Attayde and Ripa \(2008\)](#) found that enrichment had parallel effects on green and brown food chains, [Wollrab et al. \(2012\)](#) highlighted that green and brown food chains could also have contrasted responses to nutrient enrichment depending on food chain structure. Our results thus further reveal that species persistence in green and brown food webs can show either similar or contrasted responses to nutrient enrichment depending on the fraction of direct recycling, despite the fact that both primary production and decomposer production vary always in parallel when nutrient enrichment increases in our case (Fig.A1-4).

It should also be noted that while [Daufresne and Loreau \(2001\)](#) showed that primary producers and decomposers can only coexist if decomposers are limited by carbon, we see that green and brown food webs can coexist for a large range of limitation coefficients of decomposers, and even if decomposers are mainly limited by nutrients. [Zou et al. \(2016\)](#) also obtained coexistence when decomposers are limited by nutrients in their model containing consumers. In food webs, consumers can promote the coexistence of basal species competing for the same resource by lowering their biomass ([Brose, 2008](#)), which could also promote the coexistence between primary producers and decomposers limited by nutrients.

### Effects of interweb generalism on stability

Interweb generalism deeply affects the stability of food webs and their functioning. It has a dramatic positive effect on consumer persistence and biomass (Fig.A1-5B) that may be explained by the increase of the number of available prey when consumers have access to prey from both the green and brown food webs ([Post et al., 2000](#); [Attayde and Ripa, 2008](#)). This result is consistent with previous studies where generalist consumers have a higher biomass than specialists [Thebault and Loreau \(2003\)](#). Primary producers persistence is weakly affected while decomposer persistence and biomass (Fig.A1-5B) are lower in food webs with interweb generalism, probably because of the increased number of predator that increases decomposer mortality. This destabilising effect of interweb generalism can be view as due to an apparent competition between green and brown food webs. In fact, the presence of primary producers must enhance the survival and the biomass density of decomposer predators and then lead to an increased top-down control of decomposers. Similar effects have been reported in connected food chain models ([Attayde and Ripa, 2008](#); [Wollrab et al., 2012](#)) but they strongly depend on food chain length and on the trophic distance between consumers and decomposers. [Ward et al. \(2015\)](#) observed opposite effects in natural communities with an increased productivity in the detritus channel that leads to an increased top down control in the grazing channel.

[Rooney et al. \(2006\)](#) found that top consumers linking two food chains with different biomass productions and turnovers make food web more stable (stability defined as resilience). The fast channel enables the food web to recover faster from perturbations while the slow channel dampens the variations of the fast channel. In our model, the green food web can be assimilated to a slow channel and the brown food web to a fast channel (Fig.A1-3D) for low fractions of direct recycling as decomposer biomass turnover is higher than primary producer biomass turnover. While interweb generalism promotes consumer persistence in our model, CV of consumers are not decreased in such case contrary to what we could have expected from the results of [Rooney et al. \(2006\)](#).

## Conclusion and perspectives

The brown food web is more destabilised by nutrient enrichment than the green food web. Such a difference may be due to the accumulation of detritus that is stronger than the accumulation of mineral nutrients which strongly increases resource availability for the brown food web and would make it more prone to the paradox of enrichment. This effect is modulated by the fraction of direct recycling that partitions recycled nutrients from all trophic levels between the mineral nutrient compartment or the detritus compartment. A high fraction of direct recycling has destabilising effects on the green food web because of the increased mineral nutrient availability. Interweb generalism has a strong positive effect on consumers because of the increased number of available prey and of the different biomass turnover of the green and brown food webs. It has also a negative effect on the decomposer stability probably because of the increased top-down control due to the green food web that may promote the survival of shared consumers. Our results could be tested in aquatic mesocosms. The fraction of direct recycling may be manipulated through the nutritious quality of phytoplankton. If daylight is reduced by shading and limiting nutrients abundant, the C:N and C:P ratio of phytoplankton decreases (Dickman et al., 2006; Rowland et al., 2015) and may promote mineral nutrients by organisms. The effect of interweb generalism may be tested by preventing the generalist consumer from moving between the benthic (brown food web) and the pelagic (green food web) compartments. A grid would keep fish in one compartment or in another but would not prevent nutrient diffusion or detritus sedimentation.

Our model allows studying the interactions between primary producers, decomposers, mineral nutrients and detritus in the framework of a complex food web model. However, this model still simplifies strongly recycling processes as we only consider one nutrient and one detritus pool. Including two nutrients such as nitrogen and phosphorus that have different characteristics (respectively high/low input and output rates) and different ratios in organisms (high N:P in primary producers and low N:P in consumers) could lead to additional effects of consumers that are likely to immobilise phosphorus in their biomass (Danger et al., 2007b; Cebrian et al., 2009; Cherif and Loreau, 2009; Evans-White and Halvorson, 2017). Including different pools of detritus with different degradability (Loreau, 2001; Moore et al., 2004; Harraut et al., 2012; Perveen et al., 2014) could also be interesting to take into account the functional diversity of decomposers with different detritus pathways (Moore and Hunt, 1988; Rooney and McCann, 2012) and to better model the interaction between species richness and carbon storage in soil for instance.

Including more diverse basal species such as nitrogen fixers or mixotrophs would be interesting as these organisms avoid nitrogen limitation by respectively fixing nitrogen from the atmosphere (additional input of nitrogen in the system) and consuming other organisms in addition to do photosynthesis. Nitrogen fixers constitute a very important functional group in aquatic (cyanobacteria) and terrestrial ecosystems (Fabaceae and their symbionts) and mixotrophy is widely represented among large phytoplankton (Karnatak and Wollrab, 2017; Selosse et al., 2017).

At last, interweb generalism occurs in all consumers in our model while only large consumers are likely to couple green and brown food webs (McCann et al., 2005; Rooney et al., 2006; Arim et al., 2010). Thus, including an allometric scaling of interweb generalism would better represent food web structure. Furthermore, considering spatially separated green and brown food webs would better represent the natural systems with benthic-pelagic (Vadeboncoeur et al., 2005; Wolkovich et al., 2014) or below ground-above ground (Olf et al., 2009; Wolkovich et al., 2014; Hawlena and Zaguri, 2016; Koltz et al., 2017) compartments. Flows of matter (nutrient diffusion or leaf fall) and organism migrations between the spatially separated green and brown food webs and the subsidy hypothesis framework (Leroux and Loreau, 2008; Gravel et al., 2010; Leroux and Loreau, 2012; Gounand et al., 2014) could also better represent green brown interactions.

## A1 Appendix - Parameter calculation

### Allometric parameter calculation

The value of the primary producers growth rate was taken from [Savage et al. \(2004a\)](#) and [Binzer et al. \(2012\)](#):

$$r_i = e^{I_r} M_i^{-1/4} e^{E a_r (T_0 - T / k T T_0)} \quad (2.15)$$

$e^{I_r}$	allometric scaling constant at 20°C ( $g^{1/4} \cdot s^{-1}$ )
$M_i$	body mass ( $g$ )
$e^{E a_r (T_0 - T / k T T_0)}$	temperature dependency term

We considered temperature was constant at 20°C and with  $I_r = -15.68$  ([Binzer et al., 2012](#)) we have:

$$r_i = r M_i^{-1/4} \quad (2.16)$$

With  $r = 0.87 \text{ kg}^{1/4} \cdot \text{year}^{-1}$ . Metabolic rates were taken from [Brose et al. \(2006b\)](#); [Brose \(2008\)](#) with  $x/r = 0.138$  for primary producers,  $x/r = 0.314$  for invertebrates and  $x/r = 0.88$  for ectotherm vertebrates. Since we did not apply the time scale normalisation by the growth rate of primary producers as done in [Brose et al. \(2006b\)](#), we have  $x = 0.12$  for primary producers,  $x = 0.27$  for invertebrates and  $x = 0.78$  for ectotherm vertebrates. For the simulation we used the values for invertebrates for consumers.

### Handling time

In this model, the handling time  $h_{ij}$  also follows an allometric scaling. We used the expression defined by [Petchey et al. \(2008\)](#) and also used by [Thierry et al. \(2011\)](#). The original expression has been divided by the prey body mass to have a mass specific allometric parameter:

$$h_{ij} = \begin{cases} \frac{h_i}{b - \frac{M_j}{M_i}} \frac{1}{M_j} & \text{si } \frac{M_j}{M_i} < b \\ \infty & \text{si } \frac{M_j}{M_i} > b \end{cases} \quad (2.17)$$

$h_i$	allometric scaling constant ( $\text{year} \cdot \text{kg}^{-1}$ )
$b$	maximum prey-predator body mass ratio (0.05)
$M_i$	body mass of the predator ( $kg$ )
$M_j$	body mass of the prey ( $kg$ )

The maximum prey-predator body mass ratio  $b$  delimits the diet breadth. If the prey-predator body mass ratio is below  $b$ , the handling time function has a U-shape as shown in Fig. A1-1, otherwise the handling time tends to infinity and the prey is not consumed by the predator. Unfortunately, no value of the allometric scaling constant  $h_i$  could be found in the literature. However, the maximum ingestion rate  $y_i$  is well quantified ([Yodzis and Innes, 1992](#); [Brose et al., 2006b](#); [Vucic-Pestic et al., 2010](#)) and corresponds to the reverse of the handling time. Following [Brose et al. \(2006b\)](#), the ingestion rate is set proportional to the metabolic rate:

$$y_i = y x_i \quad (2.18)$$

With  $y = 8$  for invertebrates and  $y = 4$  for ectotherm vertebrates. Then, we assumed that the values from [Brose et al. \(2006b\)](#), that do not depend on the body mass of the prey, are the average over all possible prey body masses (interval  $[0, bM_i]$  defined in equation 2.17). Thus, we can state that:

$$y_i = \frac{1}{bM_i} \int_0^{bM_i} \frac{1}{h_{ij}} dM_j \quad (2.19)$$

Thus, by replacing  $h_{ij}$  by the expression from equation 2.17:

$$\begin{aligned}
 y_i &= \frac{1}{bM_i} \int_0^{bM_i} \frac{1}{\frac{h_i}{b - \frac{M_j}{M_i}} \frac{1}{M_j}} dM_j \\
 &= \frac{1}{h_i b M_i} \int_0^{bM_i} \left(b - \frac{M_j}{M_i}\right) M_j dM_j \\
 &= \frac{1}{h_i b M_i} \left[ \frac{bM_j^2}{2} - \frac{M_j^3}{3M_i} \right]_0^{bM_i} \\
 &= \frac{b^2 M_i}{6h_i}
 \end{aligned} \tag{2.20}$$

Thus:

$$h_i = b^2 M_i / 6y_i \tag{2.21}$$

And by replacing  $h_i$  in equation 2.17 by the expression found in equation 2.21:

$$h_{ij} = \frac{b^2}{6y_i} \frac{M_i}{\left(b - \frac{M_j}{M_i}\right) \frac{M_j}{M_i}} \tag{2.22}$$

$y_i$  is defined as in equation 2.4a:

$$y_i = y M_i^{-0.25} \tag{2.23}$$

$y$  | allometric scaling constant ( $year.kg^{0.25}$ ) expressed as  $8.x$  (Brose et al., 2006b)  
 $M_i$  | body mass of the organism ( $kg$ )

Handling time is minimum for  $M_j = \frac{b}{2} M_i$ . The value of the maximum prey-predator body mass ratio  $b$  is set to 0.05 so that we have minimum handling time for prey 40 times smaller than predators. This value is consistent with the prey-predator body mass ratio found by Brose et al. (2006a). To limit the number of equations, the interactions involving prey out of the interval  $[0.1bM_i, bM_i]$  were neglected.

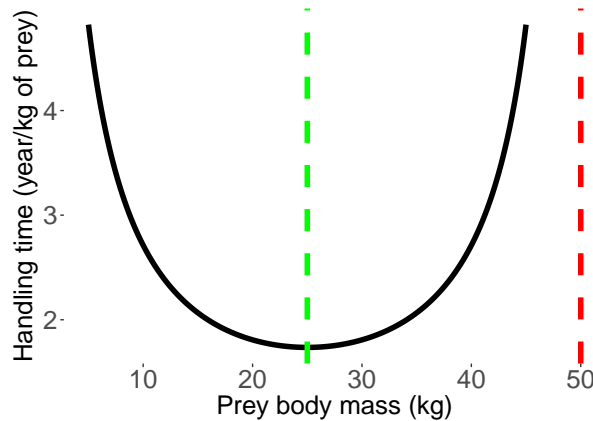


Figure A1-1: Handling time as a function of prey body mass ( $b = 0.05$ ,  $M_i = 1000kg$ ). The red dashed line represents the upper limit of body mass of prey that the predator can handle ( $M_i/M_j < b$ ) and the green dashed line represents the optimal prey body mass minimising the handling time ( $M_j = \frac{b}{2} M_i$ ).

## Stoichiometry and C:N ratios

The limiting nutrients taken into account in our model could be any mineral nutrient but we chose nitrogen to parametrise the carbon to nutrient ratio. The C:N ratio was taken from data of pelagic communities (Anderson, 1992). We took phytoplankton C:N ratio as the C:N ratio of primary producers (6.6) and for consumers the C:N ratio was set to 5 as the average of C:N ratios of bacteria (5.1), protozoa (5.5)

and copepods (4.67). The amount of nutrients released by consumers from non-assimilated prey biomass depends on both the C:N ratio of prey and consumers. The C:N ratio of non-assimilated biomass  $\alpha_{Dij}$  can be calculated by using the constraints on mass conservation and maintenance of species homeostasis (equation 2.9). The ingested biomass by consumer species  $i$  of prey species  $j$  contains a mass  $C_j$  of C and  $N_j$  of nutrient ( $\alpha_j = C_j/N_j$ ). A fraction  $e_{ij}$  of  $C_j$  is converted into a mass  $C_i$  of C of the consumer while the remaining fraction  $1 - e_{ij}$  is converted into a mass  $C_{Dij}$  of detritus. We define  $N_i$  as the assimilated mass of nutrient by the consumer ( $\alpha_i = C_i/N_i$ ), and  $N_{Dij}$  as the non assimilated mass of nutrient excreted to the detritus pool (with  $\alpha_{Dij} = C_{Dij}/N_{Dij}$ ). By law of conservation of mass, we have the two following relations:

$$N_j = N_i + N_{Dij} \quad (2.24a)$$

$$C_j = C_i + C_{Dij} = e_{ij}C_j + (1 - e_{ij})C_j \quad (2.24b)$$

By adding conditions on the maintenance of species homeostasis ( $\alpha_i$  and  $\alpha_j$  are constant), we can then derive the expression of  $\alpha_{Dij}$  as a function of  $e_{ij}$ ,  $\alpha_i$  and  $\alpha_j$ :

$$\begin{aligned} \frac{C_j}{\alpha_j} &= \frac{C_i}{\alpha_i} + \frac{C_{Dij}}{\alpha_{Dij}} \\ \frac{C_j}{\alpha_j} &= \frac{e_{ij}C_j}{\alpha_i} + \frac{(1 - e_{ij})C_j}{\alpha_{Dij}} \\ \frac{1}{\alpha_j} &= \frac{e_{ij}}{\alpha_i} + \frac{1 - e_{ij}}{\alpha_{Dij}} \\ \alpha_{Dij} &= \frac{\alpha_j\alpha_i(1 - e_{ij})}{\alpha_i - \alpha_j e_{ij}} \end{aligned} \quad (2.25)$$

### Affiliation to the green or the brown food web and energy flow

Each species is arbitrary attributed to the green or to the brown food web during the construction of the food web. Such attribution sets the possible interactions but we aim to measure the energy flows in the green and the brown food webs at the species level and food web level. Thus, we define  $\gamma_i$  as the proportion of the biomass of species  $i$  that was originally produced by photosynthesis.  $\gamma_i = 1$  for primary producers and  $\gamma_i = 0$  for decomposers. For consumers  $i$ ,  $\gamma_i$  is the sum of the  $\gamma_j$  of prey  $j$  weighted by their fraction in the diet of consumer  $i$ :

$$\gamma_i = \frac{\sum_{j=prey} e_{ji}B_iF_{ji}\gamma_j}{\sum_{j=prey} e_{ji}B_iF_{ji}} \quad (2.26)$$



## A2 Appendix - Complementary results

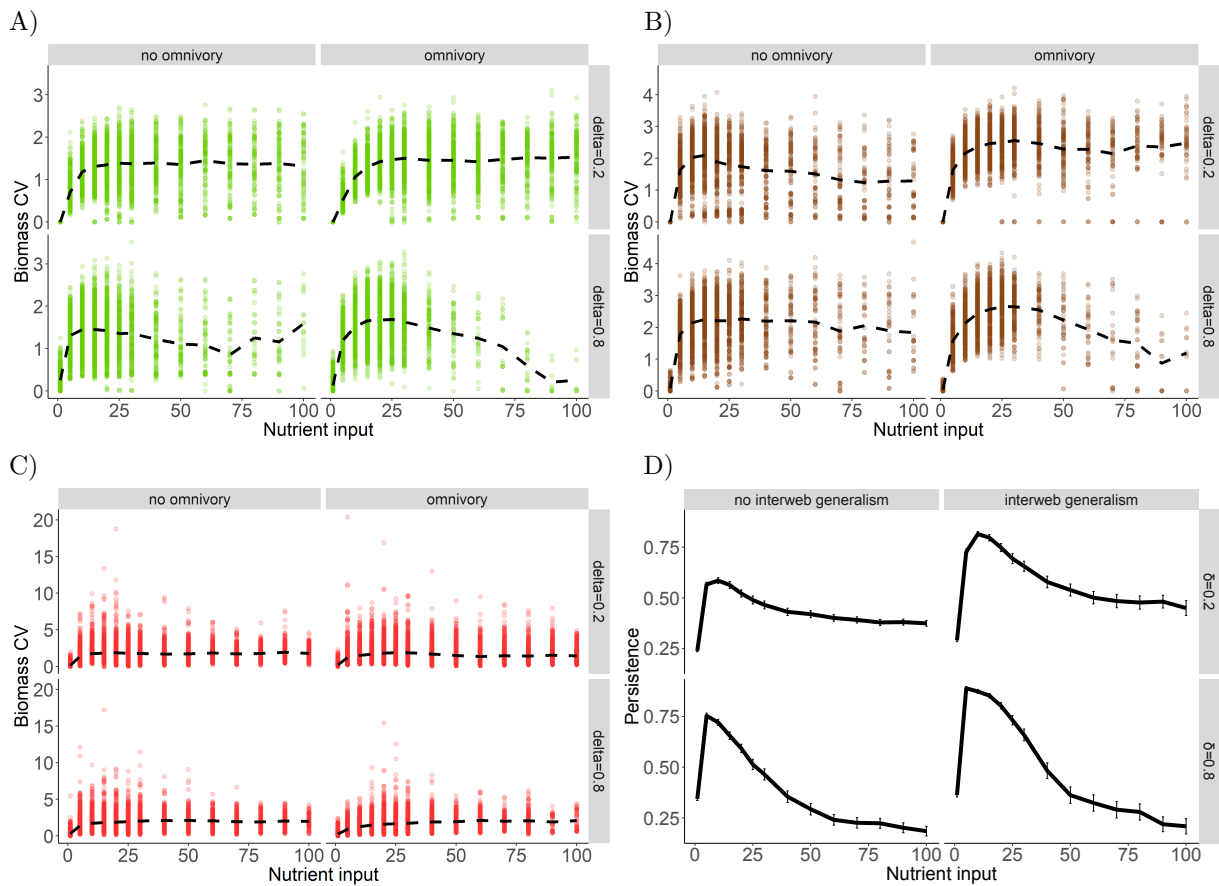


Figure A1-1: Average coefficient of variation of the biomass of each species along a nutrient input gradient ( $CN_{PP} = 11$ ). **A)** Primary producers. **B)** Decomposers. **C)** Consumers. The dotted lines represent the mean. **D)** Average species persistence among simulated food webs. Error bars represent the confidence interval of the mean.

The biomass CVs at the species level form a cluster around the mean (Fig.A1-1A-C), we do not see subgroups. Thus, the figures 2.3C and D are representative of the global response at the species level. At low nutrient inputs, species persistence sharply increases with increasing nutrient inputs and decreases as nutrient input increases further (Fig.A1-1D). The maximum species persistence is higher in food webs with interweb generalism because of the better persistence of consumers that have more available prey (Fig.2.3B). At a fraction of direct recycling  $\delta = 0.8$ , the maximum species persistence is higher than for  $\delta = 0.2$  in food webs without interweb generalism in particular. The decrease of species persistence with increasing nutrient inputs is also sharper and stronger for  $\delta = 0.8$  as the enrichment effect due to direct recycling promotes the paradox of enrichment. This results are consistent with our previous model (Quévrex et al., 2018).

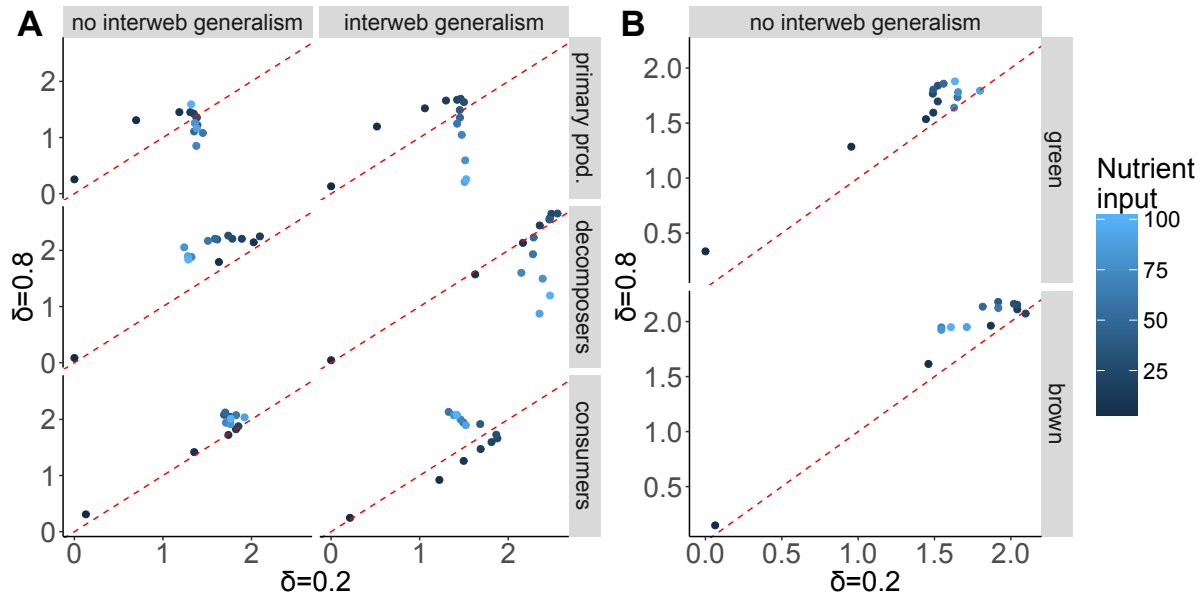


Figure A1-2: Average coefficient of variation of species among simulated food webs for  $\delta = 0.2$  versus  $\delta = 0.8$  along a nutrient input gradient (in colour scale) ( $CN_{PP} = 11$ ). **A**) CV of primary producers, decomposers and consumers in food webs without and with interweb generalism. **B**) CV of species from the green and the brown food webs in food webs without interweb generalism. The dashed red line is the bisector representing food webs where biomass CVs is the same for  $\delta = 0.2$  and  $\delta = 0.8$ .

Increasing the fraction of direct recycling  $\delta$  has a destabilising effect (*i.e.* increase of biomass CV) on primary producers at low nutrient inputs but has a stabilising effect at high nutrient inputs in both food webs without and with interweb generalism (Fig.A1-2A). Increasing  $\delta$  is always destabilising for decomposers in food webs without interweb generalism while it is stabilising at high nutrient inputs in food webs with interweb generalism. Increasing  $\delta$  is destabilising for consumers in food webs without interweb generalism while it slightly stabilising at low nutrient input in food webs with interweb generalism. In food webs without interweb generalism, increasing  $\delta$  is always destabilising for species from both green and brown food webs (Fig.A1-2B).

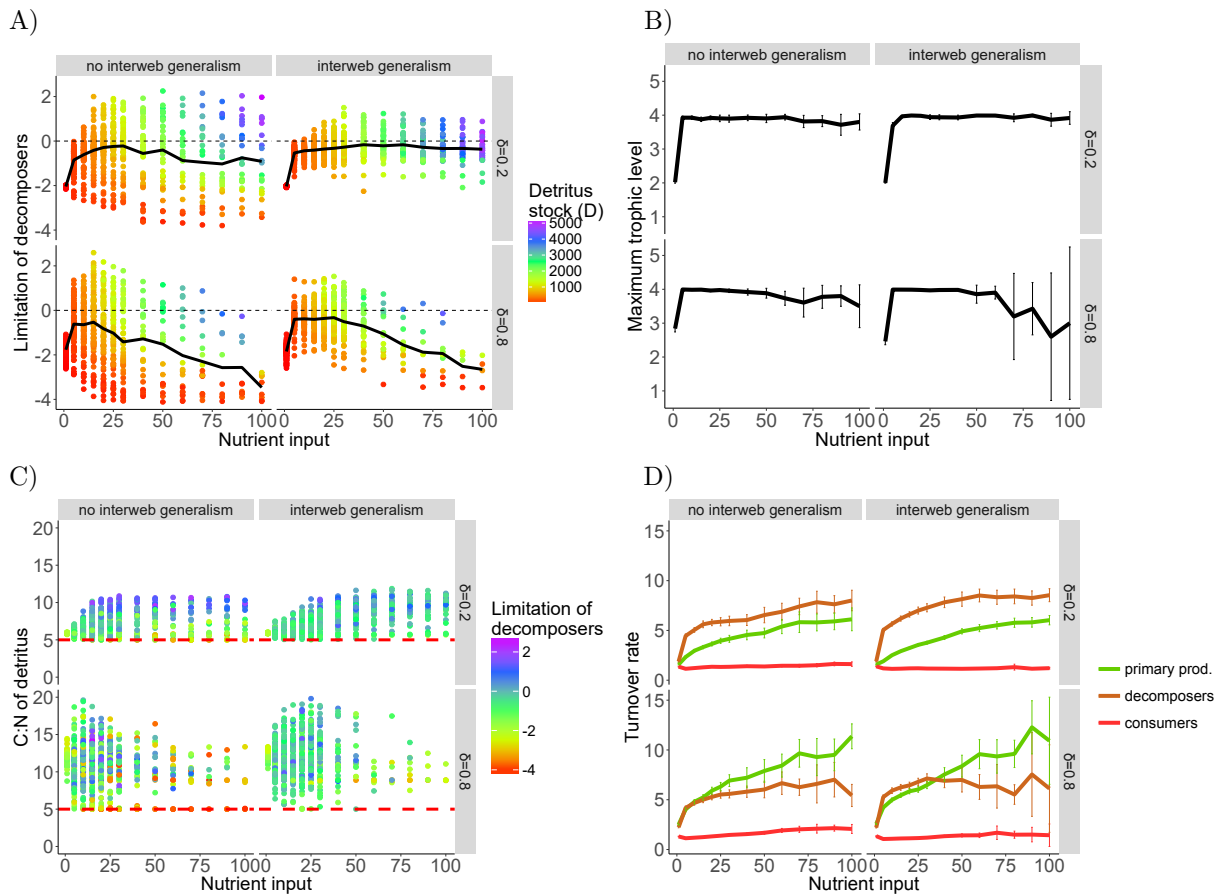


Figure A1-3: **A)** Average limitation of decomposers. Positive values represent nutrient limitation while negative values represent carbon limitation. The dotted line represents the co-limitation. Solid lines represent the average among simulated food webs. **B)** Average maximum trophic level. **C)** C:N of detritus. The dashed red line represents the C:N of decomposers. **D)** Turnover of biomass stock of primary producers, decomposers and consumers. Error bars represent the confidence interval of the mean. ( $CN_{PP} = 11$ ).

Fig.A1-3A is the same than Fig.2.4D but with the detritus stock as colour scale. Carbon limitation corresponds to food webs with a low detritus stock while nutrient limitation corresponds to food webs with a high detritus stock. Fig.2.4D displays the reversed pattern and thus decomposer limitation is ruled by the stocks of mineral nutrients and detritus.

We observe a strong increase of the average maximum trophic level (Fig.A1-3B) with increasing nutrient input. The increased energy flow sustains higher trophic levels. The maximum trophic level also decreases at high nutrient inputs for  $\delta = 0.8$  in particular because of the enrichment effect that leads to a paradox of enrichment driving higher trophic levels to extinction.

The C:N of detritus is always higher than the C:N of consumers and decomposers represented by the dashed red line (Fig.A1-3C). As consumer eat prey that have a C:N superior or equal to their C:N, they excrete detritus with a C:N superior or equal to their C:N to maintain their stoichiometry. Decomposer limitation is also weakly related to the C:N of detritus compared to the strong impact of mineral nutrient and detritus stocks.

The biomass turnover (ratio of biomass production to biomass stock) of consumers does not change significantly between the different conditions tested (Fig.A1-3D). The turnover of primary producers biomass is lower than the turnover of decomposers for  $\delta = 0.2$  and this difference is stronger in food webs with interweb generalism. For  $\delta = 0.8$ , the turnovers are different only for higher nutrient inputs and

primary producers have a higher turnover.

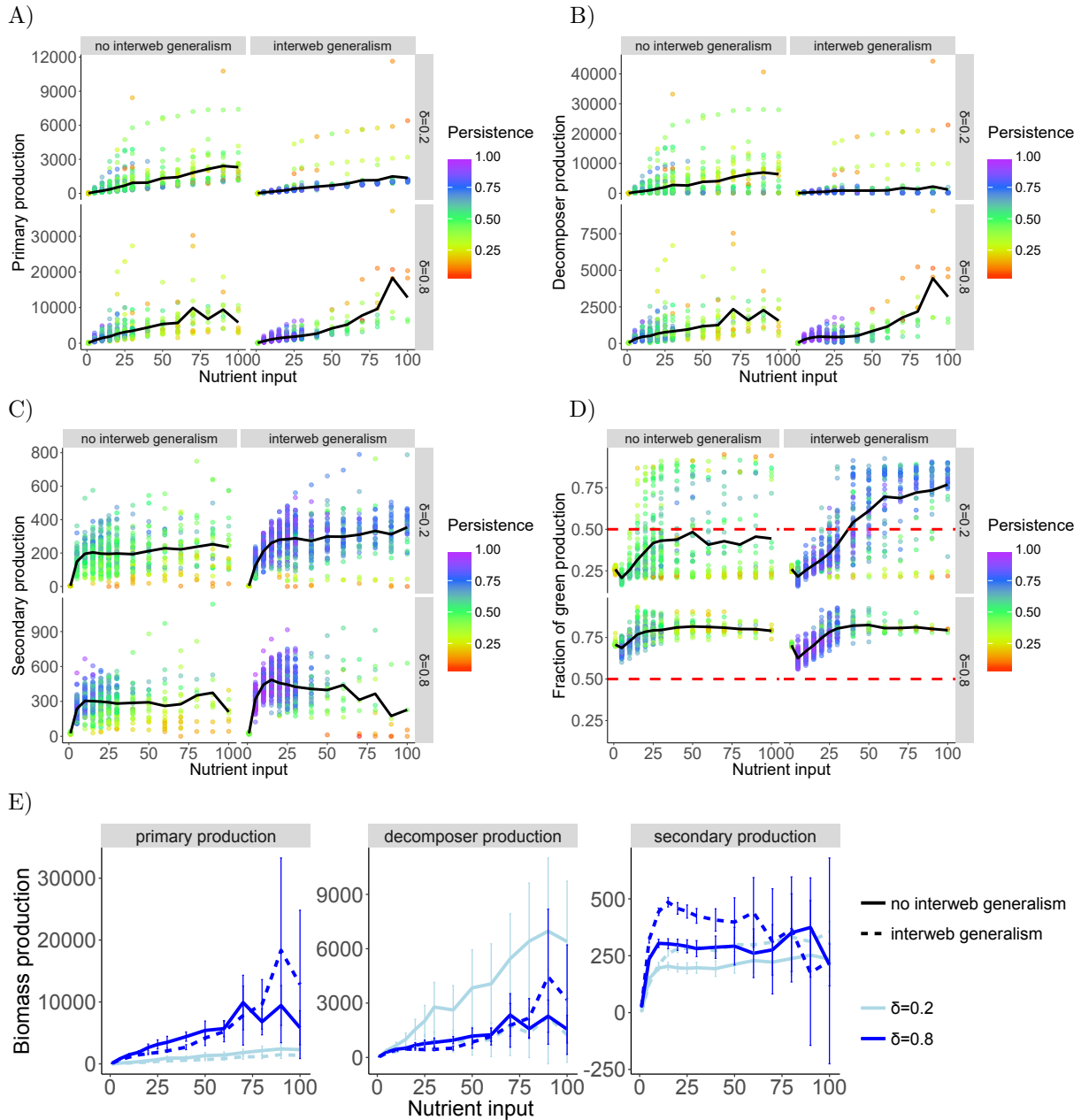


Figure A1-4: **A)** Primary production. **B)** Decomposer production. **C)** Secondary production. **D)** Ratio of green production to brown production. The red dotted line represents ecosystem where production is equally partitioned between green and brown food webs. The solid lines represent the mean among simulations. **E)** Means presented in the previous graphs. Error bars represent the confidence interval of the mean.

Increasing nutrient inputs increases primary production (Fig.A1-4A) and decomposer production (Fig.A1-4B). As primary producers create the biomass that ultimately becomes detritus, it is not surprising that decomposer production has a response to nutrient enrichment similar to primary producers. Primary production is only affected by  $\delta$  (Fig.A1-4E), increasing  $\delta$  increases mineral nutrient availability and stimulates primary production. Decomposer production is only higher in food webs without interweb generalism at  $\delta = 0.2$  (no difference between the other simulated food webs in average) (Fig.A1-4E). Decomposer production is also higher than primary production for  $\delta = 0.2$  and lower for  $\delta = 0.8$ . Such a difference is due to the increased direct recycling that increases mineral nutrient availability (Fig.2.4A and C) and reduces the quantity of excreted detritus that promotes primary production and reduces

decomposer production.

Secondary production strongly increases at low nutrient input as the number of consumers increases strongly (Fig.A1-4C) and reach a plateau probably because the biomass of consumers is maximum due to the quadratic mortality term. Secondary production is higher in food webs with interweb generalism, probably because of the increased number of possible prey, and in food webs with  $\delta = 0.8$  probably because of the increased primary production that increase the energy flow towards consumers (Fig.A1-4E).

The fraction of the total production performed by the green food web is under 0.5 at low nutrient inputs for  $\delta = 0.2$  (Fig.A1-4D). Thus, most of the production is ensured by the brown food web. This is confirmed by the larger decomposer production in Fig.A1-4B. However, when nutrient inputs increase, the production is mostly performed by the green food web with interweb generalism. In food webs without interweb generalism, two types of food webs appear at high nutrient inputs: food webs dominated by the brown production and food webs dominated by the green production. These two extreme cases are associated with food webs with a low species persistence where some basal species may escape predation because of the extinction of consumers and then have a huge production because of the lack of top-down control. For  $\delta = 0.8$ , food webs are always dominated by the green food web whose production is stimulated by the huge amount of recycled nutrients (Fig.2.4C).

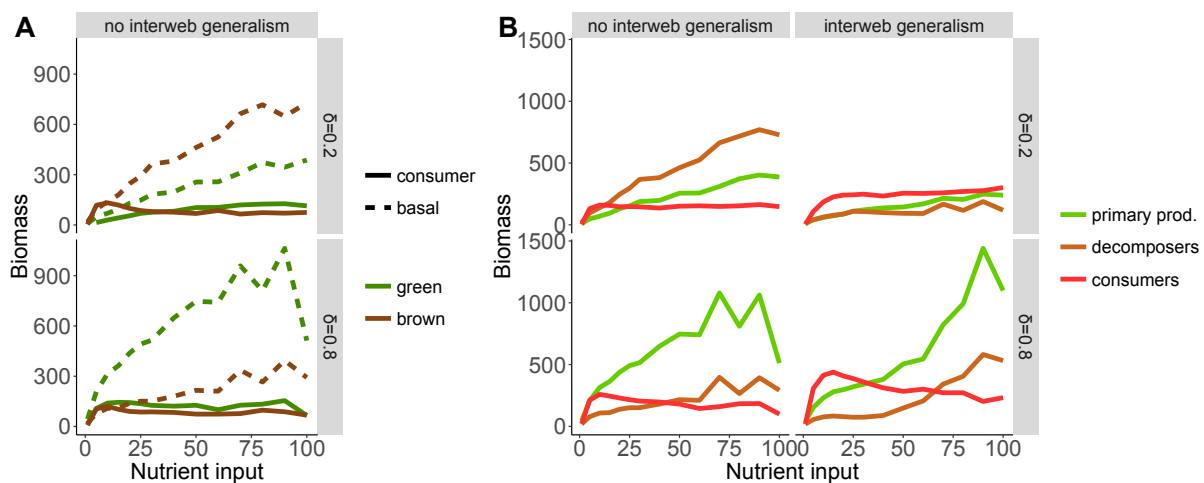


Figure A1-5: **A)** Average cumulated biomass of species from the green and the brown food webs in each simulated food web. Basal species are primary producers in the green food web and decomposers in the brown food web. **B)** Average cumulated biomass of primary producers, decomposers and consumers in each simulated food web. ( $CN_{PP} = 11$ ).

In food webs without interweb generalism, decomposers are the dominant basal species at  $\delta = 0.2$  while primary producers are dominant at  $\delta = 0.8$  (Fig.A1-5A). This corresponds to the partition of nutrients between the mineral pool and detritus by the fraction of direct recycling (Fig.2.4A and B). However, the same pattern does not hold for consumers whose total biomasses remain similar in the green and the brown food webs.

In food webs with interweb generalism, consumer biomass is higher than in food webs without interweb generalism (Fig.A1-5B) that must be due to the improved consumer persistence (Fig.2.3B). For  $\delta = 0.8$ , we have the biomasses of the three species types that are similar to food webs without interweb generalism while they are different for  $\delta = 0.2$ . In fact, for  $\delta = 0.2$ , decomposers have the lowest biomass in food webs with interweb generalism while they were dominant in food webs without interweb generalism. A small diminution of the biomass of primary producers is also present. Such a strong decrease of decomposer biomass must be due to the increased top-down control of consumers whose survival and biomass is

improved by the increased access to potential prey. In food webs without interweb generalism, consumers in the brown food web do not survive well and cannot control decomposers.

## Chapter 3

# Interactions between green and brown food webs in freshwater ecosystems: a mesocosm experiment

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## Key words

Nutrient cycling, mixotroph, light, DOC, fish, allochtone carbon, top-down, bottom-up, trophic cascade

## Abstract

The classical concepts of top-down and bottom-up cascading effects in ecosystems are challenged by the interactions between green and brown food webs. The green food web relies on photosynthesis and the brown food web relies on carbon in detritus. The interactions between these two food webs are crucial for ecosystem functioning because a major fraction of carbon enters through the green food web while nutrients are mainly recycled through the brown food web. However, green and brown food webs can compete for mineral nutrients if decomposers are nutrient limited. Thus, bottom-up or top-down effect on one food web can have major cascading effects on the other one. In our fresh water mesocosm experiment, we tested such cascading effects by selective bottom-up effects on the green food web through daylight filtration, on the brown food web through organic carbon addition, and by top-down effects mediated by fish presence or absence. The presence of fish did not shift drastically zooplankton grazing pressure as the biomass of zooplankton did not change and as large Cladocerans were absent in the initial community. However, we found a positive effect of fish on phytoplankton density in mesocosms where daylight was filtered. When daylight exposure was reduced, phytoplankton generally had higher C:nutrient ratios and fish excretion probably reduced nutrient limitation of phytoplankton that increased its density in these conditions where cells require more nutrients for division. Fish effect was also visible through positive effects on both sediment production and DOC accumulation. Fish only affected the brown food web through the reduction of the degradation capacity of benthic bacteria while pelagic bacteria were unaffected. We did not observe any cascading effect of the light treatment on the brown food web, and of organic carbon treatment on the brown food web. Our organic carbon treatment had nearly no effect on the brown food web probably because of the moderate quantity of added carbon and of the non-degradation of some of the added molecules. Our experiment shows that fish can strongly affect phytoplankton through bottom-up effects due to nutrient cycling and not only through the classic trophic cascade due to the top-down control on large herbivorous zooplankton.



## Introduction

The relative importance of bottom-up and top-down controls on ecosystem functioning has received a lot of attention in food web ecology (*e.g.* [Hunter and Price \(1992\)](#); [Hulot et al. \(2014\)](#)). However, most experimental and theoretical studies on this topic have ignored a fundamental aspect of ecosystem functioning: flows of matter and energy are divided in two pathways in ecosystems: the pathway that relies on photosynthesis and constitutes the green food web, and the pathway that relies on carbon in detritus and constitutes the brown food web ([Moore et al., 2004](#)). The close interactions between these two pathways are crucial for ecosystem functioning because a major fraction of carbon enters through the green pathway while nutrients are mainly recycled through the brown pathway.

Green and brown food webs have often been studied independently ([Rosemond et al., 2001](#); [Jones and Sayer, 2003](#); [Jardillier et al., 2004](#)), and most studies have focused on green food webs, in particular in aquatic ecosystems ([Carpenter et al., 1985](#); [Kagata and Ohgushi, 2006](#); [Heath et al., 2014](#)). However, green and brown food webs strongly interact, and these interactions are complex. First, they interact at the base of the food webs through mutualistic interactions via nutrient recycling, as well as through competition between decomposers and primary producers for nutrients. Thus, primary producers and decomposers can be either mutualists or competitors depending on whether decomposers are limited by carbon or by nutrients such as nitrogen or phosphorus ([Daufresne and Loreau, 2001](#); [Danger et al., 2007a](#)). Second, green and brown food webs also interact at higher trophic levels via generalist predators that consume preys in both green and brown webs ([Rooney et al., 2006](#); [Wolkovich et al., 2014](#)). A few theoretical studies show that the coupling of distinct energy pathways by top predators can have strong consequences on ecosystem structure and stability ([Rooney et al., 2006](#); [Wollrab et al., 2012](#)). These predators can have a stabilising effect by controlling preferentially the food web where species are the most abundant, but they might also lead to apparent competition between the coupled food webs ([Vadeboncoeur et al., 2005](#)). Last, interactions between green and brown webs at the base and at the top of food webs are not independent. For example, ecosystems dominated by planktivorous fish as top predators produce more degradable detritus than ecosystems dominated by large herbivorous zooplankton ([Harrault et al., 2012](#)). These differences in detritus degradability can have bottom-up cascading effects on the brown food web and consequently modify the type of interactions between primary producers and decomposers. Predators also strongly modify the composition and size structure of food webs ([Lazzaro et al., 2009](#); [Gauzens et al., 2016](#)), which could affect the interactions at the bottom of the food webs.

Despite the importance of these interactions for our understanding of ecosystem functioning, very few experimental ([Daufresne et al., 2008](#); [Faithfull et al., 2011](#); [Degerman et al., 2018](#)) and theoretical ([Attayde and Ripa, 2008](#); [Boit et al., 2012](#); [Wollrab et al., 2012](#); [Zou et al., 2016](#)) studies have considered the consequences of the coupling between green and brown food webs. The theoretical study of [Zou et al. \(2016\)](#) showed that the interactions between green and brown food webs questioned the classical concepts of top-down and bottom-up cascading effects in ecosystems. This study further revealed that cascading effects between green and brown webs are determined by the structure of these food webs as well as by the type of interactions between primary producers and decomposers. The aim of this study is to investigate further the cascading effects between green and brown food webs and their consequences on ecosystem functioning through an experimental study. By manipulating in a factorial design light availability, level of added carbon organic matter and fish predator presence in freshwater mesocosms, we investigated the following questions:

1. Is the bottom-up coupling between green and brown food web mutualistic or competitive? In other words, does an increase in primary production (resp. in production of decomposers via addition of carbon organic matter) increase (mutualism) or decrease (competition) the production of the brown web (resp. green web)?

2. How does the presence of fish top predators interact with the bottom-up coupling between green and brown food webs? How does fish presence affect the impact of light and carbon organic matter addition on ecosystem functioning?

## Material and methods

### Experimentation site and experimental design

The experiment was set in the Experimental Lake Platform (ELP, 48° 16' 57" N, 2° 40' 20" E) of the PLANAQUA facility ("Plateforme nationale expérimentale en écologie aquatique"), located at the field station of the Ecole Normale Supérieure, nearby Paris. The ELP includes 16 artificial lakes with an individual volume of 700 m<sup>3</sup>, complemented with a storage pond and a sewage pond of 4000 m<sup>3</sup> each, which can accommodate the inputs and outputs of water needed for the functioning of the artificial lakes (Mougin et al., 2015). All these artificial ponds, constructed in 2014, are isolated from their immediate environment by two successive sets of geotextiles and two HDPE geomembranes, and received 30 cm of washed sand originating from the river Loire at the end of spring 2014. The lakes were filled with a mixture of rainwater and drinking water from August 2014, but natural colonisation of the ponds occurred earlier, due to accumulation of rainwater as soon as the liners had been installed. We installed a floating pontoon (27 × 5 m) in the storage pond (125 m × 15 m × 3 m deep). The pontoon delimitates two blocks of 12 × 3 m, on which enclosure can be suspended.

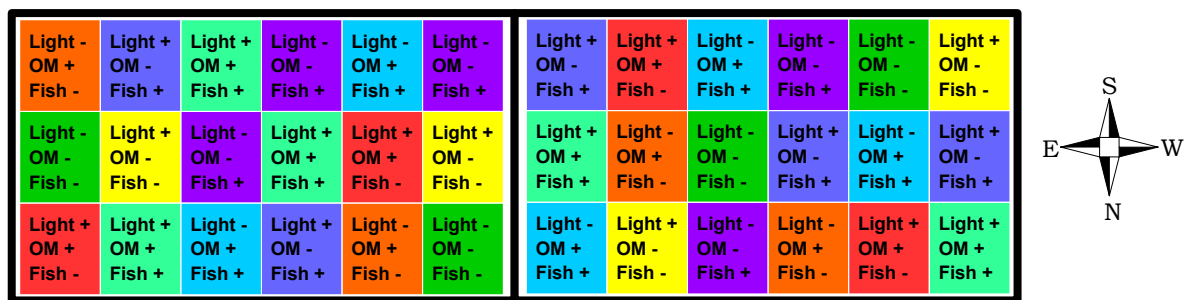


Figure 3.1: Plan of the experimental setting. Three treatments are crossed: light filtration, soluble organic carbon addition and fish addition, each category of treatment combination is represented by a different colour. The cells represent the mesocosms with detailed combinations of manipulated treatments.

The mesocosm study was performed from the end of June 2015 to the beginning of November 2015, and thus, began one year after the beginning of pond colonisation. Thirty-six translucent polyethylene enclosures (2 × 1 × 2.75 m deep), sealed at the bottom, were suspended 25 cm above the lake surface on a floating pontoon, as previously done with the same experimental setting by Danger et al. (2008a, 2012) and Harrault et al. (2014). Thus, each enclosure was a closed mesocosm benefiting from the thermostatic effect of the lake. The volume of water in each enclosure was 5 m<sup>3</sup> (2 × 1 × 2.5 m depth). Three enclosures were side by side along the width of the pontoon and each block contained 3 × 6 enclosures. The different enclosures with the same combination of treatment were uniformly distributed in order to avoid any bias due to the sun exposure or the proximity of the edges of the pontoon. The enclosures were filled with water from the storage lake hosting the pontoon during two days at the end of June. All enclosures were successively filled during two minutes to avoid any bias due to variations water composition during the day. Then, the water was enriched at the beginning of July with N and P to sustain the development of the community (the storage lake was extremely poor). We added two times (separated by seven days) 1.27 g NH<sub>4</sub>NO<sub>3</sub>, 0.65 g KH<sub>2</sub>PO<sub>4</sub> and 0.39 g K<sub>2</sub>HPO<sub>4</sub>·3H<sub>2</sub>O in each enclosure. Such addition corresponded to 140 μgN.L<sup>-1</sup> and 56 μgP.L<sup>-1</sup> (*i.e.* P:N ratio of 2.5). Zooplankton was also introduced from the experimental lakes of the platform to the enclosures to initialise the community. Three treatments (with

two modalities) were crossed in each enclosure: light, organic carbon and fish, leading to eight different combinations. Each combination with fishes had five replicates and each combination without fishes had four replicates (see Fig.3.1 for an explicit representation of the experimental design).

## Experimental treatments

### Light treatment

The filtration of day light to limit photosynthesis was performed by two types of shade meshes used for crops, filtering 10% (Diatex FOM20B200CR) and 30% (Diatex F1038T-200BLANC) of day light without changing the spectra quality. All enclosures were covered by shade meshes in order to avoid differential access by flying insects: the 10% shade mesh acted as a null treatment, while the light-depleted enclosures were covered by one layer of 30% and two layers of 10% shade mesh for a total reduction of 50% of light intensity in water (confirmed by a Li Cor measure). The shade mesh was sewn to parallel aluminum bars, making a structure that could be rolled up for sampling (Fig. 2).

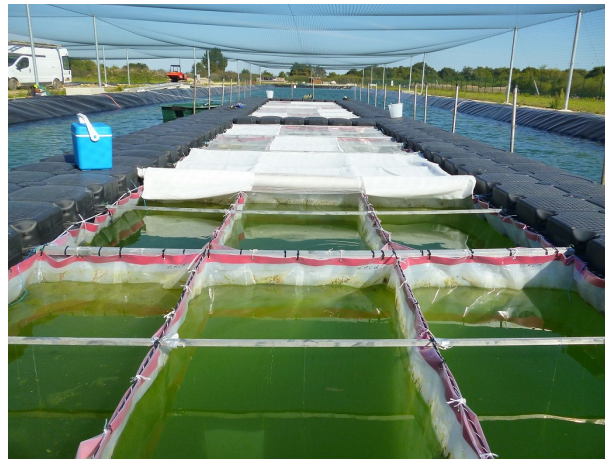


Figure 3.2: Photo of the experiment during a sampling session. The six mesocosms at the front are uncovered for allowing sampling.

### Organic matter treatment

Dissolved organic carbon (DOC) was added each week from the end of July to the beginning of November (for a total of 15 weeks) to stimulate bacterial activity. Each week, a total of 1.8 g C was added in half of the enclosures as a mixture of three organic molecules providing one third of the carbon each: glucose, cellobiose and  $\alpha$ -cyclodextrine (Sigma-Aldrich). These molecules are respectively more and less easily degraded by bacteria and also are substrates of the Biolog Ecoplate 96-well microplates (see the Functional diversity of bacteria section). A total of 5.4 mg C.L<sup>-1</sup> has been added in each treated enclosure, thus more than doubling the dissolved carbon stock of the system (initial DOC of the water: 3.96 mg C.L<sup>-1</sup>).

### Fish treatment

Fishes were used as top predators for the last treatment. Some enclosures received in the middle of July four planktonophagous rudds (*Scardinius erythrophthalmus*) with an average length of 8 cm and an average weight of 7 g (we did not have enough rudds and then we used a few roaches (*Rutilus rutilus*) with a similar size and weight as substitutes). The fishes were removed when the experiment was stopped in November. Fishes were anaesthetised before manipulation with MS222 at 0.3g.mL<sup>-1</sup>, they were photographed and weighted before and after the experiment. Each fish was also injected a nanotech pit-tag (Lutronic International, 1×6 mm) in the peritoneal cavity to have the weight of each fish at the beginning and at the end of the experiment. Thus, the individual growth rate was calculated by dividing

the difference of weight of each fish between the end and the start of the experiment by the time spent in the enclosures. The three fishes that died during the few weeks following the operation were replaced, no other fishes died until the end of the experiment. At the end of the experiment, fishes were euthanised with an overdose of MS222.

## Sampling and measurements

### Phytoplankton

Phytoplankton was sampled weekly from the end of July to November with a 2 L sampling bottle (Uwitec). A total of 6 L was sampled at three different depths ([0;50cm], [50;100cm], [100;150cm]) and mixed together. Lugol was added to 200 mL of this water for later identification of phytoplankton taxa. 3 mL were added to 150  $\mu$ L of 20% paraformaldehyde and incubated at 4°C for one hour before liquid nitrogen freezing, then samples were kept at -80°C for later FACS analysis (see the FACS analysis of microorganisms section). At last, 50 mL were directly analysed after sampling by a BBE fluoroprob (Bionef), determining the abundance of three main taxa: green algae, cyanobacteria and diatoms. At the very beginning of October, the same sampling protocol was applied to collect the seston (particulate matter between 0.7 and 50  $\mu$ m). The sampled water was first filtered through a 50  $\mu$ m nylon filter to remove zooplankton and was then filtered through a pre-weighed and carbonised Whatman GF/F glass-fiber filter (nominal cut-off 0.7  $\mu$ m). Filters were dried overnight at 60°C and weighed to determine seston mass.

### Zooplankton

Zooplankton were sampled weekly from the end of July to November with a 2-L sampling bottle (Uwitec). A total of 24 L was sampled at four different locations in the enclosures and at three different depths ([0;50cm], [50;100cm], [100;150cm]). Then, the water was filtered through a 50- $\mu$ m nylon filter and zooplankton was stored in 96% ethanol for later estimation of the main taxa abundance. At the very beginning of October, the same protocol was applied to collect zooplankton that was dried for 24 hours at 60°C just after sampling. The dry biomass of zooplankton was assessed by weighting the nylon filter before and after the sampling.

### FACS analysis of microorganisms

The frozen samples collected (see the Phytoplankton section) were analysed by FACS (Accuri C6 Plus, Becton Dickinson) as described by Zubkov et al. (2007). Samples were defrosted at 4°C for at least one hour and then filtered through a 50- $\mu$ m nylon filter to remove large particles that could plug the cytometer. Samples for protists and bacteria counting were stained with SYBR Green I DNA stain (Sigma-Aldrich, Poole, UK), 1:5000 final dilution of initial stock, in the dark at 20°C for one hour. Cells were enumerated by two detectors: the 90° or side light scatter (SSC) and the green (FL1 or FITC 533 $\pm$ 30 nm for the SYBR Green), orange (FL2 or PE 585 $\pm$ 40 nm for the phycoerythrine) or red (FL3 or PerCP 670 nm for chlorophyll *a*) fluorescence. Phytoplankton, mixotrophs and heterotroph eukaryotes were enumerated at a flow rate of 100  $\mu$ L.min<sup>-1</sup> and a core size of 40  $\mu$ m while bacteria were enumerated at the "slow" predefined flow rate.

### Water physico-chemistry

The main characteristics of the water were measured weekly with a multiparameters probe (Kor Exo) at three different depths ([0;50cm], [50;100cm], [100;150cm]). Chlorophyll *a*, pH, O<sub>2</sub> concentration, turbidity and temperature were thus measured. In addition, water filtered through pre-weighed and carbonised Whatman GF/F glass-fibre filters (nominal cut-off 0.7  $\mu$ m) was used to determine water chemistry. Two 200-mL samples were collected at two different dates in October and were frozen at -20°C for later P and

N analysis with a continuous segmented flow analyser (SEAL AA3 HR). Every two weeks, approximately 30 mL of samples plus 35  $\mu\text{L}$  of 85% phosphoric acid was stored in dark at room temperature in carbonised glass tubes with Teflon lids. Dissolved organic carbon (DOC) concentration was determined using a total organic carbon analyser (TOC-5000A; Shimadzu, Kyoto, Japan). Unfortunately, because of conservation issues, we do not have reliable data for the end of the experiment.

## Sediments

Sediments were also collected in each enclosure thanks to 5-cm diameter and 30 cm high PVC tubes hung at 1.5 m deep. Tubes were set in the middle of July and were removed in the middle of November after a total of four months. The supernatant water in the tube was removed and then sediments were collected in 200 mL plastic jars and dried at 60°C for several days.

## Functional diversity of bacteria

The catabolic capacity of each aquatic microbial community was determined using Biolog Ecoplate 96-well microplates as performed by [Pommier et al. \(2014\)](#). Two different bacterial communities were sampled: the pelagic community was sampled like phytoplankton (see Phytoplankton section) at the end of September and at the end of October (with a total of two measures for each enclosure), and the benthic community was sampled at the end of November in the supernatant of the tubes collecting the sediments (with two replicates per enclosure). The microplates include 31 different carbon-based substrates and one water control in triplicates. Each well, which contained growth media and a tetrazolium violet dye that becomes purple when the substrate is oxidised, was inoculated with 150  $\mu\text{L}$  of sample. The plates were incubated in the dark at lake temperature for seven days. Colour development (OD at 590 nm) was measured using a Bio-Rad Laboratories, Model 680 Microplate Reader every 24h just after inoculation ( $d_0$ ) and at  $d_0 + 1$ ,  $d_0 + 2$ ,  $d_0 + 3$ ,  $d_0 + 4$  and  $d_0 + 7$ . We calculated average colour development for each group of substrates (Supporting Information) after subtraction of the appropriate water blanks.

## Statistical analysis

Measure	Fixed effects	Random effects	Distribution	Test
BBE probe data	-	mesocosm+date	Gaussian	Chi <sup>2</sup>
Multiparameter probe data	depth	mesocosm+date	Gaussian	Chi <sup>2</sup>
Fish growth rate	-	-	Gaussian	F
Seston, zooplankton and sediment mass	-	-	Gaussian	F
Cell concentrations (FACS)	-	mesocosm+date	Poisson	Chi <sup>2</sup>
Algae concentration (count)	-	-	Gaussian	F
Zooplankton (count)	date	-	quasi-Poisson	F
EcoPlates Biolog	substrate+date	-	Gaussian	F

Table 3.1: Summary of the statistical models. Our three treatments and their interactions are considered as fixed effects.

We used linear mixed effect models with mesocosm and sampling date as random effects when the response variable was repeatedly measured in time (*i.e.* concentration of chlorophyll *a*, parameters of water physico-chemistry and FACS analysis). We used generalised linear models for data from the FACS analysis with a Poisson distribution and offset equal to the logarithm of the analysed volume and for data from the zooplankton counting with a quasi-Poisson distribution. For each response variable, all combinations of experimental variables and their interactions were tested to determine the best-fit model. The statistical significance of the fixed effects and corresponding p-values were obtained from backward

simplifications (Chi<sup>2</sup> test for Poisson distributions and mixed models and F test for Gaussian and quasi-Poisson distributions). *Post hoc* Tukey's tests (Tukey) were performed to compare the different modalities of treatment interactions.

## Results

### General response of the green food web

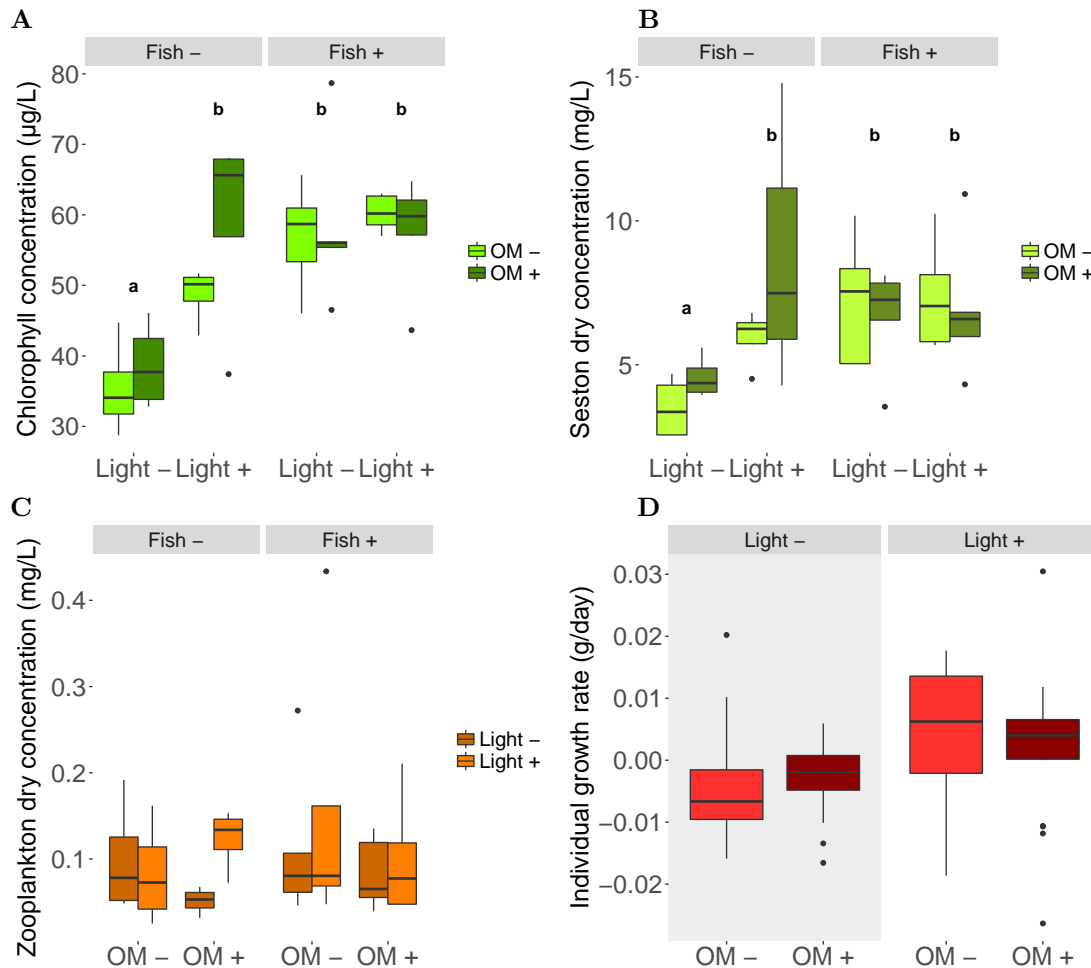


Figure 3.3: Response of compartments related to the green food web. **A)** Chlorophyll *a* concentration ( $\mu\text{g.L}^{-1}$ ) measured by the BBE probe. **B)** Seston dry mass concentration ( $\text{mg.L}^{-1}$ ). **C)** Zooplankton dry biomass concentration ( $\text{mg.L}^{-1}$ ). **D)** Growth rate of fishes ( $\text{g.day}^{-1}$ ) calculated over 133 days in average.

Chlorophyll *a* concentration (Fig.3.3A) and dry concentration of seston (Fig.3.3B) responded positively to fish presence and light exposure. We also notice a significant effect of the interaction between fish and light treatment (Table 3.2): in enclosures with fish, filtering light did not have significant effects while it strongly decreased chlorophyll *a* and seston concentration in enclosures without fish. The total dry mass concentration of zooplankton (Fig.3.3C) did not respond significantly to any treatment (Table 3.2). Fish in enclosures fully exposed to daylight grew significantly more ( $+ 0.007 \pm 0.002 \text{ g.day}^{-1}$ ) than fishes in light depleted enclosures (Fig.3.3D)(Table 3.2).

## General response of the brown food web

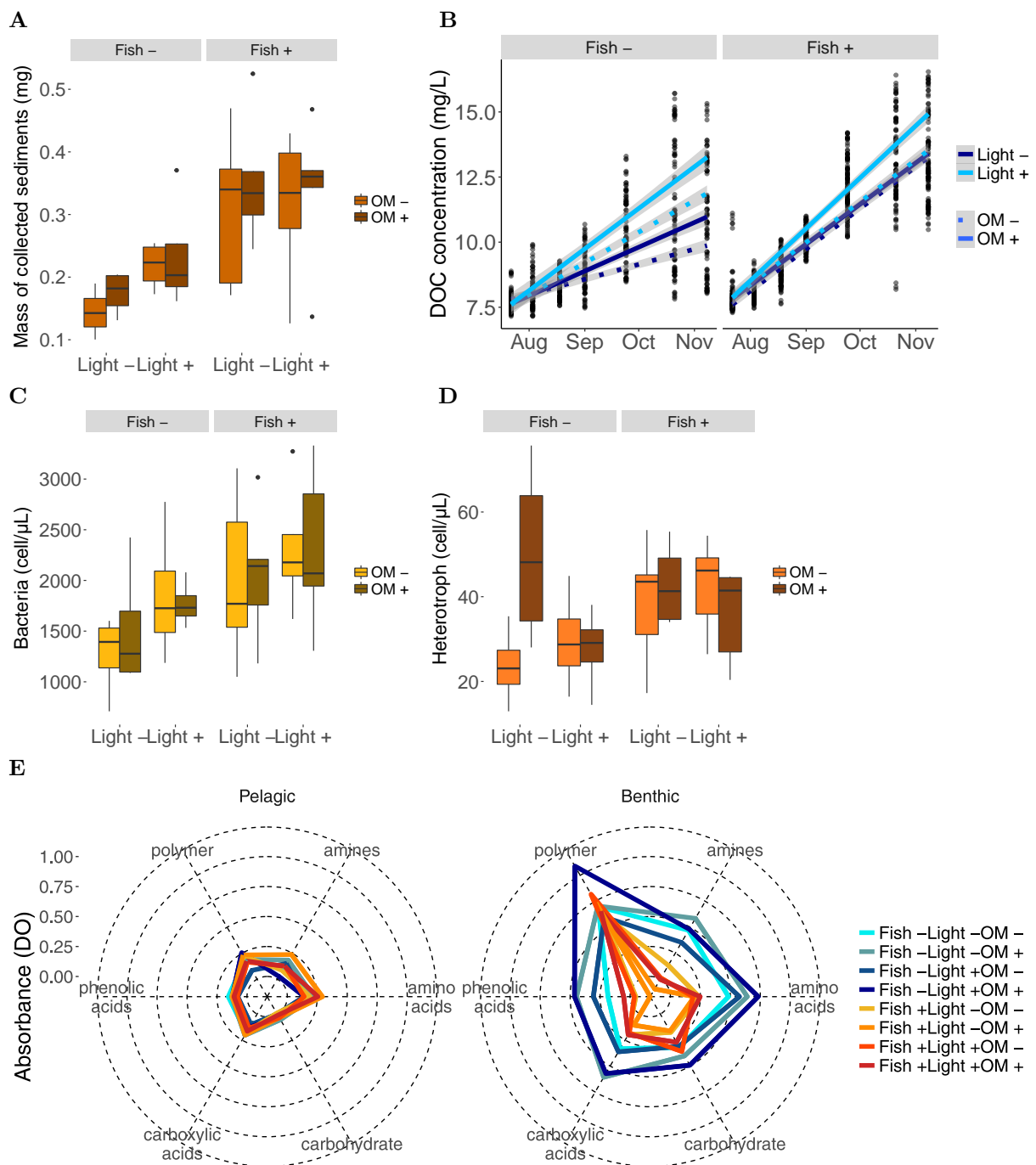


Figure 3.4: Response of compartments related to the brown food web. **A)** Sediment dry mass (mg). **B)** Dissolved organic carbon (DOC) concentration over time ( $\text{mg}\cdot\text{L}^{-1}$ ). **C)** Bacteria concentration measured by FACS ( $\text{cell}\cdot\mu\text{L}^{-1}$ ). **D)** Heterotroph concentration measured by FACS ( $\text{cell}\cdot\mu\text{L}^{-1}$ ) **E)** Metabolic profile of the bacterial community in the pelagic and benthic compartments (measured by EcoPlates Biolog). The position on each of the six axes indicates the average absorbance for that group of substrates after 7 days of incubation.

Sediment mass (Fig.3.4A) and DOC accumulation (Fig.3.4B) were significantly higher in enclosures with fish (respectively  $+ 0.508 \pm 0.122$  mg and  $+ 0.0024 \pm 0.0003$   $\text{mg}\cdot\text{L}^{-1}\cdot\text{day}^{-1}$ ) (Table 3.2). DOC accumulation also responded positively to full daylight exposition ( $+ 0.0018 \pm 0.0003$   $\text{mg}\cdot\text{L}^{-1}\cdot\text{day}^{-1}$ ) and organic carbon addition ( $+ 0.0029 \pm 0.0003$   $\text{mg}\cdot\text{L}^{-1}\cdot\text{day}^{-1}$ ). The interaction between fish and light treatments is also significant (Table 3.2). Bacteria and heterotroph eukaryote concentrations (Fig.3.4C and D) did

not respond significantly to any treatment (Table 3.2). However, fish presence significantly decreased the degradation capacity of the benthic community for all substrate families present in the EcoPlates Biolog except polymers (statistics summarised in table 3.5 in the appendix), but not for the pelagic community. The light and the organic carbon addition treatments also significantly affected a few substrate families but no general trend can be identified (Detailed results per substrate family are given in Fig.3.5 in the appendix).

### Response of phytoplankton

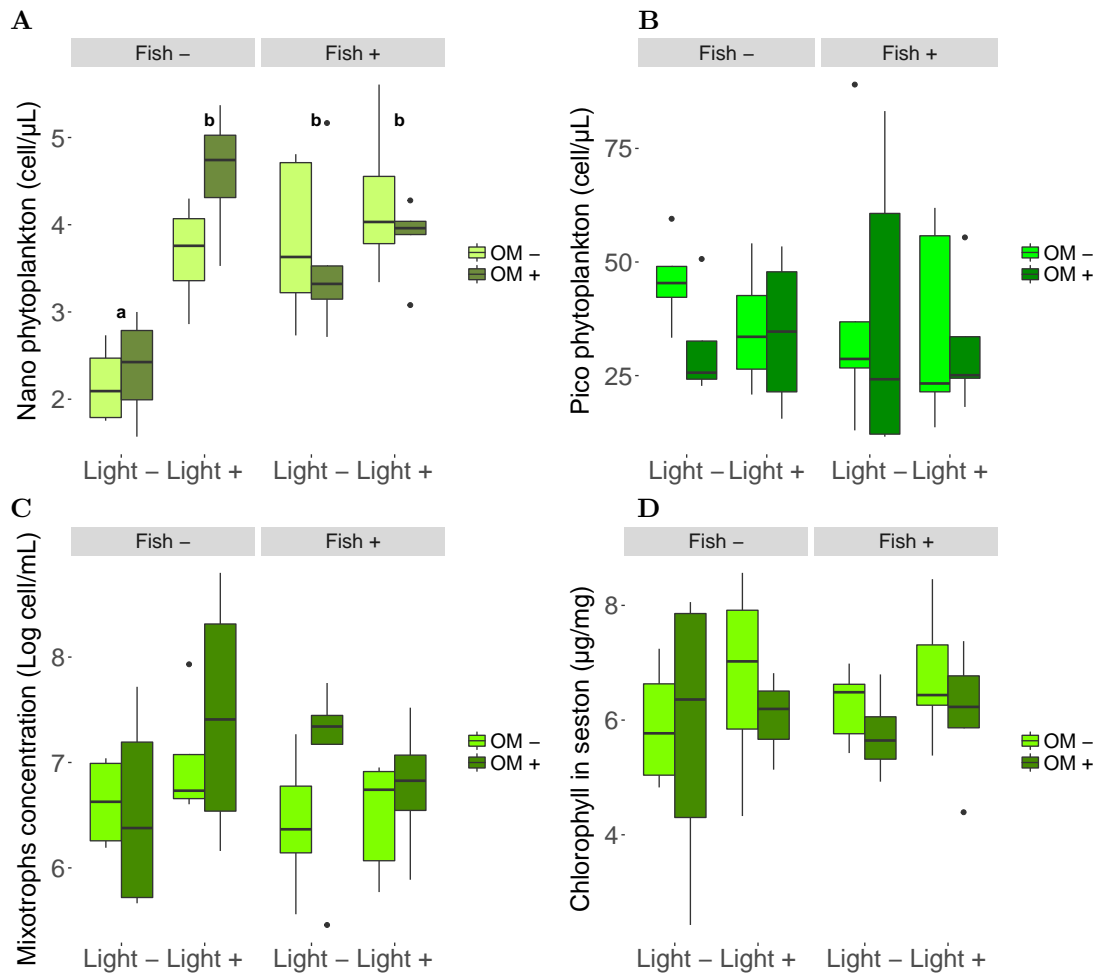


Figure 3.5: Response of phytoplankton. **A)** Nanophytoplankton concentration measured by FACS ( $\text{cell} \cdot \mu\text{L}^{-1}$ ). **B)** Picophytoplankton concentration measured by FACS ( $\text{cell} \cdot \mu\text{L}^{-1}$ ). **C)** Concentration of mixotroph algae (from the taxa identification) ( $\text{cell} \cdot \mu\text{L}^{-1}$ ). **D)** Ratio chlorophyll *a* concentration to seston concentration ( $\mu\text{g} \cdot \text{mg}^{-1}$ ).

The concentration of nanophytoplankton (Fig.3.5A) was significantly effect by the interaction between fish and light treatments (Table 3.2): light had a positive effect only in enclosures without fish and fish had an effect only in enclosures where daylight was filtered. The concentration of picophytoplankton (Fig.3.5B), the concentration of mixotrophic algae identified at the species level (Fig.3.5C) and the chlorophyll *a* concentration in seston, representing the quantity of chlorophyll *a* per seston mass unit (Fig.3.5D) did not respond significantly to any treatment (Table 3.2).



### Response of zooplankton

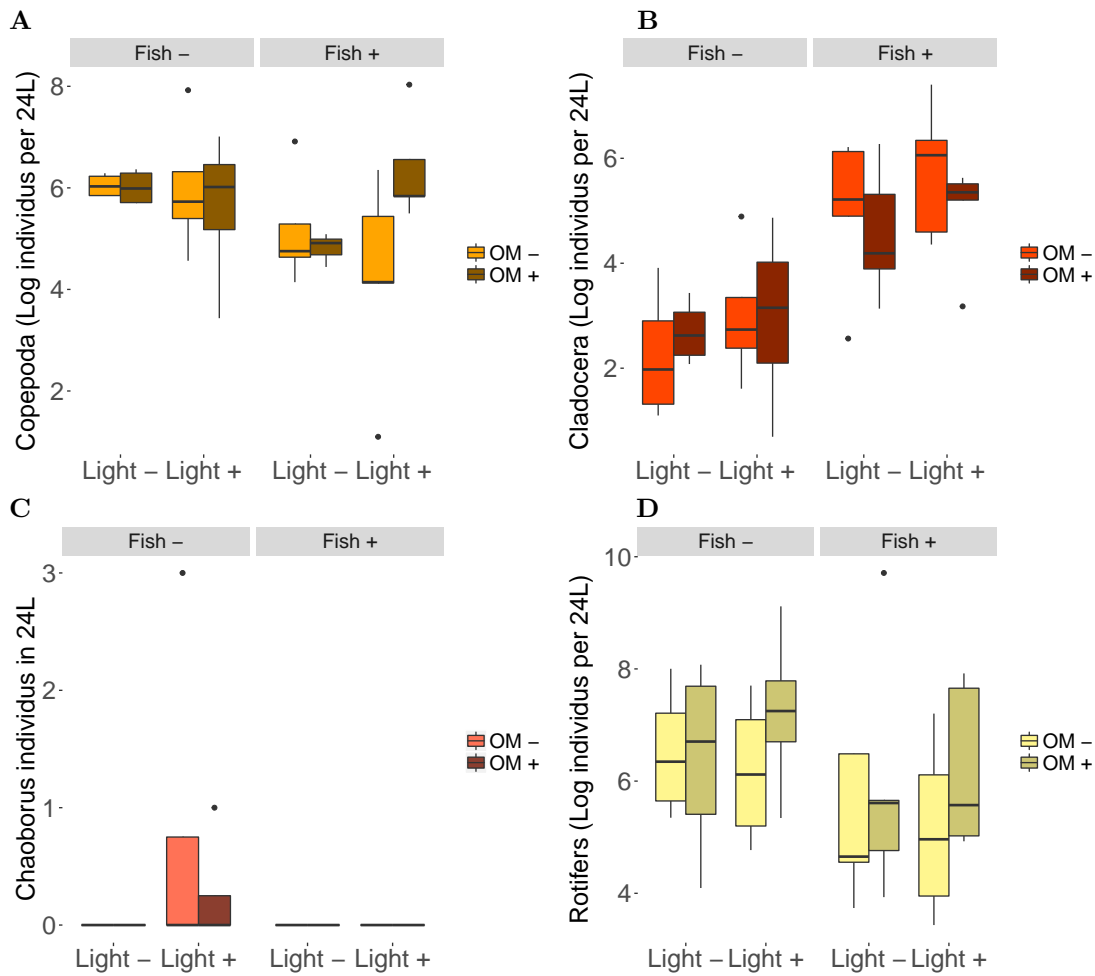


Figure 3.6: Response of zooplankton from three main aggregated groups. **A)** Cladocerae (Chydoridae and Bosminiae), **B)** Copepods (adults and nauplii), **C)** Chaoborus and **D)** rotifers (Lecanes, Lepadella, Bdelloid, Polyarthra, Brachionus, Hexarthra and Anuraepsis), Keratella were not included because of their strong variance.

Variable	Fish (F)	Light (L)	OM	F:L	F:OM	L:OM	F:L:OM
Chlorophyll	<b>0.0001</b>	<b>0.0077</b>	0.31	<b>0.0043</b>	0.16	0.88	0.26
Fish growth	-	<b>0.0011</b>	0.77	-	-	0.343	-
Seston	<b>0.0187</b>	<b>0.0319</b>	0.49	<b>0.0237</b>	0.095	0.98	0.97
Zooplankton	0.42	0.29	0.56	0.74	0.54	0.3	0.17
Sediments	<b>0.0002</b>	0.3	0.3	0.12	0.97	0.58	0.88
DOC (slopes)	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0053</b>	<b>0.0068</b>	0.31	0.35	0.25
Bacteria	0.22	0.13	0.83	0.76	0.93	0.39	0.91
Heterotroph	0.93	0.36	0.27	0.20	0.22	0.053	0.34
Nanophyto	<b>0.0043</b>	<b>0.0001</b>	0.76	<b>0.0019</b>	0.076	0.64	0.6
Picophyto	0.45	0.91	0.4	0.7	0.64	0.56	0.82
Mixotrophs	0.4	0.38	0.2	0.16	0.61	0.92	0.42
Chloro:seston	0.81	0.27	0.28	0.91	0.84	0.73	0.81
Copepoda	0.34	<b>0.037</b>	0.68	0.81	0.28	0.95	0.28
Cladocera	<b>10<sup>-8</sup></b>	0.072	0.078	0.52	0.39	<b>0.039</b>	0.80
Chaoborus	-	-	-	-	-	-	-
Rotifer	0.98	0.85	0.18	0.83	0.87	0.39	0.51

Table 3.2: Significance of treatments (p-values). Each subpart of the table corresponds to a figure panel.

The density of Copepoda (Fig.3.6A) responded positively to the light treatment, however, this effect is very weak. The density of Cladocera (Fig.3.6B) responded positively to fish presence ( $+ 2.26 \pm 0.7$  (Log individus per 24L) and Chaoborus were only present in enclosures without fish (Fig.3.6C). Rotifers (Fig.3.6D) did not respond significantly to any treatment (Table 3.2).

## Discussion

The results of our experiment can be summarised in a few major points. First, we observe consistent top-down effects of fish presence on both components of the green food web (phytoplankton abundance and composition and zooplankton composition) and the brown food web (catabolic activity of benthic microbial community), and on water physico-chemistry variables (DOC). This top-down effect of fish also interacts with the bottom-up effect of light to change phytoplankton abundance and composition, suggesting a reduction of nutrient limitation of phytoplankton by fish. Second, our results suggest only weak cascading effects between the green and the brown food webs so far, since light filtration does not clearly affect measured components of the brown food web (abundance and catabolic activity of microbial communities) and addition of organic carbon has no clear effect on main components of the green food web (no effects on fish growth, zooplankton and phytoplankton). Below we discuss these main results.

### Top-down effects of fish on green food web: importance of direct nutrient cycling through fish excretion?

We observed in all the enclosures a very important growth of phytoplankton as demonstrated by the very high values of chlorophyll *a* during August and September (Fig.A-2 in the appendix). Zooplankton biomass remained low in all treatments. The measured biomass, close to  $100 \mu\text{g DW}\cdot\text{L}^{-1}$ , corresponds to a low zooplankton biomass when compared to similar mesocosm experiments in temperate systems where it tended to attain values 3 to 5 times higher (Bertolo et al., 1999a; Danger et al., 2012). We found that small herbivorous and detritivorous species (Chydoridae, and small rotifers such as Lecane which are more typical of littoral areas than of strictly pelagic habitats), and omnivorous Cyclopidae dominated zooplankton. Large zooplanktonic organisms, such as Daphnidae and Calanoida, capable of exerting a strong grazing pressure on phytoplankton, were absent in our mesocosms. Clearly, the very low zooplankton biomass, the absence of efficient grazers, and the very high level of chlorophyll *a* in the enclosures strongly suggest that primary producers were not controlled by herbivores in our experiment. Such an absence of control by herbivory due to the absence of efficient grazers has also been reported in some previous studies (Leibold, 1989; Pace et al., 1998; Faithfull et al., 2011).

In spite of this absence of top-down control of phytoplankton by zooplankton, fish occurrence induced a positive effect on phytoplankton. This increase of phytoplankton in presence of fish was clear only when the level of photosynthetically active radiation was strongly reduced by shading mesh treatment. This fish $\times$ light effect was robust and was confirmed by the estimates of seston biomass, total chlorophyll *a* (multi-parameter probe in Fig.A-3A in the appendix), the values of chlorophyll *a* measurements associated to green algae (BBE probe) and also the turbidity (Fig.A-3F in the appendix). More precisely, this positive effect is seen on nanophytoplankton. Positive effect of fish on phytoplankton has been very frequently observed and has been interpreted as a classical cascading effect of top-predators on primary producers, mediated by a reduction of grazing pressure by zooplankton (see the meta-analysis of Hulot et al. (2014)). This reduction of top-down control has not always been associated to a decrease in zooplankton biomass, in particular when the fishes belonged to rather generalist filter feeders, such as Cyprinids (Bertolo et al., 1999b; Danger et al., 2008b) or Cichlids (Okun et al., 2007). However, in the experiments of Bertolo et al. (1999b) and Danger et al. (2008b), that were very similar to our own

experimental approach, the presence or absence of Cyprinids was always accompanied by a shift in the grazing pressure exerted by large Cladocerans. Given the absence of efficient grazers in the initial zooplankton community and the significant fish×light interaction, other factors than changes in top-down control performed by fish alone must be taken into account for explaining the response of phytoplankton. One potential explanation might be the resuspension of settled phytoplankton by fish, as demonstrated in an enclosure experiment with common carp (*Cyprinus carpio*) by [Roizen et al. \(2007\)](#). However, two results lead us to reject this hypothesis. First, it is difficult to explain differential resuspension effects in low and high light conditions. Second, the stratification of chlorophyll *a* distribution measured by the multiparameter prob (Fig.A-3B in the appendix) occurred both with and without fishes. This suggests that algal resuspension was probably not the mechanism explaining the increase in algal biomass in presence of fish.

An alternative, and more probable, explanation is associated to nutrient excretion by fish and to the reduction of the C:nutrient ratio of phytoplankton when daylight is reduced. The water of the stocking lake is nutrient-poor (P-PO<sub>4</sub>  $\simeq$  5  $\mu\text{g.L}^{-1}$ , N-NO<sub>3</sub>  $\simeq$  50  $\mu\text{g.L}^{-1}$ ). Nitrogen and phosphorus were only added at the beginning of the experiment (56  $\mu\text{g P.L}^{-1}$  and 140  $\mu\text{g N.L}^{-1}$ ). Considering, the rapid and important growth of primary producers in the first weeks of the experiment (Fig.A-2 in the appendix), phytoplankton probably became rapidly nutrient-limited (Fig.A-1 in the appendix). Phytoplankton is known to have highly plastic C:nutrient ratios depending on nutrient availability and daylight exposure ([Sterner et al., 1997, 2002](#); [Dickman et al., 2006](#); [Mette et al., 2011](#)). Indeed, when light exposure is reduced, phytoplankton cells compensate the lack of energy by an increased demand of nitrogen or phosphorus to produce more proteins, RNA ([Rhee et al. 1981](#)) or chlorophyll *a* ([Felip, 2000](#)). Consumer-driven recycling (in particular excretion by fish) has been proposed to play a key role in determining nutrient availability for phytoplankton ([Vanni and Layne, 1997](#); [Vanni et al., 1997](#); [Vanni, 2002](#)). In the enclosures, zooplankton excretion was probably negligible compared to fish one, as zooplankton represented less than 2% of fish biomass. Nitrogen is a component of the chlorine ring of the molecule of chlorophyll *a*. Thus, photosynthesis efficiency and energy acquisition and transformation should be lower in N-limited algae ([Ballin et al., 1988](#)). Moreover, an increase in chlorophyll content per cell when light is limiting has been frequently observed ([Felip, 2000](#)). However, this hypothesis of the compensation of the lack of light by an increased production of chlorophyll *a* is not supported by the ratio chlorophyll:seston that does not show any response of the chlorophyll *a* concentration in phytoplankton biomass to treatments. In addition, the counting by both FACS and microscope identification showed that some phytoplankton taxa responded similarly to chlorophyll *a* concentration (nanophytoplankton in particular). Thus, the observed increase of chlorophyll *a* concentration in presence of fish in mesocosm where daylight was filtered seems to be mainly associated to the increased density of particular phytoplankton taxa in response to the increased nutrient availability due to fish excretion.

Taking into account the very low level of zooplankton biomass in the enclosures, the question of the main resources that allowed fish to stimulate new primary production by phytoplankton is of interest. Although we do not have quantitative estimates of macro-invertebrate abundance, they were frequent in enclosures without fish and virtually absent in fish ones (pers. obs.). Thus, they clearly constituted a food source for rudds and roaches, in total accordance with other mesocosm results ([Dorenbosch and Bakker, 2012](#)). Moreover, filamentous green algae developed rapidly and formed large aggregates after nutrient addition (this led us to stop nutrient loading after two weeks). Rudds and roaches are the most herbivorous fishes under our temperate climates ([Dorenbosch and Bakker, 2012](#)). They are clearly unable to eat efficiently small algal particles, but they are totally able to consume filamentous algae that form large aggregations ([Prejs, 1984](#)). Thus, they probably consumed filamentous algae in the enclosures. In addition, algal development and settling organic matter in the enclosures may have favoured more the benthic and the littoral (walls of the mesocosms) secondary food chains (for example, through periphyton consumers and detritivorous micro-invertebrates and macro-invertebrates up to fish consumers) that were

not efficiently detected when sampling zooplankton. These direct and indirect positive bottom-up effects of primary producers on fish are supported by the positive effect of light (which increased phytoplankton biomass) on fish growth rate.

### **Top-down effects of fish on brown food web: importance of the quality of settling organic matter?**

The main argument in favour of an impact of fish on the microbial loop is only indirect and associated to a significant fish effect on the catabolic activity of the free microbial communities collected in the sediment traps. The utilisation patterns of the 31 substrates of the Biolog EcoPlates<sup>TM</sup> suggest that the relative oxidation of amines, amino acids, carbohydrates, phenolic acids and carboxylic acids were lower in the sediment of fish enclosures. The relative metabolic potential of the microbial community on a particular category of substrate has been interpreted as dependent upon its availability (Leflaive et al., 2008) or upon its relative concentration within the bulk of dissolved organic matter (Pommier et al., 2014). It had also been observed in a previous experiment that the presence of Cyprinids increased the production of labile organic matter, in particular exopolysaccharides such as transparent exopolymer particles (TEP), which aggregated with particulate matter and were transported downward (Danger et al., 2012; Harrault et al., 2012). Our results on the benthic microbial communities are in total agreement with those of Pommier et al. (2014), who observed that the addition of highly bioavailable organic matter to aquatic microbial communities favoured more specialised communities and reduced their metabolic potential. Interestingly, this specialisation trend was not observed within pelagic microbial communities. This might be associated to the fact that a large part of fresh organic matter settled, probably associated to TEPS, at the bottom of the lakes as shown by the positive effect of fish on sediment accumulation. All things being equal, pelagic microbial communities should maintain on less abundant and more diverse resources, and thus remain more generalist, than benthic microbial communities. In addition, the non-modification of the metabolic potential of the pelagic community is accompanied by a non-significant effect of the fish treatment (and of the other treatments as well) on the density of bacteria and heterotroph eukaryotes. This may be explained by the diversity of bacteria and heterotroph eukaryotes forming a generalist community that is not described by FACS analysis and that easily adapts to different conditions and thus poorly responds to our treatments.

### **Effects of light and organic matter addition: weak cascades between the green and the brown food web?**

Light had clear bottom-up effects on the green food web, in particular on total chlorophyll *a* and green algae, with clear bottom-up repercussions on the top-consumers, as discussed above. Our results also showed that an increase of light resulted in an increase of DOC, which is produced during active photosynthesis by phytoplankton. First, this increase of DOC might be simply an effect of phytoplankton biomass (more primary producers proportionally imply more exudation). Indeed, the significant interaction between light filtration and fish presence on DOC could be related to weaker light effects on phytoplankton concentration in fish enclosures. Second, this increase could partly reflect the hypothesis of Sterner et al. (1997): a higher light:nutrient ratio should induce a higher C:nutrients cell ratio (see for example Danger et al. (2009b)), and thus a higher percentage of primary production lost to exudation. Primary production is considered as an important autochthonous source of DOC for heterotrophic microbial communities in aquatic ecosystems (*e.g.* Baines and Pace (1991) and Morana et al. (2014)). However, despite the positive effect of light on DOC, light filtration did not affect significantly the abundance of bacterial and heterotroph microbial communities, and it only marginally affected microbial metabolic activities. Similarly, the addition of direct organic matter appeared to have only limited effects on bacterial community functioning. The relative metabolic potential of the microbial community was only marginally

affected by DOC addition, in contrast with the results of [Pommier et al. \(2014\)](#) and the bacteria density did not change across treatments, maybe because of the large diversity of the bacterial community that compensate any environmental change.

Concerning the cascading effects from brown to green food webs, DOC addition did not affect green algae concentration nor algae taxa composition. This absence of effect is in contradiction with previous experiments showing reduced phytoplankton biomass in response to addition of labile DOC ([Joint et al., 2002](#); [Degerman et al., 2018](#)). However, [Faithfull et al. \(2011\)](#) did not find such effects because of the dominance of mixotrophic organisms in the phytoplankton community, but we did not observe a similar community in our experiment. The contrast between our results and those of [Joint et al. \(2002\)](#) and [Degerman et al. \(2018\)](#) might be partly explained by the strong differences in experiment duration and levels of organic carbon added in the two studies (we added  $5.4 \text{ mg C.L}^{-1}$  over a period of 15 weeks while [Joint et al. \(2002\)](#) added between 4.5 and  $9 \text{ mg C.L}^{-1}$  over a period of 6 days only)(Table 3.3). In addition, our organic matter addition relied on a mixture of three molecules but the low degradation capacity of two of them (Fig.A-5A and B) might have made this treatment less efficient than pure glucose addition as done in previous studies. [Joint et al. \(2002\)](#) and [Degerman et al. \(2018\)](#) also found an increase in bacterial production following DOC addition. So far, the strongest response of bacterial communities to experimental treatments were in the benthic compartment, which may indicate that most of the brown food web activity could occur in this compartment whereas the phytoplankton and the rest of the green food web stay mostly in the pelagic compartment. Such a spatial separation between the two food webs may explain the weak response of the system to the organic matter addition.

Study	Light	Fish	OM ( $\text{mg C .L}^{-1}$ )	Nutrient	Duration
Our study	10-50%	rudds	5.4 (mixture)	-	105 days
<a href="#">Joint et al. (2002)</a>	-	-	4.5-9	NP	6 days
<a href="#">Faithfull et al. (2011)</a>	-	perch	4.2-21 (glucose)	-	45 days
<a href="#">Mette et al. (2011)</a>	4-40%	gizzard shad	-	NP	56 days
<a href="#">Hitchcock et al. (2016)</a>	-	-	1.5-16 (leachate)	-	22
<a href="#">Degerman et al. (2018)</a>	-	stickle-back	120.5 (glucose)	NP	63 days

Table 3.3: Summary of experimental treatments in previous studies testing the effects of light reduction, fish presence, organic carbon addition and nutrient addition in aquatic mesocosms.

## Conclusion and perspectives

Our results show some bottom-up effects of light and addition of organic matter on green and brown food webs, but the cascading effects from bottom-up effects in one web on the other seem to be weak, maybe due to the spatial separation of the pelagic phytoplankton community and the benthic bacterial community. Fish presence had a strong effect on both green and brown food webs: it changes taxa abundance in the green web as well as the metabolic activity of the bacterial community, and it interferes with the bottom-up effects of light and organic carbon addition. Our results suggest that fish effects were mostly mediated by their impact on detritus decomposition and nutrient recycling in this experiment, in contrast with other ones where phytoplankton was strongly controlled by large Cladocerans in absence of fish ([Danger et al. 2009](#)). Future studies may take into account the zooplankton composition (presence or absence of large Cladocerans) in the top-down (presence of fish) and bottom-up effects. The interaction between light availability and fish presence also requires more attention to be fully understood. To our knowledge, our experiment is the first one testing such an interaction.

## Acknowledgement

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## A1 Appendix - Additional results

### Water physico-chemistry

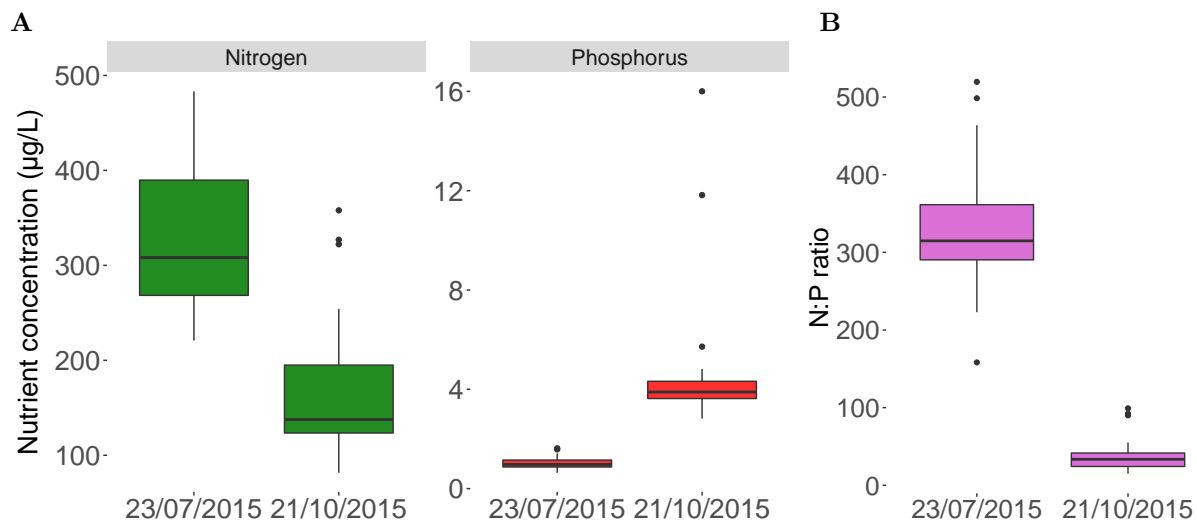


Figure A-1: Mineral nutrient concentration. **A)** Total nitrogen and total phosphorus concentrations ( $\mu\text{g}\cdot\text{L}^{-1}$ ). **B)** N:P ratio in mesocosms (mass ratio). The average N:P is equal to 330 at the beginning of the experiment and equal to 40 at the end of the experiment.

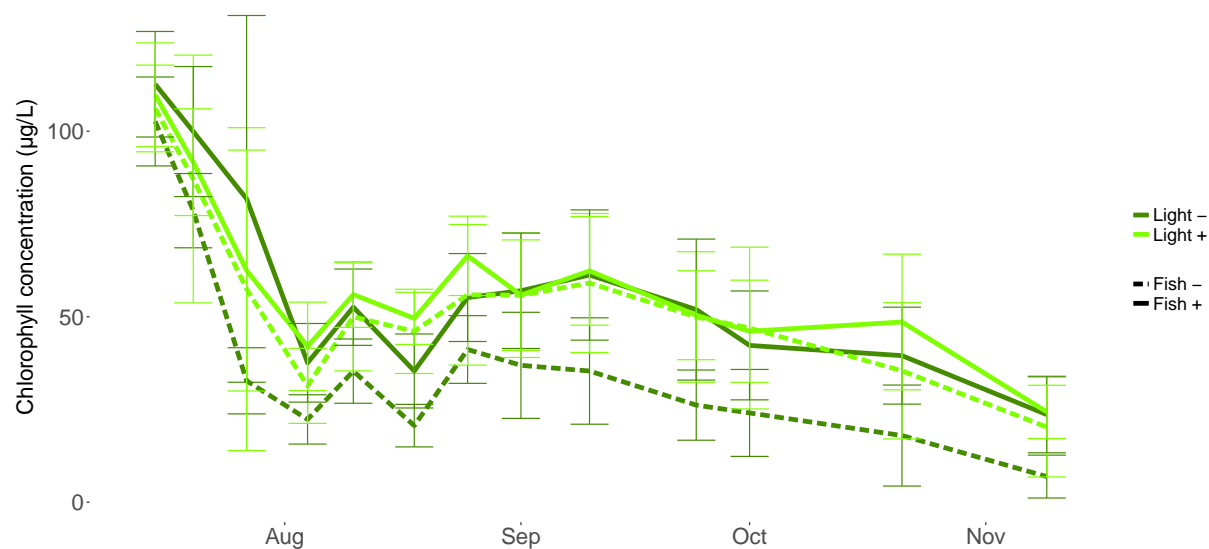


Figure A-2: Dynamics of chlorophyll *a* concentration measured by the BBE probe ( $\text{Log } \mu\text{g}\cdot\text{L}^{-1}$ ).

Variable	Fish (F)	Light (L)	OM	F:L	F:OM	L:OM	F:L:OM	depth	depth:F
chloro.	$10^{-5}$	<b>0.0001</b>	0.76	<b>0.016</b>	0.39	0.7	0.83	$10^{-16}$	0.48
temp.	0.96	0.056	0.68	0.57	0.23	0.20	0.55	<b>0.003</b>	0.79
O <sub>2</sub>	$10^{-6}$	0.70	0.067	0.21	0.15	0.81	0.60	$10^{-8}$	0.16
pH	<b>0.0003</b>	0.47	0.18	0.29	0.47	0.9	0.86	<b>0.04</b>	0.94
turbidity	$10^{-7}$	<b>0.001</b>	0.91	<b>0.012</b>	0.15	0.94	0.86	$10^{-10}$	0.22

Table 3.4: Significance (p-values) of treatments on water physico-chemistry.

Chlorophyll *a* concentration measured by the multiparameter probe (Fig.A-3A) had the same response to our treatments than the chlorophyll *a* concentration measured by the BBE probe (Fig.3.3A) with positive effects of light and fish and a fish×light interaction. The water column was stratified for all parameters

(but the difference between 50 cm and 150 cm is in average equal to  $0.5^{\circ}\text{C}$  for temperature) with a larger chlorophyll *a* concentration at greater depth (Fig.A-3B). However, fish presence did not decrease chlorophyll *a* concentration stratification, thus fish did not affect phytoplankton through water mixing and resuspension. Oxygen concentration (Fig.A-3D) and pH (Fig.A-3E) were positively affected by fish but not by light, while turbidity responded to our treatments similarly to chlorophyll *a* (Fig.A-3F).

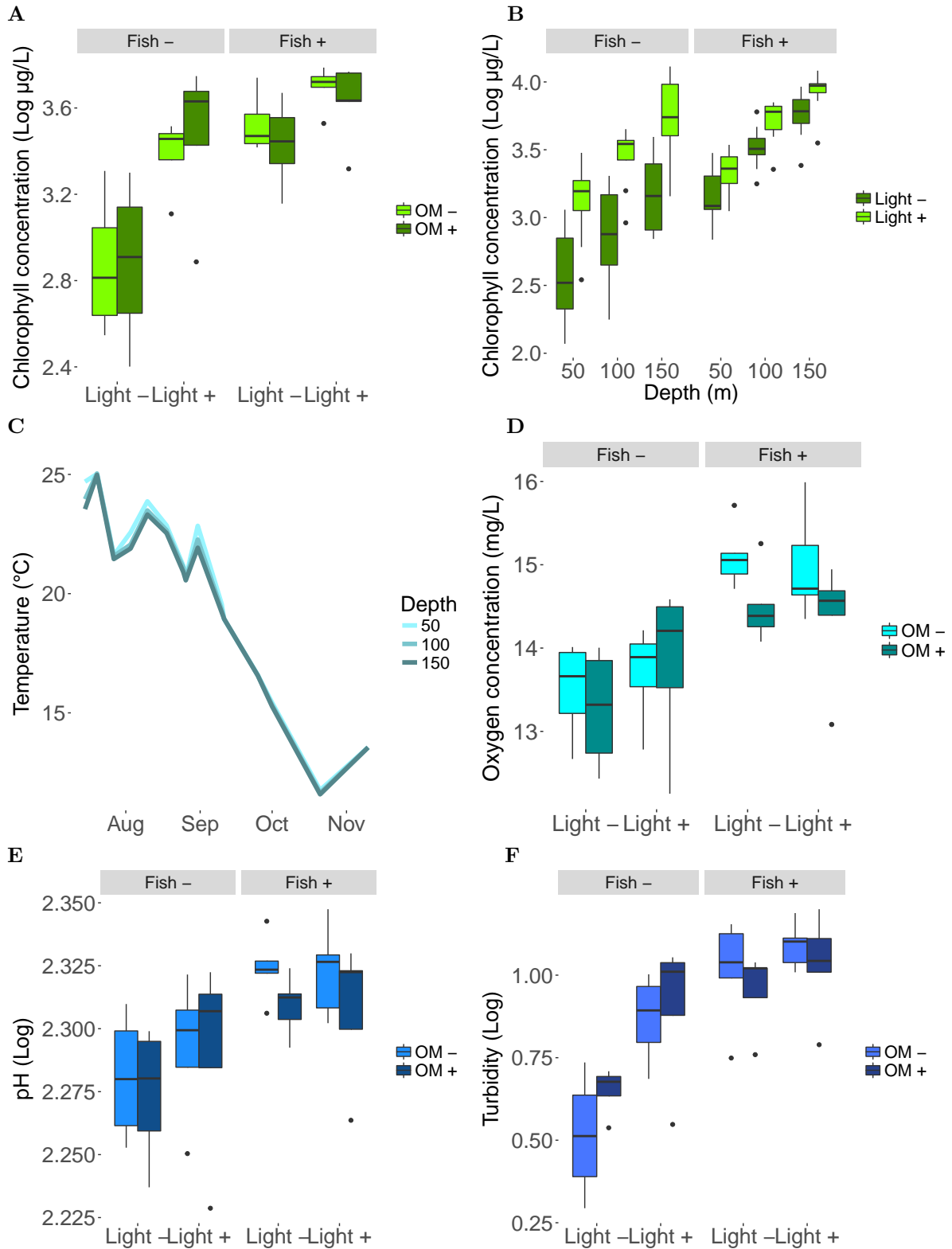


Figure A-3: Physico-chemistry of the water measured the multiparameter prob and aggregated from July to November. **A)** Chlorophyll concentration **B)** Chlorophyll concentration at three depths **C)** Temperature at three depths **D)** Oxygen concentration. **E)** pH **F)** Turbidity.



## Ecoplates

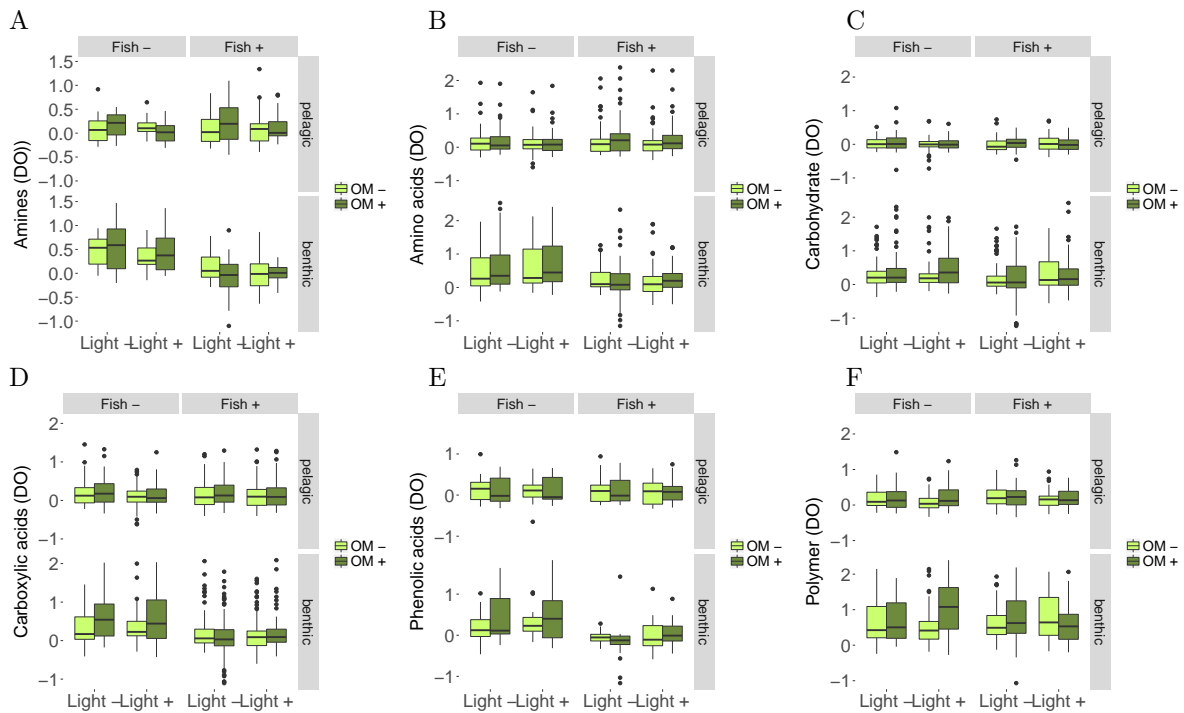


Figure A-4: DO after 7 days for the different families of substrates.

	Fish (F)	Light (L)	OM	F:L	F:OM	L:OM	F:L:OM	date	substrate
<b>Pelagic</b>									
Amines	0.62	0.34	0.55	0.80	0.30	0.077	0.85	$10^{-8}$	0.14
Amino acids	0.16	0.13	<b>0.041</b>	0.80	0.19	0.90	0.73	$10^{-16}$	$10^{-16}$
Carbohydrates	0.67	0.80	0.21	0.32	0.43	0.18	0.32	$10^{-6}$	$10^{-14}$
Carboxylic acids	0.50	<b>0.012</b>	0.19	0.31	0.80	0.95	0.98	$10^{-16}$	$10^{-16}$
Phenolic acids	0.75	0.39	0.79	0.86	0.997	0.51	0.82	$10^{-10}$	$10^{-15}$
Polymer	0.58	0.18	0.17	0.56	0.25	0.21	0.17	$10^{-9}$	$10^{-13}$
<b>Benthic</b>									
Amines	$10^{-12}$	0.34	0.84	0.45	<b>0.05</b>	0.30	0.41	-	<b>0.0008</b>
Amino acids	$10^{-16}$	0.37	0.090	0.30	0.10	0.54	0.58	-	$10^{-16}$
Carbohydrates	<b>0.0002</b>	<b>0.008</b>	0.41	0.16	<b>0.015</b>	0.98	0.24	-	$10^{-16}$
Carboxylic acids	$10^{-16}$	0.56	<b>0.012</b>	0.55	$10^{-5}$	0.63	0.21	-	$10^{-16}$
Phenolic acids	$10^{-9}$	0.12	0.18	0.71	0.073	0.58	0.21	-	$10^{-10}$
Polymer	0.41	0.21	0.21	0.53	0.055	0.63	<b>0.011</b>	-	$10^{-6}$

Table 3.5: Significance (p-values) of treatments on the degradation capacity by bacteria of substrate families present in the EcoPlates Biolog.

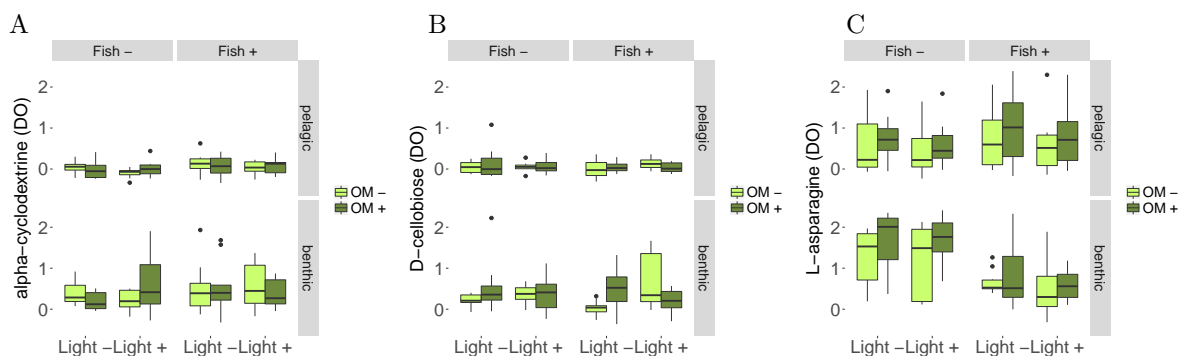


Figure A-5: DO after 7 days for: **A)**  $\alpha$ -cyclodextrine, **B)** D-cellobiose and **C)** L-asparagine.

Pelagic	Fish (F)	Light (L)	OM	F:L	F:OM	L:OM	F:L:OM	date
$\alpha$ -cyclodextrine	0.051	0.32	0.92	0.89	0.65	0.12	0.69	<b>0.0072</b>
D-cellobiose	0.63	0.79	0.76	0.27	0.37	0.13	0.75	0.031
L-asparagine	0.18	0.22	0.12	0.85	0.79	0.95	0.98	<b><math>10^{-7}</math></b>
Benthic	Fish (F)	Light (L)	OM	F:L	F:OM	L:OM	F:L:OM	date
$\alpha$ -cyclodextrine	0.78	0.30	0.96	0.48	0.45	0.50	0.096	-
D-cellobiose	0.48	0.27	0.76	0.24	0.24	<b>0.0086</b>	0.30	-
L-asparagine	<b><math>10^{-6}</math></b>	0.47	0.081	0.76	0.19	0.88	0.86	-

Table 3.6: Significance (p-values) of treatments on the degradation capacity of  $\alpha$ -cyclodextrine, D-cellobiose (two of the molecules used in the organic carbon addition treatment (OM)) and L-asparagine by bacteria.

As presented in Fig.3.4E, fish had a strong negative effect on the degradation capacity of the substrates of the EcoPlates (Fig.A-4). In addition, bacteria had a poor degradation capacity of the two recalcitrant molecules of our organic matter addition:  $\alpha$ -cyclodextrine (Fig.A-5A) and cellobiose (Fig.A-5B), compared to asparagine (Fig.A-5C) for instance. The degradability capacity for both molecules was not significantly affected by our organic matter addition treatment (table 3.6). This might explain the weak general effects of our organic matter addition compared to previous studies (Faithfull et al., 2011; Degerman et al., 2018).

## Zooplankton

Zooplankton counting at the genus level. Two dates are represented: August (Fig.A-6) and September (Fig.A-7). We aggregated the two dates or treated them as independent data sets to test the robustness of the effects of our treatments over time. When dates were aggregated, sampling date was included in the model.

Copepoda were positively affected by light when Cyclopidae and nauplii were aggregated over the two sampling dates (Fig.3.6A and table 3.2). However, we only see a positive effect of fish in August sampling (Fig.A-6A and B, Fig.A-7A and B and table 3.7) for aggregated and non aggregated data and light effect is not significant. Thus, fish had a positive effect on Copepoda at the beginning of the experiment but this effect vanished later while the positive effect of fish on Chydoridae (the only Cladocera in our experiments, except in one mesocosm) held at the two sampling dates (Fig.A-6C and Fig.A-7C).

Rotifers were not affected by our treatments when the two sampling dates were aggregated (Fig.3.6D). However, a significant effect of the addition of organic matter was observed in September (table 3.7). This effect was observed in September for Bdelloid, Brachionus (positive effect) and Polyarthra (negative effect). Polyarthra were negatively affected by organic matter addition while full light exposure had a positive effect. Thus Bdelloid and Brachionus can be associated to the brown food web while Polyarthra would be assimilated to the green food web. Fish had a negative effect on Bdelloid (Fig.A-6G) and Polyarthra (Fig.A-6H) and a positive effect on Keratella (Fig.A-6I) in August. In September, the effect of fish on Bdelloid (Fig.A-7G) and Keratella (Fig.A-7I) was still visible. Anuraeopsis (Fig.A-7K) and Lecane (Fig.A-7E) were negatively affected by fish. Thus, except for Keratella, fish had a negative effect on many rotifer species.

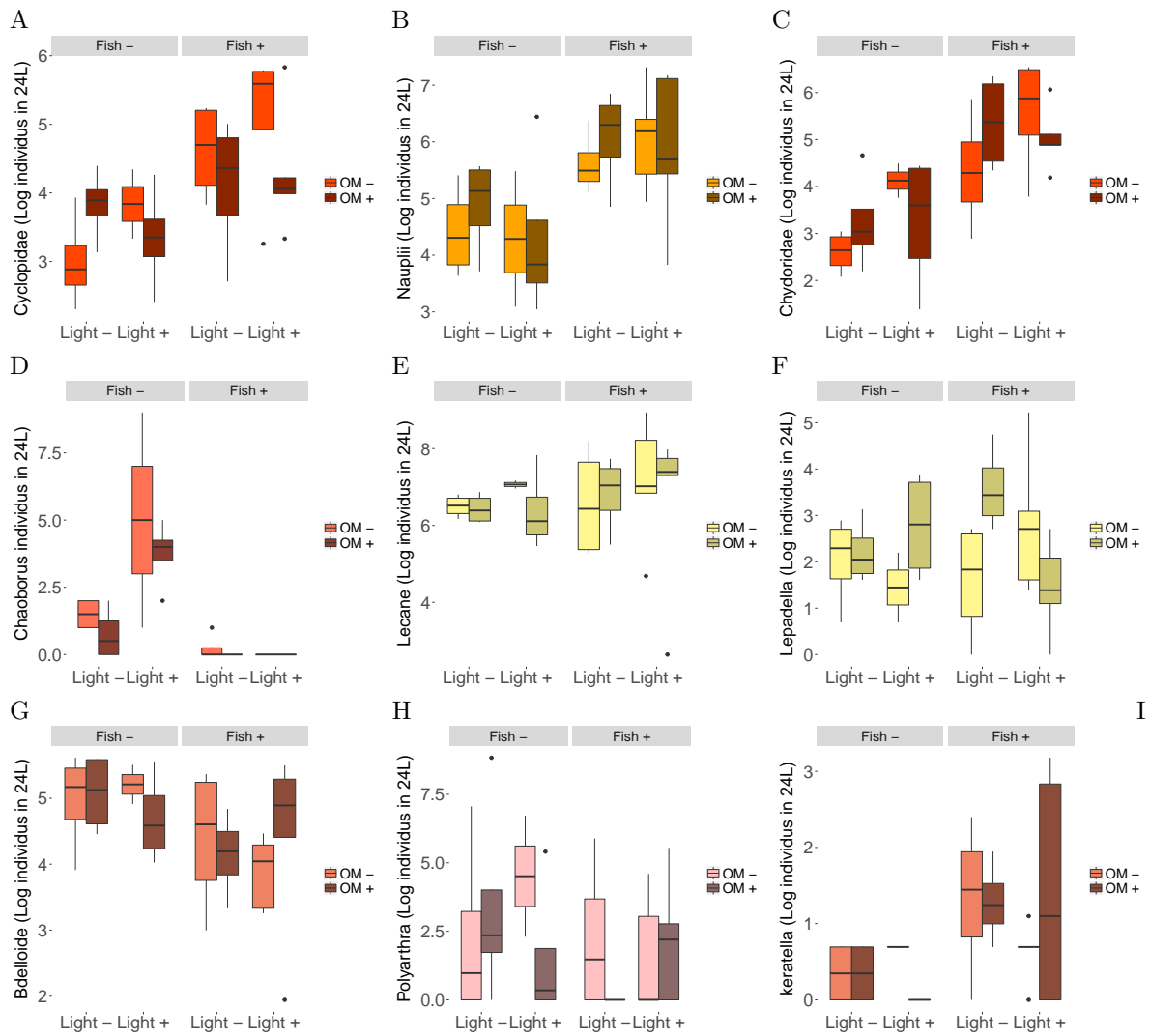


Figure A-6: Zooplankton numeration from 24 L samples (19/08/2015) **A)** Cyclopidea (large Copepoda) **B)** Nauplii (Copepoda juveniles) **C)** Chydoridae (small Cladocera) **D)** Chaoborus (large Diptera larvae) **E)** Lecane (rotifer) **F)** Lepadella (rotifer) **G)** Bdelloid (rotifer) **H)** Polyarthra (rotifer) **I)** Keratella (rotifer).

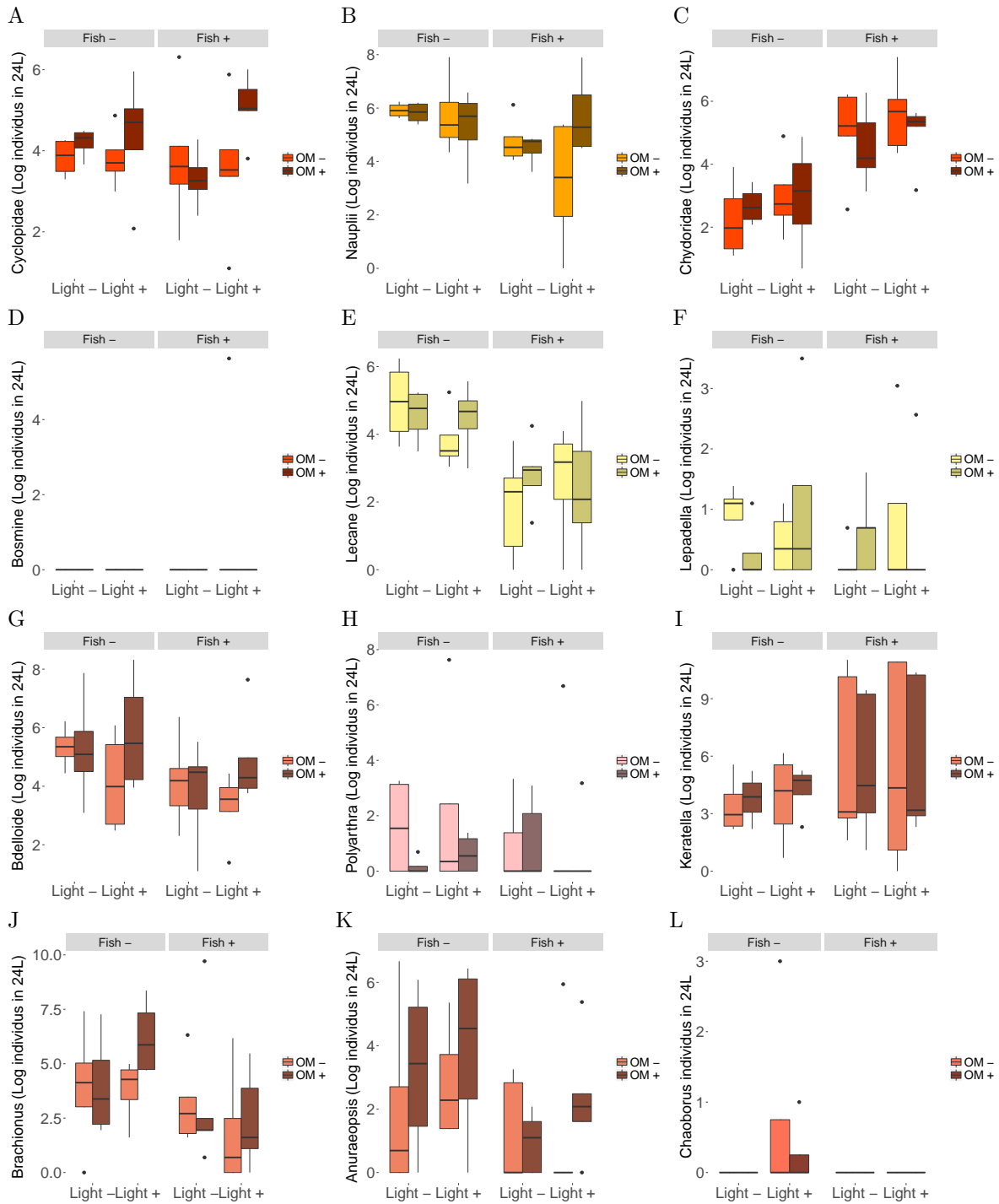


Figure A-7: Zooplankton numeration from 24 L samples (25/09/2015) **A)** Cyclopidae (large Copepoda) **B)** Nauplii (Copepoda juveniles) **C)** Chydoridae (small Cladocera) **D)** Bosmine (small Cladocera) **E)** Lecane (rotifer) **F)** Lepadella (rotifer) **G)** Bdelloid (rotifer) **H)** Polyarthra (rotifer) **I)** Keratella (rotifer) **J)** Brachionus (rotifer) **K)** Anuraeopsis (rotifer) **L)** Chaoborus (large Diptera larvae).

Taxa	Fish (F)	Light (L)	OM	F:L	F:OM	L:OM	F:L:OM
Cyclopidae	<b>0.014</b>	0.053	0.79	0.69	0.13	0.25	0.51
Nauplii	0.60	0.052	0.61	0.75	0.11	0.84	0.32
Chydoridae	<b>10<sup>-8</sup></b>	0.11	0.11	0.51	0.42	0.055	0.83
Lecane	<b>0.033</b>	0.73	0.20	0.75	0.79	0.64	0.77
Lepadella	0.28	0.62	0.84	0.22	0.25	<b>0.030</b>	<b>0.0051</b>
Bdelloide	<b>0.0083</b>	0.40	<b>0.011</b>	0.59	0.55	0.12	0.38
Polyarthra	<b>0.0055</b>	0.50	0.80	0.79	0.76	<b>0.023</b>	0.25
Keratella	<b>10<sup>-8</sup></b>	0.19	<b>0.015</b>	0.98	0.91	0.36	0.90
Brachionus	0.47	0.076	<b>0.0038</b>	<b>0.045</b>	0.38	0.60	0.10
Chaoborus	-	-	-	-	-	-	-
19/08/2015	Fish (F)	Light (L)	OM	F:L	F:OM	L:OM	F:L:OM
Cyclopidae	<b>0.0012</b>	0.16	0.13	0.69	0.36	0.43	0.58
Nauplii	<b>0.0021</b>	0.34	0.41	0.86	0.93	0.52	0.82
Chydoridae	<b>10<sup>-5</sup></b>	0.36	0.76	0.56	0.77	<b>0.022</b>	0.93
Chaoborus	-	-	-	-	-	-	-
Lecane	0.054	0.15	0.33	0.97	0.81	0.67	0.93
Lepadella	0.29	0.91	0.93	0.36	0.43	0.066	<b>0.034</b>
Bdelloide	<b>0.033</b>	0.72	0.85	0.79	0.55	0.45	0.062
Polyarthra	<b>0.017</b>	0.087	0.23	0.82	0.76	0.32	0.23
Keratella	<b>0.0005</b>	0.68	0.16	0.99	0.43	0.061	0.12
Brachionus	-	-	-	-	-	-	-
25/09/2015	Fish (F)	Light (L)	OM	F:L	F:OM	L:OM	F:L:OM
Cyclopidae	0.40	0.20	0.56	0.74	0.35	0.070	0.41
Nauplii	0.28	0.12	0.77	0.57	0.094	0.78	0.098
Chydoridae	<b>10<sup>-5</sup></b>	0.18	0.085	0.69	0.53	0.50	0.81
Bosmine	-	-	-	-	-	-	-
Lecane	<b>0.0001</b>	0.30	0.81	0.26	0.64	0.17	0.42
Lepadella	0.66	0.055	0.51	0.81	0.30	0.70	0.11
Bdelloide	<b>0.044</b>	0.42	<b>0.029</b>	0.66	0.64	0.26	0.52
Polyarthra	0.12	<b>0.0050</b>	<b>0.0046</b>	0.89	0.66	0.59	0.95
Keratella	<b>10<sup>-5</sup></b>	0.36	0.087	0.99	0.93	0.53	0.93
Brachionus	0.61	0.21	<b>0.042</b>	0.17	0.55	0.72	0.26
Anuraeopsis	<b>0.037</b>	0.65	0.66	0.10	0.25	0.19	0.85
Chaoborus	-	-	-	-	-	-	-
09/08/2015	Fish (F)	Light (L)	OM	F:L	F:OM	L:OM	F:L:OM
Copepods	<b>0.0009</b>	0.26	0.67	0.81	0.80	0.46	0.92
Chladocerans	<b>10<sup>-5</sup></b>	0.36	0.76	0.56	0.77	0.022	0.93
Chaoborus	-	-	-	-	-	-	-
Rotifers	0.81	0.89	0.97	0.36	0.51	0.37	0.50
25/09/2015	Fish (F)	Light (L)	OM	F:L	F:OM	L:OM	F:L:OM
Copepoda	0.41	0.11	0.7	0.72	0.22	0.50	0.093
Chladocera	<b>10<sup>-5</sup></b>	0.11	<b>0.05</b>	0.70	0.48	0.41	0.78
Chaoborus	-	-	-	-	-	-	-
Rotifers	0.74	0.70	<b>0.046</b>	0.24	0.44	0.89	0.38

Table 3.7: Significance (p-values) of treatments on zooplankton taxa abundance. Each subpart corresponds respectively to data at the genus level aggregated for dates, data at the genus level analysed independently for the two dates and aggregated genus analysed independently for the two dates.

## Chapter 4

# Metabolic adjustment enhances food web stability

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### Abstract

Understanding ecosystem stability is one of the greatest challenges of ecology. Over several decades, it has been shown that allometric scaling of biological rates and feeding interactions provide stability to complex food web models. Moreover, introducing adaptive responses of organisms to environmental changes (*e.g.* like adaptive foraging that enables organisms to adapt their diets depending on resources abundance) improved species persistence in food webs. Here, we introduce the concept of metabolic adjustment, *i.e.* the ability of species to slow down their metabolic rates when facing starvation and to increase it in time of plenty. We study the reactions of such a model to nutrient enrichment and the adjustment speed of metabolic rates. We found that increasing nutrient enrichment leads to a paradox of enrichment (increase in biomasses and oscillation amplitudes and ultimately extinction of species) but metabolic adjustment stabilises the system by dampening the oscillations. Metabolic adjustment also increases the average biomass of the top predator in a tri-trophic food chain. In complex food webs, metabolic adjustment has a stabilising effect as it promotes species survival by creating a large diversity of metabolic rates. However, this stabilising effect is mitigated in enriched ecosystems. Phenotypic plasticity of organisms must be considered in food web models to better understand the response of organisms to their environment. As metabolic rate is central in describing biological rates, we must pay attention to its variations to fully understand the population dynamics of natural communities.

## Introduction

Identifying the mechanisms responsible for ecosystem stability is one of the main scientific tasks in ecology (de Ruiter, 2005; Montoya et al., 2006; Rooney and McCann, 2012; Loreau and de Mazancourt, 2013; Brose et al., 2017). A prevailing view in ecology is that large, complex ecosystems were particularly stable (in the sense of dynamic stability, defined by the equilibrium stability and the variability (Pimm, 1984; McCann, 2000)) thanks to many mechanisms resulting from the diversity of interacting species (MacArthur, 1955; Elton, 1958), but early mathematical models predicted the opposite results. However, mathematical models of ecosystems predicted opposite results. For instance, the theoretical study performed by May (1972) demonstrated that diversity, complexity (measured by the linkage probability between pairs of species) and the average interaction strength decreased the stability of random interaction networks (assessed by a linear stability analysis).

Subsequently, many mechanisms promoting food web stability were identified (McCann, 2000; Loeuille, 2010; Jacob et al., 2011; Rooney and McCann, 2012; Brose et al., 2017) and two of them inspired us to implement a new one in food web models. The first mechanism is the allometric scaling of biological rates (*e.g.* metabolic rate, feeding strength), describing them as power functions of individual body mass (Yodzis and Innes, 1992; Brown et al., 2004b; Savage et al., 2004b; Brose et al., 2008; Pawar et al., 2012; Kalinkat et al., 2013). These relationships provided a better prediction of species biomasses in empirical data than any other model parametrisation (Boit et al., 2012; Hudson and Reuman, 2013). In addition, allometric scaling coupled with size structured communities (*i.e.* consumers larger than their prey) lead to more stable food webs with fewer extinctions (Brose et al., 2006b; Brose, 2008; Kartascheff et al., 2010). The second mechanism is adaptive foraging. Kondoh (2003) included adaptive foraging behaviour into food web models to enable the consumers to maximise their biomass income by preferentially hunting more abundant prey. The result is dramatic, with a reversion of the pattern predicted by May (1972): with adaptive foragers, increasing species richness and complexity enhances species persistence. Furthermore, food webs with randomly set interactions and adaptive foraging converge towards size-structured food webs with predators systematically larger than their prey (Heckmann et al., 2012). In such models, species biomasses are not the only dynamic variables, food web structures and interaction parameters are also dynamic (de Ruiter, 2005). However, one central parameter has always been considered constant in food web models: the metabolic rate. The closest examples to adjustable metabolic rates were given by Kuwamura et al. (2009), Nakazawa et al. (2011) and Wang and Jiang (2014) who considered simple models with a structured population of *Daphnia* including metabolically active adults and dormant eggs. In nature, however, many organisms exhibit phenotypic plasticity in the expression of metabolism (Brown et al., 2004b; Glazier, 2005; Jeyasingh, 2007; Glazier, 2009a; Carey et al., 2013; Norin et al., 2015). In fact, Makarieva et al. (2005) pointed out that organisms with different body sizes can display similar metabolic rates depending on their activity. Moreover, animals from all major phyla are able to slow down their activity to face harsh conditions such as drought and starvation using body mass reduction (DeLong et al., 2014b), torpor, diapause (depression of 60-95%) or cryptobiosis (depression of 99-100%) (Guppy and Withers, 1999). Considering the metabolic activity of organisms as a constant parameter is a strong assumption despite its central role in food web models. In this study, we model the plastic response of metabolism similarly to adaptive foraging. As adaptive foraging maximises the growth rate of consumers by varying the foraging effort for the different prey, we propose that metabolic adjustment maximises the growth rate by varying the metabolic rate.

Based on prior studies on adaptive foraging, we can predict consequences of this adjustable metabolism for food web models. First, this adjustable behaviour should have a substantial impact on population dynamics. For instance, when the population density of the prey increases, consumers will raise their metabolic activity that is directly related to their consumption rate. The consequence is an increase in

the predation pressure and top-down control imposed by consumers on their prey at high densities. On the contrary, in periods of starvation, consumers slow down their metabolic rate to minimise their loss in biomass caused by respiration, which keeps predator biomasses at a level high enough to avoid extinction (Chesson and Huntly, 1989; Polis et al., 1996; Chesson, 2000). In this study, we address whether the combination of these two effects stabilises the dynamics of the species (decreased amplitude and increased minima of population oscillations). In consequence our second prediction is that adaptive metabolic rates increase the persistence of complex food webs. As a measure of stability, we use the time variability of species biomasses (existence of fixed points and amplitude of biomass oscillation) and species persistence (proportion of surviving species in a food web).

## Material and Methods

We study the impact of metabolic adjustment on a simple tri-trophic food chain and complex food webs. Both are modified versions of the Allometric Trophic Network (ATN) (Brose et al., 2006b) (Parameters listed in table 4.1). The complex food webs rely on the Williams and Martinez (2000) niche model for their structure and on the Yodzis and Innes (1992) predator-prey model for the dynamic equations and their parameters.

### Food web structure

The construction of the complex food webs follows the niche model (Williams and Martinez, 2000; Brose et al., 2006b; Heckmann et al., 2012; Binzer et al., 2016) as it successfully predicted the food web structures of natural communities. The trophic interactions across species are set according to the algorithm detailed by Williams and Martinez (2000) with an expected connectance equal to 0.15. The basal species described by Williams and Martinez (2000) are set as primary producers and the others as consumers. The niche values  $n_i$  (uniformly drawn in a  $[0, 1]$  interval for each of the 40 initial species) used to parametrise the niche model are also used to calculate species body mass as follows (Heckmann et al., 2012).

$$M_i = 10^{N \cdot n_i} \quad (4.1)$$

Here  $N$  is equal to 6, that means the biggest species is one million times larger than the smallest ones.

### Predator-prey population dynamics

The population dynamics of the food web follows the ATN model (Brose et al., 2006b; Williams et al., 2007).

$$\frac{dB_i}{dt} = r_i G_i B_i - \sum_{j=\text{consumers}} x_j y_j B_j F_{ji} / e_{ji} \quad (4.2a)$$

$$\frac{dB_i}{dt} = -x_i B_i + \sum_{j=\text{prey}} x_i y_i B_i F_{ij} - \sum_{j=\text{consumers}} x_j y_j B_j F_{ji} / e_{ji} \quad (4.2b)$$

These equations describe changes in relative, biomass densities of primary producers (4.2a) and consumer species (4.2b). In these equations  $B_i$  is the biomass of species  $i$ ,  $r_i$  is the mass-specific maximum growth rate of primary producers,  $G_i$  is the logistic growth rate of primary producers (Equation (4.3)),  $x_i$  is  $i$ 's mass-specific metabolic rate,  $y_i$  is the maximum consumption rate of consumers relative to their metabolic rate,  $e_{ji}$  is  $j$ 's assimilation efficiency when consuming population  $i$  and  $F_{ij}$  describes the realised fraction of  $i$ 's maximum rate of consumption achieved when consuming  $j$  (equation (4.4)). Primary producers growth rate is modelled by a logistic growth with a shared carrying capacity  $K$  which ensures a comparable



primary production among food webs, regardless the number of primary producers (equation 4.3).

$$G_i = (K - \sum_{\substack{j=\text{primary} \\ \text{producers}}} B_j)/K \quad (4.3)$$

The consumption rate of prey depends on a Holling type II functional response with predator interference (Equation (4.4)). The preference of consumers for their prey  $\omega_{ij}$  are set to  $1/p_i$  with  $p_i$  the number of consumer  $i$ 's prey as we have no a priori information on preferences. Thus, all consumption rates are only driven by consumer body masses and prey biomass densities.  $\omega_{ij}$  are recalculated after each extinction to follow the changes of the number of prey  $p_i$ .

$$F_{ij} = \frac{\omega_{ij}B_j}{B_0 + cB_iB_0 + \sum_{k=\text{prey}} \omega_{ik}B_k} \quad (4.4)$$

Here  $B_0$  is the half-saturation density of  $i$  and  $c$  the predator interference.

Basically, mass specific biological rates (biomass production, metabolic rate and maximum consumption rate) follow the negative-quarter power-law relationship with species body masses as described by the metabolic theory of ecology (Brown et al., 2004b; Savage et al., 2004b). The time scale of the system is defined by normalising the biological rates to the mass-specific growth rate of the smallest primary producer as performed by Yodzis and Innes (1992); Brose et al. (2006b); Williams et al. (2007) (Equations 4.5a and 4.5b). Then the maximum consumption rates are normalised by the metabolic rates (Equations 4.5c). Thus, the loss due to respiration and the gain due to consumption both directly depend on the metabolic rate (Equation (4.2b)).

$$r_i = \left( \frac{M_i}{M_{ref}} \right)^{-0.25} \quad (4.5a)$$

$$x_i = \frac{a_x}{a_r} \left( \frac{M_i}{M_{ref}} \right)^{-0.25} \quad (4.5b)$$

$$y_i = \frac{a_y}{a_x} \quad (4.5c)$$

With  $M$  the body mass of species  $i$ ,  $M_{ref}$  the body mass of the smallest primary producer,  $a_r$ ,  $a_x$  and  $a_y$  are allometric constants (see Brose et al. (2006b) and Williams et al. (2007) for more details on the normalisation).

This model relies on strong assumptions such as the negative-quarter power-law relationship followed by all biological rates (not observed by Pawar et al. (2012), Rall et al. (2012) for the feeding rate and Hirt et al. (2017) for the maximal speed of animals), the independence of the maximum consumption rate to prey body mass or metabolic rate or values of parameters such as  $B_0$  or  $c$ . The sensitivity of the results to these parameters or assumptions is assessed in the Supplementary material Appendix A2, Fig.B1-B4 and Fig.B12-B14.

### Metabolic adjustment model

We propose to model the metabolic adjustment by an optimisation of the mass-specific net growth rate  $g_i$  as in adaptive foraging models (Kondoh, 2003; Uchida et al., 2007) or in body mass plasticity models (DeLong et al., 2014b). Thus, the consumer adjusts its metabolic rate to maximise the balance between ingestion and respiration that both depend on metabolic rate. Metabolic adjustment does not apply to primary producers that are considered as basal resources species with constant resource supply (see

quation (4.2a)).

$$\frac{dx_i}{dt} = x_i X \frac{\partial g_i}{\partial x_i} = x_i X \left( -1 + \sum_{j=prey} e_{ij} y F_{ij} \right) \quad (4.6a)$$

$$g_i = -x_i + \sum_{j=prey} e_{ij} x_i y F_{ij} \quad (4.6b)$$

$\partial g_i / \partial x_i$  (Equation 4.6a) is the variation of the net growth rate  $g_i$  when  $x_i$  increases (its sign drives the increase or decrease of the metabolic rate),  $x_i$  is the metabolic rate (the higher is the metabolic rate, the faster is the physiological response) and  $X$  is the metabolic adjustment coefficient representing the speed of the adjustment. The higher  $X$  is, the faster the response of species to modifications of their growth rate is. The metabolic rate is bounded by 1 and 0.001 to ensure a minimum metabolic rate and to prevent a destabilising high metabolic rate. The values predicted by the equation 4.5b fall in this interval that is consistent with Makarieva et al. (2005) (Supplementary material Appendix A2, Fig.B5, B6,B7,B8). Such a large interval is meant to take into account the large variety of metabolic scopes across phyla: typically 10 for vertebrates and  $10^5$  for some tardigrades (Guppy and Withers, 1999).

### Simulations

The model is coded in *C++* and the simulations performed with the *GSL* ODE solver. The simple tri-trophic food chain only contains a primary producer, a herbivore and a carnivore. Their body masses are respectively set to 1,  $10^2$  and  $10^4$ . A more simple predator-prey system is studied in the Supplementary material Appendix A1, Fig.A2 and Fig.A3. For the complex food webs, each simulation is independent from the other and only differs in the body mass distribution and the architecture of the food web. The system starts with 40 species that all have an initial biomass density of 0.1 and the metabolic rates are initialised with the values predicted by the metabolic theory of ecology (Equation 4.5). The simulations are performed for 10,000 time steps and only the last 1000 steps are recorded. Species persistence is the proportion of the 40 initial species that survives until the end of the simulation (a species is considered as extinct if its biomass density falls below  $10^{-30}$ ). Each combination of parameters (carrying capacity  $K$  and metabolic adjustment coefficient  $X$ ) is tested for 100 different food webs yielding a total of 555,100 simulated replicates. We use species persistence (fraction of surviving species at the end of the simulation) and biomass oscillation amplitude as measures of stability. Persistence represents the global stability of the food web as it shows the ability of species to coexist and the amplitude of biomass oscillations represents the time variability of species biomass. The amplitude of biomass oscillations is presented by bifurcation diagrams representing the local extrema of dynamics along a gradient in a parameter.

Table 4.1: Parameters and variables used in the model

Variable	Value	Description
$B_i$	$\text{kg.m}^{-2}$	biomass density of species $i$
$r_i$	dimensionless	scaled mass specific maximum growth rate of species $i$
$x_i$	dimensionless	scaled mass specific metabolic rate of species $i$
$y_i$	8	scaled mass specific maximum consumption rate
$e_{ji}$	0.45	assimilation efficiency of species $i$ by species $j$ (herbivores)
	0.85	assimilation efficiency of species $i$ by species $j$ (carnivores)
$G_i$	dimensionless	density dependent growth rate of species $i$
$F_{ij}$	dimensionless	functional response of species $i$ feeding on species $j$
$B_0$	$0.5 \text{ kg.m}^{-2}$	half saturation density for consumer functional response
$c$	$0.5 \text{ m}^2.\text{kg}^{-1}$	predator interference
$\omega_{ij}$	1/nbr prey	predator $i$ preference for species $j$
$a_x/a_r$	0.138	metabolic rate allometric constant (primary producers)
	0.314	metabolic rate allometric constant (invertebrates consumers)
$X$	dimensionless	metabolic adjustment coefficient
$K$	$\text{kg.m}^{-2}$	carrying capacity of primary producers

Note: All these parameters come from [Brose et al. \(2006b\)](#).

## Results

### Effect of adaptive metabolic rate on tri-trophic chains

The first system we consider is a simple tri-trophic food chain containing a primary producer, a herbivore and a carnivore. The effects of the resource availability on species dynamics are represented by bifurcation diagrams (Fig.4.1). The food chain without metabolic adjustment ( $X = 0$ ) displays large biomass oscillations whose amplitude increases with the carrying capacity  $K$  (Fig.4.1a) and the minima reaches extremely low values, especially for the herbivore (Supplementary material Appendix A1, Fig.A1a). As there is no metabolic adjustment, the metabolic rates are constant (Fig.4.1b) and their values are those predicted by the metabolic theory of ecology (Equations 4.5a,b,c). The food chain with metabolic adjustment ( $X = 2$ ) has fixed points for  $K \leq 7$  and oscillations for  $K > 7$  (Fig.4.1a). Despite the multi-period oscillations, the system is not chaotic (Supplementary material Appendix A1, Fig.A4a). The amplitude of oscillations increases with the carrying capacity for all species but remains lower than in the food chain without metabolic adjustment. The biomass minima increases with higher values of the metabolic adjustment coefficient (Supplementary material Appendix A1, Fig.A1a). The herbivore metabolic rate remains constantly at the maximum value allowed by the model, whereas the carnivore metabolic rate increases with carrying capacity  $K$  until it oscillates for  $K > 7$  (Fig.4.1b).

The tri-trophic food chain has fixed points along a gradient in metabolic adjustment coefficients for a carrying capacity  $K = 2$  (Fig.4.2), except for  $X = 0$  (origin of the x-axis corresponding to the situation described in Fig.4.1a). Increasing the metabolic adjustment coefficient increases the biomass of the herbivore and of the carnivore while it decreases the biomass of the primary producer. However, we observe an increase in the primary producer biomass and a decrease in the herbivore biomass for the low values of  $X$ . The metabolic rate of the herbivore is maximum for  $X > 0$  and the metabolic rate of the carnivore first sharply increases with the increasing metabolic adjustment coefficient  $X$  and then it decreases (Fig.4.2b). The response is similar for  $K = 5$  and  $X < 4$  but for  $X \geq 4$  the system oscillates

(Fig.4.2a), yet it is not chaotic (Supplementary material Appendix A1, Fig.A4b). Increasing the metabolic adjustment coefficient does not increase the amplitude of biomass oscillations, it even decreases them for the primary producer. The biomass of the carnivore increases with  $X$ , the amplitude of the oscillations of its metabolic rate increases (Fig.4.2b) while the amplitude of its biomass oscillations remains mostly unchanged. Increasing the metabolic adjustment coefficient also increases the biomass minima of each species (Supplementary material Appendix A1, Fig.A1b).

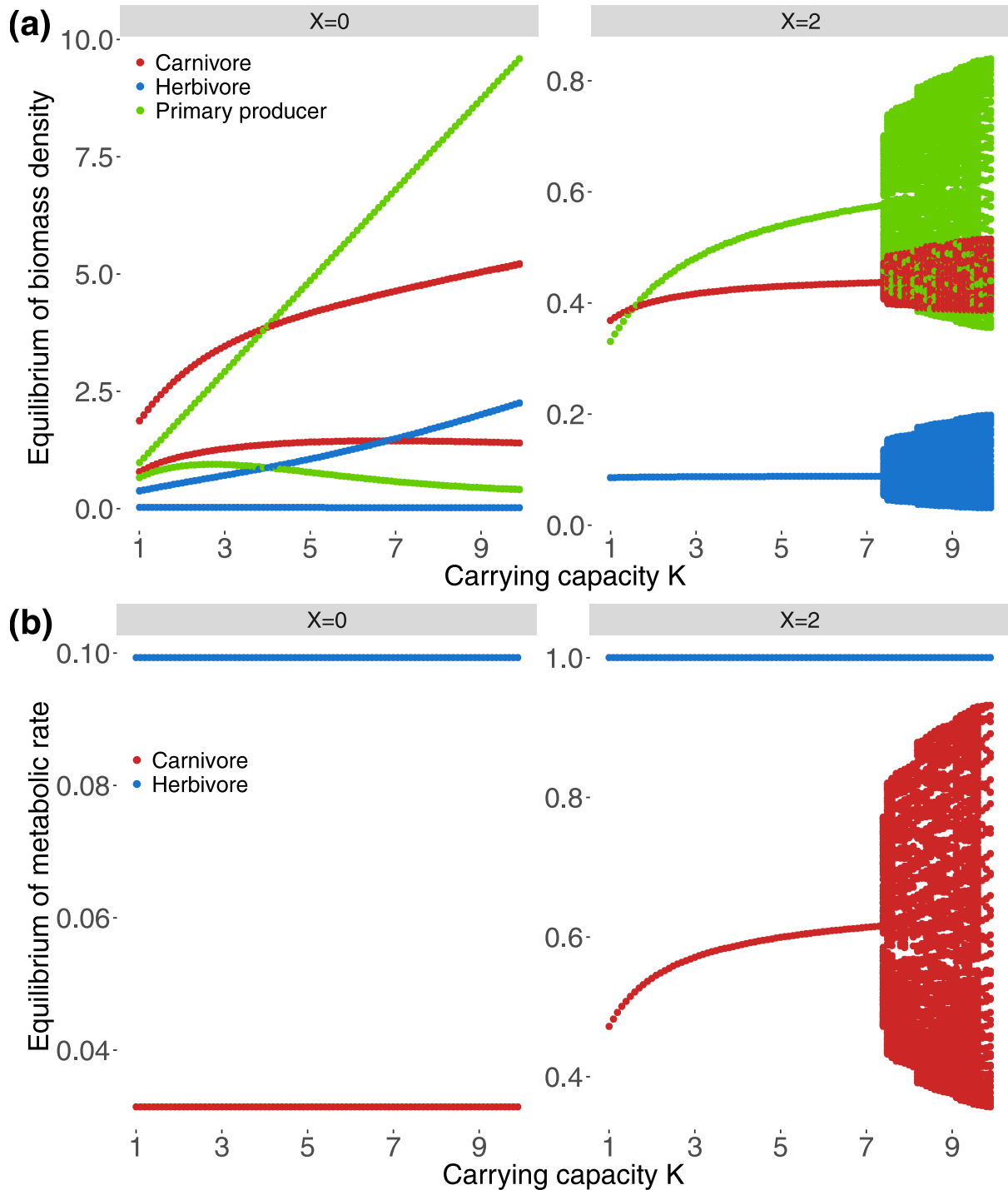


Figure 4.1: Bifurcation diagrams of the tri-trophic food-chain containing a primary producers (green), a herbivores (blue) and a carnivores (red). The bifurcation is performed along gradients in the carrying capacity  $K$  for (a) biomass density and (b) metabolic rate for a metabolic adjustment coefficient  $X = 0$  or  $X = 2$ .

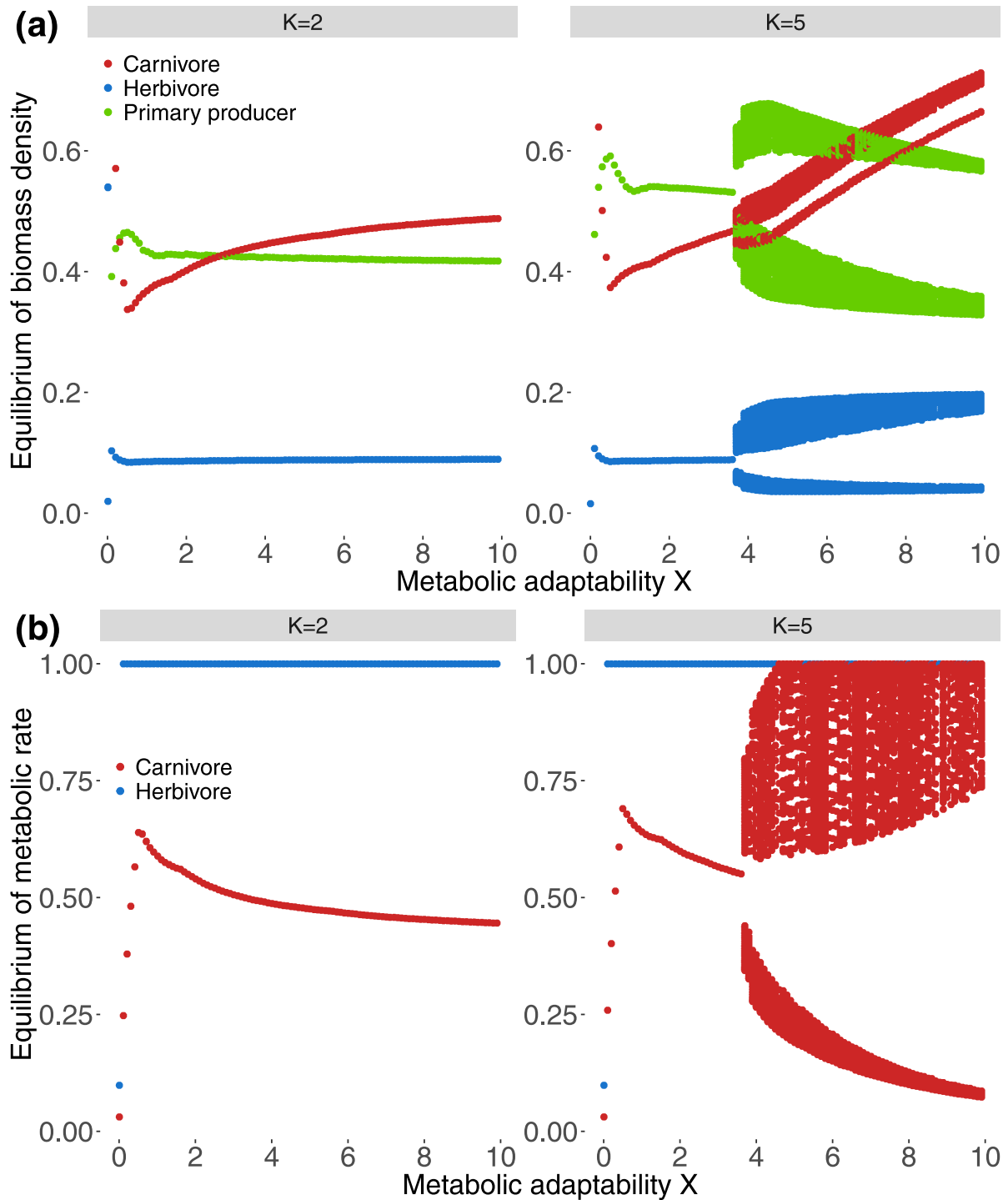


Figure 4.2: Bifurcation diagrams of the tri-trophic food-chain containing a primary producers (green), a herbivores (blue) and a carnivores (red). The bifurcation is performed along gradients in the metabolic adjustment coefficient  $X$  for (a) biomass density and (b) metabolic rate for a carrying capacity  $K = 1$  or  $K = 2$ .

### Effect of adaptive metabolic rates on persistence

The response of stability to metabolic adjustment and enrichment in complex food webs is assessed through the average species persistence (Fig.4.3a). In food webs without metabolic adjustment ( $X = 0$ ), increasing  $K$  does not significantly change species persistence that stays around 0.3. In food webs with metabolic adjustment ( $X > 0$ ), for a fixed carrying capacity  $K$ , increasing  $X$  promotes species persistence, especially at low values of  $K$  where all species can survive. If  $K > 3$ , species persistence first decreases and then increases as  $X$  increases. For a fixed value of  $X$ , increasing  $K$  decreases species

persistence and thus leads to an example of the paradox of enrichment. To sum up, enrichment through the increase of the carrying capacity has a destabilising effect on species persistence, whereas metabolic adjustment increases it substantially.

We can identify two groups of species in complex food webs: 'slow species' with a low biomass ( $< 10^{-2}$ ) and a low metabolic rate ( $< 10^{-2.5}$ ) and 'fast species' with a high biomass ( $> 10^{-2}$ ) and a high metabolic rate ( $> 10^{-2.5}$ ) (Fig.4.3b and 4.3c). Increasing the carrying capacity  $K$  does not seem to change the repartition of species in these two categories (Fig.4.3b) while more species are in an intermediate category (low biomass and high metabolic rate) at low values of metabolic adjustment coefficient  $X$  (Fig.4.3c). This difference is confirmed in Fig.4.3d where three groups of species can be identified for  $X > 0.002$ : (a) species with minimum or low metabolic rate, (b) species with intermediate metabolic rate and (c) species with maximum metabolic rate. (a) species correspond to the slow species, (b) and (c) to the fast species. Such a non-differentiation of the metabolic profile of species for low metabolic adjustment coefficients may be the origin of the first decrease of species persistence with increasing  $X$  for  $K > 3$  (Fig.4.3a).

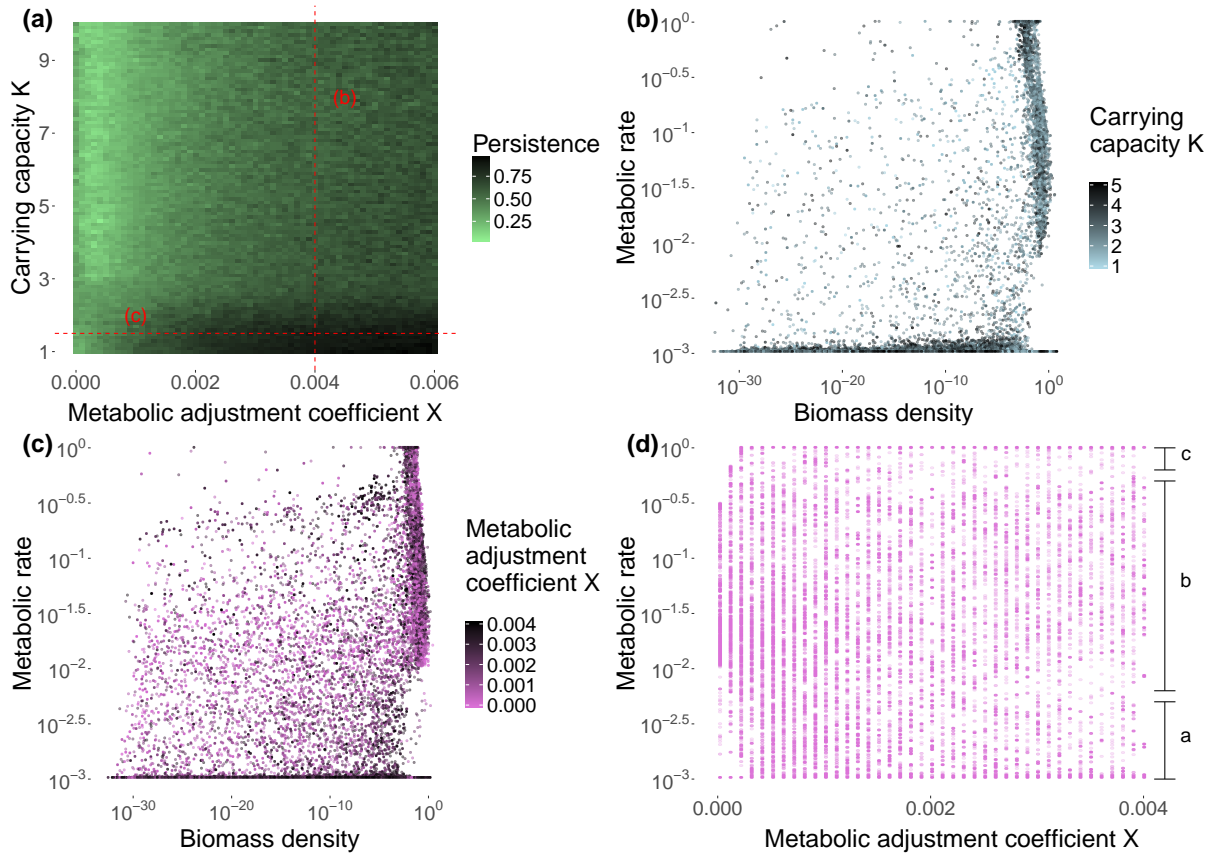


Figure 4.3: Effects of metabolic adjustment on complex food webs. **(a)** Persistence of species for different values of metabolic adjustment coefficient  $X$  and carrying capacity  $K$ . Each square represent the average persistence for 100 replicates. The dashed red lines represent the food webs whose species are represented in figures (b) and (c). **(b)** Metabolic rate versus biomass density along gradient in carrying capacity  $K$  ( $X = 0.004$ ). **(c)** Metabolic rate versus biomass density along a metabolic adjustment coefficient gradient ( $K = 1.5$ ). Each point represents one species and 100 food webs are tested for each combination of  $K$  and  $X$ . **(d)** Distribution of the average metabolic rate of each species along a metabolic adjustment coefficient gradient ( $K = 1.5$ ). The domains a, b and c represent respectively species with minimum or low metabolic rate, species with intermediate metabolic rate and species with maximum metabolic rate.

## Discussion

We studied the consequences of an adaptive metabolic rate for different aspects of food web stability. We predicted that metabolic adjustment enables species to fit their metabolic rate to their energy budget and the resource availability. In times of bonanza, it allows species to increase their activity and then to exploit more resources. In harsh times, however, metabolic adjustment also lets organisms slow down their activity to save their energy until the next season of plenty (Polis et al., 1996). This behaviour is typically the case for microbial organisms that can get encysted or can produce spores (Dawes and Ribbons, 1962; Fenchel and Finlay, 1983; Glazier, 2009b) but also larger organisms that can shift between resting and activity metabolism (Glazier, 2008; Hudson et al., 2013) or hibernating (Guppy and Withers, 1999). In the case of our models, adjustable metabolic rates reduce the magnitude of biomass oscillations and increase the average biomass of carnivores. Additionally, they greatly increase the stability of complex food webs by increasing species persistence at low resource densities.

### Effect of adaptive metabolic rate on tri-trophic food chains

Our first aim was to provide a mechanistic insight in the consequences of metabolic adjustment for population dynamics. We followed prior studies employing tri-trophic food chains with allometric scaling of population parameters, which provides a fully deterministic and easily tractable system (Otto et al., 2007; Binzer et al., 2012). First, enrichment, through the increase of the carrying capacity  $K$ , has a destabilising effect on population dynamics (Rall et al., 2008; Schwarzmüller et al., 2015). Such a destabilisation, called paradox of enrichment, is due to the unbalance between the growth and the mortality of organisms (Rosenzweig, 1971; DeAngelis, 1992; Roy and Chattopadhyay, 2007; Rip and McCann, 2011). However, this destabilising effect is dampened by metabolic adjustment that promotes fixed points or reduces the amplitude of biomass oscillations and increases the biomass minima. Increasing the speed of adjustment (*i.e.* increasing the metabolic adjustment coefficient  $X$ ) is destabilising because it promotes biomass oscillations, but it also increases the biomass of carnivores. We can compare our results to prior studies using adaptive foraging that inspired our modelling of metabolic adjustment (Kondoh, 2003, 2010; Křivan and Diehl, 2005; Mougi and Nishimura, 2008). The adaptability of predator attack rates or prey defences (Vos et al., 2004; Verschoor et al., 2004) also decreases in the amplitude of biomass oscillations, increases the average biomass of carnivores and keeps the minima away from the extinction threshold (Mougi and Nishimura, 2007). The outcome of these processes are similar because both rely on growth rate optimisation, which seems to highly improve the persistence of higher trophic levels that are generally most prone to extinction (Binzer et al., 2011). However, metabolic adjustment affects both the growth and the biomass loss rates of consumers while adaptive foraging only increases the growth rate and inducible defences decrease the mortality rate. In consequence, adaptive metabolic rates enables a better control of species dynamics, especially for top consumers whose loss rate only depends on the metabolic rate and not on predation. In our tri-trophic food chain, carnivores have a highly variable metabolic rate while the herbivore's metabolic rate always stays at the upper limit of metabolic rate range. This can be attributed to a trophic cascade: the carnivore controls the herbivore population and the primary producer thrives. Thus, the herbivore always has plenty of resources, and increasing the metabolic rate increases more the ingestion rate and the growth rate compared to the loss rate.

### Effect of adaptive metabolic rate on species persistence

Our second aim was to address the impact of an adjustable metabolic rate on the species persistence of complex food webs. The null model is a classic allometric model (Brose et al., 2006b) that displays an increase in persistence with increasing carrying capacity and increase in the energy flow in the system (Dunne et al., 2005; Rall et al., 2008). As expected, adding an adjustable metabolic rate increases the species persistence at low resources levels. Similarly to the results of studies on adaptive foraging

(Kondoh, 2003; Heckmann et al., 2012), higher adjustment coefficients (the metabolic adjustment in our case) increase species persistence. These slow species could be species with few available resources that keep their metabolic rate low most of the time, and therefore they cannot build up a high biomass densities. In contrast, fast species can exploit abundant resources and maintain a high metabolic rate to build up a high biomass density. In nature, such a pattern is represented by algal blooms and "seed banks" of micro-organisms (Lennon and Jones, 2011). However, no positive relationship between biomass density and metabolic rate has been reported across phyla in previous studies (DeLong et al., 2014a; Yashchenko et al., 2016). An opposite pattern can be seen in the tri-trophic food chain where the carnivore has a higher biomass than the herbivore and has a lower average metabolic rate. Alternatively, these slow species could just be slow in getting extinct because of their very low metabolic rate (which is the loss rate in our model). However, the substantial variation in metabolic rates of the fast species enables these species to better adapt to the specific situation concerning top-down control and resource availability in each food web, leading to an increased species persistence. The improvement in species persistence by the metabolic adjustment slips away as the carrying capacity increases. Our results obtained for the tri-trophic food chain demonstrate that metabolic adjustment dampens the paradox of enrichment but does not resolve it as in models with adaptive foraging (Mougi and Nishimura, 2007, 2008).

## Conclusion and perspectives

Previous models studied mechanisms similar to the metabolic adjustment by using structured populations of consumers with active adults and dormant eggs (Kuwamura et al., 2009; Nakazawa et al., 2011; Wang and Jiang, 2014). In these models, the resting eggs act as a refuge for the consumer, enabling them to escape from starvation. This mechanism is very different from our representation of metabolic adjustment because metabolic adjustment is an energy budget optimisation process whereas the production of resting eggs forms a kind of seed bank maintaining a high biodiversity (Jones and Lennon, 2010). This difference is emphasised by our divergent results. In fact, Nakazawa et al. (2011) found that the production of resting eggs leads to more stable population dynamics as it responds more to seasonality than to non-seasonal variation in resource availability (in this case the effect of resting eggs is weak). Metabolic adjustment (*i.e.* response to resource availability) in food webs deeply changes the outcome of the model. In fact, adjustable metabolic rates greatly increase stability regarding many criteria: they increase the average biomass of top trophic levels, decrease the variability in population biomass density and increase the minima of population biomass density, keeping them away from the extinction threshold. Including metabolic adjustment in food web models improves the representation of a highly diverse group of organisms whose metabolic activity is not predicted by the metabolic theory of ecology (Guppy and Withers, 1999; Glazier, 2005; Makarieva et al., 2008; DeLong et al., 2014b). More broadly, considering phenotypic plasticity (as it was extensively done for adaptive foraging or inducible defences for instance) is crucial to better understand the fast response of organisms to environmental changes (Marshall and McQuaid, 2011; Marshall et al., 2011; Magozzi and Calosi, 2015) and must be disentangled from variability across the individuals of a population. Interesting future directions in this research agenda would be to extend metabolic adjustment to primary producers depending on the supply of non-biotic resources affected by seasonality (*e.g.* nutrients, sun light, water...) or to include more parameters such as the attack rate in the list of biological rates directly affected by the adjustable metabolic rate. Integrating metabolic adjustment in other food web models is also essential to test for the reproducibility of our results across different food web modelling frameworks. Finally, it would also be interesting to set the metabolic adjustment coefficient  $X$  as an allometric parameter because single cell organisms are expected to respond faster than large animals for instance. Overall, adjustable metabolic rates holds great potential to represent the biology of many species in natural communities as the metabolic rate plays a central role in describing species biological functions. Hence, more experimental and field studies are



necessary to better quantify metabolic rate dynamics while former studies generally focused on measuring resting or active metabolic rate. Integrated with our modelling approach, this will provide a deepened mechanistic understanding of how adjustable metabolic rates drive population and community dynamics and eventually food-web stability.

## **Acknowledgments**

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## **Data accessibility**

All data are included in the manuscript and its supporting information. The codes are available on Zenodo and GitHub (doi:[10.5281/zenodo.1170138](https://doi.org/10.5281/zenodo.1170138)).

## A1 Appendix - Complementary results

### Effects of metabolic adjustment and carrying capacity on biomass extrema

Here are presented the minima from diagrams of bifurcation. Log transformations of minima presented in Fig.4.1 and 4.2 are used to show how the risk of extinction (i.e. having a biomass density close to zero) is affected by the carrying capacity  $K$  and the metabolic adjustment coefficient  $X$ .

Fig.A1a shows the minimal values of the diagrams of bifurcation presented in Fig.4.1 for different values of the metabolic adjustment coefficient  $X$  (represented by the color scale). In the null model ( $X = 0$ ) coloured in light blue, the minimal values of biomass density of the primary producer and the carnivore tend to be much higher than for herbivore. Then adding an adjustable behaviour to the metabolic rates of the herbivore and the carnivore (darker curves in Fig.A1a) increases the minima of the herbivore while it decreases the minima of the primary producer and of the carnivore. Increasing the value of the metabolic adjustment coefficient  $X$  decreases the minima of the primary producer and of the herbivore while it increases the minima of the carnivore.

Fig.A1b shows the minimal values of the diagrams of bifurcation presented in Fig.4.2 for different values of carrying capacity  $K$  (represented by the colour scale). The null model ( $X = 0$ ) is represented by the first points at the origin of the x-axis. For the herbivore and the carnivore, increasing metabolic adjustment coefficient  $X$  rises up minima, whatever the value taken by the carrying capacity  $K$ . But for the primary producer, the effect depends on the carrying capacity: at low carrying capacity, minima first sharply decrease, then increase and finally decrease with increasing carrying capacity.

This representation of minima gives us a more accurate insight of the stability of the system. In fact, a population with oscillating biomass densities is assumed to be more stable if the minima biomass densities stay far from zero. Here, metabolic adjustment only improves the stability of the herbivore and of the carnivore. We also notice that in food chains with metabolic adjustment, increasing resources availability rises up biomass density minima and thus partially counters effects of "paradox of enrichment".

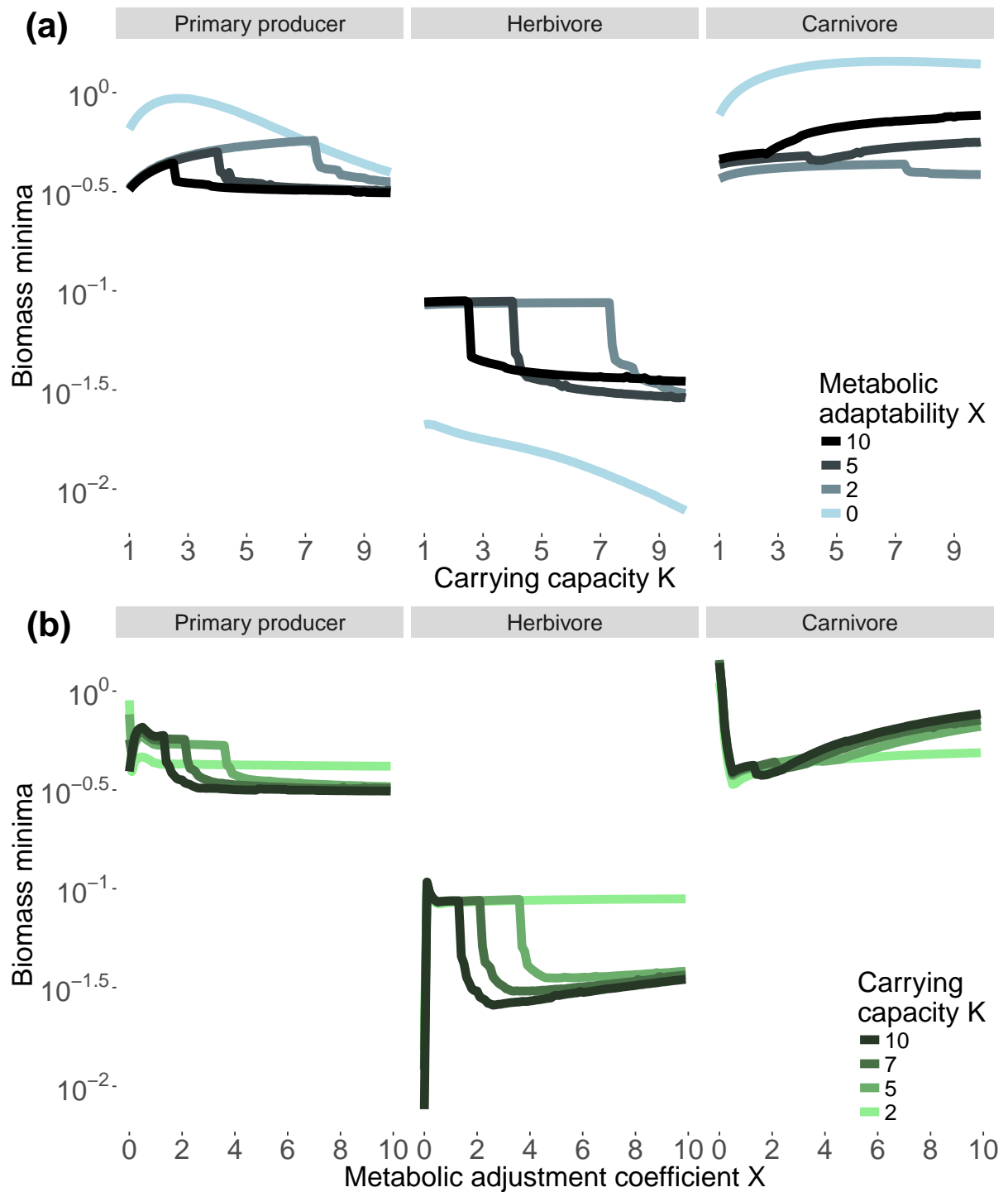


Figure A1: (a) Log transformation of minimum values taken by biomass densities in the tri-trophic food chain presented in Fig.4.1. The colour scale represents different values of metabolic adjustment coefficient  $X$ . (b) Log transformation of minimum values taken by biomass densities in the tri-trophic food chain presented in Fig.4.2. The colour scale represents different values of carrying capacity  $K$ .

## Simple predator-prey system

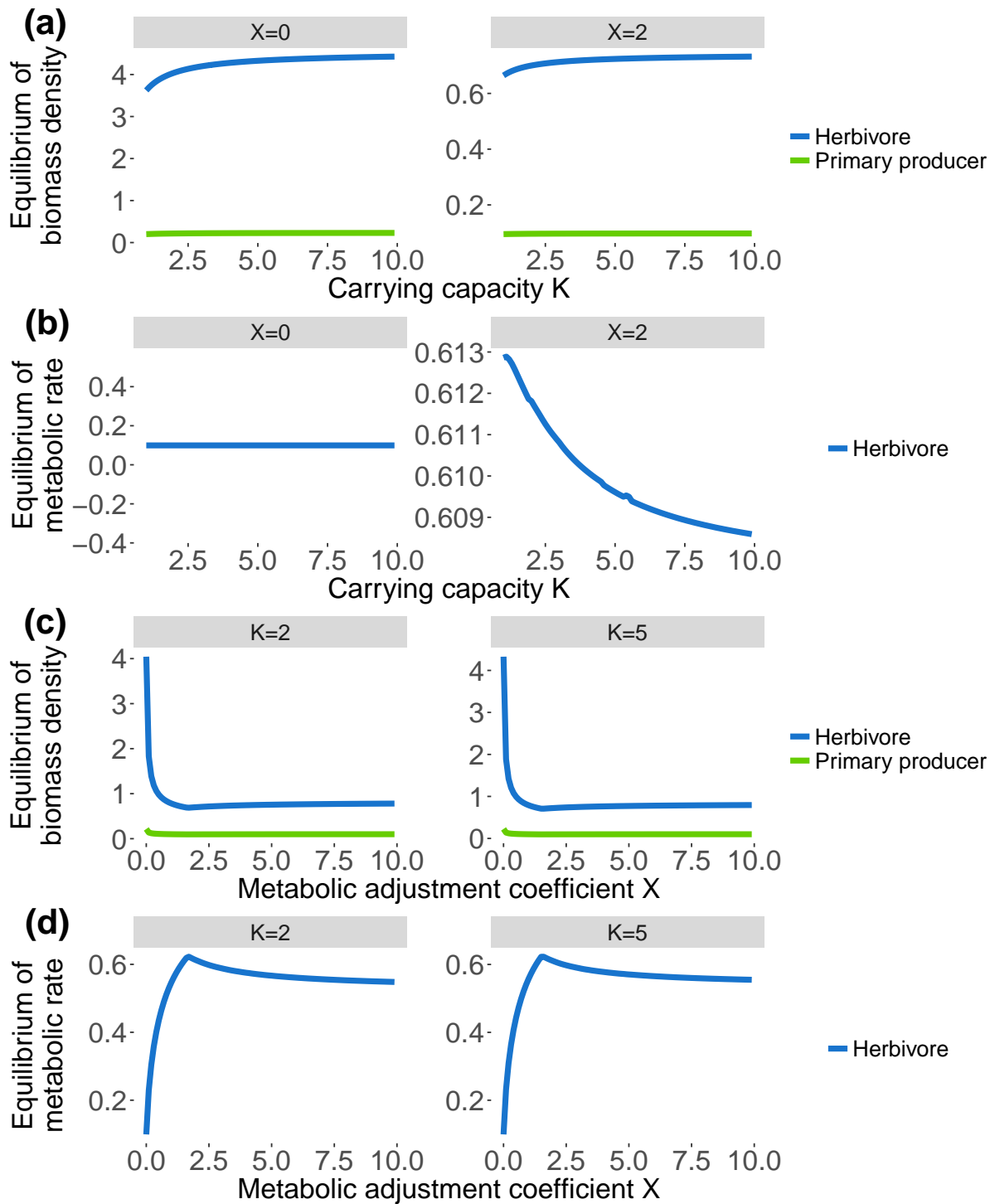


Figure A2: Predator-prey dynamics in a two species food chain. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient  $X = 0$  and  $X = 2$ . (c) Bifurcation diagrams of biomass density and (d) metabolic rate along a metabolic adjustment gradient for a carrying capacity  $K = 2$  and  $K = 5$ . The two species are a primary producer (green) and a herbivore (blue).

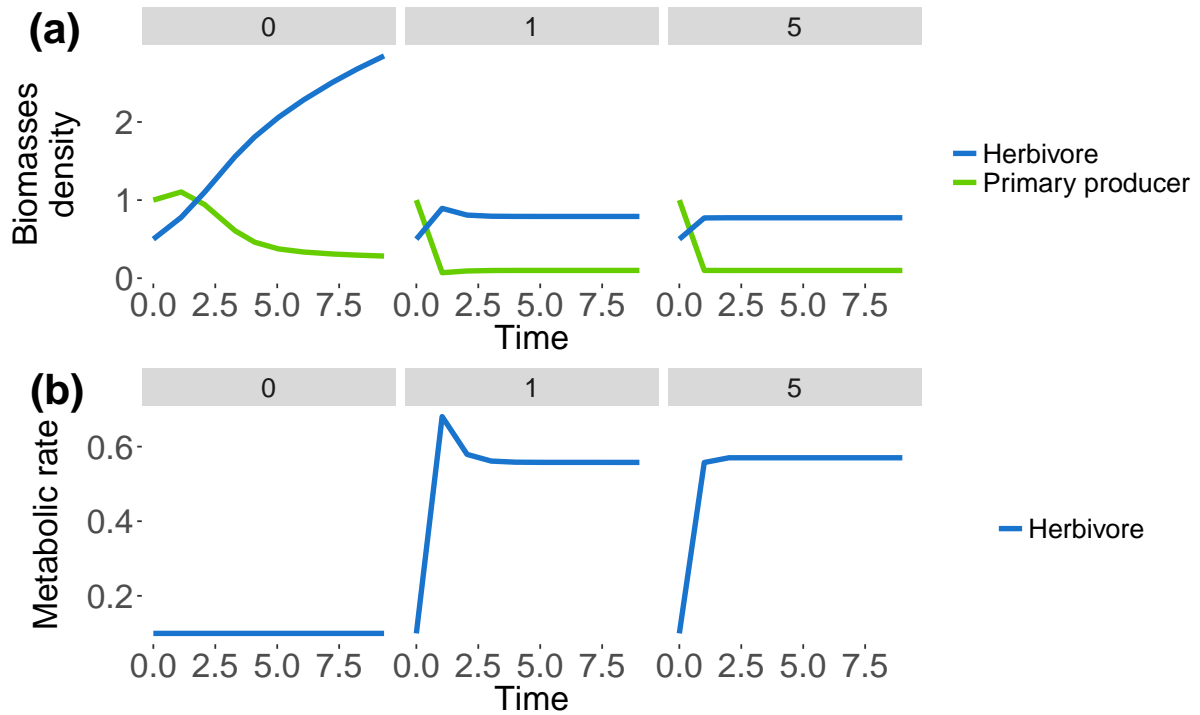


Figure A3: Predator-prey dynamics in a two species food chain. (a) Biomass densities and (b) metabolic rate dynamics for a metabolic adjustment coefficient  $X = 0$  and  $X = 2$  (carrying capacity  $K = 5$ ). The two species are a primary producer (green) and a herbivore (blue).

No oscillations are observed in the predator-prey system containing a primary producer and a herbivore. The herbivore biomass is higher without metabolic adjustment (Fig.A2a) because the metabolic rate is higher with metabolic adjustment (Fig.A2b). This leads to higher loss of biomass and thus a reduced biomass stock at equilibrium. Increasing the carrying capacity weakly affects the biomass stock and the metabolic rate of the herbivore. Increasing the metabolic adjustment coefficient  $X$  strongly decreases the biomass of the herbivore whatever the value of the carrying capacity (Fig.A2c). This decrease is due to the increase of the metabolic rate with the carrying capacity (Fig.A2d). The decrease of the biomass of the herbivore at equilibrium in systems with metabolic adjustment is due to the increase of the metabolic rate (Fig.A3a and b). Metabolic adjustment maximises the growth rate and the system quickly reach its equilibrium: primary producer biomass decreases quickly and the herbivore cannot accumulate biomass (Fig.A3a). At last, the two species food chain only has fixed points while the tri-trophic food chain is oscillating at steady state in the same parameter space.

### Lyapunov exponents of the food chain

The calculation of the Lyapunov spectrum is performed according to the method described by [Wolf et al. \(1985\)](#) and [Ramasubramanian and Sriram \(2000\)](#) (originally developed by [Shimada and Nagashima \(1979\)](#) and [Benettin et al. \(1980\)](#) independently). The ODE system comprises the non linear equations of the three-trophic food chain (equations 4.7a-e describing the dynamics of species biomasses  $B_i$  and their metabolic rates  $x_i$ ) and the linearised equations defined by the matrix product  $J.X$ , where  $J$  is the Jacobian matrix (the elements  $j_{ij}$  defined in the equations 4.8a-y) and  $X$  the tangent vectors. The maximum Lyapunov exponent corresponding to the three-trophic food chain, whose diagram of bifurcations are drawn in Fig.4.1 and 4.2, is given in Fig.A4. The value of the maximum Lyapunov

exponent is very close to zero ( $\sim 10^{-4}$ ) and the system can be considered as non chaotic.

$$\frac{dB_1}{dt} = r\left(\frac{K - B_1}{K}\right)B_1 - \frac{x_2yB_1B_2}{e_2(B_0 + cB_2B_0 + B_1)} \quad (4.7a)$$

$$\frac{dB_2}{dt} = -x_2B_2 + \frac{x_2yB_1B_2}{B_0 + cB_2B_0 + B_1} - \frac{x_3yB_2B_3}{e_3(B_0 + cB_3B_0 + B_2)} \quad (4.7b)$$

$$\frac{dB_3}{dt} = -x_3B_3 + \frac{x_3yB_2B_3}{B_0 + cB_3B_0 + B_2} \quad (4.7c)$$

$$\frac{dx_2}{dt} = x_2X\left(-1 + \frac{yB_1}{B_0 + cB_2B_0 + B_1}\right) \quad (4.7d)$$

$$\frac{dx_3}{dt} = x_3X\left(-1 + \frac{yB_2}{B_0 + cB_3B_0 + B_2}\right) \quad (4.7e)$$

$$j_{11} = \frac{\partial^2 B_1}{\partial t \partial B_1} = r\left(\frac{K - 2B_1}{K}\right) - \frac{x_2yB_2B_0(1 + cB_2)}{e_2(B_0 + cB_2B_0 + B_1)^2} \quad (4.8a)$$

$$j_{12} = \frac{\partial^2 B_1}{\partial t \partial B_2} = -\frac{x_2yB_1(B_0 + B_1)}{e_2(B_0 + cB_2B_0 + B_1)^2} \quad (4.8b)$$

$$j_{13} = \frac{\partial^2 B_1}{\partial t \partial B_3} = 0 \quad (4.8c)$$

$$j_{14} = \frac{\partial^2 B_1}{\partial t \partial x_2} = -\frac{yB_1B_2}{e_2(B_0 + cB_2B_0 + B_1)} \quad (4.8d)$$

$$j_{15} = \frac{\partial^2 B_1}{\partial t \partial x_3} = 0 \quad (4.8e)$$

$$j_{21} = \frac{\partial^2 B_2}{\partial t \partial B_1} = \frac{x_2yB_2B_0(1 + cB_2)}{(B_0 + cB_2B_0 + B_1)^2} \quad (4.8f)$$

$$j_{22} = \frac{\partial^2 B_2}{\partial t \partial B_2} = -x_2 + \frac{x_2yB_1(B_0 + B_1)}{(B_0 + cB_2B_0 + B_1)^2} - \frac{x_3yB_3B_0(1 + cB_3)}{e_3(B_0 + cB_3B_0 + B_2)^2} \quad (4.8g)$$

$$j_{23} = \frac{\partial^2 B_2}{\partial t \partial B_3} = -\frac{x_3yB_2(B_0 + B_2)}{e_3(B_0 + cB_3B_0 + B_2)^2} \quad (4.8h)$$

$$j_{24} = \frac{\partial^2 B_2}{\partial t \partial x_2} = -B_2 + \frac{yB_1B_2}{B_0 + cB_2B_0 + B_1} \quad (4.8i)$$

$$j_{25} = \frac{\partial^2 B_2}{\partial t \partial x_3} = -\frac{yB_2B_3}{e_3(B_0 + cB_3B_0 + B_2)} \quad (4.8j)$$

$$j_{31} = \frac{\partial^2 B_3}{\partial t \partial B_1} = 0 \quad (4.8k)$$

$$j_{32} = \frac{\partial^2 B_3}{\partial t \partial B_2} = \frac{x_3yB_3B_0(1 + cB_3)}{(B_0 + cB_3B_0 + B_2)^2} \quad (4.8l)$$

$$j_{33} = \frac{\partial^2 B_3}{\partial t \partial B_3} = -x_3 + \frac{x_3yB_2(B_0 + B_2)}{(B_0 + cB_3B_0 + B_2)^2} \quad (4.8m)$$

$$j_{34} = \frac{\partial^2 B_3}{\partial t \partial x_2} = 0 \quad (4.8n)$$

$$j_{35} = \frac{\partial^2 B_3}{\partial t \partial x_3} = -B_3 + \frac{yB_2B_3}{B_0 + cB_3B_0 + B_2} \quad (4.8o)$$

$$j_{41} = \frac{\partial^2 x_2}{\partial t \partial B_1} = \frac{x_2XyB_0(1 + cB_2)}{(B_0 + cB_2B_0 + B_1)^2} \quad (4.8p)$$

$$j_{42} = \frac{\partial^2 x_2}{\partial t \partial B_2} = -\frac{x_2XyB_1cB_0}{(B_0 + cB_2B_0 + B_1)^2} \quad (4.8q)$$

$$j_{43} = \frac{\partial^2 x_2}{\partial t \partial B_3} = 0 \quad (4.8r)$$

$$j_{44} = \frac{\partial^2 x_2}{\partial t \partial x_2} = X \left( -1 + \frac{yB_1}{B_0 + cB_2B_0 + B_1} \right) \quad (4.8s)$$

$$j_{45} = \frac{\partial^2 x_2}{\partial t \partial x_3} = 0 \quad (4.8t)$$

$$j_{51} = \frac{\partial^2 x_2}{\partial t \partial B_1} = 0 \quad (4.8u)$$

$$j_{52} = \frac{\partial^2 x_2}{\partial t \partial B_2} = \frac{x_3 X y B_0 (1 + cB_3)}{(B_0 + cB_3B_0 + B_2)^2} \quad (4.8v)$$

$$j_{53} = \frac{\partial^2 x_2}{\partial t \partial B_3} = -\frac{x_3 X y B_2 c B_0}{(B_0 + cB_3B_0 + B_2)^2} \quad (4.8w)$$

$$j_{54} = \frac{\partial^2 x_2}{\partial t \partial x_2} = 0 \quad (4.8x)$$

$$j_{55} = \frac{\partial^2 x_2}{\partial t \partial x_3} = X \left( -1 + \frac{yB_2}{B_0 + cB_3B_0 + B_2} \right) \quad (4.8y)$$

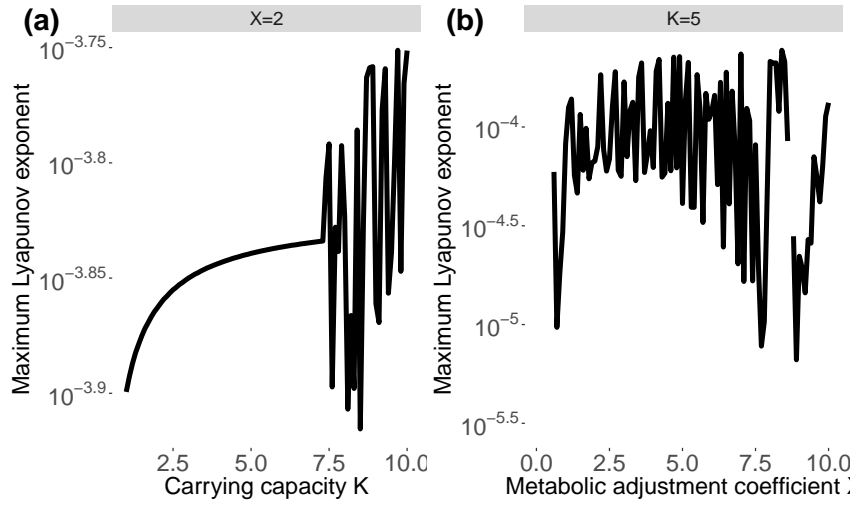


Figure A4: Maximum Lyapunov exponent of the tri-trophic food chain (a) along a carrying capacity gradient for  $X = 2$  and (b) along a metabolic adjustment coefficient gradient for  $K = 5$ .

## A2 Appendix - Sensitivity analysis

### Predator-prey interactions

#### Complex food webs

Increasing the half saturation density  $B_0$  increases species persistence at low carrying capacity  $K$  and low metabolic adjustment  $X$  in particular (Fig.B1a). A very low value of  $B_0$  leads to a low species persistence for all combinations of  $K$  and  $X$ , and species persistence becomes insensitive to enrichment (*i.e.* increase of  $K$ ). At low half saturation density  $B_0$ , consumers can strongly exploit their prey even if their density is low, leading to an increased risk of overexploitation and extinction. At higher  $B_0$ , the consumption rate of prey is lower when their density is higher. Thus, increasing  $B_0$  and  $X$  decreases the risk of overexploitation and promotes species persistence. Whatever the value of  $B_0$ , we always observe an increase of species persistence when metabolic adjustment  $X$  increases, thus the stabilising effect of metabolic adjustment on food web is robust to variations of  $B_0$ .

Predator interference  $c$  has only slight effect (Fig.B1b). There is only an increased species persistence in food webs without metabolic adjustment as seen in [Rall et al. \(2008\)](#). Our results are then not sensitive to predator interference at all.

Type III functional response leads to extremely stable food webs and increasing carrying capacity  $K$  weakly increases persistence only at low metabolic adjustment  $X$  (Fig.B1c). As in [Rall et al. \(2008\)](#), species persistence reaches a plateau when  $K$  increases, the paradox of enrichment is not visible. Increasing metabolic adjustment  $X$  strongly increases species persistence whatever the value of the carrying capacity  $K$ . Thus, the stabilising effect of metabolic adjustment exists whatever the functional response type but it is less robust at higher carrying capacity  $K$  due to the paradox of enrichment.



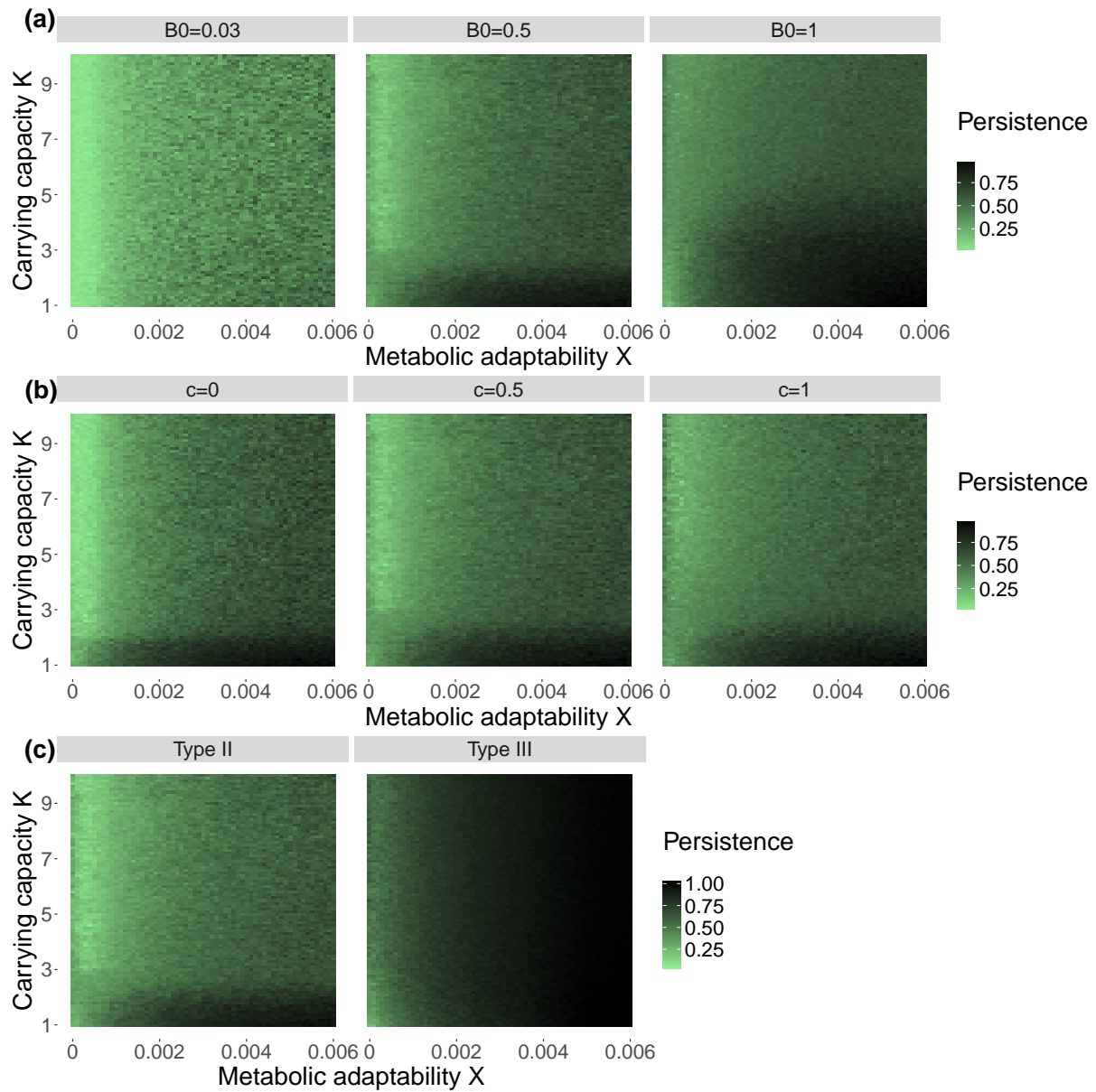


Figure B1: Effects of the predator-prey interaction parameters on species persistence in complex food webs for different values of metabolic adjustment coefficient  $X$  and carrying capacity  $K$ . Effect of (a) half saturation density  $B_0$ , (b) predator interference  $c$  and (c) functional response type. Each square represents the average persistence in 100 simulated food webs.

### Tri-trophic food chains

The dynamics in the tri-trophic food chain are highly sensitive to the half saturation density  $B_0$  (Fig.B2). In a tri-trophic food chain with metabolic adjustment ( $X=2$ ),  $B_0 = 0.03$  drives consumers to extinction,  $B_0 = 0.5$  (value used in the main study) enables the coexistence of the three species with oscillation of species biomasses at higher carrying capacity  $K$  while  $B_0 = 1$  leads to fixed points for the three species (Fig.B2a). Increasing the metabolic adjustment coefficient  $X$  leads to the survival of all species for the three values of  $B_0$  (Fig.B2c). Increasing  $B_0$  decreases the amplitude of species biomass oscillations and even leads to fixed points. The metabolic rate of the carnivore responds similarly and the metabolic rate of herbivore is always equal to its maximum possible value (Fig.B2b and B2D). The results are sensitive to  $B_0$  but increasing the metabolic adjustment always stabilises the biomass dynamics by promoting survival and by reducing the amplitude of biomass oscillations.

Predator interference  $c$  has similar effects on dynamics. Increasing  $c$  stabilises species biomass dynamics along the enrichment gradient (Fig.B3a) and metabolic adjustment coefficient gradient (Fig.B3c) by reducing the amplitude of biomass oscillations and promoting fixed points. The same response is observed for the metabolic rates (Fig.B3b and B3D) and the herbivore has always its metabolic rate equal to its maximum possible value. Such a stabilising effect of predator interference confirms previous results (Skalski and Gilliam, 2001; Lang et al., 2012)

The type III functional response always leads to fixed points for biomasses and metabolic rates (Fig.B4). The herbivore has also its metabolic rate equal to its maximum possible value.

The half saturation density  $B_0$ , the predator interference  $c$  and the functional response change the response of the tri-trophic food chain dynamics to metabolic adjustment. The dynamics observed in the main study are thus sensitive to these parameters. However, the stabilising effect of metabolic adjustment is always observed, thus the stabilising effect of metabolic adjustment is robust to these parameters.

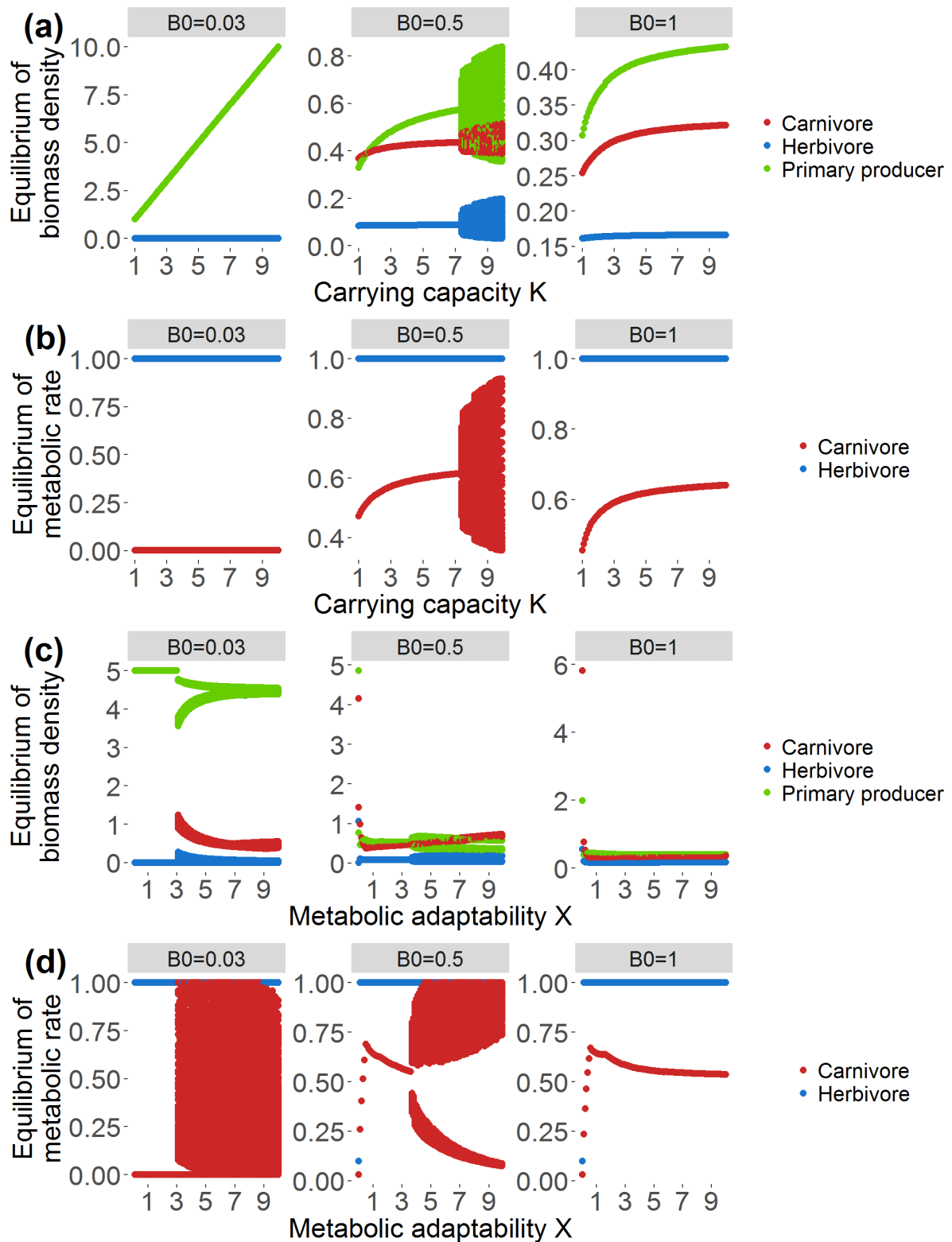


Figure B2: Effect of half saturation density  $B_0$  on three trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient  $X = 2$ . (c) Bifurcation diagrams of biomass density and (d) metabolic rate along a gradient in metabolic adjustment for a carrying capacity  $K = 5$ . The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

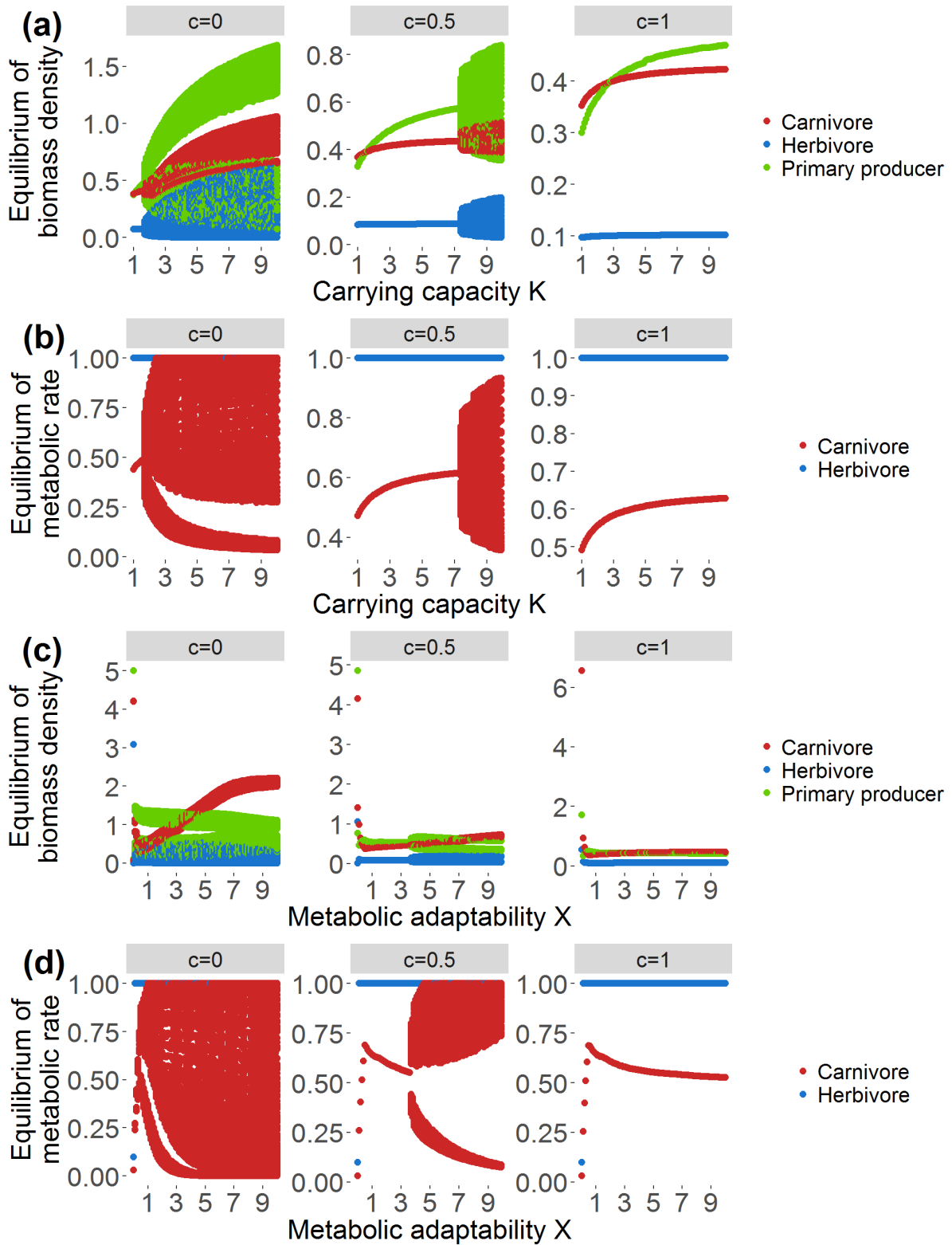


Figure B3: Effect of predator interference  $c$  on three trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient  $X = 2$ . (c) Bifurcation diagrams of biomass density and (d) metabolic rate along a gradient in metabolic adjustment for a carrying capacity  $K = 5$ . The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

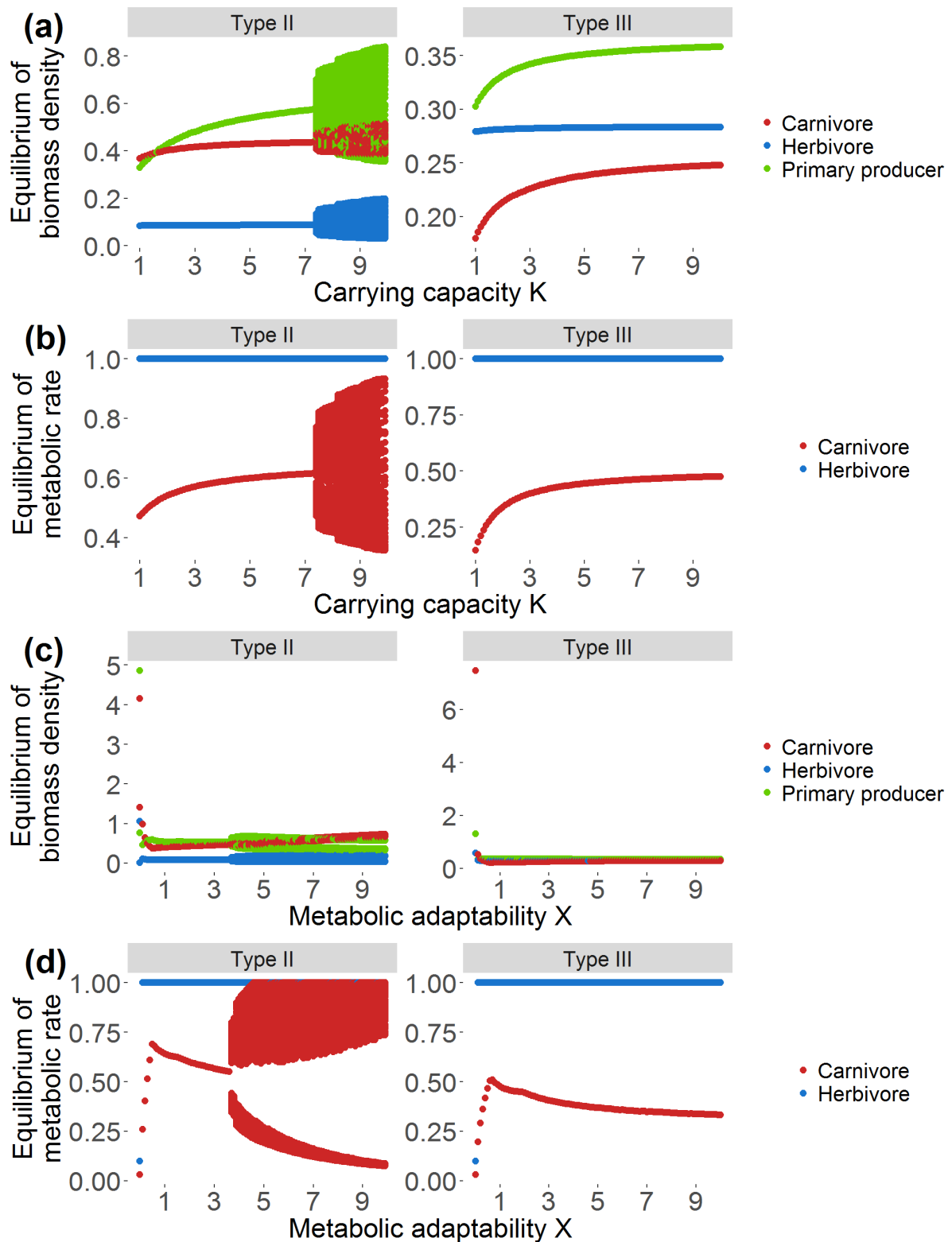


Figure B4: Effect of the functional response type on three trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient  $X = 2$ . (c) Bifurcation diagrams of biomass density and (d) metabolic rate along a gradient in metabolic adjustment for a carrying capacity  $K = 5$ . The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

## Metabolic rate boundaries

### Minimum and maximum of metabolic rate

The boundaries of the metabolic rate were chosen to include the values predicted by the MTE (Fig.B5). We tested metabolic intervals ranging over four orders of magnitude to be consistent with [Makarieva et al. \(2005\)](#). Changing the lower limits of metabolic rates does not affect species persistence in complex food webs (Fig.B6) and species biomass or metabolic rate dynamics in tri-trophic food chains (Fig.B7). Changing the upper limit does not affect species persistence in complex food webs (Fig.B6) but it can lead to the extinction of the carnivore in tri-trophic food chains (Fig.B8). Thus, to ensure species survival, we set the lower limit at  $x_{min} = 0.001$  and the upper limit at  $x_{max} = 1$  for simulations.

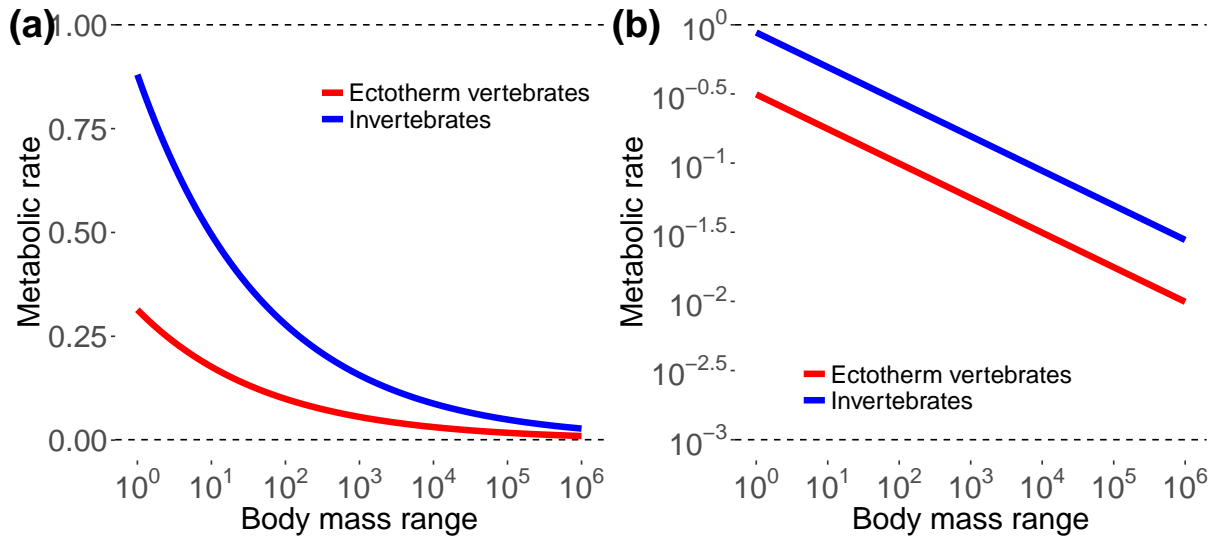


Figure B5: Normalised values of metabolic rates predicted by the MTE. Metabolic rates are calculated for invertebrates (blue) and ectotherm vertebrates (red) whose body mass ranges over six orders of magnitude. The values are represented in linear (a) and log scales (b).

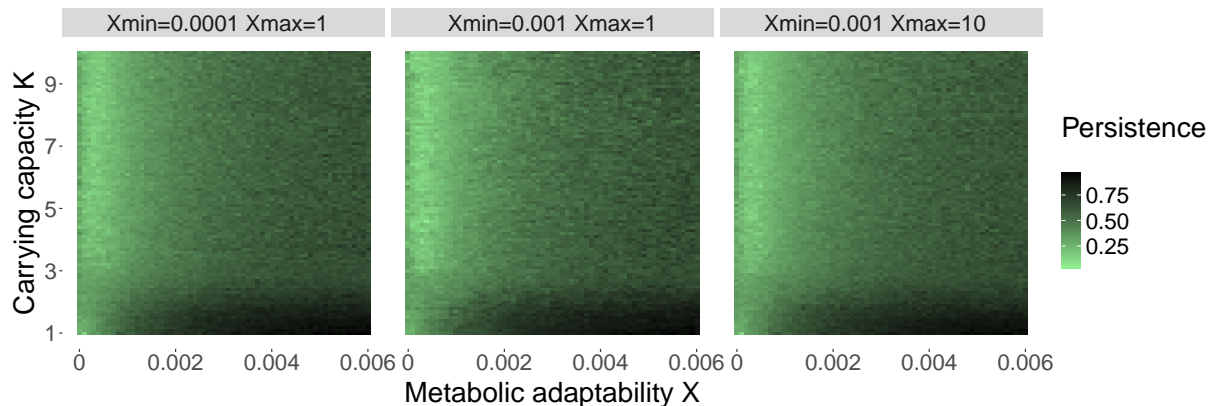


Figure B6: Effect of metabolic rate boundaries on species persistence for different values of metabolic adjustment coefficient  $X$  and carrying capacity  $K$ . Each square represents the average species persistence in 100 simulated food webs.

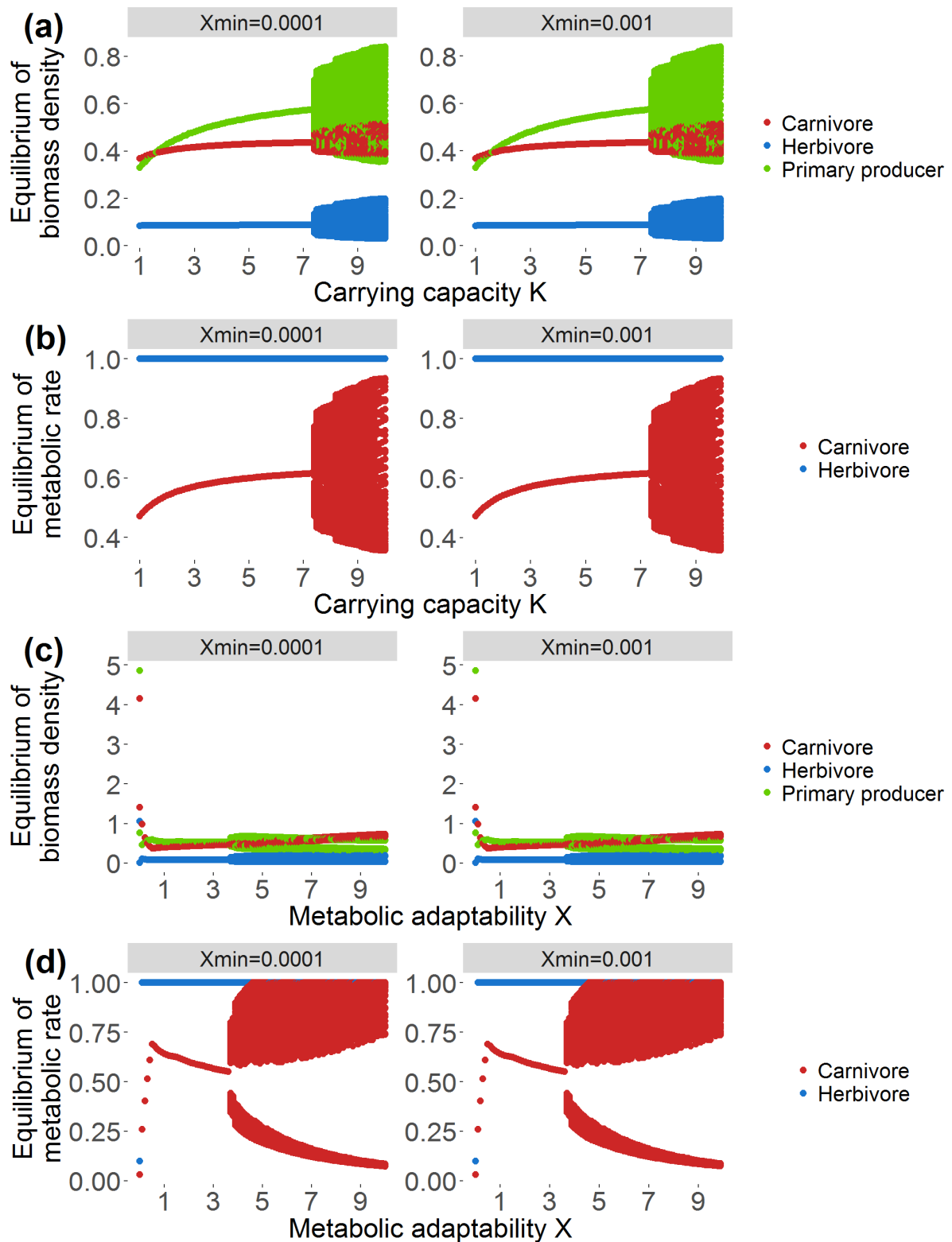


Figure B7: Effect of the lower limit of the metabolic rate in tri-trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient  $X = 2$ . (c) Bifurcation diagrams of biomass density and (d) metabolic rate along gradient in metabolic adjustment for a carrying capacity  $K = 5$ . The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

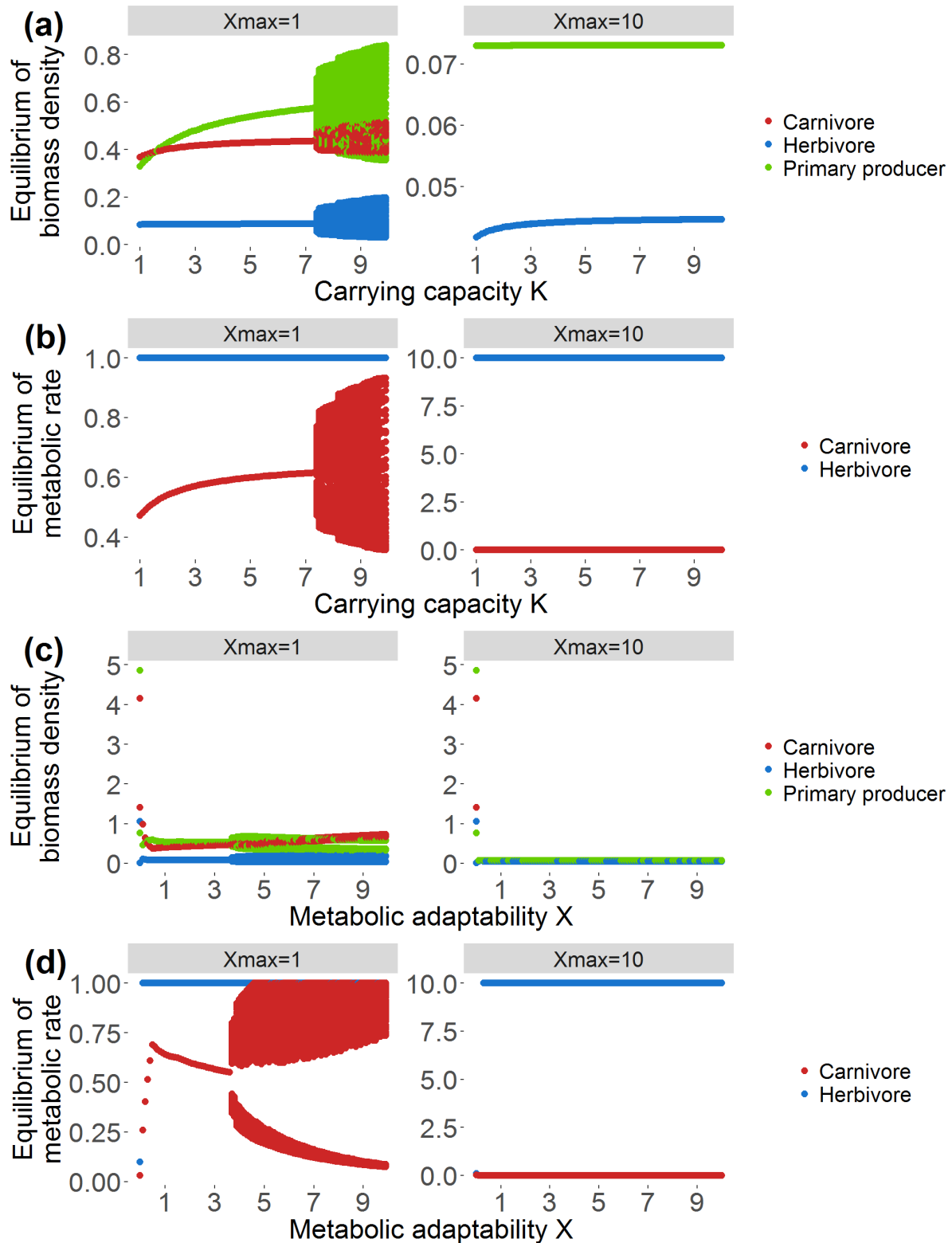


Figure B8: Effect of the upper limit of the metabolic rate in tri-trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient  $X = 2$ . (c) Bifurcation diagrams of biomass density and (d) metabolic rate along a gradient in metabolic adjustment for a carrying capacity  $K = 5$ . The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

#### Amplitude of metabolic rate variations

We also varied the maximal amplitude of the variations of metabolic rates. As the values predicted by the MTE range over two orders of magnitude (Fig.B5), the intervals of one and two orders of magnitudes



were log centred on the values predicted by the MTE (the interval is also bounded by the absolute limits). Thus, the metabolic rates vary in intervals consistent with the values predicted by the MTE (see Fig.B10).

We observe a poor persistence over all the values of metabolic adjustment coefficient  $X$  and carrying capacity  $K$  in food webs where metabolic rates vary in one or two order of magnitude (even if the interval is centred or not)(Fig.B9a,b and d) compared to the three order of magnitude interval used in the main study (Fig.B9c). This could be due to the impossibility of species to lower their metabolic rate low enough to balance their energy budget in periods of starvation. However, we see a better persistence in food webs with no centring of the interval of metabolic rate variations (Fig.B9d), probably because small species can decrease their metabolic rate at lower values. We also see that the improvement of species persistence only occur at high values of metabolic adaptability coefficient  $X$ , then a higher speed of adjustment may be necessary to compensate the narrower interval of possible variations.

In the tri-trophic food chain (Fig.B11), we do not see strong oscillations when the interval of metabolic rate variations is centred. The food chain with a two orders of magnitude wide interval, that is not centred on the values predicted by the MTE, displays similar variations than in the food chain with a three orders of magnitude interval (Fig.4.2 and Fig.4.1). This is explained by the convergence of metabolic rates to constant values (Fig.B11b and d). However, we still see an increase of primary producer and carnivore biomasses with the carrying capacity (Fig.B11a and c).

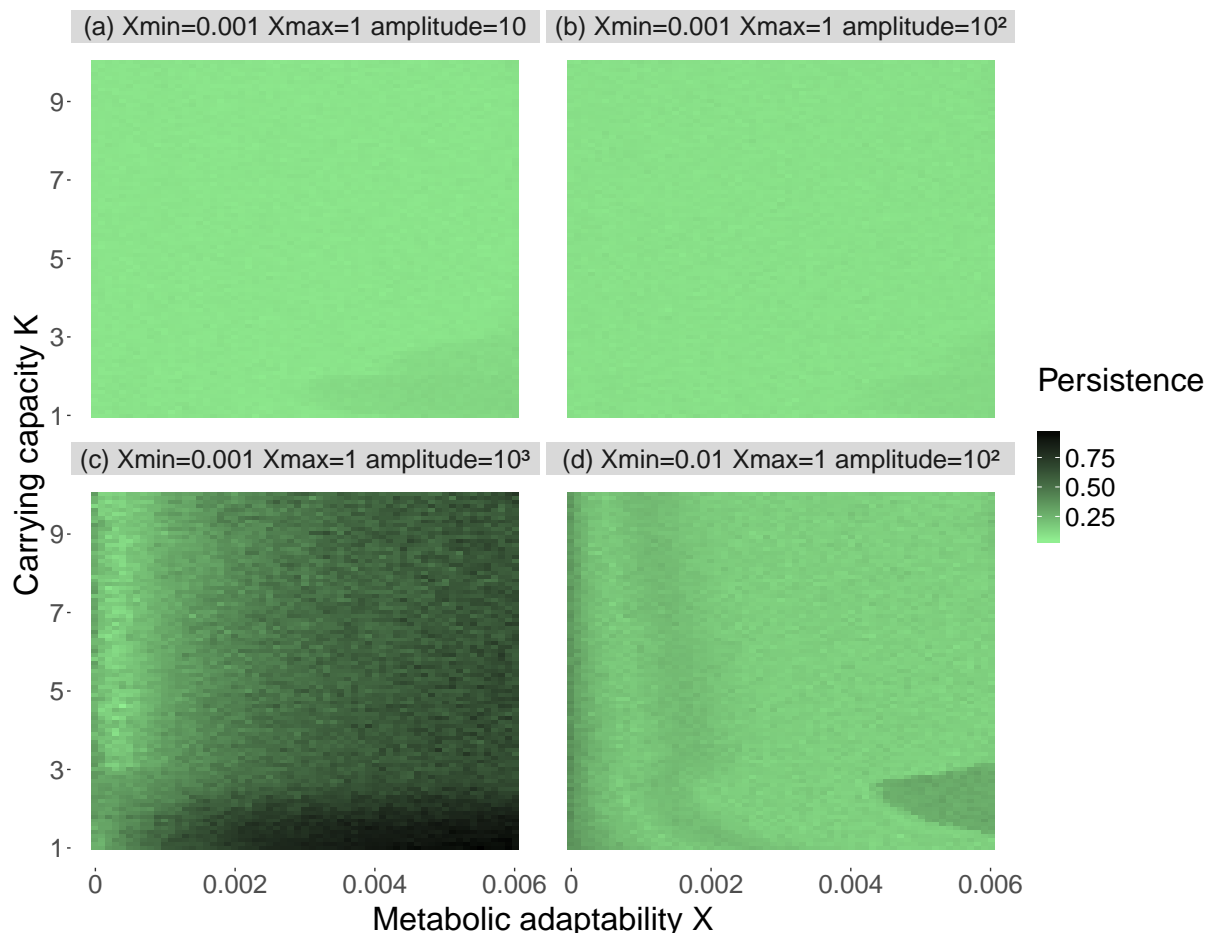


Figure B9: Effect of the amplitude of metabolic rates on species persistence for different values of metabolic adjustment coefficient  $X$  and carrying capacity  $K$ . **(a)** One order of magnitude interval of metabolic rate centred on the values predicted by the MTE. **(b)** Two orders of magnitude interval of metabolic rate centred on values predicted by the MTE. **(c)** Absolute interval used in the main study. **(d)** Two order of magnitude interval with absolute boundaries for all species (no centring of the interval). Each square represents the average species persistence of 100 simulated food webs.

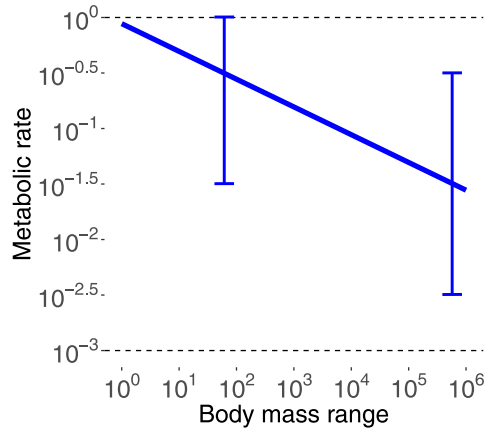


Figure B10: Example of the interval of variation of metabolic rates (blue vertical segments) centred on the values predicted by the MTE (blue line). Here metabolic rates vary in a two orders of magnitude wide interval but it is still bounded by absolute limits that are represented by the dotted lines.

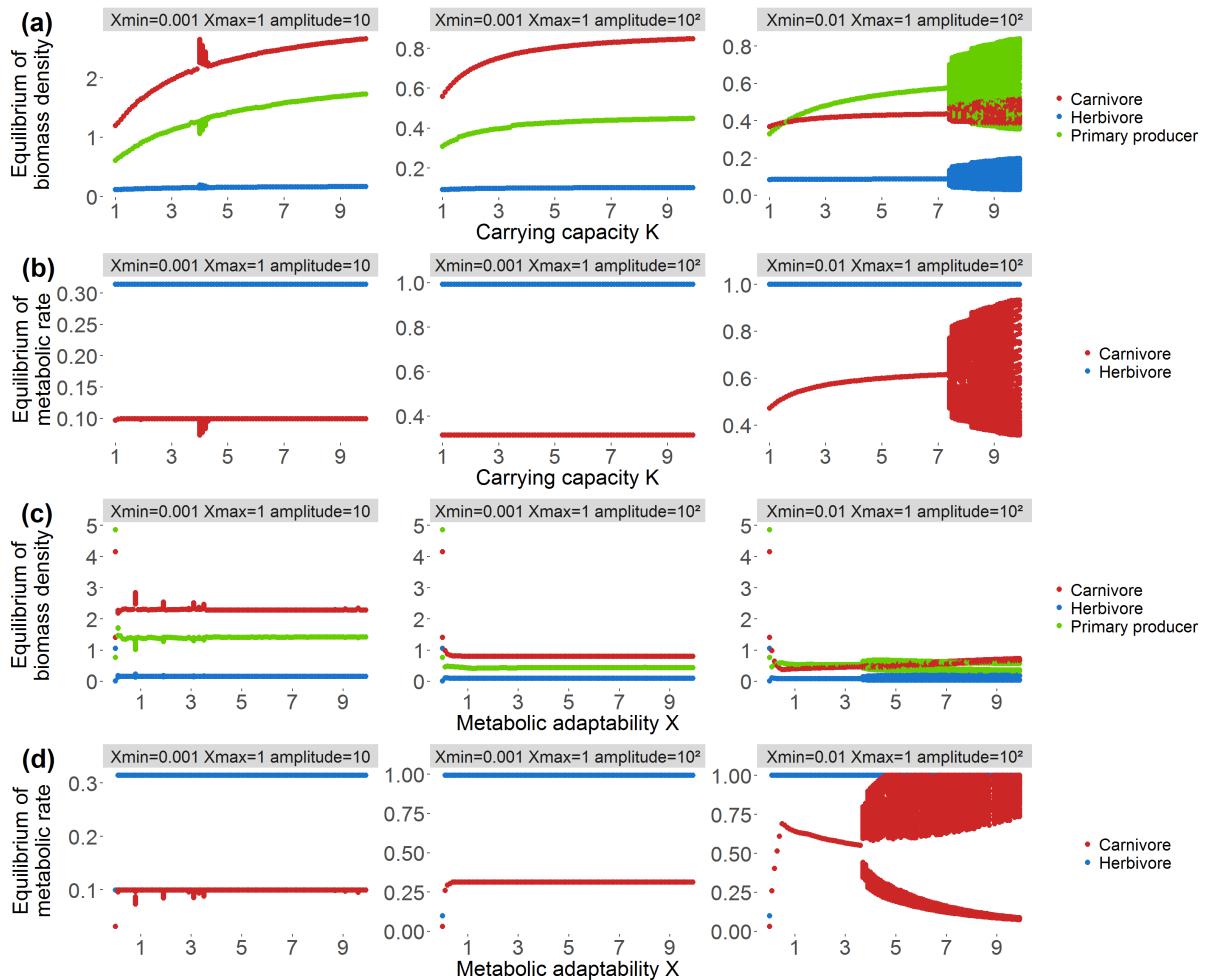


Figure B11: Effect of the amplitude of metabolic rates on tri-trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient  $X = 2$ . (c) Bifurcation diagrams of biomass density and (d) metabolic rate along gradient in metabolic adjustment for a carrying capacity  $K = 5$ . Each time, food chains with metabolic rates varying in intervals of respectively one and two orders of magnitude (centred on the value predicted by the MTE) and on two orders of magnitude not centred, are represented. The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

## Allometric scaling of biological rates

### Metabolic type

Consumer organisms can be considered as ectotherm vertebrates ( $a_x = 0.88$  and  $y_i = 4$ ) or as invertebrates ( $a_x = 0.314$  and  $y_i = 8$ ) (Brose et al., 2006b), thus changing the values of metabolic rates and ingestion rates. In our main study, we use values for invertebrates but we see a similar response of species persistence to the metabolic adjustment coefficient  $X$  and the carrying capacity  $K$  with ectotherm vertebrates parameters (Fig.B12a). The increase of species persistence is less sharp with the increase of the metabolic adjustment coefficient  $X$  (see Fig.B12b to see the response for higher values of  $X$ ). Food webs are also less sensitive to enrichment and persistence stays high for higher values of the carrying capacities  $K$ . In spite of these differences, the overall response of species persistence remains unchanged.

However, species biomasses and metabolic rates are more stable with the ectotherm vertebrates parameters (only fixed points and no oscillations) but the three species persist whatever the metabolic types (Fig.B13a and B13b). Increasing the metabolic adjustment coefficient  $X$  also increases the average biomass of the carnivore (Fig.B13c) and the metabolic rate of herbivore still has its maximum possible value (Fig.B13b and B13d).

Whatever the metabolic type we always observe a stabilising effect of metabolic adjustment on food webs by increasing species persistence and by reducing the amplitude of species biomass oscillations compared to food chains without metabolic adjustment.

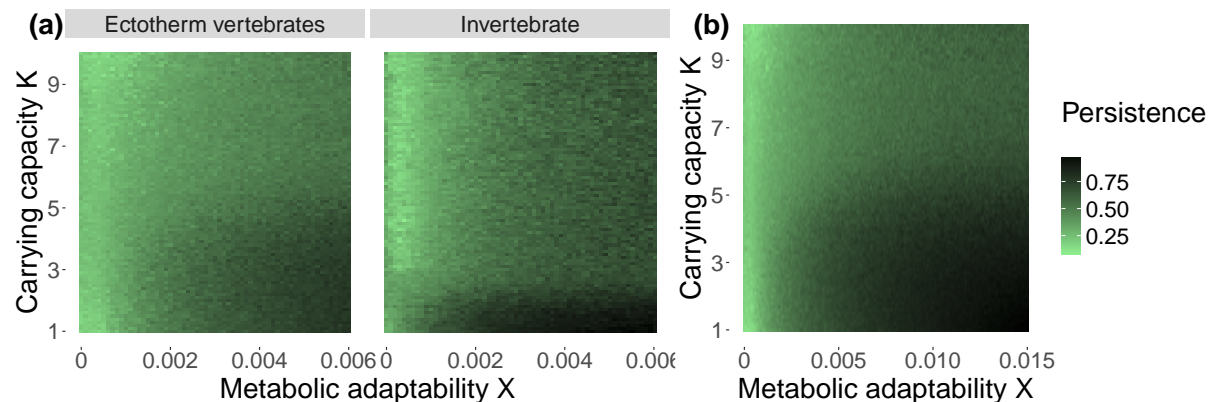


Figure B12: Effect of the metabolic type of consumers ( $y_i = 4$  for ectotherm vertebrates and  $y_i = 8$  for invertebrates) on (a) species persistence for different values of metabolic adjustment coefficient  $X$  and carrying capacity  $K$  and (b) for an extended range of values of metabolic adjustment  $X$ . Each square represents the average persistence of 100 simulated food webs.

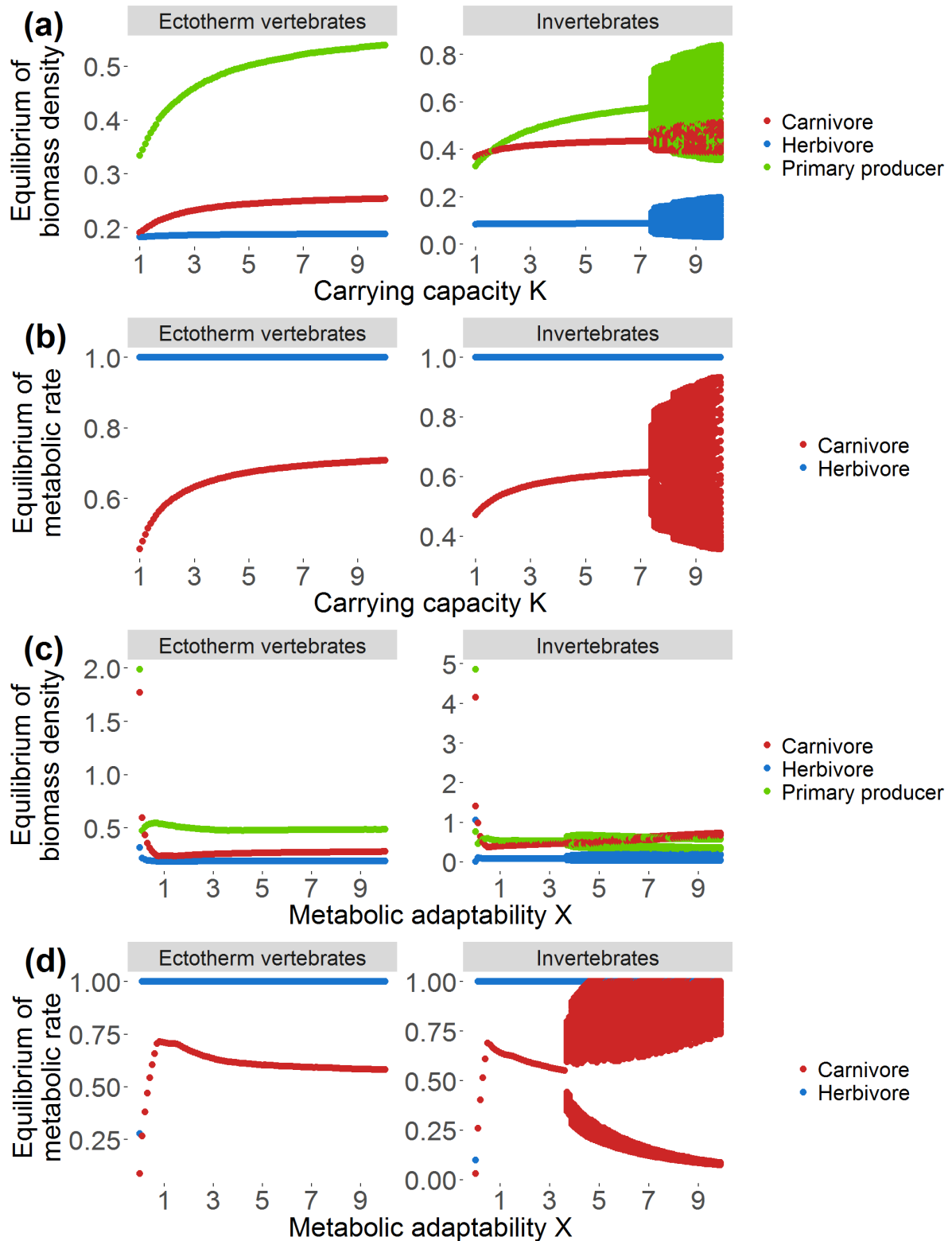


Figure B13: Effect of the metabolic type of consumers ( $y_i = 4$  for ectotherm vertebrates and  $y_i = 8$  for invertebrates) on three trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient  $X = 2$ . (c) Bifurcation diagrams of biomass density and (d) metabolic rate along a gradient in metabolic adjustment for a carrying capacity  $K = 5$ . The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

**Deviation from the quarter power law**

The Allometric Trophic Network (ATN) model (Brose et al., 2006b) was chosen to conduct this study because of the direct relationship between the maximum ingestion rate and the metabolic rate.  $y_i$  is constant because the metabolic rate and the maximum ingestion rate follow quarter power law of the body mass of consumers. However, Pawar et al. (2012) showed that the consumption rate allometric exponent depends on the dimensionality of consumers search space. Thus, we have a new expression of the standardised ingestion rate:

$$\frac{Y_C}{X_C} = \frac{a_y M_C^{s_y}}{a_x M_C^{s_x}} = \frac{a_y}{a_x} M_C^{s_y - s_x} = y_i M_C^{s_y - s_x} \quad (4.9)$$

With  $Y_C$  the ingestion rate of consumers,  $X_C$  the metabolic rate of consumers,  $a_y$  and  $a_x$  their allometric coefficients,  $s_y$  and  $s_x$  their allometric scaling exponents, and  $M_C$  the body mass of the consumer.  $M_C^{s_y - s_x}$  corresponds to the deviation of the ingestion rate from the quarter power law and is estimated in Fig.B14b for 2D and 3D search spaces.  $s_x = -0.25$ ,  $s_y = -0.15$  in 2D and  $s_y = 0.06$  in 3D search spaces.

Species persistence increases in 2D environment at low carrying capacity for ectotherm invertebrates but it decreases for invertebrates (Fig.B14a). In 3D environments species persistence is lower and the area of maximum persistence for low carrying capacity  $K$  is nearly absent. However, increasing the metabolic adjustment coefficient  $X$  increases species persistence for each metabolic type and each dimensionality. The stabilising effect of metabolic adjustment is preserved even if the ingestion rate is not a linear function of metabolic rate. The difference of species persistence can be due to the deviation from the quarter power law that strongly increases the ingestion rate for large consumers that have a 3D search space. Such a high consumption rate might promote prey overexploitation and thus leads to extinctions.

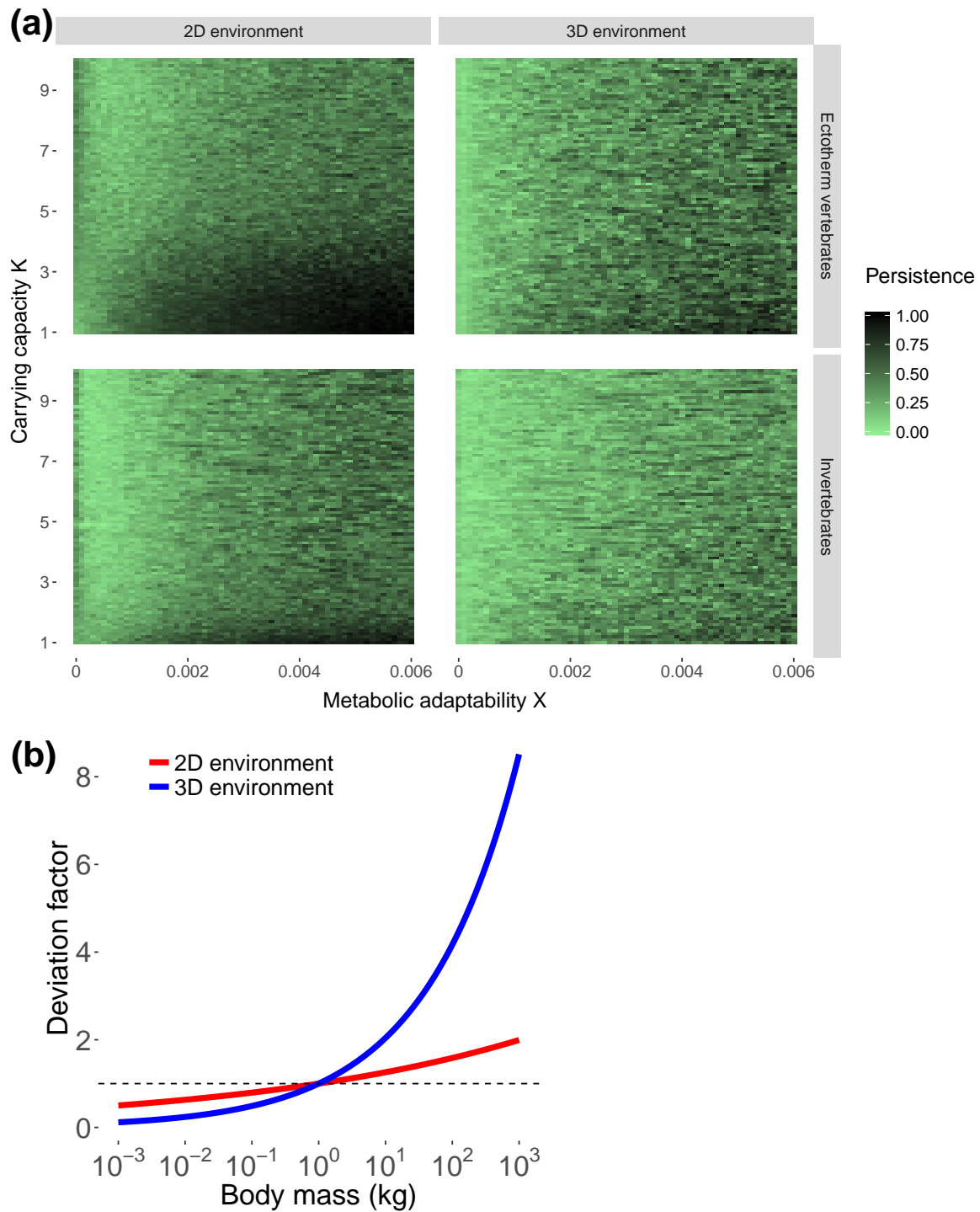


Figure B14: Sensitivity to deviations of allometric scaling of the maximal consumption rate from the quarter-power law. **(a)** Effect of metabolic type and space dimensionality on species persistence for different values of metabolic adjustment coefficient  $X$  and carrying capacity  $K$ . Each square represent the average persistence in 20 simulated food webs. **(b)** Deviation factor of the ingestion rate from the quarter power law along a gradient in species body mass in 2D (red) and 3D (blue) environments. The dashed line ( $y_i = 1$ ) represents the non-deviation from the quarter-power law.

# Discussion générale

Cette thèse avait pour but de mieux comprendre les conséquences des interactions entre réseau trophique vert et réseau trophique brun sur la stabilité du réseau trophique global. La discussion générale qui suit met en relation les résultats tirés des différents chapitres afin de les discuter avec les cadres conceptuels de l'écologie fonctionnelle et de l'écologie des communautés. Cependant, cette discussion vise surtout d'une part à discuter les grands thèmes liés à ces deux disciplines qui se sont croisées dans ce projet et d'autre part à discuter à la lumière de nos résultats les limites des outils méthodologiques que nous avons utilisés.

## Réseau vert et réseau brun, du modèle de réseau trophique au modèle d'écosystème

La modélisation du réseau brun dans un modèle de réseau trophique complexe permet enfin d'inclure la complexité des réseaux d'interactions dans un modèle minimal d'écosystème. Cependant, cela complique en de nombreux points le modèle de réseaux trophiques allométrique classique en ajoutant : 1) un effet enrichissement 2) une boucle de rétroaction positive due au recyclage des nutriments 3) un réseau trophique parallèle au réseau vert mais différent 4) une dimension stœchiométrique au modèle qui doit tenir compte des flux parallèles de carbone et de nutriments.

## Disponibilité en nutriments et paradoxe de l'enrichissement

Le point commun des deux chapitres théoriques et du chapitre annexe (aussi basé sur un modèle) est qu'ils présentent la réaction de réseaux trophiques à la disponibilité en nutriments. Depuis les travaux de [Rosenzweig \(1971\)](#) qui ont mis en lumière le paradoxe de l'enrichissement, c'est-à-dire l'effet déstabilisant d'une disponibilité accrue en ressources (nutriments minéraux en particulier) sur les dynamiques de chaînes et réseaux trophiques, de nombreuses études ont cherché à retrouver ce paradoxe dans des systèmes expérimentaux. Or le paradoxe de l'enrichissement n'a été observé que peu de fois dans des systèmes vivants qui se limitaient souvent à un couple proie-prédateur ([Persson et al., 2001](#); [Roy and Chattopadhyay, 2007](#)) et il ne peut être comparé directement à l'eutrophisation des milieux naturels. En effet, l'eutrophisation est une dégradation du milieu due par exemple à la prolifération d'algues dont la décomposition va priver le milieu d'oxygène, tuant ainsi nombre d'organismes. Le paradoxe de l'enrichissement fait lui appel à l'augmentation de l'écart entre taux de croissance et taux de mortalité des organismes qui augmente les amplitudes des variations de biomasse ([Rip and McCann, 2011](#)) rapprochant ainsi les densités des organismes du seuil critique d'extinction. L'existence du paradoxe de l'enrichissement semble intimement lié à la modélisation de la consommation des proies par les prédateurs puisque la réponse fonctionnelle de type III, contrairement à la II, ne provoque pas de paradoxe de l'enrichissement ([Rall et al., 2008](#)) comme le montre également nos résultats. [Fussmann and Blasius \(2005\)](#) ont également montré que d'autres réponses fonctionnelles avec une courbe très similaire à celle de la réponse fonctionnelle de type II ne provoquaient que peu ou pas de paradoxe de l'enrichissement. De nombreuses études théoriques ont également cherché à découvrir des mécanismes éliminant l'effet déstabilisant lié à l'enrichissement

tout en conservant une réponse fonctionnelle de type II. L'inclusion de mécanismes adaptatifs (Mougi and Nishimura, 2007, 2008, 2009), comme dans les résultats présentés dans le chapitre 4, ou la prise en compte de l'espace avec les méta-écosystèmes (Hauzy et al., 2013; Gounand et al., 2014) peuvent par exemple tamponner le paradoxe de l'enrichissement. Le paradoxe de l'enrichissement ne pourrait être alors que dû à la simplicité des modèles classiques d'interaction proie-prédateur.

Le recyclage des nutriments ne résout pas le paradoxe de l'enrichissement dans les modèles de réseaux trophiques mais il interfère avec lui en augmentant la disponibilité en nutriments comme montré dans le chapitre 1. Cependant, nous ne disposons pas d'un aperçu clair de l'importance du recyclage des nutriments par rapport aux entrées externes de nutriments et nous n'avons pas non plus d'estimation de la fraction de recyclage direct des organismes pour les principaux phylums, des méta-analyses seraient donc essentielles pour mieux cadrer nos résultats avec la réalité du fonctionnement des écosystèmes. Par l'effet enrichissement, le recyclage des nutriments permet donc à une communauté diversifiée avec une longueur de chaîne importante de se maintenir avec une entrée externe de nutriments faible. Par contre le recyclage a rendu le système plus sensible au paradoxe de l'enrichissement dans le sens où la déstabilisation survient à une entrée de nutriment plus faible que dans les modèles sans recyclage. Dans le modèle présenté au chapitre 2, le partitionnement des nutriments entre nutriments minéraux et détritux modifie la sensibilité des réseaux vert et brun à l'enrichissement, les hypothèses expliquant cet effet étant discutées par la suite. Le recyclage des nutriments a d'une part un effet enrichissement plutôt prévisible mais il a d'autre part des effets peu intuitifs sur les dynamiques des différents organismes car il génère une boucle de rétroaction reliant chaque d'eux à la ressource basale que sont les nutriments minéraux.

### **Le recyclage des nutriments, une boucle de rétroaction comme les autres ?**

Les boucles de rétroactions de manière générale peuvent être positives ou négatives. Lorsqu'elles sont positives, comme dans le cas des interactions plantes-pollinisateurs (Fig.4.15A), elles sont déstabilisantes puisqu'elles conduisent à des phénomènes d'emballement (Levins, 1974) comme dans le cas des réactions nucléaires. Les boucles de rétroaction négatives, comme dans le cas du système proie-prédateur (Fig.4.15B), conduisent à un système plutôt stable qui converge sur des points fixes ou une orbite (Voir Fig.3A et Fig.5 en introduction) car l'effet négatif du prédateur sur sa proie est plus fort que l'effet positif de la proie sur le prédateur (Neutel et al., 2002), ce qui empêche le système de s'emballer. Le recyclage des nutriments, en reliant chaque organisme à la ressource basale que sont les nutriments minéraux, couple alors les interactions top-down et bottom-up dans le réseau trophique. En effet, la consommation de la proie (effet négatif top-down sur la proie par le prédateur) augmente la disponibilité en nutriments via le recyclage qui augmente alors la production de biomasse par du producteur primaire puis de la proie (effet positif bottom-up). Ces effets sont cependant modulés par la longueur de chaîne, c'est-à-dire le nombre d'organismes entre le producteur primaire et le prédateur de sommet de chaîne (Leroux and Loreau, 2010). La boucle de rétroaction est donc positive puisque le prédateur a un effet positif sur sa proie (Fig.4.15C).



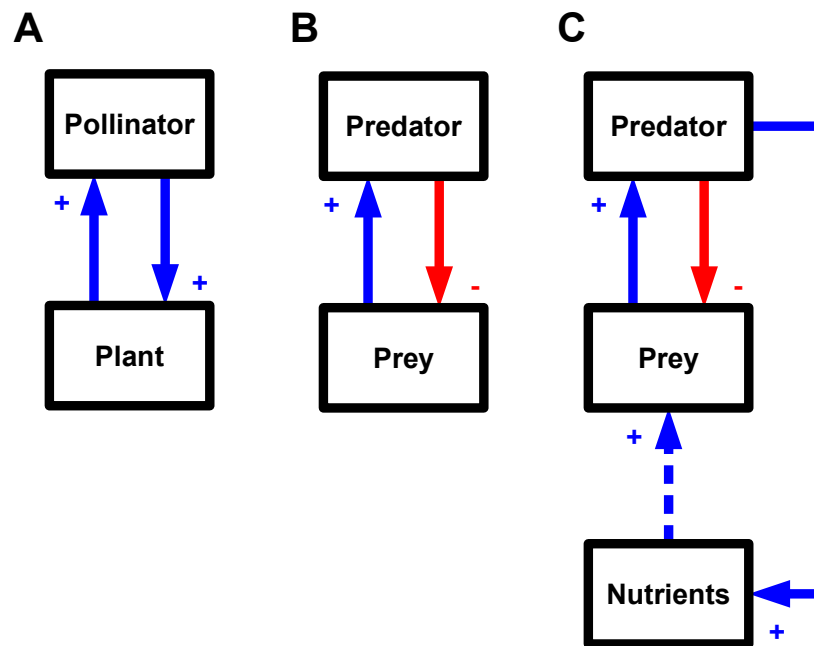


Figure 4.15: **A)** Interaction plante-pollinisateur basique. La plante et le pollinisateur ont chacun un effet positif sur l'autre, ce qui peut provoquer un emballement du système avec une augmentation exponentielle des biomasses des deux espèces. **B)** Interaction proie-prédateur classique. L'effet négatif du prédateur sur sa proie finit par limiter la croissance du prédateur. Une telle interaction donne lieu soit à des densités fixes ou des oscillations, mais les biomasses ne deviennent jamais infinies. **C)** Système proie-prédateur avec recyclage des nutriments. Le recyclage des nutriments génère une boucle de rétroaction positive sur la ressource du prédateur par une augmentation du flux d'énergie dans la chaîne trophique. On a donc un système hybride mutualiste-antagoniste.

La présence d'une telle boucle de rétroaction positive est donc susceptible de modifier la stabilité des réseaux trophiques. Les études précédentes sur la stabilité (DeAngelis, 1980, 1992; Loreau, 1994) ont montré que le recyclage des nutriments diminue la résilience du réseau trophique et a donc un effet déstabilisant. Cependant, cette mesure ne représente que la stabilité locale au voisinage des points d'équilibre du système. Les résultats de Brown et al. (2004a) ainsi que les nôtres au chapitre 1 montrent au contraire un effet stabilisant dans une chaîne trophique par une réduction de la variabilité temporelle des densités de chaque espèce une fois l'effet déstabilisant de l'effet enrichissement du recyclage corrigé. Ici, le recyclage des nutriments permet de tamponner les variations des biomasses de chaque espèce car il augmente la disponibilité en nutriments, et donc la productivité, lorsque la densité de producteurs primaires est au plus bas. Ainsi, l'effet positif des consommateurs sur la disponibilité en nutriment, et donc leur effet positif sur leurs proies, n'est pas constant au cours du temps mais intervient lorsque l'effet top-down est le plus fort. La simple présence de la boucle de rétroaction positive n'est pas suffisante pour déterminer la stabilité du système, c'est le timing de ses variations d'intensité par rapport aux dynamiques des espèces qui est la clef. Tester de tels effets expérimentalement s'avère en revanche assez compliqué techniquement. Les effets de la présence du recyclage sur la production primaire ont pu être observés dans des microcosmes où des algues peuvent être maintenues en conditions axéniques (Danger et al., 2007b) car l'absence de bactéries empêchait la décomposition de la matière organique morte. Cependant refaire des expériences similaires en chémostat en incluant des herbivores comme des daphnies est presque impossible.

L'effet stabilisant exposé précédemment n'est cependant valable que dans une chaîne trophique. Comme prédit par Brown et al. (2004a), l'effet stabilisant du recyclage des nutriments n'est pas visible dans notre modèle de réseau trophique complexe. En effet, la diversité des espèces avec des réponses non synchrones tend à lisser les grands processus écosystémiques (Doak et al., 1998; Gonzalez and Loreau, 2008; Loreau and de Mazancourt, 2013) comme le recyclage des nutriments qui devient alors presque constant au cours

du temps. Le recyclage des nutriments n'est donc plus couplé aux dynamiques des espèces et l'effet stabilisant de la boucle de rétroaction est alors perdu. Cependant, ceci est probablement dû à deux caractéristiques de notre modèle : l'absence de phénologie (*i.e.* absence de variabilité environnementale) et la grande similarité entre les espèces. La phénologie tend à synchroniser les dynamiques des espèces qui dépendent de paramètres environnementaux similaires. [Boit et al. \(2012\)](#) ont pris en compte la température, l'intensité lumineuse et la disponibilité en nutriments au fil des saisons dans leur modèle de réseau trophique représentant la communauté du lac de Constance. Le résultat a été la succession d'une phase de bloom algal puis d'une phase de forte croissance du zooplancton à l'instar des séries temporelles du lac. L'introduction d'une telle saisonnalité dans notre modèle pourrait refaire apparaître l'effet stabilisant du recyclage des nutriments. Ensuite, la grande similarité entre les espèces dans les modèles allométriques structurés en taille vient du fait qu'elles ne sont décrites que par leur masse corporelle. Ainsi, seul le nombre de proies et/ou de prédateurs est susceptible de changer d'une espèce à l'autre, ce qui fait que l'on observe une alternance entre les espèces (de même niveau trophique) de pics de biomasses et non la présence de quelques espèces dominantes dans l'écosystème comme cela peut se voir dans la nature ([Hubbell, 1997](#)). La présence de quelques groupes très abondants pourrait alors casser la constance des processus écosystémiques à cause de leur forte contribution dans ces processus. Par exemple, la présence ou l'absence de grands cladocères comme les daphnies a un impact majeur sur la densité du phytoplancton ([Danger et al., 2009a, 2012](#); [Mette et al., 2011](#); [Harrault et al., 2014](#); [Rowland et al., 2015](#); [Gauzens et al., 2016](#)) alors que les autres espèces plus petites ne sont pas capables de le contrôler comme cela était le cas dans notre expérience ou celle de ([Faithfull et al., 2011](#)).

### Réseau vert et réseau brun, parallèles mais non identiques

Le recyclage des nutriments ne doit pas être considéré comme le seul retour des nutriments dans le réservoir minéral, mais comme une fonction écosystémique assurée par une fraction à part entière du réseau trophique : le réseau brun. Les réseaux trophiques vert et brun forment deux sous-réseaux parallèles avec chacun une ressource basale (sachant que les nutriments sont aussi partagés par les deux réseaux), un type d'espèce basal qui consomme cette ressource et des consommateurs. Au-delà des rôles fonctionnels de chacun des deux réseaux, la simple présence de deux ressources basales différentes affecte profondément la production de biomasse à la base du réseau trophique puisque cela limite la compétition (sauf peut-être dans le cas de la limitation des décomposeurs par les nutriments). La suite du travail sur le modèle présenté dans le chapitre 2 consistera donc à comparer un modèle de réseau trophique à deux réseaux verts et un modèle de réseau trophique avec un réseau vert et un réseau brun pour séparer les effets dus au couplage de deux réseaux parallèles des effets des différences vert-brun.

Le réseau vert et le réseau brun sont dissymétriques sur deux points fondamentaux : l'asymétrie des ressources basales et l'asymétrie des espèces basales qui les consomment. Là où le réseau vert ne dépend que d'une seule ressource basale, le réseau brun dépend de deux ressources. Les décomposeurs sont donc soumis à des contraintes stœchiométriques et non les producteurs primaires. Cependant la situation est différente d'une croissance deux nutriments minéraux limitants ([Brose, 2008](#)) puisque les détritiques sont d'une part un mélange de carbone et de nutriments minéraux, et sont d'autre part produits par les organismes du système et non soumis à une entrée extérieure. Les compartiments nutriments minéraux et détritiques n'ont alors pas la même réponse à l'enrichissement en nutriments. Ce point est notamment lié à la stœchiométrie du système et sera discuté dans la section suivante. Une telle asymétrie dans les ressources basales expliquerait pourquoi les réseaux vert et brun réagissent de façon différente à l'enrichissement comme c'est montré dans le chapitre 2. Cependant, cette asymétrie au sein de notre modèle est à nuancer par rapport aux systèmes naturels. Par exemple, l'entrée de l'azote dans les écosystèmes dépend principalement de la fixation biologique et non de l'érosion ([Gruber and Galloway, 2008](#)). Les détritiques ne sont également pas un compartiment homogène mais un assemblage de sous-compartiments avec des

stœchiométries et des potentiels de dégradabilité variables (Moore et al., 2004) qui peuvent être modélisés séparément (Perveen et al., 2014). Une telle description des détritits pourrait alors fortement modifier la limitation des décomposeurs et donc leur réponse à l'enrichissement.

L'autre point d'asymétrie entre les réseaux vert et brun vient des espèces basales : les producteurs primaires produisent leur propre biomasse *de novo* à partir des nutriments minéraux alors que les décomposeurs convertissent les détritits en biomasse. Ceci pose un gros problème de modélisation car là où l'absorption des nutriments minéraux et la photosynthèse ont bénéficié de beaucoup d'attention (Farguhar et al., 1980; Aksnes and Egge, 1991; Fiksen et al., 2013) avec une l'utilisation de fonction de type Michaelis-Menten pour l'absorption des nutriments minéraux, la décomposition de la matière organique par les bactéries et les champignons est représentée par un simple taux linéaire tirée de mesures empiriques (Hunt et al., 1987; Moore et al., 1993; Neutel et al., 1994; Perveen et al., 2014). Cependant, des modèles plus poussés existent (Manzoni and Porporato, 2007, 2009; Manzoni et al., 2012, 2016) en tenant compte de la qualité des détritits comme évoqué précédemment ou d'effets non linéaires dus à l'interférence entre les espèces de bactéries par exemple. De plus, les détritits sont principalement composés d'agrégats et de particules solides aux-quelles se fixent les micro-organismes décomposeurs (Moore et al., 2004) contrairement aux nutriments minéraux qui sont des ions en solution. Le modèle de cinétique de Michaelis-Menten tirée de la chimie des solutions semble donc peu adapté à la consommation des détritits. Dans notre modèle, nous avons choisi de modéliser les décomposeurs de façon similaire aux producteurs primaires (donc avec une consommation des détritits de type Michaelis-Menten) afin d'apporter un minimum de modifications au modèle de réseau trophique purement vert du chapitre 1, cependant nous devons encore déterminer en quoi cela affecte la réponse des décomposeurs par rapport aux producteurs primaires.

Mis à part les deux points évoqués précédemment, nos modèles de réseaux vert et brun sont pour le reste très symétriques puisque les consommateurs de chacun d'eux sont identiques dans leur modélisation, que les masses corporelles sont tirées dans la même gamme et que les paramètres allométriques sont identiques. Or dans les systèmes naturels, les organismes du réseau brun ont tendance à être plus petits car les bactéries en sont à la base, contrairement au réseau vert avec les systèmes terrestres en particulier où des arbres peuvent assurer la majeure partie de la production primaire. Une telle différence peut alors augmenter la longueur de chaîne dans le réseau brun, diminuant ainsi le transfert d'énergie vers les prédateurs de sommet de chaîne dépendant du réseau brun (Berghlund et al., 2007). C'est le résultat obtenu par l'expérience en mésocosmes de Degerman et al. (2018) où l'ajout de matière organique défavorise les poissons qui sont en sommet de chaîne. De telles différences de tailles influent aussi sur le taux métabolique qui est d'autant plus grand par unité de masse que l'organisme est petit. Ainsi, le flux d'énergie est plus grand dans un réseau trophique comportant des organismes de petite taille. Or Rooney et al. (2006) ont montré dans leur modèle théorique que deux chaînes trophiques avec des flux d'énergie asymétriques donnent un réseau trophique plus stable. Une telle asymétrie est fréquente dans les écosystèmes avec par exemple une voie pélagique plus rapide que la voie benthique (McCann and Rooney, 2009; Rooney and McCann, 2012). Cependant, Zou (2016) a montré qu'une telle asymétrie appliquée entre une chaîne verte et une chaîne brune donne des résultats dépendants de la chaîne qui est la plus rapide et la limitation par les nutriments minéraux ou par le carbone les décomposeurs. Ces résultats n'ont pas encore été confrontés à des modèles de réseaux trophiques complexes comme ceux développés ici, ce qui représente une nouvelle piste de recherche prometteuse.

## La stœchiométrie, quand la matière croise l'énergie

Les modèles de réseaux trophiques complexes se sont pour l'instant focalisés sur des flux d'énergie (mis à part Wang and Brose (2017)) sur la base du modèle proposé par Yodzis and Innes (1992) et développé

ensuite par [Brose et al. \(2006b\)](#) and [Williams et al. \(2007\)](#). L'inclusion du recyclage des nutriments dans le modèle présenté au chapitre 1 a également apporté une dimension stœchiométrique puisqu'il était nécessaire de faire le lien entre les flux dans les réseaux trophiques allométriques classiques exprimés en carbone et les flux de nutriments des compartiments abiotiques. Cependant la stœchiométrie n'a qu'un rôle faible dans le modèle présenté au chapitre 1 puisque les organismes ne sont jamais face à une limitation par le carbone ou par les nutriments compte tenu du ratio C:N de leurs ressources. Dans le modèle présenté au chapitre 2, la présence de décomposeurs se nourrissant de détritiques et devant maintenir leur ratio C:N rend la stœchiométrie très importante puisque le ratio C:N des détritiques et la disponibilité en nutriments minéraux définissent la limitation des décomposeurs. Les différents rapports stœchiométriques des organismes qui rendent le carbone plus abondant que les nutriments minéraux apportent également une asymétrie supplémentaire dans le réseau trophique comme évoqué dans la section précédente. En effet, le recyclage des nutriments implique également un recyclage du carbone dont l'accumulation dans le compartiment détritiques avec l'enrichissement est plus importante que l'accumulation de nutriments dans le compartiment minéral. Cette accumulation plus importante expliquerait la plus grande sensibilité de la stabilité du réseau brun à l'enrichissement. Un tel effet pourrait être testé en étudiant des réseaux trophiques dont les ratios C:N de tous les organismes varient simultanément de 1 (cas où le carbone est aussi abondant que les nutriments dans l'ensemble de l'écosystème) à des valeurs utilisées dans le chapitre 2.

Nous avons également pris le parti d'une modélisation simple des flux de matière entre les organismes et leur environnement. Dans nos modèles, le flux entrant doit avoir la même stœchiométrie que l'organisme, si la ressource consommée n'a pas le même ratio C:N, alors l'ajustement se fait au niveau de la fraction de biomasse non assimilée pour les consommateurs ou via l'immobilisation ou la minéralisation de nutriments minéraux pour les décomposeurs. Cependant, le modèle de [Cherif and Loreau \(2013\)](#) gère de façon plus complexe l'ingestion, la digestion et l'assimilation du carbone et des nutriments par les herbivores. Ainsi, la prise en compte du budget en carbone et en nutriments de chaque organisme à la façon de [Cherif and Loreau \(2013\)](#) couplé à la relation d'allométrie liant excrétion d'azote et de phosphore à la masse corporelle des animaux mis en évidence par [Vanni and McIntyre \(2016\)](#) permettrait de mieux lier stœchiométrie et théorie métabolique de l'écologie ([Allen and Gillooly, 2009](#)).

Inclure plus de diversité des ratios C:N des divers organismes de notre modèle pourrait également avoir des conséquences importantes. Nous avons choisi un ratio égal à 5 pour les consommateurs et les décomposeurs et un ratio supérieur ou égal à 6,6 pour les producteurs primaires. Or ces ratios sont très variables ([Sternier et al., 1992](#); [Evans-White and Halvorson, 2017](#)) et ont de fortes conséquences sur le ratio C:N des détritiques et donc sur la limitation par le carbone ou les nutriments des décomposeurs ([Cherif and Loreau, 2009, 2013](#)), sur la limitation en nutriments des producteurs primaires ([Daufresne and Loreau, 2001](#)) et sur les effets en cascade de la prédation sur les décomposeurs ([Zou et al., 2016](#)). De plus, la variabilité des ratios C:N ne se manifeste pas seulement par une diversité de ce ratio entre les espèces, mais aussi par une plasticité de ces ratios au sein même des espèces. Les organismes photosynthétiques en particulier sont susceptibles de fortement modifier leur stœchiométrie pour s'adapter à la limitation aux divers nutriments minéraux ou à l'intensité lumineuse qui augmente la fixation du carbone ([Sternier et al., 1997](#); [Dickman et al., 2006](#); [Danger et al., 2007b](#); [Mette et al., 2011](#)). La stœchiométrie des producteurs primaires conditionne leur qualité nutritionnelle qui a alors un fort impact sur l'efficacité du transfert d'énergie dans le réseau trophique ([Cebrian et al., 2009](#)). Couplée avec le modèle de ([Cherif and Loreau, 2013](#)), la plasticité de la stœchiométrie des producteurs primaires pourrait profondément impacter la structure et la persistance des espèces dans un modèle réseau trophique complexe.

## Vers une diversification des espèces basales

Les descriptions des réseaux trophiques, qu'ils soient théoriques ou empiriques, ont tendance à agréger fortement les espèces en bas du réseau (Gauzens et al., 2013). Par exemple, Boit et al. (2012) ont regroupé toutes les bactéries en un seul compartiment ! De manière générale, là où les consommateurs se différencient par leur taille et donc leur régime alimentaire (qui est déterminé par le ratio de taille en prédateur et proie), les producteurs primaires se partagent la même ressource. Les producteurs primaires avec le plus fort taux de croissance (les plus petits organismes donc) sont alors privilégiés et excluent les autres, seule la présence de consommateurs permettant alors la coexistence (Brose, 2008; Wang and Brose, 2017). L'inclusion du réseau trophique brun ajoute également un nouveau type d'espèce basale qui augmente la production de biomasse et facilite la persistance des consommateurs. La présence des décomposeurs rajoute des interactions à la base du réseau trophique puisque le recyclage des nutriments induit par la consommation des détritiques engendre une interaction mutualiste entre les décomposeurs et les producteurs primaires. Kéfi et al. (2012) avaient déjà inclus du mutualisme entre producteurs primaires dans leurs modèles mais l'effet positif obtenu sur la persistance des espèces était faible dans un réseau trophique complexe alors que le gain de persistance dans une communauté exclusivement composée de plantes était énorme. Deux explications peuvent être apportées : d'une part l'existence de consommateurs dans le réseau trophique limite la compétition entre les espèces basales en diminuant leurs densités (Brose, 2008), d'autre part, les espèces basales sont toutes similaires. Les études précédentes et nos résultats sur les réseaux verts et bruns montrent que les interactions entre producteurs primaires et décomposeurs et leur réponse aux conditions environnementales influent fortement sur le reste du réseau trophique (Attayde and Ripa, 2008; Wolkovich et al., 2014; Zou et al., 2016) même si la présence de consommateurs diminue l'importance des interactions entre producteurs primaires et décomposeurs dans la survie de ces derniers (Daufresne and Loreau, 2001). L'introduction dans les modèles d'espèces basales avec des rôles fonctionnels différents permettrait donc de mieux tenir compte de l'importance de ces organismes essentiels au fonctionnement des écosystèmes réels (Cotner and Biddanda, 2002; Danger et al., 2007a; Degerman et al., 2018). Notre modèle de réseau trophique vert/brun pourrait également inclure des organismes fixateurs d'azote (Koffel et al., 2018) et des mixotrophes (Jones, 2000; Andersen et al., 2015; Chakraborty et al., 2017) qui, tout en gardant seulement un compartiment minéral et un compartiment détritiques, pourraient modifier la réponse de notre modèle à la disponibilité en nutriments. Par exemple, les fixateurs auraient un effet stabilisant à faible entrée de nutriments mais déstabilisant à forte entrée à cause de leur effet enrichissement. Les mixotrophes, en consommant d'autres organismes, pourraient quant à eux avoir un effet stabilisant en lissant les effets de la limitation par les nutriments grâce à la flexibilité apportée par leur capacité à être à la fois producteur primaire et consommateur. L'impact de ces deux types d'organismes sur les modèles réseaux trophiques reste cependant largement inconnu (Karnatak and Wollrab, 2017).

## Critique du modèle structuré en taille et à paramétrisation allométrique

Les trois modèles présentés aux chapitres 1, 2 et 4 reposent sur la théorie métabolique de l'écologie et la structuration en taille des réseaux trophiques pour leur paramétrisation et leur construction. L'utilisation de ces deux cadres conceptuels a prouvé son efficacité à créer des modèles de réseaux trophiques où de nombreuses espèces peuvent se maintenir à l'instar des réseaux observés dans la nature (Brose et al., 2006b). Cependant, si ces modèles représentent bien les écosystèmes aquatiques pélagiques fondés sur des producteurs primaires microscopiques (Boit et al., 2012; Hudson and Reuman, 2013), ils s'avèrent incapables de modéliser correctement un réseau trophique de forêt où le producteur primaire est l'organisme le plus gros.

Les modèles de réseaux trophiques sont très similaires à des modèles de cinétiques chimiques, c'est-à-dire

que le milieu est considéré comme homogène avec une large diffusion des organismes. Ceci peut être relativement vrai dans des milieux aquatiques pélagique mais devient par exemple absurde dans le sol qui est un milieu solide poreux. En effet, là où des animaux sont capables de creuser le substrat pour se déplacer (comme les vers de terre), les plus petits organismes comme les bactéries s'avèrent incapables de bouger seul de leur micro-région de sol. D'autres organismes comme les plantes et les champignons produisent de la biomasse de façon fractale pour explorer le milieu. La question qui se pose est : Faut-il modéliser un champignon à l'échelle du mycélium (donc une masse corporelle conséquente) ou à l'échelle de l'hyphe et donc comme un ensemble d'organismes plus petits ? J'ai dû faire face à ces questions lors de mon stage chez Ulrich Brose où je devais modéliser avec l'approche allométrique classique le réseau trophique d'un champs de maïs qui avait été décrit empiriquement (Brose and Scheu, 2014). Ce modèle était une catastrophe sans nom ! Impossible de faire coexister le système puisque le producteur primaire, le maïs en l'occurrence, se faisait éradiquer par le moindre phytophage en raison du ratio de taille désavantageux. En effet, les modèles de réseaux trophiques allométriques sont plus stables si les prédateurs sont plus gros que leurs proies (Brose et al., 2006b; Heckmann et al., 2012) et gèrent très mal des herbivores qui ne consomment qu'une partie de chaque plante qu'ils consomment contrairement au milieu aquatique où l'herbivorie s'apparente plus à de la prédation. La modélisation de ces écosystèmes nécessitera donc une représentation plus détaillée des végétaux avec par exemple une séparation entre les différents organes de la plante.

La théorie métabolique de l'écologie considère également le métabolisme comme constant au cours du temps alors que les organismes sont capables de fortement moduler leurs dépenses en énergie (Makarieva et al., 2005). En réponse à mon échec de modéliser la communauté du sol, j'ai développé un modèle tenant compte d'un métabolisme plastique plus à même de représenter les micro-organismes capables d'entrer en dormance (Guppy and Withers, 1999). Cette capacité des organismes à entrer en sorte de dormance crée un genre de banque de graine qui permet de maintenir la diversité des espèces même si l'environnement est peu favorable. La prise en compte de réponses plastiques des organismes, comme nous l'avons fait en incluant l'adaptive foraging dans les chapitres 1 et 2, est alors également une piste prometteuse pour mieux rendre compte de la dynamique des organismes dans leur environnement.

## L'expérimentation en mésocosmes

L'étude empirique entre les réseaux trophiques vert et brun peut se faire à trois échelles : microcosme, mésocosme et écosystème entier. Les expériences en microcosmes ont l'avantage d'être relativement simple, c'est-à-dire que l'environnement peut être maintenu en chemostat et que des communautés très simples d'organismes peuvent être maintenues. Ce type de système a été particulièrement utilisé pour tester des hypothèses précises sur les interactions entre bactéries et phytoplancton (Gurung et al., 1999; Danger et al., 2007a,b; Daufresne et al., 2008). La simplicité de tels systèmes permet entre-autre de facilement les relier à des modèles théoriques (Daufresne and Loreau, 2001). Cependant, les systèmes expérimentaux cités ci-dessus ne comportaient que des ressources abiotiques, un producteur primaire (*e.g. Scenedesmus obliquus*) et une communauté de bactéries issue d'un milieu naturel. Or la présence de niveaux trophiques supérieurs a une forte influence sur les relations entre producteurs primaires et décomposeurs comme le suggère par exemple la coexistence de ces deux groupes même s'ils sont en compétition pour les nutriments minéraux dans les modèles de Attayde and Ripa (2008), Zou et al. (2016) et nos résultats présentés au chapitre 2. Expérimentalement, il faut alors des dispositifs plus grands, le mésocosme, afin de maintenir des populations d'animaux.

L'expérimentation en mésocosmes se rapproche elle beaucoup plus des conditions naturelles puisque la communauté d'organismes qui y est étudiée peut comporter des consommateurs aussi gros que des pois-

sons. Cependant, la diversité de la communauté est également une grande source de variabilité. A l'échelle des producteurs primaires, la forte présence d'organismes mixotrophes dans le lac où [Faithfull et al. \(2011\)](#) ont fait leur expérience a fait que le phytoplancton n'a pas été significativement affecté par l'ajout de glucose contrairement à d'autres études ([Joint et al., 2002](#); [Degerman et al., 2018](#)). A l'échelle du zooplancton, les effets en cascade liés à la prédation par les poissons sont très fortement dus à la présence ou non de grands cladocères comme les daphnies dans la communauté d'origine : s'ils sont présents alors la cascade est forte ([Danger et al., 2009a, 2012](#); [Mette et al., 2011](#); [Harrault et al., 2014](#); [Rowland et al., 2015](#); [Gauzens et al., 2016](#)) alors que s'ils sont absents la cascade est faible comme dans nos résultats et ceux de [Faithfull et al. \(2011\)](#). Une telle variabilité dans la réponse pourrait cependant être intéressante pour séparer les effets top-down des effets bottom-up liés à la présence des poissons. En effet, comme le zooplancton ne contrôle pas le phytoplancton dans nos dispositifs expérimentaux, la présence des poissons ne modifie que peu le contrôle top-down sur le phytoplancton et seul l'effet bottom-up du aux poissons reste. Or les poissons modifient profondément la composition et la quantité des sédiments ([Danger et al., 2012](#); [Harrault et al., 2012](#)), ce qui a pour conséquence d'augmenter la disponibilité en nutriments et donc l'abondance du phytoplancton ([Vanni and Layne, 1997](#); [Vanni et al., 1997](#); [Vanni, 2002](#); [Danger et al., 2009b](#)). Ainsi, l'interaction que nous avons observée dans notre expérience entre la lumière et les poissons, interprétée comme un effet de l'excrétion des poissons qui diminue la limitation du phytoplancton par les nutriments, n'aurait peut-être pas été vue à cause de l'effet top-down écrasant des cladocères. Comparer l'interaction entre lumière et charge en nutriments d'une part, et lumière et poissons d'autre part serait intéressant pour continuer d'évaluer l'effet bottom-up lié aux poissons, la charge en nutriments servant à mimer l'effet des poissons sur la disponibilité en nutriments. A notre connaissance, l'interaction lumière×poissons n'a été testée que par [Mette et al. \(2011\)](#) et notre propre expérience et mériterait donc d'être étudiée plus en profondeur.

L'expérimentation en mésocosmes, en plus de manipuler une communauté proche de celles observées en milieux naturels, permet de travailler sur des temps relativement long. Notre expérience a duré plus de quatre mois, ce qui nous a permis par exemple de nous affranchir de la dynamique transitoire liée au lancement de l'expérience. Même si certaines expériences ont duré jusqu'à quatorze mois ([Danger et al., 2008b](#)), la plupart durent rarement plus de deux mois ([Mette et al., 2011](#); [Faithfull et al., 2011](#); [Degerman et al., 2018](#)) et parfois seulement quelques jours ! ([Joint et al., 2002](#)). Cependant, cette durée d'expérimentation ne permet pas d'avoir une vraie dynamique de population des poissons. Seuls des juvéniles en nombre fixe de gardons, rotengles ou perches sont utilisés et leur taux de croissance est mesuré. Des études à plus long terme avec des petits poissons formant une population viable seraient importantes.

Les études en mésocosmes ont enfin tendance à se focaliser sur le compartiment pélagique (mis à part [Harrault et al. \(2012, 2014\)](#) et [Danger et al. \(2012\)](#)). Or la nature même du dispositif expérimental fait que le ratio surface sur volume est relativement important comparé au lac qu'il essaie d'approximer. Ainsi, le périphyton s'avère être un compartiment assurant une part importante de la production primaire et réagit à la structure du réseau trophique ([Danger et al., 2008b, 2009b](#)). Malheureusement nous n'avons pas réussi à échantillonner correctement le périphyton lors de notre expérience et n'avons donc pas pu le quantifier. Nous nous sommes également rendu compte que certaines larves d'insectes comme celles des éphémères étaient très présentes sur les parois des mésocosmes et étaient absentes en présence de poissons. Nous ne les avons pas non plus prises en compte mais leur nombre devrait être quantifié dans des expériences futures. Enfin, le compartiment benthique est lui aussi peu étudié alors que la quantité et la qualité des sédiments répond à la présence de poissons ([Danger et al., 2012](#); [Harrault et al., 2012](#)) et a une influence en retour sur la communauté d'organismes plus petits ([Harrault et al., 2014](#)). Nous avons également vu que la communauté bactérienne se trouvant au niveau des sédiments réagissait aux traitements expérimentaux alors que la communauté pélagique y était insensible. Une meilleure prise en compte des communautés d'organismes vivant sur les parois et le fond des mésocosmes est donc impor-

tante pour pouvoir pleinement apprécier la réponse de l'écosystème dans sa globalité.

L'expérimentation en écosystèmes entiers, comme par exemple les expériences d'enrichissement en nutriments ou d'exclusion de prédateurs dans des lacs naturels (Carpenter et al., 2001) (voir Fig.8 en introduction), tient compte de l'écosystème dans sa globalité et sa complexité, avec par exemple les interactions avec le reste du bassin versant. Cependant, ce type d'expérience ne permet pas la réplication, chaque lac étant unique. La plateforme des lac artificiels au CEREEP Ecotron IleDeFrance (Mougin et al., 2015), où l'expérience présentée au chapitre 3 a été faite, est un ensemble de seize lacs artificiels de 700 m<sup>3</sup> chacun avec une zone littorale contenant des macrophytes et subissant des traitement croisés d'enrichissement au phosphore et de présence de poisons piscivores. Une telle plateforme permet donc à la fois d'avoir des systèmes représentatifs d'un lac naturel (avec des populations viables de poissons) mais également de bénéficier de la répliquabilité des mésocosmes.

## Expériences versus modélisation

Cette thèse regroupe à la fois des travaux théoriques et expérimentaux. Ces deux façons d'aborder des questions scientifiques se placent sur un gradient allant de l'omniscience au réalisme total. Les modèles mathématiques très simples étudiés de façon analytique (DeAngelis, 1992; Loreau, 2010) sont à l'extrémité de l'omniscience puisque le calcul donne la réponse exacte du système à chacun des paramètres. Cependant, la possibilité de faire de telles études ne peut se faire qu'au prix d'une simplification importante du modèle avec souvent un nombre limité d'entités en interaction et des représentations biologiques simplistes des mécanismes biologiques (représentés de façon linéaire). Malgré cette simplicité, ces modèles permettent d'explorer de façon efficace de nouvelles hypothèses et même de mettre en évidence des mécanismes contre-intuitifs qui ont donné lieu à de vifs débats comme la relation diversité-stabilité (McCann, 2000) ou encore le paradoxe de l'enrichissement (Roy and Chattopadhyay, 2007). Les observations de terrain sont elles à l'extrémité du réalisme total puisqu'elles rendent directement compte des systèmes vivants, cependant les résultats sont parfois difficiles à interpréter à cause de la multiplicité des variables et de la covariation d'un certain nombre d'entre-elles. Ces observations permettent cependant de théoriser de nouveaux mécanismes du fonctionnement du vivant mais aussi de borner dans des limites réalistes tout modèle. La biologie, et l'écologie en particulier, sont avant tout des sciences fondées sur des travaux empiriques et expérimentaux, faire de modèles qui ne sont pas discutés par rapport à des systèmes réels n'aurait pas de sens. Entre les deux, on retrouve les expériences en milieu contrôlé et les modèles fondés sur les simulations.

On retrouve dans les expériences un gradient de simplicité-réalisme qui a déjà été discuté dans la section précédente. Ces expériences sont elles aussi des modèles représentant des systèmes plus complexes (le mésocosme approximant le lac) mais il est parfois difficile d'isoler des mécanismes particulier comme le recyclage des nutriments qui est quasiment indissociable du fonctionnement d'un écosystème. C'est pour cela que la discussion de l'effet du recyclage des nutriments sur la stabilité des réseaux trophiques a été assez difficile. Les modèles théoriques fondés sur des simulation numériques se situent entre les modèles analytiques et les expériences. En effet, le chercheur est toujours omnipotent face à ce modèle car il est possible de séparer ou de mimer presque n'importe quel mécanisme comme nous l'avons fait avec le recyclage des nutriments dans le chapitre 1. Cependant, l'étude de ces modèles s'apparente plus à une expérience puisque la réponse du système ne peut être étudiée qu'au travers de variables de sorties mises en relations avec des paramètres d'entrée. Même si l'accès à l'information est très facile, par exemple il est possible de mesurer parfaitement le recyclage de chaque espèce ou d'enregistrer la production primaire, le système reste une grosse boîte noire requérant des analyses de sensibilité et des simulations croisant de nombreux paramètres pour avoir une compréhension fine du système (tâche fastidieuse et presque



impossible). Malgré ces inconvénients, ces modèles numériques permettent de complexifier les modèles analytique pour d'une part augmenter le nombre d'entités en interaction (augmentation de la complexité) et d'autre part pour représenter de façon plus réaliste les mécanismes biologiques (réponses non linéaires). Ils font ainsi le lien entre théorie et expérience dans le continuum évoqué précédemment.

Un prochaine étape possible pour les études présentées dans ce manuscrit serait de paramétrer notre modèle pour chercher à reproduire notre expérience en mésocosmes, comme l'ont fait [Boit et al. \(2012\)](#) avec le lac de Constance, afin de mieux relier notre modèle à la réalité et pour mieux comprendre la réponse de nos mésocosmes à nos traitements.

## Conclusion

Cette thèse a permis de mieux relier l'écologie des communautés au fonctionnement des écosystèmes en étudiant le recyclage des nutriments dans sa représentation minimale puis en étudiant comment la fraction du réseau trophique assurant cette fonction, le réseau brun, interagit avec le réseau vert et modifie la stabilité du réseau global. La dimension "réseau complexe" était la grande nouveauté dans le cadre de l'étude du recyclage des nutriments et des interactions entre réseau trophique vert et réseau trophique brun. Le chapitre 1 a montré que cette nouveauté changeait les conséquences du recyclage des nutriments sur la stabilité et le chapitre 2 a montré que les réseaux trophiques vert et brun réagissaient différemment à l'enrichissement. Le chapitre 3 a permis d'explorer les interactions entre réseaux vert et réseau brun sur un système aquatique réel en croisant pour la première fois des traitements qui avaient jusqu'à présent été considéré séparément. Le chapitre annexe 4 a quant à lui montré comment la modification d'un point central des modèles de réseaux trophiques allométriques, la modélisation du taux métabolique par une grandeur constante, pouvait fortement modifier la stabilité du réseau.

Ces études ouvrent la voie à de nombreuses autres. Notre expérience en mésocosmes devrait être refaite en repensant le traitement consistant en l'ajout de matière organique qui probablement a été trop faible et n'a eu que des effets mineurs. Le rôle des grands cladocères dans les couplages vert/brun est aussi prometteur car dans les études précédentes l'absence de ces derniers était presque toujours couplée à la présence de poissons, or ces derniers ont aussi un effet bottom-up fort via le recyclage des nutriments. Notre modèle de réseau trophique avec un réseau vert et un réseau brun pourrait être encore largement étudié avec des modifications minimales. Le rôle des prédateurs de sommet de chaîne dans le couplage des deux réseaux pourrait être abordé via un généralisme inter-réseau qui dépendrait de la taille corporelle des consommateurs, c'est-à-dire que seuls les consommateurs le plus gros assureraient ce couplage par exemple. L'inclusion d'organismes fixateurs d'azote ou de mixotrophes serait également prometteur pour mieux explorer les stratégies des organismes à la base du réseau pour faire face à la limitation en nutriments. Le modèle de plasticité phénotypique pourrait être étendu à d'autres traits comme par exemple la stœchiométrie des producteurs primaires.

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