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# Effects of interactions between the green and brown food webs on ecosystem functioning

Kejun Zou

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Université Pierre et Marie Curie

Ecole doctorale : 227 Science de la Nature et de l'Homme

*Laboratoire : Institut d'Ecologie et des Sciences de l'Environnement de Paris*

**Effects of interactions between the green and brown food  
webs on ecosystem functioning**

*Effets des interactions entre les réseaux vert et brun sur le  
fonctionnement des écosystèmes*

Par Kejun ZOU

Thèse de doctorat d'Ecologie

Dirigée par Dr. Sébastien BAROT et Dr. Elisa THEBAULT

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## **Abstract**

This thesis studies through three models and an experiment the important effects of the interactions between the green (based on primary production) and brown (based on decomposition) food webs on ecosystem functioning. Three interactions between the two food webs are studied: 1) nutrients recycled from all organisms in the food web couple the green and brown food webs through mutualistic/competitive interaction between primary producers and decomposers; 2) generalist consumers feed on prey from both food webs; and 3) the spatial connections between the two food webs through mobile generalist consumers at the top and through nutrient and detritus fluxes at the bottom of the food webs.

The first model couples the green and brown food webs by nutrient cycling and demonstrates that the top-down trophic cascading effects of one food web can affect the production of the other food web. These cascading effects are driven by distinct mechanisms based on nutrient cycling. The second model couples the two food webs by nutrient cycling and generalist consumers and shows that the stabilizing effects of asymmetry between green and brown energy channels depend on the mutualistic/competitive relationship between autotrophs and decomposers. The third model couples the two food webs through spatial connections and finds that the relative importance of the green and brown pathways (i.e. the green- or brown-dominance) are determined by interacting effects between top and bottom spatial couplings. The experiment results are used to test the predictions of models through the independent manipulation of the green and brown food webs in aquatic mesocosms.

These results lead to new (1) insights on the way to model food webs, (2) predictions on food web functioning, (3) interpretation of empirical results, (4) ideas to compare the functioning of different ecosystem types and (5) predictions on food web responses to global changes.

## Résumé

Cette thèse étudie par trois modèles et une expérience les effets des interactions entre le réseau vert (basé sur la production primaire) et brun (basé sur la décomposition) sur le fonctionnement des écosystèmes. Trois interactions entre les deux réseaux sont étudiées: 1) les nutriments recyclés par tous les organismes couplent les réseaux verts et bruns par une relation de mutualisme/compétition entre les producteurs primaires et les décomposeurs; 2) les consommateurs généralistes se nourrissent de proies des deux réseaux trophiques et 3) les connexions spatiales par les consommateurs généralistes mobiles en haut des réseaux trophiques et les flux de nutriments et de détritiques en bas.

Le premier modèle couple les chaînes vertes et brunes par le recyclage des nutriments et démontre que les effets top-down en cascade d'une chaîne peuvent affecter la production de l'autre chaîne. Ces effets en cascade sont entraînés par des mécanismes distincts basés sur le recyclage des nutriments. Le deuxième modèle couple les deux chaînes par le recyclage des nutriments et des consommateurs généralistes et montre que les effets stabilisants de l'asymétrie entre la chaîne verte et brune dépendent de la relation de mutualisme/compétition entre les autotrophes et les décomposeurs. Le troisième modèle couple les deux chaînes par des connexions spatiales et montre que l'importance relative de la chaîne verte et brune est déterminée par des interactions entre les couplages spatiaux en haut et en bas des chaînes trophiques. Les résultats de l'expérience en mésocosmes aquatiques sont utilisés pour tester les prédictions des modèles en manipulant indépendamment la chaîne verte et brune.

Ces résultats conduisent à (1) de nouvelles perspectives sur la modélisation du fonctionnement des réseaux trophiques, (2) des prédictions originales, (3) des nouvelles interprétations de résultats empiriques, (4) des idées sur des différences fondamentales de fonctionnement entre types d'écosystèmes, (5) des prédictions sur la réponse des écosystèmes aux changements globaux.

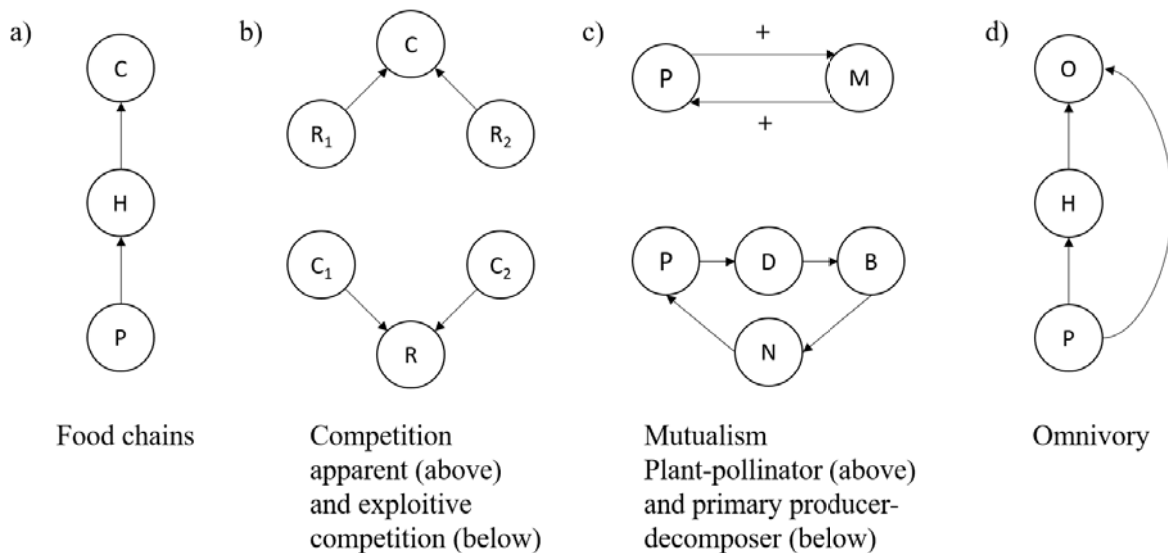
# Chapter 1

## Introduction

This chapter provides the background of my work. At first, I present an overview of how food web structure can affect ecosystem functioning (1.1) and the principal approaches for modelling the food web structure (1.2). Then, I summarize the importance of the two new processes I integrated into food web models: the nutrient cycling (1.3) and the interactions between the green and brown food webs (1.4), which are the key aspects investigated in my thesis. Finally, a brief overview of the structure of the thesis can be found in section 1.5.

### 1.1 Food web structure and ecosystem functioning

Food web structure and dynamic are key factors of ecosystem functioning and the response of communities to environmental perturbations. Relevant researches are very dynamic in this field of ecology (Pimm 1982; Duffy 2002; Thebault & Loreau 2003; Rooney & McCann 2012; Thompson *et al.* 2012). These studies have led to the development of an extensive theoretical and empirical corpus that aims at determining the influence of food web structure on the stability of communities (Neutel *et al.* 2002), and the respective impact on ecosystem functioning of the control by resources (bottom-up) and by predation (top-down) (Hunter & Price 1992). I summarize here: 1) what specific food web structures are considered important to determine ecosystem functioning in current ecological research (Fig. 1); and 2) how human impacts can modify food web structure and what are the consequences on respective ecosystem functioning (Table 1).



**Figure.1** Important food web structures determining ecosystem functioning in current ecological research. a) Food chains,  $P, H, C$  represent primary producers, herbivores and carnivores respectively. b) Competition,  $R_i, C_i$  represent the resources and consumers respectively. c) Mutualism, two types of mutualism are presented. The first is the interaction between plant and pollinator ( $P, M$  represent plants and pollinators respectively). The second is the interaction between primary producers and decomposers  $P, B, N, D$  represent primary producers, decomposers, nutrients and detritus respectively). d) Omnivory,  $P, H, O$  represent primary producers, herbivores and omnivores respectively.

- Food chains

Food chains are linear structures of trophic links in food webs from producers (bottom) to predators (top) (Fig.1-a). In a food chain, organisms are connected with each other by trophic interactions and categorized into specific trophic levels (e.g. carnivore, herbivores, producers etc.) (Loreau 2010). The indirect regulations of different trophic levels by the top predators (top-down) and by the availability of resource (bottom-up) (Oksanen *et al.* 1981; Carpenter *et al.* 1985) have been documented as trophic cascades in diverse ecological systems (Brett & Goldman 1996; Micheli 1999; Pinnegar *et al.* 2000; Schmitz *et al.* 2000). Trophic cascades have been considered as important factors determining key ecosystem functions such as biomass distribution, nutrient cycling, and primary productivity within food webs (Pace *et al.* 1999; Post 2002).

Human activities can strongly modify the structure of food chains and have severe consequences in impacted ecosystems. On one hand, harvesting of organisms and habitat

fragmentation can cause large removals of top predators, resulting in herbivory out of control and dramatic reduction in the density of primary producers (Jackson 2001; Ripple *et al.* 2001; Terborgh 2001). On the other hand, farming, industrial and urban effluents can lead to enrichment in mineral nutrients and higher inputs of organic matter to ecosystems, which greatly disturbs the functioning of these ecosystems and can lead to explosive growth of herbivores (Jefferies 2004) or bacteria (Dodds & Cole 2007). Thus human impacts at the top and at the bottom of food chains drive cascades of consequences, which usually cause great losses of biodiversity and ecosystem functions.

- Competition

The role of interspecific competition in structuring communities has been long studied both theoretically and empirically (Holt *et al.* 1994; Worm *et al.* 2002). In exploitative competition two consumers compete for the same resource while apparent competition occurs among species consumed by a shared natural enemy (Fig.1-b). In both cases, species interact with each other in an indirect manner. Studying competition can help ecologists understand a large body of ecological patterns such as the coexistence and the dominance of species within communities (Tilman 1982), and the increase in ecosystem stability related to dampened oscillations between consumers and resources (McCann *et al.* 1998).

The responses of different species to global change can shift competitive balances to favor certain species (Tylianakis *et al.* 2008). For example, certain plant species can have a competitive advantage in environmental conditions with eutrophication or increased temperature and become dominant in the community (Tilman & Lehman 2001; Zavaleta *et al.* 2003). Invasive species can outcompete native species by enhancing the population of shared predators or through more effective exploitation on the resource (Snyder & Evans 2006). All these influences can drastically modify species distributions in the ecosystem and impact the main ecological processes such as primary productivity, nutrient cycles and stability.



- Mutualism

Mutualism is an interspecific interaction in which both partners benefit from the activity of each other (Fig.1-c). Mutualism is ubiquitous and exists in diverse forms in nature (Polis & Strong 1996). The interaction between plants and pollinators is one of the most well-known mutualistic interaction in which animals help plant reproduction through pollination and receive nectar as a reward (Memmott 1999). Another important mutualistic interaction is between primary producers and decomposers: most primary production becomes detritus thus providing the resource for decomposers and in return the decomposition process provides mineral nutrient which is essential for the growth of primary producers (Daufresne & Loreau 2001). These structures of mutualistic interactions are indispensable for contributing to the healthy functioning of ecosystems such as primary productivity (plant – pollinator interaction) and nutrient dynamics (primary producer – decomposer interaction, developed in following sections).

Both forms of mutualistic interactions and related ecosystem functioning can be negatively affected by anthropogenic changes. For example, global warming and habitat loss can reduce the spatial and seasonal overlap of plant flowering and pollinator activities (Fortuna & Bascompte 2006; Memmott *et al.* 2007). Eutrophication and enhanced atmospheric CO<sub>2</sub> level can induce changes in stoichiometric composition of detritus and decomposers, which play an important role in stabilizing the ecosystem (chapter 2). Overall the loss or modification of such mutualistic interactions within food webs can result in severe degradation of the related ecosystem functions.

- Omnivory

Omnivory are consumers feeding on more than one trophic level (Pimm 1982), e.g., the omnivores consume resources from both plant and animal origins. Omnivory has been found ubiquitous in food webs and represents an important structural component in determining

ecosystem functioning. The presence of omnivores can eliminate effects of trophic cascade as they can switch to feed on different resources (Pace *et al.* 1999). More specifically, omnivores feeding on detritus can have important effects on nutrient cycling and facilitate primary productivity to compensate negative cascading effects through herbivory (Thompson *et al.* 2007). Omnivory has been also included in discussions of food web structure and ecosystem stability. Classical food web theory has suggested destabilizing effects of omnivory (Pimm & Lawton 1978; Pimm 1982). However, more recent theory and experiments indicate that omnivory can be an important stabilizing structure (McCann & Hastings 1997; Holyoak & Sachdev 1998; Fussmann & Heber 2002) due to the “weak” link effects within food webs (McCann 2000; de Ruiter 2005).

While omnivory has important effects on regulating trophic cascades and promoting ecosystem stability, human impacts potentially reduce the positive effects of omnivory on ecosystem functioning. For example, reduced food web productivity due to reduced omnivory is reported in a decomposer-based food web (Kuijper *et al.* 2005). Ecosystems might require an increasing amount of omnivory to offset the destabilizing effects of spatial compression due to the reduced resource habitat scales compared with consumer foraging scale (McCann *et al.* 2005).

In summary, examples of species interactions listed above demonstrate that food web characteristics are important to determine ecosystem functioning. Due to human impacts, we can expect complex changes in food web structure, with potential major changes in ecosystem functioning (Jeppesen *et al.* 2010). Therefore studying the basic food web structure and related effects on ecosystem functioning is essential to understand and predict the consequences of such changes. This thesis is based on this principle to study the determining effects of specific food web structure on ecosystem functioning.

**Table 1.** Summary of examples of food web structure and related ecosystem functioning. The consequences of human impacts on corresponding ecosystem functioning.

<b>Food web structure</b>	<b>Related ecosystem functioning</b>	<b>Human impacts</b>	<b>Consequences</b>
Food chains	- Top-down trophic cascades - Bottom-up trophic cascades	- Removal of top predators - Enrichment in mineral nutrients and organic matters	- Explosion of herbivores or decomposers - Complete destruction of the food web
Competition	- Species dominance - Stability	- Global change - Invasive species	- Modification of species distributions - Reduce stability
Mutualism	- Primary productivity - Nutrient cycling	- Global change - Habitat loss	- Reduced primary productivity - Reduced stability
Omnivory	- Regulate trophic cascade - Nutrient cycling - Stability	- Global change - Species loss - Spatial compression	- Reduced food web productivity - Reduced stability

## 1.2 Modeling the food web structure

Understanding and modelling food web structure is an active area of theoretical ecology. From mathematical perspectives, food webs are complex dynamic systems consisting of many biological species that interact in many different ways (i.e. trophic interaction, competition, mutualism etc. as listed in the previous section) and cause changes in time and space (McCann 2011). Using systems of differential equations is the main theoretical approach to describe the

dynamics of interacting populations and the patterns of connections among them. These descriptions of food webs can be at different levels of complexity (i.e. from simple consumer-resource trophic interaction to large networks of different interactions) and there are numerous ways of analyzing the response of ecosystem functioning to the specific food web structure.

One of the fundamental building block of food web models is the consumer-resource trophic interaction (Fig. 2-a). In a consumer-resource relationship, the consumer depends for subsistence on the resource. Denoting the number of consumers at time  $t$  by  $C(t)$  and the number of resources by  $R(t)$ , the dynamics of the consumer-resource relationship can be described by equations:

$$\frac{dR}{dt} = \phi(R) - f(C, R)R \quad (1)$$

$$\frac{dC}{dt} = ef(C, R)R - d_C C$$

where  $\phi(R)$  is the growth of the resources in the absence of the consumers,  $f(C, R)$  is the functional response of the consumers feeding on the resources,  $e$  is the consumption efficiency (i.e. the proportion of resource biomass assimilated by the consumers) and  $d_C$  is the natural loss rate of the consumers. The growth of the resources can be either a linear function (i.e.  $\phi(R) = rR$ ) or including intra-species competition to have the logistic form (i.e.  $\phi(R) = rR(1 - R/K)$ , where  $K$  is the carrying capacity). The functional response of the consumers  $f(C, R)$  has also different forms. The first consumer-resource model was the Lotka-Volterra model that uses a linear functional response,  $f(C, R) = aR$ , where  $a$  is the attack rate. More realistic functional responses are used in later research such as the Holling Type II functional response  $f(C, R) = \frac{aR}{1+ahR}$ , where  $h$  is the handling time that represents the time used for consuming the resource.

The consumer-resource dynamics with realistic growth and functional responses can be generalised in population dynamics equations describing more complex food webs of

interacting species. The generalized model is thus (assuming  $B_i$  is the population size or population density of species  $i$ ):

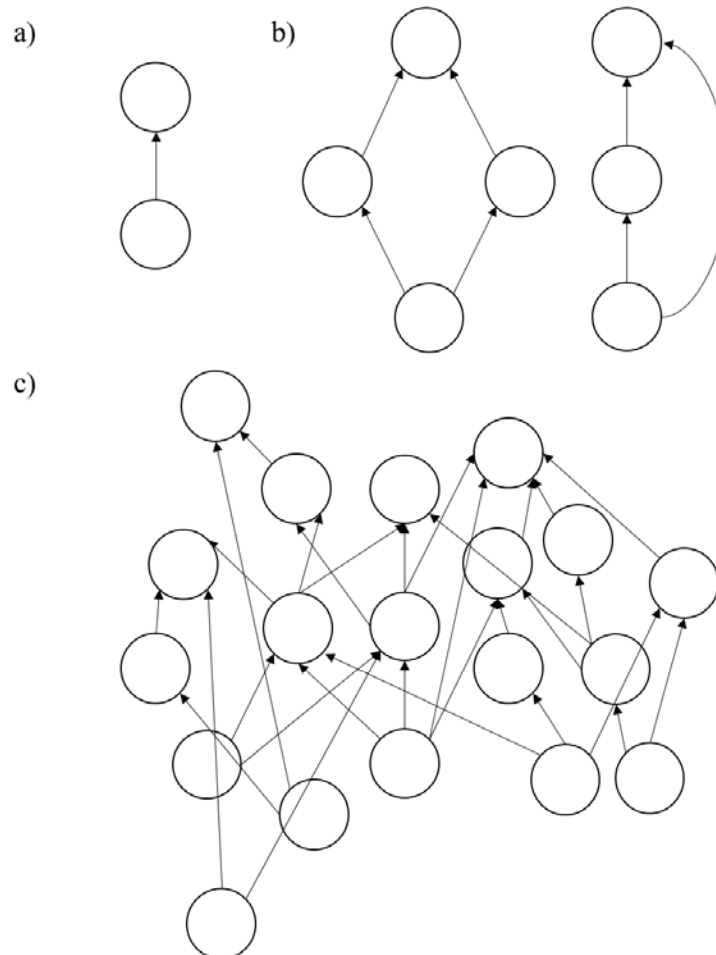
$$\frac{dB_i}{dt} = e \sum_j B_j f_{j,i} - \sum_j B_j f_{i,j} - d_i B_i \quad (2)$$

with the first term representing the growth of species  $i$  feeding on other species, the second term is representing the predation by other species, and the last term is the natural loss of species  $i$ . Applying the generalized consumer-resource dynamics in food web models, there are mainly two ways of looking at the dynamics of ecological systems.

The first is the concept of modules in ecology introduced by Robert Holt (1997). Here “modules” can be seen as sub-systems which are of intermediate complexity beyond consumer-resource interactions but below the diversity found in most ecosystems (Fig. 2-b). This way of modelling food webs assembles species into taxonomic entities or functional groups and generally consists of three to six interacting compartments (Holt & Hochberg 2001; Milo 2002). Theories are developed to understand how species interact and to study the mechanisms underlying the effects of food web structure by analysing the role of specific parameters (e.g. growth rate, attack rates etc.). For example, the study of consumer-resource interaction modules showed that weak attack rates can have stabilizing effects in ecosystems (McCann *et al.* 1998).

The second way of modelling food web structure is based on complex sets of interactions of many species with many links, which captures more realistic properties of real ecosystems (Pascual & Dunne 2006) (Fig.2-c). The network structure is either extracted from empirical studies or derived from some stochastic algorithm. For example, in the well-known niche model, species are characterized by their feeding centre and feeding range along a niche axis which determine a niche interval delimiting niche values of their prey (Williams & Martinez 2000). These network models are mainly used to investigate the effects of network structure on ecosystem stability (Montoya *et al.* 2006; Allesina & Pascual 2008; Thébault & Fontaine 2010).

Some important mechanism underlying network structure such as adaptive foraging and allometric structures are found to enhance the stability of ecosystems (Kondoh 2003; Brose *et al.* 2006).



**Figure.2** Schematic presentation of different approaches for modeling food webs. a) The fundamental building block of food web models: the consumer-resource interactions. b) The “modules” in food web models. Modules are sub-systems which are of intermediate complexity beyond consumer-resource interactions but below the diversity found in most ecosystems. c) The network structure of food webs, which is based on complex sets of interactions of many species with many links. The circles in the figure represent different species or functional groups (i.e. compartments) and the arrows represent trophic links between species or compartments.

The two ways of modelling food web structure (modules and networks) clearly interact: the modules are the basic building blocks of complex networks (Milo 2002). Further, spatial structuring (McCann *et al.* 2005; Gravel *et al.* 2010b) and evolutionary processes (Loeuille &

Loreau 2005) also have significant influences on food web structure and related ecosystem functioning. From the simplest consumer-resource interaction to the most complex ecological networks, modelling approaches help ecologists to explore and understand the relationship between food web structure and ecosystem functioning.

Many ecological properties can be easily measured in food web models. Analytic methods and simulations are widely used to decipher the dynamical outcomes of food web models based on differential equations (Brose *et al.* 2006; Attayde & Ripa 2008; Wollrab *et al.* 2012). The distribution of species and functional groups are revealed by the species biomass or the density of population in dynamic system models (Leroux & Loreau 2010). The coexistence of species under different conditions can also be predicted by such distribution (Daufresne & Loreau 2001). Estimations of primary and secondary productions are based on consumer and resource biomass and the functional responses among them (Zou *et al.* 2016). A measure of ecosystem stability, the coefficient of variation (variation/mean), examines the temporary variability of population dynamics in cyclic dynamics (Tilman 1999). These examples for measuring ecosystem functioning and stability are key methods in studying effects of food web structure and will be performed in this thesis.

The modeling approaches mentioned above so far discussed the importance of studying the dynamics of interacting populations to understand effects of food web structure on ecosystem functioning. Nevertheless, most of these studies ignore the overall functioning of the ecosystems: the energy and material flows. In particular, the nutrient material flows potentially introduce new interactions and have important consequences on ecosystem functioning. In the following sections I will summarize the importance of including nutrient cycling in food web studies and introduce the method used to integrate nutrient cycling into food web models in the thesis.

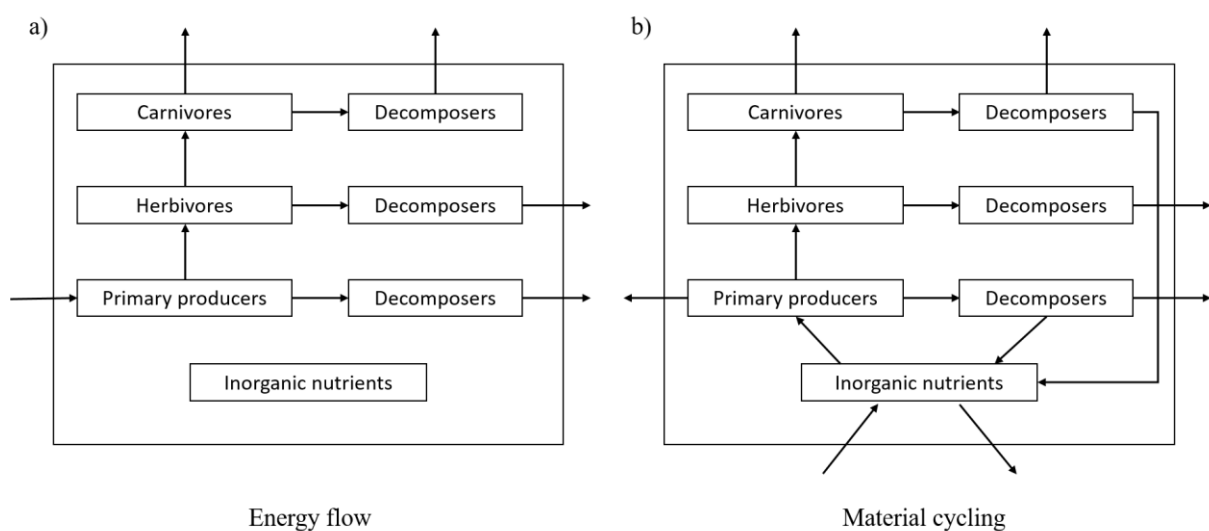
### 1.3 Nutrient cycling

While studies of population dynamics in communities focus on biotic interactions, the flows of energy and nutrient material in ecological systems are also important aspects to consider for understanding ecosystem functioning (DeAngelis 1980). These two aspects are interrelated: on the one hand, energy and nutrient materials can limit the species populations and influence the food web structures; on the other hand, interactions among species / functional groups may influence energy and material flows. Energy transfers are generally modeled as linear flows through trophic interactions (Fig. 3-a). Energy is seldom recycled within ecosystems due to its gradual dissipation through respiration. By contrast, nutrient materials can generate circular flows among all ecosystem components (Fig.3-b). Mineral nutrients are heavily recycled within ecosystems, which represents another important interaction among ecosystem components and may offer new challenges and questions compared with the population-community perspective. In many ecosystems, the internal recycling can account for a larger amount of nutrients than the inputs and the outputs to the ecosystem and has the potential to compensate nutrient limitation (Vitousek & Matson 2009). Therefore, nutrient cycling is one of the key processes in the overall ecosystem functioning.

To integrate nutrient cycling into food web studies, it is necessary to consider at least two additional components representing the limiting nutrient in their inorganic and organic forms: the mineral nutrient pool and the detritus pool respectively. Accordingly, nutrients that are unassimilated or lost from organisms (excretions, faeces, dead individuals or materials, etc.) return to the ecosystem via two main types of nutrient cycling processes. On the one hand, organisms release mineral nutrients in inorganic form via excretory processes (i.e. urine production), which is directly available for autotrophs and bacteria uptakes and termed as direct nutrient cycling (Vanni 2002). On the other hand, unassimilated organic matters (faeces), dead individuals and dead parts of higher plants return to the environment as detritus that need to be



remineralized by decomposers before being available to autotrophs and bacteria (Moore *et al.* 2004). The process is named indirect nutrient cycling. Further, the availability of limiting nutrient is not only dependent on recycling within the local community but also on external nutrient inputs and outputs. Transportation of nutrients by physical forces (e.g. water, wind etc.) or by organisms at larger scales are also essential processes for nutrient dynamics. All above processes introduce new dynamical behaviors in food web models, which potentially lead to significant consequences on ecosystem functioning.



**Figure.3** Contrasting patterns of energy flow and material cycling in ecosystems (adapted from (Loreau 2010)). a) Linear flows of energy through trophic interactions. b) Circular flows of materials among all ecosystem components.

Nutrient cycling and its potential effects on ecosystem functioning have been addressed in theoretical studies. In his work, DeAngelis (1980; 1989) discussed the effects of nutrient cycling on the resilience of the ecosystem (measured by the dominant eigenvalue of the Jacobian matrix at equilibrium) in models with increasing complexity. These models suggest that a high degree of nutrient cycling tends to increase the rate of biomass production but biomass is then restored less quickly after removal, making ecosystems less resilient to perturbations. Other studies have explored the impacts of nutrient cycling on trophic cascading effects (De Mazancourt *et al.* 1998; Leroux & Loreau 2010) and demonstrated that consumer-mediated nutrient cycling generally positively affected primary production due to indirect

mutualism between ecosystem components. The meta-ecosystem theory connects a set of ecosystems by fluxes of organisms, dead organic matter and mineral nutrients, which reflects the nutrient dynamics in spatial context. The nutrient flux among ecosystems can affect the diversity and coexistence of organisms (Daufresne & Hedin 2005), the stability and the functioning of ecosystems (Loladze *et al.* 2000; Miller *et al.* 2004). However, modeling nutrient dynamics is still not very common in food web models compared to its importance on ecosystem functioning. In this thesis, I focus on the inclusion of nutrient dynamics in food web models, including both direct and indirect nutrient cycling among ecosystem components and spatial fluxes of nutrients in both inorganic and organic forms.

To do so, I use dynamic systems to describe nutrient fluxes in open ecosystems in which the limiting nutrient (in most ecosystems either nitrogen or phosphorus) is recycled between biotic and abiotic compartments. The mineral nutrient pool and detritus pool are denoted as  $N_i$  and  $D_i$  respectively. They are supplied by constant inputs  $I_{N_i}$  and  $I_{D_i}$ , and they lose nutrients from the ecosystem at constant rates  $l_{N_i}$  and  $l_{D_i}$  respectively. The nutrients that are lost by living compartments ( $B_i$ ) are recycled back to the ecosystem. There are two origins for these losses: one corresponds to natural loss such as excretion and death of individuals (occurs at rate  $m_{B_i}$ ); the other is the fraction of nutrients that is not assimilated by consumers ( $1 - e_{i,j}$ ). We assume that only a fraction ( $\partial_i$ ) of the recycled nutrients goes to the mineral nutrient compartments ( $N_i$ ) that can be directly used by primary producers (direct nutrient cycling):  $\sum \partial_i B_i (m_{B_i} + (1 - e_{i,j}) f_{i,j})$ . Meanwhile the other fraction ( $1 - \partial_i$ ) goes to the detritus compartment ( $D_i$ ) that needs to be mineralized before being available to primary producers (indirect nutrient cycling):  $\sum (1 - \partial_i) B_i (m_{B_i} + (1 - e_{i,j}) f_{i,j})$ . Note that primary producers are generally considered unable to excrete mineral nutrients directly, thus the  $\partial_i$  for primary producers is set to 0. The spatial flows between nutrient and detritus compartments are modelled after a meta-ecosystem model (Gravel *et al.* 2010a) as  $\Delta N = d_N(pN_i - (1 - p)N_j)$  and

$\Delta D = d_D(qD_i - (1 - q)D_j)$  respectively for the patch  $i$  and the opposite for the patch  $j$ .

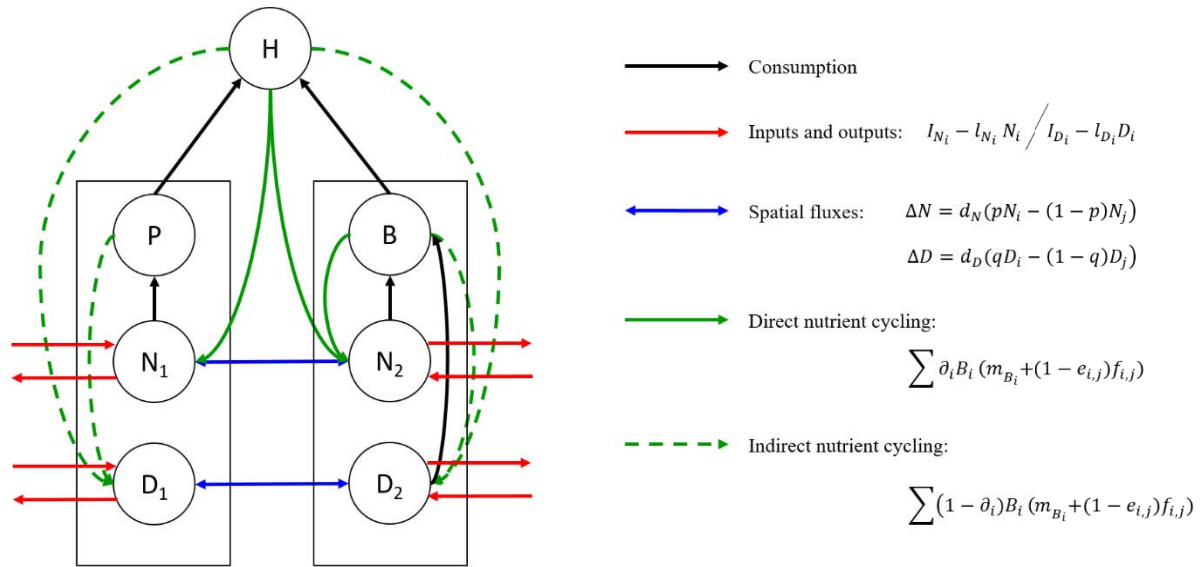
Here  $d_N$  and  $d_D$  are constant diffusion rates for nutrient and detritus respectively and  $p$  and  $q$  are indexes determining the asymmetry of nutrient and detritus fluxes between patches. Thus

the differential equations describing the dynamics of  $N_i$  and  $D_i$  are:

$$\frac{dN_i}{dt} = I_{N_i} - l_{N_i} N_i + \sum \partial_i B_i (m_{B_i} + (1 - e_{i,j}) f_{i,j}) + \Delta N - \text{consumption} \quad (3)$$

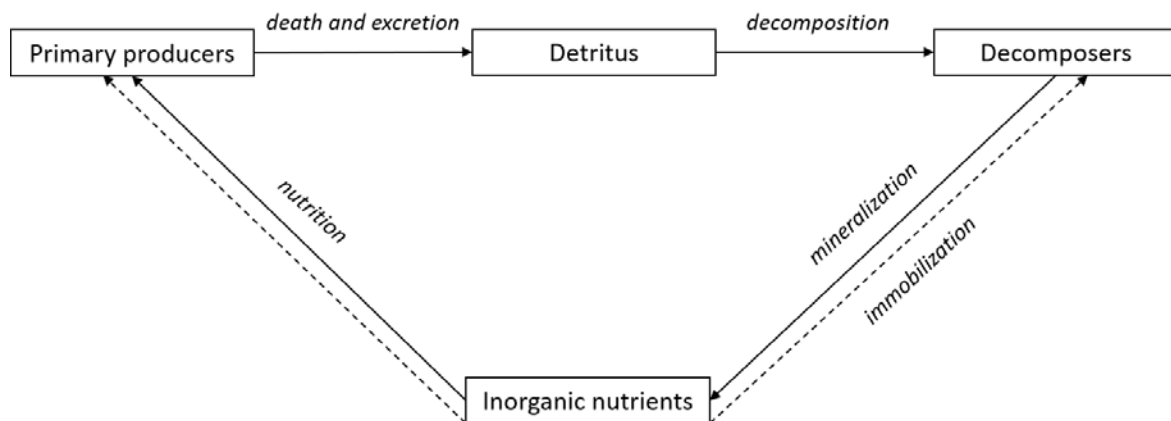
$$\frac{dD_i}{dt} = I_{D_i} - l_{D_i} D_i + \sum (1 - \partial_i) B_i (m_{B_i} + (1 - e_{i,j}) f_{i,j}) + \Delta D - \text{consumption}$$

Thus, in general, the dynamics of mineral nutrient and detritus consist of the following ingredients: inputs and outputs, nutrient fluxes due to direct and indirect nutrient cycling respectively, spatial fluxes between patches and the consumption by autotrophs and/or decomposers (Fig.4).



**Figure. 4** Schematic fluxes of mineral nutrient and detritus in the ecosystems. Black arrows represent the consumption of nutrients and detritus by primary producers and decomposers. Red arrows represent inputs and outputs of nutrients and detritus. Blue arrows represent spatial fluxes of nutrients and detritus between patches. Green arrows represent nutrient fluxes due to direct (solid arrows) and indirect (dashed arrows) nutrient cycling respectively.  $P, B, H$  are biotic components of the ecosystem which can represent primary producers, decomposer and herbivores respectively. Symbols and expressions are indicated in the text.

With the perspective of nutrient cycling, new components and new interactions are introduced to food web models. The interaction between autotrophs and decomposers is particularly interesting: on one hand, the production of both autotrophs and decomposers can be limited by the mineral nutrients; on the other hand, autotrophs produce organic matter which is the energy source of decomposers while decomposers in return mineralize mineral nutrients to support the production of autotrophs (Fig.5). Further, both autotrophs and decomposers support upper trophic levels within the ecosystem: there is a green food web based on the production of autotrophs (i.e. primary production) and a brown food web based on decomposition of organic matters (i.e. detritus). The complex interaction between autotrophs and decomposers reveals the complex interaction between the green and the brown food webs, which is a fundamental structure of ecosystems. This particular structure of food webs can have important consequences on ecosystem functioning. In the following section I summarize the interactions between these two food webs and how I plan to integrate these interactions into food web models to study their effects on ecosystem functioning.



**Figure. 5** Indirect mutualism and resource competition in a primary producer-decomposer system with nutrient recycling (adapted from (Daufresne & Loreau 2001)). Solid and dashed arrows represent respectively the indirect mutualism (i.e. the primary producers provide detritus through death and excretion, which constitutes the energy resource for decomposers, and decomposers decompose the detritus and recycle the nutrient by mineralization) and the competition for mineral nutrients between primary producers and decomposers.

#### **1.4 Interactions between the green and brown food webs**

Classical studies on trophic dynamics mediated by top consumers and resources consider exclusively the green food web based on primary production. However, in most ecosystems, the green food web is not the only pathway of energy and nutrient (Polis & Strong 1996; Cebrian 1999). The majority of primary production and the organic matters excreted by herbivores and carnivores go directly to detritus and support a diverse collection of consumers: the brown food web. In addition to its importance in ecosystem energy flows, the brown food web based on detritus play a significant role in nutrient cycling due to the decomposition process which regenerate nutrients back to the ecosystem (DeAngelis 1992; Moore *et al.* 2004). As mentioned in the previous section, primary producers in the green food web and decomposers in the brown food web have both competitive (i.e. growth based on mineral nutrients) and mutualistic (i.e. production of detritus by primary producers and remineralization of nutrients by decomposers) interactions (Fig.5). These interactions may extend to the whole food web and generate complex interactions between the green and the brown food webs.

At the food web scale, interactions between the green and the brown food webs often occur through three major ways:

- 1) Nutrient cycling

All organisms of both food webs lead to direct and indirect nutrient cycling that support the mineral nutrient and detritus pool respectively. This leads to the competitive and indirect mutualistic interactions between primary producers and decomposers mentioned above. It has been demonstrated that these complex interactions are dependent on the limitation types of decomposers and the stoichiometry mismatches between decomposers and their resources (Daufresne & Loreau 2001). According to ecological stoichiometry, the mismatch in elemental quality (i.e. nutrient to carbon ratios) between decomposers and their resources can determine decomposers nutrient uptakes. Increasing mismatch means that the decomposers need to take

more nutrients, and the competition intensity between primary producers and decomposers then increases. Thus, through nutrient cycling, the green and the brown food webs are linked at the bottom of the food webs.

## 2) Generalist consumers

There are generalist predators that feed on prey from both the green and the brown food webs. For example, many aquatic consumers (e.g. filter-feeding organisms, planktivorous and piscivorous fish) consume prey on the basis of body size and can be trophic generalists which potentially link the autotroph-based pelagic webs and detritus-based benthic webs in freshwater ecosystems (Vander Zanden & Vadeboncoeur 2002; Vadeboncoeur *et al.* 2005; Shurin *et al.* 2006). In terrestrial ecosystems, the generalist predators (e.g. spiders, staphylinid and carabid beetles) are known to rely on food resources from both above-ground (i.e. feeding on plant herbivores) and below-ground (i.e. feeding on systems microbial detritivores) (Polis & Strong 1996; Wardle *et al.* 2004). Therefore, through generalist consumers, the green and the brown food webs are linked at the top of the food webs.

## 3) Spatial couplings

The green and brown food webs may occupy spatially separated habitats. For example, pelagic (based mainly on phytoplanktonic production, the green food web) and benthic (based mainly on detritus, the brown food web) habitats are spatially decoupled but there are many cross-habitat interactions between them (Jäger & Diehl 2014). Since nutrient cycling and generalist consumers link the green and the brown food webs at the bottom and at the top of food webs respectively, the spatial fluxes of nutrient and detritus and the mobility of consumers and predators lead to spatial couplings of the green and the brown food webs.

The effects of interactions between the green and the brown food webs on food web functioning have been largely documented in empirical studies. For example, the concept of 'microbial loop' demonstrate that predators in the brown food web can increase nutrient

mineralization, which can indirectly affect primary production (Azam et al. 1983; Bonkowski 2004). It has also been shown that decomposer-mediated remineralization responds strongly to the quality and quantity of dead organic matter produced by the green food web (Wardle et al. 2003; Harrault et al. 2012). By contrast, interactions between the green and brown food webs have only been increasingly explored in recent theoretical studies. Attayde and Ripa (2008) have constructed a food web model comprising a green and a brown food chains coupled by nutrient cycling and a generalist carnivore. They demonstrated that both couplings interact to affect the mean abundance of the food web components along a gradient of nutrient enrichment. Generalist predators consuming prey from both food webs are reported to stabilize or destabilize the ecosystem under distinct conditions (Wolkovich *et al.* 2014). However, there is still a very large gap between empirical observations and theoretical studies on the interactions between the green and brown food webs and their important effects on ecosystem functioning.

A more complete framework integrating the interactions between the green and brown food webs is needed to study their effects on the ecosystem functioning. This is the goal of the thesis. The main interactions between both food webs and the related ecosystem functions studied in the thesis are briefly listed in Table 2. A more detailed plan of the thesis is given in the next section.

**Table 2.** Summary of the main interactions between the green and the brown food webs and the related major ecosystem functions studied by modelling approaches in the thesis

<b>Chapter</b>	<b>Interactions</b>	<b>Ecosystem functioning</b>
2	- Nutrient cycling	Top-down trophic cascades extending from one food web to the other food web
3	- Nutrient cycling - Generalist consumers	Stability of the ecosystem
4	- Nutrient cycling - Generalist consumers - Spatial couplings	Relative dominance of the green or the brown food web in the ecosystem

### 1.5 Structure of the thesis

This thesis contains three modelling studies and one experimental study. Each of these studies is presented in one chapter and the chapters are linked by the principal idea: the interactions between the green and brown food webs are key to understand ecosystem functioning. I start by connecting the green and brown food chains by nutrient cycling in the first model (Chapter 2) and show how the top-down trophic cascading effects of one food chain can affect the production of the other food chain. The second model (Chapter 3) integrates additionally another important interaction: the generalist consumers feeding on prey from both food chains. Effects of the asymmetry in energy channel/turnover between the two food chains and nutrient cycling mediated competitive/mutualistic relationship between primary producers and decomposers on ecosystem stability are explored. The third model (Chapter 4) puts the interactions at bottom through nutrient cycling and at top through generalist consumers into a spatial context. It examines how the spatial fluxes of nutrient and detritus and spatial coupling by mobile consumers interact to affect the relative dominance of the green or the brown food



webs. I also include an experimental study (Chapter 5) in which the theoretical predictions can be tested in the aquatic environment. In particular, the mesocosm experiment examines the top-down and bottom-up cascades under different scenarios of coupling between the green and brown food webs. Results in the Chapter 5 are still preliminary. Here I present an overview of the results from these four studies and a general discussion and perspectives of the thesis can be found in the last chapter (Chapter 6).

## **Chapter 2. Nutrient cycling and trophic cascades between the green and brown food webs**

(Published as Zou, K., Thébault, E., Lacroix, G. and Barot, S., 2016. Interactions between the green and brown food web determine ecosystem functioning. *Functional Ecology*.)

In this chapter the primary producer-based green chain and the decomposer-based brown chain are connected by nutrient cycling in a dynamical food web model. The model explores analytically the conditions that determine the direction of cascading effects from one food web to the other in different scenarios based on various assumptions. These assumptions include: 1) donor vs recipient control of decomposer production; 2) the limitation type of decomposers (i.e. carbon or nutrient limitation) and 3) different trophic lengths in both food chains. Numerical analysis are used to confirm the analytical predictions, with an additional analysis to compare linear vs type II functional responses. Results derived from different assumptions and under different functional responses provide a solid analysis on the robustness of the model predictions. Experiments published on cascading effects from one food web to the other are reinterpreted in relation to this work.

The originality of this work is the modelling of nutrient cycling through mineral vs detrital pathways (i.e. direct and indirect nutrient cycling respectively). The recycled nutrients supporting both the nutrient and detritus compartments lead to a complex relationship between

primary producers in the green food chain and decomposers in the brown food chain. Depending on their limitation type, decomposers either compete with primary producers for nutrients or benefit from detritus mainly provided by primary producers and support primary producers through remineralization of nutrients. These two aspects of nutrient cycling determine distinctly the cascading effects of the brown food web on primary production and of the green food web on decomposer production:

- The effects of the brown food web on primary production are mainly driven by the relative proportion of direct/indirect nutrient cycling in the brown web. When predators of decomposers recycle directly a larger (smaller) proportion of their nutrient than decomposers, their consumption of decomposers increases (decreases) primary production.

- The signs and strength of cascading effects of the green food web on decomposer production are determined by the carbon/nutrient limitation of decomposers. When decomposers are C-limited, the relation between primary producers and decomposers is strictly mutualistic, and carnivores, herbivores and primary producers have, respectively, positive, negative and positive effects on decomposer production. However, the signs of above cascading effects become condition-dependent when decomposers are N-limited, that is when producers and decomposers are competing for the same mineral resource.

Overall, this chapter shows the importance of integrating nutrient cycling into food web models. Nutrient cycling can question the traditional concept of top-down and bottom-up controls because consumers of one food web can affect the other one in a bottom-up way. Ecological processes behind the distinct mechanisms determining the two cascading effects and effects of other factors (e.g. the trophic length) are further developed in this chapter.

### **Chapter 3. Consequences of asymmetry between green and brown food webs on stability of aquatic and terrestrial ecosystems**

Top generalist predators can act as couplers of distinct energy channels that differ in turnover rates. Coupled fast and slow channels are found to convey both local and non-local stability to food webs in previous theoretical studies (Rooney *et al.* 2006). In this chapter the green and the brown food chains are connected by both nutrient cycling and by multi-chain feeding of generalist predators. Like the first model, integrating nutrient cycling results in complex interactions between primary producers and decomposers: they are linked by both indirect mutualistic and competitive interactions as a consequence of stoichiometric mismatches between decomposers and their resources. Additionally, the energy and nutrient flows between the green and the brown pathways coupled by generalist consumers can be asymmetric. With both modelling approach and reanalysis of published data, this study explores the interacting effects of interactions at the bottom and the top of the food web on ecosystem stability and generate two new insights:

- 1) The increase in stability due to turnover asymmetry between predator-coupled food chains (Rooney *et al.* 2006) is not always true in coupled green and brown food chains.

Nutrient cycling and the complex relationship between autotrophs and decomposers can influence the effects of asymmetry on ecosystem stability. In particular, only asymmetry towards a faster green food chain can increase the stability at relatively low competition intensity between chains. Conversely, asymmetry towards a faster brown food chain can stabilize the ecosystem when competition intensity between primary producers and decomposers is high. Increased nutrient cycling tends to attenuate the destabilizing effects of asymmetry when competition between decomposers and primary producers is weak but it has a destabilizing effect when competition is strong especially when the strength of the two food

chains are symmetric. Increased nutrient cycling also amplifies the destabilizing effect of symmetry between coupled green chains.

2) Difference in asymmetry degree and competition intensity among different types of ecosystems may lead to difference in stability.

The reanalysis of already published data indicates that both turnover asymmetry degree and competition intensity between green and brown food webs might differ among ecosystem types. Aquatic ecosystems tend to have faster green chains whereas terrestrial ecosystems tend to have faster brown chains. The stoichiometric mismatch between detritus and decomposer determining the competition intensity also varies between ecosystems. For example, it is assumed that aquatic detritus have higher mineral nutrient concentrations than terrestrial detritus. Thus the stoichiometric mismatches might be smaller in aquatic ecosystems, leading to weaker competition between primary producers and decomposers. These results may lead to different stability constraints in aquatic and terrestrial ecosystems.

Overall, this chapter highlights the complex effects of interactions at the bottom and the top of the food web on ecosystem stability. It helps to further disentangle the fundamental differences between the functioning of aquatic and terrestrial ecosystems and to predict potential changes in ecosystem stability under global change.

#### **Chapter 4. Linking the green and brown food webs through spatial coupling and consequences on ecosystem functioning**

This chapter puts the interactions between the green and brown food chains into a spatial context. Green and brown food webs can be spatially separated and the interactions between these two food webs can be affected by space. On the one hand, the interaction at the bottom of

food webs can be affected by spatial fluxes of nutrients and detritus between heterogeneous habitats (Gravel et al. 2010a; Gounand et al. 2014). On the other hand, the interaction at the top of food webs can be influenced by the mobility of the generalist consumers (Post et al. 2000; McCann et al. 2005). This study examines how the spatial couplings of the green and the brown food chains through generalist consumers at the top and resource fluxes at the bottom of food webs affect ecosystem functioning.

The model considers two asymmetries for the spatial flows: 1) the asymmetric consumption on prey from the green and the brown patches of the generalist consumers; and 2) the asymmetric fluxes of nutrients and detritus between the two patches. The results demonstrate that the two asymmetries in the spatial flows interact and determine the relative dominance of the green or the brown food webs in the ecosystems:

- The asymmetry favoring nutrient and detritus fluxes from the green patch to the brown patch provides relatively more resources to the brown patch. With herbivores as the top consumer this can amplify the predation effects of the consumer on autotrophs in the green patch. With carnivores as the top consumer, this asymmetry can dampen the negative trophic controls of top consumers on decomposers. Both effects favor the brown patch and the dominance of decomposers.

- The asymmetry favoring nutrient and detritus fluxes from the brown patch to the green patch provides more resources to autotrophs and limits the decomposers. These fluxes dampen the predation effects of consumers on autotrophs with herbivores as the top consumer and amplify the negative effects of trophic controls on decomposers with carnivores as the top consumer. Both effects lead to more autotroph dominated ecosystems.

Overall, this chapter integrates space into interactions between the green and brown food webs, which can provide a more realistic view of such food web interactions in ecosystems. Asymmetric spatial flows affect the dominance of either the primary producer in the green patch

or the decomposers in the brown patch, thus potentially affecting the relative importance of primary or decomposer production in the whole ecosystem.

## **Chapter 5. Studying the interactions between the green and brown food webs in a freshwater mesocosm experiment**

This chapter presents the preliminary results of a freshwater mesocosm experiment which aims at investigating the cascading effects between green and brown food webs and their consequences on ecosystem functioning predicted by previous modelling results (chapter 2).

The experiment takes into account two main interactions between the green and brown food webs:

- 1) The interactions 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.
- 2) The interactions at the top of the food webs via generalist predators (i.e. fish) that consume preys in both green and brown webs.

The mesocosm study was performed from the end of June 2015 to the beginning of November 2015. Thirty-six translucent polyethylene enclosures ( $2.0 \times 1.0 \times 2.75$  m deep) are constructed and suspended on a floating pontoon in the artificial lake located at the Experimental Lake Platform (ELP,  $48^{\circ} 16' 57''$  N,  $2^{\circ} 40' 20''$  E) nearby Paris. Three treatments are crossed in each enclosure:

- 1) Light treatment directly affecting the green food web. The day light is filtered by 10% (as the control) or 50% in order to limit the photosynthesis of phytoplankton.
- 2) Organic matter treatment directly affecting the brown food web. Three organic molecules (glucose, cellobiose and  $\alpha$ -cyclodextrin) are added or not (as the control)

to stimulate the activity of the decomposers

- 3) Fish treatment changing the overall structure of the food web. Fish are added or not (as the control) as the generalist predators coupling the green and brown pathways at the top of food webs.

The preliminary results of our experiment can be summarized in a few major points.

- 1) We observe consistent top-down effects of fish presence on both components of the green food web (phytoplankton abundance and composition) and the brown food web (catabolic activity of benthic microbial community) and on water physico-chemistry variables (turbidity, dioxygen concentration and DOC).
- 2) Our results suggest only weak interactions between the green and the brown food webs so far since light filtration does not affect 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).

Several analyses of the samples collected during the experiment are still in progress (determination of zooplankton and phytoplankton composition, flow cytometry to determine functional structure of microbial communities, analysis of water nutrient concentration). This additional data will give a better understanding of the interactions between green and brown food webs in our experiment.

## **Chapter 2**

**Interactions between the green and brown food web  
determine ecosystem functioning.**





# **Interactions between the green and brown food web determine ecosystem functioning**

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running headline : Food webs with nutrient cycling

## **Summary**

1. The concepts of top-down and bottom-up controls are central to our understanding of cascading trophic effects on ecosystem functioning. Classical food-web theory has focused either on food webs based on primary production (green food webs) or on food webs based on detritus (brown food webs) and generally ignored nutrient cycling.
2. We argue that nutrient cycling connects the two food webs, which questions the traditional concept of top-down and bottom-up controls.
3. By integrating these two food webs and nutrient cycling into simple models we investigate the cascading effects from one food web to the other one. Both analytical calculations and simulations show that these two cascading effects depend on simple but distinct mechanisms that are derived from different ecological processes.
4. Predators of decomposers can affect primary production in the green food chain. The signs of these effects are determined by relative proportions of nutrient cycling within the brown food chain.
5. Cascading effects within the green food chain can affect decomposer production in a bottom-up way. The carbon/nutrient limitation of decomposers determines the way the green food chain affects decomposer production.
6. These theoretical findings are applicable to explore real interactions and cascading effects between the green and the brown food webs, such as pelagic - benthic interactions or above-ground - below-ground interactions.

## **Key words**

Food web, trophic cascade, nutrient cycling, microbial loop, above-ground – below-ground interactions, pelagic - benthic interactions, detritus, competition, ecosystem functioning

## Introduction

Cascading effects mediated by top consumers and resources on primary production have received particular attention in food web ecology (Hunter & Price 1992). However, ecosystem processes are not only determined by a green food web based on primary producers but also by a brown one based on decomposers, and by complex interactions between these two webs. Empirical studies reveal that predators in one food web have cascading effects that extend to the other one (Wardle *et al.* 2004). The concept of “microbial loop” highlights that predators of the brown food web can increase nutrient mineralization in aquatic (Azam *et al.* 1983; Fenchel 1988) and terrestrial (Clarholm 1985; Bonkowski 2004) ecosystems, which can indirectly affect primary production (Azam *et al.* 1991; Stone & Weisburd 1992). Experiments have also shown that brown food webs respond strongly to the quality and quantity of dead organic matter, which is controlled by the structure of the green food web in both aquatic (Danger *et al.* 2012; Harrault *et al.* 2012) and terrestrial ecosystems (Bardgett & Wardle 2003; Wardle *et al.* 2003, 2005). Cascading effects from one web to the other vary in intensity (Wardle *et al.* 2004) and sometimes in sign (e.g. contrasting effects of herbivory on recycling processes (Wardle *et al.* 2001)). Understanding the mechanisms driving these cascading effects is therefore a challenge.

Existing theories on trophic cascades (Oksanen *et al.* 1981; Carpenter *et al.* 1985; Leroux & Loreau 2010) have focused on food webs based either on primary production (green food webs) (Wollrab *et al.* 2012; Heath *et al.* 2014) or on detritus (brown food webs) (Post & Kwon 2000; Moore *et al.* 2004). The few models that studied both food webs together highlighted important consequences of such coupling for ecosystem stability (Rooney *et al.* 2006; Boit *et al.* 2012). However, they only modelled the brown food web as an energy source for green food-web consumers, omitting nutrient dynamics that strongly connect the two webs. Nutrient cycling is known to mediate important indirect effects in ecosystems. Ecologists have long recognized that recycling activities mediated by consumers in green (De Mazancourt *et al.* 1998;

Attayde & Hansson 2001; Leroux & Loreau 2010) and brown (Nagata & Kirchman 1992; Berdjeb *et al.* 2011) food webs can positively affect resource production. We argue that nutrient cycling can question the traditional concept of top-down (the different trophic levels are determined by the abundance of top predators) and bottom-up control (the different trophic levels are determined by the availability of resource) in food-web theory (Oksanen *et al.* 1981) because consumers of one food web can affect the other one in a bottom-up way (Moore *et al.* 2003; Leroux & Loreau 2015). Studying the mechanisms driving cascading effects between green and brown food webs is crucial to understand the functioning of ecosystems. We intend here to start building a theoretical framework on this issue.

Nutrients that are unassimilated or lost from organisms (excretions, feces, dead individuals or materials, etc.) return to the ecosystem via two main types of nutrient cycling processes. Consumers release mineral nutrients via excretory processes (i.e. urine production), which is the most direct way by which animals can support primary producers (Vanni 2002) (hereafter direct recycling). Unassimilated organic matter (feces), dead individuals and dead parts of higher plants return to the environment as detritus that are mineralized by microbes before being available to primary producers (Vanni 2002; Moore *et al.* 2004) (hereafter indirect recycling). Mineral nutrients released by direct and indirect cycling not only control primary production (Hecky & Kilham 1988) but also potentially support production of decomposers. If decomposers are only limited by carbon, their mineralization of detritus benefits primary producers and leads to a mutualistic interaction with primary producers (Daufresne & Loreau 2001). If decomposers are limited by mineral nutrient or co-limited by carbon and nutrient, they compete for nutrient with primary producers (Daufresne *et al.* 2008). The carbon/nutrient limitation of decomposers depends on the gap between C:N demand of decomposers and C:N of supplied detritus resources (Bosatta & Berendse 1984; Daufresne *et al.* 2008). The relative

importance of direct/indirect recycling and carbon/N limitation of decomposers interact in real ecosystems and should thus affect the interaction between the green and brown food webs.

We develop a general model integrating both the green and brown food webs through nutrient cycling to answer the following questions: 1) Does nutrient cycling affect the signs of cascading effects of one food web on the productivity of the other? 2) In the affirmative, what are the influences of the proportion of direct/indirect recycling and carbon/nutrient limitation of decomposers? 3) Are there general conditions determining the signs of these effects? 4) Could other factors such as food chain length and functional responses affect these effects? We explore analytically the conditions that determine the signs of cascading effects from one food web to the other and reinterpret the experiments published on these effects.

## **Methods**

### ***Model formulation***

We model simple food webs consisting of one green food chain and one brown food chain. These two chains are linked in an open ecosystem in which a limiting nutrient (in most ecosystems either nitrogen or phosphorus) is recycled between biotic and abiotic compartments (Figure 1). The food web includes 7 compartments: inorganic nutrients ( $N$ ), detritus ( $D$ ), primary producers ( $P$ ), primary consumers ( $H$ ), predators of primary consumers ( $C$ ) (the green food chain), decomposers ( $B$ ) and predators of decomposers ( $F$ ) (the brown food chain).  $P$ ,  $H$ ,  $C$ ,  $B$  and  $F$  could be respectively phytoplankton, zooplankton, fish, heterotrophic bacteria and flagellates/ciliates in aquatic ecosystems, and plants, caterpillars/aphids, wasps/birds, soil bacteria and flagellates/mites/nematodes in terrestrial ecosystems.

Pools of  $N$  and  $D$  are supplied by constant inputs of mineral nutrients ( $I_N$ ) and detritus ( $I_D$ ) and they lose mineral nutrients and detritus at constant rates ( $l_N$  and  $l_D$  respectively). All trophic interactions between consumer  $i$  and resource  $j$  follow *Lotka-Volterra* functional responses with consumption rate  $a_{ij}$ , except for the decomposers. Previous studies modelled decomposition

processes either as donor controlled (Pimm 1982; Daufresne & Loreau 2001) or *Lotka-Volterra* functional responses (Zheng *et al.* 1997). Therefore we considered both cases to model the consumption of mineral nutrients and detritus by decomposers.

The green and the brown food chains are linked by nutrient cycling. Nutrients are released by all living compartments ( $P$ ,  $H$ ,  $C$ ,  $B$  and  $F$ ) to feedback to the bottom of the ecosystem ( $N$  and  $D$ ). Released nutrients originate from two pathways. One corresponds to excretion (both mineral nutrient and dead organic materials) and death of individuals, and occurs at a density-independent rate  $d_i$ . The other is linked to trophic interactions. The uptake of resource by each consumer is converted into its own biomass with efficiency  $e_{ij}$  and the remaining fraction of nutrients  $(1 - e_{ij})$  is released. We do not include efficiency terms for the nutrient uptake of primary producers and decomposers because corresponding efficiencies are likely to be close to one. We assume that only a fraction ( $\delta_i$ ) of the released nutrients from all compartments (except primary producers) goes to the organic material pool as detritus (hereafter indirect recycling). Meanwhile the other fraction  $(1 - \delta_i)$  goes to the  $N$  pool, allowing instantaneous recycling (hereafter direct recycling). The primary producers are generally considered unable to excrete mineral nutrients directly, all the nutrients they released thus go to the  $D$  compartment.

We assume decomposer growth is either limited by carbon/energy (hereafter C-limited) or by a single mineral nutrient (hereafter N-limited) (Daufresne *et al.* 2008). The type of limitation of decomposer growth at equilibrium is determined by the relative abundances of  $D$  and  $N$  and by the carbon-to-nutrient stoichiometry of detritus and decomposers. If detritus have low abundance and low carbon-to-nutrient ratio in comparison to that of decomposers, decomposer growth is C-limited. On the contrary, if detritus are abundant and relatively rich in carbon then decomposers are N-limited. When decomposition follows a *Lotka-Volterra* function, decomposer growth is expressed as:

$$\min[e_{BD}a_{BD}DB \frac{q_B}{q_D}, (e_{BD}a_{BD}DB + a_{BN}NB)] \quad (1)$$

where  $q_B$  and  $q_D$  are the nutrient-to-carbon ratios of decomposers and detritus, respectively. The left term corresponds to the C-limited case where all assimilated detrital nutrients is converted into decomposer biomass. The right term corresponds to the N-limited case where all assimilated detrital and mineral nutrients are converted into decomposer biomass.

Note that typically  $q_B > q_D$  (at least in systems where plant litter is the dominant detrital component). This means that even when they are C-limited, the decomposers may take up some mineral nutrients. Thus the term describing nutrient uptake by decomposers also depends on the type of limitation of decomposer growth. It is expressed as:

$$-\min[e_{BD}a_{BD}DB\left(\frac{q_B}{q_D} - 1\right), a_{BN}NB] \quad (2)$$

The left term corresponds to C-limitation and the right one to N-limitation. In case of C-limitation, decomposers can either excrete or take up nutrients depending on the nutrient-to-carbon ratios of decomposers and detritus.

The general model (with *Lotka-Volterra* function for decomposers) is described as follows (see Table 1 for definitions and units of parameters):

$$\begin{aligned} \dot{N} = & I_N - l_N N - a_{PN}NP + (1 - \delta_H)(d_H H + (1 - e_{HP})a_{HP}PH) + (1 - \delta_C)(d_C C + (1 - \\ & e_{CH})a_{CH}HC) + (1 - \delta_B)(d_B B + (1 - e_{BD})a_{BD}DB) + (1 - \delta_F)(d_F F + (1 - e_{FB})a_{FB}BF) - \\ & \min[e_{BD}a_{BD}DB\left(\frac{q_B}{q_D} - 1\right), a_{BN}NB] \end{aligned} \quad (3)$$

$$\dot{P} = a_{PN}NP - d_P P - a_{HP}PH \quad (4)$$

$$\dot{H} = e_{HP}a_{HP}PH - d_H H - a_{CH}HC \quad (5)$$

$$\dot{C} = e_{CH}a_{CH}HC - d_C C \quad (6)$$

$$\begin{aligned} \dot{D} = & I_D - l_D D - a_{BD}DB + d_P P + \delta_H(d_H H + (1 - e_{HP})a_{HP}PH) + \delta_C(d_C C + (1 - \\ & e_{CH})a_{CH}HC) + \delta_B(d_B B + (1 - e_{BD})a_{BD}DB) + \delta_F(d_F F + (1 - e_{FB})a_{FB}BF) \end{aligned} \quad (7)$$

$$\dot{B} = \min[e_{BD}a_{BD}DB\frac{q_B}{q_D}, (e_{BD}a_{BD}DB + a_{BN}NB)] - d_B B - a_{FB}BF \quad (8)$$

$$\dot{F} = e_{FB}a_{FB}BF - d_F F \quad (9)$$



The case with *donor-controlled* function for decomposers is obtained by removing  $B$  from terms describing decomposer consumption.

We consider here a model with a 3-level green food chain and a 2-level brown food chain (model 3-2 hereafter, detailed results in Appendix 1). However, food web structure varies between ecosystems. In some systems, carnivores are absent or too rare to be functionally important (2-level green food chain, Pace *et al.* 1999); secondary carnivores have been documented at the top of other ecosystems (4-level green food chain, Casini *et al.* 2008). The length of the brown food chain can vary too; existence of consumers of bacterivores is ubiquitous. Thus, apart from the model 3-2, we consider three other examples of food-web structure in the last section of the results and in Appendix 2, with either 2 or 4 trophic levels in the green food chain (i.e. models 2-2 and 4-2) and with 3 trophic levels in brown food chain (model 3-3). This allows to start testing the robustness of our results for other food-web structures.

### ***Model analysis***

We analytically derive the steady state expressions of each compartment. To investigate the cascading effects of one web on the functioning of the other, we calculate primary production ( $\varphi_{PP}^*$ ) and decomposer production ( $\varphi_{PB}^*$ ) at steady states (Eq.10-11 below), and study the signs of partial derivatives of both productions with respect to model parameters.

$$\varphi_{PP}^* = a_{PN}N^*P^* \quad (10)$$

$$\varphi_{PB}^* = e_{BD}a_{BD}D^*B^* + a_{BN}N^*B^* \quad (11)$$

$\partial\varphi_{PP}^*/\partial a_{FB}$  and  $\partial\varphi_{PP}^*/\partial d_F$  describe the signs and strengths of the effects of predators of decomposers on primary production of the green food web while  $\partial\varphi_{PB}^*/\partial a_{PN}(\partial\varphi_{PB}^*/\partial d_P)$ ,  $\partial\varphi_{PB}^*/\partial a_{HP}(\partial\varphi_{PB}^*/\partial d_H)$ , and  $\partial\varphi_{PB}^*/\partial a_{CH}(\partial\varphi_{PB}^*/\partial d_C)$  measure respectively the effects of primary producers, herbivores and carnivores on decomposer production in the brown food web.

To evaluate how interactions between green and brown food chains through nutrient cycling could determine the signs of cascading effects, we consider two key factors: 1) the relative proportion of direct/indirect recycling, and 2) whether decomposer growth is C-limited or N-limited. The effects of the relative proportion of direct/indirect recycling are analysed in two ways. We first calculate  $\partial\varphi_{PP}^*/\partial\delta_i$  and  $\partial\varphi_{PB}^*/\partial\delta_i$  to study the effects of the proportion of direct/indirect nutrient cycling at all trophic levels on primary production and decomposer production. Then, to analyse the effect of direct / indirect nutrient cycling on cascading effects between the two webs, we examine their impacts on the signs of the partial derivatives (Appendix 1 Table S2). The effects of growth limitation of decomposers are examined by using either the left (C-limited) or the right term (N-limited) in the minimum function.

### ***Model parameterization***

Our simple models allow exploring the signs of cascading effects between green and brown food webs. In order to investigate the potential magnitude of these effects in real ecosystems, we further parameterize the model 3-2 for a nitrogen-limited aquatic ecosystem, using a set of parameters derived from literature (Table 1, Fig. 2 and Fig. 3). To test whether our predictions are qualitatively robust to the type of functional response, we also conducted numerical simulations with type II functional responses instead of linear trophic interactions (Appendix 3).

## **Results**

### ***General results***

Limitation type is determined by the same condition in both donor-controlled and *Lotka-Volterra* cases. If  $e_{BD}a_{BD}D^*\left(\frac{q_B}{q_D} - 1\right) < a_{BN}N^*$ , the decomposers in the food web are C-limited. Otherwise, they are N-limited. Decomposer limitation thus strongly depends on the relative nutrient to carbon ratios of decomposers and detritus, and on the relative equilibrium stocks of detritus and mineral nutrients.

Overall coexistence for all scenarios requires sufficiently high inputs and low outputs of mineral nutrients and organic materials (Table S1). Equilibrium stocks of mineral nutrients ( $N^*$ ), herbivores ( $H^*$ ), detritus ( $D^*$ ) and decomposers ( $B^*$ ) depend either only on the green or the brown food web, and they are independent of decomposer limitation and functional response (Table S1). The stock of mineral nutrient ( $N^*$ ) is controlled by the green food chain. The equilibrium stock of detritus ( $D^*$ ) depends on inputs and outputs of both mineral nutrients and detritus, as well as on  $N^*$ ; it does not depend on parameters of the brown food chain. Herbivores ( $H^*$ ) and decomposers ( $B^*$ ) are strictly controlled by their respective predators. To the contrary, primary producers ( $P^*$ ), carnivores ( $C^*$ ) and predators of decomposers ( $F^*$ ) depend on parameters from both the green and brown food webs, on whether the consumption of decomposers is donor-controlled or recipient-controlled (*Lotka-Volterra* function) and on whether decomposers are C-limited or N-limited. Consequently, the total amounts of nutrients stored in the green and the brown chains also depend on parameters from both the green and brown food webs and on decomposer limitation and functional response (Table S1).

### ***Effects of the brown food chain on primary production***

Primary production is directly proportional to the stock of mineral nutrients and primary producers ( $\varphi_{PP}^* = a_{PN}N^*P^*$ ). Since  $N^*$  is independent of parameters from the brown food chain when the green food chain length is 3-level, the stock of primary producers ( $P^*$ ) is essential to understand the effects of the brown food chain on primary production.

First, direct nutrient cycling ( $1 - \delta_i$ ) by all compartments always increases primary production. Indeed, all  $\delta_i$  terms contribute negatively to  $C^*$ , which is positively correlated with  $P^*$  (Table S1). Therefore primary production always decreases when  $\delta_i$  increases (i.e. when a higher proportion of nutrient is recycled in organic form). The signs of partial derivatives (Appendix 1 Table S2) confirm this result,  $\partial\varphi_{PP}^*/\partial\delta_i$  is always negative.

Second, primary production is affected by both decomposers and their predators in the brown food chain. The signs of the effects of decomposer and predator parameters are condition-dependent except for the effects of decomposer nutrient uptake rate (Table S2).

When decomposers are N-limited, primary production always decreases with the rate of mineral nutrient consumption by decomposers ( $a_{BN}$ ). As mentioned above (Table S1),  $N^*$  does not change with  $a_{BN}$ . Instead, increasing  $a_{BN}$  leads to a larger amount of nutrients being stored in the brown food chain ( $F^*$  increases with  $a_{BN}$ ) and a smaller amount of nutrient being stored in the green chain including the primary producer compartment ( $C^*$  and, thus,  $P^*$  decrease when  $F^*$  increases). Since primary production is directly proportional to producer biomass  $P^*$ , primary production decreases as  $a_{BN}$  increases.

In most cases for other parameters of the brown food chains, the difference between  $\delta_B$  and  $\delta_F$  (relative proportion of direct/indirect nutrient cycling by decomposers and their predators) is the key factor determining the effect of the brown food web on the production of the green food web. When  $\delta_B - \delta_F > 0$ , i.e. when decomposers recycle a higher proportion of nutrients in organic form than their predator, the effects of nutrient release rate ( $d_B$ ) by decomposers on primary production are negative, otherwise the effects are positive. The effects of detritus consumption rates by decomposers ( $a_{BD}$ ) on primary production are also partly determined by the sign of  $\delta_B - \delta_F$ . They depend on the sign of  $(1 - \delta_B) + e_{BD}(\delta_B - \delta_F \frac{q_B}{q_D})$  when decomposers are C-limited and the sign of  $(1 - \delta_B) + e_{BD}(\delta_B - \delta_F)$  when decomposers are N-limited. Thus, if decomposers recycle a larger proportion of nutrients in organic form than their predators, larger decomposer consumption rate of detritus will generally result in larger primary production. Otherwise, the effects of this parameter might be negative on primary production.

Further, when decomposers are donor-controlled, the same condition  $\delta_B - \delta_F$  determines the effects of predators of decomposers on primary production. When  $\delta_B > \delta_F$ , decomposers

recycle a higher proportion of nutrients in organic form than their predators, and consumption of predators of decomposers increases primary production ( $\partial\varphi_{PP}^*/\partial a_{FB} > 0$  and Fig. 2a, see also Fig. S2 in Appendix 3 for Type II functional responses). The primary production increases by 36.9% (29% when N-limited) when the consumption rate of predators of decomposers ( $a_{FB}$ ) increases from 0.1 to 0.2 L ( $\mu\text{g N}$ )<sup>-1</sup> day<sup>-1</sup>. Meanwhile, the rate of nutrient release from predators of decomposers affects negatively primary production ( $\partial\varphi_{PP}^*/\partial d_F < 0$ , Fig. 2b). The primary production decreases by 22.8% (25.6% when N-limited) when the rate of nutrient release of predators ( $d_F$ ) increases from 0.5 to 1.0 day<sup>-1</sup>. The condition  $\delta_B < \delta_F$  leads to the opposite results (Fig. 2c,d, see also Fig. S2 in Appendix 3 for Type II functional responses). The primary production decreases by 59.7% (29.8% when N-limited) with increase in  $a_{FB}$  (i.e. negative effects of  $a_{FB}$  on primary production) and increases by 58.7% (44.9% when N-limited) with increase in  $d_F$  (i.e. positive effects of  $d_F$  on primary production).

However, when decomposers are recipient-controlled (*Lotka-Volterra* function), although the effects of predators of decomposers on primary production still depend on  $\delta_B$  and  $\delta_F$ , they are not determined by the difference between these two parameters. The direction of predator effects then depends on the sign of  $-a_{BD}D^* + a_{FB}\delta_FF^* + \delta_B(d_B + (1 - e_{BD})a_{BD}D^*)$ . If  $\delta_B$  and  $\delta_F$  are large, the effects of the consumption rate of the predators of decomposers tend to be positive on primary production while their mortality has a negative effect. Otherwise, predators of decomposers have a negative effect on primary production. This case is exemplified through numeric simulations (Fig 2e. f). Differences in the effects of predators of decomposers between the donor-controlled and the *Lotka-Volterra* cases can be explained by negative effects of decomposer predators on decomposer production in the *Lotka-Volterra* case whereas they have no effect otherwise. The positive effect of predators in the *Lotka-Volterra* case then does not arise from positive effects on direct recycling (as in the donor-control case) but from a decrease in the total amount of nutrients immobilized in the brown food chain.

### ***Effects of the green food chain on decomposer production***

Traditional top-down regulations in the green food web follow a cascade – the non-adjacent levels have the same effects on primary production while the adjacent trophic levels have opposite effects (Leroux & Loreau 2008). We show that these cascading top-down effects of the green food web climb up the brown one and affect decomposer production. In all cases, the effects of carnivores and primary producers on decomposer production are always of the same sign while the effects of herbivores are opposite. Interestingly, when decomposers are N-limited, effects of the green food chain on decomposer production are condition-dependent (Table S2, conditions detailed below).

In any case, decomposer production does not depend on the relative proportion of direct/indirect nutrient cycling ( $\partial\varphi_{PB}^*/\partial\delta_i = 0$  in all scenarios) because stocks of mineral nutrients and detritus at steady states are independent of  $\delta_i$ . Effects of the green food chain on decomposer production are thus independent of the proportion of direct/indirect nutrient cycling too.

In case of C-limitation, the consumption rate of carnivores ( $a_{CH}$ ) and the nutrient uptake rate of primary producers ( $a_{PN}$ ) have positive effects on decomposer production while the consumption rate of herbivores ( $a_{HP}$ ) has a negative effect (Table S2 and Fig. 3). Decomposer production increases by 30.8% (for both donor-controlled and *Lotka-Volterra* functions) when  $a_{CH}$  increases from 0.3 to 0.6 L ( $\mu\text{g N}$ )<sup>-1</sup> day<sup>-1</sup>. It increases by 33.1% (for both donor-controlled and *Lotka-Volterra* functions) when  $a_{PN}$  increases from 0.3 to 0.6 L ( $\mu\text{g N}$ )<sup>-1</sup> day<sup>-1</sup>. To the contrary, decomposer production decreases by 61.5% (61.6% for *Lotka-Volterra* function) when  $a_{HP}$  increases from 0.8 to 1.6 L ( $\mu\text{g N}$ )<sup>-1</sup> day<sup>-1</sup>.

In case of N-limitation, the signs of these cascading effects is governed by the sign of  $e_{BD}a_{BD}/l_D - a_{BN}/l_N$ . The ratios  $a_{BN}/l_N$  and  $e_{BD}a_{BD}/l_D$  represent the consumption rates of mineral nutrients and detritus by decomposers divided by the rate of nutrient loss from these

compartments. A higher ratio implies that a higher proportion of nutrients and detritus is assimilated by decomposers rather than being lost from the ecosystem. The signs and magnitude of cascading effects of carnivores, herbivores and primary producers remain the same as in the C-limited case if  $e_{BD}a_{BD}/l_D > a_{BN}/l_N$  (Fig. 3a. b. c). If  $e_{BD}a_{BD}/l_D < a_{BN}/l_N$ , the directions of the cascading effects are opposite (Fig. 3d. e. f). The production of decomposers decreases by 7.9% (7.7% for *Lotka-Volterra* function) and by 8.4% (8.4% for *Lotka-Volterra* function) respectively with an increase in  $a_{CH}$  and  $a_{PN}$  while it increases by 15.5% (15.7% for *Lotka-Volterra* function) with an increase in  $a_{HP}$ . The condition is independent of decomposer functional response. Thus, the cascading effects of the green food web on the production of decomposers strongly depend on the limitation of decomposers.

### ***Effects of the green and brown food chain lengths***

To test whether our results can be generalized to other food-web structures, we consider three additional examples of food webs with varying green and brown chain lengths (Appendix 2, model 2-2, model 4-2 and model 3-3).

When the green food chain has 3 levels,  $N^*$  and  $H^*$  are controlled by the green chain while  $P^*$  and  $C^*$  are determined by parameters from both the green and the brown food chains. The effects of the brown food chain on primary production are then determined mainly through its effects on  $P^*$ . When the green food chain is one link shorter or longer (i.e. 2 or 4 levels),  $N^*$  and  $H^*$  (and eventually the 4<sup>th</sup> level top predator  $Y^*$ ) depend on both food chains' parameters while  $P^*$  and  $C^*$  become independent of parameters of the brown food chain (Appendix 2). Consequently, the stocks of nutrients  $N^*$  determine the effects of the brown food chain on primary production. Despite these changes, the conditions determining the effects of the brown food chain on primary production and of the green food chain on decomposer production stay the same as in model 3-2 (Appendix 2 Table S3, S5, S6, S8, S9). The only important change is

that decomposer production is affected by all  $\delta_i$  (positive or condition dependent effects) since  $N^*$  becomes dependent on  $\delta_i$  (Appendix 2 Table S4, S7).

To the contrary, results partly depend on the length of the brown food chain. In model 3-3 ( $A$  as the 3rd trophic level in the brown food chain), the food web cannot maintain when decomposition follows a *Lotka-Volterra* function because the green and brown chains are very unlikely to control  $N^*$  at exactly the same level. In that case, the top consumer of the chain with the higher nutrient requirement  $N^*$  goes extinct (Wollrab *et al.* 2012). If decomposers are donor-controlled, as long as the green chain goes up to carnivores (3 levels), the length of the brown chain is irrelevant to the effects of the green food chain on decomposer production. The reason is that the green chain still exclusively controls the nutrient level  $N^*$  (i.e. the brown chain has no influence on  $N^*$ ) and therefore affects the brown chain as in the model 3-2. Thus if we extend the brown food chain by one link (model 3-3, or any other brown food chain lengths i.e. 3-1, 3-4 etc.), the effects of the green food chain on decomposer production does not change from the model 3-2 (Table S3, S12). However the effects of the brown food chain on primary production change (Table S3, S11). The sign of  $\partial\varphi_{PP}^*/\partial a_{FB}$  is determined by  $(\delta_B - \delta_F) + e_{FB}(\delta_F - \delta_A)$ . If the efficiency rate for decomposer consumption by their predators is low ( $e_{FB}$  close to 0), the effects of predators of decomposers on primary production are determined by the difference between the proportion of indirect nutrient cycling by decomposers and their predators ( $\delta_B - \delta_F$ ) as in model 3-2. If the consumption efficiency of predators of decomposers is high ( $e_{FB}$  close to 1), these effects depend mainly on the difference between the proportion of indirect nutrient cycling by decomposers and top predators of the brown food chain ( $\delta_B - \delta_A$ ). Further, the sign of  $\partial\varphi_{PP}^*/\partial d_F$  is determined by  $\delta_F - \delta_A$ , which is the difference between the proportion of indirect nutrient cycling by predator of decomposers and their predators. Despite varying conditions for the effects of the brown food chain on primary production, the



relative proportions of indirect nutrient cycling in the brown food web are still key factors for these effects in the donor-controlled case.

In conclusion, apart from influences of functional responses, (i) the conditions determining the effects of predator of decomposers are only affected by the length of the brown food chain, and (ii) the condition determining the effects of carnivores on decomposer production is independent from the lengths of both food chains (Table S3).

## **Discussion**

We link the green and the brown food webs by nutrient cycling and reveal key mechanisms that contribute to trophic cascades between the two webs. We show that the cascading effects of the brown food web on primary production and of the green food web on decomposer production are driven by distinct mechanisms: (i) the signs and strength of cascading effects of the green food web on decomposer production are determined by the carbon/nutrient limitation of decomposers; (ii) the effects of the brown food web on primary production are mainly driven by the relative proportion of direct/indirect nutrient cycling in the brown web. These findings are applicable to explore interactions and cascading effects between the green and the brown food webs, such as pelagic - benthic interactions or above-ground - below-ground interactions. The parameterization of the model for an aquatic system allows comparing our predictions to existing empirical results. Moreover, the comparison of the results obtained with different food chain lengths (Table S3) and with different functional responses (donor-controlled, *Lotka-Volterra* and Type II functional responses in Appendix 3) shows that our predictions are mostly robust to a large range of scenarios.

### ***Cascading effects of the brown food chain on primary production***

The predation on decomposers in the brown food web is thought to have a major influence on primary production in all ecosystems. Most empirical studies predict that predators of decomposers increase primary production by raising nutrient availability. In terrestrial

ecosystems, the “microbial loop” hypothesis suggests that bacterial grazers, e.g. protozoa or nematodes, liberate nutrients locked up in bacterial biomass, thus increasing nutrient availability to primary producers (Krome *et al.* 2009; Irshad *et al.* 2011). In aquatic ecosystems, bacterivorous protozoa mostly act as remineralizers of the limiting nutrient (Caron *et al.* 1988) and induce growth of autotrophic plankton (Ferrier & Rassoulzadegan 1991). Models have rarely addressed direct positive effects of predators of decomposers on primary production but have focused on their beneficial effects on primary production in the context of algal-bacterial competition (Bratbak & Thingstad 1985; Thingstad & Lignell 1997; Thingstad 1998). Nevertheless, these models suggest that predators of decomposers allow coexistence of phytoplankton and bacteria on the same limiting mineral nutrient when bacteria are the superior competitors, and thus indirectly demonstrate that predators of decomposers can benefit primary production. Our model is the first to explain observed cases of positive effects of predators of decomposers on primary production through nutrient cycling. It also suggests that the effect of predators of decomposers on primary production can be negative depending on the relative ability of decomposers and their predators to recycle nutrients. To our knowledge, such issue has never been tested experimentally.

Previous food-web studies that included recycling processes modelled either direct (Leroux and Loreau 2010) or indirect (De Mazancourt *et al.* 1998) nutrient cycling in ecosystems. In real ecosystems (Vanni 2002), both direct and indirect nutrient cycling contribute to affect ecosystem functioning. For example, direct nutrient excretion by fish and zooplankton could meet respectively 5% and 26% of phosphorus demand of phytoplankton (Schindler *et al.* 1993). Indirect nutrient cycling through the remineralisation of detritus affects the productivity of lakes (Jansson *et al.* 2000). The integration of both direct and indirect nutrient cycling is one of the major novelties in our model. We show that the effects of predators of decomposers on primary production depend strongly on their relative proportion of direct/indirect nutrient cycling

compared to those of decomposers. When predators of decomposers recycle directly a larger (smaller) proportion of their nutrient than decomposers, their consumption of decomposers increases (decreases) primary production. We propose a possible mechanism behind the positive effects of “microbial loop” on primary production by linking the proportion of direct nutrient cycling to stoichiometric mismatches between decomposers and their predators and between detritus and decomposers. Due to stoichiometric constraints (Vanni 2002), a species with a relatively low mineral nutrient content should excrete more nutrients than a species with a higher nutrient content. Therefore, if predators of decomposers have a higher carbon-to-nutrient ratio than their prey, they might recycle a higher proportion of inorganic nutrients than their prey, leading to positive effects on primary production (i.e. predators have a relatively low value of  $\delta_F$  thus  $\delta_B > \delta_F$ ). This condition is likely to be met since predators of decomposers such as flagellates prefer prey rich in nutrients (i.e. lower C:N) (Grover & Chrzanowski 2009). Besides, decomposers might recycle directly less mineral nutrients than predators of decomposers because of the higher C:N ratio in detritus than in decomposers (Caron *et al.* 1988; Thingstad & Lignell 1997). This should lead to a relatively high value of  $\delta_B$ , and again to positive effects of predators of decomposers on primary production.

By measuring the C:N ratios and/or the proportion of direct/indirect recycling of decomposers and their predators, we may predict the impact of predators in the brown food web on primary production. An empirical study in an aquatic ecosystem reported that the presence of bacterivorous protozoa increased diatom density by 130% when bacteria used glucose as substrate (Caron *et al.* 1988). These results are in agreement with our predictions because a high C:N ratio in bacterial substrate should lead to a relatively high value of  $\delta_B$ . We can hardly compare our predictions with other empirical results in aquatic ecosystems where, in most cases, only the effects on the production of decomposers (but not effects on primary production) are analysed (Jacquet *et al.* 2005; Berdjeb *et al.* 2011; Bouvy *et al.* 2011) or predators are

generalists and consume both primary producers and decomposers (Sherr & Sherr 2002). Our predictions can be also compared with the empirical results in terrestrial ecosystems. Irshad *et al.* (2011) found that addition of predator of decomposers increased plant biomass by 30% and increased plant N and P content by 75% and 50% while Krome *et al.* (2009) found an increase of 66% in biomass.

Additionally, our results show that the effects of predators of decomposers on primary production might depend on the length of the brown food chain as well as on the functional response of decomposers for detritus and mineral nutrient consumptions. In particular, the conditions determining effects of predators of decomposers change when decomposition follows a *Lotka-Volterra* function. These results demonstrate that the structure, the functional response and, most importantly, nutrient cycling within the brown food chain modulate the effects of predators of decomposers on primary production. To our knowledge, these different points have not been studied empirically. Specifically designed empirical studies are thus required to test these predictions.

### ***Cascading effects of the green food web on the production of decomposers***

The green food web is known to have cascading effects on the production of decomposers. In aquatic ecosystems, the green food web can control the quantity, quality and biodegradability of sediment dead organic matter (Danger *et al.* 2011, Harrault *et al.* 2012) therefore affecting the productivity in the brown food web. In terrestrial ecosystems, productive plants have strong effects on microflora through their control on litter quality (Wardle *et al.* 2003). Herbivores and carnivores are also likely to control the brown food-web production by returning dung and urine to the ecosystem or altering plant composition (Bardgett & Wardle 2003; Wardle *et al.* 2005). However, the sign of above cascading effects are hard to predict empirically. For instance, scientists have found positive, negative, or no effects of herbivores on decomposers even among relatively similar locations (Wardle *et al.* 2001).

Our results show that the carbon/nutrient dependence of decomposers is not only crucial to the coexistence of primary producers and decomposers (Daufresne *et al.* 2008), but also to the cascading effects of the green food web on decomposer production. When decomposers are C-limited, the relation between primary producers and decomposers is strictly mutualistic, and carnivores, herbivores and primary producers have respectively positive, negative and positive effects on decomposer production. However, the signs of above cascading effects become condition-dependent when decomposers are N-limited, i.e. when producers and decomposers are competing for the same mineral resource. This provides a mechanism explaining why the effects of the green food web on the production of the brown one may be negative or positive. The cascading effect of the green food web on decomposers depends not only on the top-down effect of the green web on detritus (as previously emphasized, e.g. Bardgett and Wardle 2003) but also on the top-down effect of the green web on mineral nutrients when there is competition (Fig. 4). These top-down effects on the availability of detritus and mineral nutrients have opposite signs and propagate to the brown food web through the dependence of decomposers on detritus and mineral nutrients (Fig. 4). The difference between  $e_{BD} a_{BD}/l_D$  and  $a_{BN}/l_N$  regulates the demands of decomposers on detritus and mineral nutrients. When the production of decomposers depends more on detritus ( $e_{BD} a_{BD}/l_D > a_{BN}/l_N$ ), the directions of the effects of carnivores, herbivores and primary producers on decomposer production correspond to the signs of the cascading effects of these trophic groups on detritus (Fig. 4-a). When the production of decomposers depends more on mineral nutrients than on detritus ( $e_{BD} a_{BD}/l_D < a_{BN}/l_N$ ), the signs of top-down effects of carnivores, herbivores and primary producers on decomposer production correspond to the signs of the cascading effects on mineral nutrients (Fig. 4-b). In this case, increasing consumption of primary producers and predators decreases the production of decomposers whereas increasing consumption of herbivores increases decomposer production. Interestingly, the condition determining the signs of cascading effects of the green

food web on decomposers remains the same whether we consider a green food chain with 2, 3 or 4 trophic levels, as long as the brown food chain is of length 2 or decomposers have a donor-controlled functional response.

Our results are consistent with a recent model showing that the balance between mineralization and immobilization by decomposers affects the impacts of herbivores on decomposition (Cherif & Loreau 2013). We further develop this idea by demonstrating that carbon/nutrient limitation of decomposers regulates the signs of cascading effects of the green food web on the brown one.

### ***Conclusion and perspectives***

Despite its simplicity, our model sheds new lights on how interactions between the green and the brown food webs affect ecosystem functioning. Previous theoretical studies have paid little attention on interactions between green and brown webs mediated by nutrient cycling. However, they have highlighted the effects of food-web structure (i.e. length of food chains and presence/absence of generalist predators) on trophic cascades (Attayde & Ripa 2008; Wollrab *et al.* 2012) and ecosystem stability (Rooney *et al.* 2006; Wolkovich *et al.* 2014) in food webs with multiple food channels, including green and brown ones. Future studies will thus need to tackle a larger set of food-web structures (Wollrab *et al.* 2012). In particular, generalist predators, such as filter feeders (Sherr & Sherr 2002), will need to be included because they are ubiquitous, at least in aquatic ecosystems. Mesocosm experiments manipulating mesozooplankton (Zöllner *et al.* 2003) or fish (Nishimura *et al.* 2011) suggest that generalist predators have complex cascading effects on the components of both green and brown food webs. In terrestrial ecosystems, generalist predators linking green and brown food webs might not be as common because organisms tend to live and feed either belowground (where most decomposition occurs) or aboveground. These differences might explain why predators of decomposers have been shown to increase primary production more clearly in terrestrial

ecosystems (Bonkowski 2004) than in aquatic ecosystems (Caron *et al.* 1988; Sherr & Sherr 2002).

We focused on mechanisms solely based on nutrient fluxes and basic stoichiometric hypotheses. The literature often assumes that other mechanisms are involved in interactions between green and brown food webs: for example, communities may produce litters of different qualities depending on food-web structure (Wardle *et al.* 2004; Canuel *et al.* 2007; Allard *et al.* 2010; Danger *et al.* 2012), or different pools of dead organic matter with contrasting mineralization rates co-occur due to the characteristics of soil /sediment and of brown food-web (Wolters 2000; Fontaine & Barot 2005; Harrault *et al.* 2014). In this way, our model can be viewed as a null model that should be compared to experimental results and to future models including other influential mechanisms.

## Tables

**Table 1** Parameter definitions and proposed values in simulations of model 3-2

Symbol	Definition	Dimension	Value
$I_N$	Constant input of mineral nutrients	$\mu\text{gN L}^{-1} \text{ day}^{-1}$	0.125*
$I_D$	Constant input of organic materials	$\mu\text{gN L}^{-1} \text{ day}^{-1}$	0.625†
$l_N$	Loss rate of mineral nutrients	$\text{day}^{-1}$	0.1 <sup>α</sup>
$l_D$	Loss rate of organic materials	$\text{day}^{-1}$	0.01†
$a_{PN}$	Intrinsic growth rate of primary producers	$\text{L } (\mu\text{gN}^{-1}) \text{ day}^{-1}$	0.3-0.6*
$a_{HP}$	Attack rate of herbivores on primary producers	$\text{L } (\mu\text{gN}^{-1}) \text{ day}^{-1}$	0.8–1.6*
$a_{CH}$	Attack rate of carnivores on herbivores	$\text{L } (\mu\text{gN}^{-1}) \text{ day}^{-1}$	0.3-0.6*
$a_{BN}$	Intrinsic growth rate of decomposers	$\text{day}^{-1}$ or $\text{L } (\mu\text{gN}^{-1}) \text{ day}^{-1}$	0.1, 0.5, 1.0*
$a_{BD}$	Attack rate of decomposers on organic materials	$\text{day}^{-1}$ or $\text{L } (\mu\text{gN}^{-1}) \text{ day}^{-1}$	0.83 <sup>¶</sup> or 0.083* in LV
$a_{FB}$	Attack rate of predators of decomposer on decomposers	$\text{L } (\mu\text{gN}^{-1}) \text{ day}^{-1}$	0.1-0.2*
$e_{HP}$	Nutrients conversion efficiency of herbivores	Dimensionless	0.8*
$e_{CH}$	Nutrients conversion efficiency of carnivores	Dimensionless	0.8*
$e_{BD}$	Nutrients conversion efficiency of decomposer	Dimensionless	0.8*
$e_{FB}$	Nutrients conversion efficiency of predators of decomposer	Dimensionless	0.8*
$d_P$	Loss rate from primary producers	$\text{day}^{-1}$	0.145 <sup>δ</sup>
$d_H$	Loss rate from herbivores	$\text{day}^{-1}$	0.17 <sup>δ</sup>



$d_C$	Loss rate from carnivores	day <sup>-1</sup>	0.125 <sup>δ</sup>
$d_B$	Loss rate decomposers	day <sup>-1</sup>	1.0 <sup>*</sup>
$d_F$	Loss rate from predators of decomposers	day <sup>-1</sup>	0.9 <sup>*</sup>
$\delta_H$	Proportion of indirect nutrient cycling by herbivores	Dimensionless	0.5 <sup>*</sup>
$\delta_C$	Proportion of indirect nutrient cycling by carnivores	Dimensionless	0.5 <sup>*</sup>
$\delta_B$	Proportion of indirect nutrient cycling by decomposers	Dimensionless	varied
$\delta_F$	Proportion of indirect nutrient cycling by predators of decomposers	Dimensionless	varied

\* Assumed values

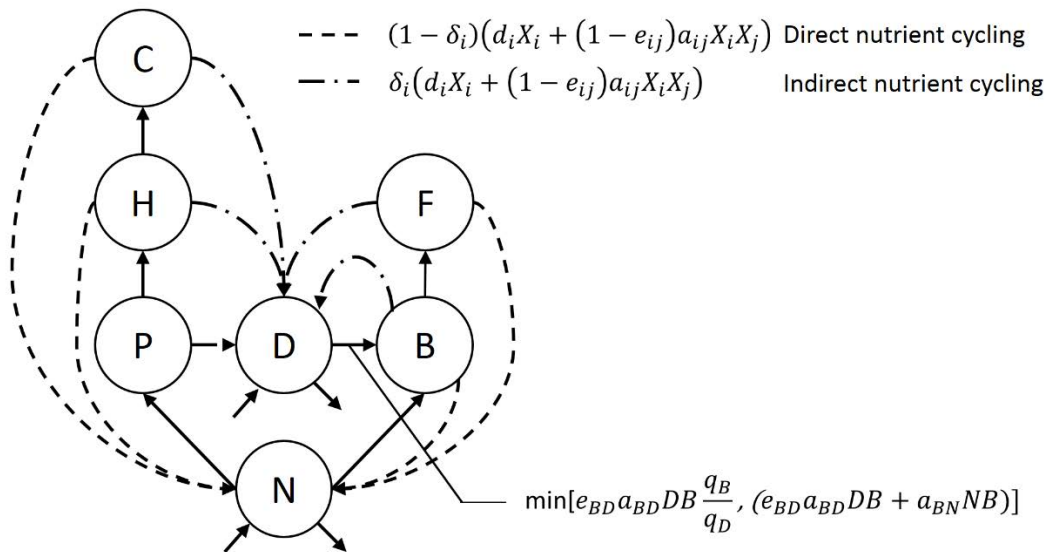
† This value is taken from Miki et al. 2008 (unit changed and converted to nitrogen content)

<sup>α</sup> This value is from Miki et al. 2011 (unit changed and converted to nitrogen content)

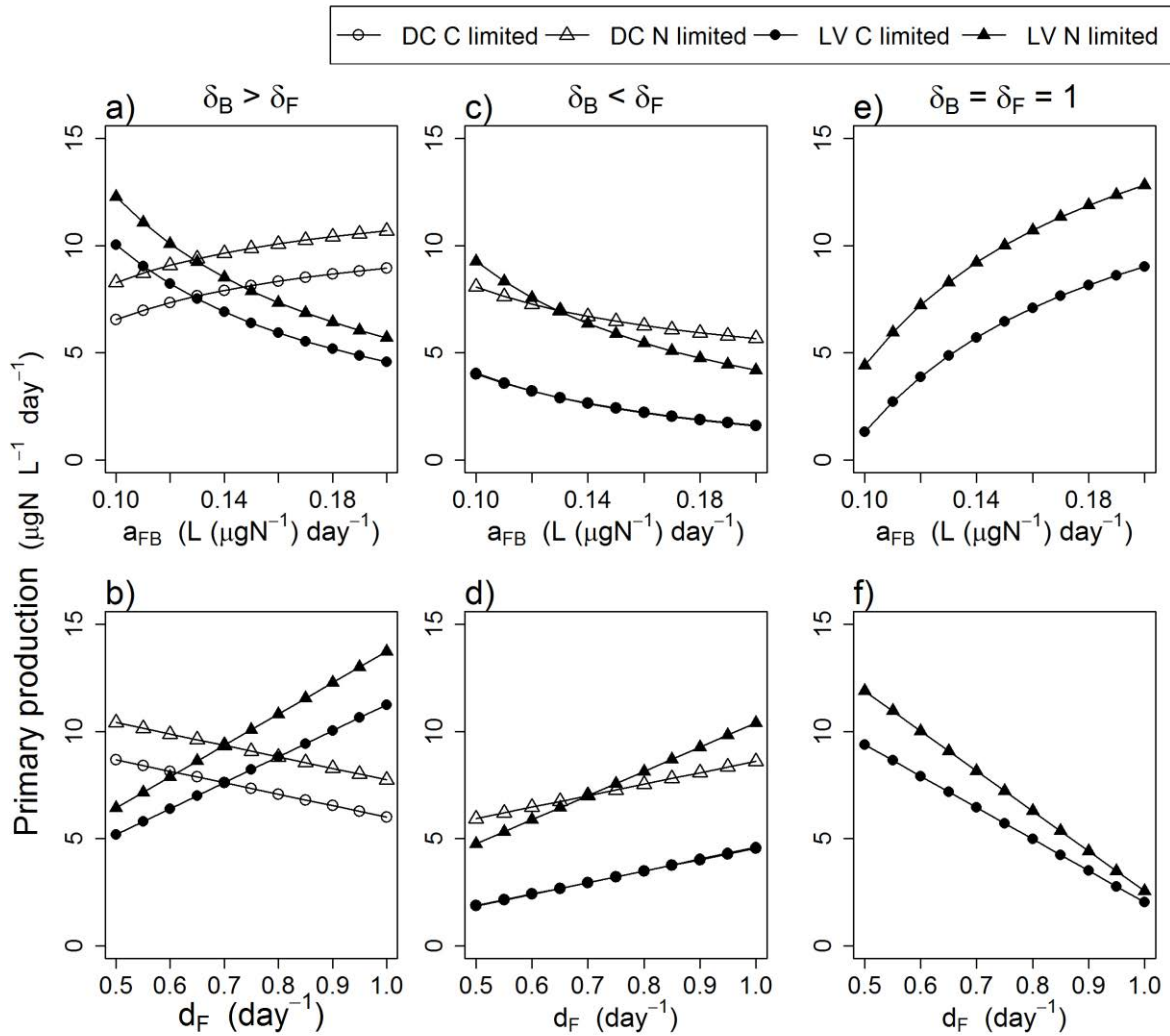
<sup>¶</sup> The value is taken from Boit et al. 2012 (unit changed and converted to nitrogen content)

<sup>δ</sup> The value is taken from Vos et al. 2004

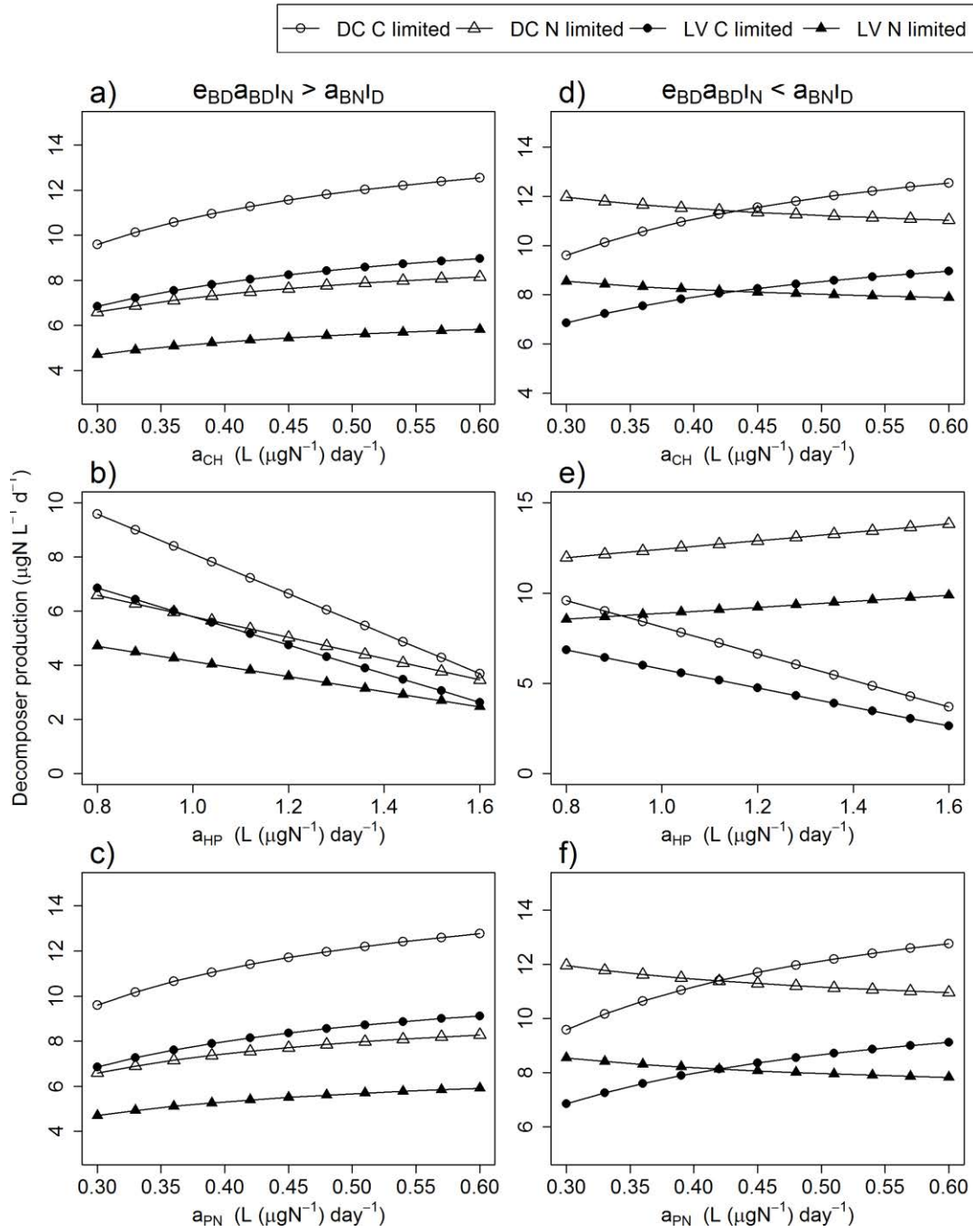
## Figures



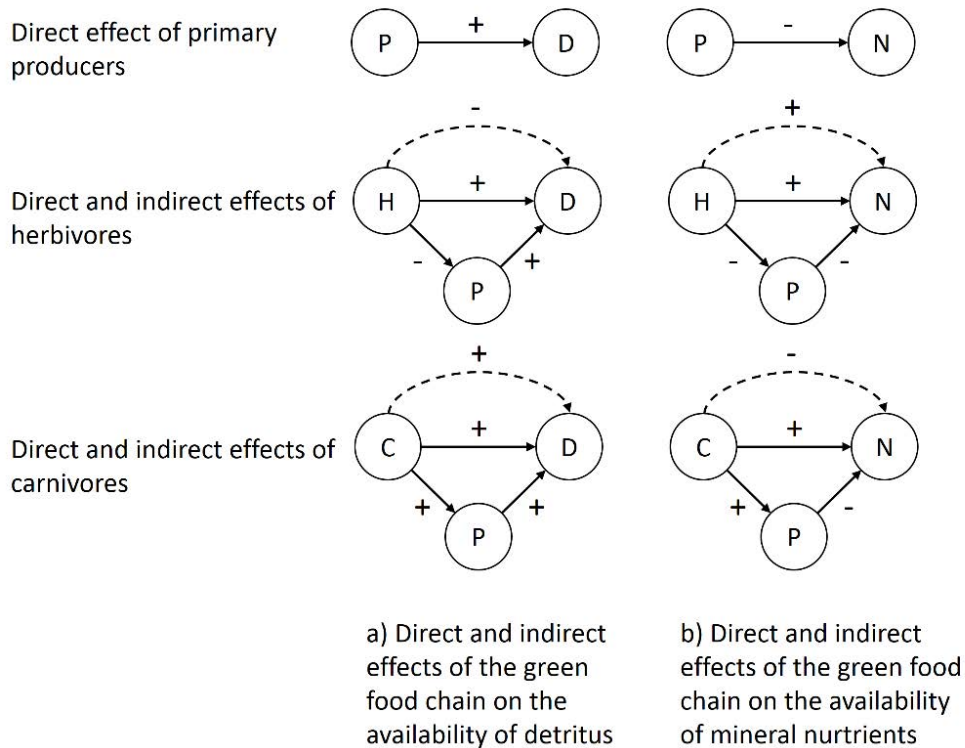
**Figure.1** Schematic diagram of the food web model. Circles represent compartments of mineral nutrients ( $N$ ), primary producers ( $P$ ), herbivores ( $H$ ), carnivores ( $C$ ), detritus ( $D$ ), decomposers ( $B$ ) and predators of decomposers ( $F$ ). Solid arrows indicate fluxes of nutrients between compartments related to consumption. Dashed and dash-dotted arrows represent direct and indirect nutrient cycling respectively. Parameters are explained in Table 1.



**Figure.2** Effects of predators of decomposers (attack rate  $a_{FB}$ , and nutrient loss rate  $d_F$ ) on primary production ( $\mu\text{gN L}^{-1} \text{ day}^{-1}$ ) predicted by the parameterized model. The 1<sup>st</sup> and 2<sup>nd</sup> columns represent respectively the cases  $\delta_B > \delta_F$  ( $\delta_B=0.5$ ,  $\delta_F=0.3$ ) and  $\delta_B < \delta_F$  ( $\delta_B=0.5$ ,  $\delta_F=0.7$ ). Simulation results include both donor-controlled and Lotka-Volterra functional responses, for both carbon and nutrient limitation of decomposers. The 3<sup>rd</sup> column represents only the results with Lotka-Volterra functional responses in which  $\delta_B = \delta_F = 1$  (no direct recycling).



**Figure.3** Cascading effects of carnivores (C), herbivores (H) and primary producers (P) (attack rates  $a_{CH}$ ,  $a_{HP}$  and  $a_{PN}$  respectively) on the production of decomposers ( $\mu\text{gN L}^{-1} \text{day}^{-1}$ ) predicted by the parameterized model for both donor-controlled and Lotka-Volterra functional responses, and both carbon and nutrient limitation of decomposers. The two columns represent respectively the cases  $e_{BD}a_{BD}/l_D > e_{BN}a_{BN}/l_N$  and  $e_{BD}a_{BD}/l_D < e_{BN}a_{BN}/l_N$ .



**Figure.4** Schematic diagram depicting the direct and indirect effects of primary producers (*P*), herbivores (*H*) and carnivores (*C*) on the availability of (a) detritus (*D*) and (b) mineral nutrients (*N*) through the balance between the effects of direct nutrients/organic materials release and the effects of trophic controls on lower trophic levels. The relative strength of these different direct and indirect effects determine the cascading effects of the green food web on the brown food web in our model. All “+” represent positive effects and “-” represent negative effects. Straight arrows represent direct and indirect effects mediated through trophic and recycling links, and dotted arrows represent net effects. (a) Plants have positive effects on detritus via recycling. Herbivores provide detritus through recycling but this positive effect is exceeded by their negative effects on plants by grazing, leading to net negative effects on detritus. Carnivores directly provide detritus through recycling and enhance indirectly plants' supply of detritus by controlling herbivores. (b) Primary producers, herbivores and carnivores affect the availability of mineral nutrients as traditionally predicted by trophic cascade theory (carnivores and primary producers increase the availability of mineral nutrients and herbivores decrease its availability).

## Supporting Information

Additional supporting information may be found in the online version of this article.

### Appendix 1 Equilibrium results and related signs of partial derivatives for model 3-2

Table S1: Equilibrium stocks of nutrient for all compartments in model 3-2

Table S2: Signs of partial derivatives reporting the effects of the brown food chain on primary production and of the green food chain on decomposer production

### Appendix 2 Other models with different food chain lengths

Table S3: Comparisons between models with different food chain lengths

Table S4: Equilibrium results for all compartments in model 2-2

Table S5: Signs of partial derivatives of primary production (PP) in model 2-2

Table S6: Signs of partial derivatives of decomposers production (PB) in model 2-2

Table S7: Equilibrium results for all compartments in model 4-2

Table S8: Signs of partial derivatives of primary production (PP) in model 4-2

Table S9: Signs of partial derivatives of decomposers production (PB) in model 4-2

Table S10: Equilibrium results for all compartments in model 3-3

Table S11: Signs of partial derivatives of primary production (PP) in model 3-3

Table S12: Signs of partial derivatives of decomposers production (PB) in model 3-3

### Appendix 3 Simulations of models with type II functional responses

Table S13 Parameters definitions and proposed values in simulation of type II functional responses

Fig. S1 Effects of  $a_{FB}$  on primary production when  $\delta_B > \delta_F$ . (a), (b) and (c) represent respectively three cases under different conditions:  $\delta_B = 0.7, \delta_F = 0.5$ ,  $\delta_B = 0.5, \delta_F = 0.3$  and  $\delta_B = 0.3, \delta_F = 0.1$ .

## Appendix 1 Equilibrium results and related signs of partial derivatives for model 3-2

**Table S1** Equilibrium stocks of nutrient for all compartments in model 3-2 for donor-controlled (DC) and Lotka-Volterra (LV) functional responses and for carbon (C limited) and nutrient (N limited) limitation of decomposers

	DC & C limited	DC & N limited	LV & C limited	LV & N limited
<b>N*</b>			$\frac{d_P + a_{HP}H^*}{a_{PN}}$	
<b>P*</b>			$\frac{d_H + a_{CH}C^*}{e_{HP}a_{HP}}$	
<b>H*</b>			$\frac{d_C}{e_{CH}a_{CH}}$	
<b>C*</b>	$\frac{e_{HP}a_{HP}[a_{BD}D^*(1-\delta_B(1-e_{BD}))-\delta_F d_F F^*-\delta_B d_B B^* - \delta_F a_{FB}(1-e_{FB})B^*F^* - I_D + l_D D^*] - d_H(d_P + \delta_H a_{HP}H^*)}{a_{CH}(d_P + a_{HP}(\delta_H(1-e_{HP}) + \delta_C e_{HP}(1-e_{CH}))H^*) + e_{HP}a_{HP}\delta_C d_C}$			$\frac{e_{HP}a_{HP}[a_{BD}B^*D^*(1-\delta_B(1-e_{BD}))-\delta_F d_F F^*-\delta_B d_B B^* - \delta_F a_{FB}(1-e_{FB})B^*F^* - I_D + l_D D^*] - d_H(d_P + \delta_H a_{HP}H^*)}{a_{CH}(d_P + a_{HP}(\delta_H(1-e_{HP}) + \delta_C e_{HP}(1-e_{CH}))H^*) + e_{HP}a_{HP}\delta_C d_C}$
<b>D*</b>			$\frac{I_N + I_D - l_N N^*}{l_D}$	
<b>B*</b>			$\frac{d_F}{e_{FB}a_{FB}}$	
<b>F*</b>	$\frac{e_{BD}a_{BD}D^*}{a_{FB}B^*} \cdot \frac{q_B}{q_D} - \frac{d_B}{a_{FB}}$	$\frac{e_{BD}a_{BD}D^* + a_{BN}N^*}{a_{FB}B^*} - \frac{d_B}{a_{FB}}$	$\frac{e_{BD}a_{BD}D^*}{a_{FB}} \cdot \frac{q_B}{q_D} - \frac{d_B}{a_{FB}}$	$\frac{e_{BD}a_{BD}D^* + a_{BN}N^*}{a_{FB}} - \frac{d_B}{a_{FB}}$

**TNG\***

**(Total N in green  
chain)**

$$\frac{d_C}{e_{CH}a_{CH}} + \frac{d_H + (a_{CH} + e_{HP}a_{HP})}{e_{HP}a_{HP}} C^*$$

**TNB\***

**(Total N in brown  
chain)**

$$\frac{d_F - d_B e_{FB}}{e_{FB} a_{FB}} + \frac{e_{FB} e_{BD} a_{BD}}{d_F} \cdot$$

$$\frac{q_B}{q_D} D^*$$

$$\frac{d_F - d_B e_{FB}}{e_{FB} a_{FB}} +$$

$$\frac{e_{BD} a_{BD} D^* + a_{BN} N^*}{a_{FB} B^*}$$

$$\frac{d_F - d_B e_{FB}}{e_{FB} a_{FB}} + \frac{e_{BD} a_{BD}}{a_{FB}} \cdot$$

$$\frac{q_B}{q_D} D^*$$

$$\frac{d_F - d_B e_{FB}}{e_{FB} a_{FB}} +$$

$$\frac{e_{BD} a_{BD} D^* + a_{BN} N^*}{a_{FB}}$$

**Total N in food web**

$$N^* + \frac{I_N + I_D - l_N N^*}{l_D} + TNG^* + TNB^*$$



**Table S2** Signs of partial derivatives reporting the effects of the brown food chain on primary production and of the green food chain on decomposer production. “+” means that an increase in the corresponding parameter increases decomposer production, i.e. a positive effect. “-” correspond to a negative effect.  $f_1, f_2, f_3, f_4$  are conditions that determine the signs of corresponding effects.

	DC & C limited		DC & N limited		LV & C limited		LV & N limited	
$\frac{\partial \varphi_{PP}^*}{\partial \delta_i}$	-							
$\frac{\partial \varphi_{PP}^*}{\partial a_{BD}}$	$f_1 > 0$	+	$f_2 > 0$	+	$f_1 > 0$	+	$f_2 > 0$	+
	$f_1 < 0$	-	$f_2 < 0$	-	$f_1 < 0$	-	$f_2 < 0$	-
$\frac{\partial \varphi_{PP}^*}{\partial a_{BN}}$	0		-		0		-	
$\frac{\partial \varphi_{PP}^*}{\partial d_B}$			$\delta_B - \delta_F > 0$				+	
			$\delta_B - \delta_F < 0$				-	
$\frac{\partial \varphi_{PP}^*}{\partial a_{FB}}$	$\delta_B - \delta_F > 0$		+		$f_3 > 0$		+	
	$\delta_B - \delta_F < 0$		-		$f_3 < 0$		-	
$\frac{\partial \varphi_{PP}^*}{\partial d_F}$	$\delta_B - \delta_F > 0$		-		$f_3 > 0$		-	
	$\delta_B - \delta_F < 0$		+		$f_3 < 0$		+	
$\frac{\partial \varphi_{PB}^*}{\partial \delta_i}$	0							
$\frac{\partial \varphi_{PB}^*}{\partial a_{CH}}, \frac{\partial \varphi_{PB}^*}{\partial a_{PN}}$	+		$f_4 > 0$		+		$f_4 > 0$	
			$f_4 < 0$				$f_4 < 0$	
$\frac{\partial \varphi_{PB}^*}{\partial d_C}, \frac{\partial \varphi_{PB}^*}{\partial d_P}$	-		$f_4 > 0$		-		$f_4 > 0$	
			$f_4 < 0$		+		$f_4 < 0$	
$\frac{\partial \varphi_{PB}^*}{\partial a_{HP}}$	-		$f_4 > 0$		-		$f_4 > 0$	
			$f_4 < 0$		+		$f_4 < 0$	
$\frac{\partial \varphi_{PB}^*}{\partial d_H}$	0							

$$f_1: (1 - \delta_B) + e_{BD}(\delta_B - \delta_F q_D/q_B)$$

$$f_2: (1 - \delta_B) + e_{BD}(\delta_B - \delta_F)$$

$$f_3: -a_{BD}D^* + a_{FB}\delta_F F^* + \delta_B(d_B + (1 - e_{BD})a_{BD}D^*)$$

$$f_4: e_{BD}a_{BD}l_N - a_{BN}l_D$$

## Appendix 2 Other models with different food chain lengths

**Table S3** Comparisons between models with different food chain lengths for the effects of predator or decomposer on primary production (effect of consuming rate  $\alpha_{FB}$ ) and the effects of carnivore on decomposer production through their consuming rates (effect of consuming rate  $\alpha_{CH}$ ). The expressions in the table give the conditions that determine the direction of these effects, if positive the effects of increasing consuming rate are positive on production. Differences in shading highlight different conditions between functional responses and between models.

	Green food chain length modified								Original model				Brown food chain length modified	
	Model 2-2				Model 4-2				Model 3-2				Model 3-3	
	DC & C limited	DC & N limited	LV & C limited	LV & N limited	DC & C limited	DC & N limited	LV & C limited	LV & N limited	DC & C limited	DC & N limited	LV & C limited	LV & N limited	DC & C limited	DC & N limited
Effects of $\alpha_{FB}$ on PP	$\delta_B - \delta_F$	$\delta_B - \delta_F$	$f_1$	$f_1$	$\delta_B - \delta_F$	$\delta_B - \delta_F$	$f_1$	$f_1$	$\delta_B - \delta_F$	$\delta_B - \delta_F$	$f_1$	$f_1$	$f_2$	$f_2$
Effects of $\alpha_{CH}$ on PB	Always positive	$e_{BD}a_{BD}l_N - a_{BN}l_D$	Always positive	$e_{BD}a_{BD}l_N - a_{BN}l_D$	Always positive	$e_{BD}a_{BD}l_N - a_{BN}l_D$	Always positive	$e_{BD}a_{BD}l_N - a_{BN}l_D$	Always positive	$e_{BD}a_{BD}l_N - a_{BN}l_D$	Always positive	$e_{BD}a_{BD}l_N - a_{BN}l_D$	Always positive	$e_{BD}a_{BD}l_N - a_{BN}l_D$

$$f_1: -a_{BD}D^* + \alpha_{FB}\delta_FF^* + \delta_B(a_B + (1 - e_{BD})a_{BD}D^*)$$

$$f_2: (\delta_B - \delta_F) + e_{FB}(\delta_F - \delta_A)$$

**The model 2-2 (model with a 2-level green food chain and a 2-level brown food chain):**

$$\dot{N} = I_N - l_N N + (1 - \delta_H)(d_H H + (1 - e_{HP})a_{HP}PH) + (1 - \delta_B)(d_B B + (1 - e_{BD})a_{BD}D(B)) + (1 - \delta_F)(d_F F + (1 - e_{FB})a_{FB}BF) - a_{PN}NP - \min\left[\left(\frac{q_B}{q_D} - 1\right)e_{BD}a_{BD}D(B), a_{BN}N(B)\right]$$

$$\dot{P} = a_{PN}NP - d_P P - a_{HP}PH$$

$$\dot{H} = e_{HP}a_{HP}PH - d_H H$$

$$\dot{D} = I_D - l_D D + d_P P + \delta_H(d_H H + (1 - e_{HP})a_{HP}PH) + \delta_B(d_B B + (1 - e_{BD})a_{BD}D(B)) + \delta_F(d_F F + (1 - e_{FB})a_{FB}BF) - a_{BD}D(B)$$

$$\dot{B} = \min\left[e_{BD}a_{BD}D(B)\frac{q_B}{q_D}, e_{BD}a_{BD}D(B) + a_{BN}N(B)\right] - d_B B - a_{FB}BF$$

$$\dot{F} = e_{FB}a_{FB}BF - d_F F$$

**Table S4:** Equilibrium results for all compartments in model 2-2

	DC & C limited	DC & N limited	LV & C limited	LV & N limited
<b>N*</b>			$\frac{d_P + a_{HP}H^*}{a_{PN}}$	
<b>P*</b>			$\frac{d_H}{e_{HP}a_{HP}}$	
<b>H*</b>	$H_{DC-C}^*$	$H_{DC-N}^*$	$H_{LV-C}^*$	$H_{LV-N}^*$
<b>D*</b>			$\frac{I_N + I_D - l_N N^*}{l_D}$	
<b>B*</b>			$\frac{d_F}{e_{FB}a_{FB}}$	
<b>F*</b>	$\frac{e_{BD}a_{BD}D^*}{a_{FB}B^*} \cdot \frac{q_B}{q_D} - \frac{d_B}{a_{FB}}$	$\frac{e_{BD}a_{BD}D^* + a_{BN}N^*}{a_{FB}B^*} - \frac{d_B}{a_{FB}}$	$\frac{e_{BD}a_{BD}D^*}{a_{FB}} \cdot \frac{q_B}{q_D} - \frac{d_B}{a_{FB}}$	$\frac{e_{BD}a_{BD}D^* + a_{BN}N^*}{a_{FB}} - \frac{d_B}{a_{FB}}$

$$H_{DC-C}^* = \frac{a_{BD}(a_{PN}(l_D + l_N) - d_P l_N)(a_{FB}B^*((1 - \delta_B(1 - e_{BD}))q_D - \delta_F e_{BD}(1 - e_{FB})q_B) - \delta_F d_F e_{BD}q_B) - l_D q_D B^*(a_{FB}(d_P l_N + a_{PN}(d_B B^*(\delta_B - \delta_F(1 - e_{FB})) - l_N + d_P P^*) - a_{PN}d_B d_F \delta_F))}{a_{FB}l_D q_D B^*(a_{HP}l_N + a_{PN}\delta_H(d_H + a_{HP}P^*(1 - e_{HP}))) + a_{BD}a_{HP}l_N(a_{FB}B^*((1 - \delta_B(1 - e_{BD}))q_D - \delta_F e_{BD}(1 - e_{FB})q_B) - \delta_F d_F e_{BD}q_B)}$$

$$H_{DC-N}^* = \frac{a_{BD}(a_{PN}(l_D + l_N) - d_P l_N)(a_{FB} B^* ((1 - \delta_B(1 - e_{BD}) - \delta_F e_{BD}(1 - e_{FB})) - \delta_F d_F e_{BD}) - l_D(a_{FB} B^* (a_{PN}(d_B B^* (\delta_B - \delta_F(1 - e_{FB})) - l_N + d_P P^*) + d_P(a_{BN} \delta_F(1 - e_{FB}) + l_N)) + \delta_F d_F(a_{BN} d_P - a_{PN} d_B B^*)))}{a_{FB} B^* (a_{HP} l_N (a_{BD}(1 - \delta_B(1 - e_{BD}) - \delta_F e_{BD}(1 - e_{FB}) + l_D) + a_{PN} \delta_H l_D (d_H + a_{HP} P^* (1 - e_{HP}))) + a_{BN} a_{HP} \delta_F (d_F + a_{FB} B^* (1 - e_{FB})) l_D - e_{BD} a_{BD} a_{HP} \delta_F d_F l_N)}$$

$$H_{LV-C}^* = \frac{a_{BD}(a_{PN}(l_D + l_N) - d_P l_N)(a_{FB} B^* ((1 - \delta_B(1 - e_{BD})) q_D - \delta_F e_{BD}(1 - e_{FB}) q_B) - \delta_F d_F e_{BD} q_B) - l_D q_D (a_{FB} (d_P l_N + a_{PN}(d_B B^* (\delta_B - \delta_F(1 - e_{FB})) - l_N + d_P P^*) - a_{PN} d_B d_F \delta_F))}{a_{FB} l_D q_D (a_{HP} l_N + a_{PN} \delta_H (d_H + a_{HP} P^* (1 - e_{HP}))) + a_{BD} a_{HP} l_N (a_{FB} B^* ((1 - \delta_B(1 - e_{BD})) q_D - \delta_F e_{BD}(1 - e_{FB}) q_B) - \delta_F d_F e_{BD} q_B)}$$

$$H_{LV-N}^* = \frac{a_{BD}(a_{PN}(l_D + l_N) - d_P l_N)(a_{FB} B^* ((1 - \delta_B(1 - e_{BD}) - \delta_F e_{BD}(1 - e_{FB})) - \delta_F d_F e_{BD}) - l_D(a_{FB} (a_{PN}(d_B B^* (\delta_B - \delta_F(1 - e_{FB})) - l_N + d_P P^*) + d_P(a_{BN} \delta_F B^* (1 - e_{FB}) + l_N)) + \delta_F d_F(a_{BN} d_P - a_{PN} d_B)))}{a_{FB} (a_{HP} l_N (a_{BD} B^* (1 - \delta_B(1 - e_{BD}) - \delta_F e_{BD}(1 - e_{FB}) + l_D) + a_{PN} \delta_H l_D (d_H + a_{HP} P^* (1 - e_{HP}))) + a_{BN} a_{HP} \delta_F (d_F + a_{FB} B^* (1 - e_{FB})) l_D - e_{BD} a_{BD} a_{HP} \delta_F d_F l_N)}$$

**Table S5:** Signs of partial derivatives of primary production (PP) in model 2-2.  $f_1, f_2, f_3, f_4$  are conditions that determine the signs of corresponding effects

	DC & C limited		DC & N limited		LV & C limited		LV & N limited	
$\frac{\partial \varphi_{PP}^*}{\partial \delta_i}$	-		-		-		-	
$\frac{\partial \varphi_{PP}^*}{\partial a_{BD}}$	$f_1 > 0$	+	$f_2 > 0$	+	$f_1 > 0$	+	$f_2 > 0$	+
	$f_1 < 0$	-	$f_2 < 0$	-	$f_1 < 0$	-	$f_2 < 0$	-
$\frac{\partial \varphi_{PP}^*}{\partial a_{BN}}$	0		-		0		-	
$\frac{\partial \varphi_{PP}^*}{\partial d_B}$	$f_3 > 0$	-	$f_3 > 0$	-	$f_4 > 0$	-	$f_4 > 0$	-
	$f_3 < 0$	+	$f_3 < 0$	+	$f_4 < 0$	+	$f_4 < 0$	+
$\frac{\partial \varphi_{PP}^*}{\partial a_{FB}}$	$f_3 > 0$	+	$f_3 > 0$	+	$f_4 > 0$	+	$f_4 > 0$	+
	$f_3 < 0$	-	$f_3 < 0$	-	$f_4 < 0$	-	$f_4 < 0$	-
$\frac{\partial \varphi_{PP}^*}{\partial d_F}$	$f_3 > 0$	-	$f_3 > 0$	-	$f_4 > 0$	-	$f_4 > 0$	-
	$f_3 < 0$	+	$f_3 < 0$	+	$f_4 < 0$	+	$f_4 < 0$	+

$$f_1: (1 - \delta_B) + e_{BD} \left( \delta_B - \delta_F \frac{q_B}{q_D} \right)$$

$$f_2: (1 - \delta_B) + e_{BD} (\delta_B - \delta_F)$$

$$f_3: \delta_B - \delta_F$$

$$f_4: -a_{BD}D^* + a_{FB}\delta_FF^* + \delta_B(d_B + (1 - e_{BD})a_{BD}D^*)$$

**Table S6:** Signs of partial derivatives of decomposers production (PB) in model 2-2.  $f_1$  is the condition that determines the signs of corresponding effects

	DC & C limited	DC & N limited		LV & C limited	LV & N limited	
$\frac{\partial \phi_{PB}^*}{\partial \delta_i}$	+	$f_1 > 0$	+	+	$f_1 > 0$	+
		$f_1 < 0$	-		$f_1 < 0$	-
$\frac{\partial \phi_{PB}^*}{\partial a_{HP}}$	-	$f_1 > 0$	-	-	$f_1 > 0$	-
		$f_1 < 0$	+		$f_1 < 0$	+
$\frac{\partial \phi_{PB}^*}{\partial d_H}$	+	$f_1 > 0$	+	+	$f_1 > 0$	+
		$f_1 < 0$	-		$f_1 < 0$	-
$\frac{\partial \phi_{PB}^*}{\partial a_{PN}}$	+	$f_1 > 0$	+	+	$f_1 > 0$	+
		$f_1 < 0$	-		$f_1 < 0$	-
$\frac{\partial \phi_{PB}^*}{\partial d_P}$	+	$f_1 > 0$	+	+	$f_1 > 0$	+
		$f_1 < 0$	-		$f_1 < 0$	-

$$f_1: e_{BD}a_{BD}l_N - a_{BN}l_D$$

**The model 4-2 (model with a 2-level green food chain and a 2-level brown food chain):**

$$\begin{aligned}\dot{N} = & I_N - l_N N - a_{PN} NP + (1 - \delta_H)(d_H H + (1 - e_{HP})a_{HP} PH) + (1 - \delta_C)(d_C C + (1 - e_{CH})a_{CH} HC) \\ & + (1 - \delta_Y)(d_Y Y + (1 - e_{YC})a_{YC} CY) + (1 - \delta_B)(d_B B + (1 - e_{BD})a_{BD} D(B)) \\ & + (1 - \delta_F)(d_F F + (1 - e_{FB})a_{FB} BF) - \min\left[\left(\frac{q_B}{q_D} - 1\right)e_{BD}a_{BD}D(B), a_{BN}N(B)\right]\end{aligned}$$

$$\dot{P} = a_{PN} NP - d_P P - a_{HP} PH$$

$$\dot{H} = e_{HP} a_{HP} PH - d_H H - a_{CH} HC$$

$$\dot{C} = e_{CH} a_{CH} HC - d_C C - a_{YC} CY$$

$$\dot{Y} = e_{YC} a_{YC} CY - d_Y Y$$

$$\begin{aligned}\dot{D} = & I_D - l_D D + d_P P - a_{BD} D(B) + \delta_H(d_H H + (1 - e_{HP})a_{HP} PH) + \delta_C(d_C C + (1 - e_{CH})a_{CH} HC) \\ & + \delta_Y(d_Y Y + (1 - e_{YC})a_{YC} CY) + \delta_B(d_B B + (1 - e_{BD})a_{BD} D(B)) + \delta_F(d_F F + (1 \\ & - e_{FB})a_{FB} BF)\end{aligned}$$

$$\dot{B} = \min\left[e_{BD}a_{BD}D(B)\frac{q_B}{q_D}, e_{BD}a_{BD}D(B) + a_{BN}N(B)\right] - d_B B - a_{FB} BF$$

$$\dot{F} = e_{FB} a_{FB} BF - d_F F$$

**Table S7:** Equilibrium results for all compartments in model 4-2

	DC & C limited	DC & N limited	LV & C limited	LV & N limited
$N^*$			$\frac{d_P + a_{HP} H^*}{a_{PN}}$	
$P^*$			$\frac{d_H + a_{CH} C^*}{e_{HP} a_{HP}}$	
$H^*$			$\frac{d_C + a_{YC} Y^*}{e_{CH} a_{CH}}$	
$C^*$			$\frac{d_Y}{e_{YC} a_{YC}}$	
$Y^*$	$Y_{DC-C}^*$	$Y_{DC-N}^*$	$Y_{LV-C}^*$	$Y_{LV-N}^*$
$D^*$			$\frac{I_N + I_D - l_N N^*}{l_D}$	
$B^*$			$\frac{d_F}{e_{FB} a_{FB}}$	
$F^*$	$\frac{e_{BD} a_{BD} D^*}{a_{FB} B^*} \cdot \frac{q_B}{q_D} - \frac{d_B}{a_{FB}}$	$\frac{e_{BD} a_{BD} D^* + a_{BN} N^*}{a_{FB} B^*} - \frac{d_B}{a_{FB}}$	$\frac{e_{BD} a_{BD} D^*}{a_{FB}} \cdot \frac{q_B}{q_D} - \frac{d_B}{a_{FB}}$	$\frac{e_{BD} a_{BD} D^* + a_{BN} N^*}{a_{FB}} - \frac{d_B}{a_{FB}}$

$$\begin{aligned}
& a_{BD}(e_{CH}a_{CH}(a_{PN}(l_D + l_N) - d_P l_N) - a_{HP}d_C l_N)(a_{FB}B^*((1 - \delta_B(1 - e_{BD}))q_D - \delta_F e_{BD}(1 - e_{FB})q_B) \\
& \quad - \delta_F d_F e_{BD}q_B) - l_D q_D B^*(a_{FB}d_C(a_{HP}l_N + a_{PN}\delta_H(d_H + a_{HP}P^*(1 - e_{HP}))) + a_{CH} \\
Y_{DC-C}^* = & \frac{(a_{FB}(e_{CH}d_P l_N + a_{PN}(\delta_C d_C C^* + e_{CH}(d_B B^*(\delta_B - \delta_F(1 - e_{FB}))) - l_N + d_P P^*)) - e_{CH}a_{PN}d_B d_F \delta_F)}{a_{FB}l_D q_D B^*(a_{YC}(a_{HP}l_N + a_{PN}\delta_H(d_H + a_{HP}P^*(1 - e_{HP}))) \\
& \quad + a_{CH}a_{PN}(a_{YC}C^*(\delta_C(1 - e_{CH}) + \delta_Y e_{CH}(1 - e_{YC})) + e_{CH}d_Y \delta_Y) \\
& \quad + a_{BD}a_{HP}a_{YC}l_N(a_{FB}B^*((1 - \delta_B(1 - e_{BD}))q_D - \delta_F e_{BD}(1 - e_{FB})q_B) - \delta_F d_F e_{BD}q_B)}
\end{aligned}$$

$Y_{DC-N}^*$

$$\begin{aligned}
& a_{BD}(e_{CH}a_{CH}(a_{PN}(l_D + l_N) - d_P l_N) - a_{HP}d_C l_N)(a_{FB}B^*(1 - \delta_B(1 - e_{BD}) - \delta_F e_{BD}(1 - e_{FB})) \\
& \quad - \delta_F d_F e_{BD}) - l_D(d_C(a_{BN}a_{HP}\delta_F(d_F + a_{FB}B^*(1 - e_{FB})) + a_{FB}B^*(a_{HP}l_N + a_{PN}\delta_H(d_H + a_{HP}P^*(1 - e_{HP})))) + a_{CH} \\
& \quad (e_{CH}\delta_F d_F(a_{BN}d_P - a_{PN}d_B B^*) + a_{FB}B^*\left(\frac{e_{CH}d_P(a_{BN}\delta_F(1 - e_{FB}) + l_N)}{+a_{PN}(\delta_C d_C C^* + e_{CH}(d_B B^*(\delta_B - \delta_F(1 - e_{FB}))) - l_N + d_P P^*}\right))) \\
= & \frac{a_{CH}a_{PN}a_{FB}l_D B^*(a_{YC}C^*(\delta_C(1 - e_{CH}) + \delta_Y e_{CH}(1 - e_{YC})) + \delta_Y d_Y e_{CH})}{a_{YC}(a_{FB}B^*(a_{HP}(a_{BD}(1 - \delta_B(1 - e_{BD}) - \delta_F e_{BD}(1 - e_{FB}) + l_D)l_N + a_{PN}\delta_H l_D(d_H + a_{HP}P^*(1 - e_{HP}))) \\
& \quad + a_{BN}a_{HP}\delta_F(d_F + a_{FB}B^*(1 - e_{FB}))l_D - e_{BD}a_{BD}a_{HP}\delta_F d_F l_N)} \\
& a_{BD}(e_{CH}a_{CH}(a_{PN}(l_D + l_N) - d_P l_N) - a_{HP}d_C l_N)(a_{FB}B^*((1 - \delta_B(1 - e_{BD}))q_D - \delta_F e_{BD}(1 - e_{FB})q_B) \\
& \quad - \delta_F d_F e_{BD}q_B) - l_D q_D(a_{FB}d_C(a_{HP}l_N + a_{PN}\delta_H(d_H + a_{HP}P^*(1 - e_{HP}))) + a_{CH} \\
Y_{LV-C}^* = & \frac{(a_{FB}(e_{CH}d_P l_N + a_{PN}(\delta_C d_C C^* + e_{CH}(d_B B^*(\delta_B - \delta_F(1 - e_{FB}))) - l_N + d_P P^*)) - e_{CH}a_{PN}d_B d_F \delta_F)}{a_{FB}l_D q_D(a_{YC}(a_{HP}l_N + a_{PN}\delta_H(d_H + a_{HP}P^*(1 - e_{HP}))) \\
& \quad + a_{CH}a_{PN}(a_{YC}C^*(\delta_C(1 - e_{CH}) + \delta_Y e_{CH}(1 - e_{YC})) + e_{CH}d_Y \delta_Y) \\
& \quad + a_{BD}a_{HP}a_{YC}l_N(a_{FB}B^*((1 - \delta_B(1 - e_{BD}))q_D - \delta_F e_{BD}(1 - e_{FB})q_B) - \delta_F d_F e_{BD}q_B)}
\end{aligned}$$

$Y_{LV-N}^*$

$$\begin{aligned}
& a_{BD}(e_{CH}a_{CH}(a_{PN}(l_D + l_N) - d_P l_N) - a_{HP}d_C l_N)(a_{FB}B^*(1 - \delta_B(1 - e_{BD}) - \delta_F e_{BD}(1 - e_{FB})) \\
& \quad - \delta_F d_F e_{BD}) - l_D(d_C(a_{BN}a_{HP}\delta_F(d_F + a_{FB}B^*(1 - e_{FB})) + a_{FB}B^*(a_{HP}l_N + a_{PN}\delta_H(d_H + a_{HP}P^*(1 - e_{HP})))) + a_{CH} \\
& \quad (e_{CH}\delta_F d_F(a_{BN}d_P - a_{PN}d_B) + a_{FB}B^*\left(\frac{e_{CH}d_P(a_{BN}\delta_F(1 - e_{FB}) + l_N)}{+a_{PN}(\delta_C d_C C^* + e_{CH}(d_B B^*(\delta_B - \delta_F(1 - e_{FB}))) - l_N + d_P P^*}\right))) \\
= & \frac{a_{CH}a_{PN}a_{FB}l_D(a_{YC}C^*(\delta_C(1 - e_{CH}) + \delta_Y e_{CH}(1 - e_{YC})) + \delta_Y d_Y e_{CH})}{a_{YC}(a_{FB}(a_{HP}(a_{BD}B^*(1 - \delta_B(1 - e_{BD}) - \delta_F e_{BD}(1 - e_{FB}) + l_D)l_N + a_{PN}\delta_H l_D(d_H + a_{HP}P^*(1 - e_{HP}))) \\
& \quad + a_{BN}a_{HP}\delta_F(d_F + a_{FB}B^*(1 - e_{FB}))l_D - e_{BD}a_{BD}a_{HP}\delta_F d_F l_N)}
\end{aligned}$$



**Table S8:** Signs of partial derivatives of primary production (PP) in model 4-2.  $f_1, f_2, f_3, f_4$  are conditions that determine the signs of corresponding effects

	DC & C limited		DC & N limited		LV & C limited		LV & N limited	
$\frac{\partial \varphi_{PP}^*}{\partial \delta_i}$	-		-		-		-	
$\frac{\partial \varphi_{PP}^*}{\partial a_{BD}}$	$f_1 > 0$	+	$f_2 > 0$	+	$f_1 > 0$	+	$f_2 > 0$	+
	$f_1 < 0$	-	$f_2 < 0$	-	$f_1 < 0$	-	$f_2 < 0$	-
$\frac{\partial \varphi_{PP}^*}{\partial a_{BN}}$	0		-		0		-	
$\frac{\partial \varphi_{PP}^*}{\partial d_B}$	$f_3 > 0$	-	$f_3 > 0$	-	$f_4 > 0$	-	$f_4 > 0$	-
	$f_3 < 0$	+	$f_3 < 0$	+	$f_4 < 0$	+	$f_4 < 0$	+
$\frac{\partial \varphi_{PP}^*}{\partial a_{FB}}$	$f_3 > 0$	+	$f_3 > 0$	+	$f_4 > 0$	+	$f_4 > 0$	+
	$f_3 < 0$	-	$f_3 < 0$	-	$f_4 < 0$	-	$f_4 < 0$	-
$\frac{\partial \varphi_{PP}^*}{\partial d_F}$	$f_3 > 0$	-	$f_3 > 0$	-	$f_4 > 0$	-	$f_4 > 0$	-
	$f_3 < 0$	+	$f_3 < 0$	+	$f_4 < 0$	+	$f_4 < 0$	+

$$f_1: (1 - \delta_B) + e_{BD} \left( \delta_B - \delta_F \frac{q_B}{q_D} \right)$$

$$f_2: (1 - \delta_B) + e_{BD} (\delta_B - \delta_F)$$

$$f_3: \delta_B - \delta_F$$

$$f_4: -a_{BD} D^* + a_{FB} \delta_F F^* + \delta_B (d_B + (1 - e_{BD}) a_{BD} D^*)$$

**Table S9:** Signs of partial derivatives of decomposers production (PB) in model 4-2.  $f_1$  is the condition that determines the signs of corresponding effects

	DC & C limited	DC & N limited	LV & C limited	LV & N limited
$\frac{\partial \varphi_{PB}^*}{\partial \delta_i}$	+	$f_1 > 0$ +	+	$f_1 > 0$ +
		$f_1 < 0$ -		$f_1 < 0$ -
$\frac{\partial \varphi_{PB}^*}{\partial a_{\gamma C}}$	-	$f_1 > 0$ -	-	$f_1 > 0$ -
		$f_1 < 0$ +		$f_1 < 0$ +
$\frac{\partial \varphi_{PB}^*}{\partial d_{\gamma}}$	+	$f_1 > 0$ +	+	$f_1 > 0$ +
		$f_1 < 0$ -		$f_1 < 0$ -
$\frac{\partial \varphi_{PB}^*}{\partial a_{CH}}$	+	$f_1 > 0$ +	+	$f_1 > 0$ +
		$f_1 < 0$ -		$f_1 < 0$ -
$\frac{\partial \varphi_{PB}^*}{\partial d_C}$	-	$f_1 > 0$ -	-	$f_1 > 0$ -
		$f_1 < 0$ +		$f_1 < 0$ +
$\frac{\partial \varphi_{PB}^*}{\partial a_{HP}}$	-	$f_1 > 0$ -	-	$f_1 > 0$ -
		$f_1 < 0$ +		$f_1 < 0$ +
$\frac{\partial \varphi_{PB}^*}{\partial d_H}$	+	$f_1 > 0$ +	+	$f_1 > 0$ +
		$f_1 < 0$ -		$f_1 < 0$ -
$\frac{\partial \varphi_{PB}^*}{\partial a_{PN}}$	+	$f_1 > 0$ +	+	$f_1 > 0$ +
		$f_1 < 0$ -		$f_1 < 0$ -
$\frac{\partial \varphi_{PB}^*}{\partial d_P}$	-	$f_1 > 0$ -	-	$f_1 > 0$ -
		$f_1 < 0$ +		$f_1 < 0$ +

$$f_1: e_{BD}a_{BD}l_N - a_{BN}l_D$$

**The model 3-3 (model with a 3-level green food chain and a 3-level brown food chain):**

$$\begin{aligned}\dot{N} = & I_N - l_N N + (1 - \delta_H)(d_H H + (1 - e_{HP})a_{HP}PH) + (1 - \delta_C)(d_C C + (1 - e_{CH})a_{CH}HC) \\ & + (1 - \delta_B)(d_B B + (1 - e_{BD})a_{BD}D) + (1 - \delta_F)(d_F F + (1 - e_{FB})a_{FB}BF) \\ & + (1 - \delta_A)(d_A A + (1 - e_{AF})a_{AF}FA) - a_{PN}NP - \min\left[\frac{q_B}{q_D}\right. \\ & \left. - 1\right)e_{BD}a_{BD}Da_{BN}N\end{aligned}$$

$$\dot{P} = a_{PN}NP - d_P P - a_{HP}PH$$

$$\dot{H} = e_{HP}a_{HP}PH - d_H H - a_{CH}HC$$

$$\dot{C} = e_{CH}a_{CH}HC - d_C C$$

$$\begin{aligned}\dot{D} = & I_D - l_D D + d_P P - a_{BD}D + \delta_H(d_H H + (1 - e_{HP})a_{HP}PH) \\ & + \delta_C(d_C C + (1 - e_{CH})a_{CH}HC) + \delta_B(d_B B + (1 - e_{BD})a_{BD}D) + \delta_F(d_F F + (1 \\ & - e_{FB})a_{FB}BF) + \delta_A(d_A A + (1 - e_{AF})a_{AF}FA)\end{aligned}$$

$$\dot{B} = \min\left[e_{BD}a_{BD}D \frac{q_B}{q_D}, e_{BD}a_{BD}D + a_{BN}N\right] - d_B B - a_{FB}BF$$

$$\dot{F} = e_{FB}a_{FB}BF - d_F F - a_{AF}FA$$

$$\dot{A} = e_{AF}a_{AF}FA - d_A A$$

**Table S10:** Equilibrium results for all compartments in model 3-3

	DC & C limited	DC & N limited
$N^*$		$\frac{d_P + a_{HP}H^*}{a_{PN}}$
$P^*$		$\frac{d_H + a_{CH}C^*}{e_{HP}a_{HP}}$
$H^*$		$\frac{d_C}{e_{CH}a_{CH}}$
$C^*$	$\frac{e_{HP}a_{HP}[a_{BD}D^*(1-\delta_B(1-e_{BD}))-\delta_F d_F F^*-\delta_B d_B B^*-\delta_F a_{FB}(1-e_{FB})B^*F^*-\delta_A A^*(d_A+a_{AF}(1-e_{AF})F^*-I_D+l_D D^*)]-d_H(d_P+\delta_H a_{HP}H^*)}{a_{CH}(d_P+a_{HP}(\delta_H(1-e_{HP})+\delta_C e_{HP}(1-e_{CH}))H^*)+e_{HP}a_{HP}\delta_C d_C}$	
$D^*$		$\frac{I_N+I_D-l_N N^*}{l_D}$
$B^*$	$\frac{e_{BD}a_{BD}D^*}{d_B+a_{FB}F^*} \cdot \frac{q_B}{q_D}$	$\frac{e_{BD}a_{BD}D^*+a_{BN}N^*}{d_B+a_{FB}F^*}$
$F^*$		$\frac{d_A}{e_{AF}a_{AF}}$
$A^*$		$\frac{e_{FB}a_{FB}B^*-d_F}{a_{AF}}$

**Table S11:** Signs of partial derivatives of primary production (PP) in model 3-3.  $f_1, f_2, f_3, f_4$  are conditions that determine the signs of corresponding effects

	DC & C limited	DC & N limited
$\frac{\partial \varphi_{PP}^*}{\partial \delta_i}$	-	-
$\frac{\partial \varphi_{PP}^*}{\partial a_{BD}}$	$f_1 > 0$ $f_1 < 0$	+ -
$\frac{\partial \varphi_{PP}^*}{\partial a_{BN}}$	0	-
$\frac{\partial \varphi_{PP}^*}{\partial d_B}$	$f_3 > 0$ $f_3 < 0$	- +
$\frac{\partial \varphi_{PP}^*}{\partial a_{FB}}$	$f_3 > 0$ $f_3 < 0$	+ -
$\frac{\partial \varphi_{PP}^*}{\partial d_F}$	$f_4 > 0$ $f_4 < 0$	- +

$$f_1: e_{AF}a_{AF}d_B[(1 - \delta_B)q_D + \delta_B e_{BD}(q_B - q_D)] + a_{FB}d_A[(1 - \delta_B)q_D + e_{BD}(\delta_B q_D - \delta_F q_B) + e_{FB}q_B(\delta_F - \delta_A)]$$

$$f_2: (1 - \delta_B)(a_{FB}d_A + e_{AF}a_{AF}d_B) + a_{FB}d_A[e_{BD}(\delta_B - \delta_F) + e_{FB}(\delta_F - \delta_A)]$$

$$f_3: (\delta_B - \delta_F) + e_{FB}(\delta_F - \delta_A)$$

$$f_4: \delta_F - \delta_A$$

**Table S12:** Signs of partial derivatives of decomposers production (PB) in model 3-3.  $f_1$  is the condition that determines the signs of corresponding effects

	DC & C limited	DC & N limited	
$\frac{\partial \varphi_{PB}^*}{\partial \delta_i}$	0		0
$\frac{\partial \varphi_{PB}^*}{\partial a_{CH}}$	+	$f_1 > 0$	+
		$f_1 < 0$	-
$\frac{\partial \varphi_{PB}^*}{\partial d_C}$	-	$f_1 > 0$	-
		$f_1 < 0$	+
$\frac{\partial \varphi_{PB}^*}{\partial d_H}$	-	$f_1 > 0$	-
		$f_1 < 0$	+
$\frac{\partial \varphi_{PB}^*}{\partial d_H}$	0		0
$\frac{\partial \varphi_{PB}^*}{\partial a_{PN}}$	+	$f_1 > 0$	+
		$f_1 < 0$	-
$\frac{\partial \varphi_{PB}^*}{\partial d_P}$	-	$f_1 > 0$	-
		$f_1 < 0$	+
$f_1: e_{BD}a_{BD}l_N - a_{BN}l_D$			

### Appendix 3 Simulations of models with type II functional responses

Models and parameters:

$$\begin{aligned}
 \frac{dN}{dt} &= I_N - l_N N + (1 - \delta_H)(d_H H + (1 - e_{HP}) \frac{a_{HP} PH}{P + K_H} + eH^2) \\
 &+ (1 - \delta_C)(d_C C + (1 - e_{CH}) \frac{a_{CH} HC}{H + K_C} + eC^2) + (1 - \delta_F)(d_F F + (1 - e_{FB}) \frac{a_{FB} BF}{B + K_F} + eF^2) \\
 &+ (1 - \delta_B)(d_B B + (1 - e_{BD}) a_{BD} D + eB^2) - \frac{r_{PN} NP}{N + K_P} - r_{BN} N \\
 \frac{dP}{dt} &= \frac{r_{PN} NP}{N + K_P} - d_P P - \frac{a_{HP} PH}{P + K_H} - eP^2 \\
 \frac{dH}{dt} &= \frac{e_{HP} a_{HP} PH}{P + K_H} - d_H H - \frac{a_{CH} HC}{H + K_C} - eH^2 \\
 \frac{dC}{dt} &= \frac{e_{CH} a_{CH} HC}{H + K_C} - d_C C - eC^2 \\
 \frac{dD}{dt} &= I_D - l_D D + \delta_H (d_H H + (1 - e_{HP}) \frac{a_{HP} PH}{P + K_H} + eH^2) \\
 &+ \delta_C (d_C C + (1 - e_{CH}) \frac{a_{CH} HC}{H + K_C} + eC^2) + \delta_F (d_F F + (1 - e_{FB}) \frac{a_{FB} BF}{B + K_F} + eF^2) \\
 &+ \delta_B (d_B B + (1 - e_{BD}) a_{BD} D + eB^2) + eP^2 + d_P P - a_{BD} D \\
 \frac{dB}{dt} &= r_{BN} N + e_{BD} a_{BD} D - d_B B - \frac{a_{FB} BF}{B + K_F} - eB^2 \\
 \frac{dF}{dt} &= \frac{e_{FB} a_{FB} BF}{B + K_F} - d_F F - eF^2
 \end{aligned}$$

The model is set in an aquatic ecosystem limited by nitrogen and is parameterized by using values from the literature. All parameters (with definition, dimension and values) and their literature sources are listed in Table S10. The functional responses of trophic interactions for all organic compartments are type II, except for decomposers where we keep the functional responses as donor-controlled in accordance with the model in the main text. This is the main difference with the equations presented in the main text. We also add a parameter  $e$  to represent the intra-specific competition within each compartment. This term facilitates the coexistence of

all compartments and stabilizes the dynamic of the ecosystem. We analyze the results at equilibrium to investigate the effects of parameters on ecosystem functioning.

**Table S13** Parameter definitions and proposed values in simulation of type II functional responses

Symbol	Definition	Dimension	Value
$I_N$	Constant input of mineral nutrients	$\mu\text{gN L}^{-1} \text{ day}^{-1}$	0.125*
$I_D$	Constant input of organic materials	$\mu\text{gN L}^{-1} \text{ day}^{-1}$	0.625 <sup>†</sup>
$l_N$	Loss rate of mineral nutrients	$\text{day}^{-1}$	0.05 <sup>α</sup>
$l_D$	Loss rate of organic materials	$\text{day}^{-1}$	0.01 <sup>†</sup>
$r_{PN}$	Intrinsic growth rate of primary producers	$\text{day}^{-1}$	0.805 <sup>¶</sup>
$a_{HP}$	Attack rate of herbivores on primary producers	$\text{day}^{-1}$	0.062 <sup>¶</sup>
$a_{CH}$	Attack rate of carnivores on herbivores	$\text{day}^{-1}$	0.03 <sup>¶</sup>
$r_{BN}$	Intrinsic growth rate of decomposers	$\text{day}^{-1}$	varied
$a_{BD}$	Attack rate of decomposers on organic materials	$\text{day}^{-1}$	0.83 <sup>¶</sup>
$a_{FB}$	Attack rate of predators of decomposer on decomposers	$\text{day}^{-1}$	0.5-1.0*
$e_{HP}$	Nutrients conversion efficiency of herbivores	Dimensionless	0.5*
$e_{CH}$	Nutrients conversion efficiency of carnivores	Dimensionless	0.5*
$e_{BD}$	Nutrients conversion efficiency of decomposer	Dimensionless	0.5*
$e_{FB}$	Nutrients conversion efficiency of predators of decomposer	Dimensionless	0.5*
$K_P$	Half saturation of primary producers	$\mu\text{gN L}^{-1}$	1.0*
$K_H$	Half saturation of herbivores	$\mu\text{gN L}^{-1}$	10.0*
$K_C$	Half saturation of carnivores	$\mu\text{gN L}^{-1}$	1.0*
$K_F$	Half saturation of predators of decomposer	$\mu\text{gN L}^{-1}$	1.0*
$d_p$	Loss rate from primary producers	$\text{day}^{-1}$	0.145 <sup>δ</sup>
$d_H$	Loss rate from herbivores	$\text{day}^{-1}$	0.17 <sup>δ</sup>
$d_C$	Loss rate from carnivores	$\text{day}^{-1}$	0.125 <sup>δ</sup>

$d_B$	Loss rate decomposers	day <sup>-1</sup>	0.72 <sup>‡</sup>
$d_F$	Loss rate from predators of decomposers	day <sup>-1</sup>	0.9*
$\delta_H$	Proportion of indirect nutrient cycling by herbivores	Dimensionless	0.5*
$\delta_C$	Proportion of indirect nutrient cycling by carnivores	Dimensionless	0.5*
$\delta_B$	Proportion of indirect nutrient cycling by decomposers	Dimensionless	varied
$\delta_F$	Proportion of indirect nutrient cycling by predators of decomposers	Dimensionless	varied
$e$	Loss rate from each compartment due to intra-specific competition	day <sup>-1</sup>	0.01*

\* Assumed values

<sup>†</sup> This value is taken from Miki et al. 2008 (unit changed and converted to nitrogen content)

<sup>α</sup> This value is from Miki et al. 2011 (unit changed and converted to nitrogen content)

<sup>¶</sup> The value is taken from Boit et al. 2012 (unit changed and converted to nitrogen content)

<sup>δ</sup> The value is taken from Vos et al. 2004

<sup>‡</sup> The biggest value in Servais et al. 1985 (unit changed from h<sup>-1</sup> to day<sup>-1</sup>)

Parameters taken from literature are mainly based on carbon fluxes. We divide these values by C:N ratios of each compartment (from literature) to get corresponding values for nitrogen fluxes. The C:N ratios used in our estimation are 6:1 (Tezuka 1989) for primary producers (algae), 4.5:1 (Walve 1999) for herbivores (zooplankton), 15:1 (Sterner & George 2000) for carnivores (fish), 6.5:1 (Chrzanowski *et al.* 1996) for decomposers (bacteria) and 8.96:1 (Sin *et al.* 1998) for predators of bacteria (flagellates). We assume the environmental C:N ratio to be 6.625:1 and deduce the C:N ratio of the autochthonous organic matter pool. The value 8:1 (Ogawa & Tanoue 2003) is taken for allochthonous organic matter. We also set all units of stock to  $\mu\text{g}$  of nitrogen, all units of volume to liter and all units of time to day.

We assume the value of inputs of inorganic mineral nutrients to be 1/5 of the inputs of organic matters. Depending on the “microbial loop” hypothesis, predators of decomposers often

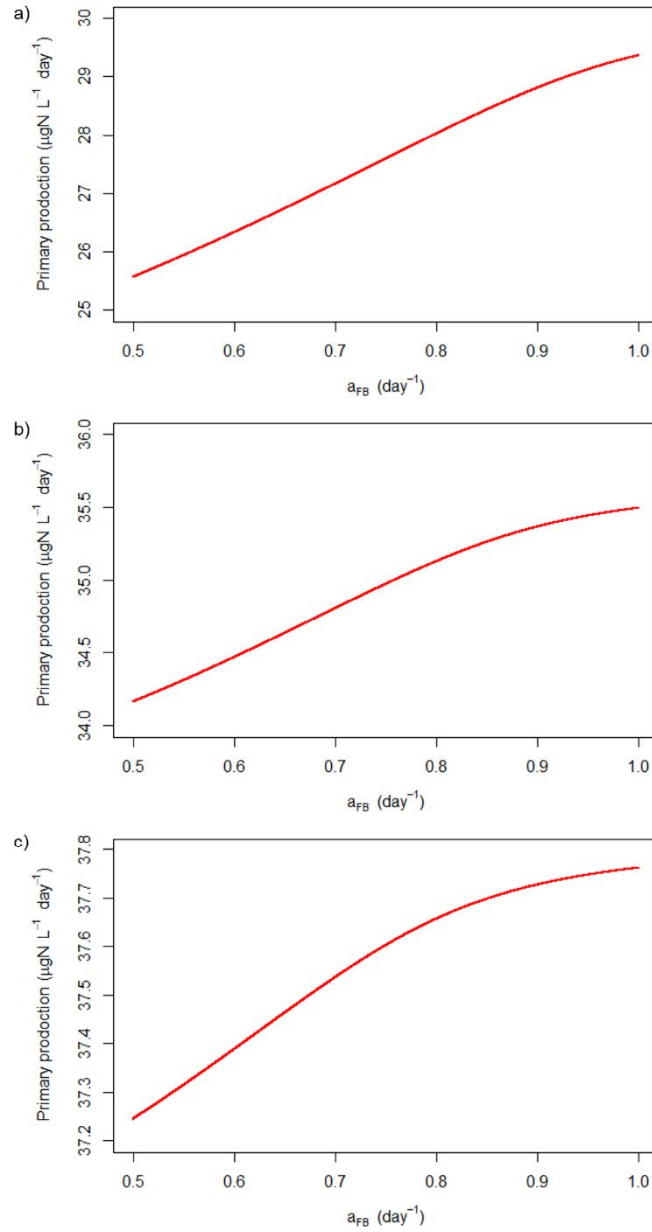


play a role in releasing unassimilated bacterial materials into the environment (Moore *et al.* 2004; Fenchel 2008). Indeed, predators of decomposers have a higher C:N ratio than that of decomposers. Therefore we consider a higher release rate of mineral nutrient from predators of decomposer ( $d_F = 0.9 \text{ day}^{-1}$ ) than that from bacteria ( $d_F = 0.72 \text{ day}^{-1}$ ). The value of  $\delta_B$ ,  $\delta_F$  and  $a_{BN}$  were varied to analyse their effects on the modelling results.

### **Results of numerical simulations for the model with type II functional responses:**

#### **Effects of predators of decomposers on primary production**

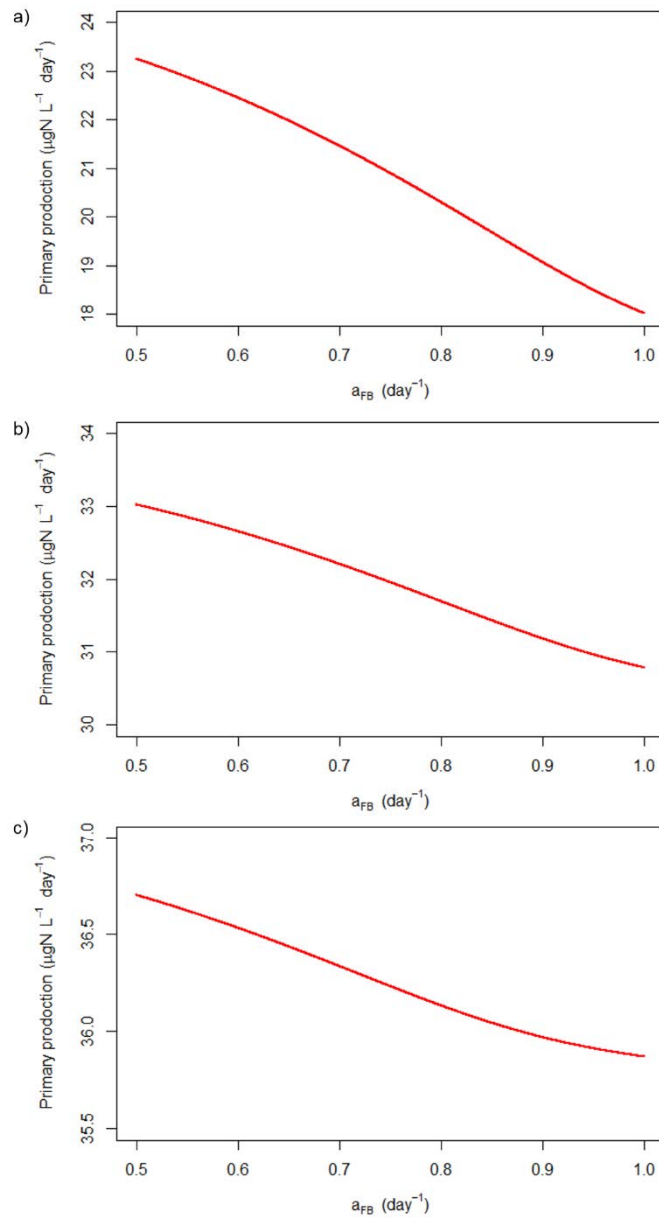
Primary production increases with increasing attack rate of predators of decomposer on decomposers ( $a_{FB}$ ) if and only if  $\delta_B > \delta_F$ . We examined 3 different values (high, medium and low) of  $\delta_B$ :  $\delta_B = 0.7$  (Fig.S1-a),  $\delta_B = 0.5$  (Fig.S1-b) and  $\delta_B = 0.3$  (Fig.S1-c), corresponding values of  $\delta_F$  are  $\delta_F = 0.5$ ,  $\delta_F = 0.3$ ,  $\delta_F = 0.1$  respectively. The primary production increases by 15.2%, 3.89% and 1.39% respectively.



**Fig. S1** Effects of  $a_{FB}$  on primary production when  $\delta_B > \delta_F$ . (a), (b) and (c) represent respectively three cases under different conditions:  $\delta_B = 0.7$   $\delta_F = 0.5$ ,  $\delta_B = 0.5$   $\delta_F = 0.3$  and  $\delta_B = 0.3$   $\delta_F = 0.1$ .

Primary production decreases with increasing attack rate of predators of decomposer on decomposers ( $a_{FB}$ ) when  $\delta_B < \delta_F$ . We also examined 3 different values (high, medium and low) of  $\delta_B$ :  $\delta_B = 0.7$  (Fig.S2-a),  $\delta_B = 0.5$  (Fig.S2-b) and  $\delta_B = 0.3$  (Fig.S2-c), corresponding

values of  $\delta_F$  are  $\delta_F = 0.9, \delta_F = 0.7, \delta_F = 0.5$  respectively. The primary production decreases by 22.5%, 6.83% and 2.26% respectively.



**Fig. S2** Effects of  $a_{FB}$  on primary production when  $\delta_B < \delta_F$ . (a), (b) and (c) represent respectively three cases under different conditions:  $\delta_B = 0.7 \delta_F = 0.9$ ,  $\delta_B = 0.5 \delta_F = 0.7$  and  $\delta_B = 0.3 \delta_F = 0.5$ .

Above results are consistent with analytical and numerical results of models with type 1 functional responses: the signs of the effects of predators of decomposers depend on the relative values of  $\delta_B$  and  $\delta_F$ . We also found that when both  $\delta_B$  and  $\delta_F$  decrease, which means higher proportion of direct nutrient cycling conducted by decomposers and their predators, the absolute value of primary production increases (see y axis from (a) to (c) in both Fig. S1 and Fig. S2) and the magnitude of change in primary production by increase of  $a_{FB}$  decreases. The increase in primary production could be explained by the fact that higher proportion of direct nutrient cycling corresponds to more available mineral nutrients returned to primary producers. The higher proportion of direct nutrient cycling (i.e. low  $\delta_B$  and  $\delta_F$ ) also reduces the effects of  $a_{FB}$  on primary production. We suppose that in this case nutrient cycling is a dominant factor and is more influential for primary production than predation on decomposers.



## **Chapter 3**

# **Consequences of asymmetry between green and brown food webs on stability of aquatic and terrestrial ecosystems**



# **Consequences of asymmetry between green and brown food webs on stability of aquatic and terrestrial ecosystems**

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## **Abstract**

Recent advances in food-web ecology highlight 1) the prevalence of multiple energy channels originating from different groups of basal trophic levels and 2) the increase in stability with turnover asymmetry between predator-coupled energy channels. Here, we show that, in contrast to previous prediction, turnover asymmetry between channels do not necessarily stabilize the ecosystem. The impact of asymmetry depends on mutualistic/competitive interactions at the bottom of the coupled channels based on stoichiometry constraints. In particular, within ecosystems integrating both green (based on primary producers) and brown (based on detritus) food channels, only asymmetry towards a faster green food channel can increase the stability at relatively low competition intensity between channels. Conversely, asymmetry towards a faster brown food channel can stabilize the ecosystem when the intensity of competition for mineral nutrients between primary producers and decomposers is high. The reanalysis of already published data indicates that both 1) asymmetry degree and 2) competition intensity might differ among ecosystem types. These results suggest stability differences between aquatic and terrestrial ecosystems which might arise from the differences in above two determining factors. Our study helps to further disentangle the fundamental differences between the functioning of aquatic and terrestrial ecosystems and to predict potential changes in ecosystem stability under global change.

## Introduction

Ecologists have long recognized the prevalence of multiple channels of energy in ecosystem food webs, originating from different groups of basal trophic levels (Moore & William Hunt 1988; Polis & Strong 1996; McCann *et al.* 2005; Gauzens *et al.* 2015). For example, pelagic and benthic pathways represent the most general energy channels in aquatic ecosystems (Jäger & Diehl 2014), most terrestrial ecosystems have explicit above-ground and below-ground energy pathways (Wardle *et al.* 2004), and the existence of bacterial and fungal pathways is a common feature in detritivore soil food webs (Moore *et al.* 2004). These energy channels are frequently coupled by multi-channel feeding of consumers at higher trophic levels (Polis & Strong 1996; McCann *et al.* 2005; Vadeboncoeur *et al.* 2005; Rooney *et al.* 2008), which has stabilizing consequences on food web dynamics (McCann & Hastings 1997; Rooney *et al.* 2006). There has been a recent surge of interest to compare the speed (or the strength) of energy/nutrient transfer between channels (i.e. fast-slow pathways or strong-weak pathways) (Rooney *et al.* 2006; McCann & Rooney 2009; Rooney & McCann 2012). For example, pelagic pathways and bacterial pathways are considered to grow and turn over faster than benthic pathways and fungal pathways respectively (Rooney & McCann 2012). Remarkable progresses have been made towards understanding how this asymmetry between coupled fast and slow channels affects ecosystem stability (Rooney *et al.* 2006; Wolkovich *et al.* 2014). It has been suggested that coupled fast and slow channels convey stability to ecosystems (Rooney *et al.* 2006; McCann & Rooney 2009). The fast channel allows rapid recoveries of the predators from large perturbations while the slow channel mitigates the impact of the fast channel that could amplify the effect of large perturbations.

While existing studies have highlighted the importance of asymmetry and predator coupling between energy channels, they generally ignored nutrient cycling and the particular interactions between primary producers and decomposers when both green (i.e. based on primary

production) and brown (i.e. based on decomposition) food channels are considered. Recent models showed that interactions between the green and the brown channels have important consequences on ecosystem functioning and stability (Attayde & Ripa 2008; Wollrab *et al.* 2012; Wolkovich *et al.* 2014; Ward *et al.* 2015; Zou *et al.* 2016). Nutrient cycling is a fundamental interaction between green and brown channels (DeAngelis *et al.* 1989a), which determine cascading effects between green and brown food channels in ecosystems (Zou *et al.* 2016). Due to nutrient cycling, interactions between the green and the brown channels at the bottom of ecosystems are much more complex than those between only green or only brown channels. Autotrophs in the green food channel benefit from inorganic nutrients supplied by decomposers in the brown food channel and provide in return carbon resources to decomposers, whereas decomposers can also compete with autotrophs for mineral nutrient uptake (Daufresne & Loreau 2001; Daufresne *et al.* 2008). Producers in both channels are thus linked by both indirect mutualistic and competitive interactions as a consequence of stoichiometric mismatches among themselves and their resources (Harte & Kinzig 1993; Daufresne & Loreau 2001; Zou *et al.* 2016). Larger difference in carbon to nutrient ratio between producers and their resources can lead to a higher demand for nutrients, resulting in stronger competition between green and brown channels and vice versa. These particular interactions between primary producers and decomposers are likely to affect ecosystem stability and the effects of turnover asymmetry. Indeed, Wolkovich *et al.* (2014) revealed that the effect of turnover asymmetry between green and brown food channels when coupled by recycling and first-consumer level were not necessarily stabilizing, contrary to the stabilizing effect found for top-consumer coupling (Rooney *et al.* 2006). We thus argue that it is fundamental to consider nutrient cycling and complex interactions between green and brown food channels to understand the consequences of asymmetry between energy channels in ecosystems.

The asymmetry between coupled green and brown channels and its consequences on ecosystem stability might also depend on the type of ecosystem considered. There is accumulating evidence that differences in ecological attributes between ecosystems likely have profound influences on ecosystem functioning (Shurin *et al.* 2002; Borer *et al.* 2005; Rip & Mccann 2011; Sardans *et al.* 2012b). Meanwhile, it has been shown that population growth and biomass turnover in green and brown food webs differ among different ecosystem types (Cebrian 1999, 2004; Cebrian & Lartigue 2004; Ward *et al.* 2015). Aquatic autotrophs and decomposers are reported to exhibit faster turnover rates than their terrestrial counterparts (Cebrian 1999). Furthermore, several comparative studies have noticed differences between ecosystems in resource quality for decomposers (Chase 2000; Grimm *et al.* 2003; Shurin *et al.* 2006; Manzoni *et al.* 2010). According to ecological stoichiometry, the mismatch in elemental quality (i.e. C:Nutrient ratio) between decomposers and their resources can lead to difference in decomposers nutrient uptakes, further influencing nutrient mineralization and immobilization processes. Because this mismatch likely differs between ecosystems, this may lead to differences between ecosystems in the decomposer-primary producer interactions, e.g. in the strength of competition between the two (Daufresne & Loreau 2001). All these studies suggest differences between aquatic and terrestrial ecosystems regarding the degree of turnover asymmetry between green and brown food channels and the interactions between primary producers and decomposers. These differences and their consequences for ecosystem stability remain however unclear because they have not been explicitly studied yet. Therefore, we suggest that studying interactions between structural asymmetry, nutrient cycling and complex interactions at the bottom of ecosystems is essential to improve our understanding and predictions of how coupled green and brown food channels affect stability in aquatic and terrestrial ecosystems.

To address this broad issue, we combine modelling and data analyses to investigate the following questions: 1) What are the consequences of considering nutrient cycling and complex interactions between green and brown food channels in studying the effects of asymmetry between channels on ecosystem stability? 2) Do asymmetry degree and interactions (e.g. intensity of competition) between green and brown food channels likely differ between aquatic and terrestrial ecosystems? 3) In the affirmative, what would be the consequences of these differences on ecosystem stability between aquatic and terrestrial ecosystems?

## **Methods**

### *The model*

We study the flux of a limiting nutrient (in most ecosystems either nitrogen or phosphorus) in food-web models consisting of two distinct channels (Fig.1). We first consider two green channels (hereafter G-G model) to assess the consequences of nutrient cycling on effects of asymmetry on stability. Second, we consider one green channel and one brown channel (hereafter G-B model). In both cases, the two channels are linked at the top by a generalist predator and additionally linked by nutrient cycling between biotic and abiotic compartments. Each channel in both food-web models contains the nutrient ( $N_i$ ) and the detritus ( $D_i$ ) compartments. The modelled ecosystems are open: these compartments receive constant inputs of nutrients and detritus ( $I_{N_i}$  and  $I_{D_i}$  respectively) and lose nutrients and detritus at constant rates ( $l_{N_i}$  and  $l_{D_i}$  respectively). There are constant exchanges between the two channels via their mineral nutrient (between  $N_1$  and  $N_2$ ) and detritus (between  $D_1$  and  $D_2$ ) compartments (with constant exchange rates  $p$  and  $q$ ). Apart from the top predator and abiotic compartments, each channel includes a basal trophic level (i.e. primary producers such as plants in the green channel and decomposers such as bacteria in the brown channel) and a consumer trophic level (i.e. primary consumers for both green and brown channels).

The rates of change in nutrient content of all compartments are described by differential equations. For intermediate trophic levels except decomposers (the producers e.g.  $P_i$ , and the consumers e.g.  $H_i$ ), the equation is:

$$\frac{dY_i}{dt} = Y_i(e_{X_iY_i}A_{X_iY_i}X_i - d_{Y_i} - A_{Y_iZ_i}Z_i) \quad (1)$$

where  $X_i$  is the resource/prey of  $Y_i$  and  $Z_i$  is the predator of  $Y_i$ . The term  $d_{Y_i}$  is the natural loss rate of  $Y_i$ . The term  $e_{X_iY_i}A_{X_iY_i}X_i$  describes the growth of  $Y_i$  induced by consuming  $X_i$  and  $A_{Y_iZ_i}Z_i$  describes the decrease in  $Y_i$  due to consumption by  $Z_i$  ( $e_{X_iY_i}$  is the conversion efficiency. Efficiency terms are not included for the nutrient uptake by primary producers and by decomposers because corresponding efficiencies are likely to be close to one.). The equation for decomposers is described below since we include stoichiometric constraints for their nutrient uptake. The top generalist predator ( $T$ ) feeds on prey from both channels, thus its equation is:

$$\frac{dT}{dt} = T(e_{X_iT}A_{X_iT}X_i + e_{X_jT}A_{X_jT}X_j - d_T) \quad (2)$$

In above equations,  $A_{XY}$  represents a type II functional response of  $Y$  feeding on  $X$ . For all compartments except the top predator:  $A_{XY} = \frac{a_{XY}XY}{X+K_Y}$ ; while for the generalist top predator:  $A_{X_iT} = \frac{\delta a_{X_iT}X_iT}{\delta X_i + (1-\delta)X_j + K_T}$ ,  $A_{X_jT} = \frac{(1-\delta)a_{X_jT}X_jT}{\delta X_i + (1-\delta)X_j + K_T}$  where  $\delta = \frac{\pi X_1}{\pi X_1 + (1-\pi)X_2}$ .  $a_{XY}$  is the growth rate/attack rate of  $Y$  feeding on  $X$  and  $K_Y$  is the half saturation of the consumer  $Y$ .  $\pi$  is the predator preference for consumer  $X_i$ .

To include nutrient cycling, we assume that a fraction ( $n_{Y_i}$ ) of nutrients that are lost by living compartments ( $P$ ,  $H$ ,  $C$ ,  $B$  and  $F$ ) is recycled back to the ecosystem. There are two origins for these losses: one corresponds to natural loss such as excretion and death of individuals (occurs at rate  $d_{Y_i}$ ); the other is the fraction of nutrients that is not assimilated by consumers ( $1 - e_{X_iY_i}$ ). We assume that only a fraction ( $s_{Y_i}$ ) of the recycled nutrients goes to the mineral

nutrient compartments ( $N_i$ ) that can be directly used by primary producers (hereafter called direct nutrient cycling):  $\sum n_{Y_i} s_{Y_i} Y_i (d_{Y_i} + (1 - e_{X_i Y_i}) A_{X_i Y_i} X_i)$ . Meanwhile the other fraction  $1 - s_{Y_i}$  goes to the detritus compartment ( $D_i$ ) that needs to be mineralized before being available to primary producers (hereafter indirect nutrient cycling):  $\sum n_{Y_i} (1 - s_{Y_i}) Y_i (d_{Y_i} + (1 - e_{X_i Y_i}) A_{X_i Y_i} X_i)$ . In G-G model, the mineralization process is modelled by a direct flow ( $m_{D_i} D_i$ ) from  $D_i$  to  $N_i$ .

In G-B model, mineralization requires decomposers ( $B$ ) that consume both mineral nutrients and detritus and release mineral nutrients. Primary producers are generally considered unable to excrete mineral nutrients directly, thus we set  $s_{P_i} = 0$ . We assume that the carbon-to-nutrient stoichiometry of detritus and decomposers determines the detritus and nutrient uptake by decomposers, which further influences the relationship between primary producers and decomposers (Zou *et al.* 2016). Thus we modelled the decomposers by:

$$\frac{dB}{dt} = B(e_{BD} A_{BD} D \frac{q_B}{q_D} - d_B - A_{FB} F) \quad (3)$$

where  $q_B$  and  $q_D$  are the nutrient-to-carbon ratios of decomposers and detritus, respectively (note that typically  $q_B > q_D$ ). Detritus consumption by decomposers (from  $D$  compartment) is  $e_{BD} A_{BD} DB$ , their nutrient uptake (from  $N$  compartment) is therefore  $e_{BD} A_{BD} DB (\frac{q_B}{q_D} - 1)$ . A higher  $\frac{q_B}{q_D}$  ratio corresponds to a larger difference in elemental quality between detritus and decomposers, thus decomposers have to uptake more nutrients to balance this mismatch, which induces stronger competition between primary producers and decomposers.

Following Rooney *et al.* (2006), we modify the growth rate/attack rates of producers/decomposers, consumers and predators (attack rate for one channel) in one channel to reflect the asymmetry of nutrients flow between channels. The second green channel in G-G model and the brown channel in G-B model are assumed to have constant attack rates, while

the growth rate/attack rates in the other channel in both models are multiplied by  $\alpha$ . Thus the modified channels are forced to be slower or faster than the constant channels.

We derive most of our parameters (Table 1) from the parameter set of Rooney et al. (2006). To investigate the effects of the interactions between asymmetry ( $\alpha$ ) and nutrient cycling ( $n_{Y_i}$ ) on ecosystem stability in model G-G, we run the model for 1661 ( $151 \alpha$  values ranging from 0.5 to  $2.0 \times 10^{-11}$   $n_{Y_i}$  values ranging from 0 to 0.5) combinations of these two parameters. To investigate the impact of the interactions between asymmetry ( $\alpha$ ) and competition ( $\frac{q_B}{q_D}$ ) on ecosystem stability in model G-B, we run the model for 1510 ( $151 \alpha$  values ranging from 0.5 to  $2.0 \times 10^{-11}$   $\frac{q_B}{q_D}$  values ranging from 1 to 2.8) combinations of these two parameters. We also test the effects of nutrient cycling and the fraction of direct/indirect nutrient cycling in model G-B, results are displayed in Appendix 1. Each simulation is run 60000 time steps and most of them do not reach a stable equilibrium and lead to cyclic dynamics. We then use 1) bifurcation diagrams (i.e. the highest and the lowest nutrient content in cyclic dynamics in predator compartment), and 2) the temporal variability – the coefficient of variation ( $CV: 100 \times \text{standard deviation} / \text{mean}$ , i.e.,  $100\sigma/\pi$ ), for measuring ecosystem stability. Note that smaller  $CV$  values represent greater stability (Tilman 1999). We calculate the bifurcation diagram and the  $CV$  for the top generalist predator of the last 2000 time steps of all simulations. All simulations are performed in R, we use the function “lsoda” in package “deSolve” for numerical integration of the dynamics.

### *Data analysis*

Additionally, we examine data from real food webs to quantify how the asymmetry between green and brown channels and the relationship between producers and decomposers might differ between ecosystems and thus affect their stability.

We first calculate the asymmetry degree between the green and the brown food channels by using a published dataset (Cebrian 1999) that documents the primary producer turnover rate



(the green channel) and the decomposition rate (the brown channel) across a continuum of diverse aquatic (freshwater macrophyte meadows, brackish and marine marshes, marine and freshwater benthic microalgal beds and seagrass meadows) and terrestrial communities (grasslands, shrublands and forests). This study indicates that based on differences in plant nutritional quality, the rapidity of energy/nutrient transfer in both green and brown food channels differs among community types, however it did not compare the asymmetry degree between green and brown channels among different ecosystem types. We use the turnover rate of primary producers and the decomposition rate as proxies of the speed of the green and brown channels and compute the ratio of primary producer turnover rate ( $\text{day}^{-1}$ ) to decomposition rate ( $\text{day}^{-1}$ ) as the asymmetry degree in 60 systems. We test whether the log ratio of asymmetry degree differed between ecosystem types via a one-way ANOVA.

We next compare the nutrient concentration in primary producers among different ecosystems (one-way ANOVA) by using the same data set. This theoretically might provide an estimation of difference in detritus quality (Cebrian 2004) and further in primary producer-decomposer relationship across diverse ecosystems. All statistical analyses are performed in R.

## Results

### *Model results*

In model G-G, the widest limit cycles and highest  $CV_C$  values occur when the two channels are symmetrical (i.e.  $\alpha = 1$ ), thus the asymmetry between coupled green channels can stabilize the ecosystem (Fig.2a, 2c). Increasing nutrient cycling rates ( $n_i$ ) leads to little more unstable systems (i.e. wider cycle limits and higher  $CV_C$ ) and slightly expands the range of cyclic dynamics along the asymmetry gradients (Fig. 2c). However, nutrient cycling does not change the impact of asymmetry between the distinct green channels on ecosystem stability. In

presence of only green channels, nutrient cycling destabilizes the ecosystem without interacting with asymmetry.

In model G-B, the asymmetry between the coupled green and brown channels does not always stabilize the ecosystem and effects of nutrient cycling interact with asymmetry effects on ecosystem stability (Figure 2 and 3, Appendix Figure S1). When there is no competition between decomposers and primary producers (i.e. no stoichiometric difference between detritus and decomposers,  $\frac{q_B}{q_D} = 1$ ), asymmetry towards slower green channel (i.e.  $\alpha < 1$ ) is always destabilizing (Fig.2b, 2d). On the contrary, asymmetry towards faster green channel leads to stable dynamics when nutrient cycling is high, while such asymmetry prevents species coexistence when nutrient cycling is low. The pattern of stabilizing/destabilizing effects of asymmetry also strongly depends on nutrient competition between primary producers and decomposers, which is determined by the relative stoichiometric composition of detritus and decomposers ( $\frac{q_B}{q_D}$ ) (Figure 3, Appendix Figure S1). As competition between primary producers and decomposers increases (i.e. increasing stoichiometric mismatch  $\frac{q_B}{q_D}$ ), the critical value of  $\alpha$  for which stability is lowest increases from values lower than 1 (i.e. asymmetry towards slower green channel is destabilizing) to values higher than 1 (i.e. asymmetry towards faster green channel is destabilizing). At intermediate stoichiometric mismatches (i.e.  $\frac{q_B}{q_D}$  around 2), decomposers take up the same amount of nutrient from the mineral nutrient compartment and from the detritus compartment and symmetry is destabilizing as found in model G-G. When the stoichiometric mismatch is relatively large (i.e.  $\frac{q_B}{q_D} > 2$ ), competition between decomposers and primary producers is strong and the most unstable cases occur when the green channel is faster than the brown channel ( $\alpha > 1$ ), which is the opposite pattern from the one found in systems with weak competition. In addition, increasing the stoichiometric mismatches between

detritus and decomposers produces more cyclic dynamics and enlarges the range of unstable dynamics.

### *Data analysis*

#### 1) Asymmetry between green and brown food channels among different ecosystem types

Overall, we find that the asymmetry degree between green and brown food channels is significantly different between aquatic and terrestrial ecosystems ( $F_{1,58}=7.144$ ,  $p<0.01$ , Fig. 4) and among different ecosystem types ( $F_{5,54}=5.9063$ ,  $p<0.001$ ). In 23 ecosystems, the green food channel is faster than the brown food channel (i.e. asymmetry degree  $\alpha > 1$ ) while other 37 ecosystems have faster brown food channels (i.e. asymmetry degree  $\alpha < 1$ ). In particular, in terrestrial ecosystems, the asymmetry degree of shrublands and forests is significantly different from that of grasslands (post-hoc tests,  $p<0.05$ ). Most of shrublands and forests (19 out of 26) have faster brown food channels while the number of ecosystems with either faster green or faster brown channels in grasslands is close (10 to 12). In aquatic ecosystems, due to fewer observations, there is no significant statistical difference in asymmetry degree among community types (post-hoc tests, all  $p>0.05$ ). We observe (Fig.4) that all freshwater macrophyte meadows have faster green food channels while all seagrass meadows have faster brown food channels. Brackish and marine marshes have similar numbers of systems with faster green or faster brown food channels. With only one observation, the marine and freshwater benthic microalgae beds are strongly asymmetrical with much faster green food channels than the brown food channels.

#### 2) Nutrient concentration in primary producers among different ecosystems types

Both nitrogen and phosphorus concentration are significantly higher in aquatic primary producers than terrestrial producers ( $F_{1,63}=91.622$ ,  $p<0.001$  for nitrogen and  $F_{1,63}=6.0869$ ,  $p<0.001$  for phosphorus respectively, Fig. 5).

## Discussion

In this study, we show that stabilizing effects of asymmetry between green and brown energy channel depend on the mutualistic/competitive relationship between autotrophs and decomposers. Our data analysis suggests that ecosystems may differ in the asymmetry degree between the green and brown food webs as well as in competition intensity between primary producers and decomposers. We thus predict that stability might differ among ecosystem types (e.g. aquatic and terrestrial ecosystems) due to differences in the degree of asymmetry between the green and the brown channels and in the relationship between producers of the two channels.

### *Does asymmetry always stabilize ecosystems?*

Our results show that asymmetry is not always stabilizing in ecosystems and that asymmetry consequences strongly depend on the nature of interactions at the bottom of food webs and on whether we consider the coupling between two green or one green–one brown webs. The results derived from the G-G model demonstrate that the asymmetry in growth/attack rates between coupled green channels stabilizes the ecosystem. This is consistent with earlier modelling results showing that contrasted speeds of energy channels are essential to ecosystem stability (Rooney *et al.* 2006). However, results of the G-B model show that asymmetry does not necessarily increase stability and can instead be strongly destabilizing depending on stoichiometry-based interactions between primary producers and decomposers. These predictions contradict those of Rooney *et al.*'s (2006) model which did not integrate the coupling of green and brown food channels. However, a recent modelling study that considered the coupling of autotrophs and detritus by first-consumer level has also noted that asymmetry might have destabilizing effects on certain conditions (Wolkovich *et al.* 2014).

Previous studies on the stability consequences of asymmetry have focused on top-down effects from the generalist predator that couples two asymmetrical channels: the fast channel

allows rapid recoveries of the predator from large perturbations while the slow channel dampens the strong responses of the fast channel (Rooney *et al.* 2006). Our results highlight that the bottom-up effects due to the complex relationship between autotrophs and decomposers is also influential for the effects of asymmetry on stability. In particular, effects of asymmetry on stability are strongly driven by the strength of competition between the producers of the two channels. When there is no competition between autotrophs and decomposers, asymmetry towards a slower green food channel is highly destabilizing whereas when competition is strong, asymmetry towards a faster green food channel tends to destabilize the ecosystem. The competition between autotrophs and decomposers is based on the consumer-driven nutrient recycling theory (CNR), that homeostatic organisms maintain their elemental composition by taking up mineral nutrients when their resource C:nutrient ratio is higher than their own C:nutrient ratio (Daufresne & Loreau 2001). The CNR theory has been recognized as key to understand ecosystem processes such as mineralization as well as interactions between green and brown food webs in both aquatic and terrestrial ecosystems (Chase 2000; Sardans *et al.* 2012; Daufresne & Loreau 2001; Cherif & Loreau 2007, 2013; Zou *et al.* 2016). Our results thus suggest that the stoichiometric compositions of detritus and decomposers are also key to understand the effects of asymmetry between energy channels on ecosystem stability. While we did not model different scenarios of competition between the coupled green channels, competition might also vary between primary producers as different autotrophs might be limited by different nutrients. Consequently, we might expect that asymmetry could also destabilize the dynamics of coupled green channels when producers weakly compete.

Nutrient cycling, a major component of the interaction between green and brown food channels, also affect ecosystem stability, in interaction with the effects of asymmetry between these food channels. While increased nutrient cycling tends to attenuate the destabilizing effects of asymmetry when competition between decomposers and primary producers is weak, it has a

destabilizing effect when competition is strong especially when the strength of the two food channels are symmetric. Increased nutrient cycling also amplifies the destabilizing effect of symmetry between coupled green channels.

### ***Differences in asymmetry degree and competition between basal trophic levels in aquatic and terrestrial ecosystems***

Our model results suggest that the degree of asymmetry between green and brown food channels, as well as its direction (i.e. faster green or faster brown food channel), are fundamental to our understanding of ecosystem stability. So far, asymmetry between green and brown food channels within ecosystems has been rarely investigated (Rooney *et al.* 2008), and the few existing studies have not compared how this asymmetry varies among ecosystem types. Meta-analyses have focused on the comparison of the turnover of either green or brown food channels between aquatic and terrestrial ecosystems (Cebrian 1999, 2004; Cebrian & Lartigue 2004). They found that aquatic herbivores turn over slightly faster (i.e. 1.3 times on average) than terrestrial herbivore while aquatic detritus consumers turn over much faster (i.e. over 10 times faster) than their terrestrial counterparts. By further analyzing the data compiled by these meta-analyses, we suggest that turnover rates of green and brown channels are often asymmetric within an ecosystem, and that this asymmetry depends on ecosystem type. In aquatic ecosystems, the green channel seems to turnover faster than the brown channel, while it tends to be the opposite in terrestrial ecosystems. Future studies will need to further compare asymmetry degree between aquatic and terrestrial ecosystems to assess the robustness of this result. In particular, freshwater pelagic ecosystems were lacking from the dataset we analyzed. Several mechanisms might explain the difference in asymmetry degree between aquatic and terrestrial ecosystems. First, due to the negative relationship between body size and biomass turnover rate (Peters 1986), terrestrial autotrophs that are relatively large (e.g. vascular plants),

tend to have relatively low turnover rates in comparison with aquatic autotrophs. The difference in body size ratios between herbivores and autotrophs and between decomposers and their consumers between aquatic and terrestrial ecosystems (Shurin *et al.* 2006) leads to difference in asymmetry degree, which may explain why terrestrial ecosystems tend to have a relatively faster brown channel. A second possibility is that terrestrial autotrophs may allocate more energy to defence against herbivory, resulting in slower growth and turnover than their aquatic counterparts (Strong 1992), which leads to relatively slower green food channels. Further studies exploring these mechanisms should help to test the robustness of our predictions on differences between ecosystem types.

Our model also reveals that consequences of food channel asymmetry on stability is likely to strongly depend on competition between primary producers and decomposers, which is linked to stoichiometric mismatch between detritus and decomposer. Thus, one important question is whether this stoichiometric mismatch also varies between ecosystems, as found for asymmetry between green and brown channels. A few studies have shown differences in producer and detritus nutrient concentrations between aquatic and terrestrial ecosystems. Our data analysis suggests significant higher nitrogen and phosphorus concentrations in aquatic primary producers than in terrestrial producers, in agreement with previous studies reporting C:N ratios at least three times higher for terrestrial autotrophs than lake seston (Elser *et al.* 2000; Sardans *et al.* 2012b). If fresh detritus tend to have the same elemental composition as primary producers (Cebrian & Lartigue 2004, but see Danger *et al.* 2012), it can be assumed that aquatic detritus have higher mineral nutrient concentrations than terrestrial detritus. Grimm *et al.* (2003) also suggested that nutrient-poor detritus likely occur more often in terrestrial than in aquatic ecosystems. We might thus hypothesize that due to higher nutrient concentration in detritus, the stoichiometric mismatches might be smaller in aquatic ecosystems, leading to weaker competition between primary producers and decomposers. However, competition for limiting

nutrients between primary producers and decomposers still exists in oligotrophic systems (Cotner & Biddanda 2002; Danger *et al.* 2007). Moreover, aquatic ecosystems usually receive inputs of terrestrial original detritus, which represents a second organic source for decomposers (Shurin *et al.* 2006; Danger *et al.* 2016). In terrestrial ecosystems, detritus nutrient quality differs also strongly due to their different origins: fine root, leaf litter and woody debris have distinct range of elemental composition (Freschet *et al.* 2013; Mooshammer *et al.* 2014).

There are very few available data allowing to compare the stoichiometric composition of decomposers between ecosystems, in particular aquatic and terrestrial ones (Danger *et al.* 2016), and only a few tentative hypotheses can be proposed. Fungi might represent a larger part of decomposers in terrestrial ecosystems than in aquatic systems, where decomposers are dominated by bacteria (del Giorgio & Cole 1998; Boer *et al.* 2005). However, fungal importance is not negligible in the littoral areas of lakes and in running waters, proved that sufficient oxygen is present (Guenet *et al.* 2010; Bärlocher & Boddy 2016). Fungi generally seem to have a more variable and sometimes higher C:Nutrient ratio, and consequently a smaller demand for nutrients, than bacteria (Hodge *et al.* 2000, Danger *et al.* 2016). These differences may lead to differences in nutrient uptake by decomposers and their relationship with primary producers between aquatic and terrestrial ecosystems. However, a more precise understanding of the processes determining the strength of stoichiometric mismatches between detritus and decomposers is needed to assess differences between intensities of competition between decomposers and primary producers among ecosystem types.

### ***Consequences on ecosystem stability***

Differences between ecosystem types on asymmetry between green and brown food channels and intensity of competition between primary producers and decomposers might lead to different stability constraints in aquatic and terrestrial ecosystems. Few studies compared the



difference in stability between aquatic and terrestrial ecosystems. Wolkovich *et al.*'s (2014) model demonstrated that the coupling of green and brown food channels is generally more stabilizing in terrestrial than in aquatic ecosystems due to narrower sets of stabilizing conditions found in aquatic ecosystems. Rip & Mccann (2011) have shown that aquatic ecosystems seem to be less stable than terrestrial ecosystems. Our model predicts that if aquatic ecosystems tend to have relatively weak competition between primary producers and decomposers due to smaller stoichiometry mismatches between decomposers and their resource, aquatic ecosystems might fit to the bottom area in Fig. 3b, where only asymmetry towards a faster green food channel stabilizes the ecosystem. If the competition between producers in green and the brown food channels in terrestrial ecosystem is indeed stronger, these ecosystems may fit more to the upper area of Fig. 3b, where increasing asymmetry degree towards a faster brown food channel increases stability. While differences in asymmetry and competition between primary producers and decomposers obviously need to be investigated further in aquatic and terrestrial ecosystems, these predictions provide relevant hypotheses to be further tested.

Our model can also give some insights on consequences of current global changes on ecosystem stability. Global change may indeed affect both asymmetry between green and brown food channels as well as competition between primary producers and decomposers. For example, enhanced CO<sub>2</sub> is responsible for higher C:N ratios in plant litters, resulting in slower decomposition thus potentially slower brown food channels (Zechmeister-Boltenstern *et al.* 2015). Anthropogenic N eutrophication promotes autotroph growth, leading to stronger competition for nutrients between primary producers and decomposers (Sardans *et al.* 2012a). Warming and drought can also influence the asymmetry degree and competition intensity between green and brown food channels (Sardans *et al.* 2012a). We conclude that global change may seriously threaten the stabilizing effect of asymmetry and competition between producers within complex food webs.

## ***Conclusion and perspectives***

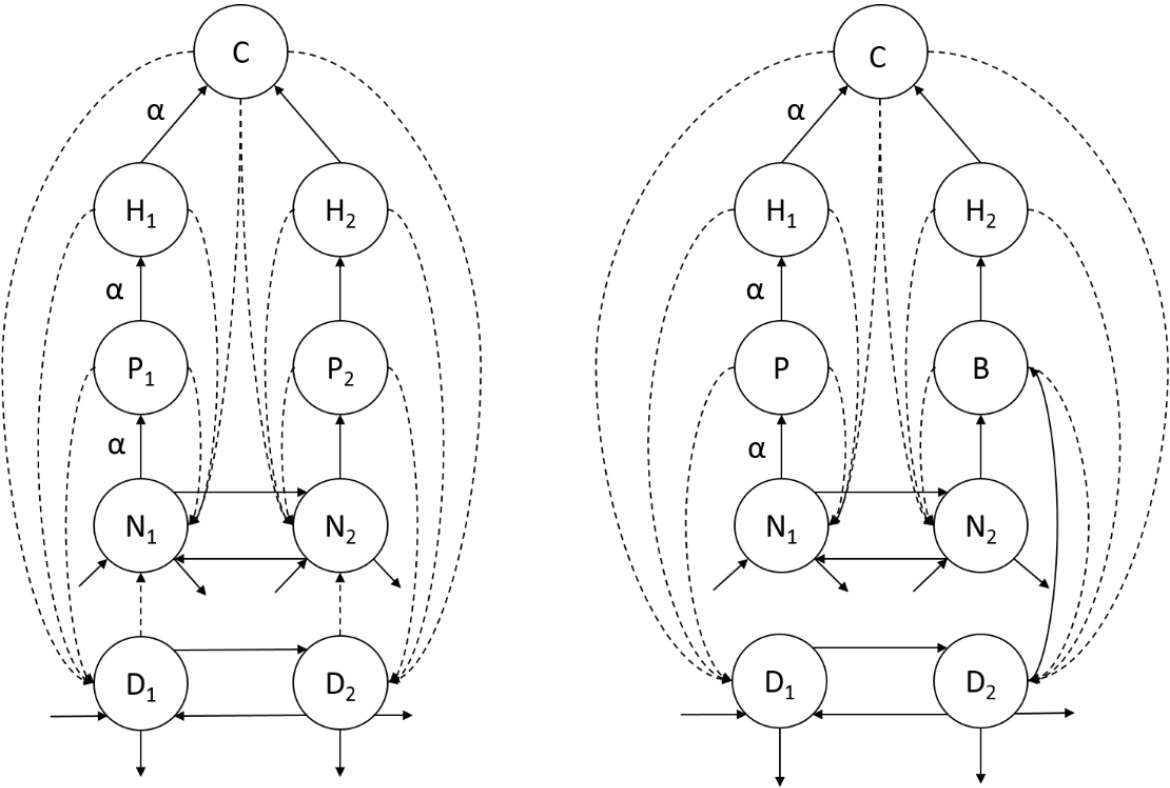
In this study, we show that turnover asymmetry between coupled food channels does not always stabilize ecosystems. Nutrient cycling and the competition for mineral nutrients between producers with distinct food channels can influence the effects of asymmetry. We have discussed the main differences in these two determining factors between different ecosystem types, which may lead to different stability constraints between aquatic and terrestrial ecosystems. There are many other essential differences between the two ecosystem types that have not been integrated in our model. Compared to terrestrial ecosystems, aquatic systems tend to have more generalist consumers (filter-feeding organisms which discriminate prey according to sizes) (Shurin *et al.* 2006), leading to more omnivory within the food web. The existence of mixotrophic organisms in aquatic ecosystems also increases the number of interactions between the green and the brown worlds (Mitra *et al.* 2014). New models should take into account these major differences that may also shape the asymmetry between food channels. Besides, we have modelled the interaction between primary producers and decomposers using basic stoichiometric hypotheses. Differences in detritus resource and quality (Wardle *et al.* 2004), differences in nutrient limitation of decomposers (Chase 2000) and differences in decomposers resource preference and use efficiency (Moore *et al.* 2004) should be analysed in more stoichiometrically-explicit models. We believe anyway that our study can serve as a conceptual framework to study fundamental differences between the functioning of aquatic and terrestrial ecosystems and to predict potential changes in ecosystem stability under global change.

## Tables

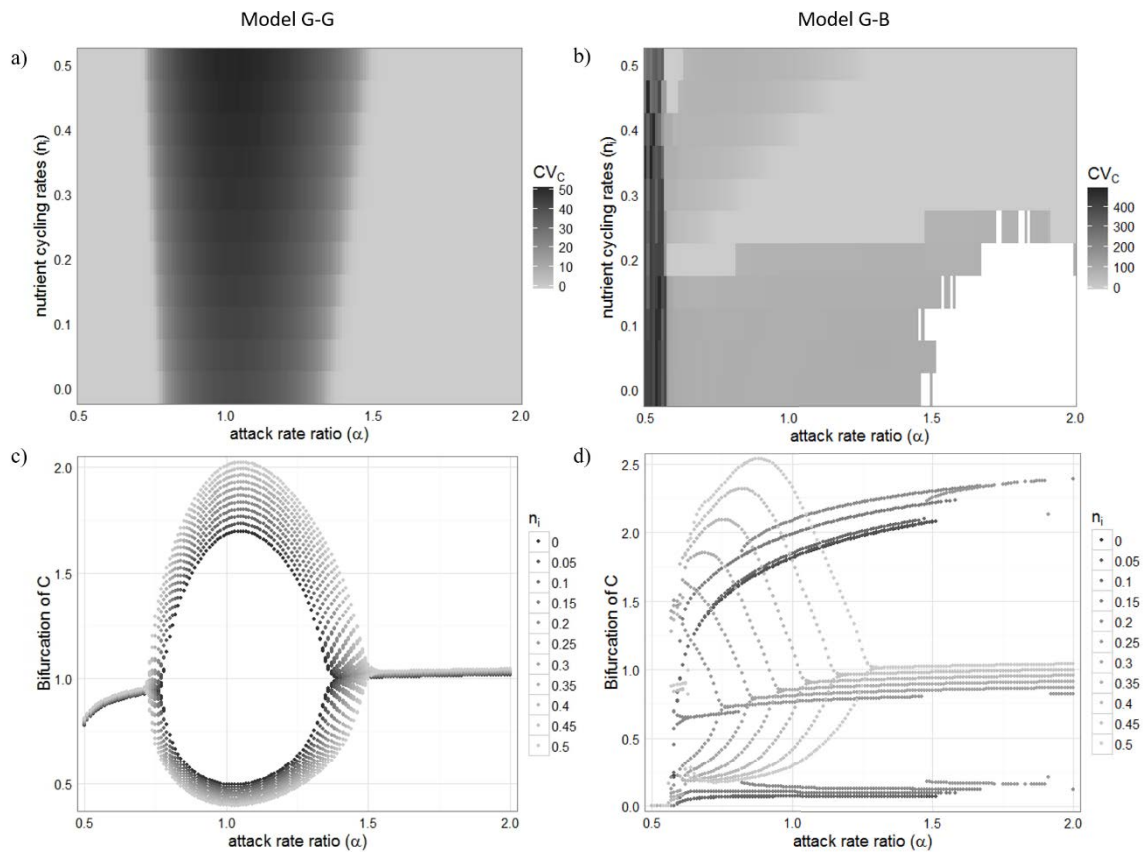
**Table 1.** Parameter definitions and proposed values in simulations

Parameter	Symbol	Value
Constant input of mineral nutrients	$I_{N_i}$	0.1
Constant input of organic materials	$I_{D_i}$	0.1
Loss rate from mineral nutrients	$l_{N_i}$	0.1
Loss rate from organic materials	$l_{N_i}$	0.1
Exchange rate from the modified channel to the constant channel	$p$	0.1
Exchange rate from the constant channel to the modified channel	$q$	0.1
Intrinsic growth rate of the producer in the modified channel	$a_{P_1N}, a_{PN}$	$1\alpha$
Intrinsic growth rate of the producer in the constant channel	$a_{P_2N}, a_{BN}$	[0-1]
Attack rate of the decomposer on the detritus	$a_{BD}$	1
Half saturation rate for the producer in the modified channel	$K_{P_1}, K_P$	1
Half saturation rate for the producer in the constant channel	$K_{P_2}, K_{BN}$	1
Half saturation rate for the decomposer on detritus	$K_{BD}$	1
Loss rate from the producer in the modified channel	$d_{P_1}, d_P$	0.4
Loss rate from the producer in the constant channel	$d_{P_2}, d_B$	0.4
Attack rate of the consumer on the producer in the modified channel	$a_{H_1P_1}, a_{HP}$	$2\alpha$
Attack rate of the consumer on the producer in the constant channel	$a_{H_2P_2}, a_{FB}$	2
Half saturation rate for the consumer in the modified channel	$K_{H_1}, K_H$	1
Half saturation rate for the consumer in the constant channel	$K_{H_2}, K_F$	1
Loss rate from the consumer in the modified channel	$d_{H_1}, d_H$	0.2
Loss rate from the consumer in the constant channel	$d_{H_2}, d_F$	0.2
Attack rate of the predator on the consumer in the modified channel	$a_{CH_1}, a_{CH}$	$1.8\alpha$
Attack rate of the predator on the consumer in the constant channel	$a_{CH_2}, a_{CF}$	1.8
Half saturation rate for the predator	$K_C$	1
Loss rate from the predator	$d_C$	0.05
Predator preference for consumer in the modified channel	$\pi$	0.5
Fast to Slow ratio	$\alpha$	[0.5-2]
Nutrients conversion efficiency	$e_{ij}$	0.8
Proportion of nutrient cycling	$n_i$	[0-0.5]
Proportion of direct nutrient cycling	$s_i$	0.5

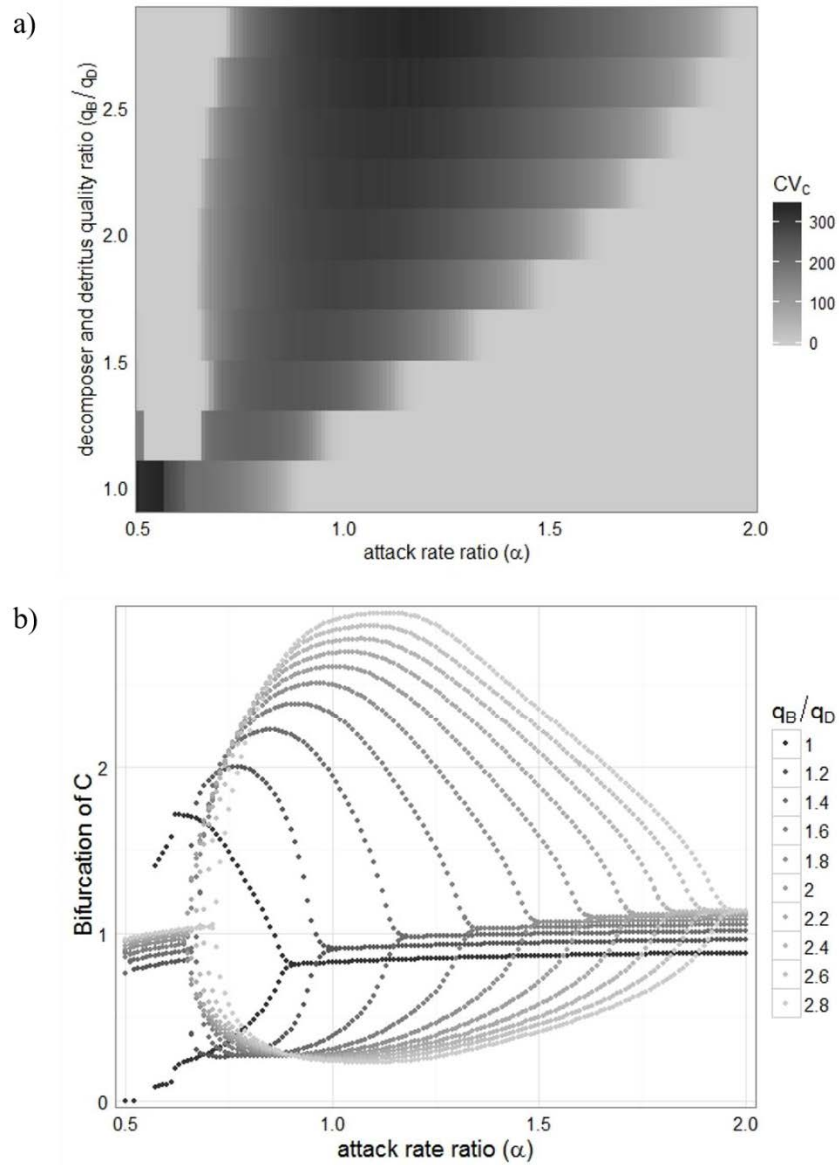
**Figures**



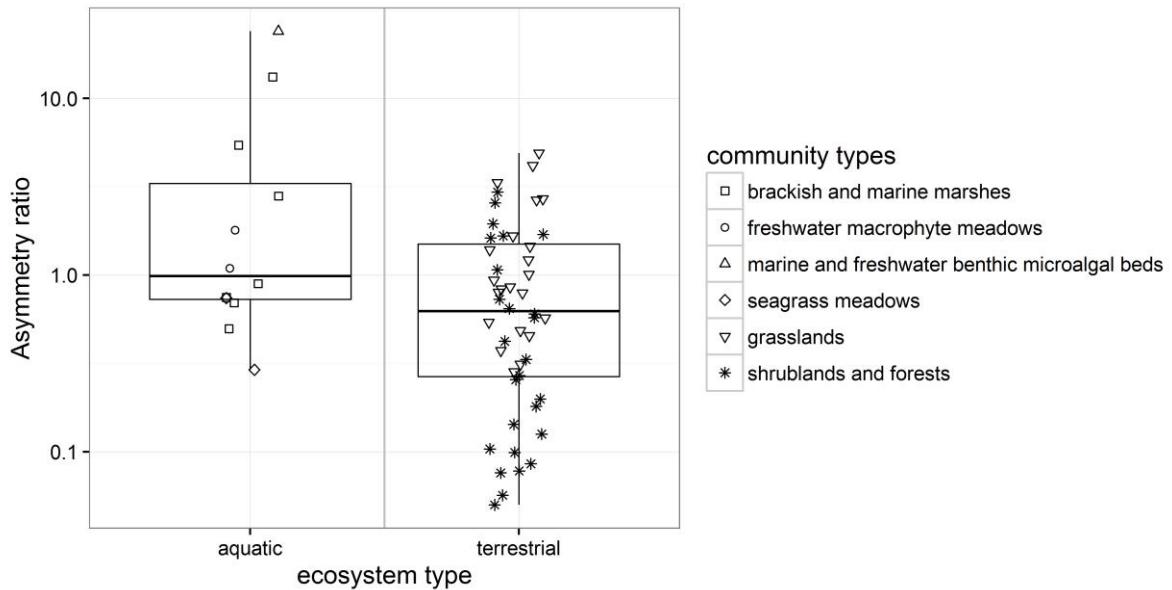
**Figure. 1** Schematic diagram of the food-web model. Left: the G-G model, right: the G-B model. Circles represent compartments of mineral nutrients ( $N_i$ ), detritus ( $D_i$ ), primary producers ( $P$ ), decomposers ( $B$ ), primary consumers ( $H_i$ ), and carnivores ( $C$ ). Solid arrows indicate fluxes of nutrients between compartments, corresponding to consumption or horizontal exchanges. Dashed arrows represent nutrient cycling. Parameters are explained in Table 1.



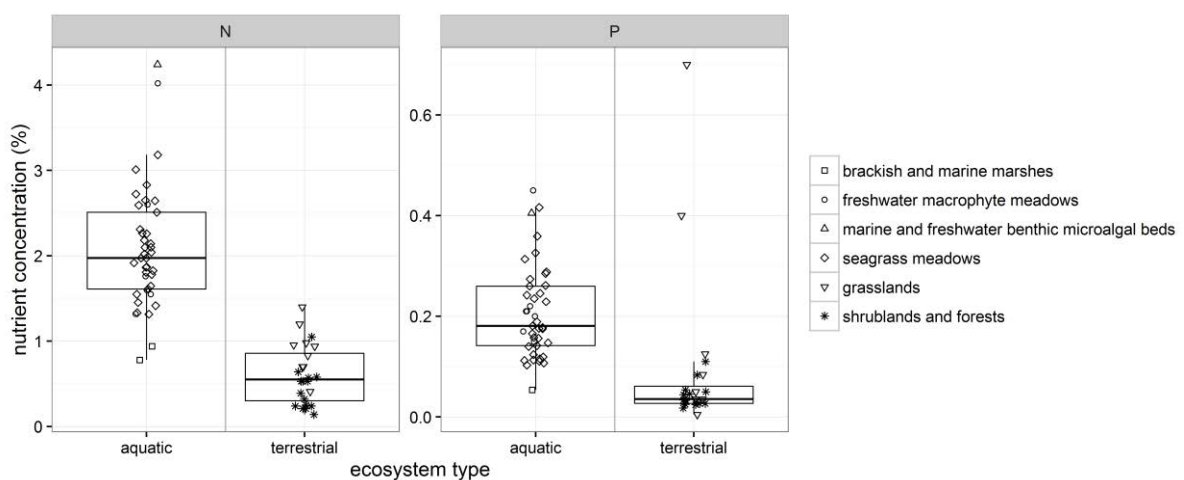
**Figure. 2** Effect of asymmetry in the growth/attack rates between coupled food channels on ecosystem stability for different values of nutrient cycling rates in model G-G (a and c) and model G-B when there is no competition between decomposers and primary producers (i.e.  $q_B/q_D = 1$ ). Other parameters are presented in Table 1. *Top* (a–b): the bifurcation of the top generalist predator (C) at different combinations of parameters (i.e.  $\alpha \times n_i$ ). *Bottom* (c–d): the coefficient of variation ( $CV$ ) of the top predator population at different combinations of parameters (i.e.  $\alpha \times n_i$ ). Symmetry occurs at  $\alpha=1$ , asymmetry towards lower and higher values corresponds to systems with faster brown channels and faster green channels respectively.



**Figure 3.** Effect of asymmetry in the growth/attack rates between coupled food channels on ecosystem stability for different values of the stoichiometric mismatch between detritus and decomposers (i.e.  $q_B/q_D$ ). Other parameters are presented in Table 1. a) The bifurcation of the top generalist predator (C) at different combinations of parameters (i.e.  $\alpha \times q_B/q_D$ ). b) The coefficient of variation ( $CV$ ) of the top predator population at different combinations of parameters (i.e.  $\alpha \times q_B/q_D$ ). Symmetry occurs at  $\alpha=1$ , asymmetry towards lower and higher values corresponds to systems with faster brown channels and faster green channels respectively.

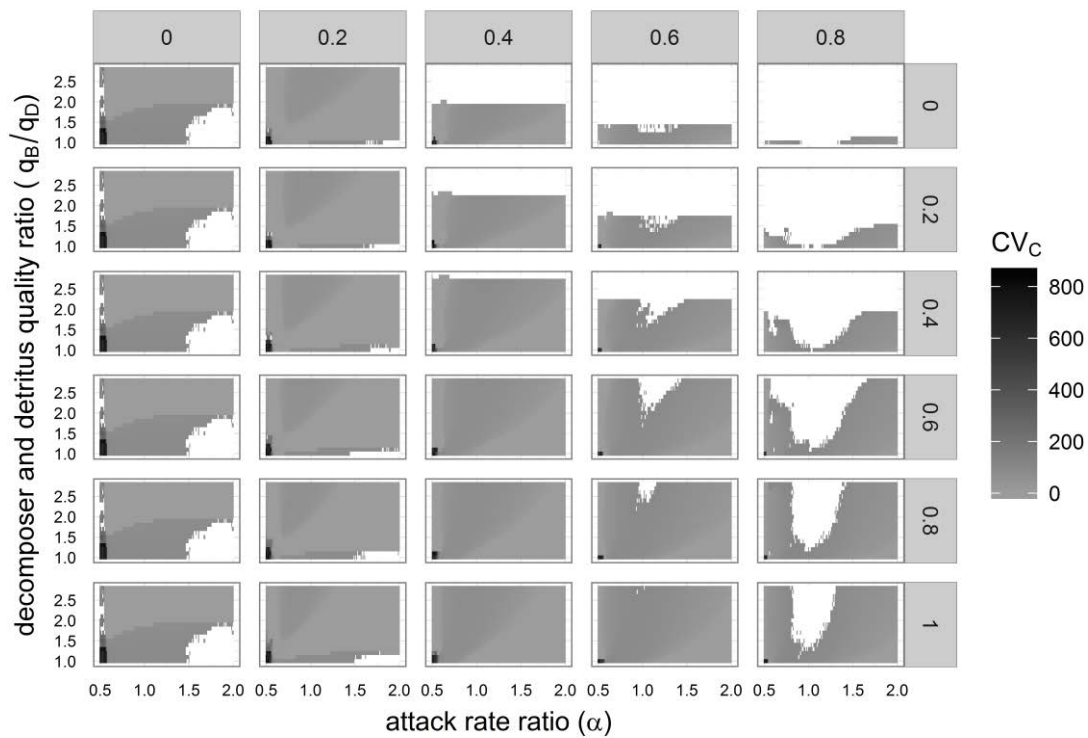


**Figure 4.** Box-plot of the log-transformed difference of the asymmetry degree between aquatic and terrestrial ecosystems. Data taken from a meta-analysis by Cebrian (1999). We used the turnover rate of primary producers and the decomposition rate as proxies of the speed of the green and brown channels and computed the ratio of primary producer turnover rate ( $\text{day}^{-1}$ ) to decomposition rate ( $\text{day}^{-1}$ ) as the asymmetry degree in 60 systems. The system is symmetrical when the asymmetry ratio equals to 1. Asymmetry ratios higher/lower than 1 represent ecosystems with a faster green or a faster brown food channel respectively.



**Figure 5.** Box-plot of the nutrient concentration in primary producers (left: nitrogen, right: phosphorus) in aquatic and terrestrial ecosystems. Data taken from a meta-analysis by Cebrian (1999).

## Appendix



**Figure S1.** Effect of asymmetry in the growth/attack rates (i.e.  $\alpha$  in x-axis) between coupled food channels on ecosystem stability for different values of the stoichiometric mismatch between detritus and decomposers (i.e.  $q_B/q_D$  in y axis), different levels of nutrient cycling (i.e.  $n_i$ , each column represents results of one value of  $n_i$ ) and different proportions of direct nutrient cycling (i.e.  $s_i$ , each line represents results of one value of  $n_i$ ). Other parameters are presented in Table 1. Symmetry occurs at  $\alpha=1$ , asymmetry towards lower and higher values corresponds to systems with faster brown channels and faster green channels respectively.





## **Chapter 4**

# **Linking the green and brown food webs through spatial coupling and consequences on ecosystem functioning**



# **Linking the green and brown food webs through spatial coupling and consequences on ecosystem functioning**

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## **Abstract**

Almost all natural communities experience strong coupling among spatially separated habitats. The green (based on primary production) and brown (based on decomposition) food webs can be spatially separated and the interactions between these two food webs can be affected by space. We use a modelling approach to combine two types of spatial couplings between the green and the brown food webs: 1) generalist consumers (herbivores or carnivores) couple the green and the brown patch at the top, and 2) reciprocal nutrient and detritus fluxes couple the two patches at the bottom of the food chains. Our analysis suggests that both 1) the asymmetric consumption of prey from the green and the brown patches by the generalist consumers and 2) the asymmetric flows of nutrients and detritus between the two patches affect ecosystem functioning and the dominance of either the green or the brown producers (i.e. autotrophs and decomposers). We propose that our food web model can be representative of many aquatic ecosystems where processes based on primary production and decomposition are at least partly spatially decoupled (benthic and pelagic compartments of the ecosystem). We therefore suggest that the relative importance of the green and the brown pathways (i.e. the green- or brown- dominance) may be very different among ecosystems depending on the type of spatial coupling between green and brown pathways.

## Introduction

Almost all natural communities experience strong coupling among spatially separated habitats (Polis *et al.* 1997; Holt 2002; Massol *et al.* 2011). On the one hand, mobile consumers link resources and their habitats at the top of food webs (Post *et al.* 2000; McCann *et al.* 2005). For example, benthic and pelagic energy flows can be coupled by the cross-habitat foraging by fishes (Vander Zanden & Vadeboncoeur 2002). On the other hand, the inorganic components of ecosystems – mineral nutrients and detritus – cross frequently spatial boundaries and couple heterogeneous habitats at the bottom of the food webs (Gravel *et al.* 2010a; Gounand *et al.* 2014). For example, processes such as sedimentation of organic matters and upwelling of nutrients represent important nutrient exchanges between the pelagic and benthic ecosystems (Müller *et al.* 2005).

A large body of theoretical research has integrated space into models by highlighting different aspects of the spatial coupling (Loreau *et al.* 2003a; Leibold *et al.* 2004; McCann *et al.* 2005; Rooney *et al.* 2006, 2008; Gravel *et al.* 2010b; Haegeman & Loreau 2014). Some studies focus on modeling the dispersion of species at different trophic levels from one patch to another (i.e. the meta-community theory) (Leibold *et al.* 2004) and the relative mobility of the organisms (McCann *et al.* 2005). In particular, it has been shown that the strong coupling by top generalist consumers has important effects on ecosystem stability (Rooney *et al.* 2006, 2008). The top-down controls on the local population dynamics either promote or depress the local prey densities, which regulates regional diversity and productivity of the whole ecosystem (Holt *et al.* 1994; Polis *et al.* 1997; McCann *et al.* 2005). The regional regulation of coupled strong-weak pathways is likely to further affect ecosystem stability (McCann *et al.* 1998; Rooney *et al.* 2008). Other studies have integrated the perspectives of landscape ecology in addition to the concept of meta-community and demonstrated that nutrient and detritus fluxes among habitats can affect the ecosystem functioning in a bottom-up way (i.e. the meta-

ecosystem concept) (Loreau *et al.* 2003b; Gravel *et al.* 2010a, b). There are clear evidences that these flows are important allochthonous subsidies to fuel local productivity in recipient habitat (Gravel *et al.* 2010a, b). This promotes regional coexistence because species that experience local extinction due to deficient resource survive with nutrient and/or detritus supply (Roos *et al.* 1991; Gounand *et al.* 2014). The nutrients and detritus fluxes also dampen local oscillations of basal resources and therefore stabilize the dynamics of spatially coupled ecosystems (Rip & Mccann 2011).

A particularly interesting feature of different types of spatial coupling is the asymmetry in the coupling. For example, the preference of generalist consumers represents the asymmetry in consumptions of prey from different habitat (McCann *et al.* 2005). This asymmetry is found to affect the ecosystem stability. The spatial nutrient flows can also be asymmetric. For example, across terrestrial-aquatic boundaries, aquatic ecosystems receive in general larger amounts of nutrient and detritus from terrestrial ecosystems than do terrestrial ecosystems from aquatic ecosystems (Jansson *et al.* 2007; Soininen *et al.* 2015). In the case of islands, the terrestrial ecosystem depend largely on the detritus brought by seabirds (Sánchez-Piñero & Polis 2000). In theoretical studies, the asymmetry of nutrient and detritus fluxes are found to impact the source-sink dynamics (i.e. alter a source habitat to a sink and verse visa) and ecosystem stability (Gounand *et al.* 2014). Overall, spatial coupling occurs from the bottom to the top of the food webs, we thus assume that the asymmetry in both top and bottom couplings can interact to influence ecosystem functioning. Although abundant studies have revealed that spatial coupling have important consequences for community dynamics and ecosystem stability, the effects of interactions between different types of spatial coupling and their asymmetry remain largely unknown, particularly on the functioning of ecosystems.

Moreover, couplings between the green (i.e. based on primary production) and the brown (i.e. based on decomposers) food chains have only recently been recognized (Attayde & Ripa

2008; Wolkovich et al. 2014; Zou et al. 2016). These couplings can also be spatialized in nature. For example, pelagic (based mainly on phytoplanktonic production) and benthic (based mainly on detritus) habitats are spatially decoupled but there are many cross-habitat interactions between them (Jäger & Diehl 2014). Due to the complex interactions between primary producers and decomposers (Daufresne & Loreau 2001; Wolkovich et al. 2014; Zou et al. 2016), the spatial couplings between the green and brown food webs can bring new insights of the consequences of spatial coupling for community dynamics and ecosystem stability. Apart from the apparent competition due to generalist consumers and the competition for nutrient uptake, primary producers in the green food chain provide detritus supporting the growth of decomposers in the brown food chain, and decomposers in turn mineralize nutrients, which is essential to the growth of primary producers. These processes lead to indirect mutualistic relations. These indirect mutualistic and competitive interactions between primary producers and decomposers are regulated by their competitive abilities and the quality of their resources (Daufresne & Loreau 2001; Zou et al. 2016). Therefore, asymmetric fluxes of nutrients and detritus should have important consequences on the complex interactions at the bottom of the coupled ecosystems, which further interacts with top-down effects to affect the functioning of the whole ecosystem. However, to our knowledge, the issues linked to these interactions between the green and the brown food webs and the spatial coupling of ecosystems have so far never been addressed.

Therefore we develop a framework to combine two types of spatial couplings between the green and the brown food webs: 1) generalist consumers (herbivores or carnivores) couple the green and the brown patches at the top, and 2) reciprocal nutrient and detritus fluxes couple the two patches at the bottom of the food chains. We aim at answering the following question: What are the interacting effects of consumers and asymmetric nutrient and detritus fluxes on the relative dominance of either green or brown producers within the coupled ecosystem? The



model predictions can help to further understand functioning of ecosystem such the productivity, nutrient cycling and stability.

## Methods

### *The model*

We study the flux of a limiting nutrient (in most ecosystems either nitrogen or phosphorus) in a model with 7 compartments (Fig. 1-a) that includes the three features we highlight in the introduction: 1) a spatial structure with both a green patch (autotrophs as producers) and a brown patch (decomposers as producers), 2) consumers that couple the two patches at the top of the ecosystem and 3) exchanges of nutrients and detritus between the two patches at the bottom of the food chains.

Each patch contains a producer compartment ( $P$  in the green patch or  $B$  in the brown patch), a nutrient ( $N_i$ ) and a detritus ( $D_i$ ) compartments. In the green patch, autotrophs ( $P$ ) only take up nutrients as their resource. In the brown patch, decomposers ( $B$ ) consume both nutrients and detritus. We assume that the consumption functions follow the Holling type II functional response:  $\frac{aX}{1+ahX}$ , where  $a$  is the attack rate for resource  $X$  and  $h$  is the saturation rate. Since decomposers are generally considered homeostatic and their nutrient-to-carbon ratios ( $q_B$ ) is typically higher than that of detritus ( $q_D$ ), decomposers need to take up nutrients to balance this mismatch, therefore we model their consumption of mineral nutrients by  $\frac{a_{BD}D_2B}{1+a_{BD}h_{BD}D_2}(\frac{q_B}{q_D} - 1)$ . All the nutrient and detritus compartments receive constant inputs ( $I_{N_i}$  and  $I_{D_i}$  respectively) and are lost from the ecosystem at constant rates ( $l_{N_i}$  and  $l_{D_i}$  respectively). All living compartments recycle a fraction of excreted or unassimilated nutrients back to the ecosystem through direct (i.e. nutrients are recycled to the nutrient pool which directly support the primary production) and indirect (i.e. nutrients are recycled to the detritus pool which need to be re-

mineralized by decomposers, thus they are only indirectly available for primary producers) nutrient cycling. The recycling functions for all living compartments except the mobile generalist consumer follow the functions used in a previous study (Zou *et al.* 2016). Due to their mobility, the generalist consumers recycle nutrients in both the green and brown patches. Their function of nutrient cycling includes a spatial term which is explained in detail in the following paragraph.

The coupling of the green and the brown patches at the top by consumers is modeled after a previous spatially coupled food web model considering the spatial scale of the consumer–resource interactions (McCann *et al.* 2005). Consumers are assumed to be more mobile than their resources and can perceive resources as patchy or not. Specifically, we define the local spatial scale of consumer foraging as  $S_C$ , in which resources are well mixed for consumers. Out of this area, consumers can forage but do not perceive resources in the larger scales as well mixed. We also define the spatial scale of the resource habitat as  $S_P$  and  $S_B$  respectively for the green and the brown patches. We can have three cases for the functional responses of the consumers according to the relative scales between  $S_C$  and  $S_P/S_B$  (we assume that  $S_P = S_B$  for simplicity) (Fig. 1).

- 1) As illustrated in Fig.1-b, the local consumer foraging scale equals to the resource habitat scale (i.e.  $S_C=S_P$ ). In this case, the consumers need to choose between the green and brown patches. The functional response is then similar to a multispecies functional response with preference:

$$F_{HP}(P, B) = \frac{W_H a P}{1 + W_H a h P + (1 - W_H) a h B} \quad (1)$$

where  $W_H = \frac{\omega P}{\omega P + (1 - \omega) B}$ ,  $\omega$  is the generalist consumers preference for prey in the green patch.

2) As illustrated in Fig.1-c, the local consumer foraging scale is larger than the sum of the resource habitat scale (i.e.  $S_C > S_P + S_B$ ). In this case, resources in the green and brown patches are well mixed for the consumers. The functional response follows the classical multispecies functional response:

$$F_{HP}(P, B) = \frac{aP}{1+ahP+ahB} \quad (2)$$

3) Fig.1-d illustrates the intermediate case between above two cases (i.e.  $S_P < S_C < S_P + S_B$ ). In this case, there are areas where consumers have to alter foraging between the green and brown patches as in case 1 and an area where resources are well mixed for the consumers as in case 2. We define the portion of the green and brown patches that are well mixed for consumers as  $Q = (S_C - S_P)/S_P$ , therefore the consumer needs to switch patch to take up resources in the portion of  $1 - Q$ . The functional response of consumers is then:

$$F_{HP}(P, B) = \frac{S_{HP}(P,B)aP}{1+S_{HP}(P,B)ahP+S_{HB}(P,B)ahB} \quad (3)$$

where  $S_{HP}(P, B) = Q + (1 - Q)W_H$ , where  $W_H = \frac{\omega P}{\omega P + (1 - \omega)B}$ . Note that this function can be generalized to all three cases: when  $S_H \leq S_P$ , consumers always need to switch patch ( $Q = 0$ ), only the habitat preference  $\omega$  affects the functional response, and when  $S_H \geq S_P + S_B$ , all resources from both patches are well mixed for consumers ( $Q = 1$ ), habitat preference  $\omega$  does not affect the functional response. We also multiply this function with the quantity of nutrient recycled by the mobile consumers to describe their nutrient cycling in the spatial context.

The mobile consumers are modelled either as herbivores and carnivores since the coupling between the green and brown patches can be at different trophic levels. For example, in aquatic ecosystems, both zooplankton (herbivore) and fish (carnivore) can couple the planktonic grazing chain (based on nutrients, the green chain) and the microbial loop (based on detritus,

the brown chain) (Rooney *et al.* 2008). Therefore, we study the effects of spatial coupling at the top of the food webs on ecosystem functioning by considering three parameters of the generalist consumers: 1) their relative foraging scale compared with the scales of resources habitat, 2) their habitat preference and 3) their trophic level.

The coupling of the green and the brown patches at the bottom of the food chains by flows between nutrient and detritus compartments is modelled after a meta-ecosystem model (Gravel *et al.* 2010a). The spatial flows of nutrient and detritus are defined as  $\Delta N = d_N(pN_1 - (1 - p)N_2)$  and  $\Delta D = d_D(qD_1 - (1 - q)D_2)$  respectively for the green patch and the opposite for the brown patch. Nutrients and detritus diffuse between patches at constant rates  $d_N$  and  $d_D$  respectively. The asymmetry of the nutrient and detritus fluxes between the green and brown patches are represented by  $p$  and  $q$  respectively. When  $p$  and  $q$  are relatively high, the signs of  $\Delta N$  and  $\Delta D$  tend to be positive, thus the flows are from the brown patch to the green patch, while lower  $p$  and  $q$  value may reverse the direction of flows.

Overall, the dynamics of the nutrient concentration in all compartments are given by the differential equations in Table 1 (symbols and values of parameters are displayed in Table 2).

### *Model Analysis*

The analytical solutions of the model with seven equations are intractable, we therefore use numerical simulations with a solver from R 3.1.2 (package deSolve). We examine how the coupling at bottom by nutrient and detritus diffusions can influence the effects of the coupling at top by the generalist consumer on the relative importance of the green and the brown pathways (i.e. the green- or brown- dominance). The spatial coupling at the top of the food webs by generalist herbivores or carnivores leads to apparent competition or apparent mutualism respectively between the autotrophs and decomposers. Through nutrient and detritus diffusion and nutrient cycling, there are also exploitative competition (i.e. consumption of nutrients by autotrophs and decomposers) and mutualism (i.e. recycling of nutrients by

decomposers and production of detritus by autotrophs) between autotrophs and decomposers, leading to more complex controls on inter-patch dominance and on the functioning of the ecosystem.

We consider four aspects of both couplings at the top and the bottom of the food webs: 1) the generalist as either herbivores or carnivores (i.e. model-H and model-C respectively), in model-C two herbivores are added respectively in the green and the brown patch; 2) the consumer preference (i.e. 101 values of  $\omega$  from 0 to 1); 3) the resource habitat scale compared to the consumer foraging scales (i.e. four levels of  $Q = 0, 0.2, 0.5, 0.8$ ) and 4) asymmetry of nutrient and detritus fluxes between the green and the brown patches (101 values of  $p$  or  $q$  from 0 to 1). Thus we analyze  $101 \times 101$  combinations of asymmetric fluxes and consumer preference in eight scenarios (two different trophic levels of the consumer  $\times$  four relative spatial scales between the consumers and the resources). We explore globally the condition under which either the autotrophs or the decomposers dominate the ecosystem (i.e. which one has the highest nutrient stock at equilibrium).

## Results

The top-down effects of the generalist consumer on the dominance of either autotrophs or decomposers in the ecosystem interact with the bottom-up effects of asymmetric nutrient and detritus flux between the green and the brown patches. The results of model-H and model-C are displayed respectively in Fig.2 and Fig.3.

In model-H where the herbivores are considered as the generalist consumers, autotrophs and detritus are under apparent competition when there is neither nutrient nor detritus diffusion. The one that is preferred by the consumer has the lower nutrient stock thus the other one dominates the ecosystem, illustrated in Fig.2-a as the dashed line separates the alternative dominance by autotrophs or by decomposers. When there is diffusion between the green and

brown patches, the asymmetry of the relative importance of nutrient or detritus compartments influences the dominance of either autotrophs or decomposers, illustrated by the solid line in Fig.2-a. Low  $p$  and  $q$  values represent cases where asymmetry favors the diffusions from the green patch to the brown patch. The green-to-brown flows provide more resources to the brown patch, thus amplifying the predation effects of the consumer on autotrophs in the green patch. Asymmetry favoring the brown patch increases the likelihood of dominance of decomposers. High  $p$  and  $q$  values, which favor the diffusions in the opposite direction, have opposite effects: the brown-to-green flows of nutrients provide more resources for autotrophs while the flows of detritus limit the decomposers. In that case, asymmetry dampens the predation effects of consumers on autotrophs and provides more autotroph dominant ecosystems. The slope of the boundary that separates the autotroph-dominant and the decomposer-dominant ecosystems increases with increasing spatial coupling strength (i.e. the foraging scale of the consumers is large compared to their resource habitat scale). Thus, the influence of the asymmetry of nutrient and detritus diffusions on the effects of consumer preference on the green- or the brown-dominance increases with larger consumer foraging scale covering more resource habitat scale (i.e.  $S_H \rightarrow 2 \times S_p, Q \rightarrow 2$ ).

In model-C where the carnivores are considered as the generalist consumers, the effects of consumer preference on the relative dominance of autotrophs and decomposers are reversed. The generalist consumer coupling the green and brown patches at one trophic level higher than in model-H, autotrophs and decomposers are therefore under apparent facilitation due to the top-down trophic cascade effects. The herbivores that are preferred by the generalist consumer are under stronger predation pressure, and their resources, either the autotrophs or the decomposers, are released from predation and thus have the higher nutrient stock and dominate the ecosystem (Fig.3). The green-to-brown nutrient and detritus flows to the brown patch still provide more resources to the decomposers. Unlike in model-H, these flows dampen the

predation effects of herbivores on decomposers due to top-down control and provides more decomposer-dominant ecosystems. Nutrient flows in opposite direction provide more resources for autotrophs while the opposite flows of detritus limit the decomposers. These flows amplify the predation effects of the herbivores on decomposers due to less control by the generalist consumers. Asymmetry favoring the green patch increases the likelihood of dominance of autotrophs. Interestingly, the slope of the boundary that separates the autotroph-dominant and the decomposer-dominant ecosystems increases slower with increasing spatial coupling strength than in model-H. This might be due to the attenuated trophic cascades effects of the carnivores which are at one trophic level higher (Leroux & Loreau 2008).

## **Discussion**

In our model, we combine two types of spatial couplings between the green and the brown food webs: 1) generalist consumers (herbivores or carnivores) couple the green and the brown patches at the top, and 2) reciprocal nutrient and detritus fluxes couple the two patches at the bottom of the food chains. Our analysis suggests that both 1) the asymmetric consumption of prey from the green and the brown patches by generalist consumers and 2) the asymmetric flows of nutrients and detritus between the two patches affect ecosystem functioning and the dominance of either the green or the brown producers (i.e. autotrophs and decomposers). We propose that our food web model can be representative of many aquatic ecosystems where processes based on primary production and decomposition are at least partly spatially decoupled (i.e. benthic and pelagic compartments of the ecosystem). We therefore suggest that the relative importance of the green and the brown pathways (i.e. the green- or brown-dominance) may be very different among ecosystems depending on the type of spatial coupling between green and brown pathways.

### ***Spatial coupling of the green and brown patches by top generalist consumers***

Consequences of spatial coupling by top consumers on ecosystem functioning depend not only on the asymmetric consumptions through distinct preference on preys in the green or the brown patches, but also on the trophic level of the top consumers. When the top consumer is an herbivore, preference on the prey of the green patch leads to the dominance of the brown producers while when it is a carnivore, such preference leads to primary producer dominance. Classic trophic cascade theory predicts that in food chains, top consumers control the abundance of the trophic level below, thus releasing the next lower trophic level from predation (Oksanen *et al.* 1981; Carpenter *et al.* 1985). Our results are in agreement with this theory since the trophic controls of generalist consumers on the producers are opposite under herbivore coupling and carnivore coupling circumstance. The preference of the top generalist consumer thus determine the relative abundance of producers within two patches (i.e. the dominance of either green or brown producers) through different intensities of top-down cascading effects in the coupled green and brown chains. The recent study of Wollrab *et al.* (2012) made detailed analyses of cascading effects in a food web comprised of two connected food chains. They showed that the bottom-up and top-down cascading effects were strongly determined by the respective lengths of the two trophic chains and the presence/absence of a generalist consumer. We focused here only on top consumer coupling of green and brown food chains with identical lengths and it would be necessary to integrate different trophic lengths in future versions of this model.

When top consumers strongly couple the green and brown patches (i.e. the foraging scale of the consumers is large compared to their resource habitat scale), the effects of consumer preference on the dominance of either green or brown producers are reduced. The weaker effects of consumer preference due to stronger coupling were also found by McCann *et al.* (2005) but on ecosystem stability. This result is directly related with the way consumer spatial coupling is modelled in our study. Unlike models in meta-community or meta-ecosystem



theories that consider dispersals of top consumers between patches (Loreau *et al.* 2003b; Leibold *et al.* 2004; Haegeman & Loreau 2014), the spatial coupling of the green and brown patches is here modelled by using a functional response of the top consumer which integrates the relative foraging/habitat scale of consumers and resources, following McCann *et al.* (2005). This functional response allows to model different levels of spatial coupling strength by the top consumers, and the consumer preference for the two patches does not appear anymore in the functional response when coupling is very strong. Results might strongly depend on the way spatial coupling is modelled at predator level. In meta-ecosystem studies focusing more on the dispersals of consumers, neutral or stabilizing effects of spatial dispersals of consumers are observed (Gounand *et al.* 2014) while McCann *et al.* (2005) highlighted a destabilizing effect of strong spatial coupling. We argue that although contradictory results are obtained, both ways of modeling spatial dynamics of consumers are reasonable and can be complementary to each other to help understanding the important factor determining effects of spatial coupling. It would also be interesting to model the dispersal of consumers among the green and brown patches in future studies.

### ***Spatial coupling of the green and brown patches by flows of nutrients and detritus***

Results show that the strength of spatial coupling by flows of nutrients and detritus as well as the asymmetry of these flows between green and brown patches affect ecosystem functioning. For both nutrient and detritus, the asymmetry favoring fluxes from the green patch to the brown patch provides more resources to the brown patch and favor the dominance of decomposers. To the contrary, the asymmetry favoring nutrient and detritus fluxes from the brown patch to the green patch provides more resources for autotrophs and limit the decomposers. The spatial coupling between green and brown compartments as well as flow asymmetries of nutrients and detritus between these compartments might differ between ecosystems (Krumins *et al.* 2013). In aquatic ecosystems, green and brown patches might be more decoupled spatially than in

terrestrial ecosystems, with highly asymmetric fluxes of nutrients and detritus between the two patches. In marine ecosystems, deep-water sediments, which constitute an important brown pathway, depend on the detritus that sink from the photosynthesis sub-surface zone. In turn, availability of nutrients decomposed in the benthic zone depends on upwelling. Thus coupling between these green and brown compartments occurs over long time scales (Menge & Menge 2013). In lakes, flow of detritus is also asymmetric and goes from the pelagic to the benthic zone through sedimentation. However, both compartments are likely to be less spatially decoupled because they are less distant than in marine ecosystems. Lake mixing indeed occurs at least on a seasonal basis (Shade *et al.* 2010).

Our results thus suggest that ecosystem differences in flows of detritus and nutrients between green and brown components might affect the relative importance of primary production and decomposition in these ecosystems. The consequences of fluxes of nutrients and detritus across ecosystem boundaries have received recently much attention in theoretical ecology (Polis *et al.* 1997; Amarasekare 2008) because they are ubiquitous in nature. At the interface between terrestrial and aquatic ecosystems, both nutrients and detritus flow asymmetrically from the terrestrial ecosystem to the aquatic ecosystems (Soininen *et al.* 2015). Terrestrial nutrients and detritus enter into water via rainfall and flood and support heterotrophic production of aquatic bacteria (Bartels *et al.* 2012). The meta-ecosystem concept has highlighted the important effects of these fluxes of matter and their asymmetry on ecosystem functioning and stability (Loreau *et al.* 2003b; Gravel *et al.* 2010b; Massol *et al.* 2011). However, so far, flows of nutrients and detritus have been considered between similar ecosystems with both green and brown compartments, and not in the context of spatial coupling of green and brown patches. Furthermore, while previous studies have proved nutrient and detritus fluxes influence the food web structure and stability in the recipient ecosystems (Ristau *et al.* 2013), few study has addressed globally the effects on overall ecosystem functioning.

We also find that the asymmetric nutrient and detritus fluxes between the green and brown patches can interact with top consumer coupling to influence the relative importance of either the producers of the green patch or the decomposers of the brown patch in the whole ecosystem. With herbivores as top consumer flux asymmetry from green to brown patches can amplify the predation effects of the consumer on autotrophs in the green patch, while with carnivores as top consumer, this can weaken the negative trophic controls of top consumers on decomposers. Asymmetry favoring nutrient and detritus fluxes from the brown patch to the green patch have opposite effects: they dampen the predation effects of consumers on autotrophs with herbivores as top consumer and amplify the negative effects of trophic controls on decomposers with carnivores as top consumers. To our knowledge, the interacting effects of asymmetric top consumption and asymmetric flows of matter predicted by our models have not been tested in empirical studies so far. It is therefore essential to measure these two key processes within different ecosystems to understand interacting effects of food web structure, space and the direction of fluxes between ecosystems on ecosystem functioning.

### ***Conclusion and perspectives***

Interactions between the green and brown food webs have become recently a key factor in food web studies due to their important effects on ecosystem functioning and stability (Attayde & Ripa 2008; Wollrab *et al.* 2012; Wolkovich *et al.* 2014; Zou *et al.* 2016). Our model is one of the first to integrate spatial dynamics into food chain coupling the green and the brown patches. We include two ways of modelling spatial coupling in recent theoretical ecology: the coupling associated with top consumer behavioral process (i.e. foraging) and the coupling associated with fluxes of resources for the bottom of the food chains as in meta-ecosystem theory. Both spatial couplings are shown to have important effects on the dominance of either the primary producer in the green patch or the decomposers in the brown patch, thus potentially on the relative importance of primary or decomposer production in the whole ecosystem.

However, our model is only an abstraction of real food webs, other essential factors should be included in future versions of the model. First, we only consider equal trophic length for the green and the brown patches, while in real food webs, the green and brown food chains can be at different length. The different length of coupled food chains have been proved to significantly affects trophic cascade effects in previous studies (Wollrab *et al.* 2012; Zou *et al.* 2016) thus it will be important to develop a more generalized model integrating different trophic lengths between spatially coupled green and brown patches. Second, as asymmetry of consumption at the top of the food web and fluxes of resources for the bottom of the food web might be very different among different ecosystem types, we should parameterize the model for different real ecosystems of contrasting types to make more specific predictions.

**Notes:**

The preliminary results of our spatial model reflect the interacting effects of coupling by the top generalist consumers and by the nutrient and detritus spatial fluxes on the dominance of green and brown patches in ecosystems. There are still many interesting questions to be addressed to complete this chapter. Here I list five aspects which we are going to develop in future works.

1. The indirect mutualistic and competitive interactions between primary producers and decomposers can be regulated by the stoichiometric mismatch between decomposers and their resources (i.e.  $\frac{q_B}{q_D}$  in the model). Increasing  $\frac{q_B}{q_D}$  means that the competition between primary producers and decomposers increases. In current simulations, we only use a constant value of  $\frac{q_B}{q_D}$  thus a fixed competition intensity between the primary producers and the decomposers. It would be interesting to study how the stoichiometry and the competition intensity affect the spatial flux of nutrients and detritus and the consequence on ecosystem functioning.

2. The spatial model can be representative of real ecosystem. For example, the green and brown patches can represent respectively the pelagic and benthic compartments of aquatic ecosystems where spatial fluxes of nutrients and detritus are differently asymmetric (e.g. nutrients diffuse more freely in the water column while detritus fluxes are more asymmetric through sedimentation from the pelagic to the benthic ecosystems). Therefore, we will use specific parameters and the different asymmetry of nutrient and detritus fluxes (i.e. represented by  $p$  and  $q$  in the model) in aquatic ecosystems to further explore the model predictions in more real conditions.
3. We have mentioned the importance of considering the relative spatial scale of the consumer–resource interactions (i.e. represented by  $Q$  in the model). We need to further study how the relative foraging scale of consumers compared with the scales of resources habitat affect primary production and decomposition to see how the strength of the spatial coupling via consumers affects the functioning of the ecosystem.
4. One of the novelties of the model is that we consider the spatial coupling between the green and brown food webs, which can have indirect mutualistic interactions through nutrient cycling. It could be very interesting to compare the results with a green-green coupling case (e.g. the G-G model in chapter 3) to understand how the interactions between green and brown affect our results.
5. In real ecosystems, there is generally the two types of food web (either green or brown) in each of the patches. Therefore, we can develop meta-ecosystem models in which each patches in the ecosystem contains both the green and brown pathways and study how this structure and affect ecosystem functioning. This could be very useful to study the coupling between adjacent ecosystems (lake-terrestrial ecosystem around the lake, ocean-island). We can also compare the asymmetry of consumption at the top of the food web and fluxes of resources for the bottom of the food web in different ecosystem types to make more specific predictions.

## Tables

**Table 1** Equations of models

Model	Herbivores as the generalist consumer (Model-H)	Carnivores as the generalist consumer (Model-C)
<b>Generalist consumer compartment</b>	$\frac{dH}{dt} = H(e_{HP}F_{HP}(P, B)P + e_{HB}F_{HB}(P, B)B - m_H)$	$\frac{dC}{dt} = C(eF_{CH_1}(H_1, H_2)H_1 + eF_{CH_2}(H_1, H_2)H_2 - m_{H_2})$
<b>Compartment in the green patch</b>	The primary producers: $\frac{dP}{dt} = P(F_P(N) - m_P - F_{HP}(P, B)H)$	The primary producers: $\frac{dP}{dt} = P(F_P(N) - m_P - F_{H_1}(P)H_1)$ The herbivores: $\frac{dH_1}{dt} = H_1(eF_{H_1}(P) - m_{H_1} - F_{CH_1}(H_1, H_2)C)$
<b>Compartment in the brown patch</b>	The decomposers: $\frac{dB}{dt} = B(eF_B(D)\frac{dB}{q_D} - m_B - F_{HB}(P, B)H)$	The decomposers: $\frac{dB}{dt} = B(eF_B(D)\frac{dB}{q_D} - m_B - F_{H_2B}(B)H_2)$ The predators of decomposers: $\frac{dH_2}{dt} = H_2(eF_{H_2}(B) - m_{H_2} - F_{CH_2}(H_1, H_2)C)$
<b>Nutrient and detritus compartments in the green patch</b>	Nutrients: $\frac{dN_1}{dt} = I_{N_1} - l_{N_1}N_1 - F_P(N)P + n_H s_H S_{HP}(P, B)(m_H + (1 - e_{HP})F_{HP}(P, B) + (1 - e_{HB})F_{HB}(P, B))H + \Delta N$ Detritus: $\frac{dD_1}{dt} = I_{D_1} - l_{D_1}D_1 + m_P P + n_H(1 - s_H)S_{HP}(P, B)(m_H + (1 - e_{HP})F_{HP}(P, B) + (1 - e_{HB})F_{HB}(P, B))H + \Delta D$	Nutrients: $\frac{dN_1}{dt} = I_{N_1} - l_{N_1}N_1 - F_P(N)P + n_C s_C S_{CH_1}(H_1, H_2)(m_C + (1 - e)F_{CH_1}(H_1, H_2) + (1 - e)F_{CH_2}(H_1, H_2))C + n_{H_1} s_{H_1}(m_{H_1} + (1 - e)F_{H_1}(P))H_1 + \Delta N$ Detritus: $\frac{dD_1}{dt} = I_{D_1} - l_{D_1}D_1 + m_P P + n_C(1 - s_C)S_{CH_1}(H_1, H_2)(m_C + (1 - e)F_{CH_1}(H_1, H_2) + (1 - e)F_{CH_2}(H_1, H_2))C + n_{H_1}(1 - s_{H_1})(m_{H_1} + (1 - e)F_{H_1}(P))H_1 + \Delta D$
<b>Nutrient and detritus compartments in the brown patch</b>	Nutrients: $\frac{dN_2}{dt} = I_{N_2} - l_{N_2}N_2 - F_B(N)B(\frac{dB}{q_D} - 1) + n_H s_H S_{HB}(P, B)(m_H + (1 - e_{HP})F_{HP}(P, B) + (1 - e_{HB})F_{HB}(P, B))H + n_B s_B(m_B + (1 - e_{BD})F_B(D))B - \Delta N$ Detritus: $\frac{dD_2}{dt} = I_{D_2} - l_{D_2}D_2 + n_H(1 - s_H)S_{HB}(P, B)(m_H + (1 - e_{HP})F_{HP}(P, B) + (1 - e_{HB})F_{HB}(P, B))H + n_B s_B(m_B + (1 - e_{BD})F_B(D))B - \Delta D$	Nutrients: $\frac{dN_2}{dt} = I_{N_2} - l_{N_2}N_2 - F_B(N)B(\frac{dB}{q_D} - 1) + n_C s_C S_{CH_2}(H_1, H_2)(m_C + (1 - e)F_{CH_1}(H_1, H_2) + (1 - e)F_{CH_2}(H_1, H_2))C + n_{H_2} s_{H_2}(m_{H_2} + (1 - e)F_{H_2}(B))H_1 - \Delta N$ Detritus: $\frac{dD_2}{dt} = I_{D_2} - l_{D_2}D_2 + n_C(1 - s_C)S_{CH_2}(H_1, H_2)(m_C + (1 - e)F_{CH_1}(H_1, H_2) + (1 - e)F_{CH_2}(H_1, H_2))C + n_{H_2}(1 - s_{H_2})(m_{H_2} + (1 - e)F_{H_2}(B))H_1 - \Delta D$

**Table 2.** Parameter definitions and proposed values in simulations

Symbol	Definition	Value
<i>Parameters in general</i>		
$I_{N_i}$	Constant input of mineral nutrients in patch $i$	0.1
$l_{N_i}$	Loss rate of mineral nutrients from patch $i$	0.1
$I_{D_i}$	Constant input of organic materials in patch $i$	0.05
$l_{D_i}$	Loss rate of organic materials from patch $i$	0.1
$d_N$	Constant nutrient diffusion rate between patches	0.02
$d_D$	Constant detritus diffusion rate between patches	0.02
$p$	Asymmetry of the nutrient fluxes between patches	0-1
$q$	Asymmetry of the detritus fluxes between patches	0-1
$e_{XY}$	Conversion efficiency from resource $X$ to consumer $Y$	0.5
$n_X$	The fraction of nutrient cycling of living compartment $X$	0.4
$s_X$	The proportion of direct nutrient cycling of $X$	0.7
$S_C$	Spatial scale of consumer foraging	1-1.8
$S_P, S_B$	Spatial scale of resource habitat (the green and brown patches)	1
<i>Parameters in model-H</i>		
$r_{PN}$	Intrinsic growth rate of primary producers	1.5
$h_P$	Half saturation rate of primary producers	0.5
$m_P$	Natural mortality of primary producers	0.05
$q_B/q_D$	Nutrient-to-carbon ratios of decomposers and detritus	1.2
$a_{BD}$	Consumption rate of decomposers on detritus	1.5
$h_{BD}$	Half saturation rate of decomposers	0.5
$m_B$	Natural mortality of decomposers	0.05
$a_{HP}$	Attack rate of herbivores on primary producers	1
$a_{HB}$	Attack rate of herbivores on decomposers	1

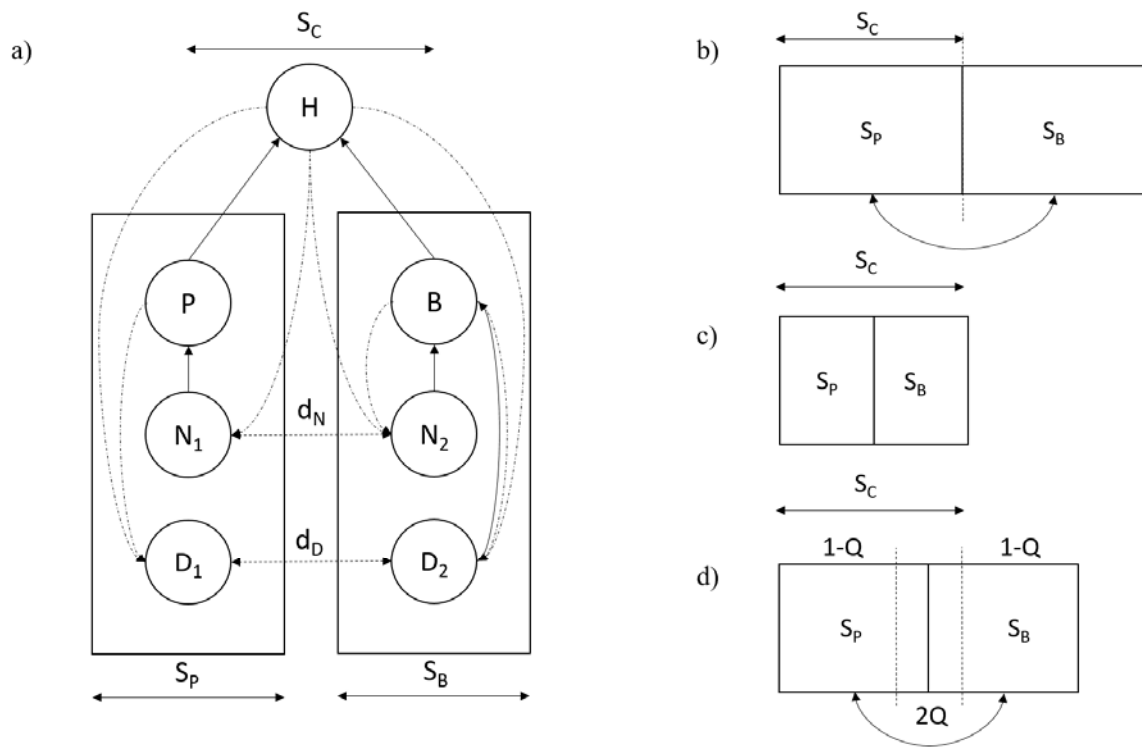
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$h_H$	Half saturation rate of herbivores	0.1
$m_H$	Natural mortality of herbivores	0.01
$\omega$	Herbivore preference for primary producers	0-1
<b><i>Parameters in model-C</i></b>		
$r_{PN}$	Intrinsic growth rate of primary producers	1.5
$h_{PN}$	Half saturation rate of primary producers	0.5
$m_P$	Natural mortality of primary producers	0.05
$q_B/q_D$	Nutrient-to-carbon ratios of decomposers and detritus	3
$a_{BD}$	Consumption rate of decomposers on detritus	1.5
$h_{BD}$	Half saturation rate of decomposers	0.02
$m_B$	Natural mortality of decomposers	0.05
$a_{HP}$	Attack rate of herbivores on primary producers in the green patch	1
$h_{HP}$	Half saturation rate of herbivores in the green patch	0.1
$m_{H_1}$	Natural mortality of herbivores in the green patch	0.1
$a_{HB}$	Attack rate of herbivores on decomposers in the brown patch	1
$h_{HB}$	Half saturation rate of herbivores in the brown patch	0.1
$m_{H_2}$	Natural mortality of herbivores in the brown patch	0.1
$a_{CH_1}$	Attack rate of generalist predators on herbivores in the green patch	1
$a_{CH_2}$	Attack rate of generalist predators on herbivores in the brown patch	1
$h_C$	Half saturation rate of generalist predators	0.1
$m_C$	Natural mortality of generalist predators	0.01
$\omega$	Generalist predators preference for herbivores in the green patch	0-1

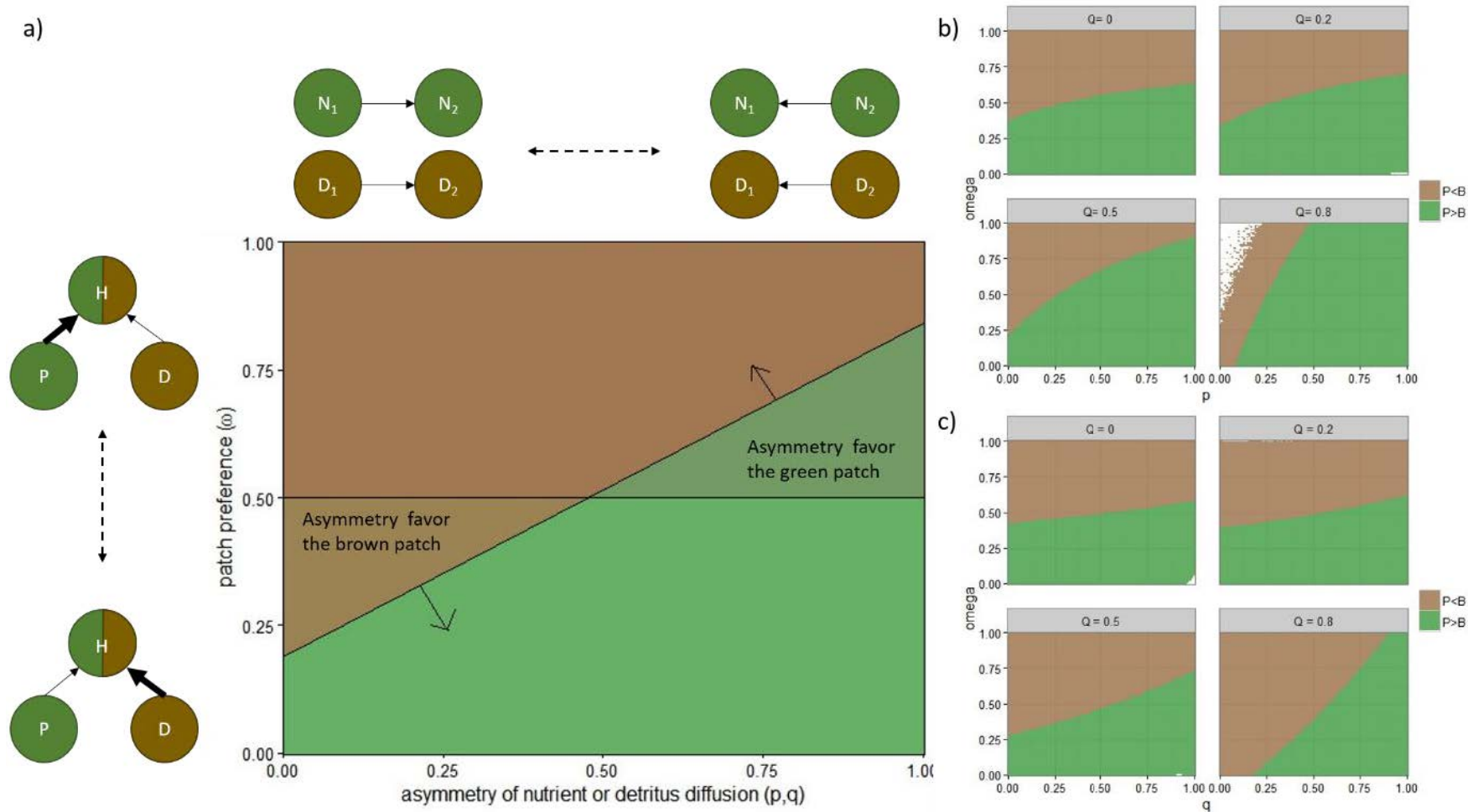
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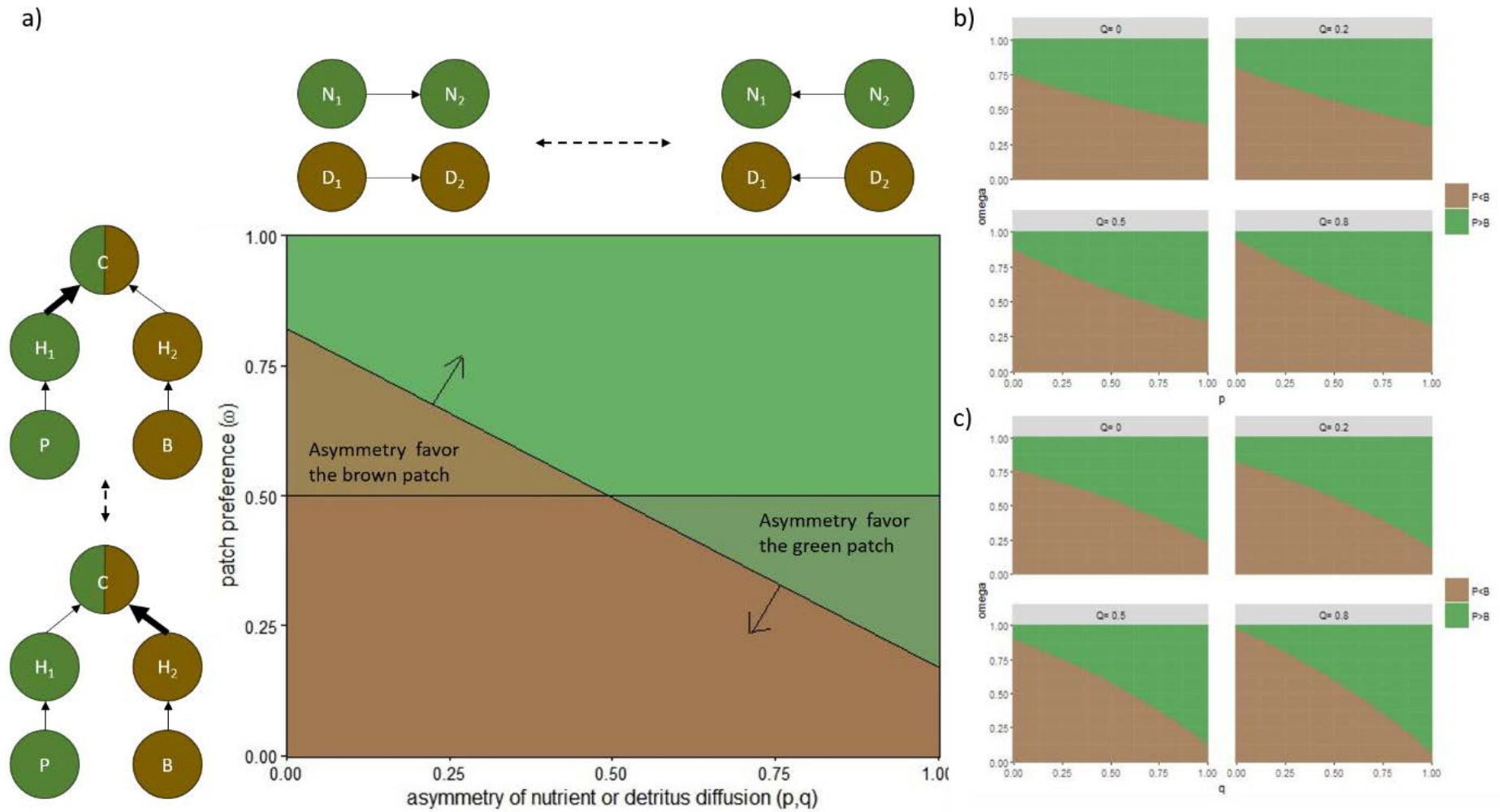
## Figures



**Figure 1.** Schematic representation of the model with herbivores as top consumers (model-H) (a) and of the consumer-resource interaction depending on spatial scale (b-d). The difference between the foraging scale of the consumer and the habitat scale of the resources determines three different cases of the functional response of consumers as explained in the text.



**Figure.2** Interacting effects of predation preference of herbivores and asymmetry of nutrient and detritus diffusion on either autotroph- or decomposer-dominance in the ecosystem. a) is a schematic presentation of the effects while b) and c) represent real simulation results for asymmetry of nutrient ( $p$ ) and detritus ( $q$ ) respectively. The brown and green areas represent respectively the autotroph-dominance and decomposer-dominance of the ecosystems.



**Figure.3** Interacting effects of predation preference of carnivores and asymmetry of nutrient and detritus diffusion on either autotroph- or decomposer-dominance in the ecosystem. a) is a schematic presentation of the effects while b) and c) represent real simulation results for asymmetry of nutrient ( $p$ ) and detritus ( $q$ ) respectively. The brown and green areas represent respectively the autotroph-dominance and decomposer-dominance of the ecosystems.

## **Chapter 5**

### **Interactions between green and brown food webs in freshwater ecosystems: preliminary results of a mesocosm experiment**



# **Interactions between green and brown food webs in freshwater ecosystems: preliminary results of a mesocosm experiment**

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## Introduction

The relative importance of bottom-up and top-down controls on ecosystem functioning has received a lot of attention in food-web ecology (Hunter & 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 & 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 & 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 & Loreau 2001). Second, green and brown food webs also interact at higher trophic levels via generalist predators that consume preys in both green and brown webs. 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 stabilizing 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 and theoretical studies have considered the consequences of the coupling between green and brown food webs (Halnes *et al.* 2007; Daufresne *et al.* 2008; Boit *et al.* 2012; Zou *et al.* 2016). 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?

## **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", <http://www.cereep.ens.fr/>), 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 colonization of the ponds occurred earlier, due to accumulation of rainwater as soon as the liners had been installed. We installed a floating a floating pontoon (27 x 5 m) in the storage pond (125 m x 15 m x 3 m deep). The pontoon delimitates two blocks of 12 x 3 m, on which enclosure can be suspended. 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 colonization. Thirty-six translucent polyethylene enclosures (2.0 × 1.0 × 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.* (2008, 2012) and Harrault *et al.* (2014). Thus, each enclosure is 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). Thus, 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 not randomly 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 is extremely poor). 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  $\text{K}_2\text{HPO}_4 \cdot 3\text{H}_2\text{O}$  were added two times (separated by seven days) in each enclosure. Such addition corresponded to  $140 \mu\text{g N L}^{-1}$  and  $56 \mu\text{g P L}^{-1}$  (i.e. C/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 figure 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).

#### 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,

1.8 g C was added in half of the enclosures as a mixture of three organic molecules: 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 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 nonatech pit-tag (Lutronic International, 1x6 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 die 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). Every two weeks, samples for FACS analysis were also stained with Lysotracker Green DND-26 (1mM final concentration, Invitrogen) in the dark at room temperature to target mixotrophic unicellular eukaryotes, prior to paraformaldehyde addition. At last, 50 mL were directly analyzed 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-weighted 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 was 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  $\mu\text{m}$  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

**Preliminary note:** these analyses are underway and their results are not yet available. However, we preferred to describe the methodology here, to provide the reader with an overall view of the methodological approach.

Frozen samples collected (see the Phytoplankton section) will be analysed by FACS as described by Zubkov *et al.* (2007). Samples will be defrosted at 4°C for at least one hour and then will be filtered through a 50- $\mu\text{m}$  nylon filter to remove large particles that could plug the cytometer. In a 5-mL cytometer tube, 1 mL of sample and 200  $\mu\text{L}$  of 3  $\mu\text{m}$  calibration beads solution, (Ready- to-use, Calibration beads for lasers with blue 488 nm excitation, Sysmex France) will be added at known dilution to determine absolute cell concentrations. Samples for protists and bacteria counting will be stained with SYBR Green I DNA stain (Sigma-Aldrich, Poole, UK), 1:50 final dilution of initial stock, in the dark at 20°C for one hour. Cells will be enumerated at  $\sim 180 \mu\text{L min}^{-1}$  flow rate for 2–3 min triggering on 90° light scatter (R1 gate). The measurements of 90° or side light scatter (SSC), green (FL1, 530 $\pm$ 15 nm), orange (FL2, 585 $\pm$ 21 nm) and red (FL3, >650 nm) fluorescence will be made with log amplification on

a four-decade scale. Flow cytometric data will be analysed using CellQuest software (Becton Dickinson) and will be plotted using WinMDI software 2.8 (Joseph Trotter, Scripps Research Institute, La Jolla, CA, USA). Mixotrophic microbial eukaryotes will be distinguished and counted by flow cytometry with a FACSCalibur flow cytometer equipped with a 488nm laser using Lysotracker Green DND-26 fluorescence collected at FL1 (530/30 bandpass filter) and side scatter (SSC).

#### Water physico-chemistry

The main characteristics of the water were measured weekly with a multi-parameter probe (KorExo) 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-weighted and carbonised Whatman GF/F glass-fibre filters (nominal cut-off 0.7 µm) 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. Every two weeks, approximately 30 mL of samples plus 35 µL 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).

#### Sediments

Sediments were also collected in each enclosure thanks to 5 cm diameter and 30 cm height PVC tubes hung at 1.5 m deep. Tubes were set in the middle of July and were removed in the middle of November for 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 triplicate. Each well also contains growth media and a tetrazolium violet dye that becomes purple when the substrate is oxidized and was inoculated with 150  $\mu$ 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 24 h 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 for the last four dates of measurement (i.e. for incubation times of 48h, 72h, 96h and 168h).

#### ***Preliminary statistical analyses***

We analysed the effects of our three treatments and their two and three-level interactions on phytoplankton (concentrations of green algae, blue green algae and diatoms estimated by BBE



fluoroprob, concentration of Chlorophyll a estimated by multiparameters probe and dry seston biomass), dry biomass of zooplankton, fish growth, water physico-chemistry (oxygen concentration measured by multiparameters probe, DOC) and catabolic capacity of microbial communities. Zooplankton counting and determination, analyses for microorganisms with FACS as well as analyses of N and P concentrations and sediment characteristics are still ongoing. Thus the corresponding variables could not be included in these preliminary statistical analyses.

We used linear mixed effect models with mesocosm position as random effects, using the package lme4 in R. When the response variable was repeatedly measured in time (i.e. concentrations of green algae, blue green algae and diatoms, concentration of Chlorophyll a and parameters of water physico-chemistry), sampling date and mesocosm identity was added as a random effect in the model. For each response variable, all combinations of experimental variables and their interactions were tested to determine the best-fit model. We selected the model that fitted best according to the Akaike information criterion (AIC) and model selection was done using MuMIn in R. P-values were obtained from backward simplifications using maximum likelihood approximation (Chi<sup>2</sup> results indicating significance).

For testing the effects of experimental treatments and their interactions on overall catabolic activity of microbial communities, we performed permutational multivariate analyses of variance (permanova) based on euclidian distances. To do so, we used the adonis function (vegan package in R), and we accounted for measure repetition by restricting permutations within each measurement date (i.e. incubation time was included as strata in adonis). We

analysed the average relative oxidation of the different types of substrates with linear mixed effect models where all combinations of experimental variables and their interactions were included as fixed effects and mesocosm identity and incubation time were considered as random effects. Model selection and calculation of statistic values were then performed as explained in the previous paragraph.

## **Results**

### *Phytoplankton*

#### Green algae

Green algae were clearly the dominant phytoplanktonic group in all treatments. Effects of fish presence on green algae interacted significantly with effects of light and organic matter treatments (Table 1). Fish presence increases less green algae concentration when light is not filtered or when organic matter is added (Figure 3). Concerning the effects of treatments alone, fish presence increases green algae concentration the most (estimate= $11.6 \pm 2.58 \mu\text{g.L}^{-1}$ ), then light (estimate= $10.67 \pm 2.56 \mu\text{g.L}^{-1}$ ), but effect of organic matter addition is not significant overall (estimate= $0.52 \pm 2.56 \mu\text{g.L}^{-1}$ ).

#### Cyanobacteria

Only fish presence significantly affects blue green algae concentrations (Table 1). Cyanobacteria concentrations are higher when fishes are present (Figure 4).

#### Diatoms

As for cyanobacteria, diatom concentrations are only significantly affected by fish presence (Table 1). However, in this case, diatom concentration is negatively affected by fish presence (Figure 5).

#### Seston and overall chlorophyll a concentration

For both seston dry concentration and chlorophyll a concentration as measured by the multi-parameter probe, we find a significant interaction between fish presence and light filtration (Table 1). Fish presence increases seston concentration and chlorophyll a concentration when light is strongly filtered (Figure 6) but it has a weaker or no effect when light availability is higher. Greater light availability increases seston concentration and chlorophyll a concentration when fishes are absent (Table 1, Figure 6) but it has a weaker effect (chlorophyll a) or no effect (seston) when fishes are present.

#### ***Zooplankton and macroinvertebrates***

The analysis using the Akaike information criterion selected a model including no treatment (Table 1). No treatment (or no interaction between treatments) has a significant effect on the zooplankton dry mass (Figure 7).

At this time, we only have partial information on zooplankton composition and we cannot estimate treatment effects. However, we can indicate that zooplankton was dominated by Rotifers (*Lecane* spp, *Lepadella* sp., *Ascomorpha* sp., Bdelloid species, and more rarely *Keratella* sp.), Cladocerans of the Chydoridae family, and Cyclopidae (nauplii, copepodites and adults).

Macroinvertebrates were not adequately sampled by the zooplankton bottles. However, several taxa (*Chaoborus* larvae, Chironomidae, Ephemeroptera, Gerridae), were always observed in fishless enclosures while they were in most cases invisible in fish ones.

### ***DOC***

Whatever the treatment, the DOC concentration in enclosures significantly increased over time (Figure 8). The increase in DOC over time depends on the interaction between the three experimental treatments (Table 1). Fish presence always leads to greater DOC accumulation and the enclosures with fishes, organic carbon addition and without light filtration have the highest DOC concentration (Figure 8). The effects of light and organic matter addition are affected by fish presence. When fishes are absent, increased light availability or organic matter addition always increase DOC accumulation over time. When fishes are present, increased light availability only increases DOC when organic matter is added while organic matter addition only increases DOC when light is not filtered.

### ***Dioxygen concentration and turbidity***

No interaction between treatments has an effect on the dioxygen concentration. Fish presence and organic matter addition have significant effects (Table 1). Fish presence increases dioxygen concentration while organic matter addition decreases it (Figure 9).

For turbidity, effects of fish presence interacted significantly with effects of light and organic matter treatments (Table 1). Light filtering decreases more turbidity when fishes are absent than when they are present, and fish presence increases more turbidity when light is

filtered (Figure 9). Organic matter addition tends to have a positive effect on turbidity in absence of fish whereas it tends to have a negative effect in fish presence.

### ***Fish***

The relative growth of fishes only depends on the light treatment and on the species (Table 1). The organic matter addition had no significant impact. Light has a positive effect on fish relative growth rate ( $0.0067 \pm 0.0019 \text{ day}^{-1}$ , Figure 10).

### ***Catabolic activity of microbial communities***

For pelagic microbial communities, overall catabolic activity is marginally affected by fish presence and by the interaction between light intensity and organic matter addition at one sampling date (Table 2). However, average relative oxidation of the different substrate types is not significantly affected by any experimental treatment (Table 3, Figure 11).

For benthic microbial communities, overall catabolic activity is significantly affected by fish presence and marginally by addition of organic matter (Table 2). Average relative oxidation of amines, amino acids, phenolic acids and carboxylic acids are significantly lower when fishes are present (Table 3, Figure 11).

## **Discussion**

The preliminary results of our experiment can be summarized 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 the brown food web (catabolic activity of benthic microbial community) and on water physico-chemistry

variables (turbidity, dioxygen concentration and DOC). Second, our results suggest only weak cascading effects between the green and the brown food webs so far, since light filtration does not affect 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 preliminary 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. Regardless of treatment, green algae dominated the biomass of phytoplankton communities. Zooplankton biomass remained low in all treatments. The measured biomass value, close to 100  $\mu\text{g DW L}^{-1}$ , 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 greater (Bertolo *et al.* 1999a; Danger *et al.* 2012). At this time, we only have partial information on zooplankton composition and we cannot estimate treatment effects. However, we can clearly state that small herbivorous and detritivorous species (with several taxa 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 all the samples already analysed. Clearly, the very low zooplankton biomass,

the absence or scarcity 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.

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 mesh treatment. However, this fish effect was robust and was confirmed by the estimates of seston biomass, total chlorophyll *a* (multi-parameter probe), the values of Chlorophyll *a* measurements associated to green algae (BBE probe), and also the turbidity and oxygen measures. Such a 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.* 2009) or Cichlids (Okun *et al.* 2007). However, in the experiments of Bertolo *et al.* (1999b) and Danger *et al.* (2009), which 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. Other factors than changes in top-down control must be taken into account for explaining the observed fish effect.

One potential explanation might be the resuspension of settled phytoplankton by fish, as demonstrated in an enclosure experiment with common carp (*Cyprinus carpio* L.) by Roozen *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, fish negatively affected diatoms, which are characterized by a high sedimentation rate. 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. The water of the stocking lake is nutrient-poor (P-PO<sub>4</sub> ≈ 5 µg L<sup>-1</sup>, N-NO<sub>3</sub> ≈ 50 µg L<sup>-1</sup>). Nitrogen and phosphorus were only added at the beginning of the experiment (56 µg P L<sup>-1</sup> and 140 µg N L<sup>-1</sup>). Considering, the rapid and important growth of primary producers in the first weeks of the experiment, phytoplankton probably became rapidly nutrient-limited (this point will be verified soon by the analyses of dissolved nutrients). Consumer-driven recycling (in particular direct excretion by fish) has been proposed to play a key role in determining nutrient availability of nutrients for phytoplankton (Vanni & Layne 1997; Vanni 2002). In the enclosures, zooplankton excretion was probably negligible compared to fish one, as zooplankton represented less than 2% of fish biomass. This probably explained the positive effect of fish on phytoplankton. Such a positive effect associated to nitrogen excretion by fish had been previously observed in very similar conditions (Danger *et al.* 2009). The fact that this positive effect was only observed in light-depleted enclosures is also in good accordance with the very probable limitation of phytoplankton by Nitrogen,



expected when taking into account the very low N:P ratio ( $N:P = 2.5$ ) of dissolved nutrients added in the systems. Such N-limitation should induce low N:P ratio within algal cells (this point will be also tested through the analysis of N:P ratio of seston). Nitrogen atoms are components of the chlorin 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). Consequently, we expect a much higher positive effect of nutrient excretion by fish in light-depleted enclosures.

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 macroinvertebrate abundance, they were frequent in fishless enclosures and virtually absent in fish ones. Thus, they clearly constituted a food source for rudd and roach, in total accordance with other mesocosm results (Dorenbosch & 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). Rudd and roach are the most herbivorous fishes under our temperate climates (Dorenbosch & Bakker 2012). If they are clearly unable to eat efficiently small algal particles, they are totally able to consume filamentous algae that form large aggregations (Prejs 1984). Thus, they probably consumed filamentous algae in the enclosures. Last, algal development and settling organic matter in the enclosures may have favoured more benthic and littoral secondary food chains (for

example, through periphyton consumers and detritivorous microinvertebrates and macroinvertebrates 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?***

At this time, the main argument in favour of an impact of fish on the microbial loop is only indirect and associated to a significant fish effect observed in the catabolic activity of the free microbial communities collected in the sediment traps. The utilization patterns of the 31 substrates of the Biolog EcoPlates<sup>TM</sup> suggest that the relative oxidation of amines, amino acids, 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). The analysis of the quantity of settled material in the sediment traps will allow us to verify the hypothesis of a greater supply of labile organic matter in the bottom of the fish enclosures. 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 specialized 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. 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.

***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 before. We cannot infer at this time on the effects of light on the microbial loop. Such effects potentially exist even if light filtration does not seem to affect significantly microbial metabolic activities on the substrates of the Biolog EcoPlates™. Our results showed that an increase of light resulted in an increase of DOC, which could impact in turn bacterial communities and their consumers. DOC is produced during active photosynthesis by phytoplankton, and primary production is considered as an important autochthonous source of DOC for heterotrophic microbial communities in aquatic ecosystems (e.g. Baines & Pace 1991; Morana *et al.* 2014). Further analyses should allow us to separate between two complementary effects for understanding light effects on DOC accumulation.

First, this increase of DOC might be simply an effect of phytoplankton biomass (more primary producers proportionally imply more exudation). Second, this increase could partly reflect the hypothesis of Sterner *et al.* (1997): a higher light:nutrient ratios should induce a higher C:nutrients cell ratio (see for example Danger et al., 2009), and thus a higher percentage of primary production lost to exudation. The light:nutrient ratio and the DOC supply might also affect the importance of mixotrophy (Jäger *et al.* 2014). The significant interaction between light, organic matter addition and fish presence on DOC accumulation suggests complex interactions between the presence of fish top predators and the bottom-up coupling between green and brown food webs. The smaller effect of light on DOC increase in presence of fish could be related to weaker light effects on phytoplankton concentration in fish enclosures. However, in the presence of fish, the effects of light on DOC concentration also depended on direct addition of organic carbon, resulting in an increase of DOC only when organic carbon was added. This complex interactive effect on DOC concentration should deserve further attention. Future FACS analyses should allow us to better understand these results and to verify the existence of light effects on the relative importance of prokaryotes and eukaryotes and the importance of mixotrophy.

At this time, the addition of direct organic matter appeared to have only limited effects on community functioning. Moreover, these effects were frequently dependent upon the effects of the other manipulated factors, such as for DOC accumulation discussed in the previous paragraph. Organic carbon addition tended to slightly decrease oxygen concentration in the water, which might reflect an increase in bacteria activity. Surprisingly,

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). The results on metabolic activities on the substrates of the Biolog EcoPlates™ at one sampling date suggest complex interaction effects between light intensity and organic matter, which should deserve further attention. DOC addition in interaction with fish presence also slightly affected green algae concentration as measured by the BBE probe: addition of DOC tended to slightly increase green algae concentration in absence of fish. This slight positive effect is in contradiction with a previous experiment showing reduced phytoplankton biomass in response to addition of labile DOC (Joint *et al.* 2002). The contrast between our results and those of Joint *et al.* (2002) 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 mg C L<sup>-1</sup> over a period of 15 weeks while Joint *et al.* added between 4,5 and 9 mg C L<sup>-1</sup> over a period of 6 days only). Joint *et al.* (2002) also found an increase in bacterial production following DOC addition. Overall effects of DOC addition on microbial communities cannot be fully inferred at this time in our experiment because we only have results on microbial metabolic activities on the substrates of the Biolog EcoPlates™. 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. The

potential direct use of DOC by algae through mixotrophy and the rather low organic carbon loads added experimentally might also explain these limited effects.

### ***Perspectives and conclusion***

Our preliminary 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 seems to be weak, maybe due to the spatial separation of the pelagic phytoplankton community and the benthic bacterial community. Fish presence has 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 preliminary 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). Additional analyses of samples for phytoplankton and zooplankton composition, flow cytometry for determining microbial functional structure and analyses of water nutrient concentration should allow us to verify the hypotheses discussed above and to investigate further the interactions between effects of fish, light and organic matter addition in this experiment. Indeed, data on phytoplankton and zooplankton composition will give more detailed insights on the response of the green food web. Meanwhile, flow cytometry will bring information on the response of interactions between primary producers and decomposers by estimating the relative abundance of photosynthetic and heterotrophic microorganisms and the importance of mixotrophy. Last, the response of nutrient concentration to experiment

treatments should allow to further test our hypothesis on fish effects on nutrient algae limitation.

## **Acknowledgments**

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## Tables

**Table 1:** Summary of the statistical models used to test the effects of the experimental treatments. The best model was that with the lowest AICc. When interaction terms were significant, the main effects presented in the table were evaluated from a model without the corresponding interactions.

Response type	Response variable	Best model	Predictors and corresponding statistic values
Phytoplankton	Green algae	L*P + M*P	P $X^2= 15.9$ $p < 0.0001$
			L $X^2= 15.1$ $p < 0.0001$
			M $X^2= 0.05$ $p =0.81$
			L:P $X^2= 9.01$ $p = 0.0026$
			M:P $X^2= 4.25$ $p = 0.039$
	Blue green algae	P	P $X^2= 6.72$ $p = 0.009$
	Diatoms	P + L	P $X^2= 5.75$ $p = 0.016$
			L $X^2= 3.34$ $p = 0.067$
	Chlorophyll a	L*P	P $X^2= 14.9$ $p=0.0001$
			L $X^2= 18.6$ $p < 0.0001$
L:P $X^2= 4.63$ $p = 0.031$			
Seston	L*P	P $X^2=6.73$ $p=0.009$	
		L $X^2=5.56$ $p=0.018$	
		L:P $X^2=6.72$ $p=0.009$	
Zooplankton	Dry biomass	n.s	n.s
Fish	Fish growth	L + Species	L $X^2=9.45$ $p=0.002$
			Species $X^2=10.7$ $p=0.001$
Water physico-chemistry	O <sub>2</sub> concentration	P + M	P $X^2=14.83$ $p=0.0001$
			M $X^2= 4.70$ $p=0.03$
	Turbidity	L*P + M*P	P $X^2= 27.34$ $p < 0.0001$
			L $X^2= 19.13$ $p < 0.0001$
			M $X^2= 0.44$ $p=0.50$
			L:P $X^2= 6.56$ $p=0.01$
			M:P $X^2= 3.88$ $p=0.048$
DOC	Time*L*P*M	L:P:M:Time $X^2=6.9$ $p = 0.008$	



**Table 2:** Summary of the results of the permanova models testing the effects of the experimental treatments on the catabolic activity of benthic and pelagic microbial communities. 10000 replicate permutations were used for the hypothesis tests. L: light intensity, M: input of organic matter, P: fish presence, : indicates interaction between two predictors.

		Pelagic community end of September			Pelagic community end of October			Benthic community end of November		
Predictors	<i>df</i>	<i>SS</i>	<i>F</i>	<i>p</i>	<i>SS</i>	<i>F</i>	<i>p</i>	<i>SS</i>	<i>F</i>	<i>p</i>
M	1	1.557	0.815	0.24	0.615	0.795	0.40	<b>4.48</b>	<b>1.499</b>	<b>0.046</b>
L	1	0.9630	0.504	0.54	0.753	0.975	0.27	2.09	0.698	0.35
P	1	<b>3.72</b>	<b>1.948</b>	<b>0.022</b>	<i>1.310</i>	<i>1.695</i>	<i>0.059</i>	<b>33.17</b>	<b>11.09</b>	<b>0.0001</b>
M:L	1	<b>3.065</b>	<b>1.605</b>	<b>0.044</b>	0.501	0.648	0.55	2.73	0.914	0.19
M:P	1	1.841	0.964	0.17	0.500	0.647	0.55	1.97	0.66	0.39
L:P	1	1.523	0.797	0.26	1.110	1.437	0.10	1.50	0.50	0.58
M:L:P	1	1.274	0.667	0.35	0.497	0.642	0.56	2.31	0.77	0.28

**Table 3:** Summary of the statistical models used to test the effects of the experimental treatments on average relative oxidation of the different types of substrates by benthic and pelagic microbial communities. The best model was that with the lowest AICc. L: light intensity, M: input of organic matter, P: fish presence.

Substrate type	Pelagic community end of September		Pelagic community end of October		Benthic community end of November	
	Best model	Statistic values of predictors	Best model	Statistic values of predictors	Best model	Statistic values of predictors
Carbohydrates	P	$X^2= 2.2$ $p=0.14$	ns	ns	P	$X^2= 3.62$ $p=0.057$
Amino acids	ns	ns	ns	ns	P	$X^2= 22.8$ $p<0.001$
Amines	ns	ns	L	$X^2= 2.6$ $p=0.11$	P	$X^2= 20.4$ $p<0.001$
Carboxylic acids	ns	ns	ns	ns	P	$X^2= 12.9$ $p<0.001$
Polymer	ns	ns	ns	ns	M	$X^2= 3.22$ $p=0.072$
Phenolic acids	ns	ns	ns	ns	M+P	M: $X^2= 3.76$ $p=0.052$ P: $X^2= 23.4$ $p<0.001$

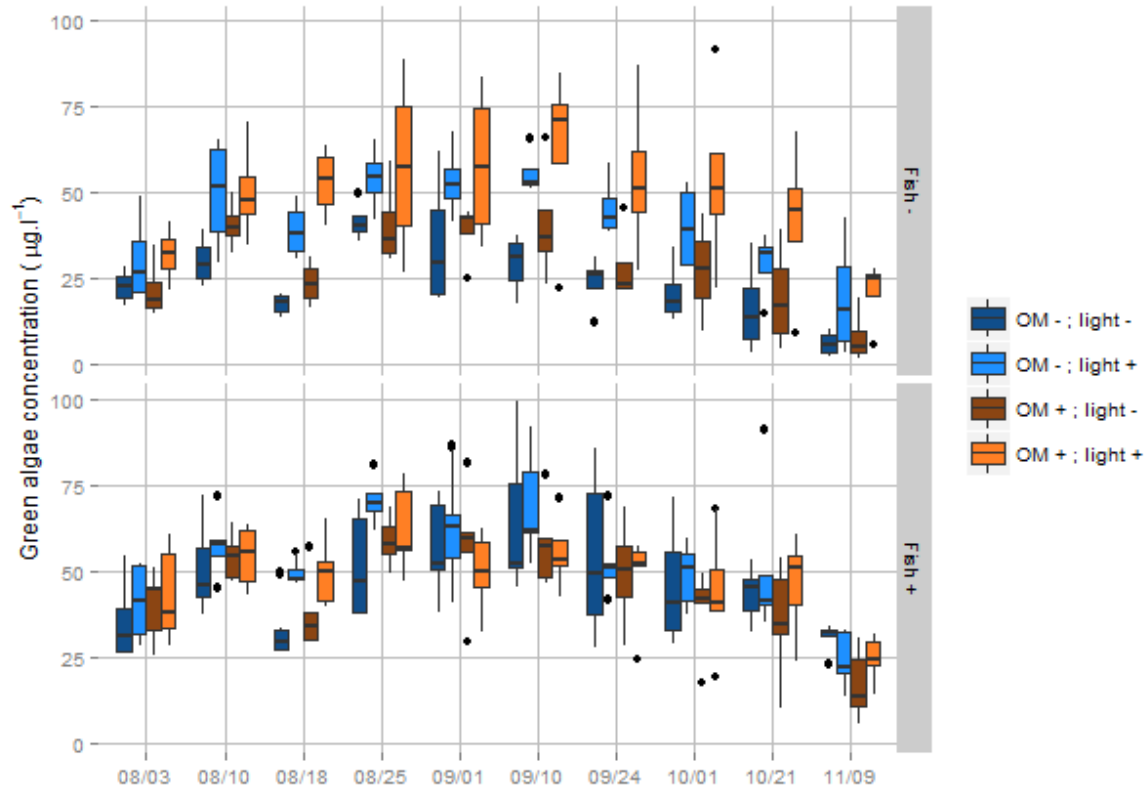
## Figures



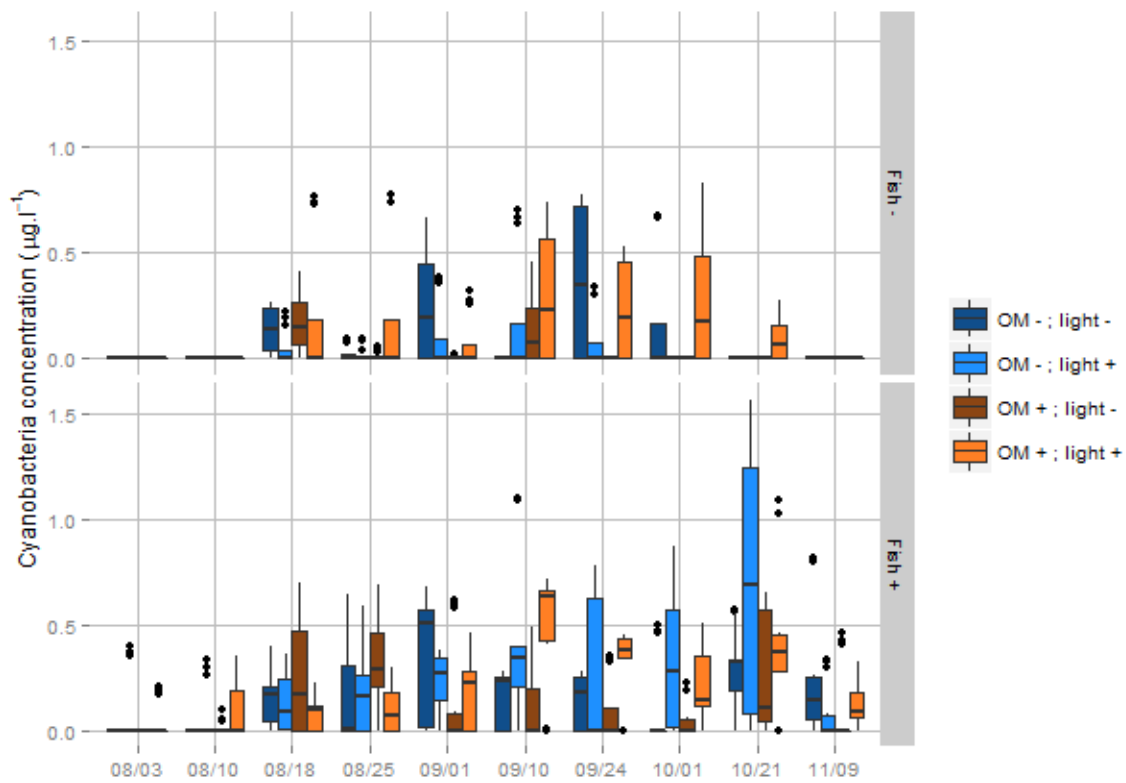
**Figure 1:** Plan of the experimental setting. Three treatments are crossed: light filtration, soluble organic carbon addition and fish, the each final treatment is represented by color. The cells represent the mesocosms and contain the list of treatments.



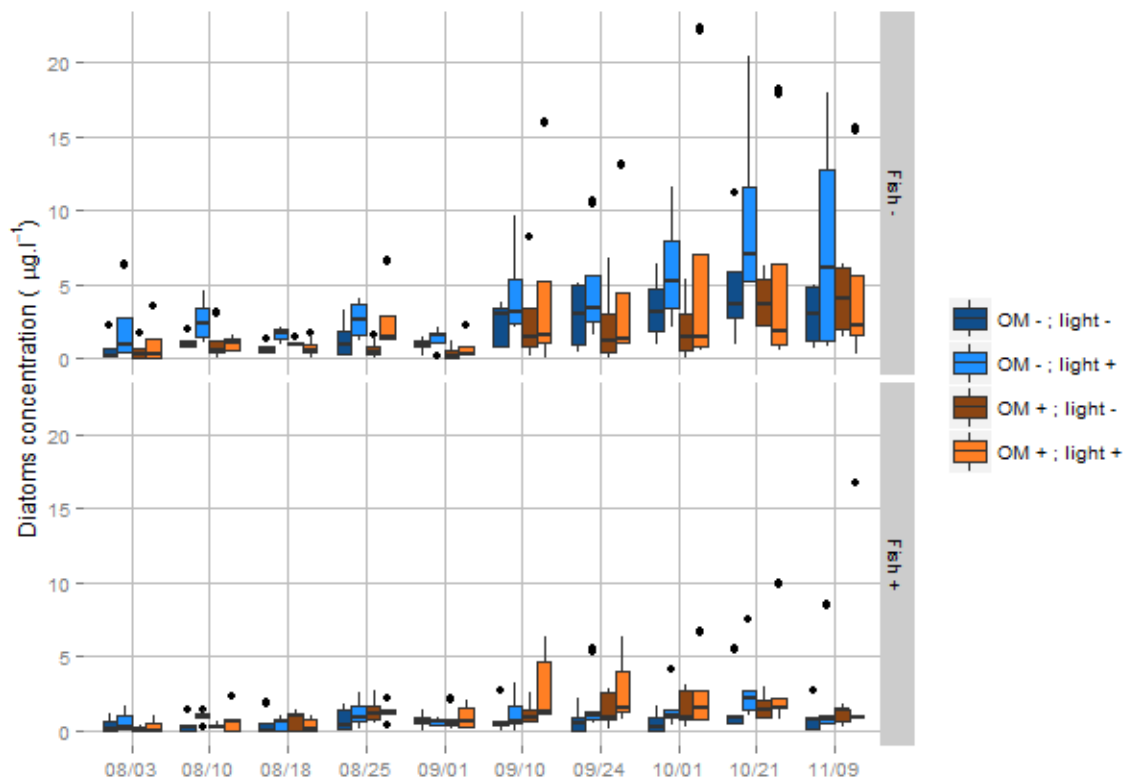
**Figure 2:** Photo of the experiment during a sampling session. The six mesocosms at the front are uncovered for allowing sampling.



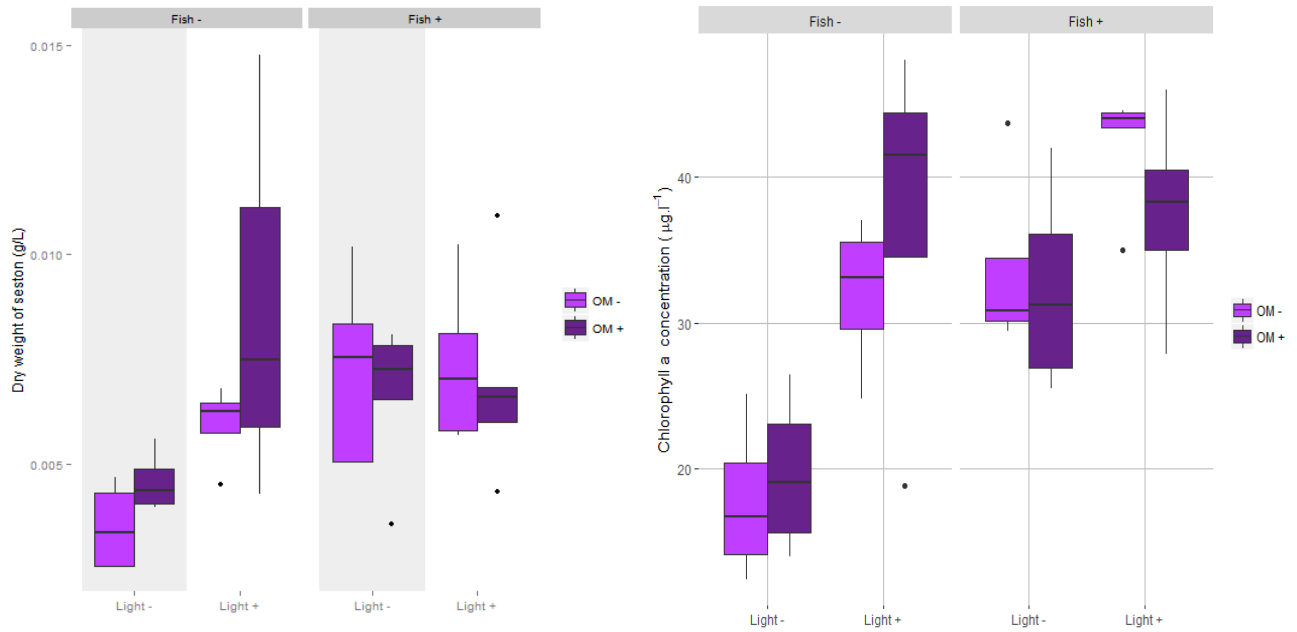
**Figure 3:** Green algae Chlorophyll a concentration ( $\mu\text{g.L}^{-1}$ ) measured by the BBE probe. Each sampling date is represented in the x-axis (the first date has been removed from the statistical analysis because of the bloom of algae after the nutrient addition). In the legend, the blue coloration corresponds to enclosures without organic matter addition and the brown coloration corresponds to the enclosures with organic matter addition. The dark colours correspond to enclosures with light filtration and the light colours to enclosures without light filtration.



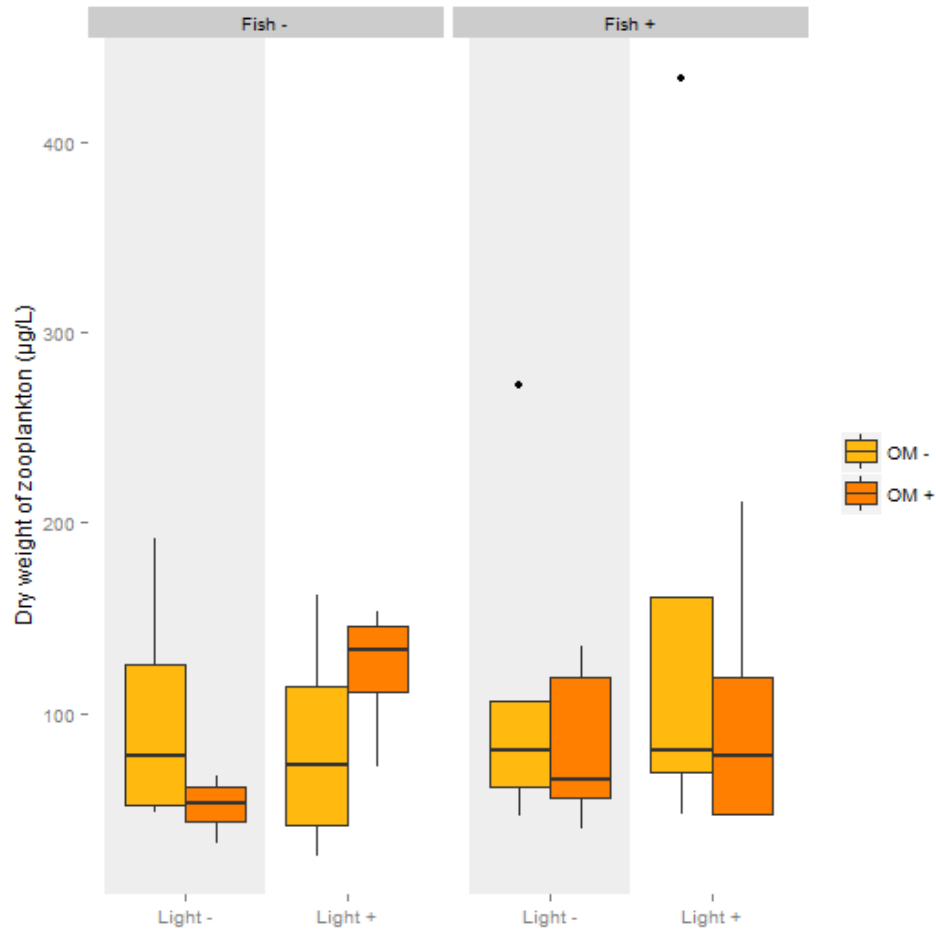
**Figure 4:** Cyanobacteria concentration ( $\mu\text{g.L}^{-1}$ ) measured by the BBE probe. Each sampling date is represented in the x-axis (the first date has been removed from the statistical analysis because of the bloom of algae after the nutrient addition). In the legend, the blue coloration corresponds to enclosures without organic matter addition and the brown coloration corresponds to the enclosures with organic matter addition. The dark colours correspond to enclosures with light filtration and the light colours to enclosures without light filtration.



**Figure 5:** Diatoms concentration ( $\mu\text{g.L}^{-1}$ ) measured by the BBE probe. Each sampling date is represented in the x-axis (the first date has been removed from the statistical analysis because of the bloom of algae after the nutrient addition). In the legend, the blue coloration corresponds to enclosures without organic matter addition and the brown coloration corresponds to the enclosures with organic matter addition. The dark colours correspond to enclosures with light filtration and the light colours to enclosures without light filtration.

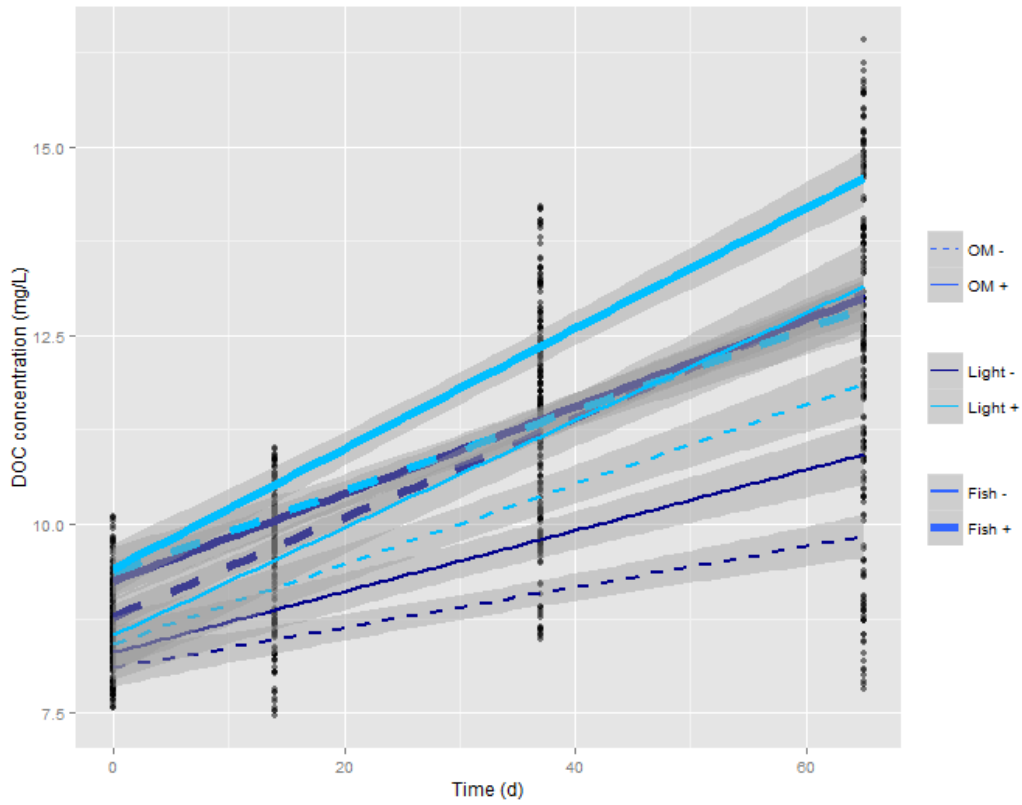


**Figure 6:** Dry mass of seston (g/L) and average chlorophyll a concentration over time measured by the multiparameter probe, regarding the three treatments. In each plot, the left panel corresponds to the enclosures without fishes, the right panel to the enclosures with fishes. The light treatment is represented by the x-axis and emphasized by a grey background corresponding to the treatment with light filtration. The colour corresponds to the organic matter treatment, the dark purple boxplot representing the enclosures that received organic carbon.

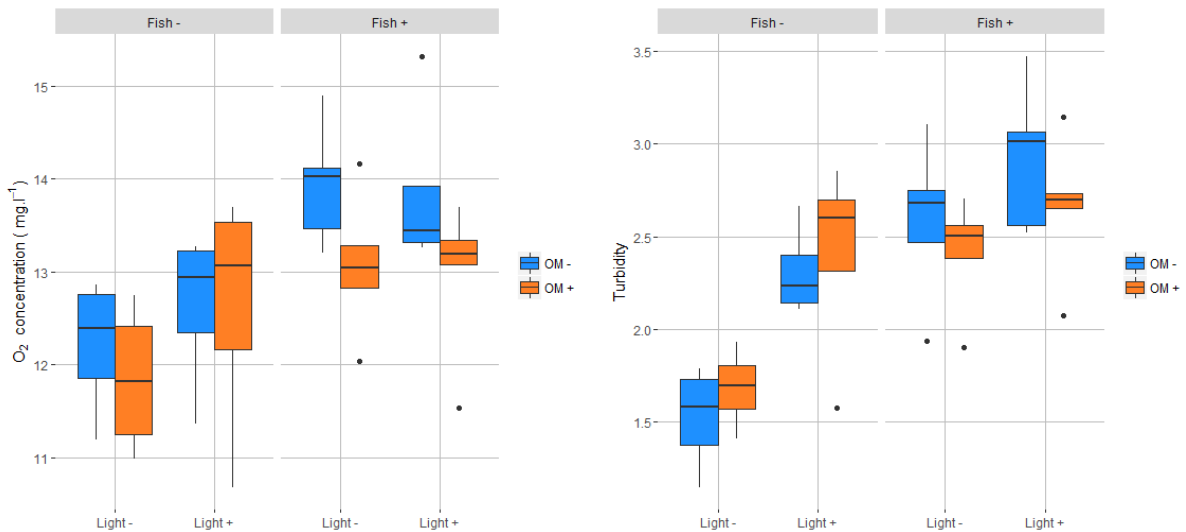


**Figure 7:** Dry biomass of zooplankton ( $\mu\text{g/L}$ ) regarding of the three treatments. The left panel corresponds to the enclosures without fishes, the right panel to the enclosures with fishes. The light treatment is represented by the x-axis and emphasized by a grey background corresponding to the treatment with light filtration. The colour corresponds to the organic matter treatment, the dark orange boxplot representing the enclosures that received organic carbon.

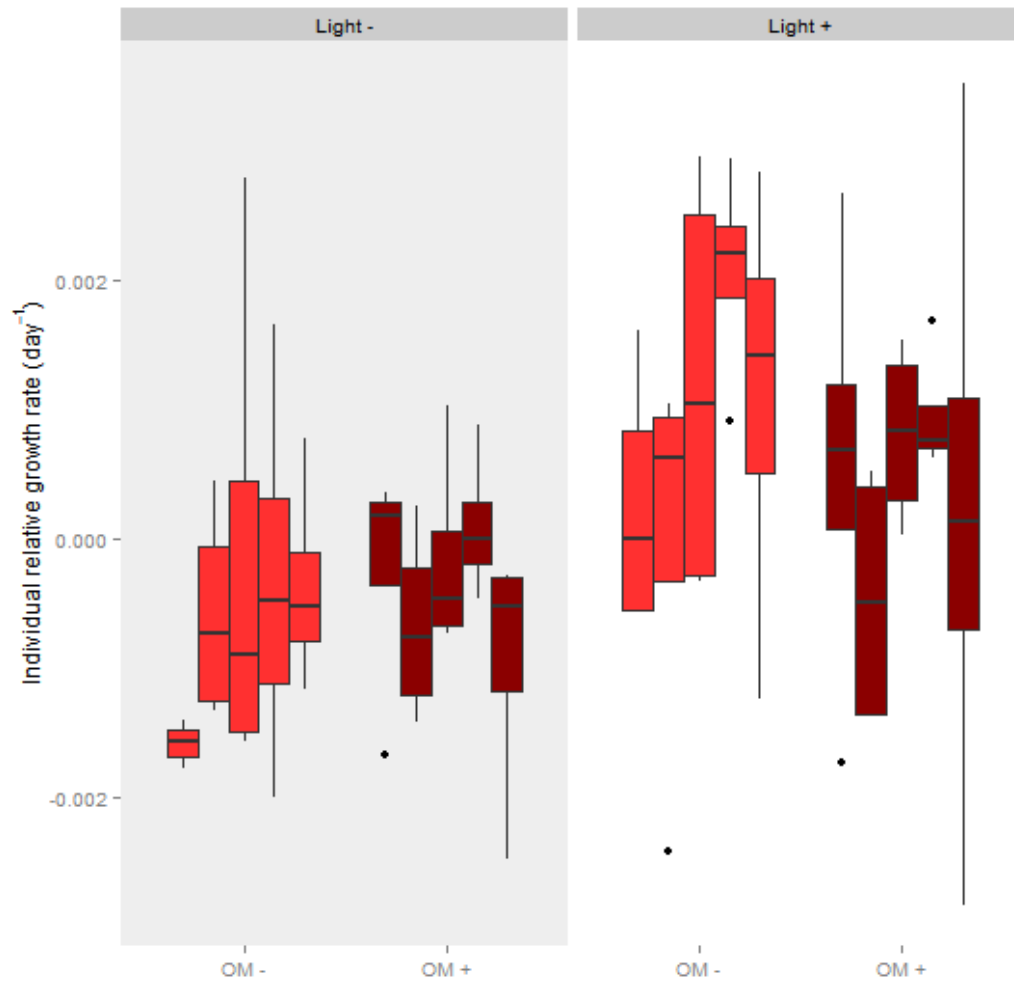




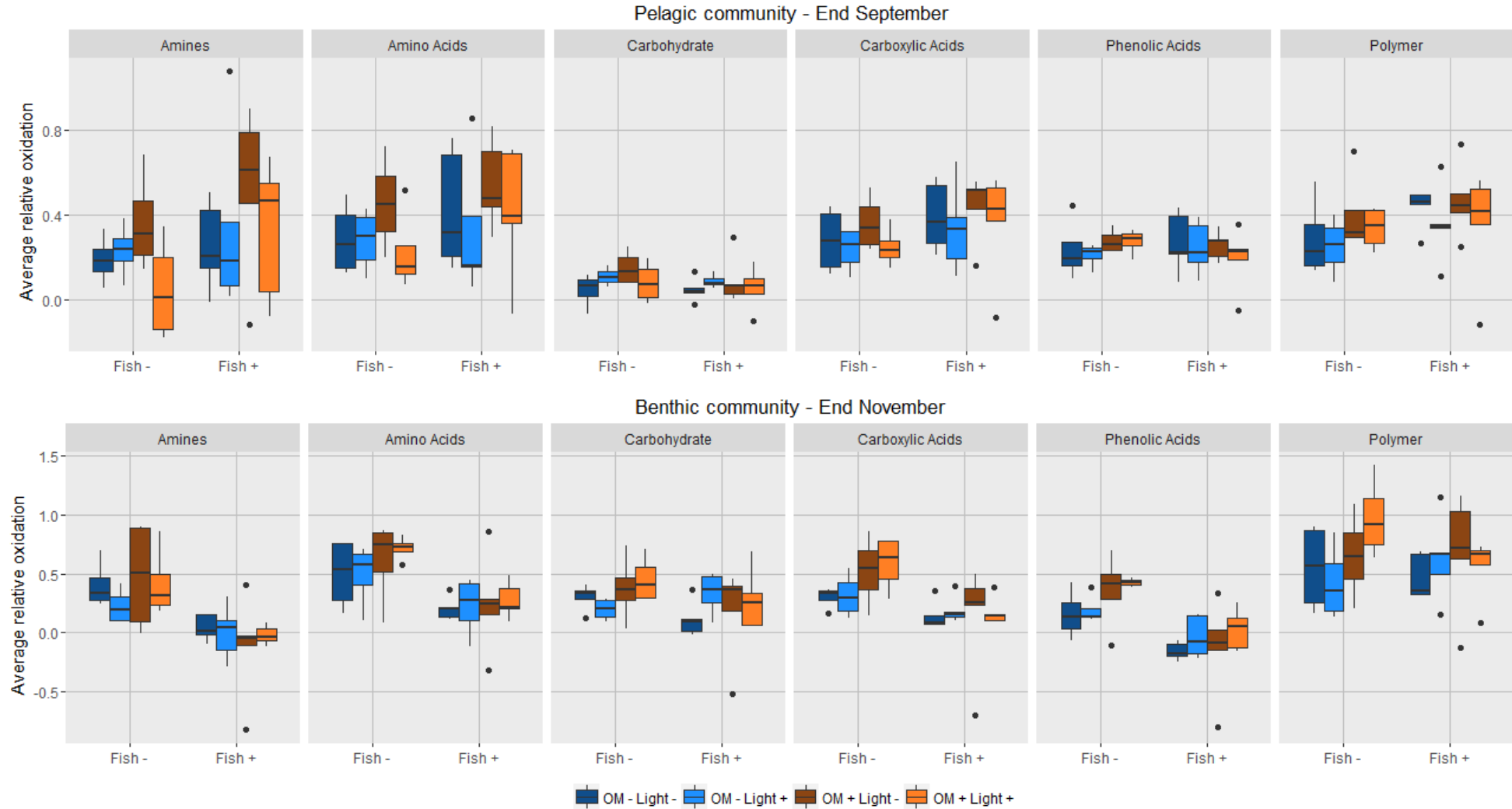
**Figure 8:** Dissolved organic carbon concentration ( $\text{mg}\cdot\text{L}^{-1}$ ) for each sampling date. Lines represent statistical model predicted values and the grey color represents the confidence interval.



**Figure 9:** Average  $\text{O}_2$  concentration ( $\text{mg}\cdot\text{L}^{-1}$ ) and average water turbidity over time, as measured by the multiparameters probe.



**Figure 10:** Individual growth rate normalized to the initial body mass of each fish. Each box plot corresponds to the fishes from one enclosure and the colour corresponds to the organic matter addition treatment (as indicated by the x-axis).



**Figure 11 :** Average relative oxidation of the different biochemical substrates in the different experimental treatments, as measured 7 days after inoculation of the microbial communities.

## **Chapter 6**

### **Discussion**

The different studies in my thesis demonstrate the importance of considering the interactions between the green and brown food webs for studying how food web structure affects ecosystem functioning. There are three interactions between the two food webs: 1) nutrients recycled from all organisms in the whole food web couple the green and brown food webs through mutualistic/competitive interactions between primary producers and decomposers; 2) generalist consumers feeding on prey from both food webs; and 3) the spatial connections through mobile generalist consumers at the top and the nutrient and detritus fluxes at the bottom of the food webs. Modeling these interactions lead to (1) new insights on the study of consequences of food web structure, (2) predictions that are different from previous modelling results, (3) new interpretation of empirical studies (e.g. exploring the underlying mechanisms behind observations), (4) new interpretations/ predictions on differences between ecosystem types and (5) novel predictions on food web responses to human impacts and the global change. Here, I first discuss the above mentioned points about the importance of integrating interactions between the green and brown food webs into food web models. Secondly, I present several ideas for future research on these topics. The discussion focuses on my modelling studies because so far I only have very preliminary results for the experimental study.

## **6.1 Importance of integrating interactions between the green and brown food webs into food web models**

### **6.1.1 New insights on the modeling of food webs**

In this thesis, the food web models not only include population dynamics but also takes into account interactions through nutrient cycling. Two compartments (i.e. nutrient and detritus) and two ways of nutrient cycling (i.e. direct and indirect) are integrated into the food web models to represent important aspects of nutrient dynamics. The decomposers can be either carbon-limited or nutrient-limited and their uptake of mineral nutrients is modelled based on the stoichiometric mismatches between decomposers and their resources (chapters 2, 3, 4). These new ways of modelling interactions in food webs introduces both mutualistic and competitive interactions between primary producers and decomposers. These specific interactions further lead to complex indirect interactions between the green and brown food webs. There are so far very few theoretically studies that have recognized the importance of considering nutrient cycling and related interactions. DeAngelis was one of the first to integrate nutrient cycling into food web models and he showed recycling effects on ecosystem stability (DeAngelis *et al.* 1989b). More recent modeling studies also begin to address nutrient cycling within food webs (De Mazancourt *et al.* 1998, 1999; Cherif & Loreau 2013; Wolkovich *et al.* 2014). However, these models only consider the green food web and the decomposers, omitting the dynamics and effects of higher trophic levels in the brown food web and most indirect nutrient cycling processes. The results obtained in this thesis highlight strong effects of both direct and indirect nutrient cycling and related complex interactions between the two food webs on ecosystem functioning. Therefore, as another modelling study by Attayde and Ripa (2008), my work

suggests new insights on the functioning of food webs by integrating both direct and indirect nutrient cycling and both green and brown food webs.

The coupling of the green and brown food webs by top generalist consumers is another important factor (chapters 3 and 4). The prevalence of multi-channel feeding by consumers at higher trophic levels have been long recognized and assumed to have stabilizing effects in ecosystems (Moore & William Hunt 1988; Polis & Strong 1996; McCann *et al.* 2005; Rooney *et al.* 2006; Gauzens *et al.* 2015). However, in these studies the coupled channels are considered as either both green or both brown channels, the interactions at the bottom of the food webs are thus different from that when both green and brown food channels are considered. Accordingly, the bottom-up effects due to specific mutualistic and/or competitive interactions between primary producers and decomposers can interact with the top-down effects of the generalist consumers to affect ecosystem functioning. Therefore, this work suggests the importance of considering both top and bottom couplings between the green and brown food webs in models.

Further, two types of spatial dynamics might be used to model interactions between green and brown food webs (chapter 4). The generalist consumers are considered to move and forage over a larger spatial scale than their prey, which leads to functional responses of the consumers that depend on the relative foraging scale of the consumers and the prey (i.e. whether the consumers need to make a choice between different prey habitat according to the scale of their foraging habitat compared with prey habitat) (McCann *et al.* 2005). This spatial dynamic has been used to highlight the role of space in changing the functional responses of consumers but previous models assumed no exchanges at lower trophic levels and between nutrient and detritus compartments (McCann *et al.* 2005). Fluxes of nutrients and detritus between patches

can be modeled as in the meta-ecosystem theory (Loreau *et al.* 2003b; Gravel *et al.* 2010a). The meta-ecosystem theory highlights the spatial exchanges in nutrient and detritus fluxes as well as the dispersals of organisms, but the different habitat scaling of different trophic levels is not considered in the dynamics. In the thesis, these two mechanisms through which nutrients are exchanged between parts of the food web are integrated into a single framework, and effects of both habitat/foraging scaling and spatial fluxes are studied, bringing another insight in food web modeling.

Overall, my thesis highlights the main interactions between the green and brown food webs and shows how to integrate them into food web models. These new interactions can bring new predictions on key aspects of ecosystem functioning such as productivity and stability.

### **6.1.2 Different predictions to previous studies**

Since new interactions have been introduced into food web models, I obtained predictions that are different from previous studies that only considered trophic interactions. 1) The top-down effects of one food chain (green or brown) can extend to affect the production of the other food chain. 2) The signs of the trophic cascades from one food web to the other are determined by nutrient cycling and the complex interactions between primary producers and decomposers. 3) The asymmetry of turnover rates between coupled green and brown food channels does not necessarily increase stability.

The classical trophic cascade theory has been questioned in chapter 2. On the one hand, the classical top-down effects only affect the production within the food chain, whereas in the new models the top-down effects of one food chain (green or brown) can extend to affect the

production of the other food chain. On the other hand, the top-down effects are generally negative to the adjacent trophic levels and positive to the next adjacent trophic levels (Carpenter *et al.* 1985). However in the new models the signs of the trophic cascades from one food web to the other depend not only on the number of trophic levels in between but also on particular conditions related to nutrient cycling and the complex interactions between primary producers and decomposers. These new predictions help to explain some complex and even contradicting observations in empirical studies. For example, the extension of trophic cascades from the brown food web to the green food web can explain the widely observed “microbial-loop” effects (i.e. positive effects of predators of decomposers on primary production through nutrient cycling) (Caron *et al.* 1988; Bonkowski 2004; Krome *et al.* 2009). The condition-dependent signs of trophic cascades can help understand the positive, negative, or absence of effect of herbivores on decomposers found among relatively similar locations (Wardle *et al.* 2001).

The stabilizing effects of asymmetric energy and material transfers between channels in food webs with multi-channel feeding generalist consumers (Rooney *et al.* 2006) have also been questioned (chapter 3). My results show that asymmetry between coupled green and brown food channels does not necessarily increase stability and can instead be strongly destabilizing depending on stoichiometry-based interactions between primary producers and decomposers. A recent modelling study that considered the coupling of autotrophs and detritus by a first consumer level is consistent with my prediction that asymmetry might have destabilizing effects under certain conditions (Wolkovich *et al.* 2014). This new finding suggests that the bottom-up effects due to the complex relationship between primary producers and decomposers should not be ignored in studying the top-down effects of asymmetry on stability.



Overall, new predictions on ecosystem production and stability can be obtained with models integrating the interactions between the green and brown food webs. These modelling results can bring insights for interpreting empirical studies and for understanding differences between ecosystem types as well as consequences of global change on ecosystems.

### **6.1.3 Implication for empirical studies**

The modelling results can inspire empirical studies in mainly two ways: 1) they might allow exploring underlying mechanisms behind empirical observations; and 2) they can suggest new measurements on specific parameters relevant to the prediction of the models.

Different mechanisms behind empirical observations have been explored in this thesis. Detailed descriptions of these mechanisms are already outlined in the discussions of previous chapters. Here I only highlight two key factors behind the mechanisms determining the effects of interactions between green and brown food webs on ecosystem functioning. The first key factor is the stoichiometric mismatches between compartments. Ecological stoichiometry proposes that heterotrophic organisms absorb nutrients to maintain a relatively constant nutrient composition and excrete nutrients that are not needed (Vanni 2002). A species with a relatively lower mineral nutrient content should excrete more nutrients than a species with a higher nutrient content. Therefore, the stoichiometric mismatches between decomposers and their predators and between detritus and decomposers can determine the relative proportion of direct nutrient cycling of predators of decomposers and of decomposers, which is responsible for the mechanism behind the positive effects of predators of decomposers on primary production, the so called “microbial loop” effects (chapter 2). The difference in carbon to nutrient ratio between

decomposers and primary producers (that are also the main producer for detritus) can lead to difference in their demand for nutrients, resulting in different competition intensity between them (Daufresne & Loreau 2001), which can explain the observed contradictory results on cascading effects of the green food chain on the decomposers (chapter 2) and the difference in ecosystem stability among different ecosystem types (chapter 3).

The second key factor for ecosystem functioning is the interactions between top and bottom couplings of the green and brown food webs. The effects of top and bottom couplings and related mechanisms have been generally studied separately in previous studies. For example, the population asynchrony resulting from the coupling of fast and slow channels by top generalist predators has been considered as a mechanism increasing stability (Rooney et al. 2006). Other studies have shown that interspecific competition for resource increases both the amplitude (destabilizing effects) and the asynchrony (stabilizing effect due to the relative constant averaging responses to environmental fluctuations) of population fluctuations, which has contrasting effects on ecosystem stability (Loreau & de Mazancourt 2013). In the thesis, both mechanisms are considered: the bottom-up effects due to competition between autotrophs and decomposers interact with effects of asymmetry between the fast and slow channels, leading to complex consequences on stability shown in our model predictions (chapter 3). In a spatial context, it has been widely observed that the mobility of consumers and spatial flows of nutrient and detritus can both affect the ecosystem functions and food web structure across ecosystem boundaries (Soininen et al. 2015). In chapter 4 these interacting effects are explored theoretically, which shows that the asymmetric nutrient and detritus fluxes between the green and brown patches can interact with the asymmetric consumption of the green and brown prey

by top consumers to influence the relative importance of either the producers of the green patch or the decomposers of the brown patch in the whole ecosystem.

After proposing mechanisms behind the empirical studies, the thesis also provides practical ways to guide experiments and test the theory. Measuring the stoichiometric composition of the components in ecosystems (chapter 2 and 3), comparing the nutrient turnover speed between consumers in the green and brown food webs (chapter 3) and studying the direction of nutrient or detritus spatial fluxes (chapter 4) are all tractable ways for observing interactions between green and brown food webs and for studying related ecosystem functions in real ecosystems.

#### **6.1.4 Comparison between different ecosystem types**

The ecological attributes determining the interactions between the green and brown food webs and corresponding ecosystem functioning can be different depending on the ecosystem types. Therefore, the modelling results in the thesis can be used to further compare differences in ecosystem functioning between different ecosystem types, especially between aquatic and terrestrial ecosystems.

A large number of fundamental ecological characteristics are tightly correlated with the body size (Rooney *et al.* 2008). For example, the biomass turnover rates decrease with increasing body size thus smaller organisms tend to have greater turnover rates than larger organisms (Brown *et al.* 2004). The primary producers in aquatic systems are generally unicellular, whereas terrestrial plants are multicellular and more complex (Shurin *et al.* 2006). The differences in body size ratios can result in differences in biomass turnover rate (Peters 1986) between the green and brown channels between aquatic and terrestrial ecosystems, which

may lead to different effects on the ecosystem stability (chapter 3). There are also differences in nutrient stoichiometry between aquatic and terrestrial primary producers. Aquatic producers are generally rich in nutrient whereas terrestrial plants have more structural and transport tissues to be carbon-rich (Polis & Strong 1996). Accordingly, nutrient-poor detritus likely occur more often in terrestrial than in aquatic ecosystems (Grimm et al. 2003). These differences in nutrient stoichiometry may lead to differences between these ecosystem types in the relative proportion of direct/indirect nutrient cycling in the brown food webs and in competition intensity between primary producers and decomposers, which can affect the trophic cascades between food webs (chapter 2) and the ecosystem stability (chapter 3). Meanwhile, in aquatic ecosystems, the green and brown patches might be more decoupled spatially than in terrestrial ecosystems. In soils, decomposer-based brown food web are more spatially connected with plant roots which excrete more rapidly detritus to support the decomposers, whereas the pelagic and benthic habitats aquatic ecosystems are more spatially decoupled and the sedimentation or upwelling processes take more time to exchange nutrient and detritus between habitats (Krumins *et al.* 2013). The relative importance of the green and the brown pathways (i.e. the green- or brown- dominance) may be very different among ecosystems depending on the type of spatial coupling between green and brown pathways.

Overall, accumulating evidence indicates that aquatic and terrestrial food webs have many differences in their structure and function. Studying interactions between the green and brown food webs can be a very relevant way to address the differences in the food web structure and differences in ecosystem functioning between aquatic and terrestrial ecosystems.

### 6.1.5 Predicting ecosystem responses to global changes

As reviewed in the very beginning of the thesis (Chapter 1, Table 1), human activities (e.g. hunting, fishing, bioaccumulation of toxicants, land use changes, and fertilization) and global changes can modify the food web structure (e.g. changes in species interactions, altered dispersal patterns etc.), leading to significant changes in ecosystem functioning. This thesis highlights that interactions between the green and brown food webs are indispensable components of food web structure. Thus, studying the effects of human activities and global changes on these interactions is important for predicting ecosystem responses to global changes.

The mechanisms that link changes in interactions between the green and brown food webs to alterations in ecosystem functioning, such as population dynamics, energy flow, productivity, nutrient cycles and stability, are diverse. I list several examples of the potential shifts in interactions between the green and brown food webs due to global change and the possible consequences on ecosystem functioning in Table 1. The mechanisms behind most of these predictions are based on the two key factors discussed in 6.1.3: 1) the stoichiometric mismatches within the food web and 2) the interactions between top and bottom couplings between the green and brown food webs. For example, enhanced atmospheric CO<sub>2</sub> and eutrophication can cause changes in C:Nutrient ratios of primary producers, detritus and decomposers (Sardans *et al.* 2012a; Zechmeister-Boltenstern *et al.* 2015), potentially leading to different stoichiometric mismatches between compartments in the ecosystem. Since stoichiometry mismatches between decomposers and detritus and between decomposers and their predators are key factors determining the direct/indirect nutrient cycling of the brown food web and the mutualistic/competitive interactions between primary producers and decomposers,

the shifts in these mismatches can result in shifts in the signs of trophic cascading effects between the green and brown food chains. The asymmetry between turnover rates of the green and brown channels coupled by generalist consumers can be modified by changes in either/both turnover of the two channels due to enhanced atmospheric CO<sub>2</sub>, eutrophication, warming or drought (Xu-Ri *et al.* 2012; Zechmeister-Boltenstern *et al.* 2015). For example, enhanced CO<sub>2</sub> can promote plant growth (i.e. faster green food channel) and is responsible for higher C:N ratios in plant litters, resulting in slower decomposition rate thus potentially slower brown food channels. Besides, climate-driven losses of species can even decouple the green and brown chains at the top of food webs (Doney *et al.* 2012). Ecosystem stability can be affected by such top-down impacts, as well as through bottom-up impacts of altered mutualistic/competitive interactions between primary producers and decomposers. Further, human induced habitat fragmentation or land reclamation in lakes can cause habitat compression (i.e. the reduction of spatial scale of resources habitat related to the foraging scale of the mobile consumers, thus consumers forages in both prey habitats simultaneously) in the ecosystems, which can alter the functional responses of generalist consumers towards preys in the green and brown patches, resulting in spatially well mixed green and brown patches with less effects of asymmetry of consumption by the generalists (McCann *et al.* 2005). Global change can alter the patterns of ocean material circulation, resulting in changes in the direction of nutrient and organic matter transports that provide important connectivity across marine ecosystems (Keeling *et al.* 2010; Doney *et al.* 2012). Changes in landscape configuration caused by human action can disrupt the exchanges of nutrient and detritus (Mumby & Hastings 2007). Both changes in top-down effects of generalist consumers and the bottom-up effects of nutrient and detritus flux can alter the

relative importance of either the producers of the green patch or the decomposers of the brown patch in the whole ecosystem.

Overall, predicting ecosystem responses to global changes requires a thorough understanding of the impact of food web structure on ecosystem functioning, which should include the interactions between the green and brown food webs.

**Table 1.** Effects of human impacts and global change on the interactions between the green and brown food webs and potential consequences on ecosystem functioning as predicted by the models developed in this thesis

<b>Human impacts and global changes</b>	<b>Results in ecosystems</b>	<b>References</b>	<b>Affected interactions</b>	<b>Potential Consequences</b>
Enhanced atmospheric CO <sub>2</sub>	Increases in plant and detritus C:nutrient ratios	(Sardans <i>et al.</i> 2012a)	Increased competition between primary producers and decomposer.	Effects on trophic cascades between food chains and on ecosystem stability
	Faster plant growth and slower decomposition	(Xu-Ri <i>et al.</i> 2012)	Asymmetry in turnover rates between the green and brown channels	Effects on ecosystem stability
Eutrophication	Increases in nutrient availability and decreases in plant and detritus C:nutrient ratios	(Zechmeister-Boltenstern <i>et al.</i> 2015)	The mutualistic/competitive interactions between primary producers and decomposer.	Effects on trophic cascades between food chains and on ecosystem stability
Warming and drought	Increases in plant and detritus C:nutrient ratios	(Sardans <i>et al.</i> 2012a)	Increased competition between primary producers and decomposer.	Effects on trophic cascades between food chains and on ecosystem stability
	Reduced green channel turnover	(Moran <i>et al.</i> 2010)	Asymmetry in turnover rates between the green and brown channels	Effects on ecosystem stability



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Species loss	Decoupling multi-channel energy and material transfers at the top of food webs	(Doney <i>et al.</i> 2012)	The coupling of asymmetric green and brown channels	Effects on ecosystem stability
Habitat fragmentation	Habitat compression and altered functional responses of generalist consumers	(McCann <i>et al.</i> 2005)	Less effects of asymmetry by generalist consumption	Effects on the dominance of either the producers or the decomposers in the whole ecosystem
Global warming	Altered material circulation. Changes in the direction of spatial nutrient and detritus flows	(Keeling <i>et al.</i> 2010)	The spatial coupling of green and brown patches at the bottom of the food webs	Effects on the dominance of either the producers or the decomposers in the whole ecosystem
Changes in landscape configuration	Disrupted exchanges of nutrient and detritus. Decoupling the energy and material transfers at the bottom of food webs	(Mumby & Hastings 2007)	The spatial coupling of green and brown patches at the bottom of the food webs	Effects on the dominance of either the producers or the decomposers in the whole ecosystem

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## 6.2 Perspectives

Here I highlight three important topics that might represent the next steps in studying how interactions between the green and brown food web can affect ecosystem functioning.

### 6.2.1 Increasing the complexity of the food web model

So far, the interactions between the green and brown food webs have been studied within a simple framework that only includes coupled green and brown food chains. Larger systems with more species/functional compartments both in the green and brown food webs would probably lead to more realistic results, which may be more representative of empirical observations. However, including too many realistic features can make the food web model too complex to understand. Therefore I focus on a few selected mechanisms to be integrated in models and that may provide useful insights.

- Stoichiometric models

The interaction between primary producers and decomposers are modelled in my thesis using basic stoichiometric hypotheses. We do not model explicitly a carbon compartment and a nutrient compartment for the components in the food web model as done in stoichiometric-explicit models (Daufresne & Loreau 2001). Using more stoichiometric-explicit models could increase our understanding of the impact of differences (1) in detritus quality (Wardle et al. 2004), (2) in nutrient limitation of decomposers (Chase 2000) and (3) in decomposers resource preference and use efficiency (Moore *et al.* 2004) on complex interactions between primary producers and decomposers and related ecosystem functioning.

- More interactions due to top and bottom couplings

The top coupling of the green and brown food webs by generalist consumers can occur at different trophic levels and with distinct trophic lengths of both food webs (Wollrab et al. 2012). Omnivores can also couple the green and brown food webs. Further, the number of top interactions can be different between different ecosystem types. For example, aquatic systems tend to have more generalist consumers and more omnivory within the food web (Shurin et al. 2006).

The bottom coupling of the green and brown food webs involves other types of interactions that I have not included in my models. The existence of mixotrophic organisms (i.e. combination of auto- and heterotrophic trophic modes) in aquatic ecosystems represents a new bottom interaction which is different from the mutualistic/competitive interaction between primary producers and decomposers (Mitra *et al.* 2014). In terrestrial ecosystems, communities may produce litters of different qualities with contrasting mineralization rates that depend on the whole food web (Wardle et al. 2004; Canuel et al. 2007; Allard et al. 2010; Danger et al. 2012) or on the brown food-web characteristics and soil /sediment characteristics (Wolters 2000; Fontaine & Barot 2005; Harrault et al. 2014), which leads to more complex interactions at the bottom of coupled green and brown food webs.

These interactions due to top and bottom couplings depend largely on specific characteristics of aquatic and terrestrial ecosystems. Thus, studying these interactions can also allow making more explicit comparison between the functioning of aquatic and terrestrial ecosystems

- Complex realistic interaction network models

We should build new models that contain more species and more connections between these species to represent more realistic interaction network structure. Network approaches can permit to better describe interactions between species in ecosystems, to integrate different types of interactions (e.g. trophic, non-trophic, indirect mutualistic etc.) and to investigate the effects of network structure on ecosystem functioning (Montoya et al. 2006; Allesina & Pascual 2008; Thébault & Fontaine 2010). The models developed in this thesis demonstrate that nutrient cycling and interactions between the green and brown food webs can affect ecosystem functioning. It will be necessary to integrate these interactions into more complex network models to explore these effects in a more realistic context.

### **6.2.2 Studying additional ecosystem functions**

The thesis focuses mainly on the primary producer and decomposer biomasses and their production and the stability of the ecosystems, however, other aspects of ecosystem functioning could be studied in future researches.

- Nutrient flows

Although the modelling approach in the thesis is based on nutrient dynamics, the nutrient fluxes within the whole food web has not been examined in great detail. There are at least four types of nutrient fluxes: 1) inputs and outputs of nutrient and detritus; 2) trophic fluxes due to consumer-resource interactions; 3) recycling fluxes of direct and indirect nutrient cycling and 4) spatial exchanges of nutrient and detritus. The relative importance of these four types of

nutrient fluxes could be studied more precisely to compare the relative importance of external (i.e. inputs and outputs) and internal (i.e. trophic, recycling and internal exchanges) ecological processes in controlling the nutrient dynamics and functioning of the whole ecosystem (De Mazancourt *et al.* 1999; Barot *et al.* 2007).

- Ecological functions related to ecosystem services

My theoretical analyses on ecosystem functioning can also be used to address critical issues about the provision of ecosystem services, for example, optimization of fish farming with minimum inputs of mineral nutrients and organic material and outputs of mineral nutrients and pollutants. Fishes are generally the top generalist consumers coupling the green and brown food webs in the ecosystems, however, how interactions between the green and brown food webs studied in the thesis can affect fish production have not been addressed. In future work, interactions between food webs, nutrient cycling and inputs / outputs of mineral nutrients and organic matters should be taken into account to provide solutions to increase the sustainability of fish farming.

### **6.2.3 Comparing model results with real data**

Food web models can be used to represent real ecosystems. However the real interactions and the underlying ecological processes are always more complex and can hardly be modeled in a comprehensive way. Therefore it is necessary to compare the model results with real data to examine the logic, the robustness and the prediction of the model.

In chapter 3, I have already made a reanalysis of already published data to serve as the evidence that key factors analyzed in models can be observed in real ecosystems. The data analysis suggests that ecosystems may differ in the asymmetry degree between the green and brown food webs as well as in competition intensity between primary producers and decomposers, leading to difference in stability as predicted by model results. More of such comparisons between model results and real data can be conducted to make more solid and robust predictions.

During the PhD work, I also conducted an experimental study with colleagues to test the predictions of the model developed in the thesis (chapter 5). We are still working on the analysis of data collected during the experiment. The results would help to test the model predictions developed in chapter 2 and observe the effects of interactions between the green and brown food webs on ecosystem functioning in real ecosystems.



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