Impact of nutrient cycling on food web stability

Pierre Quévreux[1], Sébastien Barot[1] and Élisa Thébault[1]

[1]*Sorbonne Université, Sorbonne Paris Cité, Paris Diderot Univ Paris 07, CNRS, INRA, IRD, UPEC, Institut d'Écologie et des Sciences de l'Environnement – Paris, iEES-Paris, 4 place Jussieu, F-75252 Paris, France*

Corresponding author: pierre.quevreux@cri-paris.org

Summary

1. Nutrient cycling is fundamental to ecosystem functioning. Despite recent major advances in the understanding of complex food web dynamics, food web models have so far generally ignored nutrient cycling. However, nutrient cycling is expected to strongly impact food web stability and functioning.

2. To make up for this gap, we built an allometric and size structured food web model including nutrient cycling. By releasing mineral nutrients, recycling increases the availability of limiting resources for primary producers and links each trophic level to the bottom of food webs.

3. We found that nutrient cycling can provide more than 50% of the total nutrient supply of the food web, leading to a strong enrichment effect that promotes species persistence in nutrient poor ecosystems but leads to a paradox of enrichment at high nutrient inputs, *i.e.* to destabilisation.

4. In addition to this enrichment effect, the presence of recycling loops linking each trophic level to the basal resources stabilises species biomass dynamics in food chains but has only weak stabilising effects in complex food webs.

5. By considering nutrient cycling, this new model improves our understanding of the response of food webs to nutrient availability and open perspectives to better link studies on food web dynamics and ecosystem functioning.

Key words

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

Introduction

Food web dynamics and functioning have been studied thoroughly through empirical and modelling approaches because food webs are essential to ecosystem functioning. A key issue is to determine the characteristics of food webs that stabilise their key properties, *e.g.* the number of species composing them, primary production or secondary production. Food chains (*i.e.* linear chains of species or trophic groups interacting through trophic interactions) and food

webs (*i.e.* networks of species interacting through trophic interactions) models have been extensively used to tackle these issues. In particular, dynamical models of complex food webs (*i.e.* food webs including numerous interacting species) reveal that size structured food webs (Brose *et al.*, 2006b; Heckmann *et al.*, 2012), allometric scaling of biological rates (Brose *et al.*, 2006b) and adaptive foraging (Kondoh, 2003; Heckmann *et al.*, 2012) promote species coexistence and population stability. However, these models focus on population dynamics and carbon fluxes, forgetting non-living compartments (mineral nutrients and dead organic matter) and nutrient cycling (cyclic fluxes of nutrients through living and non-living compartments). Some studies include mineral nutrients as basal resources for primary producers (Schneider *et al.*, 2016; Wang & Brose, 2017) or detritus as basal resources for bacteria (Boit *et al.*, 2012) or for species higher in the food web (Legagneux *et al.*, 2012), but they never include a complete nutrient cycling.

Nevertheless, the cycling of mineral nutrients such as nitrogen and phosphorus likely tightly interacts with food web dynamics and stability. Stability can be measured in different ways: resilience (calculated by the leading eigenvalue of the jacobian matrix of the system at equilibrium) represents the ability of the system to return to its equilibrium after a perturbation, resistance measures the degree to which a variable changes after a perturbation and temporal variability (measured for example by the coefficient of variation) represents the variance of population densities over time (McCann, 2000). Several studies indeed highlighted the importance of nutrient cycling processes for ecosystem stability, but with contrasting results (O'Neill, 1976; DeAngelis, 1980; DeAngelis *et al.*, 1989; DeAngelis, 1992; Loreau, 1994; McCann, 2011; Neutel & Thorne, 2014). DeAngelis (1980, 1992) showed that nutrient cycling affects food chain resilience, systems with tighter nutrient cycling (*i.e.* a lower proportion of mineral nutrients is lost from the ecosystem each time they cycle) being less resilient. On the other hand, Loreau (1994) suggested that tighter cycling was associated with greater food chain resistance to perturbations, and McCann (2011) found that food chains with nutrient cycling were less destabilised (*i.e.* more resilient) by nutrient enrichment than food chains without nutrient cycling. Meanwhile, Neutel & Thorne (2014) did not find clear effects of the presence of recycling loops on the resilience of complex soil food webs, some food webs being unaffected by nutrient cycling and others being either destabilised or stabilised. While the study of consequences of nutrient cycling on stability has largely been restricted to resilience of small food web motifs or food chains (but see Neutel & Thorne (2014)), understanding the consequences of nutrient cycling on the stability of complex food webs becomes crucial to predict ecosystem stability in response to perturbations. Observed contradictory results on the impact of nutrient cycling on stability might arise from the fact that nutrient cycling can affect food web stability through different mechanisms, whose importance could also differ between food chain and food web models.

First, the recycled nutrients (*i.e.* excreted nutrients that return to the mineral pool available for primary producers) are added to the external inputs of mineral nutrients and could lead to an enrichment effect (Loreau, 2010). Recent studies have emphasised that nutrient fluxes between ecosystems can strongly determine ecosystem functioning and stability (Leroux & Loreau, 2008; Gounand *et al.*, 2014). Effects on nutrient availability thus clearly need to be accounted for when studying nutrient cycling effects on food web stability (McCann, 2011). Nutrient cycling increases primary production (Loreau, 2010), which increases the energy transfer to consumers. This could increase species persistence and sustain higher trophic levels (Abrams, 1993; Binzer *et al.*, 2011). On the contrary, nutrient cycling could lead to the destabilisation of food web dynamics through the increase of basal resources availability. Indeed, increasing this availability tends to increase the amplitude of population oscillations, which increases the risk of extinction. This characterises the paradox of enrichment (Rosenzweig, 1971; Rip & McCann, 2011) predicted by several food chain and food web models (Roy & Chattopadhyay, 2007; Rall

et al., 2008; Hauzy *et al.*, 2013; Gounand *et al.*, 2014; Binzer *et al.*, 2016) and some experiments (Fussmann *et al.*, 2000; Persson *et al.*, 2001). Taken together, this leads to the hypothesis that in nutrient poor ecosystems, nutrient cycling would increase food web stability, *i.e.* species persistence and the persistence of higher trophic levels while, in nutrient rich ecosystems, nutrient cycling would destabilise food webs. Testing this hypothesis is particularly meaningful in a context of global nutrient enrichment due to human activities (Vitousek & Reiners, 1975; Smith *et al.*, 1999).

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

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

To study the consequences of nutrient cycling on food web stability, we extended the recent food web modelling approach based on allometric relations with species body mass (*e.g.* Brose *et al.* (2006b); Heckmann *et al.* (2012); Schneider *et al.* (2016); Wang & Brose (2017)) by integrating basic aspects of nutrient cycling in this framework. Species body mass is linked to with fundamental species traits such as metabolic or growth rates (Yodzis & Innes, 1992; McCann *et al.*, 1998; Brown *et al.*, 2004b) and it is also a good predictor of trophic interactions in ecosystems (Williams & Martinez, 2000; Petchey *et al.*, 2008). Models parametrised with such allometric relations have been increasingly used to study food web dynamics and stability, especially because they allow recreating observed patterns and dynamics of complex food webs (Boit *et al.*, 2012; Hudson & Reuman, 2013). This framework thus offers a good opportunity to include nutrient cycling to food web models. To disentangle the mechanisms by which nutrient cycling affects food web stability (defined by species persistence and time variability of biomass dynamics), we assessed and compared the respective impact of nutrient cycling through the addition of mineral resources and the addition of feedback loops in both a complex food web and a food chain. These aspects were critical to answer the following questions: Can nutrient cycling lead to a paradox of enrichment and how does it interact with the overall nutrient

availability in the ecosystem? Can the addition of feedback loops by nutrient cycling stabilise food chains as well as complex food webs? Do the relative importance of direct and indirect nutrient cycling and the decomposition rate influence food web stability?

Material and methods

General description of the model

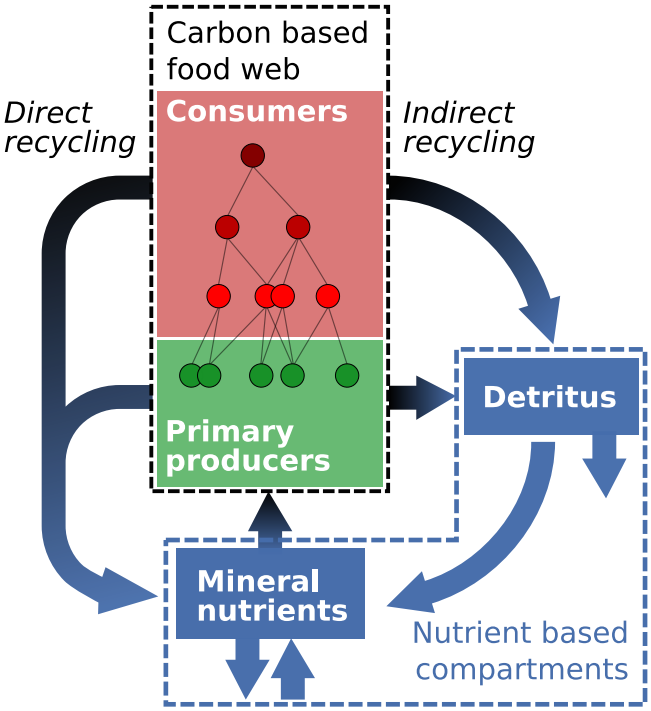

Figure 1: Schematic diagram of the modelled food web. The food web contains several primary producers and consumers forming a complex interaction network. It also includes two non-living compartments: mineral nutrients and detritus. Each organism excretes nutrients either directly as mineral nutrients (arrows on the left), or indirectly through the production of degradable detritus (arrows on the right). Stoichiometric rules ensure the conversions between the carbon based food web and the nutrient based compartments.

We developed a food web model including basic aspects of nutrient cycling by combining food web, allometry and stoichiometric theories (Fig. 1). Following classical allometric food web models (Brose, 2008; Heckmann *et al.*, 2012), that are based on carbon flows, species biological parameters and trophic interactions scale with species body mass. Our model adds two major abiotic compartments, mineral nutrients (*e.g.* mineral nitrogen pool) and detritus (dead organic matter), to food web dynamics. Since detritus and mineral nutrient compartments are expressed in mass of nutrient whereas species compartments are expressed in mass of carbon, stoichiometry rules ensure the conversion between carbon flows and nutrient flows between the biotic and abiotic compartments and account for species stoichiometric homoeostasis in the food web. Nutrients are either directly recycled (species excretion of mineral nutrients directly available for primary producers) or indirectly recycled (species excretion of detritus releasing mineral nutrients through decomposition). All stocks are expressed for an arbitrary unit of habitat either a surface or a volume. The model is parametrised for nitrogen, but could be applied to other limiting nutrients such as phosphorus. The studied food chain model is a simplified version of the food web model, with only three species, a primary producer, a herbivore

and a carnivore. It is thus built with the same equations and the same parameters as the food web model.

Predator-prey interactions in the allometric food web model

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

$$M = 10^c \tag{1}$$

The five smallest species are defined as primary producers, the other as consumers. The diet of consumers depends on the profitability of each prey based on prey handling (*i.e.* the lower is the handling time, the more profitable is the prey). Following Petchey *et al.* (2008) and Thierry *et al.* (2011), mass specific handling time h_{ij} of species j by the consumer i is defined by:

$$h_{ij} = \begin{cases} \dfrac{h_i}{b - \dfrac{M_j}{M_i}} \dfrac{1}{M_j} & \text{if } \dfrac{M_j}{M_i} < b \\ \infty & \text{if } \dfrac{M_j}{M_i} > b \end{cases} \tag{2}$$

With h_i a time constant (calculation detailed in Appendix S1 of supporting information), M_j the body mass of the prey, M_i the body mass of the consumer and b the maximum prey-predator body mass ratio above which the prey cannot be eaten. The handling time function against prey body mass is U-shaped, handling time being minimal when prey body mass is equal to $b/2 \times M_j$. We consider that predators can only interact with preys within the body-mass interval $[0.1bM_i, bM_i]$ with $b < 1$ (*i.e.* predators are always larger than their prey) as the handling time increases exponentially out of this interval. Thus, the structure of the food web (*e.g.* number of trophic levels, see Fig. S2-2C and D in supporting information) is shaped by species biomass distribution and body mass ratios between species.

The predator-prey dynamics follow previous allometric food web models (Brose, 2008; Heckmann *et al.*, 2012). The respective equations for primary producers (equation 3a) and consumers (equation 3b) are:

$$\frac{dB_i}{dt} = r_i G_i B_i - x_i B_i - \beta_i B_i^2 - \sum_{j=consumers} B_j F_{ji} \tag{3a}$$

$$\frac{dB_i}{dt} = -x_i B_i - \beta_i B_i^2 + \sum_{j=prey} e_{ij} B_i F_{ij} - \sum_{j=consumers} B_j F_{ji} \tag{3b}$$

In these equations, B_i is the biomass of population i, G_i is the nutrient-dependent growth rate of primary producers, r_i is the mass-specific maximum growth rate of primary producers, x_i is the mass-specific metabolic rate, β_i is the intraspecific competition coefficient and e_{ij} the

assimilation efficiency of species j by species i. Primary producer growth rates r_i as well as species metabolic rates x_i are defined as functions of species body masses, according to the allometric quarter-power laws as described by Yodzis & Innes (1992) and Brown *et al.* (2004b):

$$r_i = rM_i^{-1/4} \tag{4a}$$

$$x_i = xM_i^{-1/4} \tag{4b}$$

With M_i the body mass of species i and r and x allometric constants (Table 1) (See Appendix S1 in supporting information).

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

$$F_{ij} = \frac{\omega_{ij} a_i B_j^q}{1 + \sum\limits_{k=prey} \omega_{ik} a_i h_{ik} B_k^q} \tag{5}$$

Here B_j represents the biomass of the prey j, q is the Hill exponent (the functional response is of type II if $q = 1$ or type III if $q = 2$), a_i is the attack rate of consumer i and h_{ik} is the handling time of k by consumer i. ω_{ij} is the preference of i for the prey j. We chose here to model preferences as time variables and not as fixed parameters according to the adaptive foraging theoretical framework (results with preferences as fixed parameters are available in Appendix S3 in supporting information). Adaptive foraging is indeed an important aspect of predator-prey interactions (*e.g.* predator foraging efforts depend on prey availability) and it strongly affects food web dynamics (Kondoh, 2003; Uchida & Drossel, 2007; Heckmann *et al.*, 2012). The dynamics of foraging efforts were modelled through changes over time of the consumer preferences ω_{ij} according to the following equation:

$$\frac{d\omega_{ij}}{dt} = A\omega_{ij}\left(\frac{\partial g_i}{\partial \omega_{ij}} - \sum_{k=prey} \omega_{ik} \frac{\partial g_i}{\partial \omega_{ik}}\right) \tag{6}$$

Here, A represents the adaptive rate of the diet preference and g_i the total growth rate of species i defined such as $\frac{dB_i}{dt} = g_i B_i$. The initial value of ω_{ij} is set assuming a uniform distribution among preys and during the simulation, the ω_{ij} are rescaled after the resolution of equation 6 to keep the relation $\sum\limits_{k=prey} \omega_{ik} = 1$ true at each time step.

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

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

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

$$\frac{dN}{dt} = I - \ell N + dD + \underbrace{\delta \sum_{i=diversity} \frac{x_i B_i + \beta_i B_i^2}{\alpha_i}}_{direct\ recycling} - \underbrace{\sum_{\substack{i=primary \\ producer}} \frac{r_i G_i B_i}{\alpha_i}}_{primary\ producers\ uptake} \tag{7a}$$

$$\frac{dD}{dt} = -\ell D - dD + \underbrace{\sum_{i=consumer} \sum_{j=prey} \frac{(1-e_{ij}) B_i F_{ij}}{\alpha_{Dij}}}_{non\ assimilated\ biomass} + \underbrace{(1-\delta) \sum_{i=diversity} \frac{x_i B_i + \beta_i B_i^2}{\alpha_i}}_{indirect\ recycling} \tag{7b}$$

We consider an open ecosystem where I is the constant external input of nutrients (*e.g.* through erosion or atmospheric deposition) and ℓ is the rate of loss of mineral nutrients and detritus (*e.g.* through leaching, sedimentation).
The nutrient-dependent growth rate of primary producers is expressed as (DeAngelis, 1980; DeAngelis *et al.*, 1989):

$$G_i = \frac{N}{K_i + N} \tag{8}$$

where K_i is the half saturation constant of nutrient uptake of primary producer i. The nutrient uptake by primary producers (expressed as a nutrient flow) is calculated by dividing the growth rate of primary producers (expressed as a carbon flow) by their C:N ratio.
Detritus are decomposed at a constant rate d. Organisms release nutrients through excretion and mortality to the detritus and mineral nutrient pools. A fraction δ of these nutrients is released in their mineral form (urine for instance) while the remaining fraction is released as dead organic matter (detritus like feces, dead bodies, litter fall...) (Fig. 2A)(Zou *et al.*, 2016). We assume that the nutrients contained in the non-assimilated biomass (e_{ij} fraction of the eaten biomass) go in the detritus compartment.
The amount of nutrients released by species in the food web depends on their C:N ratio α_i. The carbon to nutrient ratio of non-assimilated biomass α_{Dij} depends on both the C:N ratio of the prey j and of the consumer i (calculation detailed in Appendix S1 of supporting information):

$$\alpha_{Dij} = \frac{\alpha_j \alpha_i (1 - e_{ij})}{\alpha_i - \alpha_j e_{ij}} \tag{9}$$

Assessing nutrient cycling effects on stability

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

the additional inputs of nutrients associated with nutrient cycling. To simulate the enrichment effect of nutrient cycling, we replaced the basal nutrient input by the total nutrient input I_{tot}:

$$I_{tot} = I + I_{recy} \tag{10}$$

Where I is the external nutrient input and I_{recy} is the average quantity of recycled nutrients (directly and indirectly) calculated over the last 1000 years of the simulation in the C model. Thus, in the SC model, I_{recy} is constant over time because recycling (both direct and indirect recycling) is not explicitly modelled. In the C model, these nutrient subsidies vary over time as they directly originate from the direct and indirect recycling loops and thus depend on temporal variations of species biomasses and detritus in the ecosystem.

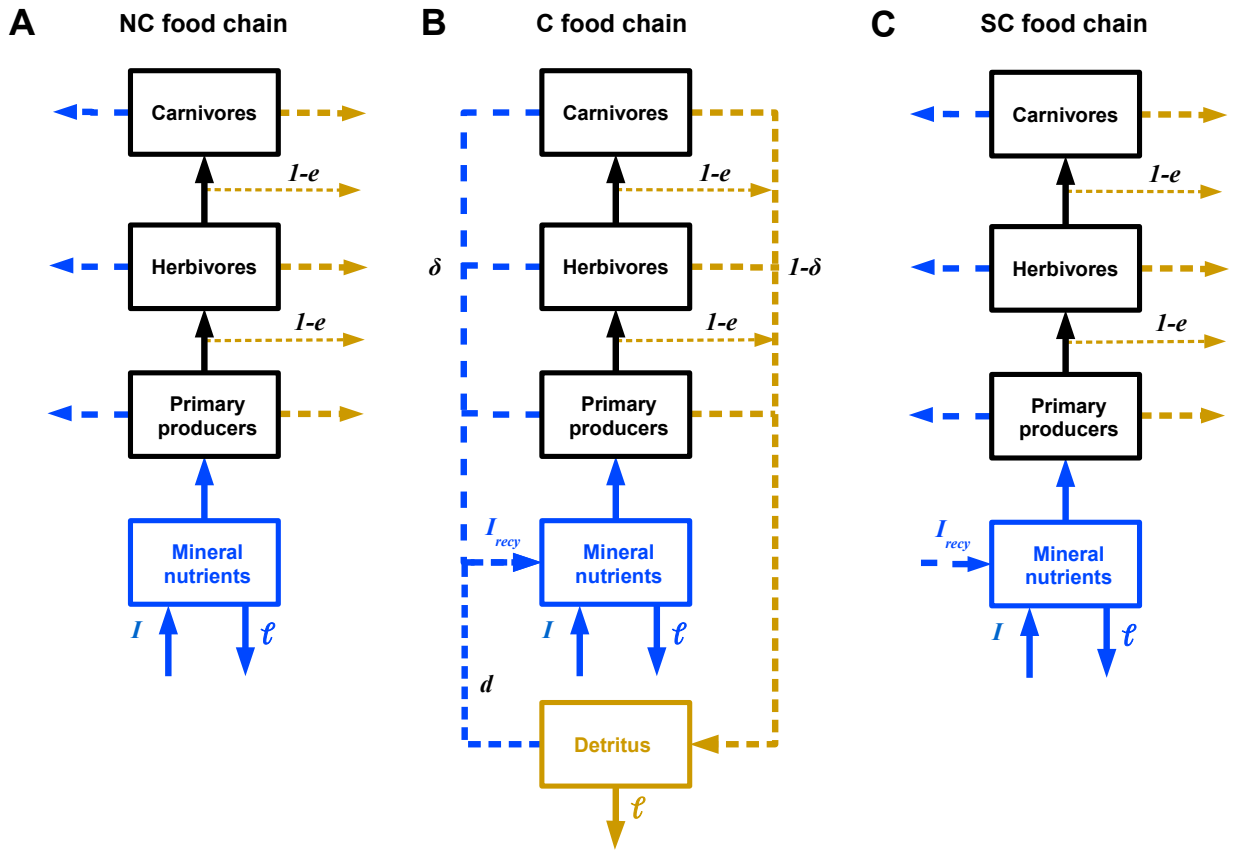

Figure 2: Diagram of the general structure of our models with and without nutrient recycling feedback loops. Food chains are represented for more simplicity but these three models are valid for food webs as well. The dotted arrows represent nutrient cycling (nutrient flux in blue, detritus in brown). **A)** NC model. Food chain without nutrient cycling. **B)** C model. Food chain with nutrient cycling. A fraction δ of nutrients is excreted as mineral nutrients (direct recycling on the left) and a fraction $1 - \delta$ plus a fraction $1 - e$ of non ingested biomass are excreted as detritus (indirect recycling on the right). The total nutrient input I_{tot} in the pool of mineral nutrients is the sum of the external nutrient input I and the recycled nutrient I_{recy}. **C)** SC model. Food chain without nutrient cycling but with a nutrient input corrected by I_{recy}. The resulting food chain does not have the feedback loop induced by nutrient recycling but has an equivalent nutrient availability as in the food web with nutrient cycling. Note that the first version of our model (NC) is based on the C model where I_{recy} is set to 0.

In addition to the complex food web, a tri-trophic food chain (*i.e.* with three species) is built to track the effects of nutrient cycling in a simpler system. The tri-trophic food chain is ruled

by the same equations as the complex food web except for the adaptive foraging that is not relevant in such a model.

	Value and units	Description	Reference
B_i	$kg.v^{-1}$	Biomass (carbon) of species i	Variable (equation 3a, 3b)
N	$kg.v^{-1}$	Mineral nutrient (nitrogen)	Variable (equation 7a)
D	$kg.v^{-1}$	Detritus (nitrogen)	Variable (equation 7b)
ω_{ij}	Dimensionless	Preference of predator j for prey i	Variable (equation 6)
r	0.87 $kg^{1/4}.year^{-1}$	Growth rate allometric constant	Binzer *et al.* (2012)
x	0.12 $kg^{1/4}.year^{-1}$	(primary prod.) Metabolic rate	Brose (2008)
	0.27 $kg^{1/4}.year^{-1}$	(consumer) allometric constant	
h_j	$year.kg^{-1}$	Handling time	Appendix S1
a_i	0.1 $v.year^{-1}$	Attack rate	Arbitrary
β_i	0.001 $v.kg^{-1}.year^{-1}$	Intraspecific competition coefficient	Arbitrary
e_{ij}	0.45 (herbivore)	Assimilation efficiency of species j	Yodzis & Innes (1992)
	0.85 (carnivore)	eaten by species i	
q	1	Hill exponent	Brose *et al.* (2006b)
A	0.01	Adaptive rate	Arbitrary
b	0.05	Max prey-predator body mass ratio	Brose *et al.* (2006a)
α_i	6.6 (primary prod.)	Carbon to nutrient ratio	Anderson (1992)
	5 (consumer)		
K_i	10 $kg.v^{-1}$	Half saturation of nitrogen uptake	Arbitrary
ℓ	0.2 $year^{-1}$	Leaching rate	Arbitrary
M_i	kg (of C)	Body mass of species i	Log uniform in $[10^{-5}, 10]$
I	$kg.v^{-1}.year^{-1}$	External nutrient input	$[0, 400]$
d	Dimensionless	Decomposition rate of detritus	$[0, 1]$
δ	Dimensionless	Fraction of direct recycling	$[0, 1]$

Table 1: Table of parameters and variables. v represents a generic metric of space (*e.g.* that could represent litres or square meters). Indeed all the parameters depending on space are set arbitrarily and thus we do not need to specify a particular unit of space.

Simulations

All the parameters, their units and their values as used in the simulations are given in table 1. The sensitivity of the results to arbitrarily set parameters is given in Appendix S3 in supporting information. The simulations are performed with $C++$ and the GSL ode solver using the Runge-Kutta-Fehlberg (4, 5) method with an adaptive time step and an absolute accuracy of 10^{-6}. Simulations are run for 10,000 years and outputs are recorded for the last 1000 years. Species persistence is measured as the ratio of the final number of species at $t = 10,000$ to the initial number of species at $t = 0$. The CV is the ratio of the standard deviation to the mean of species biomass or recycled quantity of nutrients over time, calculated for the 1000 last years of each simulation. Each combination of parameters is tested for 100 different food webs (*i.e.* different randomly drawn sets of species body mass), each of these food webs being simulated in the three configurations of nutrient cycling (*i.e.* for the NC, C and SC models). To implement the SC model, we recorded the density of each compartment in the simulation of the C model at $t = 9000$ as well as the averaged quantity of recycled nutrient I_{recy} for the last 1000 years. We then ran corresponding food web simulations for the SC model (*i.e.* with $\delta = d = 0$ and $D = 0$) for 1000 years with initial densities and a nutrient input I respectively set equal to the densities and I_{tot} recorded in the C model.

In each simulation for complex food webs, there are initially 50 species and their initial biomass is set at 10 kg.v^{-1} for primary producers and at 5 kg.v^{-1} for consumers (v is an arbitrary metric of space, see table 1). Initial quantities of nutrients in the mineral nutrients and detritus pools are set at 10 kg.v^{-1}. In the simulations for the food chain model, the body masses of the primary producer, the herbivore and the carnivore are respectively 1, 10 and 100 kg, and their initial biomass are respectively 1, 0.5 and 0.1 kg.v^{-1}.

Results

Overall effects of nutrient cycling on food web dynamics

Nutrient cycling contributes to an important part of the total mineral inputs of nutrients in the food web, and its contribution varies with the levels of external inputs of nutrients (Fig. 3A and S2-5B in supporting information), in parallel with variations of total biomass in the food web and primary production (see Fig. S2-3 in supporting information). In this study case, nutrient cycling always represents larger inputs of nutrients to the food web than external inputs (Fig. 3A). At low nutrient enrichment levels, consumers are responsible for most of the recycling. However, at high nutrient enrichment levels, the quantity of nutrient recycled by consumers stops increasing while the total quantity of nutrient recycled still increases linearly with the external nutrient input I due to a large increase in the quantity of nutrient cycled by primary producers. A similar relation is observed for the primary and the secondary productions (see Fig. S2-4C in supporting information).

Nutrient cycling affects the relationship between nutrient enrichment (*i.e.* external nutrient inputs) and food web stability (Fig. 3). First, it affects the relationship between species persistence and nutrient enrichment (Fig. 3B). In either food webs with and without nutrient cycling, persistence follows a hump-shaped relationship with external nutrient input I: first there is a sharp increase of the persistence for low nutrient inputs, then a plateau with maximum persistence (area outlined in dark grey for the C food webs) and finally a decrease of the persistence for high nutrient inputs. However, maximum persistence is reached for lower input values and effects of enrichment are sharper for the case with nutrient cycling than for the case without nutrient cycling. These sharp changes in species persistence along the gradient of nutrient enrichment are paralleled by strong changes in food web maximum trophic level with an increase and then a decrease of the maximum trophic level with increasing external nutrient input I (See Fig. S2-2C in supporting information).

Second, nutrient cycling affects the relation between the average coefficient of variation (CV) of the species biomass and nutrient enrichment (Fig. 3C). While the average CV of species biomass increases monotonically with nutrient enrichment when there is no nutrient cycling, it shows a saturating relationship in food webs with nutrient cycling. In this case, the CV of species biomass increases at low input values but it stops increasing at high nutrient enrichment. However, high CVs only occur in food webs with surviving consumers (Fig. S2-2B and S2-2D in supporting information). The CV of the quantity of recycled nutrients follows a hump-shaped relation with external nutrient input I but the temporal variability of the quantity of recycled nutrients is about 25 times smaller than the CV of species biomass (see also Fig. S2-1 in supporting information).

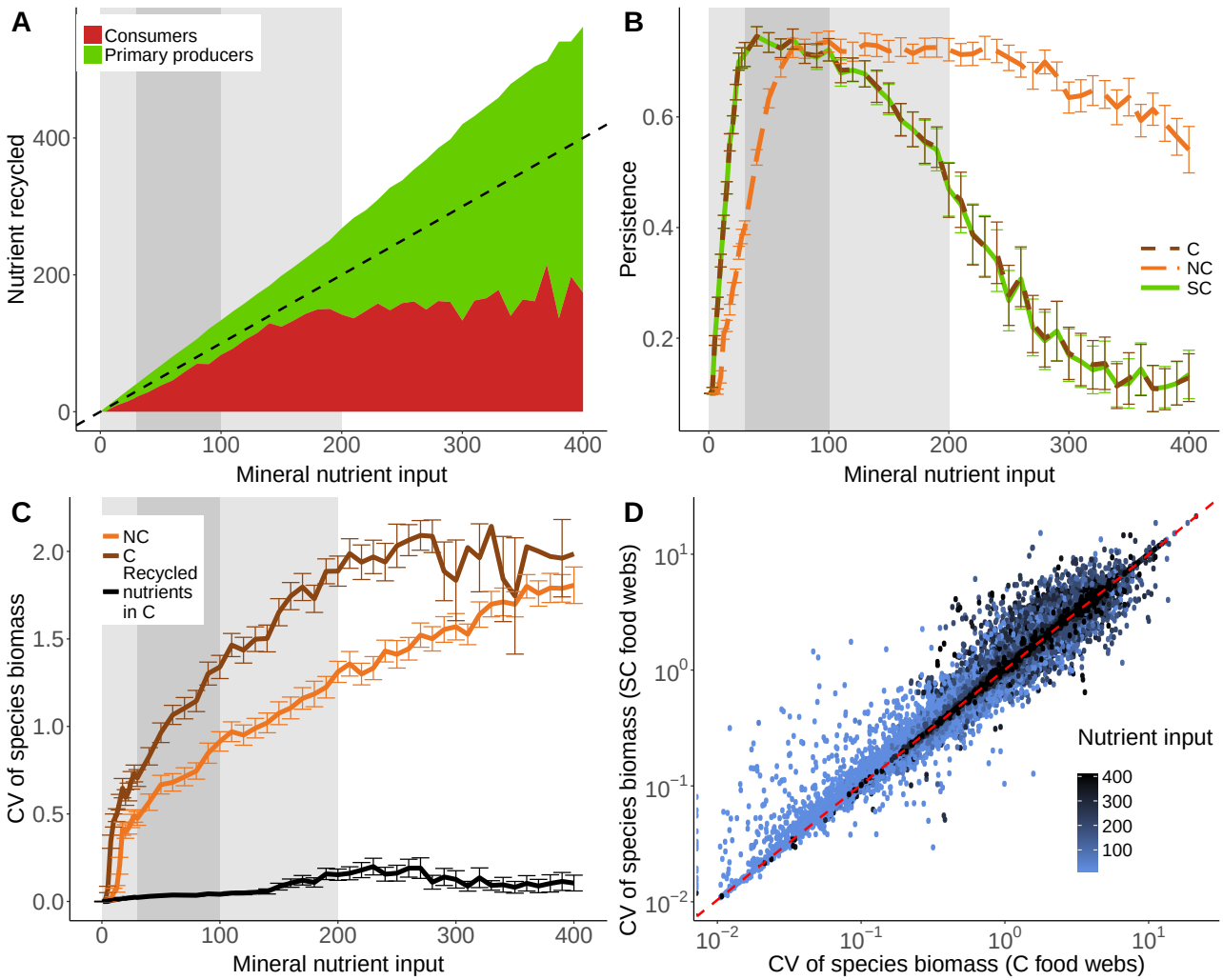

Figure 3: Overall effects of nutrient cycling on nutrient supply and food web dynamics in the complex food web model. **A)** Quantity of recycled nutrients by primary producers (green) and consumers (red) along a nutrient enrichment gradient (average of simulated food webs where at least one species persists). The dashed line is the bisector symbolising the case where the quantity of recycled nutrient is equal to the external nutrient input I. The light grey domain (for I in $[0, 200]$) emphasises the mineral nutrient input range where the quantity of nutrients recycled by consumers increases. **B)** Effects of nutrient cycling on species persistence (proportion of surviving species at the end of simulations) along a nutrient enrichment gradient. Each point represents the average persistence of 100 simulated food webs. The brown dashed curve represents the C food webs with nutrient cycling ($\delta = 0.2$, $d = 0.2$), the orange curve represents the NC food webs without nutrient cycling and the green curve represents the SC food webs without nutrient cycling but with a mineral nutrient input simulating the enrichment effect of nutrient cycling in the C food web. The dark grey domain emphasises the plateau of maximal species persistence in the C food webs. **C)** Effect of the external nutrient input I on the average coefficient of variation (CV) of species biomass (error bars represent the confidence interval of the mean) in C food web (brown) and in NC food webs (orange). Each point represents the average of simulated food webs where at least one species persists. The black curve represents the average CV of the quantity of recycled nutrients in C food webs. **D)** CV of the species biomass in C food webs versus in the SC food webs. Each dot represents the average CV of one species of one food web in its C and SC versions. The dashed red line is the bisector and the colour scale represents the external nutrient input I.

Influence of the recycling parameters

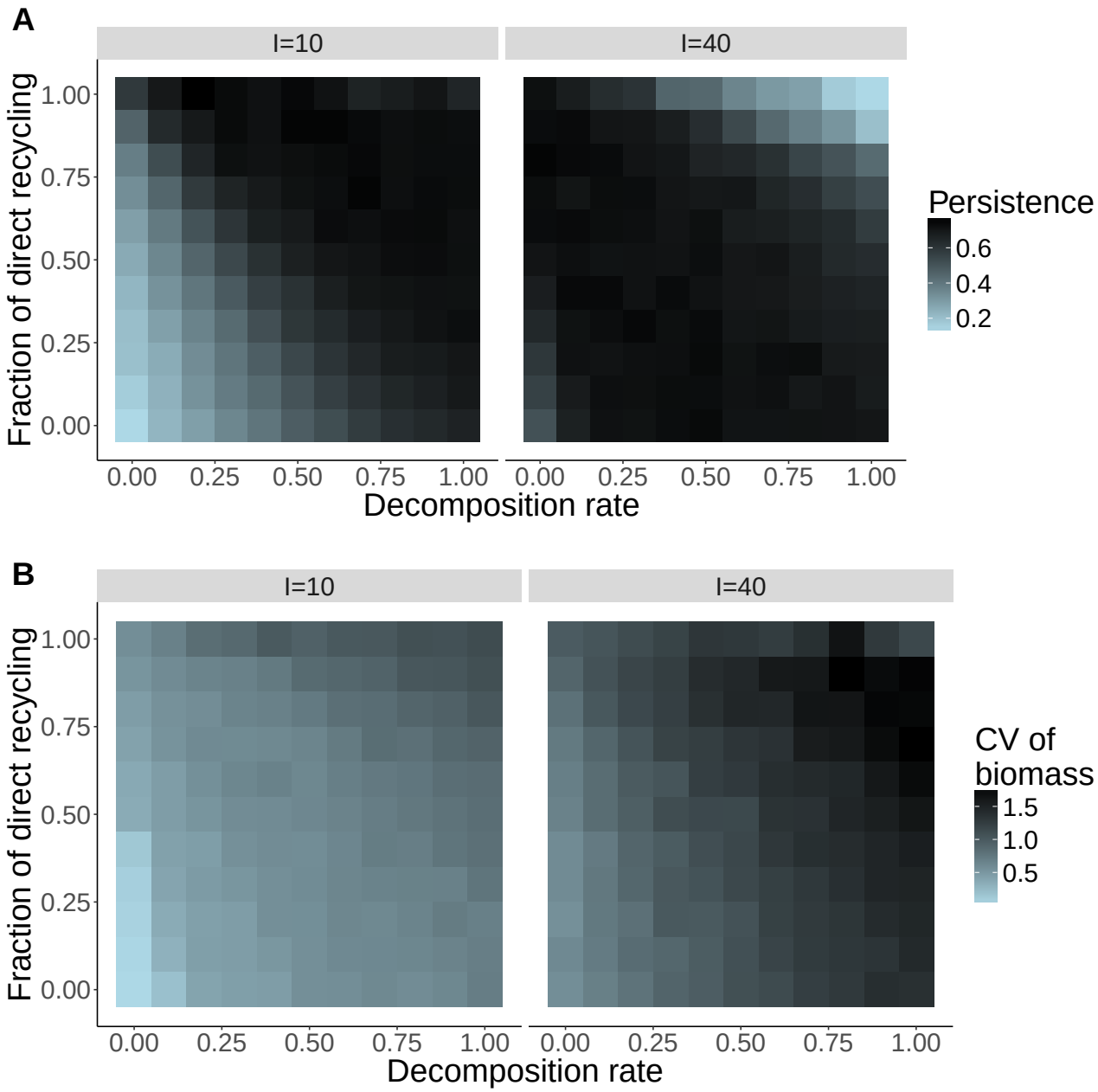

Figure 4: Effect of the recycling parameters d (detritus decomposition rate) and δ (fraction of direct recycling) in the complex food web model on **A)** species persistence and on **B)** the average coefficient of variation of the biomass of species for $I = 10$ and $I = 40$. In **A)**, each square represents the average value for 100 simulated food webs while in **B)** it represents the average value for persistent food webs only (*i.e.* food webs where at least one species persists).

Both the decomposition rate d and the fraction of directly recycled nutrients δ affect species persistence and the coefficient of variation of species biomass (Fig. 4). When $I = 10$, increasing d and δ increases the persistence (Fig. 4A) and the average CV of species biomass (Fig. 4B). When $I = 40$, increasing d and δ first increases and then decrease persistence while the average CV of species biomass increases and stays at its maximum value. Increasing d and δ always increases the quantity of recycled nutrients in the food web (Fig. S2-5 in supporting information), leading to greater inputs of nutrients than external inputs, and it further affects food web maximum trophic level in the same way as species persistence.

Effects of nutrient cycling: enrichment vs feedback loop

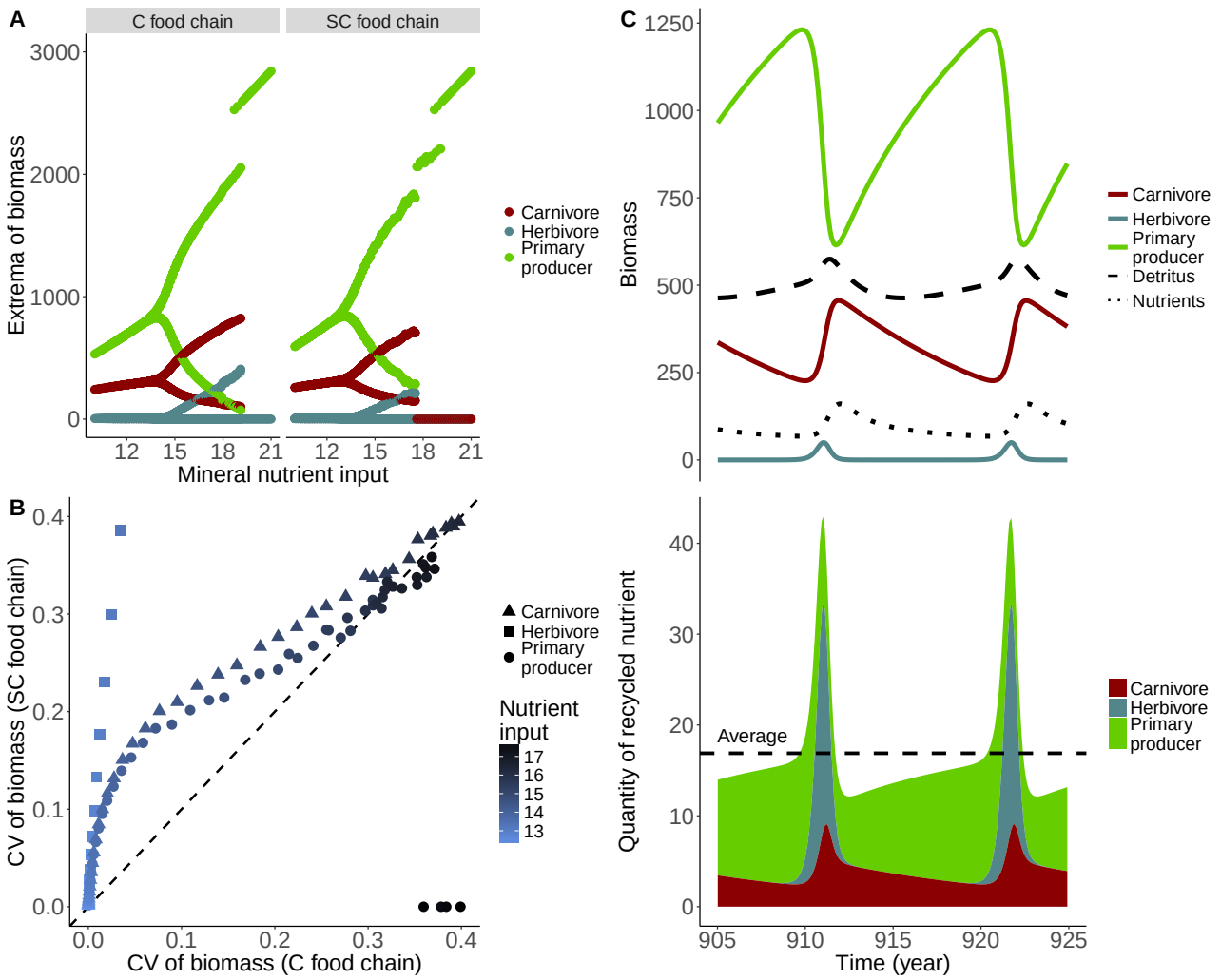

Figure 5: Effect of the feedback loop in a tri-trophic food chain. **A)** Diagram of bifurcation of species biomass (minima and maxima of biomass in dynamics) in a tri-trophic food chain (primary producer, herbivore and carnivore) along a nutrient enrichment gradient. Two cases are represented: a case with nutrient cycling (C food chain) and a case without nutrient cycling but with a simulated enrichment due to nutrient cycling (SC food chain). **B)** CV of the species biomass in the C food chain versus the SC food chain. The dashed line represents the bisector and the colour scale represents the nutrient input I. In order to improve the readability, values on the y axis above 0.4 (corresponding to herbivore CV) are not shown but herbivore CV response to enrichment is qualitatively similar to primary producer's and carnivore's one. **C)** Dynamics of the biomass of species, the mineral nutrients compartment (values magnified by 30 for more readability), the detritus compartment (values magnified by 10 for more readability) and of the quantity of nutrients recycled by each trophic level in the C food chain ($I = 15$, $\delta = 0.2$, $d = 0.2$). The dashed line represents the average quantity of recycled nutrients as simulated in the SC model.

The comparison between the case with nutrient cycling (case C) and the case without nutrient cycling but with a nutrient input simulating the enrichment effect of nutrient cycling (case SC) allows to separate the effects of nutrient cycling due to enrichment from those due to the creation of additional feedback loops from each trophic levels to the bottom of the food web. When we model food web dynamics without nutrient cycling but including the enrichment

effect of nutrient cycling (*i.e.* SC case), the relationships between external nutrient inputs and species persistence or biomass CV are the same as in presence of nutrient cycling (Fig. 3B and S2-2A in supporting information). Indeed, the curves corresponding to C and SC strongly overlap. Most of the effects of nutrient cycling on food web stability are thus due to an enrichment effect caused by recycled nutrients. Weak effects of the addition of recycling loops appear when we compare more closely the CV of species in individual food webs with or without these loops (Fig. 3D). Although the CVs of species are strongly correlated between the C and SC simulations, at low nutrient inputs species biomasses are generally less variable over time in food webs when nutrient cycling adds feedbacks loops (see Fig. S2-6 in supporting information).

In simple food chain models, as in complex food webs, effects of nutrient cycling on stability are mainly due to an enrichment effect (Fig. 3A and Fig. S2-7A in supporting information). The variability of species biomasses increases with nutrient inputs and with comparable CV values in both the C and SC cases (see Fig. S2-7B in supporting information). However, a stabilising effect of the recycling loops, already observed in the food webs, appears more clearly in the food chain model (Fig. 5B and Fig. S2-7C in supporting information). For low nutrient inputs, the CV of biomass is higher in the SC food chain, especially for herbivores. In addition, the herbivore and carnivore go extinct at lower threshold value of increased inputs in the SC case than in the C case (Fig. 5A). Contrary to what we found in the complex food web model (Fig. 3C), the temporal variabilities of the quantity of recycled nutrients and of species biomasses are of similar magnitude in the food chains and the dynamics of primary producers and of the quantity of recycled nutrients are clearly out-of-phase (Fig. 5C and S2-7B in supporting information). While the total quantity of recycled nutrient is below the average recycled quantity during most of the dynamic, it peaks for a short time when primary producer biomass and primary production decrease while herbivore and carnivore biomasses increases (see Fig.5C and S2-7D in supporting information). This peak of recycled nutrient is driven by a large increase of the quantity of nutrient recycled by the herbivore and the consumer, and coincides with a peak in the amount of detritus while primary producer biomass is almost minimal (Fig. 5C).

Discussion

By integrating nutrient cycling, our food web model allows to better link population dynamics and ecosystem functioning. Results of this model highlight that nutrient cycling strongly affects food web dynamics and its response to nutrient enrichment. We show that the effects of nutrient cycling on food web stability are mostly due to the increased nutrient availability (*i.e.* enrichment effect due to efficient recycling) that promotes species persistence at low nutrient inputs but leads to a paradox of enrichment at high level of nutrient inputs. The addition by nutrient cycling of feedback loops from each species to the bottom resource has a clear stabilising effect in food chains but only weakly affects the stability of complex food webs. These results are thoroughly discussed below and their sensitivity to the parameters (Table 1) is tested in Appendix S3 in supporting information.

Nutrient cycling and enrichment effects

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

recycling) lead to stability values that are obtained for increased levels of nutrient inputs in food webs with a slower nutrient cycling.

In agreement with previous food web studies (Rall *et al.*, 2008; Binzer *et al.*, 2016), we observe two contrasting responses of species diversity and food web stability to increased nutrient availability. While higher nutrient availability consistently increases the temporal variability of species biomasses, it also increases species persistence in nutrient poor ecosystems (*i.e.* low external nutrient inputs) but leads to decreased persistence at high inputs of nutrients. The increase in persistence at low nutrient inputs is likely due to the increased persistence of species at higher trophic levels (Fig. S2-2C). Higher trophic levels are known to require a sufficient ecosystem productivity (limited by nutrient availability) to meet their energetic requirement and persist (*e.g.* Oksanen *et al.* (1981); Abrams (1993); Leibold (1996)), which can explain why increased persistence is only found in our case for nutrient poor ecosystems. The observed increase in the amplitude of species biomass oscillations (*i.e.* increase of species CVs) with increasing nutrient inputs is typical of the well-known paradox of enrichment (Rosenzweig, 1971; DeAngelis, 1992; Roy & Chattopadhyay, 2007; Rip & McCann, 2011). In accordance with our model results, the paradox of enrichment has been found in complex food web models with type II functional responses (Rall *et al.*, 2008; Binzer *et al.*, 2016). While the use of type III functional responses removes in our model the destabilising effect of nutrient enrichment (Fig. S3-3, see also Rall *et al.* (2008)), adaptive foraging as included in our study does not prevent the occurrence of the paradox of enrichment (Fig. S3-2) as already observed by Mougi & Nishimura (2008) in a one predator-two prey model. Such destabilising effects of nutrient availability on species dynamics might explain the decrease in species persistence we observe at high levels of nutrient inputs. In case of type III functional responses where no such destabilising effects occur, persistence does not decline at high levels of nutrient availability (Fig. S3-3). Large oscillations of species biomass caused by nutrient enrichment likely trigger species extinctions as their biomass might reach the extinction threshold value, thus counteracting the positive effect of nutrient enrichment on persistence at low nutrient levels and resulting in an hump-shaped relationship between species persistence and nutrient enrichment.

Our results highlight that effects of nutrient cycling on nutrient availability are key to understand consequences of nutrient cycling on food web dynamics in ecosystems. Several mechanisms can determine how nutrient cycling affect nutrient availability in our model. First, the efficiency of nutrient cycling, as defined by the proportion of nutrient that is recycled without being leached out of the ecosystem, has been shown to increase the total amount of mineral nutrient circulating in the ecosystem and primary production (DeAngelis, 1980; de Mazancourt *et al.*, 1998; Barot *et al.*, 2007; Loreau, 2010). In our model, detritus just represent a pool of nutrient unavailable for primary producers and increase the probability of a nutrient to be lost by the ecosystem as their loss rate is the same as for the mineral nutrient pool. Increasing the direct recycling and the decomposition rate respectively decreases the proportion of nutrient passing through the detritus pool and the residence time of nutrient contained in detritus, leading to increased nutrient availability. This suggests that the impact of nutrient cycling partly arises in our models from complex interactions between the speed of recycling and nutrient losses (Fig. S3-1C and D). These interactions should be further disentangled through new simulations manipulating independently rates of mineral nutrient and detritus loss that are set equal in our model while higher losses for mineral nutrients than for detritus would be more realistic, at least in terrestrial ecosystems.

Second, the amount of recycled nutrients depends on food web species biomass and on primary production, which increases linearly with nutrient inputs (Loreau, 2010). In fact, nutrient

uptake by producers necessarily balances nutrients recycled from all trophic levels at equilibrium (Fig. S2-4C and D). At low nutrient inputs, consumers are the main contributors to nutrient cycling, in agreement with experimental and empirical studies (Vanni, 2002; Schmitz *et al.*, 2010). While nutrients recycled per unit of biomass due to species metabolism are lower for consumers because of their larger body mass, consumers also strongly contribute to recycling through nutrient losses associated to feeding inefficiency. This is particularly true for herbivores whose assimilation efficiency is low ($e_{ij} = 0.45$) so that they produce a lot of detritus by consuming primary producers, as also emphasised by previous ecosystem models (Leroux & Loreau, 2010; Krumins *et al.*, 2015). However, at high nutrient input, food webs are dominated by primary producers, which become the main contributors to nutrient cycling. In such case, primary producers release large amounts of detritus and nutrients due to high metabolic rates and large density dependent mortalities (Fig. S2-4). At high external nutrient inputs, the total quantity of recycled nutrients is lower for food webs with higher trophic levels (Fig. S2-3A). This seems contradictory to the results of Wang & Brose (2017) who found that higher vertical diversity (*i.e.* presence of species at higher trophic levels) increases the nutrient flow in food webs. However, results are not fully comparable between the two studies as we do not directly manipulate species richness and vertical diversity while Wang & Brose (2017) did not include nutrient cycling in their model.

Food web structure influences nutrient cycling through other already identified mechanisms pertaining to the quality of the produced detritus that are not included in our model. In nature, the fraction of direct recycling and the degradability of detritus can be controlled by the trophic structure of the food web. In aquatic ecosystems, top predators such as fish produce large quantities of highly degradable detritus (Harrault *et al.*, 2012) that sustain a higher biomass of phytoplankton and zooplankton (Vanni & Layne, 1997; Harrault *et al.*, 2014). In terrestrial ecosystems, herbivores also produce excrements that are easily degraded by the soil community and lead to an increase of the primary production (McNaughton, 1984; Belovsky & Slade, 2000). Primary producers can also strongly influence decomposition. In terrestrial ecosystems, plant leaf traits affect the composition and the quality of the litter (Cornwell *et al.*, 2008). Primary producer stoichiometry is also highly variable both between and within species (Sterner *et al.*, 2002; Dickman *et al.*, 2006; Danger *et al.*, 2007, 2009; Mette *et al.*, 2011), which will affect detritus quality and stoichiometry. While our results remain qualitatively robust to different average values of C:N ratios of primary producers (Fig. S3-4 and Fig. S3-5), the links between food web structure and the degradability of detritus might strongly influence food web stability through their impact on nutrient availability. Including further these mechanisms would thus need to be tested in new versions of our model.

Nutrient cycling and effects of feedback loops

Though we found that nutrient cycling mostly destabilises food webs through an enrichment effect, we also find stabilising effects of nutrient cycling through feedback loops from all trophic levels to primary producers and these effects were much stronger in our food chain model than in our food web model. These stabilising effects were visible through the decrease of the temporal variability of species biomasses between the SC and C models (Fig. S2-7A and C) that compare the effects of the addition of nutrients by nutrient cycling with and without the feedback loops. Rip & McCann (2011) showed that the destabilising effect of enrichment may occur due to an unbalance between species growth rates and loss rates. In our food chain model, such unbalance is decreased for primary producers in presence of feedback loops (Fig. S2-8) thanks to out-of-phase dynamics of recycled nutrients and primary production (Fig. S2-7D), which stabilises population dynamics in the food chain. Indeed, the increase in herbivore and carnivore biomasses results from increased consumption of their resource species, a large part of this

consumed biomass being unassimilated (15% for carnivores and 55% for herbivores, see Table 1) and thus directly going to increase the detritus pool, increasing consequently the amount of recycled nutrient (Fig. S2-7C). This increased nutrient availability boosts primary production and compensates for the increased mortality due to herbivory. On the contrary, when the herbivore and the carnivore biomasses decrease, the quantity of recycled nutrients is lower which limits the increase of the biomass of the primary producer due to a reduced mortality (Fig. S2-7D and Fig. S2-8). Similar results have been described by Brown *et al.* (2004a) who showed that a positive feedback loop in a food chain stabilises species dynamics. Although Brown *et al.* (2004a) did not consider nutrient cycling but a positive effect of predators on resource uptake by prey, our results can be understood through the same kind of mechanisms. Our results contradict previous studies on food chains suggesting that feedback loops generated by nutrient cycling are destabilising (DeAngelis, 1980). This discrepancy likely arises from these latter results being based on a different stability measure (*i.e.* resilience instead of temporal variability) and because previous studies did not separate enrichment effects from feedback loop effects of nutrient cycling.

Our results show that the stabilising effects of recycling loops are weaker in food webs than in food chains. By considering a different stability measure (*i.e.* resilience), Neutel & Thorne (2014) also suggested that the presence of recycling feedback loops have significant effects on food web stability only in food webs with low diversities and simple structures. In our case, such weaker effects in complex food webs might be explained by the low temporal variability of the total quantity of recycled nutrients observed in the food web model, which does not allow strong asynchrony between the dynamics of mineral nutrients and primary producers as found in the food chain model (Fig. S2-1, Fig. S2-7C). While the CV of recycled nutrients is in the same order of magnitude as the CV of species biomass in the food chain model (Fig. S2-7B), it is smaller by one order of magnitude in the food web model. Nutrient cycling is the outcome of the aggregated nutrient loss from numerous species whose dynamics are not synchronous and lead to compensation effects: when the biomasses of some species decrease, the biomasses of other species likely increase, thus keeping the total biomass and the total quantity of recycled nutrients less variable (Fig. S2-1C). As nutrient cycling appears to be relatively constant along time compared to species biomass dynamics, mimicking it with a constant nutrient input I_{recy} as in SC food webs leads to dynamics similar to those of C food webs. While in food chains, nutrient cycling dynamics tightly interact with species biomass dynamics, leading to an imperfect simulation of nutrient cycling by a constant nutrient input. Theory predicts that species diversity stabilises aggregated ecosystem properties through asynchronous species dynamics (Doak *et al.*, 1998; Gonzalez & Loreau, 2008; Loreau & de Mazancourt, 2013). This rationale is supported by numerous experimental studies showing that aggregated ecosystem processes, such as primary production (Tilman, 1996; Tilman *et al.*, 2006; Schläpfer & Schmid, 1999; Loreau, 2000; Hooper *et al.*, 2005) or dead biomass decomposition (Knops *et al.*, 2001; Keith *et al.*, 2008; Gessner *et al.*, 2010; Nielsen *et al.*, 2011) are more stable over time than individual species dynamics and that this stability increases with the number of species. Interestingly, our results also suggest that positive effects of biodiversity on ecosystem stability might also occur for nutrient cycling. To the best of our knowledge, this hypothesis has never been fully tested in biodiversity experiments and could lead to a new research avenue.

Conclusion and perspectives

In an ecosystem model linking population dynamics in a food web to ecosystem functioning, we found strong effects of nutrient cycling on food web stability. Thus, ecologists need to incorporate nutrient cycling in theoretical and empirical work to better predict food web stability. We

identified two distinct effects of nutrient cycling. First, an enrichment effect due to the recycled nutrients that increase species persistence at low nutrient inputs by increasing resource availability but leads to a decrease in species persistence through a paradox of enrichment at higher nutrient inputs. Second, a stabilising effect of the feedback loops that links each trophic level to the mineral resource through nutrient cycling. However, this stabilising effect is stronger in food chains than in complex food webs where nutrient cycling mainly consists in an enrichment effect.

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

The predictions of our model should be tested experimentally. For example, it would be possible in mesocosms to manipulate both inputs of mineral nutrients and the efficiency of nutrient cycling (Harrault *et al.*, 2014), *e.g.* exporting an increasing proportion of detritus, and to measure the response in terms of food web functioning and stability. It would also be interesting to compare food webs of different types of natural ecosystem with contrasting nutrient cycling and mineralisation rates. Typically, our model probably better corresponds to an aquatic food web (*i.e.* fully size-structured web) and aquatic and terrestrial food webs should be compared. It should be noted that the role of detritus cannot be fully appreciated in our model because there are no decomposers and no brown food web. In fact, detritus are more than a transient pool for nutrients since, in real food webs, they are resources for decomposers and are recycled through the whole brown food web (Moore *et al.*, 2004). Another important step will be to include in models a true brown food web containing decomposers feeding on detritus in parallel to the green food webs relying on photosynthesis (Moore *et al.*, 2004; Zou *et al.*, 2016). The interactions between green and brown food webs are conditioned by stoichiometric constrains on primary producers and detritus in particular (Daufresne & Loreau, 2001; Cherif & Loreau, 2013; Zou *et al.*, 2016) and can deeply change the functioning and the stability of ecosystems (Daufresne & Loreau, 2001; Moore *et al.*, 2005; Attayde & Ripa, 2008; Zou *et al.*, 2016) but these results have so far not been tested in complex realistic food webs.

Acknowledgement

We thank the École Normale Supérieure, the PhD program "École Doctorale Frontières du Vivant (FdV) – Programme Bettencourt" and the Initiative Structurante Ecosphère Continentale et Côtière (IS EC2CO) for their financial support. We also thank the anonymous reviewers and Shawn Leroux in particular for their detailed comments that strongly helped us to improve this manuscript.

Data accessibility

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

Conflict of interest disclosure

The authors of this preprint declare that they have no financial conflict of interest with the content of this article.

References

Abrams, P.A. (1993) Effect of increased productivity on the abundances of trophic levels. *The American Naturalist* **141**, 351–371.

Anderson, T.R. (1992) Modelling the influence of food C:N ratio, and respiration on growth and nitrogen excretion in marine zooplankton and bacteria. *Journal of Plankton Research* **14**, 1645–1671.

Attayde, J.L. & Ripa, J. (2008) The coupling between grazing and detritus food chains and the strength of trophic cascades across a gradient of nutrient enrichment. *Ecosystems* **11**, 980–990.

Barot, S., Ugolini, A. & Brikci, F.B. (2007) Nutrient cycling efficiency explains the long-term effect of ecosystem engineers on primary production. *Functional Ecology* **21**, 1–10.

Belovsky, G.E. & Slade, J.B. (2000) Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences* **97**, 14412–14417.

Binzer, A., Brose, U., Curtsdotter, A., Eklöf, A., Rall, B.C., Riede, J.O. & de Castro, F. (2011) The susceptibility of species to extinctions in model communities. *Basic and Applied Ecology* **12**, 590–599.

Binzer, A., Guill, C., Brose, U. & Rall, B.C. (2012) The dynamics of food chains under climate change and nutrient enrichment. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**, 2935–2944.

Binzer, A., Guill, C., Rall, B.C. & Brose, U. (2016) Interactive effects of warming, eutrophication and size structure: impacts on biodiversity and food-web structure. *Global Change Biology* **22**, 220–227.

Boit, A., Martinez, N.D., Williams, R.J. & Gaedke, U. (2012) Mechanistic theory and modelling of complex food-web dynamics in Lake Constance. *Ecology Letters* **15**, 594–602.

Bokhorst, S., Huiskes, A., Convey, P. & Aerts, R. (2007) External nutrient inputs into terrestrial ecosystems of the Falkland Islands and the Maritime Antarctic region. *Polar Biology* **30**, 1315–1321.

Brose, U. (2008) Complex food webs prevent competitive exclusion among producer species. *Proceedings of the Royal Society of London B: Biological Sciences* **275**, 2507–2514.

Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F., Blanchard, J.L., Brey, T., Carpenter, S.R., Blandenier, M.F.C., Cushing, L., Dawah, H.A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M.E., Martinez, N.D., Memmott, J., Mintenbeck, K., Pinnegar, J.K., Rall, B.C., Rayner, T.S., Reuman, D.C., Ruess, L., Ulrich, W., Williams, R.J., Woodward, G. & Cohen, J.E. (2006a) Consumer–resource body-size relationships in natural food webs. *Ecology* **87**, 2411–2417.

Brose, U., Williams, R.J. & Martinez, N.D. (2006b) Allometric scaling enhances stability in complex food webs. *Ecology Letters* **9**, 1228–1236.

Brown, D.H., Ferris, H., Fu, S. & Plant, R. (2004a) Modeling direct positive feedback between predators and prey. *Theoretical Population Biology* **65**, 143–152.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004b) Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.

Cherif, M. & Loreau, M. (2013) Plant–herbivore–decomposer stoichiometric mismatches and nutrient cycling in ecosystems. *Proc. R. Soc. B* **280**, 20122453.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V. & Westoby, M. (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* **11**, 1065–1071.

Danger, M., Mériguet, J., Oumarou, C., Benest, D. & Lacroix, G. (2009) Direct and indirect effects of biomanipulations on periphyton stoichiometry in shallow lakes. *SIL Proceedings, 1922-2010* **30**, 737–740.

Danger, M., Oumarou, C., Benest, D. & Lacroix, G. (2007) Bacteria can control stoichiometry and nutrient limitation of phytoplankton. *Functional Ecology* **21**, 202–210.

Daufresne, T. & Loreau, M. (2001) Ecological stoechiometry, primary producer-decomposer interactions, and ecosystem persistence. *Ecology* **82**, 3069–3082.

de Mazancourt, C., Loreau, M. & Abbadie, L. (1998) Grazing optimization and nutrient cycling : When do herbivores enhance primary production? *Ecology* **79**, 2242.

DeAngelis, D.L. (1980) Energy flow, nutrient cycling, and ecosystem resilience. *Ecology* **61**, 764.

DeAngelis, D.L. (1992) *Dynamics of nutrient cycling and food webs*. No. 9 in Population and community biology series, Chapman & Hall, London, 1. ed edn.

DeAngelis, D.L., Mulholland, P.J., Palumbo, A.V., Steinman, A.D., Huston, M.A. & Elwood, J.W. (1989) Nutrient dynamics and food-web stability. *Annual Review of Ecology and Systematics* **20**, 71–95.

Dickman, E.M., Vanni, M.J. & Horgan, M.J. (2006) Interactive effects of light and nutrients on phytoplankton stoichiometry. *Oecologia* **149**, 676–689.

Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E. & Thomson, D. (1998) The statistical inevitability of stability-diversity relationships in community ecology. *The American Naturalist* **151**, 264–276.

Fath, B.D. & Halnes, G. (2007) Cyclic energy pathways in ecological food webs. *Ecological Modelling* **208**, 17–24.

Fussmann, G.F., Ellner, S.P., Shertzer, K.W. & Jr, N.G.H. (2000) Crossing the Hopf bifurcation in a live predator-prey system. *Science* **290**, 1358–1360.

Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H. & Hättenschwiler, S. (2010) Diversity meets decomposition. *Trends in Ecology & Evolution* **25**, 372–380.

Gonzalez, A. & Loreau, M. (2008) The causes and consequences of compensatory dynamics in ecological communities. *Annual Review of Ecology, Evolution, and Systematics* **40**, 393–414.

Gounand, I., Mouquet, N., Canard, E., Guichard, F., Hauzy, C. & Gravel, D. (2014) The paradox of enrichment in metaecosystems. *The American Naturalist* **184**, 752–763.

Halnes, G., Fath, B.D. & Liljenström, H. (2007) The modified niche model: Including detritus in simple structural food web models. *Ecological Modelling* **208**, 9–16.

Harrault, L., Allard, B., Danger, M., Maunoury-Danger, F., Guilpart, A. & Lacroix, G. (2012) Influence of food-web structure on the biodegradability of lake sediment. *Freshwater Biology* **57**, 2390–2400.

Harrault, L., Allard, B., Mériguet, J., Carmignac, D., Huon, S., Gauzens, B. & Lacroix, G. (2014) Bottom-up effects of lake sediment on pelagic food-web compartments: a mesocosm study. *Freshwater Biology* **59**, 1695–1709.

Hauzy, C., Nadin, G., Canard, E., Gounand, I., Mouquet, N. & Ebenman, B. (2013) Confronting the paradox of enrichment to the metacommunity perspective. *PLoS ONE* **8**, e82969.

Heckmann, L., Drossel, B., Brose, U. & Guill, C. (2012) Interactive effects of body-size structure and adaptive foraging on food-web stability: Body size, adaptivity and food-web stability. *Ecology Letters* **15**, 243–250.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3–35.

Hopper, S.D. (2009) OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil* **322**, 49–86.

Hudson, L.N. & Reuman, D.C. (2013) A cure for the plague of parameters: constraining models of complex population dynamics with allometries. *Proc. R. Soc. B* **280**, 20131901.

Jickells, T. (2005) External inputs as a contributor to eutrophication problems. *Journal of Sea Research* **54**, 58–69.

Keith, A.M., van der Wal, R., Brooker, R.W., Osler, G.H.R., Chapman, S.J., Burslem, D.F.R.P. & Elston, D.A. (2008) Increasing litter species richness reduces variability in a terrestrial decomposer system. *Ecology* **89**, 2657–2664.

Knops, J.M.H., Wedin, D. & Tilman, D. (2001) Biodiversity and decomposition in experimental grassland ecosystems. *Oecologia* **126**, 429–433.

Kondoh, M. (2003) Foraging adaptation and the relationship between food-web complexity and stability. *Science* **299**, 1388–1391.

Krumins, J.A., Krumins, V., Forgoston, E., Billings, L. & Putten, W.H.v.d. (2015) Herbivory and stoichiometric feedbacks to primary production. *PLOS ONE* **10**, e0129775.

Legagneux, P., Gauthier, G., Berteaux, D., Bêty, J., Cadieux, M.C., Bilodeau, F., Bolduc, E., McKinnon, L., Tarroux, A., Therrien, J.F., Morissette, L. & Krebs, C.J. (2012) Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. *Ecology* **93**, 1707–1716.

Leibold, M.A. (1996) A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *The American Naturalist* **147**, 784.

Leroux, S.J. & Loreau, M. (2008) Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters* **11**, 1147–1156.

Leroux, S.J. & Loreau, M. (2010) Consumer-mediated recycling and cascading trophic interactions. *Ecology* **91**, 2162–2171.

Loreau, M. (1994) Material cycling and the stability of ecosystems. *The American Naturalist* **143**, 508–513.

Loreau, M. (2000) Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**, 3–17.

Loreau, M. (2010) *From populations to ecosystems: theoretical foundations for a new ecological synthesis*. No. 46 in Monographs in population biology, Princeton Univ. Press, Princeton, NJ, oCLC: 699867402.

Loreau, M. & de Mazancourt, C. (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters* **16**, 106–115.

McCann, K., Hastings, A. & Huxel, G.R. (1998) Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798.

McCann, K.S. (2000) The diversity–stability debate. *Nature* **405**, 228–233.

McCann, K.S. (2011) *Food webs*. No. 50 in Monographs in population biology, Princeton Univ. Press, Princeton, NJ, oCLC: 775576741.

McNaughton, S.J. (1984) Grazing lawns: animals in herds, plant form, and coevolution. *The American Naturalist* **124**, 863–886.

Mette, E.M., Vanni, M.J., Newell, J.M. & Gonzàlez, M.J. (2011) Phytoplankton communities and stoichiometry are interactively affected by light, nutrients, and fish. *Limnology and Oceanography* **56**, 1959–1975.

Moore, J.C., Berlow, E.L., Coleman, D.C., Ruiter, P.C., Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J. & Wall, D.H. (2004) Detritus, trophic dynamics and biodiversity. *Ecology Letters* **7**, 584–600.

Moore, J.C., McCann, K. & de Ruiter, P.C. (2005) Modeling trophic pathways, nutrient cycling, and dynamic stability in soils. *Pedobiologia* **49**, 499–510.

Mougi, A. & Nishimura, K. (2008) The paradox of enrichment in an adaptive world. *Proceedings of the Royal Society B: Biological Sciences* **275**, 2563–2568.

Neutel, A.M. & Thorne, M.A. (2014) Interaction strengths in balanced carbon cycles and the absence of a relation between ecosystem complexity and stability. *Ecology Letters* **17**, 651–661.

Nielsen, U.N., Ayres, E., Wall, D.H. & Bardgett, R.D. (2011) Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity–function relationships. *European Journal of Soil Science* **62**, 105–116.

Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981) Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* **118**, 240–261.

O'Neill, R.V. (1976) Ecosystem persistence and heterotrophic regulation. *Ecology* **57**, 1244.

Persson, A., Hansson, L.A., Brönmark, C., Lundberg, P., Pettersson, L.B., Greenberg, L., Nilsson, P.A., Nyström, P., Romare, P. & Tranvik, L. (2001) Effects of enrichment on simple aquatic food webs. *The American naturalist* **157**, 654–669.

Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008) Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences* **105**, 4191–4196.

Polis, G.A., Anderson, W.B. & Holt, R.D. (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* **28**, 289–316.

Rall, B., Guill, C. & Brose, U. (2008) Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos* **117**, 202–213.

Rip, J.M.K. & McCann, K.S. (2011) Cross-ecosystem differences in stability and the principle of energy flux. *Ecology Letters* **14**, 733–740.

Rosenzweig, M.L. (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science (New York, N.Y.)* **171**, 385–387.

Roy, S. & Chattopadhyay, J. (2007) The stability of ecosystems: A brief overview of the paradox of enrichment. *Journal of Biosciences* **32**, 421–428.

Schläpfer, F. & Schmid, B. (1999) Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. *Ecological Applications* **9**, 893–912.

Schmitz, O.J., Hawlena, D. & Trussell, G.C. (2010) Predator control of ecosystem nutrient dynamics. *Ecology Letters* **13**, 1199–1209.

Schneider, F.D., Brose, U., Rall, B.C. & Guill, C. (2016) Animal diversity and ecosystem functioning in dynamic food webs. *Nature Communications* **7**, 12718.

Smith, V.H., Tilman, G.D. & Nekola, J.C. (1999) Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environmental Pollution (Barking, Essex: 1987)* **100**, 179–196.

Sterner, R.W., Elser, J.J. & Vitousek, P. (2002) *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press, Princeton and Oxford, oCLC: 248866756.

Thierry, A., Petchey, O.L., Beckerman, A.P., Warren, P.H. & Williams, R.J. (2011) The consequences of size dependent foraging for food web topology. *Oikos* **120**, 493–502.

Tilman, D. (1996) Biodiversity population versus ecosystem stability. *Ecology* **77**, 350.

Tilman, D., Reich, P.B. & Knops, J.M.H. (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629–632.

Uchida, S. & Drossel, B. (2007) Relation between complexity and stability in food webs with adaptive behavior. *Journal of Theoretical Biology* **247**, 713–722.

Vadeboncoeur, Y., Jeppesen, E., Vander Zanden, M.J., Schierup, H.H., Christoffersen, K. & Lodge, D.M. (2003) From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. *Limnology and Oceanography* **48**, 1408–1418.

Vanni, M.J. (2002) Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* **33**, 341–370.

Vanni, M.J. & Layne, C.D. (1997) Nutrient recycling and herbivory as mechanisms in the "top-down" effect of fish on algae in lakes. *Ecology* **78**, 21–40.

Vitousek, P.M. & Reiners, W.A. (1975) Ecosystem succession and nutrient retention: a hypothesis. *BioScience* **25**, 376–381.

Wang, S. & Brose, U. (2017) Biodiversity and ecosystem functioning in food webs: the vertical diversity hypothesis. *Ecology Letters* .

Williams, R.J. & Martinez, N.D. (2000) Simple rules yield complex food webs. *Nature* **404**, 180–183.

Yodzis, P. & Innes, S. (1992) Body size and consumer-resource dynamics. *The American Naturalist* **139**, 1151.

Zou, K., Thébault, E., Lacroix, G. & Barot, S. (2016) Interactions between the green and brown food web determine ecosystem functioning. *Functional Ecology* **30**, 1454–1465.