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RESEARCH ARTICLE

Nutrient cycling and self-regulation determine food web stability

Kevin Theis | **Pierre Quévreux** | **Michel Loreau**

Theoretical and Experimental Ecology Station, UPR 2001, CNRS, Moulis, France

Correspondence
Pierre Quévreux
Email: pierre.quevreux@cri-paris.org

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Abstract

1. To understand ecosystems, an integrative approach combining functional ecology and community ecology is required. Nutrient cycling is a good example since it links each organism to the major flows of materials in ecosystems. Together with the demographic processes governing the mortality of organisms (and hence their nutrient losses) such as self-regulation, nutrient recycling has a major impact on ecosystem dynamics and stability.
2. By considering stochastic perturbations in the vicinity of the equilibrium affecting the top species in a food chain, we assessed stability based on the temporal variability in the different compartments of the food chain for different recycling efficiencies and self-regulation intensities.
3. Our results show that nutrient cycling always has a destabilising effect on perturbed species, while lower trophic levels are stabilised or destabilised depending on their trophic distance from the perturbed species. Thus, for species at odd distances from the top species, nutrient cycling is stabilising, whereas for species at even distances, nutrient cycling is destabilising. Self-regulation generally stabilises systems, unless its effects are too strong. Finally, nutrient cycling and self-regulation have opposite effects because nutrient cycling dampens the stabilising effect of self-regulation.
4. Considering these two phenomena together is necessary to assess the effects of perturbations on species dynamics and thus to understand the overall response of ecosystems in the context of global changes.

KEYWORDS
bottom-up, food chain, invariability, nutrients, positive feedbacks, stochastic perturbations, top-down

1 | INTRODUCTION

The study of ecosystems in light of functional ecology and community ecology frameworks has led to major research progress in recent decades (DeAngelis, 1992; Loreau, 2010; McCann, 2012). In fact, these two frameworks taken together describe how mechanisms at the individual level (i.e. growth rates and mortality rates) can impact the functioning of an entire ecosystem. For instance, nutrient cycling, which is the loss of nutrients by organisms (e.g. excretion, faeces and dead bodies) that can be reabsorbed by primary producers, perfectly illustrates the productive combination of ecosystem functioning and community ecology. In fact, nutrient cycling links each organism to the base of the food chain, thus creating feedback loops likely to affect the global dynamics of

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Kevin Theis and Pierre Quévreux contributed equally.

ecosystems (Loreau, 1998, 2010; Ulanowicz, 1990; Veldhuis, Berg, et al., 2018). Nutrient cycling can deeply alter food web dynamics, which was not considered in previous studies using community models only. For example, Leroux and Loreau (2010) showed that nutrient cycling alters the mechanisms causing trophic cascades by increasing primary producer biomass. The importance of nutrient cycling in ecosystem stability has received specific attention; nevertheless, it has led to contrasting results depending on the definition of stability considered in different studies (DeAngelis, 1980, 1992; DeAngelis et al., 1989; Loreau, 1994, 2010; McCann, 2012; Neutel & Thorne, 2014; O'Neill, 1976; Quévreux, Barot, et al., 2021).

The notion of stability is a subject of intense debate in ecology (Grimm & Wissel, 1997; McCann, 2000), and its various definitions do not measure the same features of ecosystem dynamics (Arnoldi et al., 2016). Studies considering asymptotic resilience, that is, the rate at which a system returns to equilibrium after a perturbation in a very long run, as measured by the lead eigenvalue of the Jacobian matrix of the system, showed that stability decreases when nutrient recycling becomes more efficient (DeAngelis, 1980, 1992; DeAngelis et al., 1989; Nakajima & DeAngelis, 1989; Loreau, 1994). However, Loreau (1994) tempered this conclusion by showing that nutrient recycling efficiency increases resistance (defined as the magnitude of the deviation of the system from equilibrium after being perturbed). Thus, these measures describe different facets of stability, and each of them has intrinsic limitations. In particular, asymptotic resilience has often been used to describe the stability of the entire system but Haegeman et al. (2016) and Arnoldi et al. (2018) demonstrated that it is actually driven by rare species and ignores abundant species, which contribute most to total biomass. Hence, asymptotic resilience is not a good integrative metric of ecosystem stability. Other measures, such as species persistence (the fraction of surviving species after a given time) and temporal variability (the coefficient of variation of biomass), describe the response of each species (Brose et al., 2006; Heckmann et al., 2012; Shanafelt & Loreau, 2018), and provide more insight into stability at different scales (from population to ecosystem, see Haegeman et al., 2016). Moreover, temporal variability is often used in empirical studies (Gross et al., 2014; Rakowski et al., 2019; Tilman et al., 2006); thus, using this measure of stability in mathematical models strengthens the relevance of theoretical results for empirical ecology. Quévreux, Barot, et al. (2021), who considered a food web model including up to 50 species and a maximum of four trophic levels, showed with these two measures that nutrient cycling affects food web stability mainly through its enrichment effect. At low nutrient inputs, nutrients recycled by all the organisms of the food web sustain a higher carnivore or consumer biomass and increase species persistence (stabilising effect). In contrast, at high nutrient inputs, recycled nutrients promote the paradox of enrichment and thus have a destabilising effect.

In addition to this enrichment effect, nutrient cycling creates links between each trophic level and mineral nutrients (Vanni, 2002; Veldhuis, Berg, et al., 2018; Veldhuis, Gommers, et al., 2018), thus generating feedback loops whose consequences have only been explored by a few studies. For example, Brown et al. (2004) found that such feedback loops can delay or even prevent the appearance of limit cycles due to increased external nutrient inputs. In Quévreux, Barot, et al. (2021), the effects of these feedback loops, despite being slight, depend on the considered trophic level since they are stabilising for consumers and destabilising for primary producers. In our study, we expect the feedback loops generated by nutrient cycling to interact with the effect of predation according to the trophic position of each species (Figure 1a). Shanafelt and Loreau (2018) demonstrated the existence of trophic cascades in the stability of the various trophic levels, that is, trophic levels at even distance from the top are the most stable while trophic levels at odd distance, which experience a strong top-down control, are the least stable. Hence, we expect nutrient recycled by predators to generate an indirect, positive effect on prey that would offset the negative direct effect of predation and thus to stabilise prey dynamics (Figure 1b(1)). However, this positive effect is also expected to amplify and destabilise the existing trophic dynamics of predators

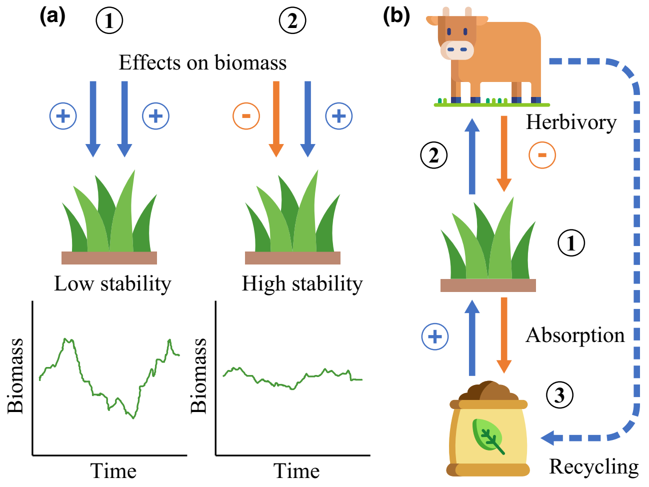

FIGURE 1 Expected effects on biomass of nutrient cycling feedback loops in a food chain with two trophic levels. (a) Net effects on biomass should translate into stability. (1) Effects with the same direction add up and lead to large variations in biomass, thus decreasing stability. (2) Effects with opposite directions cancel each other and lead to small variations in biomass, thus increasing stability. (b) In a food chain, this should lead to the stabilisation or the destabilisation of the different trophic levels. Orange arrows represent the negative effect of consumers on their resource while blue solid arrows represent the positive effect of resources on their consumer. Blue dashed arrows represent the positive effect of nutrients recycled by organisms on mineral nutrients. (1) Nutrient cycling generates a positive feedback of herbivores on primary producers due to the increased nutrient availability. This positive effect should offset the negative effect of herbivory and stabilise the dynamics of primary producer biomass. (2) Nutrient cycling generates a positive feedback of herbivores on themselves that should amplify the variations of herbivore biomass and destabilise its dynamics. (3) In a similar way, herbivores have a positive indirect effect on mineral nutrients that adds up to the positive effect of nutrient cycling feedback loop, thus leading to a destabilisation of mineral nutrients

and compartments at odd trophic distance from the considered predators (Figure 1b(2) and (3)).

These mechanisms governing stability should be modulated by demographic processes affecting both nutrient cycling and top-down control such as self-regulation, which summarises intraspecific interactions limiting population growth (e.g. territoriality and disease transmission, shading). By increasing mortality, self-regulation increases the quantity of nutrients recycled by organisms. In addition, self-regulation stabilises population dynamics by reducing interspecific interaction strength relative to intraspecific interactions, as supported by numerous theoretical and empirical studies (Barabás et al., 2017; Barbier & Loreau, 2019; Begon, Harper, et al., 1986; Begon, Mortimer, et al., 1986; Moore & Ruiter, 2012; Picoche & Barraquand, 2019, 2020; Sterner et al., 1997; Yodzis, 1981). Thus, we expect self-regulation to amplify the stabilising or destabilising effects of nutrient cycling described earlier by increasing the positive bottom-up effect of nutrient cycling and decreasing the negative top-down effect of predators on prey.

To explore these mechanisms, we extend the model developed by Shanafelt and Loreau (2018) by implementing nutrient cycling and measured its response to stochastic perturbations to assess food chain stability. This approach, which is based on stochastic perturbations of the system in the vicinity of equilibrium, considers biomass variability as a measure of stability and enables us to track the response of each compartment of the system (Arnoldi et al., 2019; Barbier & Loreau, 2019; Shanafelt & Loreau, 2018). We first explore the effect of nutrient cycling on stability by varying recycling efficiency (i.e. the fraction of excreted nutrients that returns to the mineral pool) by maintaining nutrient availability constant to disentangle feedback effects from enrichment effects according to Quévreux, Barot, et al. (2021) and McCann (2012). Then, we detail how these effects are modulated by self-regulation, which partially controls the losses of nutrients by organisms. Finally, we vary food chain length to understand how predation and trophic position influence the effects of nutrient cycling on food chain stability.

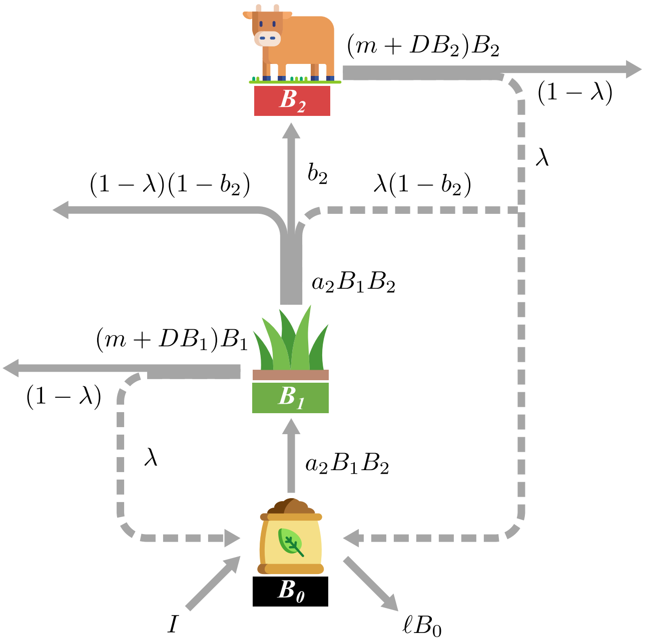

FIGURE 2 General food chain model with two trophic levels (TL2): mineral nutrients B_0, primary producers B_1 and herbivores B_2. I is the external nutrient input and ℓ is the leaching rate. b_i is the biomass conversion efficiency, a_i is the predation rate of species i on species $i - 1$, m is the loss rate due to death, respiration or excretion and D is the self-regulation. The flows of nutrients governed by these parameters are represented by solid arrows. The recycling efficiency λ is defined as the fraction of lost nutrients (due to mortality, self-regulation and inefficient feeding) returning to the mineral nutrient compartment. These flows of recycled nutrients are represented by dashed arrows

2 | MATERIALS AND METHODS

2.1 | General description of the model

We extend the model developed by Shanafelt and Loreau (2018), which consists of a food chain sustained by mineral nutrients, by adding nutrient cycling, which returns a fraction λ of nutrients lost by organisms (mortality, excretion and inefficient feeding) to the mineral nutrient compartment (Figure 2). The fraction $1 - \lambda$ leaves the ecosystem; thus, classic food chain models from the community ecology framework without nutrient cycling are completely open (i.e. $\lambda = 0$), since all the biomass lost by organisms is also lost by the ecosystem. This approach is the simplest way to model nutrient cycling (DeAngelis, 1980; Leroux & Loreau, 2010; Loreau, 1994), and is relevant here as we aim to capture the fundamental effects of recycling feedback loops on food web dynamics (Brown et al., 2004). However, more realistic models exist that involve detritus and decomposers for instance (DeAngelis et al., 1989; Loreau, 1995; Zou et al., 2016). The dynamics of mineral nutrients and species biomass are described in box_model and the parameters used in the model are listed in Table 1.

2.2 | Stochastic perturbations

Variability is generated by small stochastic perturbations affecting the system in the vicinity of the equilibrium according to the following stochastic differential equations:

$$dB_i = f_i\left(B_1, \dots, B_n\right) dt + \sigma_i B_i dW_i, \tag{2}$$

$f_i(B_1, \dots, B_n)$ represents the deterministic part of species i dynamics depending on the biomass of the n species present in the ecosystem (described by Equation 1). The right part of the equation represents the stochastic perturbations defined by their standard deviation σ_i, a white noise dW_i of mean 0 and variance 1 and

TABLE 1 Parameters derived from Shanafelt and Loreau (2018)

Parameters	Interpretation	Units	Values
I	External nutrient inputs	Density × time^{-1}	{0.05, 0.1}
ℓ	Leaching rate	Time^{-1}	0.1
D	Density-dependent mortality (self-regulation)	Density^{-1} × time^{-1}	[0, 1]
λ	Recycling efficiency	Dimensionless	[0, 1]
a_1	Attack rate of B_1 on B_0	Density^{-1} × time^{-1}	2
a_2	Attack rate of B_2 on B_1	Density^{-1} × time^{-1}	{0.4, 0.401}
a_3	Attack rate of B_3 on B_2	Density^{-1} × time^{-1}	0.5
b_2	Biomass conversion efficiency from B_1 to B_2	Dimensionless	0.5
b_3	Biomass conversion efficiency from B_2 to B_3	Dimensionless	0.8
m	Mortality rate	Time^{-1}	0.1
I/I_{recymax}	Ratio of external input to input by nutrient cycling	Dimensionless	]0, 1]

scale with species i biomass B_i (Arnoldi et al., 2016; Shanafelt & Loreau, 2018; Wang et al., 2015).

2.3 | Assessing stability

We measure stability by invariability S_i, which is defined as the inverse of the coefficient of variation of species i biomass (CV_i), that is, the ratio of the mean biomass B_i^* to its standard deviation $\sqrt{w_i}$ (Shanafelt & Loreau, 2018). Note that mean biomass is here equal to the biomass at equilibrium since we consider small perturbations in the vicinity of the equilibrium. Thus, the higher invariability, the lower the temporal variability of biomass and the higher the stability of the biomass dynamics of the considered species.

$$S_i = \frac{1}{\mathrm{CV}_i} = \frac{B_i^*}{\sqrt{w_i}}. \tag{3}$$

Biomasses at equilibrium B_i^* are calculated by numerical integration of Equation 1 with the *odeint* function from the SciPy package (version 1.5.2) of the *Python* programming language for 4,000–1,000,000 time units, which are enough to reach equilibrium. Initial biomasses are obtained by the analytic resolution of the system for $\lambda = 1$ and $D = 0$ or $D > 0$.

Variances w_i are the diagonal elements of the variance–covariance matrix C^* of the system obtained by solving the Lyapunov equation (Arnold, 1974; Arnoldi et al., 2016; Shanafelt & Loreau, 2018; Wang et al., 2015:

$$JC^* + C^*J^T + TV_ET^T = 0. \tag{4}$$

J is the Jacobian matrix, V_E is the covariance matrix of perturbations and T describes how perturbations affect the system. (Matrices are detailed in section S1-1 in the Supporting Information and see Quévreux, Barbier, et al. (2021) for a detailed description of the Lyapunov equation.)

BOX 1 Food chain model

$$\frac{dB_0}{dt} = I - \ell B_0 - a_1B_0B_1 + \sum_{i=1}^{n} \lambda \left(m + DB_i\right) B_i + \sum_{i=2}^{n} \lambda \left(1 - b_i\right) a_iB_{i-1}B_i, \tag{1a}$$

$$\frac{dB_1}{dt} = B_1 \left(a_1B_0 - a_2B_2 - m - DB_1\right), \tag{1b}$$

$$\frac{dB_i}{dt} = B_i \left(b_ia_iB_{i-1} - a_{i+1}B_{i+1} - m - DB_i\right), \tag{1c}$$

B_i is the biomass of trophic level i, where B_0 corresponds to mineral nutrients, B_1 to primary producers, B_2 to herbivores and B_i ($i > 2$) to carnivores. We consider Lotka–Volterra trophic interactions with b_i the biomass conversion efficiency (we assume that primary producers convert all the absorbed mineral nutrients into biomass) and a_i the predation rate of specie i on specie $i - 1$. Species are subject to losses m due to death, respiration or excretion and self-regulation D (negative intraspecific interactions). A fraction λ of the biomass lost by organisms (losses m and self-regulation D) and inefficient feeding (fraction $1 - b_i$ of the ingested biomass) is recycled by returning to the mineral nutrient compartment. Finally, I represents the external nutrient inputs and ℓ represents the leaching rate (nutrients running off the ecosystem). Parameters and their values are detailed in Table 1.

2.4 | Addressing nutrient availability

We aimed to study the feedback loops generated by nutrient cycling, but nutrient cycling also has an enrichment effect that must be carefully taken into account.

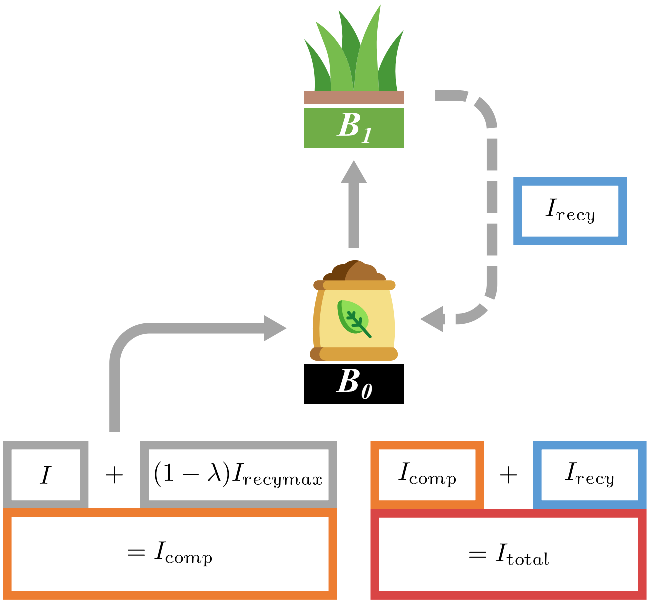

FIGURE 3 Schematic summarising the different flows of nutrients in the ecosystem. B_0 is the mineral nutrient compartment and B_1 is the primary producer biomass. I is the basal external input, I_{recy} is the quantity of recycled nutrients and $I_{recymax}$ is its value when $\lambda = 1$. I_{comp} is the additional external input offsetting fraction $1 - \lambda$ of non-recycled nutrients. Thus, I_{total} is constant regardless of the value of λ

First, the impact of nutrient cycling depends on the contribution of recycled nutrients compared to that of external nutrient inputs. Thus, in an ecosystem with low external inputs, recycling would contribute significantly to the supply of the mineral nutrient compartment. This relation is summarised by the ratio of external inputs I to internal inputs of recycled nutrients $I_{recymax}$ (i.e. maximum quantity of recycled nutrients when $\lambda = 1$). Thus, $I/I_{recymax}$ is maintained between 0.1 and 1 to ensure a significant contribution of nutrient cycling to the overall dynamics of our ecosystem model. We do not constrain $I/I_{recymax}$ to a fixed value because we already adjust the values of I and D (see Equations 3 and 4 in the Supporting Information).

Second, varying recycling efficiency λ simultaneously increases feedback and enrichment effects. To disentangle these two effects, we offset fraction $1 - \lambda$ of nutrients lost by the system due to inefficient recycling by an additional external nutrient input, as in Quévreux, Barot, et al. (2021) (Figure 3). This modified external input I_{comp} is defined by:

$$I_{comp} = I + (1 - \lambda)\, I_{recymax}. \tag{5}$$

Thus, we maintain a constant nutrient availability regardless of the value of λ, which ensures similar biomasses and species persistence for all values of λ.

3 | RESULTS

3.1 | Recycling efficiency

To understand the influence of nutrient cycling on food chain stability, we first consider a nutrient-primary producer system where only primary producers are perturbed. We choose this simple setup because it results in an easier mathematical analysis, and models with a longer food chain length are studied in Figures S2-2 and S2-3.

First, the invariability in the primary producers (B_1) decreases when the recycling efficiency λ increases regardless of the value of the self-regulation coefficients D. This decrease is due to a stronger increase in standard deviation σ_1 than in equilibrium biomass B_1^* (Figure 4). In the same way, the invariability in the mineral nutrients (B_0) is driven by the variation in the standard deviation but also depends strongly on the self-regulation coefficient D. In fact, for $D \neq 0$, we observe a maximum invariability at $\lambda = 0.53$ due to a minimum standard deviation.

These variations can be fully explained analytically by the values of the term J_{01} of the Jacobian matrix which represents the direct effect of B_1 on B_0 (see Equation 7 in the Supporting Information). This direct effect has two components with opposite effects: the absorption of B_0 by B_1 (1) and the recycling effect of B_1 (2) (Figure 5a). For low values of λ, the negative effect of absorption overwhelms the positive effect of recycling and perturbations are mainly transmitted from B_1 to B_0 through absorption, thus leading to a negative overall effect (Figure 5b). As the recycling efficiency λ increases, the recycling effect becomes stronger and finally totally offsets the absorption effect. This represents a situation where primary producers have a null net effect on nutrients and thus corresponds to the maximum invariability observed in Figure 4. Then, for high values of λ, perturbations are mainly transmitted by nutrient cycling. However, this pattern does not hold when the self-regulation coefficient D is null because the recycling effect is weak to offset the absorption effect (Figure 5b).

We obtain similar results for other food chain lengths since the top compartment is always destabilised by nutrient cycling. The other compartments are either stabilised if they are at odd distances from the top compartment or destabilised if they are at even distances (see Figure S2-2).

3.2 | Self-regulation

We explore the effects of self-regulation on food chain stability by considering a nutrient-primary producer-herbivore system. In the nutrient-primary producer system presented above, self-regulation directly affects the positive and negative effects of the primary producers on mineral nutrients. This effect leads to a specific response of the system to self-regulation, which is detailed in Figure S2-7; thus, we consider more trophic levels to derive more general conclusions on ecosystem functioning. First, the invariability of herbivores B_2 is constant for most values of self-regulation D but increases and decreases for higher values. The observed increase is due to the decrease in the standard deviation of B_2 while its biomass remains constant. The final decrease is due to a decrease in herbivore biomass because of intense self-regulation, while the decrease in the standard deviation is less strong (Figure 6).

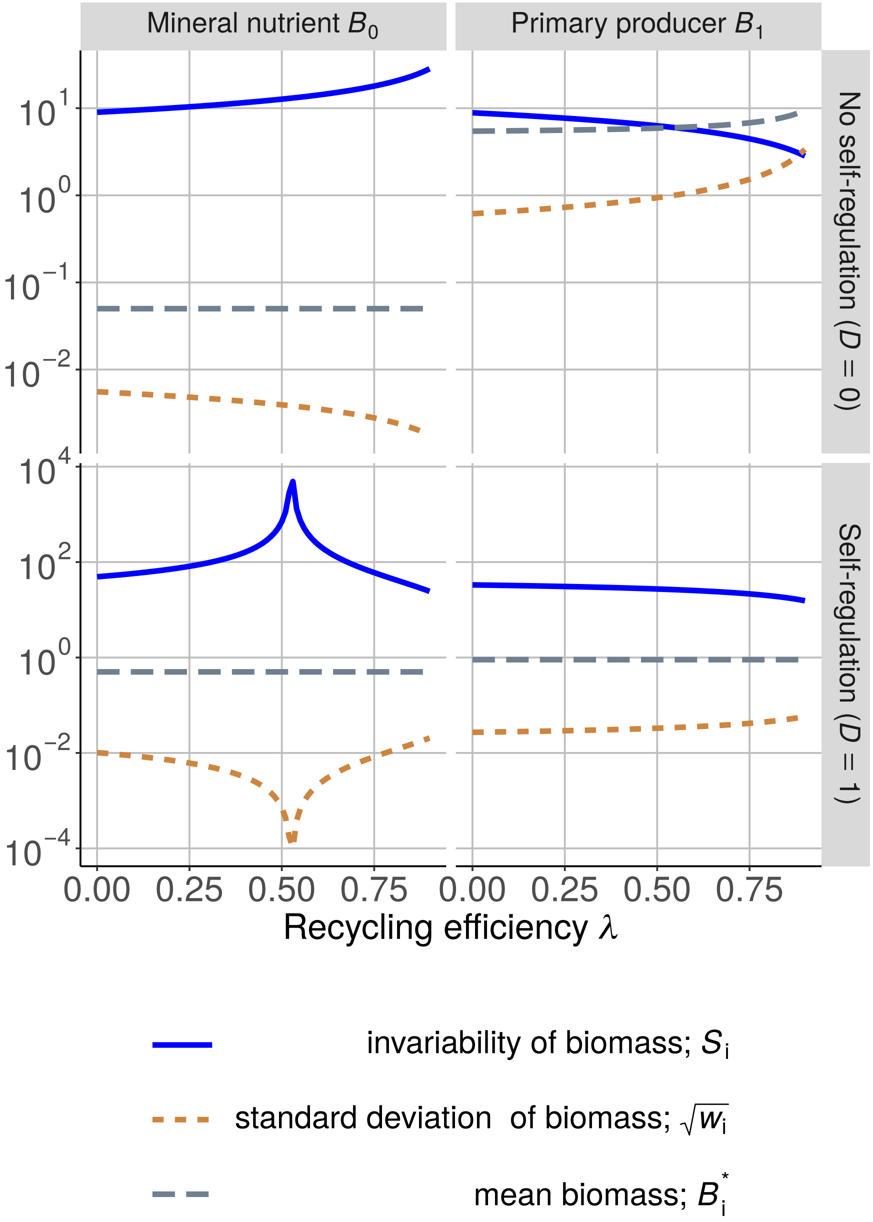

FIGURE 4 Stability (measured by invariability), standard deviation and biomass of different compartments depending on recycling efficiency λ and self-regulation coefficient D in a food chain with a chain length equal to 1 (TL1). Primary producers are perturbed and basal external inputs I are fixed to 0.05

The invariability of the mineral nutrients B_0 increases because of the decrease in the standard deviation while the nutrient stock remains constant. Again, we can explain this pattern by quantifying the direct and indirect interactions described in Figure 7. The overall effect of herbivores B_2 on mineral nutrients B_0 is mostly positive and the direct recycling effect of B_2 must prevail as the variations in the standard deviation of the nutrients are similar to those of the herbivores.

Again, we can explain this pattern based on the terms of the Jacobian matrix summarised by Figure 7a. As there are three compartments, we must consider the direct effect of herbivores on mineral nutrients represented by the recycling of B_2 (2) and the indirect effect represented by the product of the predation of B_2 on B_1 (1) and all the effects of B_1 on B_0 (3) (i.e. recycling of B_1 and predation of B_1 on B_0). According to the variations in the terms of the Jacobian matrix, the overall effect of the herbivores B_2 on the mineral nutrients B_0 is mostly positive (see Figure S2-5). The direct effect of recycling by B_2 must prevail as the variations in the standard deviation of the nutrients are similar to those of the herbivores (Figure 6).

Similarly, Figure 7b explains the variations in the invariability of primary producers B_1. The particular response to self-regulation for $\lambda = 1$ is due to the strong indirect effect of herbivore recycling on primary producers coupled with self-regulation differentially affecting B_1 and B_2 due to their different abundances (see Figure S2-5 and the detailed description in the Supporting Information). For low values of λ (i.e. $\lambda < 1$), recycling efficiency is not high enough to allow perturbations to be transmitted mainly by nutrient cycling. Thus, there is a monotonous increase in the invariability of the primary producers, as self-regulation increases B_1 by decreasing the top-down control of the primary producers by herbivores.

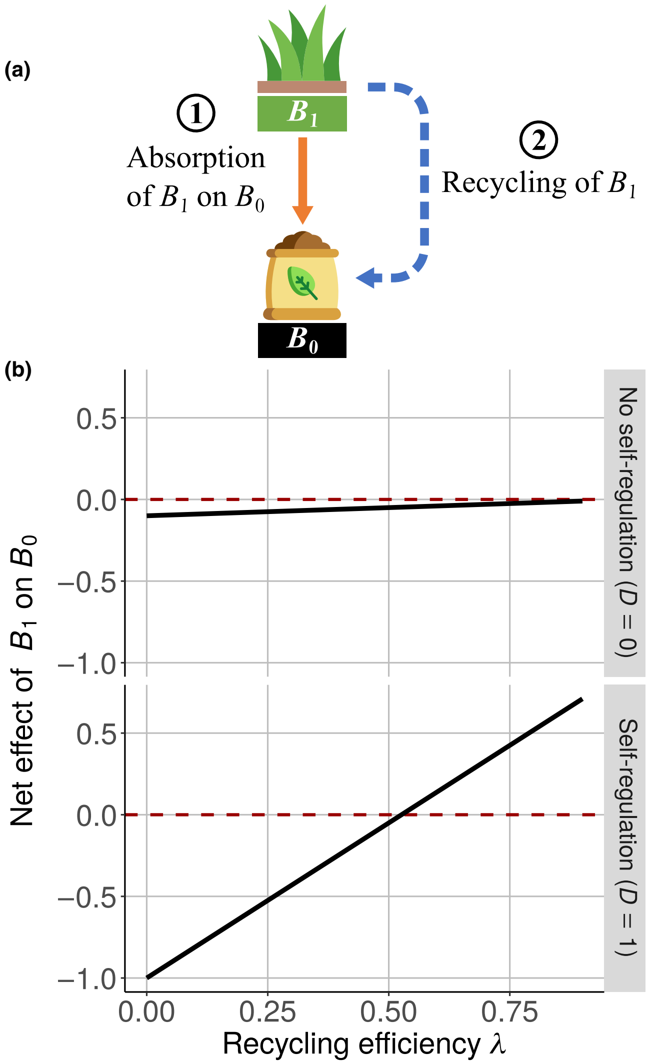

FIGURE 5 Effects of primary producers on mineral nutrients. (a) Schema of the nutrient-primary producer system. The orange arrow represents (1) the negative effect of the absorption of B_0 by B_1, and the blue dashed arrow represents (2) the positive recycling effect of B_1. (b) Variations in the direct net effects ((1) + (2)) of primary producers B_1 on mineral nutrients B_0 (equal to element J_{01} of the Jacobian matrix) depending on recycling efficiency λ and self-regulation coefficient D in a food chain with a chain length equal to 1 (TL1). The dashed red line represents a null net effect ($J_{01} = 0$)

3.3 | Food chain length

Food chain length also affects the invariability of each species since we found previously that the response of stability depends on the distance from the perturbed species (which is the highest trophic level in this study, as shown in Figure 8a). Thus, species at an odd distances from the perturbed specie are stabilised by nutrient cycling because its positive effect mitigates the negative effect of predation (Figure 8b; Figure S2-9). The invariability of primary producers increases with recycling efficiency λ when primary producers are at odd distance from the top species (TL2) with a maximum of invariability near $\lambda = 0.75$ when self-regulation is strong ($D = 0.1$) similarly to Figure 4. In contrast, species at even distances (Tl1 and TL3) from the perturbed species are destabilised by nutrient cycling. In fact, nutrient cycling enhances the transmission of perturbations through a positive bottom-up effect, which adds to the positive effect due to the top-down control of consumers at odd distances (Figure 7).

4 | DISCUSSION

Our model aimed to determine the influence of nutrient cycling and self-regulation on food chain stability with a particular focus on feedback effects. First, we showed that nutrient cycling is always destabilising for perturbed species, while lower trophic levels are stabilised or destabilised depending on their trophic distance from the perturbed species. Thus, nutrient cycling is stabilising for species at odd distances, whereas it is destabilising for species at even distances. Second, we showed that self-regulation modulates the effects of nutrient cycling by decreasing top-down control and increasing flows of recycled nutrients.

4.1 | Recycling efficiency

Our main result is that nutrient cycling has a stabilising or a destabilising effect on each species depending on its trophic distances from the perturbed species. More specifically, species at odd distances are stabilised while species at even distances are destabilised by nutrient cycling (Figure 8). The key mechanisms involved are, on the one hand, the top-down control of consumers on resources, which leads to trophic cascades (Fretwell & Barach, 1977; Hairston et al., 1960; Oksanen et al., 1981), and, on the other hand, the positive bottom-up effect of recycled nutrients (Leroux & Loreau, 2010; Loreau, 2010). In fact, nutrient cycling dampens the negative effects cascading on species at odd distances from the top predator by adding a positive bottom-up effect of predators on their prey (Figures 4 and 5). This mechanism smooths the distribution of biomass CV predicted by Shanafelt and Loreau (2018), who found a strong difference between controlled and uncontrolled species and demonstrates that ecosystem processes can deeply impact community dynamics. Conversely, nutrient cycling destabilises species at even distances as the positive bottom-up effects add to the positive cascading top-down effects, thus enhancing the transmission of perturbations. This interplay between nutrient cycling and cascading effects has also been observed for biomass by Leroux and Loreau (2010), who found that nutrient cycling increases the biomass of species at even distances from the top consumer and not that of species at even distances (controlled species).

However, these results are not consistent with the results of Quévreux, Barot, et al. (2021), who did not find this pattern. This discrepancy is due to the presence of limit cycles in their system, whereas we consider stochastic perturbations in the vicinity of equilibrium. In systems with limit cycles, nutrient cycling creates new couplings of the phase of each predator–prey oscillator, thus altering the amplitude of oscillations and biomass CVs. On the other hand,

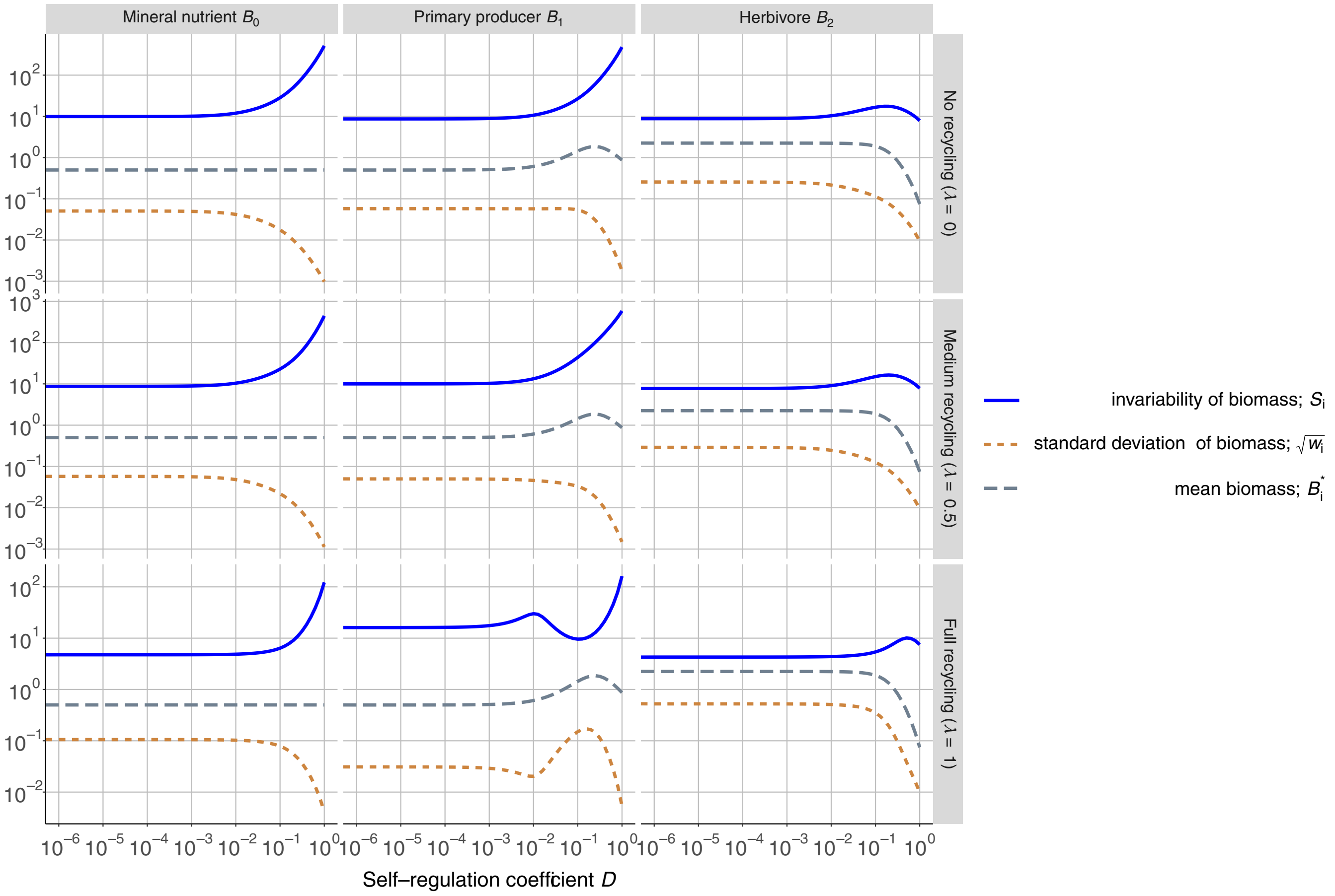

FIGURE 6 Stability (measured by invariability), standard deviation and biomass of the different compartments depending on recycling efficiency λ and self-regulation coefficient D in a food chain with a chain length equal to 2 (TL2). Basal external inputs I are fixed to 0.05, and predation rate a_2 is equal to 0.4 when $D = 0$ and to 0.401 when $D \neq 0$

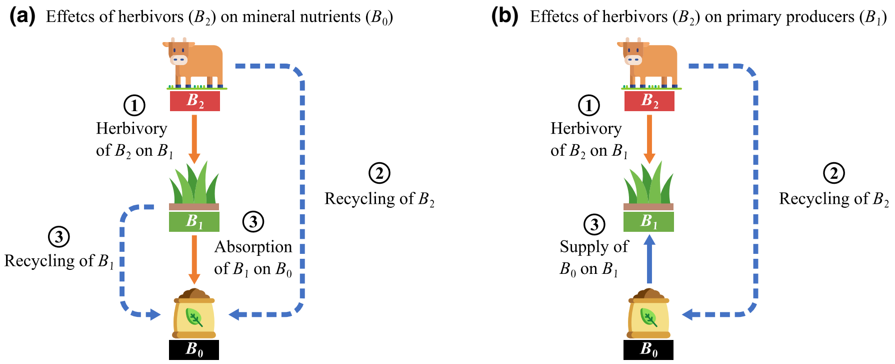

FIGURE 7 Schematic representing the direct and indirect effects of (a) herbivores on mineral nutrients. Blue arrows represent the positive terms (2) $\lambda(m + 2DB_2) + \lambda(1 - b_2)a_2B_1$, (3) $\lambda(m + 2DB_1) + \lambda(1 - b_2)a_2B_2$. Orange arrows represent the negative terms (1) $- a_2B_1$ and (3) $- a_1B_0$. Note that the direct effect of B_1 on B_0 (3) is partitioned into its positive and negative terms. (b) Effects of herbivores on primary producers. Blue arrows represent the positive terms (2) $\lambda(m + 2DB_2) + \lambda(1 - b_2)a_2B_1$, (3) a_1B_1. Orange arrows represent the negative terms (1) $- a_2B_1$. Note that the effect of nutrient absorption (3) is now positive because it is considered from the perspective of primary producers

stochastic perturbations ripple across the food chain and lead to trophic cascade-like patterns of stability. This shows that the effect of nutrient cycling on ecosystem dynamics depends on the state of the system and future studies should consider this aspect in their results. In addition, we show that asymptotic resilience is not representative of the response of the entire ecosystem (see Figures S2-1, S2-4, S2-6 and S2-8), but is mainly driven by a single compartment (Arnoldi et al., 2016; Haegeman et al., 2016). Considering invariability as a result of stochastic perturbations gives a detailed description of the stability of each ecosystem compartment.

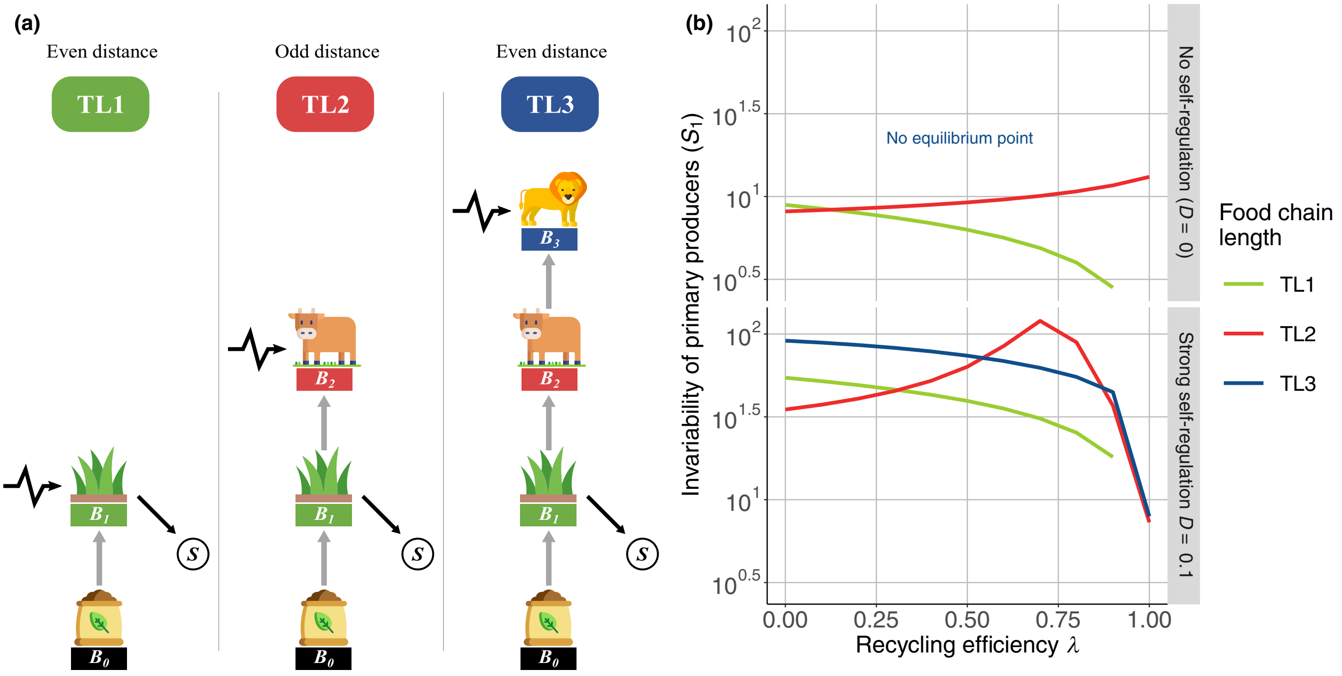

FIGURE 8 (a) Schematic representing the stability S of the primary producers B_1 depending on chain length which is set to 1, 2 or 3. Black arrows represent perturbations affecting the top species which is at odd (i.e. TL2) or even (i.e. TL1, TL3) distances from primary producers. (b) Stability of the primary producers B_1 depending on recycling efficiency λ and self-regulation coefficient D for various chain lengths. Stability is measured by invariability (i.e. inverse of CV), which is the ratio between equilibrium biomass B_i^* and standard deviation σ_i. External nutrient input I is fixed at 0.01 and attack rate a_2 is equal to 0.401

Our results demonstrate the importance of indirect effects since the indirect positive effect of nutrient cycling on resources can overcome the direct negative effect of consumers (Figure 5). The key role of long and weak loops in the stability of interaction networks has been already identified (McCann et al., 1998; Neutel et al., 2002) but Neutel and Thorne (2014) showed that feedback loops generated by nutrient cycling generally have a neutral effect on asymptotic resilience. This discrepancy can be explained by two factors. First, Neutel and Thorne (2014) did not consider self-regulation when calculating asymptotic resilience, while we show that its absence strongly reduces the response of asymptotic resilience to nutrient cycling (see Figures S2-1 and S2-4). Second, the complexity of food webs they analysed may blur the feedback effects of nutrient cycling. For instance, omnivory, by increasing the number of direct and indirect interactions, may weaken the net outcome of nutrient cycling. Such an effect can be observed with food chain length since the maximum of invariability observed for TL1 in Figure 4 is less clear for TL2 in Figure S2-2. Ultimately, nutrient cycling has almost no effect on stability in food webs with numerous interacting species (Quévreux, Barot, et al., 2021).

Finally, our model represents nutrient cycling in a very simple ways to grasp the fundamental effects of feedback loops generated by nutrient cycling on food web stability. Actually, nutrient cycling is much more complex since nutrients are also excreted as detritus that are degraded by decomposers (Moore et al., 2004). Decomposers and their consumers form the brown food web, which interacts with the green food web that relies on photosynthetic primary producers, through carbon and nutrient availability for instance (Cherif & Loreau, 2013; Danger et al., 2007; Daufresne et al., 2008; Daufresne & Loreau, 2001; Joint et al., 2002). These interactions strongly affect ecosystem functioning (Attayde & Ripa, 2008; Buchkowski et al., 2019; Zou et al., 2016) and food web stability (Gounand et al., 2014; Mougi, 2020). However, Mougi (2020) considered asymptotic resilience to measure stability and future studies should study the response to stochastic perturbations to fully understand the effects of nutrient cycling on ecosystem stability.

4.2 | Self-regulation

First, we found that self-regulation is generally stabilising when it is present for two or more trophic levels (Figure 6), although it becomes destabilising and can lead to species extinction if it is too strong (Barabás et al., 2017). The stabilising effect of self-regulation is due to a decrease in the ratio of interspecific to intraspecific interactions which leads to a lesser transmission of perturbations. However, the effects of self-regulation seem heavily dependent on food chain lengths (Figure 8). In a simple mineral nutrient-primary producer system, self-regulation has no effect on stability, as equilibrium biomass and standard deviation vary with D at the same rate (see Figure S2-7). For the system with three trophic levels, the effect of self-regulation is unclear because at a low coefficient of self-regulation D, the system does not reach equilibrium (see Figure S2-9).

In our model, self-regulation strongly interacts with nutrient cycling as it increases the quantity of nutrients released by organisms. In fact, the balance between the two mechanisms described earlier depends on the intensity of the self-regulation. For instance, nutrient cycling tends to reduce the stabilising effect of self-regulation on perturbed species and trophic levels at even distances from the perturbed species by making the perturbation loop inside the ecosystem. To our knowledge, most of the existing models studying nutrient cycling do not consider self-regulation (DeAngelis et al., 1989; Leroux & Loreau, 2010; Loreau, 1994; McCann, 2012; Nakajima & DeAngelis, 1989 but see Quévreux, Barot, et al., 2021), but given its interactions with nutrient cycling and its central role in the overall dynamics of food chains (Barbier & Loreau, 2019), self-regulation should be considered in future models combining community ecology and ecosystem functioning.

Finally, self-regulation summarises various mechanisms and is considered as an additional mortality term in our model. However, it can be seen as a decrease in the resource uptake rate, as in the Beddington–DeAngelis functional response (Beddington, 1975; DeAngelis et al., 1975), which considers mutual interference of predators. In future studies using such a model, we would expect self-regulation to decrease the quantity of recycled nutrients by reducing material flows between species, which would decrease the feedback effect of nutrient cycling. In addition, the Beddington–DeAngelis functional response alters interspecific interactions since it is nonlinear, while our study is based a linear functional response. However, we should only expect minor changes from this point for two main reasons. First, type II functional responses do not alter drastically biomass distribution among species at equilibrium (Barbier & Loreau, 2019). Second, since we consider small perturbations in the vicinity of equilibrium, our system is linearised and nonlinear functional responses act as linear Lotka–Volterra predator–prey interactions in the vicinity of the equilibrium.

4.3 | Empirical testing

Testing our results empirically is challenging because nutrient cycling is a fundamental ecosystem process that is not easy to measure and control. Nevertheless, microcosm or mesocosm experiments offer promising opportunities. For instance, Harrault et al. (2014) performed an aquatic mesocosm experiment in which they added sediments collected in a previous experiment to test the bottom-up effects of the quality of dead organic matter on pelagic food webs. In this spirit, removing the sediments produced in a mesocosm is equivalent to reducing recycling efficiency λ in our model and adding external sediments is equivalent to the compensation explained in Figure 3. However, in future experiments, recycling efficiency λ should not be considered equal among trophic levels. Harrault et al. (2012) demonstrated that detritus from mesocosms with fish were more degradable than detritus from mesocosms without fish. This increased degradability is equivalent to a higher λ and led to a stronger positive effect of nutrient cycling on phytoplankton (Harrault et al., 2014), as observed by previous experiments (Attayde & Hansson, 2001; Vanni & Layne, 1997; Vanni et al., 1997).

The crossed effects of nutrient cycling and self-regulation could be tested in microcosm experiments because micro-organisms can be easily killed and turned into labile organic matter by microwaving a sample from microcosms (Harvey et al., 2016, 2020; Jacquet & Altermatt, 2020; Jacquet et al., 2020). Thus, controlling the size of the microwaved sample depending on the density of protists would mimic variations in self-regulation, and reinjecting or not the sample would link self-regulation to nutrient cycling.

5 | CONCLUSIONS

Our study shows that the effects of nutrient cycling on ecosystem stability depend on the measure of stability since our results diverge from those in the existing literature using different measures. By considering stochastic perturbations, we found that nutrient cycling can be stabilising or destabilising depending on the positive and negative direct or indirect effects of the perturbed species on each species. This results in a trophic cascade pattern since species at even trophic distances from the perturbed species are destabilised, while species at odd distances are stabilised.

We also show that self-regulation, which is usually considered in a pure community ecology context, strongly interacts with nutrient cycling. By increasing the quantity of recycled nutrients and reducing the strength of top-down control, self-regulation strengthens the positive feedback loops generated by nutrient cycling. Thus, considering self-regulation should strongly impact the results of future studies considering similar models.

Our results provide broader insight into the mechanisms governing ecosystem stability and open models considering a more realistic representation of nutrient cycling, such as with detritus and decomposers.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

Conceptualisation (K.T., P.Q. and M.L.); Funding acquisition (M.L.); Model analysis (K.T., P.Q. and M.L.); Coding simulation (K.T.); Supervision (P.Q. and M.L.); Original draft writing (K.T. and P.Q.); Review and editing (P.Q. and M.L.).

DATA AVAILABILITY STATEMENT

The Python code of the simulations and R code of the figures are available on GitHub https://github.com/fixeight12/Nutrient-cycling-and-self-regulation-determine-food-web-stability/.

ORCID

Pierre Quévreux https://orcid.org/0000-0002-3531-1410
Michel Loreau https://orcid.org/0000-0002-0122-495X

REFERENCES

Arnold, L. (1974). *Stochastic differential equations: Theory and applications*. Wiley.

Arnoldi, J., Bideault, A., Loreau, M., & Haegeman, B. (2018). How ecosystems recover from pulse perturbations: A theory of short- to long-term responses. *Journal of Theoretical Biology*, *436*, 79–92.

Arnoldi, J., Loreau, M., & Haegeman, B. (2016). Resilience, reactivity and variability: A mathematical comparison of ecological stability measures. *Journal of Theoretical Biology*, *389*, 47–59.

Arnoldi, J., Loreau, M., & Haegeman, B. (2019). The inherent multidimensionality of temporal variability: How common and rare species shape stability patterns. *Ecology Letters*, *22*(10), 1557–1567.

Attayde, J. L., & Hansson, L.-A. (2001). Fish-mediated nutrient recycling and the trophic cascade in lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(10), 1924–1931.

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*(6), 980–990.

Barabás, G., Michalska-Smith, M. J., & Allesina, S. (2017). Self-regulation and the stability of large ecological networks. *Nature Ecology & Evolution*, *1*(12), 1870–1875.

Barbier, M., & Loreau, M. (2019). Pyramids and cascades: A synthesis of food chain functioning and stability. *Ecology Letters*, *22*(2), 405–419.

Beddington, J. R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *The Journal of Animal Ecology*, *44*(1), 331.

Begon, M., Harper, J. L., & Townsend, C. R. (1986). *Ecology: Individuals, populations and communities*. Blackwell. OCLC: 833046410.

Begon, M., Mortimer, M., & Thompson, D. J. (1986). *Population Ecology a unified study of animals and plants*. OCLC: 1185818106. John Wiley and Sons Ltd.

Brose, U., Williams, R. J., & Martinez, N. D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letters*, *9*(11), 1228–1236.

Brown, D. H., Ferris, H., Plant, R., & Fu, S. (2004). Modeling direct positive feedback between predators and prey. *Theoretical Population Biology*, *65*(2), 143–152.

Buchkowski, R. W., Leroux, S. J., & Schmitz, O. J. (2019). Microbial and animal nutrient limitation change the distribution of nitrogen within coupled green and brown food chains. *Ecology*, *100*(5), e02674. https://doi.org/10.1002/ecy.2674

Cherif, M., & Loreau, M. (2013). Plant–herbivore–decomposer stoichiometric mismatches and nutrient cycling in ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1754), 20122453.

Danger, M., Leflaive, J., Oumarou, C., Ten-Hage, L., & Lacroix, G. (2007). Control of phytoplankton-bacteria interactions by stoichiometric constraints. *Oikos*, *116*(7), 1079–1086.

Daufresne, T., Lacroix, G., Benhaim, D., & Loreau, M. (2008). Coexistence of algae and bacteria: A test of the carbon hypothesis. *Aquatic Microbial Ecology*, *53*, 323–332.

Daufresne, T., & Loreau, M. (2001). Ecological stoechiometry, primary producer-decomposer interactions, and ecosystem persistence. *Ecology*, *82*(11), 3069–3082.

DeAngelis, D. L. (1980). Energy flow, nutrient cycling, and ecosystem resilience. *Ecology*, *61*(4), 764.

DeAngelis, D. L. (1992). *Dynamics of nutrient cycling and food webs*. Number 9 in Population and community biology series (1st ed.). Chapman & Hall.

DeAngelis, D. L., Goldstein, R. A., & O'Neill, R. V. (1975). A model for tropic interaction. *Ecology*, *56*(4), 881.

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*(1), 71–95.

Fretwell, S. D., & Barach, A. L. (1977). The regulation of plant communities by the food chains exploiting them. *Perspectives in Biology and Medicine*, *20*(2), 169–185.

Gounand, I., Mouquet, N., Canard, E., Guichard, F., Hauzy, C., & Gravel, D. (2014). The paradox of enrichment in metaecosystems. *The American Naturalist*, *184*(6), 752–763.

Grimm, V., & Wissel, C. (1997). Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*, *109*(3), 323–334.

Gross, K., Cardinale, B. J., Fox, J. W., Gonzalez, A., Loreau, M., Wayne Polley, H., Reich, P. B., & van Ruijven, J. (2014). Species richness and the temporal stability of biomass production: A new analysis of recent biodiversity experiments. *The American Naturalist*, *183*(1), 1–12.

Haegeman, B., Arnoldi, J.-F., Wang, S., de Mazancourt, C., Montoya, J. M., & Loreau, M. (2016). Resilience, invariability, and ecological stability across levels of organization. *bioRxiv*.

Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist*, *94*(879), 421–425.

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*(11), 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*(8), 1695–1709.

Harvey, E., Gounand, I., Fronhofer, E. A., & Altermatt, F. (2020). Metaecosystem dynamics drive community composition in experimental, multi-layered spatial networks. *Oikos*, *129*(3), 402–412.

Harvey, E., Gounand, I., Ganesanandamoorthy, P., & Altermatt, F. (2016). Spatially cascading effect of perturbations in experimental meta-ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1838), 20161496.

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*(3), 243–250.

Jacquet, C., & Altermatt, F. (2020). The ghost of disturbance past: Long-term effects of pulse disturbances on community biomass and composition. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1930), 20200678.

Jacquet, C., Gounand, I., & Altermatt, F. (2020). How pulse disturbances shape size-abundance pyramids. *Ecology Letters*, *23*(6), 1014–1023.

Joint, I., Henriksen, P., Fonnes, G., Bourne, D., Thingstad, T., & Riemann, B. (2002). Competition for inorganic nutrients between phytoplankton and bacterioplankton in nutrient manipulated mesocosms. *Aquatic Microbial Ecology*, *29*, 145–159.

Leroux, S. J., & Loreau, M. (2010). Consumer-mediated recycling and cascading trophic interactions. *Ecology*, *91*(7), 2162–2171.

Loreau, M. (1994). Material cycling and the stability of ecosystems. *The American Naturalist*, *143*(3), 508–513.

Loreau, M. (1995). Consumers as maximizers of matter and energy flow in ecosystems. *The American Naturalist*, *145*(1), 22–42.

Loreau, M. (1998). Ecosystem development explained by competition within and between material cycles. *Proceedings of the Royal Society B: Biological Sciences*, *265*(1390), 33–38.

Loreau, M. (2010). Material cycling and the overall functioning of ecosystems. In *From populations to ecosystems: Theoretical foundations for a new ecological synthesis (MPB-46)* (pp. 164–195). Princeton University Press.

McCann, K. S. (2000). The diversity-stability debate. *Nature*, *405*(6783), 228–233.

McCann, K. S. (2012). Adding the ecosystem. In *Food webs* (pp. 189–200). Princeton University Press.

McCann, K. S., Hastings, A., & Huxel, G. R. (1998). Weak trophic interactions and the balance of nature. *Nature*, *395*(6704), 794–798.

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*(7), 584–600.

Moore, J. C., & Ruiter, P. C. D. (2012). *Energetic food webs: An analysis of real and model ecosystems*. OUP Oxford.

Mougi, A. (2020). Coupling of green and brown food webs and ecosystem stability. *Ecology and Evolution*, *10*(17), 9192–9199. https://doi.org/10.1002/ece3.6586

Nakajima, H., & DeAngelis, D. L. (1989). Resilience and local stability in a nutrient-limited resource-consumer system. *Bulletin of Mathematical Biology*, *51*(4), 501–510.

Neutel, A.-M., Heesterbeek, J. A. P., & De Ruiter, P. C. (2002). Stability in real food webs: Weak links in long loops. *Science*, *296*(5570), 1120–1123.

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*(6), 651–661.

Oksanen, L., Fretwell, S. D., Arruda, J., & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, *118*(2), 240–261.

O'Neill, R. V. (1976). Ecosystem persistence and heterotrophic regulation. *Ecology*, *57*(6), 1244.

Picoche, C., & Barraquand, F. (2019). How self-regulation, the storage effect, and their interaction contribute to coexistence in stochastic and seasonal environments. *Theoretical Ecology*, *12*(4), 489–500.

Picoche, C., & Barraquand, F. (2020). Strong self-regulation and widespread facilitative interactions in phytoplankton communities. *Journal of Ecology*, *108*(6), 2232–2242. https://doi.org/10.1111/1365-2745.13410

Quévreux, P., Barbier, M., & Loreau, M. (2021). Synchrony and perturbation transmission in trophic metacommunities. *The American Naturalist*, *197*(6), 714131. https://doi.org/10.1086/714131

Quévreux, P., Barot, S., & Thébault, É. (2021). Interplay between the paradox of enrichment and nutrient cycling in food webs. *Oikos*, *130*(1), 95–109. https://doi.org/10.1111/oik.07937

Rakowski, C. J., Farrior, C. E., Manning, S. R., & Leibold, M. A. (2019). Predator complementarity dampens variability of phytoplankton biomass in a diversity-stability trophic cascade. *bioRxiv*.

Shanafelt, D. W., & Loreau, M. (2018). Stability trophic cascades in food chains. *Royal Society Open Science*, *5*(11), 180995.

Sterner, R. W., Bajpai, A., & Adams, T. (1997). The enigma of food chain length: Absence of theoretical evidence for dynamic constraints. *Ecology*, *78*(7), 2258–2262.

Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, *441*(7093), 629–632.

Ulanowicz, R. E. (1990). Aristotelean causalities in ecosystem development. *Oikos*, *57*(1), 42.

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*(1), 21–40.

Vanni, M. J., Layne, C. D., & Arnott, S. E. (1997). 'Top–down' trophic interactions in lakes: Effects of fish on nutrient dynamics. *Ecology*, *78*(1), 1–20.

Veldhuis, M. P., Berg, M. P., Loreau, M., & Olff, H. (2018). Ecological autocatalysis: A central principle in ecosystem organization? *Ecological Monographs*, *88*(3), 304–319. https://doi.org/10.1002/ecm.1292

Veldhuis, M. P., Gommers, M. I., Olff, H., & Berg, M. P. (2018). Spatial redistribution of nutrients by large herbivores and dung beetles in a savanna ecosystem. *Journal of Ecology*, *106*(1), 422–433. https://doi.org/10.1111/1365-2745.12874

Wang, S., Haegeman, B., & Loreau, M. (2015). Dispersal and metapopulation stability. *PeerJ*, *3*, e1295.

Yodzis, P. (1981). The stability of real ecosystems. *Nature*, *289*(5799), 674–676.

Zou, K., Thébault, E., Lacroix, G., & Barot, S. (2016). Interactions between the green and brown food web determine ecosystem functioning. *Functional Ecology*, *30*(8), 1454–1465.

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