

Interactions between the green and brown food web determine ecosystem functioning

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Summary

1. The concepts of top-down and bottom-up controls are central to our understanding of cascading trophic effects on ecosystem functioning. Classical food web theory has focused either on food webs based on primary production (green food webs) or on food webs based on detritus (brown food webs) and generally ignored nutrient cycling.

2. We argue that nutrient cycling connects the two food webs, which questions the traditional concept of top-down and bottom-up controls.

3. By integrating these two food webs and nutrient cycling into simple models, we investigate the cascading effects from one food web to the other one. Both analytical calculations and simulations show that these two cascading effects depend on simple but distinct mechanisms that are derived from different ecological processes.

4. Predators of decomposers can affect primary production in the green food chain. The signs of these effects are determined by relative proportions of nutrient cycling within the brown food chain.

5. Cascading effects within the green food chain can affect decomposer production in a bottom-up way. The carbon/nutrient limitation of decomposers determines the way the green food chain affects decomposer production.

6. These theoretical findings are applicable to explore real interactions and cascading effects between the green and the brown food webs, such as pelagic–benthic interactions or above-ground–below-ground interactions.

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

Introduction

Cascading effects mediated by top consumers and resources on primary production have received particular attention in food web ecology (Hunter & Price 1992). However, ecosystem processes are not only determined by a green food web based on primary producers but also by a brown one based on decomposers, and by complex interactions between these two webs. Empirical studies reveal that

predators in one food web have cascading effects that extend to the other one (Wardle *et al.* 2004). The concept of ‘microbial loop’ highlights that predators of the brown food web can increase nutrient mineralization in aquatic (Azam *et al.* 1983; Fenchel 1988) and terrestrial (Clarholm 1985; Bonkowski 2004) ecosystems, which can indirectly affect primary production (Azam, Smith & Hollibaugh 1991; Stone & Weisburd 1992). Experiments have also shown that brown food webs respond strongly to the quality and quantity of dead organic matter, which is controlled by the structure of the green food web in both aquatic

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(Harrault *et al.* 2012; Danger *et al.* 2012) and terrestrial ecosystems (Bardgett & Wardle 2003; Wardle *et al.* 2003, 2005). Cascading effects from one web to another vary in intensity (Wardle *et al.* 2004) and sometimes in sign [e.g. contrasting effects of herbivory on recycling processes (Wardle *et al.* 2001)]. Understanding the mechanisms driving these cascading effects is therefore a challenge.

Existing theories on trophic cascades (Oksanen *et al.* 1981; Carpenter, Kitchell & Hodgson 1985; Leroux & Loreau 2010) have focused on food webs based either on primary production (green food webs) (Wollrab, Diehl & De Roos 2012; Heath, Speirs & Steele 2014) or on detritus (brown food webs) (Post & Kwon 2000; Moore *et al.* 2004). The few models that studied both food webs together highlighted important consequences of such coupling for ecosystem stability (Rooney *et al.* 2006; Boit *et al.* 2012). However, they only modelled the brown food web as an energy source for green food web consumers, omitting nutrient dynamics that strongly connect the two webs. Nutrient cycling is known to mediate important indirect effects in ecosystems. Ecologists have long recognized that recycling activities mediated by consumers in green (De Mazancourt, Loreau & Abbadie 1998; Attayde & Hansson 2001; Leroux & Loreau 2010) and brown (Nagata & Kirchman 1992; Berdjeb *et al.* 2011) food webs can positively affect resource production. We argue that nutrient cycling can question the traditional concept of top-down (the different trophic levels are determined by the abundance of top predators) and bottom-up control (the different trophic levels are determined by the availability of resource) in food web theory (Oksanen *et al.* 1981) because consumers of one food web can affect the other one in a bottom-up way (Moore *et al.* 2003; Leroux & Loreau 2015). Studying the mechanisms driving cascading effects between green and brown food webs is crucial to understand the functioning of ecosystems. We intend here to start building a theoretical framework on this issue.

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

producers (Daufresne *et al.* 2008). The carbon/nutrient limitation of decomposers depends on the gap between C:N demand of decomposers and C:N of supplied detritus resources (Bosatta & Berendse 1984; Sterner & Elser 2002; Daufresne *et al.* 2008). The relative importance of direct/indirect recycling and carbon/nutrient limitation of decomposers interacts in real ecosystems and should thus affect the interaction between the green and brown food webs.

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

Materials and methods

MODEL FORMULATION

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

Pools of N and D are supplied by constant inputs of mineral nutrients (I_N) and detritus (I_D), and they lose mineral nutrients and

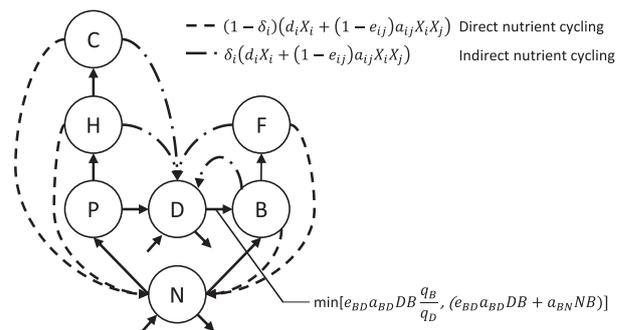


Fig. 1. Schematic diagram of the food web model. Circles represent compartments of mineral nutrients (N), primary producers (P), herbivores (H), carnivores (C), detritus (D), decomposers (B) and predators of decomposers (F). Solid arrows indicate fluxes of nutrients between compartments related to consumption.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

detritus at constant rates (I_N and I_D , respectively). All trophic interactions between consumer i and resource j follow Lotka–Volterra functional responses with consumption rate a_{ij} , except for the decomposers. Previous studies modelled decomposition processes either as donor-controlled (Pimm 1982; Daufresne & Loreau 2001) or Lotka–Volterra functional responses (Zheng, Bengtsson & Agren 1997). Therefore, we considered both cases to model the consumption of mineral nutrients and detritus by decomposers.

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

We assume decomposer growth is either limited by carbon/energy (hereafter C-limited) or by a single mineral nutrient (hereafter N-limited) (Daufresne *et al.* 2008). The type of limitation of decomposer growth at equilibrium is determined by the relative abundances of D and N and by the carbon-to-nutrient

stoichiometry of detritus and decomposers. If detritus have low abundance and low carbon-to-nutrient ratio in comparison with that of decomposers, decomposer growth is C-limited. On the contrary, if detritus are abundant and relatively rich in carbon, then decomposers are N-limited. When decomposition follows a Lotka–Volterra function, decomposer growth is expressed as:

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

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

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

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

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

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

Table 1. Parameter definitions and proposed values in simulations of models 3-2

Symbol	Definition	Dimension	Value
I_N	Constant input of mineral nutrients	$\mu\text{gN L}^{-1} \text{day}^{-1}$	0.125*
I_D	Constant input of organic materials	$\mu\text{gN L}^{-1} \text{day}^{-1}$	0.625 [†]
l_N	Loss rate of mineral nutrients	day^{-1}	0.1 [‡]
l_D	Loss rate of organic materials	day^{-1}	0.01 [†]
a_{PN}	Intrinsic growth rate of primary producers	$\text{L} (\mu\text{g N}^{-1}) \text{day}^{-1}$	0.3–0.6*
a_{HP}	Attack rate of herbivores on primary producers	$\text{L} (\mu\text{g N}^{-1}) \text{day}^{-1}$	0.8–1.6*
a_{CH}	Attack rate of carnivores on herbivores	$\text{L} (\mu\text{g N}^{-1}) \text{day}^{-1}$	0.3–0.6*
a_{BN}	Intrinsic growth rate of decomposers	day^{-1} or $\text{L} (\mu\text{g N}^{-1}) \text{day}^{-1}$	0.1, 0.5, 1.0*
a_{BD}	Attack rate of decomposers on organic materials	day^{-1} or $\text{L} (\mu\text{g N}^{-1}) \text{day}^{-1}$	0.83 [§] or 0.083* in LV
a_{FB}	Attack rate of predators of decomposer on decomposers	$\text{L} (\mu\text{g N}^{-1}) \text{day}^{-1}$	0.1–0.2*
e_{HP}	Nutrients conversion efficiency of herbivores	Dimensionless	0.8*
e_{CH}	Nutrients conversion efficiency of carnivores	Dimensionless	0.8*
e_{BD}	Nutrients conversion efficiency of decomposer	Dimensionless	0.8*
e_{FB}	Nutrients conversion efficiency of predators of decomposer	Dimensionless	0.8*
d_P	Loss rate of primary producers	day^{-1}	0.145 [¶]
d_H	Loss rate of herbivores	day^{-1}	0.17 [¶]
d_C	Loss rate of carnivores	day^{-1}	0.125 [¶]
d_B	Loss rate of decomposers	day^{-1}	1.0*
d_F	Loss rate of predators of decomposers	day^{-1}	0.9*
δ_H	Proportion of indirect nutrient cycling by herbivores	Dimensionless	0.5*
δ_C	Proportion of indirect nutrient cycling by carnivores	Dimensionless	0.5*
δ_B	Proportion of indirect nutrient cycling by decomposers	Dimensionless	varied
δ_F	Proportion of indirect nutrient cycling by predators of decomposers	Dimensionless	varied

*Assumed values.

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

[‡]This value is from Miki *et al.* (2011) (unit changed and converted to nitrogen content).

[§]The value is taken from Boit *et al.* (2012) (unit changed and converted to nitrogen content).

[¶]The value is taken from Vos *et al.* (2004).

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

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

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

$$\dot{C} = e_{CH} a_{CH} HC - d_C C \quad \text{eqn 6}$$

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

$$\begin{aligned} \dot{B} = & \min \left[e_{BD} a_{BD} DB \frac{q_B}{q_D}, (e_{BD} a_{BD} DB + a_{BN} NB) \right] \\ & - d_B B - a_{FB} BF \end{aligned} \quad \text{eqn 8}$$

$$\dot{F} = e_{FB} a_{FB} BF - d_F F \quad \text{eqn 9}$$

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

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

MODEL ANALYSIS

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

$$\varphi_{PP}^* = a_{PN} N^* P^* \quad \text{eqn 10}$$

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

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

To evaluate how interactions between green and brown food chains through nutrient cycling could determine the signs of cascading effects, we consider two key factors: (i) the relative proportion of direct/indirect recycling and (ii) whether decomposer growth is C-limited or N-limited. The effects of the relative proportion of direct/indirect recycling are analysed in two ways. We first calculate $\partial \varphi_{PP}^* / \partial \delta_i$ and $\partial \varphi_{PB}^* / \partial \delta_i$ to study the effects of the proportion of direct/indirect nutrient cycling at all trophic levels

on primary production and decomposer production. Then, to analyse the effect of direct/indirect nutrient cycling on cascading effects between the two webs, we examine their impacts on the signs of the partial derivatives (Appendix 1, Table S2, Supporting information). The effects of growth limitation of decomposers are examined by using either the left (C-limited) or the right term (N-limited) in the minimum function.

MODEL PARAMETERIZATION

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

Results

GENERAL RESULTS

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

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

EFFECTS OF THE BROWN FOOD CHAIN ON PRIMARY PRODUCTION

Primary production is directly proportional to the stock of mineral nutrients and primary producers ($\varphi_{PP}^* = a_{PN} N^* P^*$).

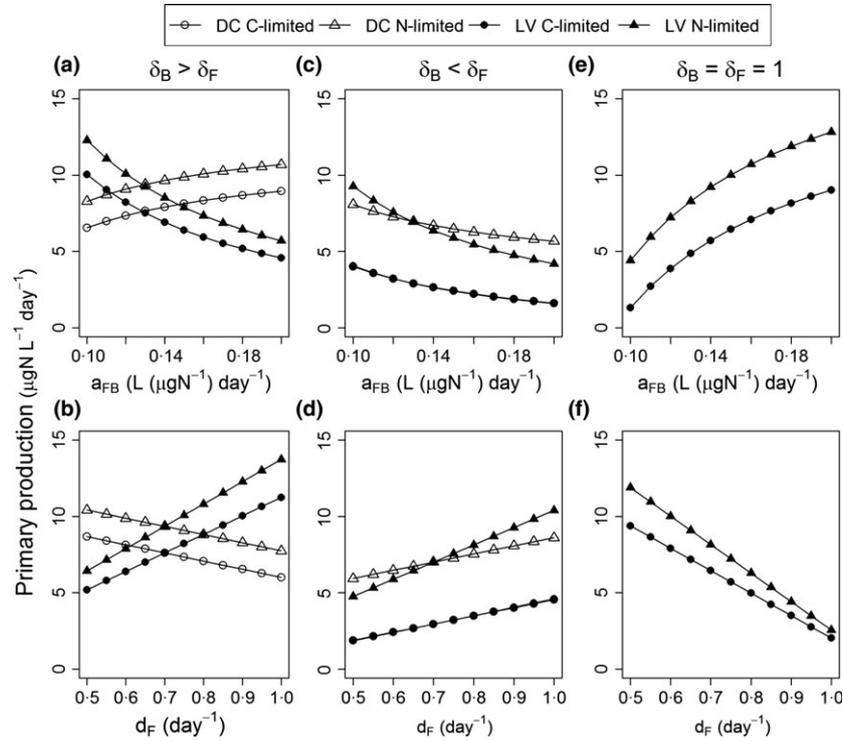


Fig. 2. Effects of predators of decomposers (attack rate a_{FB} and nutrient loss rate d_F) on primary production ($\mu\text{gN L}^{-1} \text{day}^{-1}$) predicted by the parameterized model. The 1st and 2nd columns represent, respectively, the cases $\delta_B > \delta_F$ ($\delta_B = 0.5$, $\delta_F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

Since N^* is independent of parameters from the brown food chain when the green food chain length is 3-level, the stock of primary producers (P^*) is essential to understand the effects of the brown food chain on primary production.

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

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

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

production is directly proportional to producer biomass P^* , primary production decreases as a_{BN} increases.

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

Further, when decomposers are donor-controlled, the same condition $\delta_B - \delta_F$ determines the effects of predators of decomposers on primary production. When $\delta_B > \delta_F$, decomposers recycle a higher proportion of nutrients in organic form than their predators, and consumption of

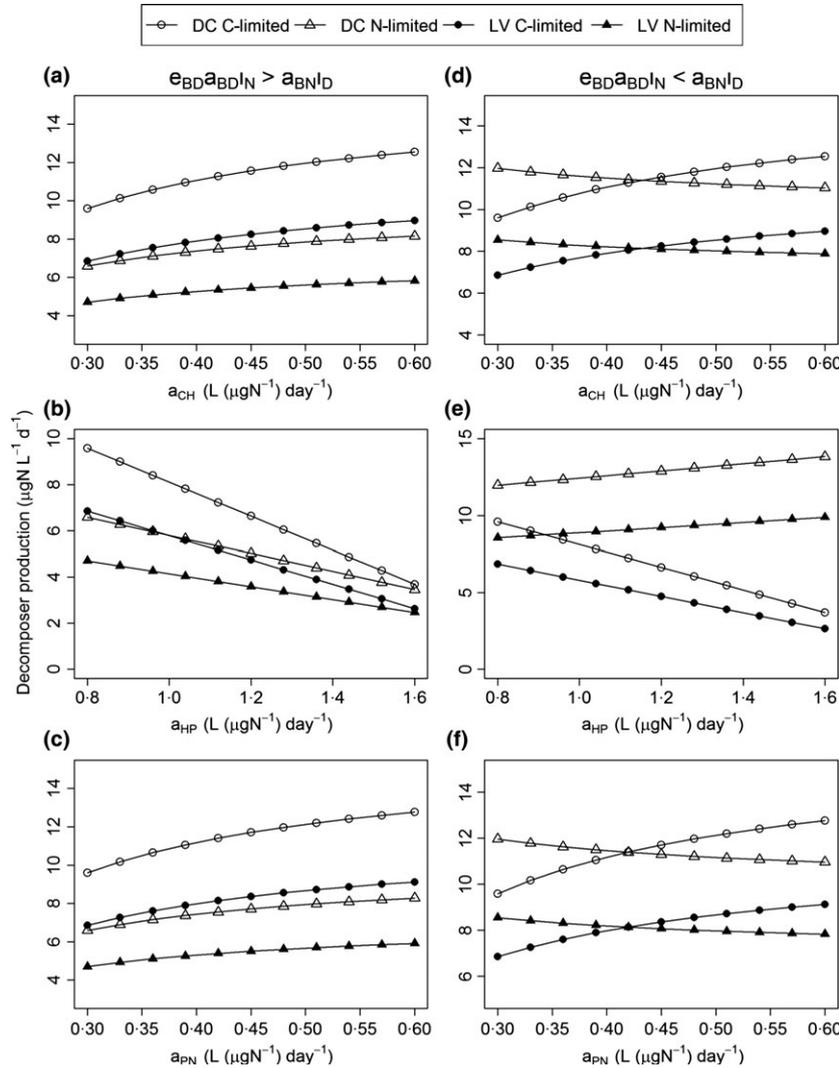


Fig. 3. Cascading effects of carnivores (*C*), herbivores (*H*) and primary producers (*P*) (attack rates a_{CH} , a_{HP} and a_{PN} , respectively) on the production of decomposers ($\mu\text{gN L}^{-1} \text{d}^{-1}$) predicted by the parameterized model for both donor-controlled and Lotka–Volterra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

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

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

case then does not arise from positive effects on direct recycling (as in the donor-controlled case) but from a decrease in the total amount of nutrients immobilized in the brown food chain.

EFFECTS OF THE GREEN FOOD CHAIN ON DECOMPOSER PRODUCTION

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

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

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

In case of N-limited, the signs of these cascading effects are governed by the sign of $e_{BD}a_{BD}/l_D - a_{BN}/l_N$. The ratios a_{BN}/l_N and $e_{BD}a_{BD}/l_D$ represent the consumption rates of mineral nutrients and detritus by decomposers divided by the rate of nutrient loss from these compartments. A higher ratio implies that a higher proportion of nutrients and detritus is assimilated by decomposers rather than being lost from the ecosystem. The signs and magnitude of cascading effects of carnivores, herbivores and primary producers remain the same as in the C-limited case if $e_{BD}a_{BD}/l_D > a_{BN}/l_N$ (Fig. 3a–c). If $e_{BD}a_{BD}/l_D < a_{BN}/l_N$, the directions of the cascading effects are opposite (Fig. 3d–f). The production of decomposers decreases by 7.9% (7.7% for Lotka–Volterra function) and by 8.4% (8.4% for Lotka–Volterra function), respectively, with an increase in a_{CH} and a_{PN} , while it increases by 15.5% (15.7% for Lotka–Volterra function) with an increase in a_{HP} . The

condition is independent of decomposer functional response. Thus, the cascading effects of the green food web on the production of decomposers strongly depend on the limitation of decomposers.

EFFECTS OF THE GREEN AND BROWN FOOD CHAIN LENGTHS

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

When the green food chain has 3 levels, N^* and H^* are controlled by the green chain while P^* and C^* are determined by parameters from both the green and the brown food chains. The effects of the brown food chain on primary production are then determined mainly through its effects on P^* . When the green food chain is one link shorter or longer (i.e. 2 or 4 levels), N^* and H^* (and eventually the 4th level top predator Y^*) depend on both food chains' parameters while P^* and C^* become independent of parameters of the brown food chain (Appendix 2). Consequently, the stocks of nutrients N^* determine the effects of the brown food chain on primary production. Despite these changes, the conditions determining the effects of the brown food chain on primary production and of the green food chain on decomposer production stay the same as in model 3-2 (Appendix 2, Tables S3, S5, S6, S8 and S9). The only important change is that decomposer production is affected by all δ_i (positive or condition-dependent effects) since N^* becomes dependent on δ_i (Appendix 2, Tables S4 and S7).

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

difference between the proportion of indirect nutrient cycling by decomposers and their predators ($\delta_B - \delta_F$) as in model 3-2. If the consumption efficiency of predators of decomposers is high (e_{FB} close to 1), these effects depend mainly on the difference between the proportion of indirect nutrient cycling by decomposers and top predators of the brown food chain ($\delta_B - \delta_A$). Further, the sign of $\partial\phi_{PP}^*/\partial d_F$ is determined by $\delta_F - \delta_A$, which is the difference between the proportion of indirect nutrient cycling by predator of decomposers and their predators. Despite varying conditions for the effects of the brown food chain on primary production, the relative proportions of indirect nutrient cycling in the brown food web are still key factors for these effects in the donor-controlled case.

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

Discussion

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

CASCADING EFFECTS OF THE BROWN FOOD CHAIN ON PRIMARY PRODUCTION

The predation on decomposers in the brown food web is thought to have a major influence on primary production in all ecosystems. Most empirical studies predict that predators of decomposers increase primary production by raising nutrient availability. In terrestrial ecosystems, the ‘microbial loop’ hypothesis suggests that bacterial grazers, for example protozoa or nematodes, liberate nutrients

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

Previous food web studies that included recycling processes modelled either direct (Leroux & Loreau 2010) or indirect (De Mazancourt, Loreau & Abbadie 1998) nutrient cycling in ecosystems. In real ecosystems (Vanni 2002), both direct and indirect nutrient cycling contribute to affect ecosystem functioning. For example, direct nutrient excretion by fish and zooplankton could meet, respectively, 5% and 26% of phosphorus demand of phytoplankton (Schindler *et al.* 1993). Indirect nutrient cycling through the remineralization of detritus affects the productivity of lakes (Jansson *et al.* 2000). The integration of both direct and indirect nutrient cycling is one of the major novelties in our model. We show that the effects of predators of decomposers on primary production depend strongly on their relative proportion of direct/indirect nutrient cycling compared to those of decomposers. When predators of decomposers recycle directly a larger (smaller) proportion of their nutrient than decomposers, their consumption of decomposers increases (decreases) primary production. We propose a possible mechanism behind the positive effects of ‘microbial loop’ on primary production by linking the proportion of direct nutrient cycling to stoichiometric mismatches between decomposers and their predators and between detritus and decomposers. Due to stoichiometric constraints (Vanni 2002), a species with a relatively low mineral nutrient content should excrete more nutrients than a species with a higher nutrient content. Therefore, if predators of decomposers have a higher carbon-to-nutrient ratio than their prey, they might recycle a higher proportion of inorganic nutrients than their prey, leading to positive effects on primary production (i.e. predators have a relatively low value of δ_F thus $\delta_B > \delta_F$). This condition is likely to be met since predators of decomposers such as

flagellates prefer prey rich in nutrients (i.e. lower C:N) (Grover & Chrzanowski 2009). Besides, decomposers might recycle directly less mineral nutrients than predators of decomposers because of the higher C:N ratio in detritus than in decomposers (Caron, Goldman & Dennett 1988; Thingstad & Lignell 1997). This should lead to a relatively high value of δ_B , and again to positive effects of predators of decomposers on primary production.

By measuring the C:N ratios and/or the proportion of direct/indirect recycling of decomposers and their predators, we may predict the impact of predators in the brown food web on primary production. An empirical study in an aquatic ecosystem reported that the presence of bacterivorous protozoa increased diatom density by 130% when bacteria used glucose as substrate (Caron, Goldman & Dennett 1988). These results are in agreement with our predictions because a high C:N ratio in bacterial substrate should lead to a relatively high value of δ_B . We can hardly compare our predictions with other empirical results in aquatic ecosystems where, in most cases, only the effects on the production of decomposers (but not effects on primary production) are analysed (Jacquet *et al.* 2005; Berdjeb *et al.* 2011; Bouvy *et al.* 2011) or predators are generalists and consume both primary producers and decomposers (Sherr & Sherr 2002). Our predictions can be also compared with the empirical results in terrestrial ecosystems. Irshad *et al.* (2011) found that addition of predator of decomposers increased plant biomass by 30% and increased plant N and P content by 75% and 50%, while Krome *et al.* (2009) found an increase of 66% in biomass.

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

CASCADING EFFECTS OF THE GREEN FOOD WEB ON THE PRODUCTION OF DECOMPOSERS

The green food web is known to have cascading effects on the production of decomposers. In aquatic ecosystems, the green food web can control the quantity, quality and biodegradability of sediment dead organic matter (Danger *et al.* 2012; Harrault *et al.* 2012) therefore affecting the productivity in the brown food web. In terrestrial ecosystems, productive plants have strong effects on microflora through their control on litter quality (Wardle *et al.* 2003). Herbivores and carnivores are also likely to control the

brown food web production by returning dung and urine to the ecosystem or altering plant composition (Bardgett & Wardle 2003; Wardle *et al.* 2005). However, the sign of above cascading effects is hard to predict empirically. For instance, scientists have found positive, negative or no effects of herbivores on decomposers even among relatively similar locations (Wardle *et al.* 2001).

Our results show that the carbon/nutrient dependence of decomposers is not only crucial to the coexistence of primary producers and decomposers (Daufresne *et al.* 2008), but also to the cascading effects of the green food web on decomposer production. When decomposers are C-limited, the relation between primary producers and decomposers is strictly mutualistic, and carnivores, herbivores and primary producers have, respectively, positive, negative and positive effects on decomposer production. However, the signs of above cascading effects become condition-dependent when decomposers are N-limited, that is when producers and decomposers are competing for the same mineral resource. This provides a mechanism explaining why the effects of the green food web on the production of the brown one may be negative or positive. The cascading effect of the green food web on decomposers depends not only on the top-down effect of the green web on detritus (as previously emphasized, e.g. Bardgett & Wardle 2003) but also on the top-down effect of the green web on mineral nutrients when there is competition (Fig. 4). These top-down effects on the availability of detritus and mineral nutrients have opposite signs and propagate to the brown food web through the dependence of decomposers on detritus and mineral nutrients (Fig. 4). The difference between $e_{BD}a_{BD}/l_D$ and a_{BN}/l_N regulates the demands of decomposers on detritus and mineral nutrients. When the production of decomposers depends more on detritus ($e_{BD}a_{BD}/l_D > a_{BN}/l_N$), the directions of the effects of carnivores, herbivores and primary producers on decomposer production correspond to the signs of the cascading effects of these trophic groups on detritus (Fig. 4a). When the production of decomposers depends more on mineral nutrients than on detritus ($e_{BD}a_{BD}/l_D < a_{BN}/l_N$), the signs of top-down effects of carnivores, herbivores and primary producers on decomposer production correspond to the signs of the cascading effects on mineral nutrients (Fig. 4b). In this case, increasing consumption of primary producers and predators decreases the production of decomposers, whereas increasing consumption of herbivores increases decomposer production. Interestingly, the condition determining the direction of cascading effects of the green food web on decomposers remains the same whether we consider a green food chain with 2, 3 or 4 trophic levels, as long as the brown food chain is of length 2 or decomposers have a donor-controlled functional response.

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

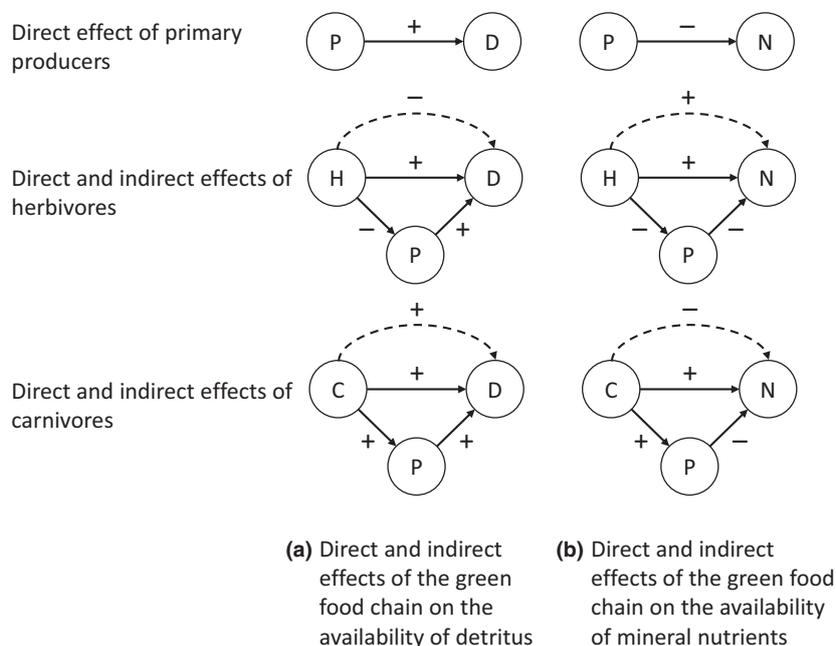


Fig. 4. Schematic diagram depicting the direct and indirect effects of primary producers (P), herbivores (H) and carnivores (C) on the availability of (a) detritus (D) and (b) mineral nutrients (N) through the balance between the effects of direct nutrients/organic materials release and the effects of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

limitation of decomposers regulates the signs of cascading effects of the green food web on the brown one.

Conclusion and perspectives

Despite its simplicity, our model sheds new lights on how interactions between the green and the brown food webs affect ecosystem functioning. Previous theoretical studies have paid little attention on interactions between green and brown webs mediated by nutrient cycling. However, they have highlighted the effects of food web structure (i.e. length of food chains and presence/absence of generalist predators) on trophic cascades (Attayde & Ripa 2008; Wollrab, Diehl & De Roos 2012) and ecosystem stability (Rooney *et al.* 2006; Wolkovich *et al.* 2014) in food webs with multiple food channels, including green and brown ones. Future studies will thus need to tackle a larger set of food web structures (Wollrab, Diehl & De Roos 2012). In particular, generalist predators, such as filter feeders (Sherr & Sherr 2002), will need to be included because they are ubiquitous, at least in aquatic ecosystems. Mesocosm experiments manipulating mesozooplankton (Zöllner *et al.* 2003) or fish (Nishimura *et al.* 2011) suggest that generalist predators have complex cascading effects on the components of both green and brown food webs. In terrestrial ecosystems, generalist predators linking green and brown

food webs might not be as common because organisms tend to live and feed either below-ground (where most decomposition occurs) or above-ground. These differences might explain why predators of decomposers have been shown to increase primary production more clearly in terrestrial ecosystems (Bonkowski 2004) than in aquatic ecosystems (Caron, Goldman & Dennett 1988; Sherr & Sherr 2002).

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

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Data accessibility

All data are included in the manuscript and its supporting information.

References

- Allard, B., Danger, M., Ten-Hage, L. & Lacroix, G. (2010) Influence of food web structure on the biochemical composition of seston, zooplankton and recently deposited sediment in experimental freshwater mesocosms. *Aquatic Sciences*, **73**, 113–126.
- 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**, 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**, 980–990.
- Azam, F., Smith, D.C. & Hollibaugh, J.T. (1991) The role of the microbial loop in Antarctic pelagic systems. *Polar Research*, **10**, 239–243.
- Azam, F., Fenchel, T., Field, J., Gray, J., Meyer-Reil, L. & Thingstad, F. (1983) The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series*, **10**, 257–263.
- Bardgett, R.D. & Wardle, D.A. (2003) Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, **84**, 2258–2268.
- Berdjeb, L., Pollet, T., Domaizon, I. & Jacquet, S. (2011) Effect of grazers and viruses on bacterial community structure and production in two contrasting trophic lakes. *BMC Microbiology*, **11**, 88.
- 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.
- Bonkowski, M. (2004) Protozoa and plant growth: the microbial loop in soil revisited. *New Phytologist*, **162**, 617–631.
- Bosatta, E. & Berendse, F. (1984) Energy or nutrient regulation of decomposition: implications for the mineralization-immobilization response to perturbations. *Soil Biology and Biochemistry*, **16**, 63–67.
- Bouvy, M., Bettarel, Y., Bouvier, C., Domaizon, I., Jacquet, S., Le Floch, E. *et al.* (2011) Trophic interactions between viruses, bacteria and nanoflagellates under various nutrient conditions and simulated climate change. *Environmental Microbiology*, **13**, 1842–1857.
- Bratbak, G. & Thingstad, T. (1985) Phytoplankton-bacteria interactions: an apparent paradox? Analysis of a model system with both competition and commensalism. *Marine Ecology Progress Series*, **25**, 23–30.
- Canuel, E.A., Spivak, A.C., Waterson, E.J. & Duffy, J.E. (2007) Biodiversity and food web structure influence short-term accumulation of sediment organic matter in an experimental seagrass system. *Limnology and Oceanography*, **52**, 590–602.
- Caron, D.A., Goldman, J.C. & Dennett, M.R. (1988) Experimental demonstration of the roles of bacteria and bacterivorous protozoa in plankton nutrient cycles. *Hydrobiologia*, **159**, 27–40.
- Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. (1985) Cascading trophic interactions and lake productivity. *BioScience*, **35**, 634–639.
- Casini, M., Lovgren, J., Hjelm, J., Cardinale, M., Molinero, J.-C. & Kornilovs, G. (2008) Multi-level trophic cascades in a heavily exploited open marine ecosystem. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 1793–1801.
- Cherif, M. & Loreau, M. (2013) Plant-herbivore-decomposer stoichiometric mismatches and nutrient cycling in ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122453.
- Clarholm, M. (1985) Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. *Soil Biology and Biochemistry*, **17**, 181–187.
- Danger, M., Allard, B., Arnous, M.B., Carrias, J.F., Mériquet, J., Ten-Hage, L. *et al.* (2012) Effects of food-web structure on the quantity and the elemental quality of sedimenting material in shallow lakes. *Hydrobiologia*, **679**, 251–266.
- Daufresne, T. & Loreau, M. (2001) Ecological stoichiometry, primary producer-decomposer interactions, and ecosystem persistence. *Ecology*, **82**, 3069–3082.
- 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.
- De Mazancourt, C., Loreau, M. & Abbadie, L. (1998) Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology*, **79**, 2242–2252.
- Fenchel, T. (1988) Microfauna in pelagic food chains. *Nutrient Cycling in Coastal Marine Environments* (eds Blackburn, B. & Sørensen, B.) pp. 59–65. John Wiley & Sons, Chichester, UK.
- Ferrier, C. & Rassoulzadegan, F. (1991) Density-dependent effects of protozoans on specific growth rates in pico- and nanoplanktonic assemblages. *Limnology and Oceanography*, **36**, 657–669.
- Fontaine, S. & Barot, S. (2005) Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. *Ecology Letters*, **8**, 1075–1087.
- Grover, J.P. & Chrzanowski, T.H. (2009) Dynamics and nutritional ecology of a nanoflagellate preying upon bacteria. *Microbial Ecology*, **58**, 231–243.
- 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., Mériquet, J., Carmignac, D., Huon, S., Gauzens, B. *et al.* (2014) Bottom-up effects of lake sediment on pelagic food-web compartments: a mesocosm study. *Freshwater Biology*, **59**, 1695–1709.
- Heath, M.R., Speirs, D.C. & Steele, J.H. (2014) Understanding patterns and processes in models of trophic cascades. *Ecology Letters*, **17**, 101–114.
- Hecky, R.E. & Kilham, P. (1988) Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. *Limnology and Oceanography*, **33**, 796–822.
- Hunter, M. & Price, P. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, **73**, 724–732.
- Irshad, U., Villenave, C., Brauman, A. & Plassard, C. (2011) Grazing by nematodes on rhizosphere bacteria enhances nitrate and phosphorus availability to *Pinus pinaster* seedlings. *Soil Biology and Biochemistry*, **43**, 2121–2126.
- Jacquet, S., Domaizon, I., Personnic, S., Pradeep Ram, A.S., Heddal, M., Duhamel, S. *et al.* (2005) Estimates of protozoan- and viral-mediated mortality of bacterioplankton in Lake Bourget (France). *Freshwater Biology*, **50**, 627–645.
- Jansson, M., Bergstrom, A.K., Blomqvist, P. & Drakare, S. (2000) Allochthonous organic carbon and phytoplankton/bacterioplankton production relationships in lakes. *Ecology*, **81**, 3250–3255.
- Krome, K., Rosenberg, K., Bonkowski, M. & Scheu, S. (2009) Grazing of protozoa on rhizosphere bacteria alters growth and reproduction of *Arabidopsis thaliana*. *Soil Biology and Biochemistry*, **41**, 1866–1873.
- 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.
- Leroux, S.J. & Loreau, M. (2015) Theoretical perspectives on bottom-up and top-down interactions across ecosystems. *Trophic Ecology* (eds T.C. Hanley & K.J. La Pierre), pp. 3–28. Cambridge University Press, Cambridge, UK.
- Miki, T., Nakazawa, T., Yokokawa, T. & Nagata, T. (2008) Functional consequences of viral impacts on bacterial communities: A food-web model analysis. *Freshwater Biology*, **53**, 1142–1153.
- Miki, T., Takimoto, G. & Kagami, M. (2011) Roles of parasitic fungi in aquatic food webs: A theoretical approach. *Freshwater Biology*, **56**, 1173–1183.
- Moore, J.C., McCann, K., Setälä, H. & De Ruiter, P.C. (2003) Top-down is bottom-up: does predation in the rhizosphere regulate aboveground dynamics? *Ecology*, **84**, 846–857.
- Moore, J.C., Berlow, E.L., Coleman, D.C., De Suiter, P.C., Dong, Q., Hastings, A. *et al.* (2004) Detritus, trophic dynamics and biodiversity. *Ecology Letters*, **7**, 584–600.
- Nagata, T. & Kirchman, D.L. (1992) Release of dissolved organic matter by heterotrophic protozoa: implications for microbial food webs. *Archiv für Hydrobiologie Beiheft, Ergebnisse der Limnologie*, **35**, 99–109.
- Nishimura, Y., Ohtsuka, T., Yoshiyama, K., Nakai, D., Shibahara, F. & Maehata, M. (2011) Cascading effects of larval Crucian carp introduction on phytoplankton and microbial communities in a paddy field: top-down and bottom-up controls. *Ecological Research*, **26**, 615–626.
- Oksanen, L., Fretwell, S., Arruda, J. & Niemela, P. (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, **118**, 240–261.

- Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, **14**, 483–488.
- Pimm, S.L. (1982) *Food Webs*. Springer, Dordrecht, The Netherlands.
- Post, W.M. & Kwon, K.C. (2000) Soil carbon sequestration and land-use change: processes and potential. *Global Change Biology*, **6**, 317–327.
- Rooney, N., McCann, K., Gellner, G. & Moore, J.C. (2006) Structural asymmetry and the stability of diverse food webs. *Nature*, **442**, 265–269.
- Schindler, D.E., Kitchell, J.F., He, X., Carpenter, S.R., Hodgson, J.R. & Cottingham, K.L. (1993) Food web structure and phosphorus cycling in lakes. *Transactions of the American Fisheries Society*, **122**, 756–772.
- Sherr, E.B. & Sherr, B.F. (2002) Significance of predation by protists in aquatic microbial food webs. *Antonie van Leeuwenhoek, International Journal of General and Molecular Microbiology*, **81**, 293–308.
- Sterner, R.W. & Elser, J.J. (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton, NJ.
- Stone, L. & Weisburd, R.S.J. (1992) Positive feedback in aquatic ecosystems. *Trends in Ecology & Evolution*, **7**, 263–267.
- Thingstad, T.F. (1998) A theoretical approach to structuring mechanisms in the pelagic food web. *Hydrobiologia*, **363**, 59–72.
- Thingstad, T. & Lignell, R. (1997) Theoretical models for the control of bacterial growth rate, abundance, diversity and carbon demand. *Aquatic Microbial Ecology*, **13**, 19–27.
- Vanni, M.J. (2002) Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics*, **33**, 341–370.
- Vos, M., Verschoor, A.M., Kooi, B.W., Wäckers, F.L., DeAngelis, D.L. & Mooji, W.M. (2004) Inducible defenses and trophic structure. *Ecology*, **85**, 2783–2794.
- Wardle, D.A., Barker, G.M., Yeates, G.W., Bonner, K.I. & Ghani, A. (2001) Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecological Monographs*, **71**, 587–614.
- Wardle, D.A., Yeates, G.W., Williamson, W.M. & Bonner, K.I. (2003) The response of a three trophic level soil food web to the identity and diversity of plant species and functional groups. *Oikos*, **102**, 45–56.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H. (2004) Ecological linkages between aboveground and belowground biota. *Science (New York, N.Y.)*, **304**, 1629–1633.
- Wardle, D.A., Williamson, W.M., Yeates, G.W. & Bonner, K.I. (2005) Trickle-down effects of aboveground trophic cascades on the soil food web. *Oikos*, **111**, 348–358.
- Wolkovich, E.M., Allesina, S., Cottingham, K.L., Moore, J.C., Sandin, S.A. & de Mazancourt, C. (2014) Linking the green and brown worlds: the prevalence and effect of multichannel feeding in food webs. *Ecology*, **95**, 3376–3386.
- Wollrab, S., Diehl, S. & De Roos, A.M. (2012) Simple rules describe bottom-up and top-down control in food webs with alternative energy pathways. *Ecology Letters*, **15**, 935–946.
- Wolters, V. (2000) Invertebrate control of soil organic matter stability. *Biology and Fertility of Soils*, **31**, 1–19.
- Zheng, D.W., Bengtsson, J. & Agren, G.I. (1997) Soil food webs and ecosystem processes: decomposition in donor-control and Lotka–Volterra systems. *The American Naturalist*, **149**, 125.
- Zöllner, E., Santer, B., Boersma, M., Hoppe, H.G. & Jürgens, K. (2003) Cascading predation effects of *Daphnia* and copepods on microbial food web components. *Freshwater Biology*, **48**, 2174–2193.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

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

Appendix 2. Other models with different food chain lengths.

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

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

Table S2. Signs of partial derivatives reporting the effects of the brown food chain on primary production and of the green food chain on decomposer production in model 3-2.

Table S3. Comparisons between models with different food chain lengths.

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

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

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

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

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

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

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

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

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

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

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