

## RESEARCH ARTICLE

# The coordination of green–brown food webs and their disruption by anthropogenic nutrient inputs

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**Abstract**

**Aim:** Our goal was to quantify nitrogen flows and stocks in green–brown food webs in different ecosystems, how they differ across ecosystems and how they respond to nutrient enrichment.

**Location:** Global.

**Time period:** Contemporary.

**Major taxa studied:** Plants, phytoplankton, macroalgae, invertebrates, vertebrates and zooplankton.

**Methods:** Data from >500 studies were combined to estimate nitrogen stocks and fluxes in green–brown food webs in forests, grasslands, brackish environments, sea-grass meadows, lakes and oceans. We compared the stocks, fluxes and metabolic rates of different functional groups within each food web. We also used these estimates to build a dynamical model to test the response of the ecosystems to nutrient enrichment.

**Results:** We found surprising symmetries between the green and brown channels across ecosystems, in their stocks, fluxes and consumption coefficients and mortality rates. We also found that nitrogen enrichment, either organic or inorganic, can disrupt this balance between the green and brown channels.

**Main conclusions:** Linking green and brown food webs reveals a previously hidden symmetry between herbivory and detritivory, which appears to be a widespread property of natural ecosystems but can be disrupted by anthropogenic nitrogen additions.

**KEYWORDS**

anthropogenic perturbations, food webs, nutrient cycling, nutrient subsidies, primary productivity

## 1 | INTRODUCTION

Food webs are supported by two energy and nutrient sources: primary production and detrital matter. These two sources, together with their respective consumers, constitute the green and brown

channels, respectively. Despite being coupled across all ecosystems to form green–brown food webs (Butler et al., 2008), investigations have only recently begun to explore the links between green and brown food webs and how these links affect their functioning (Buchkowski et al., 2019; Butler et al., 2008; Wolkovich et al., 2014;

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Zou et al., 2016). We are therefore limited in our ability to predict ecosystem responses to anthropogenic environmental change, such as the massive nutrient inputs entering all ecosystems globally (Bobbink et al., 2010; Bouwman et al., 2013).

The green channel encompasses primary producers, herbivores and their predators. Carbon enters this channel via photosynthesis and is redistributed upwards in the trophic chain, while nutrients, including nitrogen, are acquired primarily from the soil and water inorganic compartments (Buchkowski et al., 2019; Evans-White & Halvorson, 2017; Moore et al., 2004). Given that herbivores extract only a small portion of the net primary production, and particularly so in terrestrial ecosystems, a majority of carbon and nutrients from primary producers is recycled in the brown channel, which consists of detritus, microbes and the animals that consume both (Cebrian, 1999; Hairston Jr & Hairston Sr, 1997; Polis & Strong, 1996; Wetzel, 1995). Producers represent the entry point of carbon in the ecosystem, while detritus is a reservoir for both carbon and nutrients that stabilizes ecosystem dynamics and functions, including primary productivity, and promotes high biodiversity of consumers (DeAngelis, 1992; Moore et al., 1993, 2004; Polis et al., 1997).

Ecologists have long recognized these important roles but have focused mainly on the interaction of detrital matter with primary producers and decomposers (Cebrian, 1999; García-Palacios et al., 2016; Wolkovich et al., 2014), dedicating less attention to consumption and predation dynamics at higher trophic levels in the brown channel. Inquiry into trophic interactions has instead dealt almost exclusively with the green channel, largely disregarding nutrient cycling through the decomposers (Moore et al., 2004). However, understanding of green channel dynamics cannot be extrapolated readily to the brown channel.

A central difference between the green and brown food webs is their qualitatively different resource bases: primary producers versus detritus. In the green channel, primary producers are fuelled by solar energy and nutrients released by detritus. Primary production is controlled by self-regulation among primary producers and by herbivores that, in turn, can be regulated by predators (Barabás et al., 2017; Hairston et al., 1960; Paine, 2002). In the brown channel, detritus stocks depend on recycling from the primary producers and on subsidies entering the ecosystem from adjacent ecosystems or from human activities, such as agriculture (Polis et al., 1997). Nutrient limitation can occur at all trophic levels but depends on plant tissue composition in primary producers in the green channel and on nutrient enrichment from detritus decomposition in the brown channel (Sturner & Elser, 2002). These distinctions alone should lead to differences in both state and response to perturbations between channels (Attayde & Ripa, 2008; Mougi, 2020).

Although the internal processes within each channel (i.e., primary production, herbivory and predation for the green channel and decomposition for the brown channel) are relatively well characterized in isolation, the ecosystem-level consequences for stocks, fluxes and process rates of linking the two channels remain unclear. Predators consume both herbivores and detritivores, leading to an

apparent competition (Holt & Bonsall, 2017) between herbivores and detritivores, and thus between the green and brown channels overall. Moreover, given that food webs are always interlinked via both consumption and nutrient cycling, we need to consider them in concert to predict ecosystem responses to natural and anthropogenic perturbations.

Global change is expected to affect the functioning of both channels in all ecosystems (Tyllianakis et al., 2008; Woodward et al., 2012). A major driver of change is the input of nutrients into ecosystems, owing to both deliberate actions (e.g., fertilization) and side effects, such as atmospheric deposition (Bobbink et al., 2010; Bouwman et al., 2013; Galloway et al., 2008; Matson, 1997). According to the subsidy hypothesis, enriched ecosystems will show stronger top-down effects by predators on lower trophic levels (Leroux & Loreau, 2008). However, empirical tests either support or refute this prediction, possibly because outcomes are determined not only by the quantity, but also by the quality of the subsidy (Aguilera et al., 2021; Riggi & Bommarco, 2019). Altering between inorganic inputs, such as mineral fertilizer, and organic ones, for instance manure or detritus, could reverse the direction of trophic control from a top-down to a bottom-up control.

To compare stocks, fluxes and process rates in the two channels across ecosystems and to assess their responses to nutrient enrichment, in this study we synthesize data from the literature for six major ecosystems: forests, grasslands and savannas, brackish environments (marshes and mangroves), seagrass meadows, lakes and open oceans. We focus on nitrogen as a key limiting element, used here as a common currency to compare ecosystems. Values and ranges of stocks, fluxes and metabolic rates are collated from the literature for six compartments in green–brown food webs: primary producers, herbivores, predators, detritivores, organic matter and inorganic nitrogen. We use this information to parameterize a dynamical ecosystem model in which the two channels are linked, allowing us to examine how stocks and fluxes among compartments respond to an altered amount and quality of nutrient inputs. By “quality” here we refer to the chemical nature of these inputs, distinguishing between inorganic and organic forms; the former are easily taken up by the producers, whereas the latter require first to be mineralized by the decomposers. We thus gain insights on the current state of green and brown channels in major ecosystems, their similarities and differences, and how their state might change owing to the anthropogenic inputs of organic and inorganic nitrogen.

## 2 | MATERIALS AND METHODS

To quantify fluxes and stocks of nitrogen in the green and brown food webs, we first constructed a database merging existing and new datasets spanning the six ecosystems. Second, we developed a dynamical model of nitrogen cycling, which was parameterized using the new database. Third, we used the model to quantify the responses of green and brown food webs to changes in nitrogen inputs.

## 2.1 | Data synthesis

Our data synthesis is based on five main data sources: (1) two previous meta-analyses that focus on primary production, herbivory and detrital dynamics (Cebrian, 1999, 2004), containing c. 900 entries from 370 studies; (2) models that use the software ECOPATH (Christensen & Walters, 2004), mainly describing aquatic systems and focusing on food web relationships, such as predation rates; this dataset consists of 52 models, each detailing a particular ecosystem; (3) 31 studies of terrestrial food webs, reporting stocks and consumption fractions of consumers; (4) 69 studies reporting estimates of nitrogen stocks and fluxes in soil and/or water; and (5) 25 studies reporting estimations of nitrogen conversion efficiencies and weight conversions (see [Supporting Information section 1](#)).

From the first four datasets, we extracted direct estimates of nitrogen stocks of different compartments (see model description below), fluxes, such as net primary production (NPP), and flux fractions, such as how much NPP is lost to herbivory. We used all these estimates, together with non-dimensional quantities from the fifth dataset (e.g., nutrient conversion efficiencies), to calculate all the nitrogen stocks and fluxes in each ecosystem (see [Supporting Information section 2](#)). To quantify the stock and flux variability within each ecosystem type, we adopted a randomized parameter estimation approach. For each data type from our first four datasets (stocks, fluxes and flux fractions), we randomly chose two values and calculated their geometric average (more appropriate than arithmetic average when considering values changing over orders of magnitude). These averages were used to estimate the remaining values of stocks and fluxes, based on our dynamical model (see model description below), obtaining one complete set of nitrogen stocks and fluxes for that ecosystem. We repeated this procedure 1,000 times, each time randomly choosing different values, giving us a good representation of the variability of stocks and fluxes within each ecosystem type.

## 2.2 | Ecosystem structure and dynamical model

We divided each ecosystem into six compartments representing three trophic levels (primary producers, primary consumers and predators) along two parallel (green and brown) energy and nutrient flow channels ([Figure 1](#)). The three compartments that are central in the classic green food chain view are (see [Figure 1](#)):

- *P*: Primary producers, including plants, phytoplankton and algae.
- *H*: Herbivores, ranging from zooplankton, through insects, to large ungulates.
- *C*: All predators (secondary consumers), including animals that feed on insects, vertebrates, etc.

The other three compartments, forming the brown channel, include:

- *D*: Detritivores feeding on detrital matter, including animals that feed on microorganisms (which, in turn, feed on the detrital matter), but excluding the biomass of these microorganisms.
- *N*: Available inorganic nutrients in the medium (water or soil). The substrate here is the topsoil in forests and grasslands (where most of nutrient cycling occurs), but also in brackish and seagrass environments, and the top water column in the aquatic ecosystems.
- *S*: Active organic matter. In terrestrial ecosystems (forest, grassland and brackish), *S* represents the fraction of soil organic matter with relatively fast turnover time, including microbial biomass. We exclude mineral-associated or physically protected organic matter that is less sensitive to nutrient subsidies. In aquatic systems, we consider all detritus and associated microorganisms in the top water column (see details in [Supporting Information section 2.2](#)); sediments and nutrient cycling therein are not considered (except for sediment pore water in seagrass ecosystems).

Note that the predators, which constitute the higher trophic level, feed on the primary consumers: both the herbivores (green channel) and the detritivores (brown channel); hence, they represent one of the connections between the two channels.

Nutrient stock sizes were expressed as nitrogen stocks per unit surface area (in grams of nitrogen per metre squared) and flows between compartments in terms of nitrogen fluxes (in grams of nitrogen per metre squared per year). This allowed us easily to connect living and mineral compartments in the soil or water. The stoichiometric relationships in animals are relatively constrained and similar across ecosystems, whereas primary producers have more flexible nutrient contents (Elser et al., 2000; González et al., 2017). Therefore, translating our results and data to another type of currency, such as carbon, would be feasible after prescribing stoichiometric coefficients for all compartments or allowing flexible stoichiometry for the producers. This was beyond our scope here, because it would require additional assumptions that are difficult to test, such as assumptions on carbon metabolism under different degrees of nutrient limitation (Manzoni et al., 2017) and the degree of producer stoichiometric flexibility.

To model the dynamics of the ecosystem, we used six ordinary differential equations ([Equation 1](#)) that describe the change in nitrogen stocks of the six compartments of the ecosystems. By constructing a nitrogen-based model, we assumed nitrogen limitation or co-limitation in the ecosystem, which implies that our model predictions are relevant when nitrogen poses a strong limitation on growth of primary producers and detritivores. To keep the model simple and general, we followed Barbier and Loreau (2019) in defining the food web and used a type I functional response for consumption terms, meaning that the fluxes were linearly proportional to both the consumer and the resource. Additionally, two types of self-regulation were modelled: of predators attributable to intraguild predation, and of primary producers attributable to space and light limitations. With these assumptions, the nitrogen

mass balance equations for our six compartments can be written as follows (Figure 1):

$$\begin{aligned}
 \frac{d}{dt}P &= P(\varepsilon_P r_P N - r_H H - u_P - q_P P) \\
 \frac{d}{dt}H &= H(\varepsilon_H r_H P - r_C C - u_H - q_H H) \\
 \frac{d}{dt}D &= D(\varepsilon_D r_D S - r_C C - u_D - q_D D) \\
 \frac{d}{dt}C &= C(\varepsilon_C r_C H - \varepsilon_C r_C D - u_C - q_C C) \\
 \frac{d}{dt}N &= zS - IN - r_P PN + I_N \\
 \frac{d}{dt}S &= I_0 - zS - r_D DS + I_S
 \end{aligned}
 \tag{1}$$

The  $r_i$  parameters represent consumption coefficients of compartment  $i$  feeding on the trophic level below (or primary producers taking up  $N$ ),  $\varepsilon_i$  is the nutrient conversion efficiency tied to this consumption (ratio of nitrogen converted to biomass divided by the nitrogen consumed),  $u_i$  is the first-order mortality rate of the compartment, and  $q_i$  modulates the self-regulation of the compartment (e.g., light limitation for plants or intraguild predation for predators). The consumption and self-regulation coefficients are multiplied by the stocks to calculate the associated nitrogen fluxes. The coefficient  $z$  represents the rate of nutrient mineralization, and  $I$  is the loss rate of inorganic nutrient (e.g., leaching, volatilization). The flux of organic nutrient input to  $S$  from mortality of primary producers and animals is given by:  $I_0 = \gamma(u_P P + u_H H + u_D D + u_C C)$ , where  $\gamma$  is the recycling coefficient (e.g., the fraction of  $P$  mortality routed to  $S$ ). We assess a different assumption on nutrient recycling, whereby nutrients not converted into biomass are also recycled, in the Supporting Information (section 6.2). The parameters  $I_N$  and  $I_S$  are the influx rates of nutrients into the  $N$  and  $S$  compartments, respectively, interpreted as the inorganic and organic nutrient subsidy fluxes.

The connection between the green and brown channels is captured by three processes: recycling of dead material into  $S$  (modulated by  $\gamma$ ); transformation of organic material into inorganic material and its uptake by primary producers (modulated by  $z$ ); and predation of both detritivores and herbivores by predators  $P$  on top of the joint channels (Rooney et al., 2006; Scheu, 2001; Wardle et al., 2004). We note that the addition of self-regulation terms leads to more well-behaved dynamics (Barabás et al., 2017); for instance, avoiding unrealistic oscillations of the nutrient stocks under high nutrient input rates (Attayde & Ripa, 2008). Other methods of partitioning the ecosystem into compartments are possible (e.g., using more than six compartments), but our results are robust to partitioning choice because they focus on ecosystem functions, such as herbivory or predation, and not on individual species (Supporting Information section 6.1).

### 2.3 | Parameterization and simulations

Our stock and flux estimates were based on the steady-state solution of the dynamical model. The steady-state solution was used to

back-calculate the quantities that were not known from data (see Supporting Information section 3). The consumption coefficients of the type I functional responses were estimated by dividing the consumption flux by the stocks of resource and consumer, and the linear mortality rate of each compartment was estimated by dividing its mortality flux by its stock. Intraguild predation, the first type of self-regulation, was estimated directly for all ecosystems except for forest and grassland, for which we used heuristic estimations according to predation rates. The second type of self-regulation, space and light limitation, was assumed to reduce primary productivity by 10% in all ecosystems. This value did not change the results qualitatively (see details and sensitivity analysis in Supporting Information section 3.2 and section 5). Moreover, our analysis suggested that self-regulation was important only for primary producers and predators (see Supporting Information section 3.2).

To test whether our method to estimate model parameters caused spurious correlations (Brett, 2004), we adopted two Monte-Carlo approaches. In the first approach, parameters were chosen at random from independent distributions, so that they could not exhibit correlations by construction. In the second approach, we estimated the parameters from the data, but shuffling it between ecosystems. The expectation was that spurious correlations caused by our estimation approach would also emerge in these artificial datasets, whereas “real” correlations would emerge only between parameters estimated from the real data (see details in Supporting Information section 6.3).

To use our parameters for simulations (Figures 3 and 4), we chose a subset of the 1,000 parameter sets we defined in Section 2.1 (Data synthesis). However, nutrient inputs were still not known and needed to be estimated to guarantee that stocks were reasonable. For this purpose, the subset was chosen to represent parameter values that, in combination with the estimated nutrient inputs, gave viable equilibrium values for our model (i.e., they were self-consistent). This methodology, detailed in the next paragraph, was necessary because we did not have a complete set of stocks and fluxes for any specific ecosystem. Hence, choosing the most consistent parameter sets, while leaving the nitrogen input as a free parameter, ensured that we could model ecosystems with consistent properties.

For each ecosystem, we used the 1,000 parameter sets, and for each set we simulated different combinations of nutrient inputs, identifying those that produced nutrient stocks closest to those we used to estimate the parameter set. Finally, we chose the 200 sets that gave the best results (stocks closer to the data), thus focusing on viable ecosystems where our simulations were in line with the empirical estimates. The baseline input values (those obtained for these 200 sets) are shown in the Supporting Information (Figure S14), with most input values between 2 and 20 gNm<sup>-2</sup>year<sup>-1</sup>, which is consistent with observed levels (Rabalais, 2002; Zhu et al., 2015). For each of these 200 sets, we then increased the nutrient input by 10%, by adding either organic or inorganic nutrients, on top of the baseline input values, which were typically a mixture of both organic and inorganic. We chose a 10% addition to assess the sensitivity of ecosystems to nutrient addition. This nutrient addition was small

enough to have an approximately linear response. This could be contrasted with the 100% addition we considered in the Supporting Information (Figures S15 and S16). The results of the stocks and fluxes under nutrient addition are shown in Figures 3 (stocks) and 4 (fluxes), and in the Supporting Information (Figure S5) for both stocks and fluxes combined. These are shown relative to the baseline values (i.e., relative to the values of stocks and fluxes that we had from our self-consistent simulations).

### 3 | RESULTS

#### 3.1 | Nitrogen stocks and flows in green-brown food webs

Our literature review showed that predator (C) stocks, in general, were low compared with P and S stocks in the terrestrial forest and grassland ecosystems (Figure 1). Stocks were more evenly distributed across compartments in the aquatic ecosystems, in particular in the oceans. Across all ecosystems, the stocks of P and S showed similar values, as did H and D (Supporting Information Figure S2).

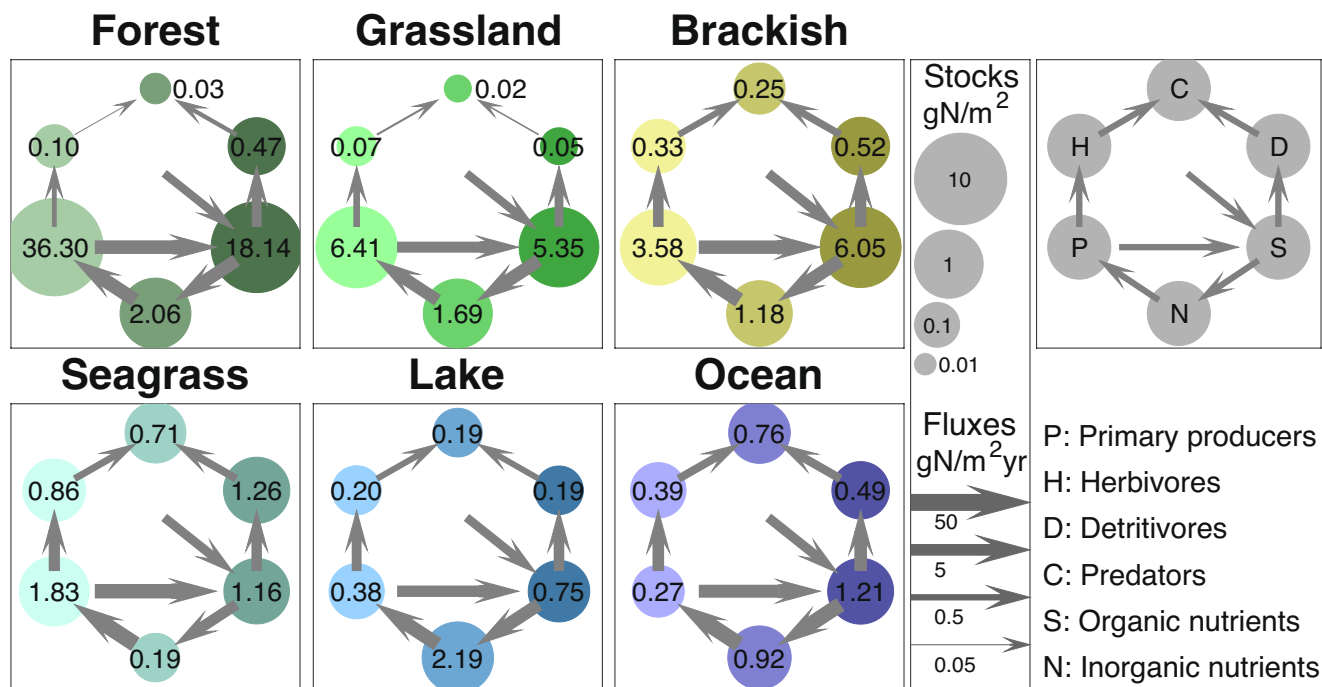
Fluxes among the three lower compartments (P, S, and N) were all of similar order of magnitude across all ecosystems, despite overall higher median nitrogen stocks in the terrestrial compared with the aquatic ecosystems. This was a result of the higher metabolic rates associated with P and S in aquatic ecosystems, which compensated for

the smaller nitrogen stocks (Cebrian, 1999). In contrast, the median fluxes among the top three compartments of H, D and C in terrestrial ecosystems were much smaller than in the aquatic ecosystems.

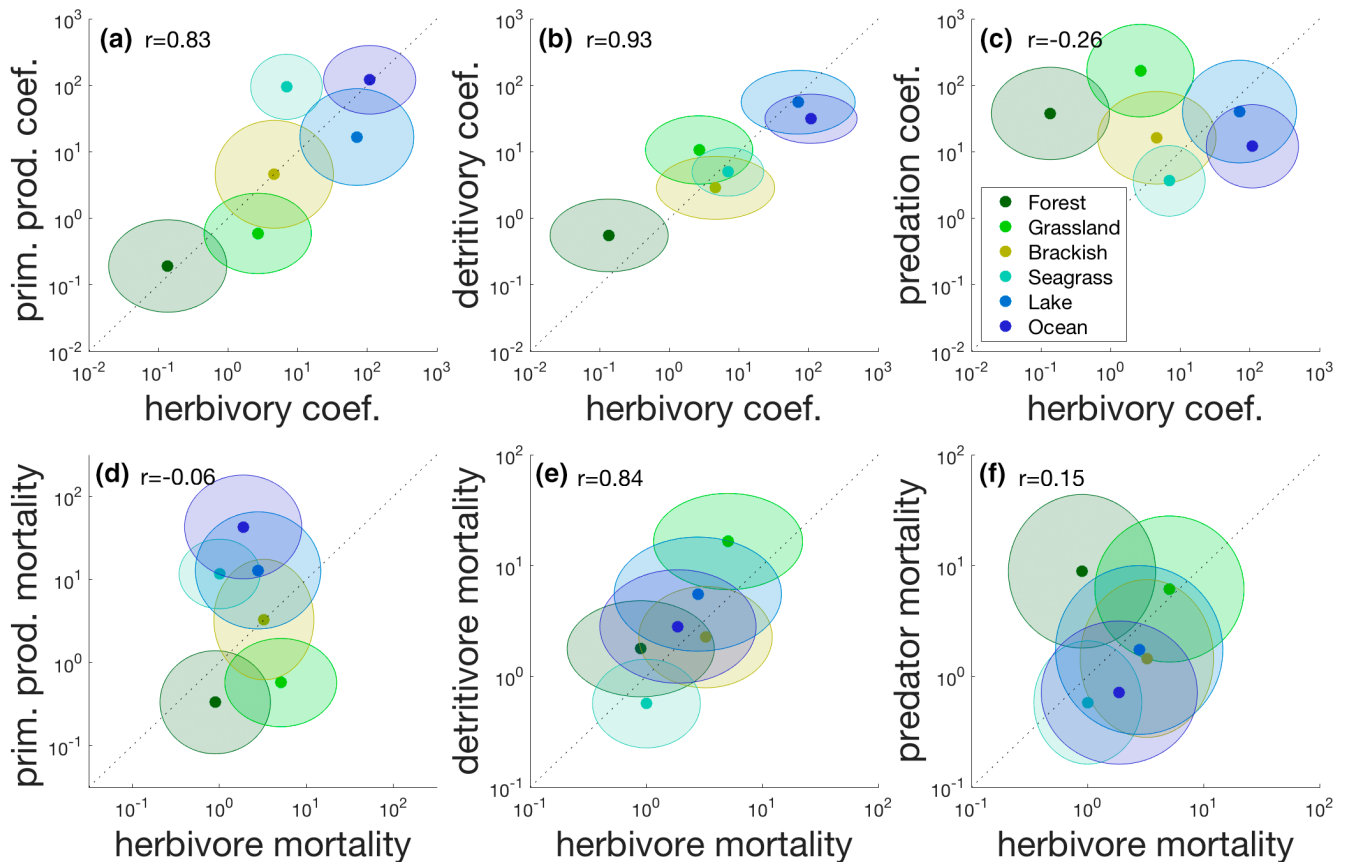
#### 3.2 | Coordination of production, consumption and mortality within and across trophic levels

Nitrogen stocks and fluxes are modulated by the rates of production, consumption and mortality of all compartments in the ecosystem. In turn, these are tied to the physiology, behaviour and metabolism of the species found at each trophic level. Combining data and modelling, we estimated the consumer consumption coefficients and mortality rates from measured nitrogen stocks and fluxes. These process rates were then used to elucidate previously hidden coordination among processes or ecosystem components within an ecosystem and across ecosystems (Figure 2).

Interestingly, we found that the consumption coefficients of P, H and D (i.e. of primary producer growth, herbivory and consumption by detritivores) were all tightly correlated across ecosystems (correlation coefficients  $>.8$ ), demonstrating a global coordination of growth capacity of producers and consumption capacity of consumers (Figure 2a-c). This coordination was evident even after accounting for the notable variation of coefficient values within each ecosystem type, as indicated by the ellipse sizes (Figure 2a-c). Furthermore, there was a strong numerical similarity between



**FIGURE 1** Median nitrogen stocks and fluxes in green-brown food webs across six ecosystem types. The six ecosystems are forests, grasslands, brackish environments (marshes and mangroves), seagrass meadows, lakes and oceans. Stock sizes for nitrogen (in grams of nitrogen per metre squared) are given within circles, with the circle areas representing stock sizes and arrow widths representing flux sizes (in grams of nitrogen per metre squared per year; also given in Supporting Information Table S2). The diagonal arrow into compartment S represents total recycling from animal compartments H, D and C.



**FIGURE 2** Comparison between consumer consumption coefficients (a–c; in metres squared per gram of nitrogen per year) and mortality rates (d–f; per year) of food web compartments. The x-axis shows values for herbivores and the y-axis values for primary producers (prim. prod.), detritivores and predators (left to right, respectively). The sizes of the ellipses correspond to variability (measured by standard deviation) within an ecosystem type in rate estimation (see Materials and Methods). The diagonal dotted line is the 1:1 line; axes are on a logarithmic scale. Pearson correlation values (based on median points per ecosystem type) for each coefficient pair are given in the top left corner of each panel (the full correlation matrix and further analysis are provided in the [Supporting Information section 5](#) and [section 6.3](#)).

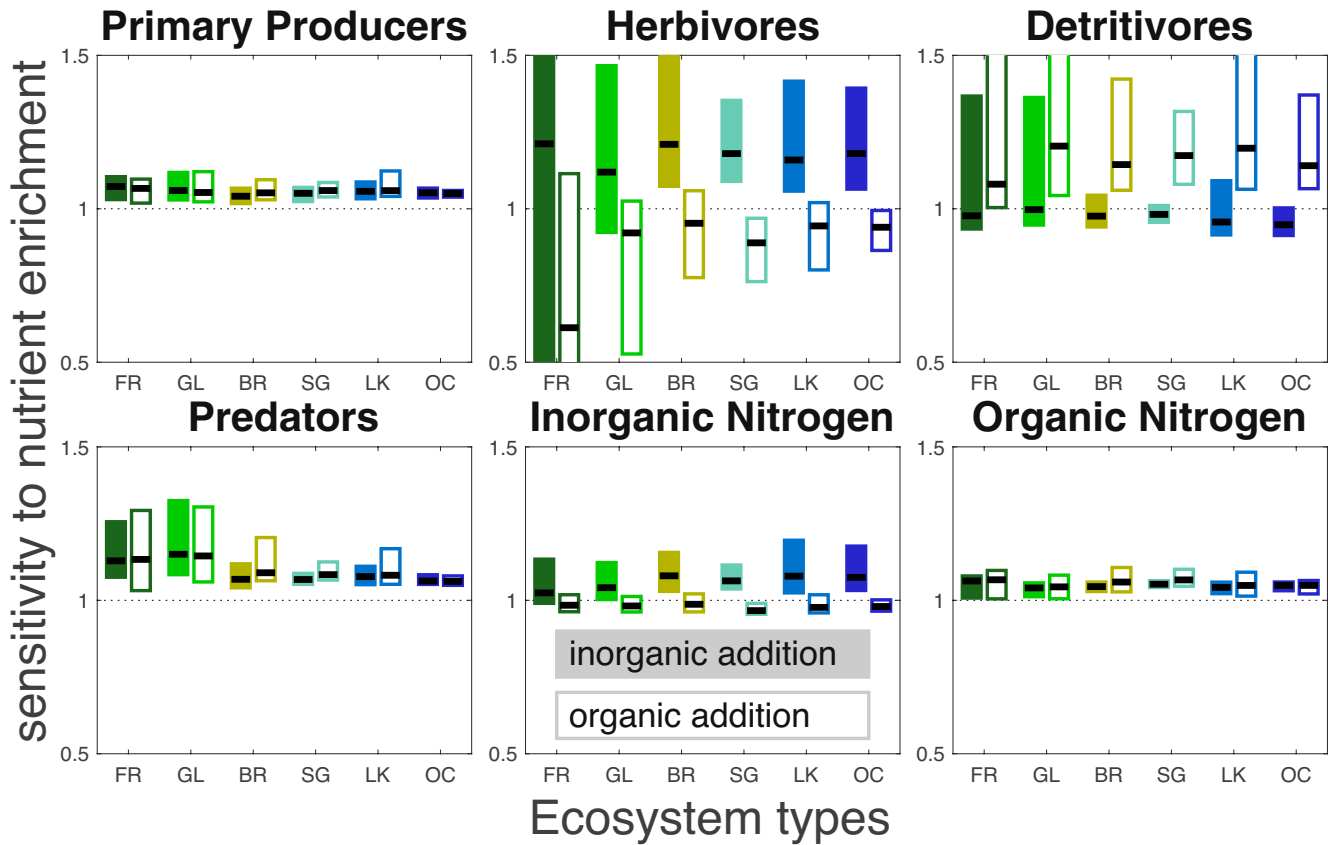
coefficients characterizing herbivores and detritivores ([Figure 2b](#)), shown by the ellipses in the middle panels lying along the 1:1 line. The correlations between consumption coefficients by detritivores and herbivores were stronger than those among mortality coefficients within ecosystems, which were more variable, as indicated by the larger ellipses in [Figure 2d–f](#). We tested whether these correlations were an artefact of our parameter estimation approach ([Supporting Information section 6.3](#)) and found that the correlation between the consumption coefficients of detritivores and herbivores was particularly robust, demonstrating a strong correlation between the two ecosystem-scale processes of herbivory and detritivory.

### 3.3 | Responses of green–brown food webs to nitrogen additions

Using our ecosystem model parameterized with data from the literature, we predicted the response of each ecosystem compartment to addition of varying proportions of organic (e.g., manure and detritus) and inorganic nitrogen (e.g., chemical fertilizers and atmospheric deposition) added to the *S* and *N* model compartments,

respectively. Using this model, we explored how ecosystem stocks and fluxes responded to simulated addition of 10% of nutrient inputs over the baseline levels. These additions altered the structure of the food webs and the relative dominance of processes in the green and brown channels, as shown in [Figure 3](#) for nitrogen stocks and in [Figure 4](#) for nitrogen fluxes.

As expected, addition of inorganic nitrogen increased the inorganic nitrogen stock (*N*), and addition of either organic or inorganic nitrogen increased the organic nitrogen (*S*) and primary producer (*P*) stocks, but only slightly. Addition of organic nitrogen increases the detritivore (*D*) stock and related fluxes, whereas inorganic additions had a weak and generally negative impact on *D*. Organic enrichment has a stronger effect on *D* than on *S*, despite *S* being directly affected by the enrichment, whereas *D* is only indirectly affected. In all six ecosystems, addition of inorganic nitrogen strongly increased the herbivore stocks (*H*) and related fluxes, with addition of organic nitrogen having the opposite effect ([Figures 3](#) and [4](#); [Supporting Information Figure S5](#)). The opposite effect of inorganic and organic nutrient enrichment on *D* and *H* stocks and associated fluxes disrupted the relative equivalence between *D* and *H* seen in [Figure 1](#). Considering the more extreme case of doubling nutrient addition,



**FIGURE 3** Change in nitrogen stocks attributable to increased nitrogen input, across ecosystems. Each panel shows relative changes in stocks (i.e., ratios of stocks after nitrogen enrichment of 10% over stocks under baseline nitrogen input) within one compartment, with values for ecosystem types as reported along the x-axis: Forest (FR), grassland (GL), brackish (BR), seagrass (SG), lake (LK) and ocean (OC). The relative changes in simulated stocks attributable to increased nutrient input of either inorganic or organic nitrogen are shown by filled and open boxes, respectively. The black line shows median values, with box edges corresponding to the 5th and 95th percentiles (a few values for herbivores, detritivores and predators go beyond the maximum value shown of 5).

inorganic enrichment increased  $H$  by a factor of three or more, while only slightly increasing  $D$ , whereas organic enrichment led to an opposite effect of more than doubling  $D$ , while decreasing  $H$  (Supporting Information Figures S15 and S16). Finally, predators ( $C$ ) benefitted from the increased stocks of herbivores and detritivores, regardless of input type, indicating that the effects of nitrogen additions cascaded through the entire food web.

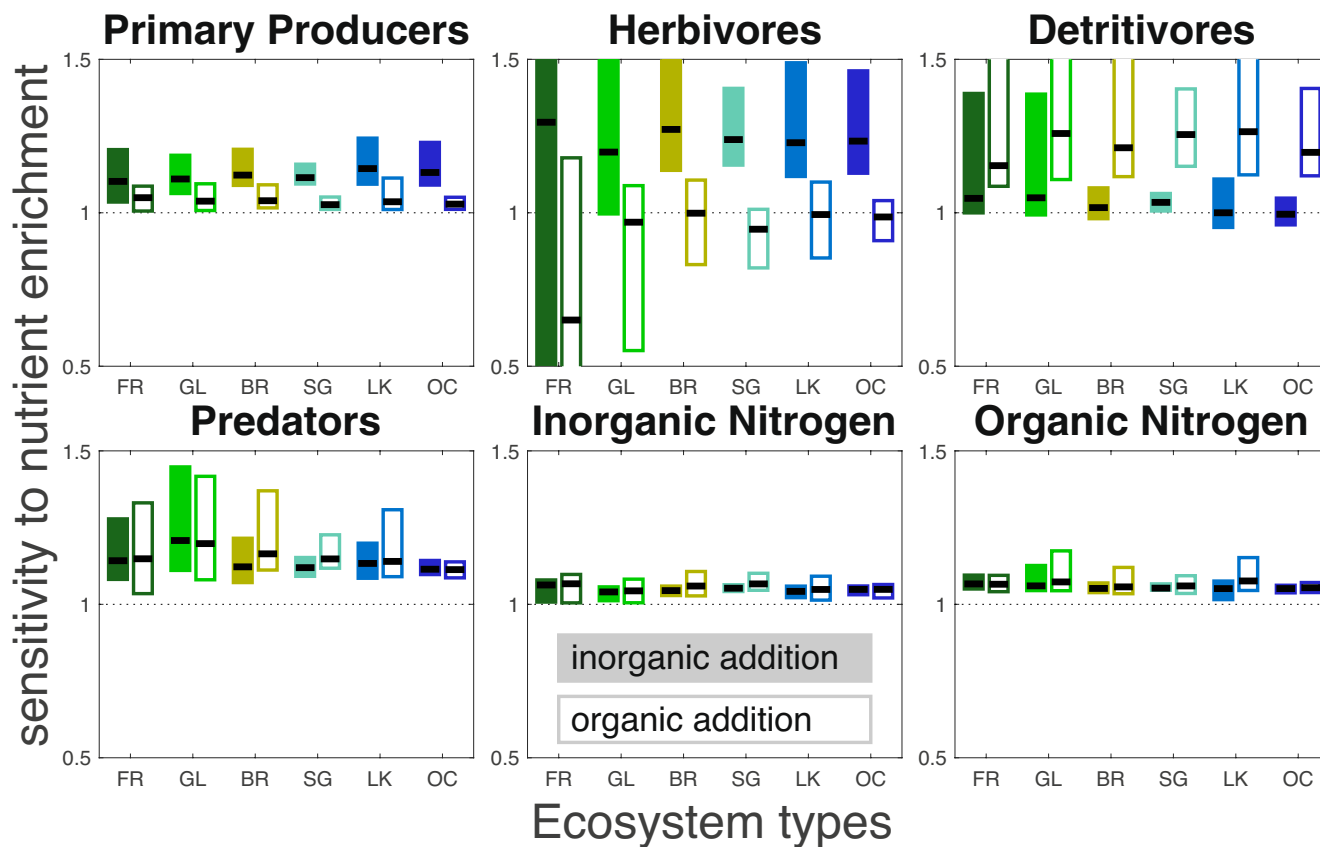
Different ecosystems responded in a consistent way to nitrogen enrichment; stocks and fluxes either increased or decreased consistently. However, predator nitrogen stocks and fluxes to predators in terrestrial ecosystems responded more strongly in comparison to aquatic ecosystems, regardless of the form of nitrogen added. Moreover, terrestrial ecosystems tended to exhibit a more variable response of both the nitrogen stocks of the animal compartments ( $H$ ,  $D$  and  $C$ ) and the nitrogen fluxes feeding them.

## 4 | DISCUSSION

Our data synthesis provides a unique overview of the dynamics of nitrogen, from inorganic stocks in soil and water, and up to the

predators, along the two parallel green and brown food webs and across major ecosystems (Figure 1). Our results bring insights on three pertinent topics: the symmetry between the green and brown channels in food webs; similarities and differences between terrestrial and aquatic ecosystems; and the response of ecosystems to the amount and quality of nitrogen addition. Moreover, our data collection highlights availability and paucity of key baseline information across ecosystems. Empirical data on food web properties, such as production fluxes of consumers at the ecosystem level, are largely missing in terrestrial ecosystems (Supporting Information Table S1). Overall, more data are available on nitrogen fluxes and stocks along the green channel compared with the brown channel, and data for estimating self-regulation are lacking throughout.

Some well-known patterns across ecosystems emerge from our analysis, such as a more pyramidal structure of food web compartments (Bar-On et al., 2018; Shurin et al., 2006) and lower herbivory rates in terrestrial than in aquatic food webs (Cyr & Face, 1993). We also find surprisingly consistent nitrogen stocks in some compartments across ecosystems, in particular for stocks of inorganic nitrogen (with the exception of seagrass meadows) and detritivores (except for grasslands). Nitrogen enrichment leads to similar



**FIGURE 4** Change in nitrogen fluxes attributable to increased nitrogen input, across ecosystems. Each panel shows relative changes of nitrogen fluxes (i.e., ratios of fluxes after nitrogen enrichment of 10% over fluxes under baseline nitrogen input) into one compartment from other compartments (i.e., excluding subsidies), with values for each ecosystem type as reported along the x-axis: Forest (FR), grassland (GL), brackish (BR), seagrass (SG), lake (LK) and ocean (OC). The relative changes in simulated fluxes attributable to increased nutrient input of either inorganic or organic nitrogen are shown by filled and open boxes, respectively. The black line shows median values, with box edges corresponding to the 5th and 95th percentiles. Note that a few values for herbivores, detritivores and predators go beyond the maximum value shown of 5.

or stronger impacts of consumers on their resources in terrestrial ecosystems, when compared with aquatic ones (Figure 4). For instance, predation fluxes in grasslands and herbivory fluxes in forests increase strongly after nutrient addition. This strong effect of the consumer on resources in terrestrial ecosystems highlights an apparent paradox: although herbivory fluxes are lower in terrestrial ecosystems (Cyr & Face, 1993), in the context of nutrient enrichment we find that consumer effects on resources are roughly equivalent in terrestrial and aquatic ecosystems, contrary to what is often suggested (Shurin et al., 2002). We can hypothesize that aquatic systems are less resource limited (and more limited by other factors, such as self-regulation) than terrestrial ones, meaning that nutrient enrichment leads to strong trophic cascades in terrestrial systems despite weaker predation and herbivory fluxes.

Within each ecosystem, we find a striking vertical symmetry, whereby the green and brown channels have similar nutrient stock sizes at any given trophic level (Figure 1; Supporting Information Figure S2). The *P* and *S* compartments have comparable sizes, as do the *H* and *D* compartments. This is notable given that the herbivory fraction (i.e., how much of the NPP flux is consumed by herbivores)

differs widely among ecosystems, ranging from <5% in forests to >40% in the oceans (Cebrian, 1999). The symmetry between the green and brown channels is also evident in the comparison of consumption coefficients and mortality rates across ecosystems (Figure 2). These coefficients are remarkably similar for herbivores and detritivores within a given ecosystem type, despite the wide range of values that these coefficients take across ecosystems (differences of two to three orders of magnitude). This result is not simply a consequence of the model definition or method of parameter estimation (see Supporting Information section 6.3), suggesting that a coordination between the green and brown channels in food webs is a fundamental property of ecosystems.

The emergence of ecosystem-level coordination could be a result of fundamental biophysical constraints, such as energy requirements at each trophic level or energy and matter conservation across trophic levels (Barnes et al., 2018). The fact that both herbivores and detritivores are, typically, mobile animals that consume immobile primary producers and organic material while being preyed upon by other moving animals could be an explanation for this intriguing correspondence between channels. Decomposers and herbivores



are often considered as functionally similar groups (Cebrian, 2004), but the correspondence we find (Figure 2; Supporting Information Figure S2) suggests that we could consider our organic nitrogen (S) compartment (consisting of detritus, organic matter and microbial decomposers) as equivalent to primary producers in its role of temporary sessile nutrient storage that feeds detritivore macrofauna, as primary producers feed herbivores. This is consistent with modelling results finding that the stability of brown and green trophic chains is similar only when the brown chain includes three or more compartments (i.e., when including detritivores in the brown food chain models; Moore et al., 2004). These two faunal groups, herbivores and detritivores, thus play a functionally comparable role, but in different channels of the food web.

In our model conception, we focused on compartments with a single functional role, such as herbivory or predation, thus considering omnivory and mixotrophy only implicitly (Stoecker et al., 2017; Thompson et al., 2007). This assumption becomes an issue if the compartment in question changes behaviour (e.g., omnivores consuming more animals than plants owing to nitrogen enrichment; Supporting Information section 6.1). However, our simulations focus on small changes with respect to the current conditions, and we can therefore reasonably assume that a large shift in behaviour does not occur. Venturing beyond this point, to enable quantitative predictions of large changes, will require an improved understanding of the prevalence and overall role of factors such as omnivory in the community and on changes in feeding attributable to altered environmental conditions, such as nutrient enrichment. Perhaps even more importantly, at high nitrogen addition levels, some processes are likely to become limited by factors other than nitrogen, meaning that explicit consideration of stoichiometric constraints (Buchkowski et al., 2019) could be a next step of investigations. The transition from carbon limitation to nutrient limitation has been studied in heterotrophs (Manzoni et al., 2017), plant-microbial systems (Čapek et al., 2018) and entire ecosystems (Cherif & Loreau, 2013), but it is still not clear how stoichiometric flexibility combines with adjustment of metabolic and excretion rates along nutrient availability gradients. Therefore, by focusing on a single limiting nutrient, our results provide only a first-order representation of nutrient cycling, but without the uncertainties related to the specific choices for implementing stoichiometric constraints.

By parameterizing a general model with empirically derived parameters, we can ask how we are affecting ecosystems by enriching them with organic and/or inorganic nutrients (Figures 3 and 4). As expected, we find that large inputs of inorganic nitrogen promote primary production and thus consumers, leading to herbivore outbreaks (Matson, 1997), but such an effect in the green channel is not mirrored in the brown channel. In fact, increasing nitrogen inputs by 10% does not lead to the same increase in nitrogen stocks of primary producers (*P*) and organic matter (*S*). For terrestrial ecosystems, the predicted increase in *P* is in line with previously reported values from nitrogen-limited systems (Čapek et al., 2018). However, this result is surprising when compared with the consistently larger increases in

predators (*C*), which are affected by nutrient addition only indirectly. This is in line with observed stronger impacts of predators on herbivore stocks than of herbivores on plant stocks (Shurin et al., 2002). It suggests that the *P* and *S* compartments are, to a large extent, regulated by the rest of the ecosystem, supporting the green-world hypothesis that consumers largely control primary producer abundance (Hairston et al., 1960). Finally, we find that compartment stocks are affected very differently depending on the quality of subsidy (i.e., whether nitrogen is added in organic or mineral form). Addition of inorganic nitrogen increases herbivore stocks while detritivore stocks decline. The opposite happens when organic nitrogen is added. These patterns are consistent with theoretical (McCary et al., 2020) and empirical (Corredor et al., 2021; Riggi & Bommarco, 2019) observations that show how subsidizing systems can lower their consumer stocks owing to predation, a phenomenon termed apparent trophic cascades (Moore et al., 2004). Here, for the first time, we demonstrate their generality across ecosystems. We also test that these results hold under different assumptions, including variations in the levels of *P* self-regulation (Supporting Information Figures S6–S13) and contrasting assumptions on nitrogen recycling (Supporting Information Figures S17 and S18).

Our results highlight the importance of the brown channel in transferring nitrogen towards higher trophic levels, in addition to the sensitivity of both green and brown channels to nutrient additions. In particular, addition of either organic or inorganic nutrients affects the two channels in opposite ways, and an increase in nutrient inputs can disproportionately increase stocks of one channel while decreasing the other (Supporting Information Figure S15), thus disrupting the coordination between the two channels. We conclude that both channels, in addition to their interactions centred around nutrient recycling and top-down control, are key for understanding ecosystem functioning, including occurrences of herbivore outbreaks driven by inorganic nitrogen enrichment. By routing nitrogen to the green channel, inorganic nitrogen inputs increase stress on the brown food web, which is crucial to nutrient cycling, carbon retention and the primary production on which most life is based.

#### AUTHOR CONTRIBUTIONS

Y.R.Z., S.M. and R.B. conceived the study and developed the model. Y.R.Z. performed the data collection, analysis and simulations. All authors interpreted the results. Y.R.Z. led the writing, which S.M. and R.B. commented on and revised.

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#### CONFLICT OF INTEREST

The authors declare no competing interests.

## DATA AVAILABILITY STATEMENT

The datasets were all collected from published sources, and can be found at the open-access repository: <https://doi.org/10.5281/zenodo.5743318>. The computer code used for the simulations is available from the corresponding author upon request.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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