When microbes and consumers determine the limiting nutrient of autotrophs: a theoretical analysis

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Ecological stoichiometry postulates that differential nutrient recycling of elements such as nitrogen and phosphorus by consumers can shift the element that limits plant growth. However, this hypothesis has so far considered the effect of consumers, mostly herbivores, out of their food-web context. Microbial decomposers are important components of food webs, and might prove as important as consumers in changing the availability of elements for plants. In this theoretical study, we investigate how decomposers determine the nutrient that limits plants, both by feeding on nutrients and organic carbon released by plants and consumers, and by being fed upon by omnivorous consumers. We show that decomposers can greatly alter the relative availability of nutrients for plants. The type of limiting nutrient promoted by decomposers depends on their own elemental composition and, when applicable, on their ingestion by consumers. Our results highlight the limitations of previous stoichiometric theories of plant nutrient limitation control, which often ignored trophic levels other than plants and herbivores. They also suggest that detrital chains play an important role in determining plant nutrient limitation in many ecosystems.

Keywords: model; ecological stoichiometry; excess C cycling; herbivory; $N:P$ ratio; detritivores

1. INTRODUCTION

Ecological stoichiometry suggests that consumer-driven nutrient recycling can change the nutrient limiting plant growth (Sterner *et al.* 1992). This hypothesis came from a thorough case analysis of the effect of *Daphnia* on nutrient limitation of phytoplankton: *Daphnia* species, which are very rich in phosphorus (Andersen & Hessen 1991), tend to experience a deficiency in this element and an excess of nitrogen in their food. They thus retain more phosphorus than nitrogen in their biomass, and excrete more nitrogen than phosphorus (Elser & Urabe 1999). By excreting more of one element than of the other, they change the balance of these elements in the chemical environment. This, in turn, can change the identity of the element that limits phytoplankton growth. Thus, in the presence of *Daphnia*, phytoplankton can switch from nitrogen to phosphorus limitation.

Current research efforts seek to expand this theory to other ecosystems (e.g. Hassett *et al.* 1997; Elser *et al.* 2000; Schade *et al.* 2003; Frost *et al.* 2005). There is indeed no theoretical reason why this effect of consumer-driven nutrient recycling should be limited to freshwater pelagic environments. In every ecosystem, nutrient recycling by dominant consumers can potentially change the limiting nutrient of plants. Cattle in pastures, mammals in savannahs and grasslands, root herbivores in soils, invertebrates and detritivores in forests and streams have the potential to change the relative availability of nutrients for primary producers.

A useful preliminary step might be to assess the conditions for the validity of the hypothesis of a consumer-driven shift in plant nutrient limitation. This hypothesis rests upon two mechanisms: (i) the relative amounts of elements recycled by consumers must be a function of the difference between the elemental compositions of plants and consumers, and (ii) this recycling must alter the availability of the various elements for plants. Numerous studies have tested the effects of plant and consumer elemental compositions on consumer-driven nutrient recycling. But, surprisingly, very few studies have tried to assess the feedback of differential consumer-driven nutrient recycling on plant limitation, and the conditions under which a shift in the element limiting plant growth happens (Elser *et al.* 1988; Carpenter *et al.* 1992; Rothhaupt 1997; Daufresne & Loreau 2001*a*). All these studies, however, considered the pairwise interaction between plants and consumers separated from the rest of the food web. Among the most important components of food webs, in terms of both activity and biomass, are microbial decomposers. We have good *a priori* reasons to think that microbial decomposers (hereafter 'decomposers') are likely to directly affect the limiting nutrient of plants and interfere with the effect of plant consumers (hereafter 'consumers').

First, there is accumulated evidence that decomposers, far from being mere kind suppliers of resources to plants through mineralization, are probably also fierce competitors for mineral elements. Numerous studies have demonstrated this in aquatic and terrestrial ecosystems, with accrued evidence that mineralization often requires

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agents that provoke the death of microbial decomposers (for terrestrial ecosystems, see Currie & Kalff 1984 and Andersen *et al.* 1986; for aquatic ecosystems, see Kaye & Hart 1997 and Raynaud *et al.* 2006; for a theoretical analysis, see Daufresne & Loreau 2001b). Recent evidence suggests that consumption of elements by decomposers might affect the nutrient that limits plants (Danger *et al.* 2007).

Second, consumers regulate their assimilation of not only nitrogen and phosphorus, but also carbon by excreting it when in excess (Darchambeau *et al.* 2003). Excreted organic carbon can fuel the growth of decomposers when they are limited by its availability (for aquatic ecosystems, see Jumars *et al.* 1989; for terrestrial ecosystems, see Lovett & Ruesink 1995, Stadler & Müller 1996 and Strom *et al.* 1997).

Finally, the supply of organic carbon to decomposers is not the only way through which consumers and decomposers interact. In many ecosystems, consumers also ingest some decomposers, because the latter are intimately interlaced with plant material, are epibionts or are within the same size range as plant cells (for aquatic ecosystems, see Brendelberger 1991 and Arndt 1993; for terrestrial ecosystems, see Curry & Schmidt 2007).

From these three observations, we hypothesize that the presence and properties of decomposers will affect the limiting nutrient of plants and interfere with the effect of consumer-driven nutrient recycling on plant limitation.

To investigate the potential effects of decomposers on the nutrient limiting plant growth and on the plant–consumer interaction, we built a model that includes all the above-mentioned interactions between plants, consumers and decomposers. We extended Daufresne & Loreau's (2001a) model, which describes the interaction between autotrophs—a more generic term than plants—and herbivores exchanging nitrogen and phosphorus, to include microbial decomposers and carbon as an additional element. Using this model, we first compare the relative net production of nitrogen and phosphorus by the food web as a whole with and without decomposers. In this first step, we assume that consumers feed only on autotrophs. To study the effect of omnivory in consumers on the nutrient limiting autotrophs, we then repeat the analysis of the model with consumers feeding also on decomposers. We also estimate model parameters for aquatic pelagic ecosystems in which the zooplankton is the main consumer, and for forest and shrubland ecosystems in which insects are the main consumers, in order to show that our model can be used as a tool for comparative analyses among ecosystems of the role of consumers and decomposers in determining the nutrient limiting autotrophs.

The analysis of the model shows that decomposers can change the element that limits the growth of plants according to their own nitrogen : phosphorus ratio. But, if consumers feed on decomposers significantly, then, decomposers then promote the same limiting element as their consumers, even if they, themselves, consume preferentially the non-limiting element. These results advocate for the importance of considering the fate of the detrital chain production when investigating the impact of microbial decomposers on the availability of nutrients.

2. MODEL DESCRIPTION

Our model (figure 1) is an extension of Daufresne & Loreau's (2001a). Along the nitrogen (N) and phosphorus (P) stocks of inorganic nutrients (N_I and P_I), autotrophs (N_A and P_A) and consumers (N_C and P_C), we introduce stocks representing the microbial decomposers (N_D and P_D). We also add carbon (C) stocks to the living compartments, C_A, C_C and C_D (note that C in the subscript always refer to consumers and never to carbon).

The three elements P, N and C are bound in the biomass of the three living compartments in fixed ratios $(N:P)_A$, $(N:P)_C$ and $(N:P)_D$ for the $N:P$ ratios of autotrophs, consumers and decomposers, respectively, and $(C:P)_A$, $(C:P)_C$ and $(C:P)_D$ for their $C:P$ ratios.

Because decomposers are generally more efficient than autotrophs in taking up P and N, we assume that C is the element that limits their growth (for aquatic ecosystems, see Bratbak & Thingstad 1985 and Carlson & Ducklow 1996; for terrestrial ecosystems, see Morita 1988 and Demoling *et al.* 2007). We also assume that the organic C produced by autotrophs and consumers is totally labile, and that decomposers use almost instantaneously and totally the entire C produced. In this work, we are interested in the role of decomposers in the stoichiometric interaction between consumers and autotrophs. Therefore, introducing a compartment of refractory carbon is not of great use because it is hardly a resource for decomposers. Also, introducing a compartment of labile carbon is unnecessary because decomposers are usually highly efficient at using labile carbon, and compartments that form a chain, as would the labile and decomposer carbon compartments, can generally be merged without much qualitative change (Puccia & Levins 1986). We checked, however, that the inclusion of a separate compartment of labile carbon does not change the conclusions qualitatively.

In our model, consumers primarily feed on autotrophs, but they can also feed on decomposers. We assume a donor-controlled function for the ingestion of autotrophs and decomposers by consumers, i.e. the amount of elements' transferred from resources to the consumers is proportional to the amount of available resources (the factor of proportionality, or ingestion rate, is i_A for autotrophs and i_D for decomposers). Our choice of a donor-controlled function is plainly justified when the main consumers are detritivores, which do not affect autotrophs directly. In the case of livestock, human management generally tends to maintain a constant exploitation of the resource. For wild herbivores, donor control of herbivory may be more likely than recipient control, according to Polis & Strong (1996), when entire trophic levels, not single species, are considered.

Consumers maintain constancy of their stoichiometry by excreting the elements that are in excess of their need. Thus, when their food is deficient in N, they reject the excess of P and C with positive fluxes WP and WC, while when their food is deficient in P, they reject the excess of N and C with positive WN and WC fluxes. WN, WP and WC are the stoichiometrically regulated release fluxes of N, P and C, respectively (Anderson *et al.* 2005). Excreted N and P are available to both autotrophs and decomposers because we made the simplifying assumption that all the recycled N and P, whether organic or inorganic, is available to both autotrophs and decomposers. Phosphatases, whether from plant (Tarafdar & Claassen 1988) or

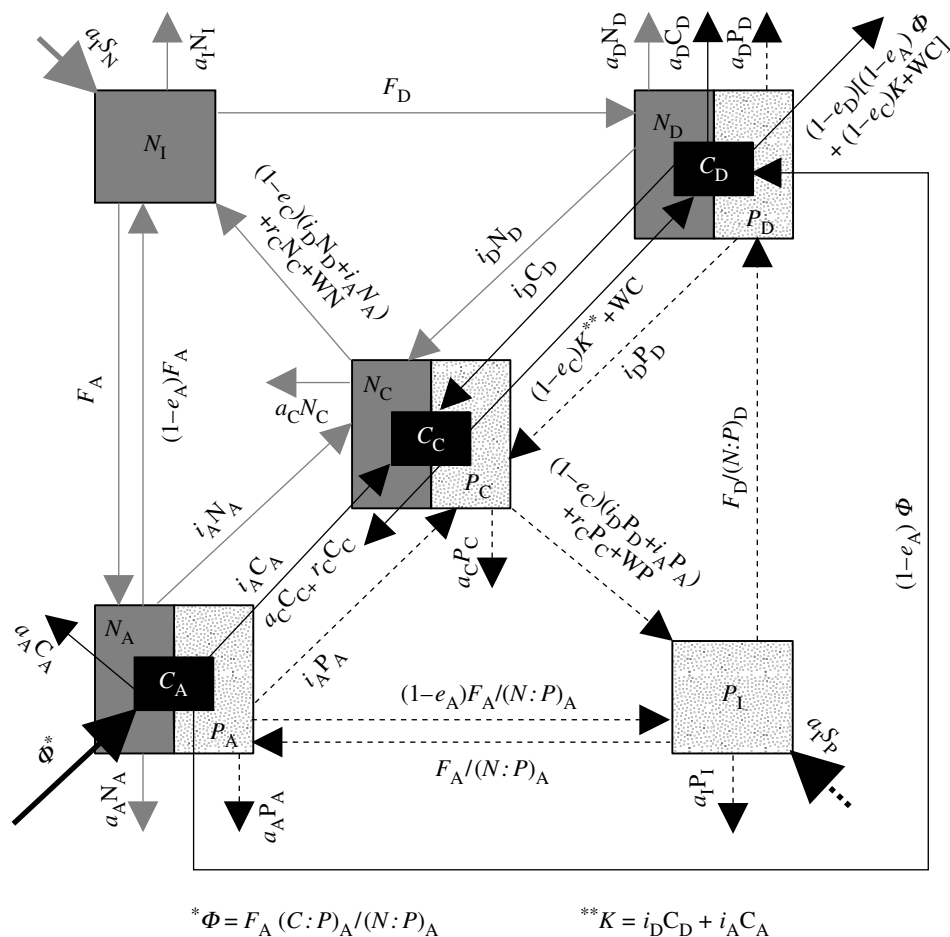$$^*\Phi = F_A\,(C:P)_A/(N:P)_A \qquad\qquad ^{**}K = i_D C_D + i_A C_A$$

Figure 1. Flow diagram of an autotroph–consumer–decomposer model that couples three elements: carbon, C; nitrogen, N; and phosphorus, P. Black, carbon stocks; grey, nitrogen stocks; dots, phosphorus stocks. C_A, C_C and C_D are the stocks of C in autotrophs, consumers and decomposers, respectively. N_I, N_A, N_C and N_D are the inorganic stock and the stock of N in autotrophs, consumers and decomposers, respectively. P_I, P_A, P_C and P_D are the inorganic stock and the stock of P in autotrophs, consumers and decomposers, respectively. a_I is the renewal rate—i.e. both the loss and the supply rate—of the inorganic resources N_I and P_I. S_N and S_P are the supplies of N and P, respectively. a_A, a_C and a_D are the loss rates of autotrophs, consumers and decomposers, respectively. F_A, $F_A/(N:P)_A$ and $F_A(C:P)_A/(N:P)_A$ are the uptake fluxes of N_I, P_I and CO_2 by autotrophs. e_A is the assimilation efficiency of autotrophs. i_A and i_D are the ingestion rates by consumers of autotrophs and decomposers, respectively. e_H is the assimilation efficiency of consumers. r_C is their respiration rate. WC, WN and WP are the stoichiometrically regulated fluxes of excess C, N and P, respectively, that are released by consumers to maintain their $C:N:P$ ratio constant. F_D and $F_D/(N:P)_D$ are the uptake fluxes of N_I and P_I by decomposers.

microbial origin (Rodríguez & Fraga 1999), make organic phosphorus available to both compartments, and there is growing evidence that organic nitrogen might also be available to autotrophs (Kaye & Hart 1997). Rejected C is organic, and is immediately taken up by decomposers.

The excess of C rejected by consumers is only one of many sources of C for decomposers. Two other sources are the C ingested by consumers but not assimilated (fraction $1-e_C$ of ingested food) and the C excreted by autotrophs (fraction $1-e_A$ of primary production). Consumers also eliminate elements as a by-product of their metabolism, but the C produced therein is not available to decomposers, as it is respired in the form of CO_2 (specific respiration rate r_C).

Of all the C they take up, decomposers assimilate only a fraction e_D, the remaining fraction $1-e_D$ being used for respiration. Decomposers might also excrete some C in an organic form. But, since, in our model, organic C is instantaneously taken up by decomposers, this excreted C is not explicitly accounted for and is considered as a part of e_D. The uptake fluxes of N_I and P_I by decomposers,

F_D and $F_D/(N:P)_D$, are totally assimilated, and are thus net uptakes.

Autotrophs also take up N_I and P_I, with fluxes denoted by F_A and $F_A/(N:P)_A$. Their growth can be limited by either of the two elements and, applying Liebig's law of the minimum, it is the element that yields the lowest growth rate that is the actual limiting element (Blackman 1905).

All compartments have loss rates: a_A, a_C, a_D and a_I for autotrophs, consumers, decomposers and both N_I and P_I, respectively. These represent all the forms of elemental losses from the ecosystem. To counterbalance these losses, N_I and P_I are supplied to the ecosystem in quantities S_N and S_P, respectively, with a rate equal to their loss rate a_I, which is *de facto* the renewal rate of inorganic resources.

3. RESULTS
(a) *The N : P ratio of food-web net production controls autotroph nutrient limitation*
As explained in Daufresne & Loreau (2001a), at equilibrium, the inorganic resource limiting autotroph

growth is at its R^* value (Tilman 1980; figure 2). Also, the food-web net production vector $N P_{ADC}$ balances the supply vector $N P_S$ (figure 2). We define food-web net production, or impact, as consumption minus recycling of inorganic nutrients (Daufresne & Loreau 2001a). Because net production is equal to loss for living compartments at equilibrium, the food-web net production vector components are more simply expressed as the sums of the losses of N and P at equilibrium from the living compartments,

$$\underbrace{\begin{pmatrix} a_I(S_N - N_I^*) \\ a_I(S_P - P_I^*) \end{pmatrix}}_{N P_S} = -\underbrace{\begin{pmatrix} a_A N_A^* + a_D N_D^* + a_C N_C^* \\ a_A P_A^* + a_D P_D^* + a_C P_C^* \end{pmatrix}}_{N P_{ADC}},$$

where the asterisk denotes equilibrium values.

The absolute value of the slope of the food-web net production vector, i.e. the $N : P$ ratio of food-web net production, $(N : P)_{ADC}$, is equal to the ratio of the N consumed by the food web to the P consumed, $(N : P)_{ADC} = (a_A N_A^* + a_D N_D^* + a_C N_C^*)/(a_A P_A^* + a_D P_D^* + a_C P_C^*)$.

For a given supply point, this ratio determines the element limiting autotroph growth and the intensity of the limitation. As illustrated in figure 2, the smaller this ratio—i.e. the smaller the net production of N by the food web in comparison with P net production—the more likely, or the more severe, the P limitation of autotrophs. Hence, in the rest of our analysis, we address the problem of the effect of decomposers on autotroph limitation by comparing the $N : P$ ratios of food-web net production with decomposers, $(N : P)_{ADC}$, and without decomposers, $(N : P)_{AC}$. If the $N : P$ ratio of food-web net production with decomposers is larger than without them, then decomposers promote N limitation of autotrophs. By contrast, if it is smaller, decomposers drive autotrophs towards P limitation.

We analyse in detail only the case where consumers are limited by P when feeding on autotrophs $((N : P)_C < (N : P)_A)$. The results for N-limited consumers $((N : P)_C > (N : P)_A)$ are symmetrical and can be found in figure 4.

First, we exclude the effects of omnivory by setting the ingestion rate of decomposers by consumers, i_D, to 0, and we proceed to analyse the influence of decomposers on autotroph limitation. Subsequently, we repeat this analysis with $i_D > 0$. We highlight the changes brought by omnivory on the effect of decomposers by comparing the results of the two analyses.

(b) The N : P ratio of decomposers determines their effect on autotroph limitation

To examine the influence of decomposers on autotroph limitation in the absence of consumer omnivory, we compare the $N : P$ ratios of food-web net production without decomposers, $(N : P)_{AC} = (a_A N_A^* + a_C N_C^*)/(a_A P_A^* + a_C P_C^*)$, and with decomposers, $(N : P)_{ADC} = (a_A N_A^* + a_C N_C^* + a_D N_D^*)/(a_A P_A^* + a_C P_C^* + a_D P_D^*)$, under the constraint $i_D = 0$. We conduct this analysis for P-limited consumers, i.e. for consumers that are richer in P than their autotroph food $((N : P)_C < (N : P)_A)$. Results for N-limited consumers are the same, *mutatis mutandis*.

In the absence of decomposers, the food-web net production vector NP_{AC} is the vectorial sum of the
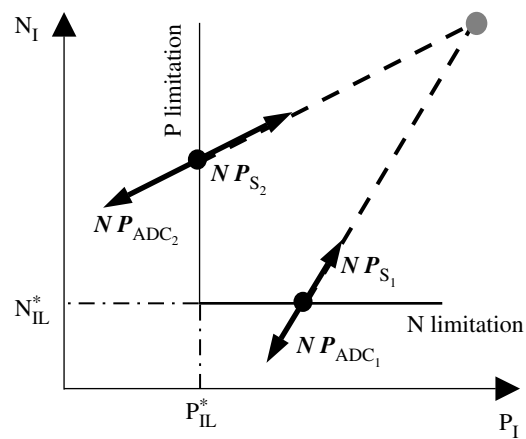

Figure 2. Graphical analysis of the autotroph–decomposer–consumer model with explicit resources at equilibrium. The coordinates represent the inorganic N and P resources, N_I and P_I. At equilibrium, N_I is equal to the R^* value N_{IL}^* when autotrophs are N limited and P_I is equal to the R^* value P_{IL}^* when they are P limited. The zero net growth isocline (ZNGI)—the set of (N_I, P_I) pairs that lead to equilibrium—is thus the joining of the horizontal solid line of resource points leading to N limitation and the vertical solid line of resource points resulting in P limitation. At equilibrium, the net production vector $N P_{ADC}$ entirely balances the supply vector $N P_S$. The supply vector always points towards the supply point (grey circle). Hence, the equilibrium resource point (black circles) lies at the intersection between the ZNGI and the dashed line, with the $N : P$ ratio of food-web net production $(N : P)_{ADC}$ as a slope and passing through the supply point. For N limitation, the closer the equilibrium point is to the co-limitation point (P_{IL}^*, N_{IL}^*), the nearer the autotrophs are to P limitation. By contrast, the farther a P-limited equilibrium point is from the co-limitation point, the more intense is the P limitation of autotrophs. For a specific supply point, the position of the equilibrium point is set by the $N : P$ ratio of food-web net production $(N : P)_{ADC}$: as illustrated by the two equilibrium points associated with the vectors $N P_{ADC_1}$ and $N P_{ADC_2}$, the gentler the slope of the net production vector—the smaller $(N : P)_{ADC}$—the more P is promoted as a limiting nutrient.

net production vectors of autotrophs $N P_A$ and consumers $N P_C$ (figure 3a),

$$-\underbrace{\begin{pmatrix} a_A N_A^* + a_C N_C^* \\ a_A P_A^* + a_C P_C^* \end{pmatrix}}_{N P_{AC}} = -a_A \underbrace{\begin{pmatrix} N_A^* \\ P_A^* \end{pmatrix}}_{N P_A} - a_C \underbrace{\begin{pmatrix} N_C^* \\ P_C^* \end{pmatrix}}_{N P_C}.$$

From this vectorial representation, it appears that the food-web ratio $(N : P)_{AC}$ is a combination of the two single-compartment ratios $(N : P)_A$ and $(N : P)_C$ (figure 3a). Thus, its value lies somewhere between these two values, i.e. $(N : P)_C < (N : P)_{AC} < (N : P)_A$. It is clear from this inequality that P-limited consumers drive autotrophs towards P limitation since $(N : P)_{AC} < (N : P)_A$, a result already found by Daufresne & Loreau (2001a). Increasing the feeding rate of consumers on autotrophs, i_A, amplifies the contribution of consumer net production to food-web net production at the expense of autotroph net production. From this fact and the analytical expression of $(N : P)_{AC}$ in table A2 of the electronic supplementary material, it appears that $(N : P)_{AC}$ moves from $(N : P)_A$ to $(N : P)_C$ as the feeding rate i_A increases from 0 to infinity (figure 3a).

In a similar way, the net production vector of the food web including decomposers, $N P_{ADC}$, is also a vectorial
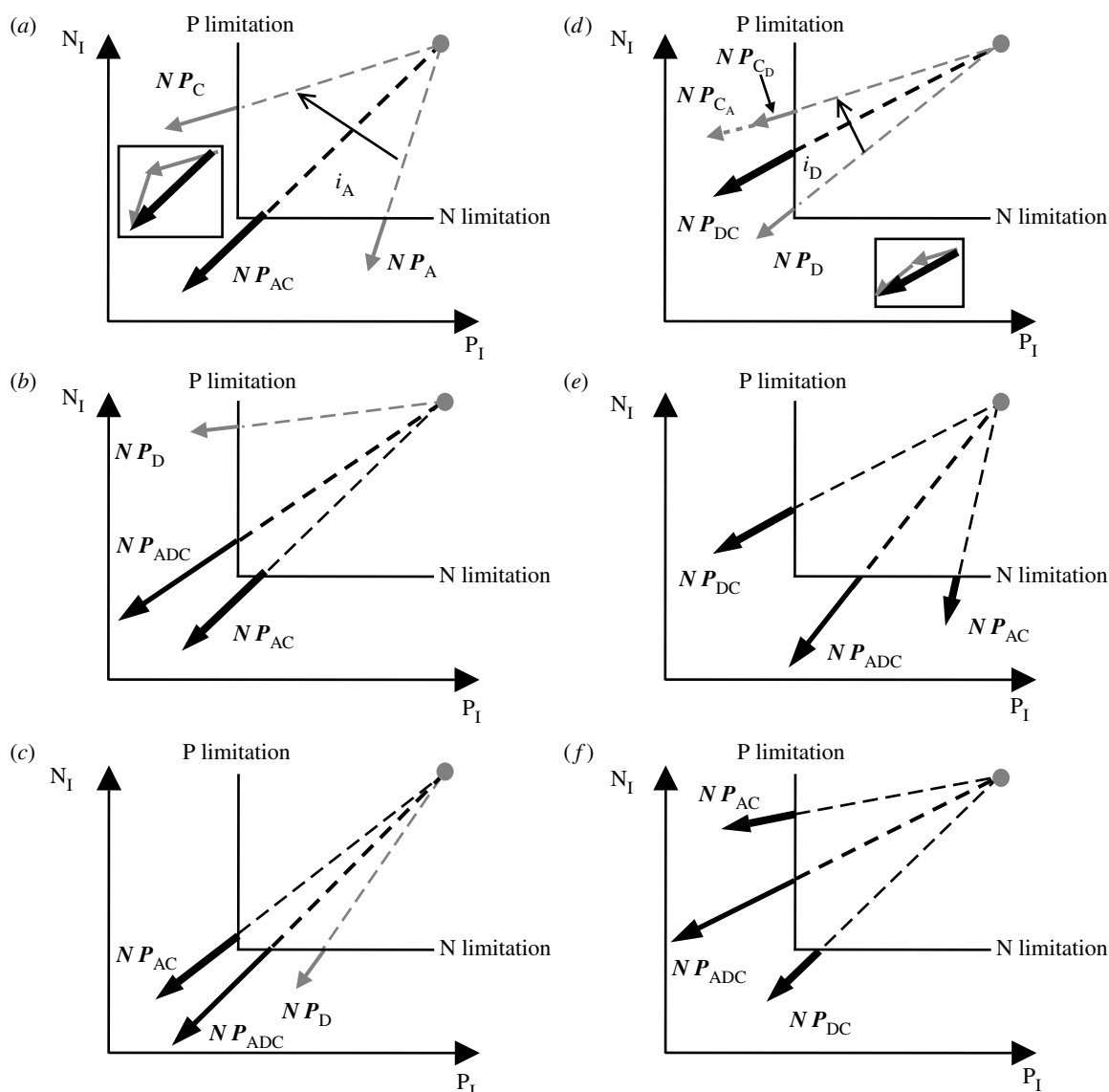
Figure 3. Graphical analysis of the effect of the presence of decomposer on autotroph limitation when consumers are not omnivorous ((a–c) the feeding rate of consumers on decomposers $i_D = 0$) and when they are omnivorous ((d–f) $i_D > 0$). (a) Graphical determination of $N P_{AC}$, the net production vector of a food web made up of autotrophs and consumers only, as the vectorial sum of autotroph and consumer net production vectors $N P_A$ and $N P_C$. As the consumer ingestion rate on autotrophs i_A increases, $N P_{AC}$ moves closer to $N P_C$. (b) Promotion of P as a limiting nutrient of autotrophs by decomposers with an $N : P$ ratio smaller than $(N : P)_{AC}$, as highlighted by the gentler slope of the food-web net production vector $N P_{ADC}$ in comparison with the slope of $N P_{AC}$. (c) Promotion of N as a limiting nutrient of autotrophs by decomposers with an $N : P$ ratio larger than $(N : P)_{AC}$, as highlighted by the steeper slope of the food-web net production vector $N P_{ADC}$ in comparison with the slope of $N P_{AC}$. (d) Graphical determination of $N P_{DC}$, the decomposer-based food-web net production vector, as the vectorial sum of decomposer and decomposer-based consumer net production vectors $N P_D$ and $N P_{C_D}$. As the consumer ingestion rate of decomposers i_D increases, $N P_{DC}$ moves closer to $N P_{C_D}$. (e) Promotion of P as a limiting nutrient of autotrophs by decomposers as a consequence of an $N : P$ ratio of decomposer-based food-web production smaller than $(N : P)_{AC}$, as highlighted by the gentler slope of the food-web net production vector $N P_{ADC}$ in comparison with the slope of $N P_{AC}$. (f) Promotion of N as a limiting nutrient of autotrophs by decomposers as a consequence of an $N : P$ ratio of decomposer-based food-web production larger than $(N : P)_{AC}$, as highlighted by the steeper slope of the food-web net production vector $N P_{ADC}$ in comparison with the slope of $N P_{AC}$.

sum of the net production vectors $N P_{AC}$ and $N P_D$,

$$\underbrace{-\begin{pmatrix} a_A N_A^* + a_D N_D^* + a_C N_C^* \\ a_A P_A^* + a_D P_D^* + a_C P_C^* \end{pmatrix}}_{N P_{ADC}}$$

$$= \underbrace{-\begin{pmatrix} a_A N_A^* + a_C N_C^* \\ a_A P_A^* + a_C P_C^* \end{pmatrix}}_{N P_{AC}} \underbrace{- a_D \begin{pmatrix} N_D^* \\ P_D^* \end{pmatrix}}_{N P_D}.$$

Therefore, the $N : P$ ratio of food-web net production, $(N : P)_{ADC}$, is bounded by the ratio of decomposers, $(N : P)_D$, and the ratio of the autotroph-based food-web net production, $(N : P)_{AC}$ (figure 3b,c). The effect of decomposer inclusion on autotroph limitation depends on these two ratios:

— if $(N : P)_D$ is smaller than $(N : P)_{AC}$, decomposers promote P as a limiting nutrient for autotrophs (figure 3b) and

—if $(N:P)_D$ is larger than $(N:P)_{AC}$, decomposers drive autotrophs towards N limitation (figure 3c).

Figure 4a summarizes the various conditions on net production $N:P$ ratios that result in decomposers promoting either P or N as the limiting nutrient of autotrophs. N-rich decomposers combined with P-limited consumers, i.e. $(N:P)_D > (N:P)_A > (N:P)_C$, promote N as the limiting nutrient of autotrophs (path 1 in figure 4a). However, when both decomposers and consumers are richer than autotrophs in P, i.e. $(N:P)_D < (N:P)_A$ and $(N:P)_C < (N:P)_A$, the resulting effect of decomposers depends on whether they consume relatively more N $((N:P)_D > (N:P)_{AC}$, path 2) or more P $((N:P)_D < (N:P)_{AC}$, path 3), respectively, than autotrophs and consumers combined. The results are the same, *mutatis mutandis*, when consumers are richer than autotrophs in N $((N:P)_C > (N:P)_A)$.

Terrestrial ecosystems, in which above-ground herbivores are the main consumers, are typically in the situation where decomposers do not contribute significantly to consumer net production ($i_D \cong 0$). We estimated the model parameters for these systems (forest and shrubland ecosystems, with herbivorous insects as the main consumers; table 1). A comparison of the estimated $N:P$ ratios suggests that both consumers and decomposers should promote P as a limiting nutrient for autotrophs (corresponding to path 3 in figure 4a). The main effect on plant limitation, however, is caused by decomposers because estimated ingestion rates by insect herbivores are low and the majority of primary production goes to decomposition.

(c) *Omnivory amplifies the effect of consumers on autotroph limitation*

Including decomposers in the diet of consumers ($i_D > 0$) means that, at equilibrium, a fraction of consumer N and P net productions comes from decomposers, while another fraction comes from autotrophs. The net production vector of consumers is thus the sum of two parallel vectors (figure 3d),

$$\boldsymbol{N}\boldsymbol{P}_C = \underbrace{-\frac{i_A}{i_A + i_D f} a_C \begin{pmatrix} N_C^* \\ P_C^* \end{pmatrix}}_{\boldsymbol{N}\boldsymbol{P}_{C_A}} \underbrace{-\frac{i_D f}{i_A + i_D f} a_C \begin{pmatrix} N_C^* \\ P_C^* \end{pmatrix}}_{\boldsymbol{N}\boldsymbol{P}_{C_D}},$$

where i_A and i_D are the feeding rates of consumers on autotrophs and decomposers, respectively, and f is the ratio between the stocks of the element that limits consumers in decomposers and autotrophs (see table A1 in the electronic supplementary material). $(i_A)/(i_A + i_D f)$ and $(i_D f)/(i_A + i_D f)$ are the respective proportions of autotrophs and decomposers in the consumer diet.

By combining the decomposer-based consumer net production vector $\boldsymbol{N}\boldsymbol{P}_{C_D}$ and the decomposer net production vector ($\boldsymbol{N}\boldsymbol{P}_D$), we obtain the decomposer-based food-web net production vector, $\boldsymbol{N}\boldsymbol{P}_{DC}$ (figure 3d). Similarly, we obtain an autotroph-based net production vector $\boldsymbol{N}\boldsymbol{P}_{AC}$ by combining the autotroph-based consumer net production vector $\boldsymbol{N}\boldsymbol{P}_{C_A}$ and the autotroph net production vector $\boldsymbol{N}\boldsymbol{P}_A$.

Because the food-web net production vector $\boldsymbol{N}\boldsymbol{P}_{ADC}$ is a combination of the autotroph-based and decomposer-based food-web net production vectors ($\boldsymbol{N}\boldsymbol{P}_{AC}$ and

$\boldsymbol{N}\boldsymbol{P}_{DC}$, respectively), assessing the change induced by decomposers on autotroph limitation is just a matter of comparing the slopes of the two vectors:

—if $(N:P)_{DC}$ is smaller than $(N:P)_{AC}$, the $N:P$ ratio of food-web net production, $(N:P)_{ADC}$, is smaller than the autotroph-based food-web ratio, $(N:P)_{AC}$, and hence decomposers promote autotroph P limitation (figure 3e) and

—if $(N:P)_{DC}$ is larger than $(N:P)_{AC}$, decomposers drive autotrophs towards N limitation (figure 3f).

As figure 3d shows, the exact position of the decomposer-based food-web net production vector $\boldsymbol{N}\boldsymbol{P}_{DC}$ between the decomposer and consumer net production vectors, $\boldsymbol{N}\boldsymbol{P}_D$ and $\boldsymbol{N}\boldsymbol{P}_C$, depends on the intensity of the feeding rate of consumers on decomposers, i_D: the larger the i_D, the closer the $\boldsymbol{N}\boldsymbol{P}_{DC}$ is to $\boldsymbol{N}\boldsymbol{P}_C$. Therefore, for specific $(N:P)_A$, $(N:P)_C$ and $(N:P)_D$ ratios, the fact that $(N:P)_{DC}$ is smaller or larger than $(N:P)_{AC}$ depends to some extent on i_D.

Similar to figure 4a, figure 4b presents the various conditions on the net production $N:P$ ratios that result in decomposers promoting either P or N limitation of autotrophs in the case of omnivorous consumers. We summarize the main results of figure 4b as follows.

—If decomposers promote the same limiting element as do consumers in the absence of omnivory $((N:P)_D < (N:P)_{AC})$, omnivory does not change the identity of the element that is promoted by decomposers (path 3 in figure 4b).

—If, however, decomposers promote a different limiting element from that of consumers in the absence of omnivory $((N:P)_D > (N:P)_{AC} > (N:P)_C)$, the outcome of the presence of decomposers on autotroph limitation depends on the feeding rate, i_D, of consumers on decomposers. By increasing the net production of consumers, decomposers increase the influence of the latter on autotroph limitation. If the feeding rate i_D is small, omnivory does not alter the limiting element promoted by decomposers (paths 1a and 2a in figure 4b). But if it is larger than a threshold value $\tilde{i}_D$, decomposers end up promoting the same limitation as do consumers, notwithstanding the fact that they do not consume relatively more of the limiting element (paths 1b and 2b in figure 4b).

Pelagic ecosystems are typically in the situation where decomposers contribute significantly to consumer net production (Azam *et al*. 1983). We estimated the model parameters for such systems (table 1). A comparison of $(N:P)_{AC}$ and $(N:P)_{ADC}$ suggests that decomposers should promote P limitation of autotrophs (path 3 in figure 4b). More interesting conclusions can be drawn from a comparison of the effects of consumers on the element limiting autotrophs with and without decomposers. On the one hand, when decomposers are not taken into consideration, consumers promote P limitation $((N:P)_{AC} < (N:P)_A)$. On the other hand, when decomposers are included, the impact of consumers on the nutrient limiting autotrophs becomes very weak (compare $(N:P)_{AD}$ and $(N:P)_{ADC}$), and they promote
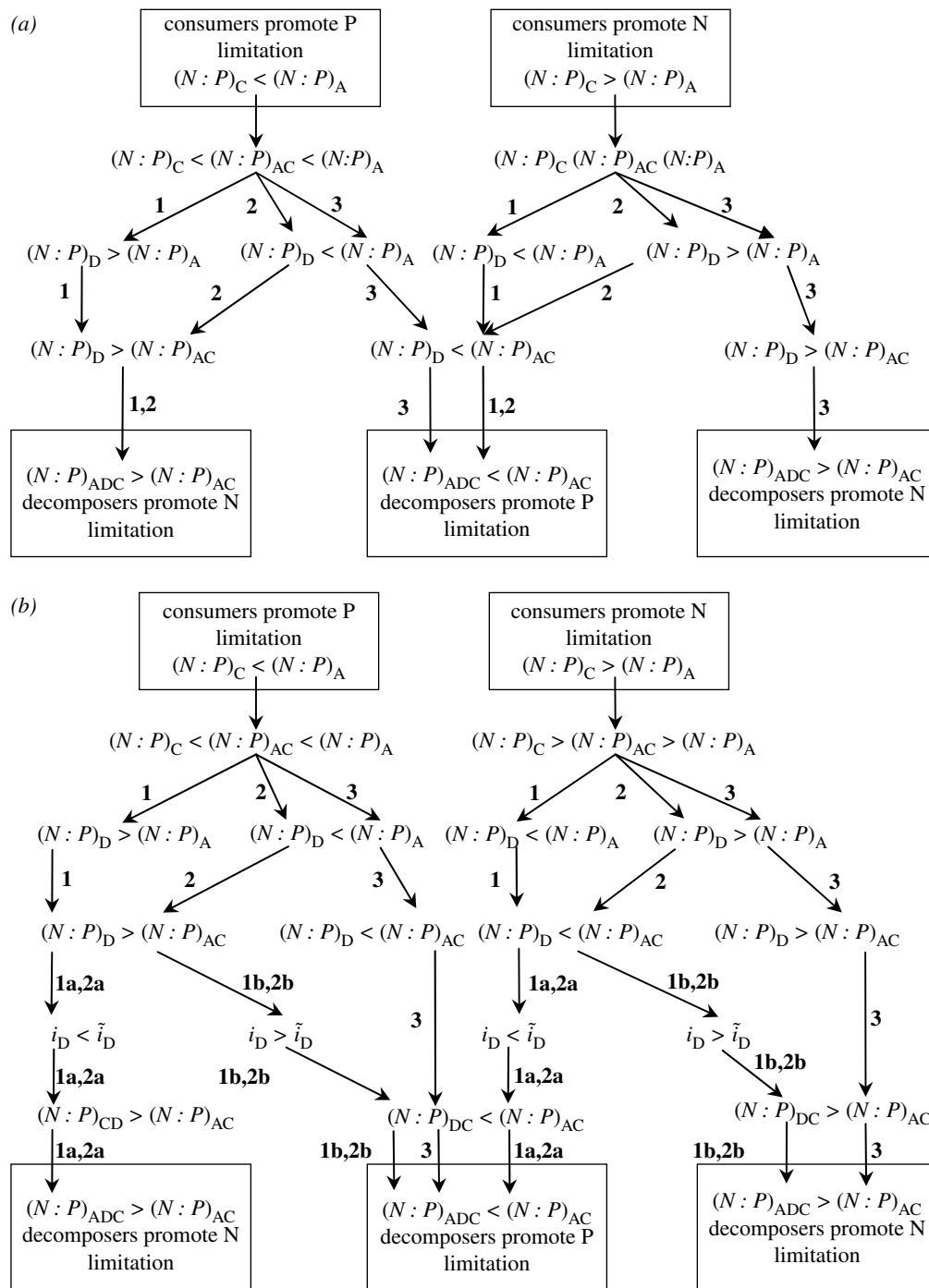
(a)

consumers promote P limitation $(N:P)_C < (N:P)_A$

consumers promote N limitation $(N:P)_C > (N:P)_A$

$(N:P)_C < (N:P)_{AC} < (N:P)_A$

$(N:P)_C (N:P)_{AC} (N:P)_A$

1 **2** **3**

$(N:P)_D > (N:P)_A$ $(N:P)_D < (N:P)_A$ $(N:P)_D < (N:P)_A$ $(N:P)_D > (N:P)_A$

1 **2** **3** **1** **2** **3**

$(N:P)_D > (N:P)_{AC}$ $(N:P)_D < (N:P)_{AC}$ $(N:P)_D > (N:P)_{AC}$

1,2 **3** **1,2** **3**

$(N:P)_{ADC} > (N:P)_{AC}$ decomposers promote N limitation

$(N:P)_{ADC} < (N:P)_{AC}$ decomposers promote P limitation

$(N:P)_{ADC} > (N:P)_{AC}$ decomposers promote N limitation

(b)

consumers promote P limitation $(N:P)_C < (N:P)_A$

consumers promote N limitation $(N:P)_C > (N:P)_A$

$(N:P)_C < (N:P)_{AC} < (N:P)_A$

$(N:P)_C > (N:P)_{AC} > (N:P)_A$

1 **2** **3**

$(N:P)_D > (N:P)_A$ $(N:P)_D < (N:P)_A$ $(N:P)_D < (N:P)_A$ $(N:P)_D > (N:P)_A$

1 **2** **3** **1** **2** **3**

$(N:P)_D > (N:P)_{AC}$ $(N:P)_D < (N:P)_{AC}$ $(N:P)_D < (N:P)_{AC}$ $(N:P)_D > (N:P)_{AC}$

1a,2a **1b,2b** **3** **1a,2a** **1b,2b** **3**

$i_D < \tilde{i}_D$ $i_D > \tilde{i}_D$ $i_D < \tilde{i}_D$ $i_D > \tilde{i}_D$

1a,2a **1b,2b** **1a,2a** **1b,2b**

$(N:P)_{CD} > (N:P)_{AC}$ $(N:P)_{DC} < (N:P)_{AC}$ $(N:P)_{DC} > (N:P)_{AC}$

1a,2a **1b,2b** **3** **1a,2a** **1b,2b** **3**

$(N:P)_{ADC} > (N:P)_{AC}$ decomposers promote N limitation

$(N:P)_{ADC} < (N:P)_{AC}$ decomposers promote P limitation

$(N:P)_{ADC} > (N:P)_{AC}$ decomposers promote N limitation

Figure 4. (*a*) Summary chart of the effect of decomposers on autotroph nutrient limitation in the case of non-omnivorous consumers ($i_D = 0$). The promotion of N or P as a limiting nutrient by decomposers depends on the relationships between $N:P$ ratios of autotroph $(N:P)_A$, consumer $(N:P)_C$, decomposer $(N:P)_D$ and autotroph-based food-web net production $(N:P)_{AC}$. (*b*) Summary chart of the effect of decomposers on autotroph nutrient limitation in the case of omnivorous consumers ($i_D > 0$). The promotion of N or P as a limiting nutrient by decomposers depends on the relationships between $N:P$ ratios of autotroph $(N:P)_A$, consumer $(N:P)_C$, decomposer $(N:P)_D$ and autotroph-based food-web net production $(N:P)_{AC}$, and also on the ingestion rate of decomposers by consumers i_D in comparison with a threshold value $\tilde{i}_D$. Different combinations of $(N:P)_A$, $(N:P)_C$, $(N:P)_D$, $(N:P)_{AC}$ and i_D, represented by different arrow paths, lead to the promotion of different limiting elements by decomposers. Each combination or path is marked by different numbers (**1**, **2** and **3** in (*a*) and **1**, **1a**, **2**, **2a**, **2b** and **3** in (*b*)).

N instead of P limitation $((N:P)_{ADC} > (N:P)_{AD})$! In this case, the effect of the whole food web on the nutrient limiting autotrophs is still to promote P $((N:P)_{ADC} < (N:P)_A)$, but decomposers are responsible for this effect (compare $(N:P)_{AD}$ and $(N:P)_A$). These comparisons show that the effects of consumers and decomposers on the nutrient limiting autotrophs are not additive but rather interactive. This is an excellent illustration of the fact that, in our model, the impact of a given trophic level on the nutrient limiting autotrophs depends on the whole food-web context.

4. DISCUSSION

Stoichiometric hypotheses that describe the effects of consumer-driven nutrient recycling on plant nutrient limitation often ignore the potential impact of other components of the food webs in which plants and

Table 1. Mean or typical values of parameters for two types of ecosystems: forests and shrublands and pelagic areas of aquatic ecosystems. (Symbol definitions can be found in the legend of figure 1. The ratio of decomposer to autotroph stocks f is calculated according to table A3 in the electronic supplementary material; $N:P$ ratios are calculated according to table A2 in the electronic supplementary material; the type of element limiting consumer growth (cons. lim.) is calculated according to table A4 of the electronic supplementary material; and the type of limiting element promoted by decomposers (el. prom.) is calculated according to figure 4.)

ecosystems	forest and shrublands	pelagic areas		
consumers	insects	zooplankton		
parameters			units	from
$(N:P)_A$	27.3	26.5	At : At	Elser *et al.* (2000)
$(C:P)_A$	799	256	At : At	Elser *et al.* (2000)
$(N:P)_C$	22.6	18.5	At : At	Elser *et al.* (2000)
$(C:P)_C$	73.2	114	At : At	Elser *et al.* (2000)
$(N:P)_D$	7	15	At : At	Makino & Cotner (2004) and Cleveland & Liptzin (2007)
$(C:P)_D$	60	72	At : At	Makino & Cotner (2004) and Cleveland & Liptzin (2007)
a_A	0.0000048	0.029	day^{-1}	Cebrián (1999)
a_C	0.01	0.15	day^{-1}	Makarewicz & Likens (1979) and Banse & Mosher (1980)
a_D	0.0033	0.048	day^{-1}	Hunt *et al.* (1987) and Pirlot *et al.* (2007)
e_A	0.1	0.6	—	Cebrián (1999)
e_C	0.6	0.6	—	Schroeder (1981)
e_D	0.3	0.2	—	del Giorgio & Cole (1998) and Moore *et al.* (2005)
r_C	0.0054	0.095	day^{-1}	Banse & Mosher (1980) and Hernández-León & Ikeda (2005)
i_A	0.000009	0.145	day^{-1}	Cebrián (1999)
i_D	0	0.072	day^{-1}	Pirlot *et al.* (2007)
calculations				
F	0.16	1.33	At : At	
$(N:P)_{AD}$	7.6	18.5	At : At	
$(N:P)_{AC}$	25.3	21.3	At : At	
$(N:P)_{DC}$	7	16.2	At : At	
$(N:P)_{ADC}$	7.9	18.6	At : At	
cons. lim.	P	P		
el. prom.	P	P		

herbivores are embedded (Sterner *et al.* 1992; Elser & Urabe 1999). This is unfortunate, especially in the case of microbial decomposers, since these are generally major players in the processing of plant-derived nutrients (Cebrián 1999; Moore *et al.* 2004). To study the effects of consumer-driven nutrient recycling on the nutrient that limits plant growth in the presence of decomposers, we used a stoichiometrically explicit model that couples the cycles of three elements, C, N and P, between autotrophs, consumers and decomposers.

Our vectorial graphical analysis demonstrates that the promotion of P or N limitation of autotrophs by decomposers depends on (i) the difference between the $N:P$ ratio of the decomposer-based food-web net production and the $N:P$ ratio of the autotroph-based food-web net production, and (ii) the degree to which decomposers are fed upon by consumers: if decomposers sustain an important fraction of consumer net production, they end up promoting the same limiting element as do consumers, even if they use more of the non-limiting element for their own production. For example, P-rich decomposers should normally drive autotrophs towards P limitation (e.g. in Danger *et al.* 2007). But if they are heavily consumed by consumers that promote N limitation, they indirectly promote N limitation. This result highlights the

importance of considering not only a trophic level's specific relative demands in elements, but also those of the trophic levels that it supports. For example, we anticipate that consumers supporting a high production of predators do not have the same impact on nutrient availability as do consumers that are almost not consumed.

The classical stoichiometric hypothesis on the effect of consumer-driven nutrient recycling assumes that the impact of a consumer on nutrient limitation in autotrophs can be deduced simply from a comparison between the $N:P$ ratio of consumers—if necessary, corrected by the assimilation efficiencies of N and P—and the $N:P$ ratio of autotrophs (Sterner 1990). This hypothesis implicitly assumes that the consumers considered are the main processors of autotroph production, or at least that their effect on nutrient limitation in autotrophs does not interfere with the effect of other trophic levels. The results from our model suggest that microbial decomposers can be more important than consumers in determining the nutrient limiting autotrophs, and that their effect can interfere with that of consumers. Our estimates of these effects for forest and pelagic ecosystems illustrate these predictions (table 1). According to our calculations, the effect of decomposers on nutrient limitation in autotrophs should dominate over that of herbivorous insects in forests and shrublands.

Incidentally, recent reviews show that terrestrial plants might be less exclusively N-limited than traditionally thought (Elser *et al.* 2007). Our prediction that consumers and decomposers alike should promote P limitation of forests represents an interesting mechanism that could explain why some terrestrial ecosystems might be P limited where we expect them to be N limited. Pelagic ecosystems offer a potential example of decomposers interfering with the impact of consumers on nutrient limitation in autotrophs since both the identity of the limiting nutrient promoted by consumers and the intensity of this promotion depend on whether decomposers are or are not included in the calculations. As with any quantitative prediction, however, our conclusions for these two types of ecosystems are as good as the available parameter estimates. We had to rely on mean or typical values published in the literature (mainly from Cebrián 1999 and Elser *et al.* 2000. Better predictions would require simultaneous estimates of all the parameters for producers, consumers and decomposers in the same ecosystem.

As any other model, our model contains assumptions that require some discussion. Among these assumptions are our choice of a donor-controlled function describing resource consumption by consumers, the possibility of an N or P, but not C, limitation of consumer growth, the use by decomposers of the totality of the organic C released by autotrophs and consumers, the limitation of decomposer growth by C, but not N or P, and constant stoichiometric ratios for all trophic levels.

While describing the model, we explained the reasons for which we feel most of these assumptions are reasonable in many ecological situations. We recognize, however, that there are other situations in which some of these assumptions might be far from reality. But since our predictions hinge only on the $N:P$ ratios of the net productions of the various parts of the food web, we have fair confidence in the robustness of our conclusions even when some assumptions are violated. As long as the appropriate N and P net productions are known in a system, our model and the vectorial method we developed should prove useful in determining the type of limiting nutrient promoted by a given trophic level. Admittedly, we represented the growth of organisms and its effect on their net production in a simplistic way. But the growth and $N:P$ ratios of autotrophs, decomposers and, to some extent, consumers vary in a very complicated fashion under the action of the various factors that control their growth (e.g. Ågren 2004; Makino & Cotner 2004; Cotner *et al.* 2006; Ballantyne *et al.* 2008). Therefore, we did not try to describe the growth and stoichiometry of organisms more precisely in this mainly theoretical paper; we leave this task to future developments.

In our model, consumers affect autotroph nutrient limitation by recycling excess C in an organic form available to decomposers (see table A3 in the appendix). However, the assumptions that lead to this prediction can be unjustified in many situations: decomposer growth might be limited by N or P instead of C (e.g. Rivkin & Anderson 1997; Ilstedt & Singh 2005), consumers themselves might be limited by C (Tiunov & Scheu 2004), in which case, they would not recycle excess C, or they can get rid of their excess C by increasing their respiration rate, not their release of organic C (Jensen & Hessen 2007). Still, many studies have found a positive, if

only temporary, effect of C recycling by consumers on the growth of decomposers in both aquatic (Jumars *et al.* 1989; Strom *et al.* 1997) and terrestrial ecosystems (Lovett & Ruesink 1995; Stadler & Müller 1996). Hence, we think that this prediction is worth investigating. If, concurrently, consumers and decomposers happened to promote different limiting elements, we would have the most blatant contradiction of the hypothesis that consumers alter the limitation of autotrophs only according to their own $N:P$ ratio.

Terrestrial and aquatic ecosystems are very different in many important features, justifying their study under different subdisciplines (Cebrián 2004; Shurin *et al.* 2006). But there has been a recent trend to reunite the two types of ecosystem under a common perspective (Elser *et al.* 2000, 2007). When doing so, one has still to be careful not to ignore the fundamental differences between the two types of ecosystem: in terrestrial ecosystems, herbivory is generally low and most primary production is channelled towards detritus production; the reverse is true in aquatic ecosystems, with a high proportion of primary production consumed by herbivores (Cebrián 1999). Hence, when transferring hypotheses and concepts about the influence of herbivores in ecosystems from water to dry land, one has to ask whether other consumers in terrestrial systems are not likely to play the role that herbivores play in aquatic systems (e.g. Cebrián 2004). Our estimates of the effects of decomposers and herbivores on plant nutrient limitation in forests and shrublands confirm that herbivores should play only a small role in the cycling of nutrients in forested ecosystems, the prime role being left to decomposers and detritivores (table 1).

The prevalence of herbivore or detritivore consumers in different ecosystems has led to another division in ecosystem ecology between those studies that concentrate on the part of food webs based on consumption of plant living tissue and those that focus on consumption of plant detritus. Aquatic ecologists soon realized that these two parts of food webs are linked together, and that part of herbivore secondary production can be fuelled by nutrients coming ultimately from detritus (Azam *et al.* 1983). We tried to include this so-called microbial loop in the simplest possible way in our model, by letting first-order consumers feed directly on decomposers. In terrestrial ecosystems, we could find no evidence in the literature that herbivore production is subsidized partly by detritus-derived nutrients. However, this might result from a narrow view of what represents the major consumers in terrestrial ecosystems. Most studies are concerned with classical herbivores, such as mammals (grazers and browsers) and insects (phytophagous and sap-feeders). It is probably true that these consumers do not derive any significant production from detritus (although some insects such as cockchafers and fungus gnats have larval stages that might derive a significant amount of their resources from detritus). But important consumers such as ants, termites and earthworms use both plant material and decomposer-derived organic matter (Curry & Schmidt 2007; Milton & Kaspari 2007). Although we did not have enough quantitative data on decomposer-based consumer production to include them in our parametrization of forest and shrubland ecosystems, this is certainly work worth doing in the future, if one is to correctly assess the role of

consumer-driven nutrient recycling in plant nutrient limitation. It would not be surprising if such an effort were to show that some of the influence of consumers on nutrient cycling is through their diversion of part of decomposer production for their own sake. On a more speculative level, it is interesting to note that many consumers of plant material—herbivores and detritivores alike—have developed symbioses with microbial species. Could this be an evolutionary mechanism developed to allow these species to access the nutrient-rich microbial production?

In both terrestrial and aquatic ecosystems, microbivorous trophic levels exist that are intermediates between decomposers and first-order consumers in microbial loops (Azam *et al.* 1983). They can also be responsible for the remineralization of the nutrients immobilized in decomposer biomass (Andersen *et al.* 1986; Raynaud *et al.* 2006).

We could have accommodated our model to include these trophic levels without much difficulty. But, we feel that this additional complication would have obscured the reader's understanding of the vectorial analytical method we developed, as well as of the general message of our work. Still, our model should be extended in the future to include these intermediary trophic levels in order to gain more accuracy in predicting the effects of decomposers and consumers on plant nutrient limitation.

In conclusion, our model makes a strong case for the inclusion of the whole food-web context in attempts to predict the impact of consumers and decomposers on nutrient limitation in autotrophs. We showed that, to determine this impact for any species or trophic level, one only has to estimate its net production at equilibrium, as well as the part of the net production of the other components of the food web that is derived from it. We also advocate that stoichiometric studies should broaden their range of consumers studied to include detritivores and omnivores if their goal is to fully understand how the biotic components of ecosystems alter the cycling of elements.

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