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Plant–herbivore–decomposer stoichiometric mismatches and nutrient cycling in ecosystems

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Plant stoichiometry is thought to have a major influence on how herbivores affect nutrient availability in ecosystems. Most conceptual models predict that plants with high nutrient contents increase nutrient excretion by herbivores, in turn raising nutrient availability. To test this hypothesis, we built a stoichiometrically explicit model that includes a simple but thorough description of the processes of herbivory and decomposition. Our results challenge traditional views of herbivore impacts on nutrient availability in many ways. They show that the relationship between plant nutrient content and the impact of herbivores predicted by conceptual models holds only at high plant nutrient contents. At low plant nutrient contents, the impact of herbivores is mediated by the mineralization/immobilization of nutrients by decomposers and by the type of resource limiting the growth of decomposers. Both parameters are functions of the mismatch between plant and decomposer stoichiometries. Our work provides new predictions about the impacts of herbivores on ecosystem fertility that depend on critical interactions between plant, herbivore and decomposer stoichiometries in ecosystems.

1. Introduction

Herbivores can have dramatic impacts on ecosystem functioning: they can alter primary production [1], change fire regimes [2], modify plant communities [3] and shift ecosystems over geological timescales [4]. However, we still have a limited understanding of the effects of herbivores on nutrient availability, a major determinant of ecosystem fertility and plant properties [5,6].

Although major advances on this topic have been made in some ecosystems, such as boreal forests [7], the Serengeti grasslands [8] and temperate managed pastures [9], the impacts of herbivores on nutrient cycling are generally hard to predict in the absence of detailed, long-term experimental manipulations. Such empirical studies have found positive, negative, or no effects of herbivores on decomposers, soil carbon respiration and net nitrogen mineralization, even among relatively similar locations [10]. This low predictability can largely be ascribed to the many ways in which herbivores affect decomposition. Bardgett & Wardle [11] grouped the various effects of herbivores into three main categories: type I mechanisms that alter the quantity of resources returned to the soil (e.g. herbivores change net primary productivity, and hence, indirectly, plant litter production); type II mechanisms that alter the quality of resources returned to the soil (e.g. herbivores return large quantities of nutrients to the soil as dung and urine, which are often more accessible to microbial decomposers than plant litter); type III mechanisms that alter the composition of plant communities (e.g. selective herbivores shift plant community composition towards unpalatable plant species, whose litter is often of lower quality to microbial decomposers). These mechanisms do not necessarily act on nutrient availability in the same direction, hence the difficulty in drawing general predictions about the effects of herbivores on soil processes.

However, there is a consensus that the effects of herbivores on nutrient availability should be largely positive in fertile ecosystems and mainly negative in unproductive ecosystems [11]. The main factor responsible for this pattern is thought to be plant and litter qualities. Plants from fertile ecosystems are often thought to have higher nutrient content and fewer secondary compounds than plants from nutrient-poor ecosystems [12]. Several conceptual models show how higher plant quality should trigger mechanisms leading to an increase in organic matter decomposition, nutrient mineralization and microbial decomposer biomasses [11,13]. Hobbs's [14] is probably the most mechanistic of these conceptual models. Relying on contemporary state of the art knowledge about the nutrient metabolism of ungulates, Hobbs estimated their nitrogen excretion as a function of the nitrogen content in their food. As the latter increases, ungulates get rid of the excess of nitrogen in their food as urine. Because N in urine is more easily available to plants and microbes, one expects an increasingly positive effect of herbivores on nutrient availability as plant nutrient content increases. Assuming that plants generally have higher nutrient content in more fertile soils, he predicted a positive effect of herbivores in enriched ecosystems. However, the only experiment known to us that tested this prediction did not support it [15].

One problem with this hypothesis is that it includes only a type II mechanism (higher return of labile N in urine as plant nutrient content increases). But the mechanisms by which herbivores affect nutrients can hardly be considered in isolation. In fact, excess N excretion by herbivores entails the prior ingestion of plants, a process that alters the magnitude of primary production, a type I mechanism. Moreover, food ingestion unavoidably results in the defaecation of the non-assimilated fractions, a process that leads to both type I and type II mechanisms.

Furthermore, this hypothesis jumps directly to the conclusion that urine has positive effects on nutrient availability, without following the fate of excreted and egested nutrients through the soil and decomposer compartments. However, we know that microbial decomposers excrete elements in mineral form when their concentration in the detritus is in excess of the microbes' physiological needs, a process called mineralization. Detritus deficient in an element, on the other hand, elicits the uptake of the same element in a mineral form from the environment as compensation, a process called immobilization. Hence, decomposition, such as herbivory, is a stoichiometrically regulated process that affects nutrient availability [16,17]. Thus, interactions between the two concurrent processes are predictable [11], but have not been fully investigated using stoichiometric approaches. We posit that the stoichiometry of decomposers is essential to understand the effects of herbivores on nutrients [18].

Consequently, we built a model for the impacts of herbivores on nutrient availability that includes the mechanisms associated with the regulation of both herbivore excretion and decomposition. We use a stoichiometrically explicit model in order to investigate the role of plant nutrient content. We do not include type III mechanisms and other mechanisms related to the physiological responses of plants to herbivory [19]; we leave those for future developments. Yet, our model makes important, novel predictions about the impacts of herbivory on nutrient availability in ecosystems. Because these predictions stem from broad stoichiometric principles, we expect them to be general and robust to the addition of mechanisms improving the realism of our model.

2. Model description

Our model represents organisms as coupled compartments of elements under a mass-balance constraint, a classical approach in ecological stoichiometry [20]. We incorporate a homeostatic constraint by setting the elemental composition of the organic compartments to constant values. Our description of decomposer nutrition is based on one of our previous models [18]. A full description and analysis of the model is provided in the electronic supplementary material, §S1.

The model describes the exchanges of carbon (C), and another essential nutrient (X) between plants consumed by herbivores and microbial decomposers via an inorganic pool of X and an organic pool of coupled C and X (figure 1). The factor on which we focus, plant nutrient content, is represented by the plant C : X ratio.

Herbivory is included in the model using a simplified version of Anderson *et al.*'s model [21]. Nutrition of herbivores is decomposed into five processes (figure 1): ingestion (I), digestion (G), assimilation (A), defaecation (D) and excretion (E). These processes, in turn, affect the variables and parameters that drive plant–decomposer interactions: I decreases plant biomass; E increases the pool of inorganic X; D adds biomass to the pool of detritus; A (assimilation across the gut wall), if its efficiency differ between C and X, leads to C : X ratios that diverge between the defaecated organic matter and plant material; finally, G, thanks to the actions of physico-chemical digestive agents, alters the decomposability of the defaecated material. These processes are indivisible components of herbivore nutrition, but are not necessarily operating at the scale at which the model applies to a specific herbivore species. Herbivores are mobile organisms that may dedicate different parts of their habitat to different activities [14,22]. Consequently, some physiological processes may not affect the flows of elements within the system under consideration, although they occur within the body of herbivores. In order to incorporate this possibility in our model, we derived a set of six sequentially ordered scenarios of herbivory (table 1): building on scenario 0, i.e. without herbivores, the next scenario (I) includes only one nutritional process, ingestion. The following scenario (IE) includes both ingestion and excretion. In scenario IED, the process of defaecation is added to the two previous processes, but with egested faeces that have the same C : X ratio and decomposability as the original plant material, thus eliminating the effects of the two remaining nutritional processes from the ecosystem: assimilation (A) and digestion (G). The two latter processes are included sequentially in the last two scenarios (IEDA and IEDAG).

We use a classical stoichiometric approach to incorporate the effect of plant nutrient content on herbivore nutrient excretion [20]. We define a C : X threshold elemental ratio for herbivores ($\mathrm{TER_H}$), which is the plant C : X ratio above which herbivore growth limitation switches from C to X and excretion of X is at its minimum [23]. When the plant C : X ratio is smaller than $\mathrm{TER_H}$, herbivore growth is limited by C availability and the excess of X in the food is excreted. Because of maintenance costs, $\mathrm{TER_H}$ was shown to vary slightly as a function of the amount of C ingested [24]. However, these variations tend to be moderate [23], so we make the simplifying assumption of a constant $\mathrm{TER_H}$.

Herbivore biomass (x_H) is held constant, assumedly under the control of some unaccounted ecological factors (predators,

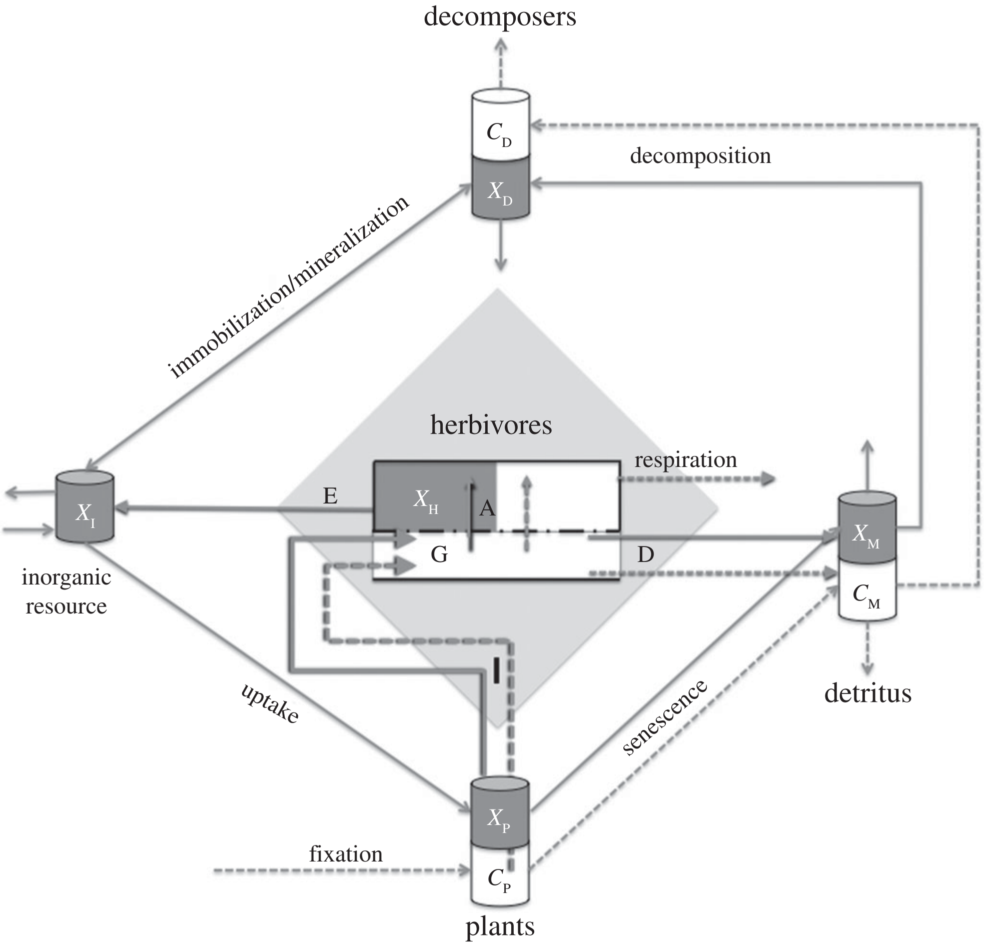

Figure 1. Flow diagram of a model that couples the cycles of carbon (in white) and another limiting element X (in grey) between plants, decomposers and herbivores. Plants (C_P and X_P combined) grow on a limiting inorganic resource containing X (X_I). They supply decomposers (C_D and X_D combined) with detritus (C_M and X_M). Decomposers either immobilize or mineralize X_I, depending on the difference between the ratios $C_D : X_D$ and $C_M : X_M$. Carbon (dashed arrows) and X (solid arrows) flow in and out of the ecosystem and between the various C and X stocks. Herbivores ingest plants (flow I). Once ingested, the resource is digested, i.e. its physical and molecular integrity are degraded (G), resulting in a changed decomposition rate for plant organic matter once defaecated. Simple molecules are then assimilated into biomass with assimilation efficiencies that are different for C and X (A). This differential assimilation results in a different C : X ratio for the organic resource after defaecation (D). Part of the assimilated nutrients is excreted (E) or respired (for C), resulting in net growth efficiencies for X and C, respectively, that are functions of both the plant and the herbivore C : X ratios, as well as of the assimilation efficiencies of C and X.

parasites, diseases or climatic factors) or anthropogenic actions (husbandry, hunting or conservation practices). Only plant consumption by herbivores varies dynamically.

Unlike herbivores, decomposers can use inorganic X as an alternative resource when their food is deficient in organic X. Thus, along an increasing gradient of detritus C : X ratios, decomposers pass through three states (figure 2*a*): (i) for C : X ratios smaller than their TER ($\mathrm{TER_D}$), their growth is C limited and they excrete—mineralize—the excess X from their resource; (ii) for moderate C : X ratios above $\mathrm{TER_D}$, their growth is also limited by the availability of organic C, but they immobilize inorganic X, instead of mineralizing it; (iii) for higher C : X ratios, growth is not limited by the availability of organic C, but rather by the availability of the inorganic X needed for immobilization. The latter process is then decoupled from the C : X ratio of detritus.

Owing to the defaecation process, the detritus is a mixture of plant- and herbivore-derived organic matter. Its C : X ratio is just a weighted average of the C : X ratios of these two sources. But because defaecated organic matter in the model is just ingested plant material with somewhat altered molecular and elemental compositions, the detritus C : X ratio is *in fine* proportional to the plant C : X ratio (see the electronic supplementary material, §S1.2.2); therefore, the state of decomposers ultimately depends on the plant C : X ratio (see the electronic supplementary material, §S1.2.3).

Plant and decomposer uptakes of resources are donor-controlled functions, that is, their rates are not proportional to their own densities, but to the densities of their resources (see the electronic supplementary material, §S5 for a detailed discussion of uptake functions).

3. Results

(a) Effects of ingestion

One noticeable effect of herbivores is a decrease in the equilibrium biomass of plants following ingestion (see the electronic supplementary material, figure S2.1*d*). As a consequence, the level of detritus is also decreased (compare the levels of detritus between the scenario without herbivores and the scenario including ingestion in figure 2*b*). Owing to the lower detritus availability, a second ensuing effect is the extension towards higher values of the range of C : X ratios for which decomposers are limited by C (figure 2*b*).

Table 1. Herbivory scenarios.

name	nutritional processes included	possible biological interpretations	mathematical derivation
0	no process	no or excluded herbivores	set ingestion rate of producers by herbivores (*h*) to 0 in full model
I	ingestion	grazing grounds or plants used only for feeding, in order to avoid predators, disease transmission, interference. . .	remove defaecation and excretion of X and C from full model
IE	ingestion, excretion	herbivores using areas dedicated to defaecation	remove defaecation of X and C from full model
IED	ingestion, excretion, defaecation	herbivores with a digestive process that does not significantly alter the physical and chemical composition of their food	set uptake rates of herbivore and plant detritus by decomposers (*j* and *a* respectively) equal in full model, as well as plant and herbivore detritus C : X ratios ($\alpha = \varphi$)
IEDA	ingestion, excretion, defaecation, assimilation	herbivores whose digestion does not significantly affect the molecular composition integrity of their food (e.g. aphids, which preferentially take up amino acids but do not modify sap molecular integrity)	set $j = a$ in full model
IEDAG	ingestion, excretion, defaecation, assimilation, digestion	whole habitat of herbivore considered, the different elements are assimilated with different efficiencies, ingested food is physically or chemically altered by digestion	no change, full model

(b) Role of plant nutrient content

The effects of ingestion on detritus levels (figure 2*b*), combined with the mineralization/immobilization pattern illustrated in figure 2*a*, are crucial to understand how plant C : X ratios modulate the effects of herbivores on nutrient availability. To show this, we plot nutrient availability (X_I^*) as a function of plant nutrient content (plant C : X ratio) for the scenario IE (ingestion plus excretion processes), with scenario 0 (no herbivory) as a baseline for comparison (figure 3*a*, see the electronic supplementary material, table S1.2 for parameter values).

In both scenarios, we see a decrease in X_I^*, as the plant C:X ratio increases, until a threshold is reached, above which X_I^* is constant (approx. 34 under scenario 0 and approx. 54 under scenario IE). This threshold marks the limit between C and X decomposer growth limitation (see also analysis in the electronic supplementary material, §S2.2). This pattern mirrors the pattern in the mineralization/immobilization rate (figure 2*a*). Mineralization and immobilization produce higher and lower X_I^*, respectively. So, as the plant C : X ratio increases, X_I^* first declines because of the gradual shift from mineralization to immobilization, then reaches a plateau when the immobilization rate becomes constant.

To interpret the effects of herbivores on nutrient availability, we have to recall that their ingestion of plant biomass results in a decrease in the level of detritus C (figure 2*b*). When decomposers are under C limitation, this decrease results in a decline of the mineralization/immobilization rate. If X_I^* is mineralized (i.e. for plant C : X ratios below TER_D), ingestion thus result in a decrease in nutrient availability (figure 3*a*). Above TER_D, the immobilization rate is decreased and so, X_I^* is increased. For better illustration, figure 3*b* plots %ΔXI, the percent change in X_I^* that result from herbivory, as a function of the plant C : X ratio. %ΔXI is calculated as

$$\%\Delta \text{XI} = \frac{X_I - X_I(\text{'0'})}{X_I(\text{'0'})} \times 100,$$

i.e. as 100× the equilibrium value of X_I under the herbivory scenario minus that for scenario without herbivory, divided by the latter. This index ranges from −100 (indicating an inorganic nutrient concentration of 0 under herbivory) to potentially +∞. %ΔXI is equal to 0 if herbivory does not alter the inorganic nutrient equilibrium level compared with no herbivory; and a %ΔXI of +100 indicates a doubling of the inorganic nutrient equilibrium level by herbivory. The figure clearly shows that herbivores decrease nutrient availability below TER_D and increase it, when the plant C : X ratios are above it. But the patterns are still more complex and the plot can actually be divided into five regions (noted I–V in figure 3*a*,*b*):

Region I. This region corresponds to C : X ratios that are smaller than the herbivore TER_H, and hence to C-limited herbivores. As a consequence of C limitation, herbivores excrete the excess of X from their food, thus partially mitigating the indirect negative impact of ingestion on the inorganic nutrient stock via decreased plant detritus production. However, as the plant C : X ratio increases, the amount of excess X in the food decreases, resulting in a lower excretion of excess X by herbivores. Thus, the relation between the impact of herbivores on nutrient availability (%ΔXI) and plant C : X ratio within this range is negative.

Region II. In this region, herbivores are limited by X (the plant C : X ratio is above TER_H). X_I excretion is thus minimal and is no longer affected by the plant C : X ratio. Here, the effect of excretion on X_I^* is constant and positive. The effect of ingestion

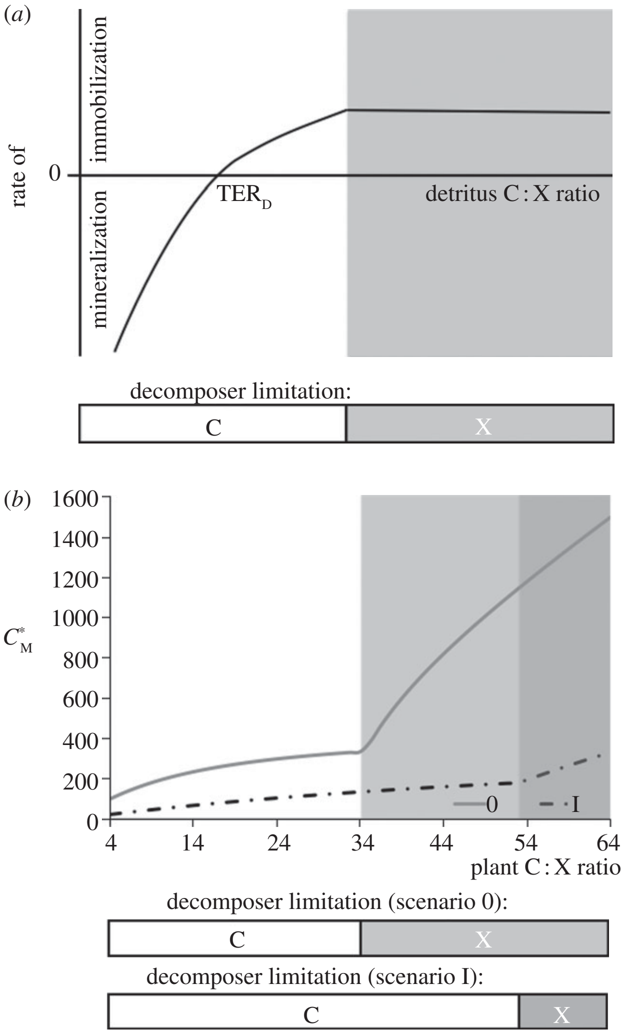

Figure 2. (*a*) Mineralization/immobilization rate from decomposers in the model as a function of the detritus C : X ratio, all else being equal. The rate is negative when decomposers mineralize the inorganic resource X_I, and positive when they immobilize it. The rate is 0 when the detritus C : X ratio is equal to TER_D, the ratio of C-to-X needed by decomposers for a balanced growth. For high detritus C : X ratios, decomposer growth is limited by X_I availability. The immobilization rate is thence decoupled from the detritus C : X ratio. (*b*) Equilibrium detritus C level (C^*_M) as a function of plant C : X ratio under scenario I (herbivory with only the ingestion process involved) with scenario 0 (no herbivores) used for baseline comparison. (see the electronic supplementary material, table S1.2 and table 1 for parameter values)

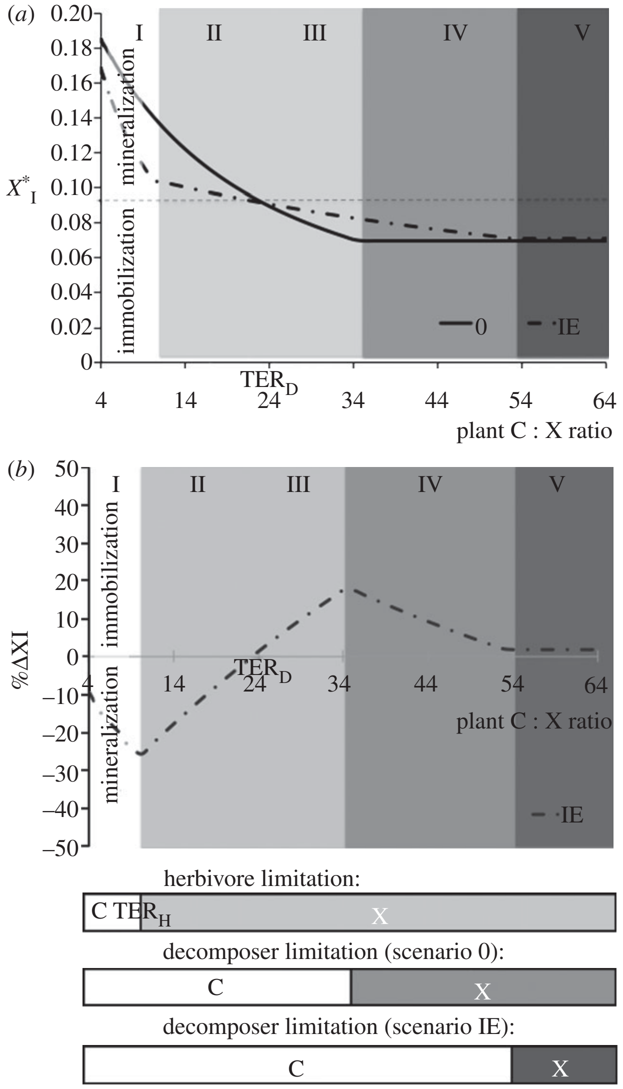

Figure 3. (*a*) Equilibrium inorganic nutrient stock, X^*_I, as a function of plant C : X ratio, under scenarios IE (ingestion + excretion only) and scenario 0. (*b*). Percent change in X^*_I owing to herbivory (%ΔXI) as a function of plant C : X ratio. %ΔX is the difference between X^*_I, in the two scenarios ($X^*_I('IE') - X^*_I('0')$) as a percent of scenario 0, $X^*_I('0')$. The results show that herbivory effects range from a decrease of approximately 26% to an increase of approximately 18% in inorganic nutrient equilibrium levels. In both panels (*a*) and (*b*), the resulting curves can be divided into five regions that correspond to specific combinations of herbivore and decomposer properties.

is negative though, because X is mineralized by decomposers (plant C : X ratios are below TER_D, the TER of decomposers). Hence, the overall effect of herbivory is negative. But as the plant C : X ratio increases, it gets closer to TER_D, resulting in a decreased mineralization rate (figure 2*a*). As the contribution of the mineralization rate to nutrient availability declines, so is the effect of herbivore ingestion. Therefore, there is a positive relationship between %ΔXI and the plant C : X ratio, up to a value of 0, which marks the C : X ratio for which the detritus C: X ratio exactly matches the needs of decomposers.

Region III. Here, the plant C : X ratio is above TER_D, leading to the immobilization of X^*_I by decomposers. The negative effect of ingestion on the immobilization rate results in an increase in nutrient availability (positive %ΔXI). As the plant C : X ratio increases above TER_D, immobilization increases, as does the relative effect of herbivores on nutrient availability.

Region IV. Here, decomposer growth is limited by X_I in the absence of herbivores (scenario 0), and by C in their presence. When the growth of decomposers is limited by X_I, the immobilization rate is unaffected by the properties of the detritus, in particular its C : X ratio. Therefore, the inorganic nutrient stock is unaffected by the plant C : X ratio under scenario 0. But it decreases in the scenario with herbivores, because of the increase in the immobilization rate as a function of plant C : X ratio (see figure 3*a* to compare the two scenarios). This explains the decrease in %ΔXI as a function of plant C : X ratio within this region.

Region V. In this region, the inorganic nutrient limits decomposer growth in both the absence (scenario 0) and presence of herbivores (scenario IE). As a result, the inorganic nutrient stock does not vary with the plant C : X ratio in both scenarios, yielding no variation in the effect of herbivory as a function of plant C : X ratio. Because, in this region of plant

C : X ratios, the detritus properties do not affect nutrient availability, the only operating herbivory process is the constant excretion rate, hence the positive value for %ΔXI.

(c) Role of herbivore characteristics

We plotted %ΔXI as a function of the plant C : X ratio for each of the herbivory scenarios (figure 4*a*).

The profiles obtained are qualitatively very similar among the various herbivory scenarios. One exception is the absence of a region I under scenario I (ingestion only), a logical outcome of the absence of excretion in this scenario (because region I is the product of the stoichiometrically regulated excretion by C-limited herbivores). The other differences between the various scenarios are only quantitative. As a rule of thumb, at a given plant C : X ratio, processes that increase the quantity (e.g. defaecation D) or quality (e.g. digestion G) of detritus dampen the effect of herbivory (bringing %ΔXI closer to 0) by counteracting the drop in detritus levels owing to ingestion (see the electronic supplementary material, §S2.2 for a thorough analysis).

There are differences also in the ranges of plant C : X ratios over which the five regions extend. For example, region IV is almost undetectable in the IEDAG scenario (all the herbivore nutritional processes included). This comes from the fact that the sums of the processes of defaecation (D), assimilation (A) and digestion (G) enrich the ecosystem in detritus to the point of almost counterbalancing the decrease in the detritus pool owing to ingestion (I). As the detritus pool increases relative to the inorganic nutrient pool, the onset of the X_I limitation of decomposition happens for smaller plant C : X ratios (notice on figure 4*a* how region V begins at increasingly smaller plant C : X ratios as one goes from the IE scenario to the IEDAG scenario, i.e. from a ratio approx. 54 to a ratio approx. 34).

It is, however, possible to observe more important qualitative differences between herbivores with differing physiologies. In particular, herbivores with a TER larger than that of decomposers can have a profile without region II, and possibly also region III. Region II corresponds to plant C : X ratios that lead simultaneously to X-limited herbivores (plant C : X ratio $> \mathrm{TER_H}$) and mineralizing decomposers (plant C : X ratio $< \mathrm{TER_D}$); these two conditions can clearly not be fulfilled simultaneously when $\mathrm{TER_H} > \mathrm{TER_D}$. Figure 4*b* illustrates such a case. Such herbivores have overall more positive effects on nutrient availability than herbivores with a lower $\mathrm{TER_H}$ because they excrete a higher proportion of the excess X in their diet, over a wider range of plant C : X ratios (compare figure 4*a* with *b*).

(d) Role of decomposer stoichiometry regulation

Our model includes a detailed description of the stoichiometric regulation of decomposition. To test the dependence of our results on this description, we devised a version of our model with a decomposition process independent from the stoichiometry of decomposers. In this version, decomposition is represented as a first-order mineralization rate, i.e. as a simple proportion of the detritus density (equations in electronic supplementary material, §S4). Figure 4*c* shows the effect of herbivory on nutrient availability (%ΔX) as a function of plant C : X ratio for this model. A comparison with the full model (figure 4*a*) highlights the additional complexity associated with an explicit stoichiometric description of decomposition. There is no equivalent to regions II, III and IV with a non-stoichiometric decomposition rate. The effect of herbivores becomes simply more negative as the plant C : X ratio increases, as predicted in Hobbs's model [14], until reaching a constant percentage change above $\mathrm{TER_H}$ (figure 4*c*). To conclude, as the plant C : X ratio increases, the stoichiometric regulation of decomposition results in a shift of herbivore effects from negative to positive, a prediction that cannot be yielded by models with non-stoichiometric decomposition.

4. Discussion

Plant nutrient content is thought to be a major driver of the impacts of herbivores on nutrient availability in ecosystems [11]. One postulated mechanism underlying this effect is that herbivores consuming more nutrient-rich plants should excrete higher levels of nutrients [14]. We tested this hypothesis with a stoichiometrically explicit model that tracks the exchange of carbon and an essential element X between plants, soil compartments and herbivores. Our work contributes three main predictions to the understanding of the role of plant nutrient content in herbivory:

- excretion of excess X affects nutrient availability as postulated by Hobbs's hypothesis [14] only when herbivores are C limited (i.e. only in region I of figure 3*a*,*b*);
- intensity of the effects of herbivores through changes in the detritus depends on the mismatch between the nutrient content of the detritus and of the demand of microbial decomposers. For example, a small mismatch should result in a negligible mineralization/immobilization flux of inorganic X. Consequently, small changes induced by herbivores in the detritus should result only in modest changes in nutrient availability (regions II and III in figure 3); and
- when both herbivores and microbial decomposers are limited by X, the effects of herbivores do not depend on plant nutrient content and are restricted to mechanisms, such as urine excretion, that bypass the detritus to affect inorganic nutrient levels directly (regions V of figure 3).

We want to emphasize that these predictions are rather general and derive from the homeostasis rules that govern the response of herbivores and microbial decomposers to mismatches between their demands in elements and the elemental compositions of their resources.

For example, the first prediction logically derives from the assumption of a post-absorption regulation of herbivore stoichiometry through the excretion of excess elements. This is a reasonably agreed upon assumption to describe the homeostasis of heterotrophic consumers [14,21]. However, various forms of pre-absorption stoichiometry regulation are also possible, through, e.g. the regulation of assimilation efficiencies [25], intake rates and gut-passage times [26] or the selection of nutritionally balanced plant species or parts [27]. If dietary excesses of nutrients are dealt with before they are absorbed, excretion (a post-absorption process) should no longer depend on plant nutrient content. So, a priori, the first prediction should not hold any more in this specific case; but we see no reason why the second and third predictions should be invalidated. In fact, these two predictions are the results of the effect of the plant C : X

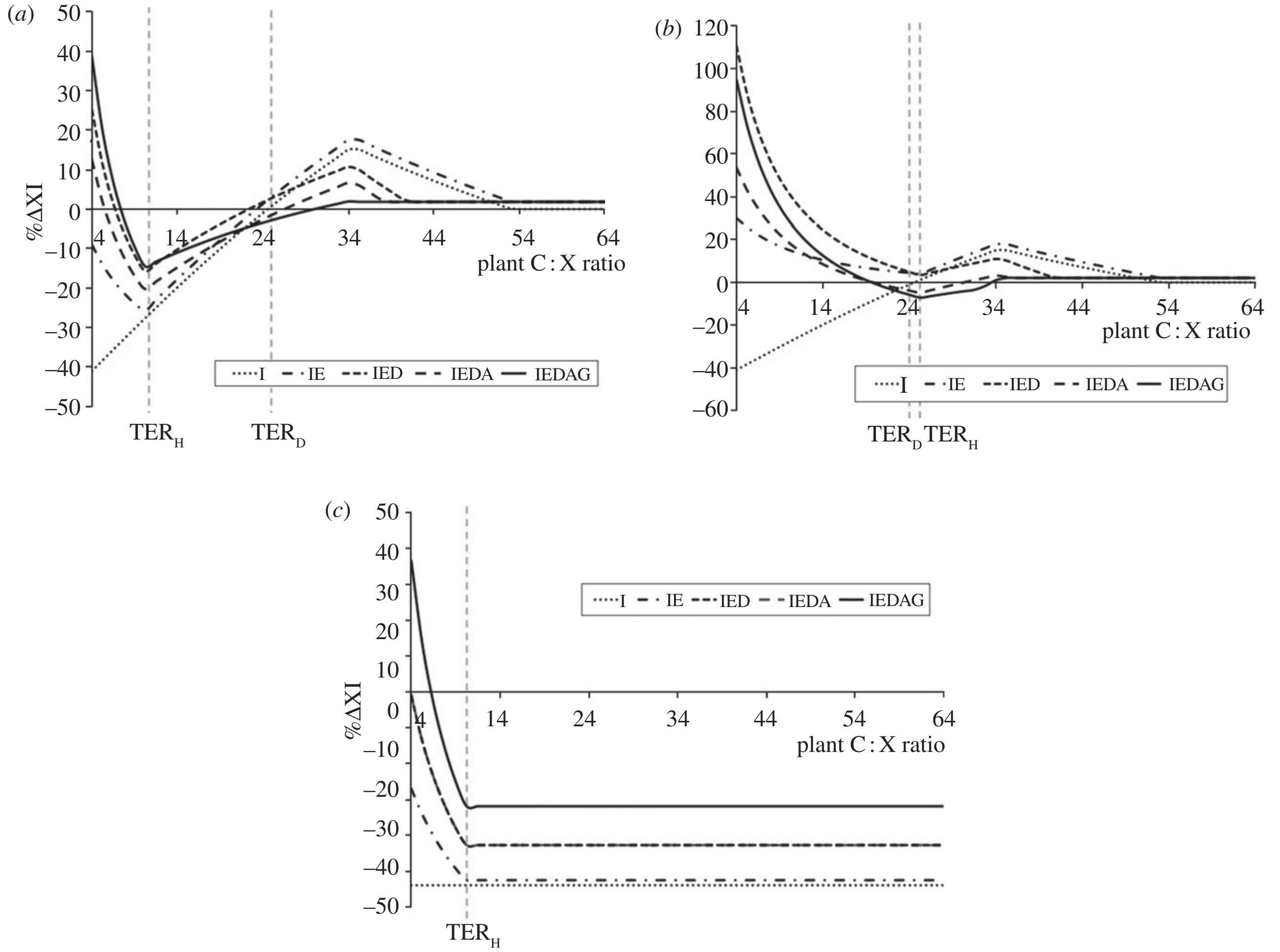

Figure 4. (*a*) %ΔXI as a function of plant C : X ratio for the various herbivory scenarios. As in figure 3, %ΔXI is X_{I}^{*} under a given herbivory scenario minus $X_{\mathrm{I}}^{*}('0')$ (X_{I}^{*} under scenario 0, i.e. no herbivores), as a percentage of $X_{\mathrm{I}}^{*}('0')$. The results show that herbivory effects range from a decrease of approximately 40% to an increase of approximately 40% in inorganic nutrient equilibrium levels. (*b*) Parameters are similar to those in (*a*), apart from $\gamma = 8$, $a_{\mathrm{X}} = 0.8$ and $n_{\mathrm{C}}^{\max} = 0.4$. These parameters result in a $\mathrm{TER_H} = 25.33$ (in place of 10.13 in figure 4*a*). The TER of decomposers ($\mathrm{TER_D}$) is equal to 24.57 in both. (*c*) Same as (*a*) and (*b*), but for a simplified version of the model in which organic X lost from plants and herbivores is recycled into inorganic X according to a first-order reaction that is not affected by the detritus and decomposer elemental compositions. Effects of ingestion (I) are not affected by the plant C : X ratio. For the other scenarios, from left to right, the effect of herbivory on nutrient availability decreases until reaching a plateau (when the plant C : X ratio $> \mathrm{TER_H}$). The plots for scenarios IED and IEDA are confounded.

ratio on the mineralization/immobilization rate (shown in figure 2*a*) more so than of any specific herbivore property. Therefore, they should prove robust to changes in how herbivore stoichiometric regulation is modelled. In conclusion, a model based on pre-absorption stoichiometry regulation in herbivores should show no equivalent to region I in figure 3, but the other regions should be present, leading to a scenario similar to scenario I in figure 4*a*.

The inclusion of a stoichiometric regulation of decomposition is the major addition in our model in comparison to previous plant–herbivore models [20,28,29–31]. On the other hand, in order to keep the model analytically tractable, we had to abandon more realistic depictions of the herbivore and plant dynamics found in other models. For example, herbivore population densities and plant C : X ratios are set to constant values in our model although they are known to vary in natural systems. Stoichiometric models that look more specifically into the dynamics of plant–herbivore models yield a set of identical predictions despite divergence in underlying assumptions: (i) X limitation of herbivores, as a result of high C : X ratios in plants, hinders the onset of limit cycles as predicted by the paradox of enrichment; (ii) alternative stable states to cycles emerge; (iii) very large stoichiometric mismatches between plants and herbivores can lead to the extinction of herbivores. These models all assume a non-stoichiometrically regulated mineralization rate. It will be important to evaluate how the addition of stoichiometry in the decomposition process in these models changes their predictions about plant–herbivore dynamics.

Most conceptual models link the effects of herbivory to ecosystem fertility. In contrast, our model links the effects of herbivory to the nutrient content of plants. Ecosystem fertility is often thought to determine plant nutrient content [12]. If this is true, an increase in ecosystem fertility would then imply a decrease in plant C : X ratios, i.e. a shift from region V towards region I in figures 2–4. However, factors other than soil fertility affect plant nutrient content, such as water availability and low light conditions [6,15,32]. Moreover, intensities and types of herbivory might differ among ecosystems with different fertilities [13,32]. Therefore, we expect our model to reliably describe the relationship between fertility and herbivory only among ecosystems with fairly similar herbivores, plants and environmental conditions. Then, our model predicts that nutrient-limited herbivores negatively affect nutrient availability as ecosystem fertility increases, provided decomposers are limited by carbon availability.

Our model includes most, but not all, of the potential mechanisms by which herbivores affect nutrient levels. For instance, following herbivory, increases in root exudation, biomass allocation to root tissues or secondary compound production have been documented in plants [19]. These changes then can affect plant contribution to detritus and eventually nutrient availability [19]. But it is as yet unclear how universal among plants are these reactions. In any case, the addition of these mechanisms to our model is not likely to change its core predictions. Our three main predictions (represented by regions I, II, III and V in figure 3) are likely to still hold, because they are the outcome only of the mismatches between plant, decomposer and herbivore stoichiometries (see the electronic supplementary material, §S3 for first proofs and a more detailed discussion).

Another way for herbivores to affect nutrient availability is by altering plant community composition. When faced with a choice between plants with different qualities, herbivores often select plants with the highest nutrient content. These plants often happen to be those whose litter decomposes faster and results in more mineralization [33]. Over the long term, this should result in a plant community skewed towards less palatable, less decomposable plants (e.g. [7], but see [34]). De Mazancourt & Loreau's [35] model expounds the conditions under which this plant community alteration should result in reduced nitrogen availability. Their model shows that herbivores need to favour plant species that are inefficient at conserving nutrients in ecosystems. But it does not include stoichiometric constraints on herbivory and decomposition. Given the important role of the mineralization/immobilization rate in our model, and its obvious influence on nutrient losses from ecosystems, a stoichiometric version of their model [35] will probably also exhibit a major influence of the stoichiometry of decomposition on how herbivore affect nutrient availability.

Empirical evidence in favour of our predictions is limited to date, owing to a scarcity of published experimental studies testing the effects of plant nutrient content on the ecosystem impacts of herbivores. Some exclosure experiments exhibit negative effects of herbivory ingestion on N mineralization via litter decrease (similarly to region II in figure 3*a*; [36,37]). Unfortunately, these experiments did not report plant nutrient content. One experiment that does is Bakker *et al.*'s [15]. Interestingly, its results contradict the predictions of Hobbs's model [14] and are compatible with our prediction 2 (compare panels *c* and *d* in their fig. 2 with regions II and III in our figure 3). However, we do not see this experiment as a formal verification of our model. Only those experiments that will concomitantly measure plant and detritus nutrient contents, mineralization/immobilization rates, and nutrient availabilities, inside and outside herbivore exclosures, and along a gradient of plant C : X ratios, will provide the kind of data necessary to test our model predictions. Moreover, such experiments will have to yield estimates for the stoichiometric requirements of both herbivores and microbial decomposers ($\mathrm{TER_H}$ and $\mathrm{TER_D}$, respectively).

Finally, the patterns of herbivory effects as a function of plant nutrient content were remarkably similar among scenarios of herbivory differing in the nutritional processes included. Herbivores with different TERs, however, can show rather divergent profiles: less X-limited herbivores (those with higher $\mathrm{TER_H}$) show more positive effects on nutrient availability, over a wider range of plant C : X ratios (compare figure 4*a* with *b*). This further emphasizes the most important insight from our model, namely that the effects of herbivores on nutrient availability depend on the mismatches among all of plant, herbivore and decomposer stoichiometries.

The study field of herbivore effects on nutrient availability is filled with contradictory results and complex ad hoc conceptual models. Our model is based on general principles linked to the stoichiometry homeostasis of organisms. From the various patterns that the model generates, we extracted three major predictions. First, herbivore excretion is important mainly when plants have very high nutrient contents. Second, at moderate plant nutrient contents, the effects of herbivores on nutrient availability are tied to the rates of mineralization/immobilization. Third, at low nutrient contents, these effects should be slightly positive and uncoupled from plant nutrient content. We hope that these new predictions will provide a guideline for more theoretically based experimental investigations of the effects of herbivores—a major constituent of food webs—on ecosystem fertility—a key feature of ecosystems that is under pressure from human exploitation.

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