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Opposite changes of whole-soil vs. pools C : N ratios: a case of Simpson's paradox with implications on nitrogen cycling

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Abstract

Ecosystem and soil scientists frequently use whole soil carbon:nitrogen (C : N) ratios to estimate the rate of N mineralization from decomposition of soil organic matter (SOM). However, SOM is actually composed of several pools and ignoring this heterogeneity leads to incorrect estimations since the smaller pools, which are usually the most active, can be masked by the larger pools. In this paper, we add new evidence against the use of C : N ratios of the whole soil: we show that a disturbance can decrease the whole-soil C : N ratio and yet increase C : N ratios of all SOM pools. This curious numerical response, known as Simpson's paradox, casts doubt on the meaning of frequently reported whole-soil C : N changes following a disturbance, and challenges the N mineralization estimates derived from whole-soil C : N ratio or single-pool modeling approaches. Whole-soil C : N ratio may not only hide features of the labile SOM pool, but also obscure changes of the large recalcitrant SOM pools which determine long-term N availability.

Key words: C : N ratio, carbon, decomposition, mineralization, nitrogen, Simpson's paradox, soil

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Introduction

The ratio of carbon (C) to nitrogen (N) content of soil organic matter (SOM) is the main indicator of its quality and has been extensively used to estimate N releases after SOM decomposition. SOM C : N ratio determines how much N is mineralized per unit of C respired and influences the amount of this N that is immobilized by decomposers (Accoe *et al*., 2004). For these reasons, the C : N ratio is a critical input of biogeochemical models used to predict the impacts of agriculture and other disturbances on organic matter decomposition and N cycling in terrestrial ecosystems (Chapin *et al*., 2002). These calculations have traditionally assumed that SOM behaved as a homogeneous pool whose global C : N ratio regulates decomposition and N release. In the last decades, however, it has been brought into attention that SOM is composed by a variety of chemical forms with different nutrient contents and turnover rates which can be grouped into fractions with different lability (Parton *et al*., 1987, 1988, 2005; Cambardella & Elliot, 1992; Accoe *et al*., 2004; McLauchlan & Hobbie, 2004). Details of these primary organic matter fractions which actually determine C and nutrient dynamics are lost when all SOM is considered as a single pool (Davidson *et al*., 2000; Melillo *et al*., 2002; Knorr *et al*., 2005). For example, in temperate ecosystems, where the largest SOM pool is generally passive, the relatively small labile fraction makes the largest contribution to short-term organic matter decomposition and N mineralization (Andriulo *et al*., 1999; Alvarez & Alvarez, 2000). Therefore, estimates of organic matter decomposition and N mineralization based on changes in whole-soil C : N ratios have been suspected because they hide features of the fractions into a general average (Fabrizzi *et al*., 2003; Accoe *et al*., 2004). In this paper, we show that changes in the overall C : N may not only hide changes in the C : N ratio of the smaller but relevant pools but also critically misrepresent the changes in all fractions, including the usually large passive pool whose dynamics is relevant for long-term N storage.

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Fractional and overall soil C : N ratio can show Simpson's paradox (Simpson, 1951), a characteristic of averages making it impossible to determine changes in the parts based on the change of the whole. The paradox implies a reversal association between two variables, after a third variable or factor is considered. A classic example is that of a university which had a higher rejection rate for women than for men, while the rejection rate was higher for men than for women in all the colleges composing that same university. When Simpson's paradox is a possibility, it is necessary to decide if the interest is focused on the whole or on the parts. In our example, what is the focus, the university as a whole or every college? With respect to SOM dynamics, Simpson's paradox appears when the whole-soil C : N changes in one direction, while the C : N ratios of every soil fraction change in the opposite direction. Whole-soil and single-fraction C : N ratios are related by the formula,

$$R = \sum r_i \rho_i$$

where R is the overall SOM ratio, r_i is the ratio of the ith SOM fraction, and ρ_i is the proportion of all organic N that is contained in the ith fraction. It is easy to verify that R will decrease after a disturbance even if every single r_i increases, provided that ρ_i decreases enough in some fraction with a relatively high r_i (Fig. 1). This is expected to occur when the proportion of such SOM fraction decreases sharply after the disturbance (see in Fig. 1, the reduction in ρ_2 from 48.5% to 27.1% after the disturbance).

If the whole-soil C : N ratio increases after a disturbance, researchers that are aware of the multiple fractions that compose SOM but unaware of Simpson's paradox will normally assume that either all or at least the larger fractions have increased their C : N ratios. However, Simpson's paradox introduces a new counterintuitive possibility: all fractions may decrease their C : N ratio in spite of the increase at the whole-soil level. This would determine that predictions of disturbance impacts on fluxes such as gross N mineralization and immobilization based on the whole-soil C : N ratio are opposite to those more realistically based on the different SOM pools (including pools of short and long-term turnover).

While Simpson's paradox has been reported for other biological properties (Thomas & Parresol, 1989; Allison & Goldberg, 2002), it has been usually ignored in ecology and soil science, and we know of no previous reports relating it to SOM C : N ratios. Since most soil biogeochemical processes are determined by the behavior of the fractions, rather than the whole, it is critical to evaluate the incidence of the paradox on SOM dynamics. In this paper, (1) we present an example of

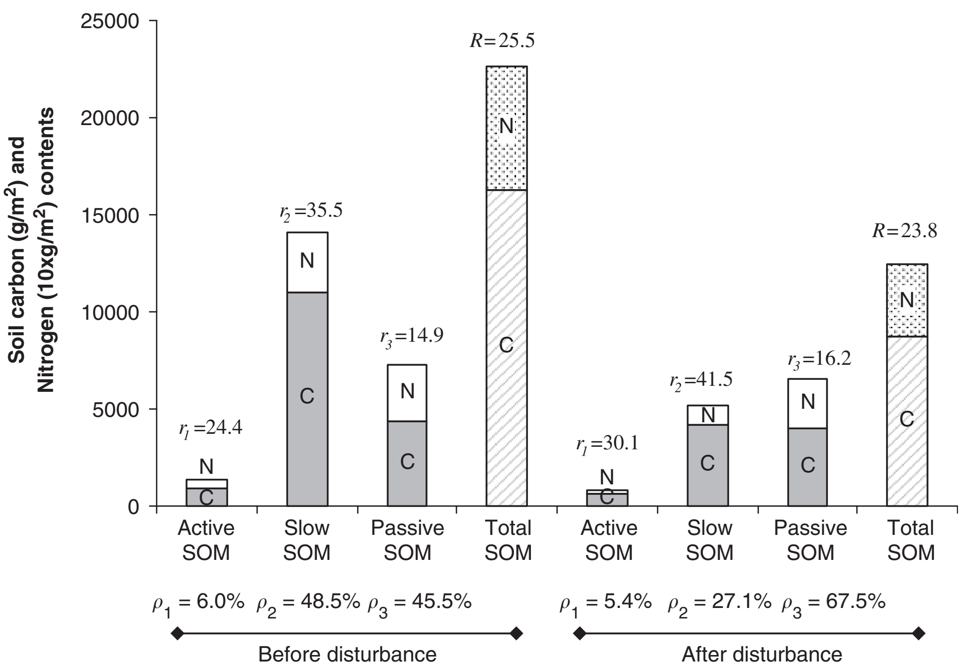

Fig. 1 A hypothetical example of Simpson's paradox for the case of changes in carbon (C) and nitrogen (N) contents in each soil pool and for the whole soil, before and after a disturbance. C : N ratios (r_i) of each soil fraction are shown above each bar. The whole-soil SOM C : N ratio (R) is shown above the total SOM bar. ρ_i values, the proportion of all organic N that is contained in the ith fraction, are shown below each SOM pool. Note that N contents are expressed as $10\,g\,m^{-2}$, to include them in the same axis as C.

changes in whole-soil and fractional C : N ratios showing Simpson's paradox and (2) we assess the implications of using either whole-soil or fractional C : N ratios to estimate gross N mineralization when Simpson's paradox occurs. Although the example presented in the paper derives from modeled data, we explain why the conclusions drawn from this paper apply also to measured data.

Methods

To document Simpson's paradox for soil C : N changes (objective 1), we compared the impact of grazing by exotic cattle on whole-soil and on fractional C : N ratios using CENTURY, a process-based biogeochemical model suitable for long-term analysis of ecosystem functioning (Parton *et al*., 1987, 1988, 1993; Glimanov *et al*., 1997). The model divides SOM into three different pools of different turnover rate: active, slow and passive (Parton *et al*., 1987; Metherell *et al*., 1993). Soil fluxes are controlled by environmental variables, and by lignin:nitrogen and C : N ratios.

We simulated the effects of 400 years of grazing by exotic cattle on SOM in 11 grassland sites of Argentina and Uruguay, South America. For each site, we obtained C and N contents in SOM and calculated overall SOM C : N ratios and C : N ratios for the three SOM pools under the two scenarios: one with no domestic grazing (named 'before domestic grazing') and the other after 400 years of domestic grazing (named 'after domestic grazing'). These simulations mimic, at each site, the introduction of domestic herbivores by Europeans occurred approximately by year 1600 (Soriano, 1992). For the simulations we used soil data published by government agencies of Argentina (INTA-SAGYP, 1990) and Uruguay (MGAP, 1979, 1994) and weather data from INIA (www.inia.org.uy) and INTA (www.inta.gov.ar) as inputs to the model. Calibration and evaluation of the CENTURY model for these sites was completed in a previous work (Piñeiro *et al*., submitted). The amount of aboveground net primary production consumed by natural and domestic herbivores at each site was derived from Oesterheld *et al*. (1992). Stocking rates at each site were increased from the expected values in year 1600 to present levels following a logistic growth curve.

To evaluate the consequences of using a whole-soil C : N ratios vs. fractional C : N ratios to estimate gross N mineralization changes after a disturbance when Simpson's paradox is observed (objective 2), we estimated the amount of total N mineralized per gram of SOM C decomposed before and after 400 years of grazing, using the two approaches. For this analysis we used C and N soil contents obtained with CENTURY as described above, but further calculations of gross N mineralization were made outside of CENTURY, in order to compare the consequences of using a whole-soil C : N ratios vs. fractional C : N ratios (CENTURY makes calculations of gross N mineralization only based on C : N ratios of each SOM pools), and to show it with readily comprehensive math. Our analysis was based on the assumption that when SOM decomposition occurs, the soil biota respires soil organic C and consequently a certain amount of N is mineralized (gross N mineralization), which depends on the C : N ratio of the organic matter respired. In experimental studies, both gross and net N mineralization are difficult to measure, because of the complexity in the estimation of the C that is actually decomposed and its specific C : N ratio (and immobilization of N in the case of measuring net mineralization) (Davidson *et al*., 1991). However, both conceptually and as considered in models of N cycling, gross N mineralization can be estimated by a simple calculation if the amount of organic matter decomposed and its C : N ratio are known (without considering immobilization) (Probert *et al*., 2005). We estimated the amount of mineralized N when 100 g of SOM C were decomposed by two approaches: first, by considering that SOM was a homogenous pool and hence gross N mineralization was calculated based on the whole-soil C : N ratios (named single-pool calculation), and second, by considering that decomposition occurred separately in each SOM fraction, and hence gross N mineralization was calculated based on the C : N ratios of each SOM fraction (named multiple-pool calculation). In this second approach, the amount of C respired from each fraction in the 100 g soil C sample was estimated based on the turnover rates proposed by Parton *et al*. (1987), 1–5, 30–40 and 200–1500 years, for the active, slow and passive SOM fraction, respectively. For simplicity, we assumed a turnover of SOM pools of 1.5, 35 and 1000 years, respectively. Finally, given the C : N ratio of each pool, we estimated the release of N from each fraction for the two grazing conditions. Assuming different SOM turnover rates within the ranges given above did not change qualitatively our results.

Results and discussion

For nine out of 11 sites tested, CENTURY simulations showed that grazing decreased the overall C : N ratio but increased it for all three – active, slow and passive – SOM pools (results for two exemplary sites are presented in Table 1). Long-term grazing resulted in drastic decreases of the slow SOM pool, which had the highest C : N ratio (*r*), reducing the proportion (ρ) of all soil N contained in this SOM fraction and generating

Table 1 Carbon (C) and nitrogen (N) contents and C : N ratios of different soil organic matter (SOM) pools before and after long-term grazing, for two localities in Argentina and Uruguay

	Carbon ($g\,m^{-2}$)		Nitrogen ($g\,m^{-2}$)		C : N		
Soil Pools	Before grazing	After grazing	Before grazing	After grazing	Before grazing	After grazing	Difference
Pergamino, Argentina							
Active	943	602	38.6	23.4	24.4	25.7	1.30
Slow	6993	4147	216	125	32.4	33.2	0.80
Passive	4339	4024	291	268	14.9	15.0	0.10
Total	12275	8773	546	416	22.5	21.1	−1.40
Canelones, Uruguay							
Active	707	504	17.5	11.2	40.4	45.0	4.60
Slow	5369	3462	163	97.9	32.9	35.4	2.50
Passive	3611	3439	247	230	14.6	15.0	0.40
Total	9687	7405	428	339	22.6	21.8	−0.80

Simpson's paradox. Although changes in C : N ratios were small, we do not intend to test the significance of these changes, as it would be of interest in experimental studies, but to clearly define the problem and illustrate why it occurs. After grazing, the slow SOM fraction with relatively high C : N (32.4 and 33.2) decreased its proportion, while the passive fraction with a relatively low C : N ratio (14.9–15.0) increased. Thus, whole soil C : N ratio, which was 22.5 and 22.6 before grazing, tended to be more similar to the passive fraction, decreasing the C : N after grazing. Such depletion of the slow-turnover SOM fraction is common after many years of agricultural use and leads to the predominance of the passive fraction in SOM (Cambardella & Elliot, 1992; Fabrizzi *et al*., 2003). Thus, although we have revealed the paradox with modeled data, we expect it to occur in experiments where a large fraction is depleted after a disturbance.

These results clearly demonstrate that whole-soil C : N ratios can erroneously assess the impact of a disturbance on organic matter quality, hence leading to incorrect estimation of gross N mineralization rates. Since it has been demonstrated that SOM fractions actually control decomposition rates (Knorr *et al*., 2005), each SOM fraction and its C : N ratio will in fact control gross and net N mineralization. Several authors indicated that the assumption of a unique homogeneous SOM pool may hide important information about the labile SOM pool, mainly because of the interference of the more recalcitrant pools (Davidson *et al*., 2000; Knorr *et al*., 2005). For example, Fabrizzi *et al*. (2003) showed that plowing can decrease the C : N ratios of the most labile SOM pool but increase it for the whole soil, due to an increase in the size of the recalcitrant pool. Hence, it has been established that consideration of the SOM as a single homogeneous pool and associated reporting of whole-soil C : N ratios can mask the dynamics of smaller pools leading to substantial error in inferences on decomposition and gross N mineralization. Here, we report new evidence against the use of whole-soil C : N ratios, by showing that the use of whole-soil C : N ratios to evaluate a disturbance may not only hide features of smaller soil fractions into a general average, but can also give opposite trends to those achieved by all the soil fractions after the disturbance. Thus, due to Simpson's paradox, whole-soil C : N ratio can mask not only the composition of the usually smaller, labile fractions, but also the changes in the large passive fractions after a disturbance. Changes of gross N mineralization of the recalcitrant SOM pools could largely increase N availability, N recycling and N losses, since large quantities of N are stored in this pool in temperate ecosystems, having great impacts on ecosystem functioning.

When Simpson's paradox occurs, it is straightforward to show that opposite estimates of gross N mineralization can be made by considering whole-soil and fractional C : N ratios. The effect of long-term grazing on gross N mineralization estimates were opposite when calculated by the single-pool calculation or by the multiple-pool calculation (Table 2). Using data from the Canelones site, estimates of N release made by considering all SOM as unique pool were 4.4 g of N/100 g of C before grazing and 4.6 g of N/100 g of C after grazing (Table 2, see single-pool calculation). This represented a 3.7% increase in gross N mineralization after grazing. In contrast, total gross N mineralization rates estimated by the multiple-pool calculation were as follows: 2.6 g of N/100 g of C before grazing and 2.4 g of N/100 g of C after grazing by domestic herbivores. This represented a 9.2% reduction of gross N mineralization after grazing.

Without considering Simpson's paradox, a decrease of whole-soil C : N ratio such as the one reported for

Table 2 Estimated nitrogen gross N mineralization rates from 100 g of soil organic matter (SOM) decomposed before and after long-term grazing, considering the whole soil as a unique homogeneous pool (single pool calculation) or separately each SOM fraction (multiple pool calculation).

	Before grazing			After grazing		
Soil Pool	C decomposed*	C : N[†]	N mineralized*	C decomposed*	C : N	N mineralized*
Single pool calculation						
Total soil	100	22.6	4.4	100	21.8	4.6
Multiple pool calculation						
Active	75.0	40.4	1.9	76.7	45.0	1.7
Slow	24.4	32.9	0.74	22.6	35.4	0.64
Passive	0.57	14.6	0.039	0.78	15.0	0.052
Total soil	100		2.6	100		2.4

*Grams of C or N.
[†]C : N ratios are the same as presented in Table 1.
C : N ratios correspond to the Canelones site.

Canelones in Table 1, could be interpreted in one of two ways: as an increase of SOM quality and a subsequent increase of gross N mineralization, or, more conservatively, as an undefined response because the whole-soil value might have obscured an increase of C : N of some fraction and, thus, no conclusions should be drawn. Simpson's paradox includes the new possibility that gross N mineralization can be reduced due to changes of all fractions opposite to the change in whole-soil C : N ratio, as shown in Table 2. This misestimate of gross N mineralization is likely to be translated to net N mineralization, since immobilization by soil biota also depends on the C : N ratio (Davidson *et al*., 1991; Probert *et al*., 2005). In this example, lower immobilization will be predicted from the single-pool calculation (as the C : N ratio decreases), while actually more immobilization is occurring because the C : N ratio of each pool has increased.

Use of whole-soil C : N ratio should be a concern not only in modeling but also in measuring and reporting data from experimental studies. Papers reporting experimental studies often show total SOM amounts and total soil C : N ratios because they are easier to measure than those of individual SOM pools. However, such results may be misinterpreted by readers that observe changes in a given direction after a disturbance, and hence derive hypotheses of changes in ecosystem functioning. We showed here that changes of all SOM fractions and, hence, the real impact of disturbance on N dynamics may be opposite to the reported from these experiments.

It has been widely discussed whether SOM models should include several pools, mainly for assessing decomposition under different climate scenarios (Fang *et al*., 2005; Knorr *et al*., 2005). Although multiple soil fractions have recently been increasingly taken into account, some work still reports total soil C : N values only (see for example Murty *et al*., 2002; Luizao *et al*., 2004).

Several models have been updated with the inclusion of different soil pools but others still are single pooled (i.e. CEVSA, Cao & Woodward, 1998; and TRIFFID, Cox *et al*., 2000). Furthermore, some models with several pools report only total C : N (see Halliday *et al*., 2003; Grunzweig *et al*., 2004) hiding features of soil fractions or potentially giving opposite trends. Here, we show that single-pool models may incorrectly assess gross N mineralization rates (and potentially net mineralization and immobilization), because they are based on whole-soil C : N ratios. An error in the estimation of gross N mineralization is likely to propagate to estimates of N availability and consequently to rates of C sequestration by plant growth. We show here that not only the labile pools (with impacts on short-term N dynamics) but also the recalcitrant pools (with impacts on long-term N dynamics), which store large amounts of N can be misrepresented by whole-soil C : N ratios. Consequently, a correct estimation of N releases from these large recalcitrant pools is crucial for assessing human induced changes in the global N cycle.

Our results indicate that projections and understanding of land-use change impacts on C and N biogeochemical cycles should be revised taking into account the effects of disturbance on different SOM pools, because trends in C : N ratio for the whole-soil can be opposite to those of the soil pools that directly control net N mineralization.

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