Nutrient cycling efficiency explains the long-term effect of ecosystem engineers on primary production

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Summary

1. Soil organisms, such as earthworms, accelerate mineralization of soil organic matter and are thought to be beneficial for plant growth. This has been shown in short-term microcosm experiments. It is thus legitimate to ask whether these increases in plant growth are due to brief pulses of mineralization or whether these increases are long-lasting.

2. This question was addressed using a system of differential equations modelling the effects of decomposers on nutrient cycling via trophic (nutrient assimilation) and nontrophic effects (through their ecosystem engineering activities).

3. The analytical study of this model showed that these processes increase primary production in the long term when they recycle nutrients efficiently, allowing a small fraction of the recycled nutrients to be leached out of the ecosystem.

4. Mineralization by the ecosystem engineering activities of decomposers seems to deprive them of a resource. However, it was shown that a decomposer may increase its own biomass, through its ecosystem engineering activities, provided the created recycling loop is efficient enough.

5. Mechanisms through which earthworms may modify the efficiency of nutrient cycling are discussed. The necessity of measuring the effect of earthworms on the nutrient input–output balance of ecosystems under field conditions is emphasized.

Key-words: earthworm, ecosystem engineers, nutrient cycling, plant growth, recycling efficiency

Introduction

Soil decomposers, particularly earthworms, are usually considered beneficial for plant growth (Brown *et al.* 1999; Scheu 2003), and their presence may facilitate plant growth via a number of different postulated mechanisms (Brown, Edwards & Brussaard 2004): (1) they enhance the activities of beneficial microorganisms; (2) in some cases they control plant pests and parasites; (3) they lead to the production of growth-regulating factors that act like hormones; (4) they change soil structure; and (5) they increase nutrient availability for plants by increasing mineralization rates. Many authors invoke this last hypothesis to explain increases in plant production of their microcosm or mesocosm experiments (Spain, Lavelle & Mariotti 1992; Scheu & Parkinson 1994; Pashanasi *et al.* 1996; Derouard *et al.* 1997; Gilot 1997; Callaham & Hendrix 1998; Araujo, Luizão & Barros 2004). However, these mechanisms are not mutually exclusive and

it is difficult to quantify the influence of different earthworm activities, particularly in short-term experiments (Carpenter 1996). First, microcosms and mesocosms might not be representative of large plots of nonmanipulated soil; for example, microcosm soils are usually homogenized and partially defaunated. Second, short-term experiments cannot faithfully reflect the long-term effect of earthworms on soil organic matter dynamics and plant growth. Indeed, short-term experiments could result in a peak of mineralization that would quickly level off when available, readily degradable fractions of organic matter have been mineralized. Moreover, soil organic matter dynamics is slow, especially when the more humified component of soil organic matter is taken into account (Martin *et al.* 1990; Schlesinger 1990). Consequently, short-term experiments may not be very informative for soil organic matter dynamics in natural ecosystems more or less at equilibrium, or agro-ecosystems where the same cultures are repeatedly applied for many years.

Previous models (de Mazancourt, Loreau & Abbadie 1998, 1999) and empirical studies (Bianchi, Jones & Shachak 1989; McNaughton *et al.* 1997) have

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shown that herbivores may increase primary production via their effects on nutrient cycling. The long-term increase in production depends on an increase in nutrient recycling efficiency due to herbivore activities rather than an increase in the turnover rate of plant biomass, which would only result in a short-term increase in plant production. More precisely, it was shown that herbivores increase nutrient recycling efficiency if they increase nutrient retention inside ecosystems and diminish nutrient losses (de Mazancourt *et al.* 1998, 1999), for example, through leaching. These results are consistent with the rationale above about the long-term effect of soil decomposers on plant growth that would not depend on a short-term increase in mineralization. It can thus be hypothesized that herbivores and soil decomposers increase plant production under the same type of condition. A compartment model (see Fig. 1) was built to test this general hypothesis.

Herbivores influence nutrient recycling efficiency through their trophic activities (de Mazancourt *et al.* 1998, 1999), i.e. through the assimilation of nutrients. However, earthworms and other soil ecosystem engineers (Jones, Lawton & Shachack 1997; Lavelle, Bignell & Lepage 1997) may affect soil organic matter mineralization both through trophic and nontrophic activities. First, they assimilate a part of the organic matter of the soil they ingest and, on their death, their own tissue decomposes quickly and releases mineral nutrients (Whalen *et al.* 1999). Second, ecosystem engineers can increase mineralization rates by modifying soil physical and chemical properties. They also modify the fraction of organic matter they ingest but cannot assimilate. In the case of earthworms: (1)

anecic and epigeic earthworms feed on litter and incorporate unassimilated vegetation fragments into soil mineral layers (especially anecic species) (Brown, Barois & Lavelle 2000); (2) soil organic matter rejected in earthworm casts is broken up in the digestion process (Martin 1991); (3) earthworms probably stimulate soil bacteria populations by increasing the availability of soil resources to them (Martin 1991; Brown *et al.* 2000). These modifications to soil organic matter can in turn facilitate assimilation by other groups of soil decomposers (Parmelee, Bohlen & Blair 1998). While the expression 'ecosystem engineer' is still controversial to some (Wilby 2002; Wright & Jones 2006), we find it useful to denote all nontrophic activities of earthworms and other soil decomposers, which are often not taken into account in models.

Ecosystem engineering activities may be incidental but some ecosystem engineers have probably evolved such activities to increase the suitability of their environment (Jones, Lawton & Shachack 1994; Odling-Smee, Laland & Feldman 2003). This is particularly clear in the well known cases of beavers and intraspecific facilitation in plants (Callaway & Walker 1997). Here, in contrast, when earthworms mineralize soil organic matter through their nontrophic effects, the corresponding mineralized nutrients are no longer available for them because they cannot assimilate mineral nutrients. Consequently, such ecosystem engineering activities lead to losses of resources for soil decomposers and should thus be detrimental for them. Is that really the case? To answer this question, both the trophic and nontrophic (through ecosystem engineering activities) effects of earthworms on nutrient cycling were included in the same compartment
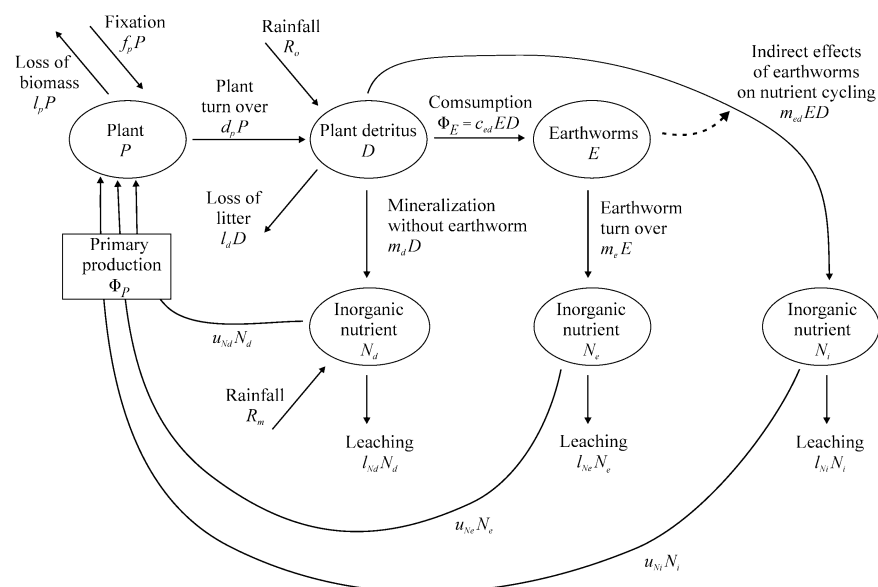

Fig. 1. Model of the cycling of a limiting nutrient. Recycling of plant detritus (soil organic matter) follows three pathways: without earthworms (subscript *d*), due to earthworm trophic effects (subscript *e*) and due to earthworm nontrophic effects (i.e. engineering effects, subscript *i*). The doted arrow denotes earthworm nontrophic effects on mineralization, while plain arrows denote fluxes. The label of each arrow indicates the formula used for the corresponding flux. Parameter definitions can be found in the text and in Table 1.

model. This permitted us to address four questions: (1) Can decomposers increase primary production through their effect on nutrient cycling? (2) Can nontrophic effects increase plant production as well as trophic effects? (3) Does this occur under the same type of conditions as trophic effects? and (4) Do nontrophic effects of decomposers on mineralization always decrease their own biomass?

Methods

Our model is very general and describes the dynamics of a limiting nutrient in a simple ecosystem. Although the model is valid for any type of soil decomposer, the decomposer is named 'earthworm' throughout the paper for heuristic simplicity. Earthworms are also perhaps one of best examples of soil ecosystem engineers and are also quantitatively very important: it is estimated that there are more than 5000 species of earthworms in the world; they are present in most terrestrial ecosystems; they often have very high biomasses (up to 2 mg ha^{-1} in some temperate pastures); and they may ingest the whole top soil layer in 2 or 3 years (Lavelle & Spain 2001).

Parameter and variable definitions are given in Table 1. The model is composed of six compartments (see Fig. 1): plants (P), plant detritus (D), earthworms (E), and three pools of inorganic nutrients resulting from the mineralization of plant detritus independently of earthworms (N_d), from the mineralization of earthworm tissues (N_e) or from earthworm nontrophic effects (N_i). These three compartments are separately taken into account to allow different leaching (l_{Nd}, l_{Ne} and l_{Ni}) and uptake rates by plants (u_{Nd}, u_{Ne} and u_{Ni}) in the three recycling pathways denoted, respectively, by the subscripts d, e and i: without earthworm, earthworm trophic effects and earthworm nontrophic

effects. These different leaching and uptake rates allow for differences in recycling efficiency between the pathways (see below). Denitrification is not explicit in the model but can be considered as incorporated into the leaching rates because it also results into an output of nutrient (nitrogen) for ecosystems. Earthworm nontrophic effects encompass all earthworm activities as ecosystem engineers that may lead to the mineralization of nutrients they do not assimilate. This involves changes in soil structure, consequent changes in soil hydrodynamics, stimulation of soil microflora, fragmentation of organic matter and incorporation of litter into the soil.

Plants build up their biomass by absorbing nutrients coming from the three recycling pathways. In turn, plant biomass mortality and herbivory lead to a flux from the plant compartment to the plant detritus compartment. For simplicity, we consider that this compartment contains all soil organic matter, i.e. litter, dead roots and humus. This organic matter is mineralized via the three pathways mentioned above. In addition to leaching leading to losses of nutrients from the mineral compartments, two other sources of nutrient loss are considered for the ecosystem: loss of plant detritus – due to erosion, movements of litter along toposequences and fires – and loss of plant biomass – mainly due to fires. There are four sources of nutrients inputs to the ecosystem: atmospheric depositions of inorganic and organic nutrients brought by winds and rains, fixation of atmospheric nitrogen by rhizospheric bacteria (valid for nitrogen only), and weathering of the parent material that generates accessible nutrients (other than nitrogen). For simplicity, immigration and emigration of earthworms was excluded. Similarly, only the input of inorganic nutrients into the compartment resulting from mineralization independent of earthworms was considered. As the 'detritus' compartment contains

Table 1. Parameters and variables of the model. Parameters denoting fluxes within the ecosystem are given before those that denote outputs and inputs

Parameter or variable	Dimension	Definition
P	kg nutrient ha^{-1}	Nutrient content of the plant biomass
D	kg nutrient ha^{-1}	Nutrient content of soil organic matter
E	kg nutrient ha^{-1}	Nutrient content of earthworm biomass
N_d	kg nutrient ha^{-1}	Mineral nutrients resulting from mineralization independently of earthworms
N_e	kg nutrient ha^{-1}	Mineral nutrients resulting from earthworm trophic effect on mineralization
N_i	kg nutrient ha^{-1}	Mineral nutrients resulting from earthworm nontrophic effect on mineralization
d_p	year^{-1}	Plan death rate
c_{ed}	kg ha^{-1} year^{-1}	Consumption rate of plant detritus by earthworm
m_{ed}	kg ha^{-1} year^{-1}	Rate of mineralization of plant detritus through earthworm nontrophic effects
m_d	year^{-1}	Mineralization rate of plant detritus (without earthworms)
m_e	year^{-1}	Mineralization rate of earthworm dead tissue
u_{Ni}, u_{Nd}, u_{Ne}	year^{-1}	Uptake rates of mineral nutrients by plants, there is a different rate for each mineral nutrient compartment
l_{Ni}, l_{Nd}, l_{Ne}	year^{-1}	Leaching rates of the three mineral nutrient compartments
l_p, l_d	year^{-1}	Rates of nutrient loss from the plant and detritus compartments
R_m, R_o	kg ha^{-1} year^{-1}	Input of mineral and organic nutrients into the system
f_p	year^{-1}	Rates of nutrient input to the system through atmospheric fixation (only for nitrogen)

both the litter and the humified fraction of soil organic matter the model holds for any ecological type of earthworm (anecic and epigeic earthworms feeding on litter, endogeic earthworm feeding on humus).

To keep the model as simple as possible, fluxes are described by simple linear functions (see Fig. 1). Most of them are donor-controlled functions. Both the consumption of organic matter and the nontrophic effects of earthworms on mineralization are considered to be proportional to both the earthworm and soil organic matter compartments (parameters c_{ed} and m_{ed}). This makes sense as these two fluxes are likely to be proportional to the amount of soil ingested, and thus to the amount of casts rejected and because earthworm biomass is known to control the production of casts and thus soil structure. Nutrient uptake by plants is considered to depend on the availability of nutrients in a linear fashion. This simplification was necessary for the model to be analytically tractable.

Creation of plant detritus depends on a fixed rate of plant mortality (d_p). Mineralization of plant detritus and earthworm tissues depend linearly on these compartments (m_d, m_e). m_e is in fact the mortality rate of earthworm biomass. As mineralization of dead earthworms is very rapid compared with other modelled processes, m_e can be considered as a mineralization rate (the compartment of earthworm dead tissues is not explicitly taken into account). Atmospheric deposits of organic and mineral nutrients are assumed to be constant (R_o R_m). R_m also takes into account the weathering of the parent material. Fixation of atmospheric nitrogen, losses of nutrients through fires and exportation of organic matter from the plant and detritus compartments are assumed to depend linearly on plant and detritus compartments (f_p, l_p, l_d). Nitrogen fixation is assumed to depend entirely on symbiotic fixation and is thus considered to be proportional to the size of the plant compartment, which is composed of a fixed proportion of Leguminosae for an ecosystem at equilibrium.

The model equations read as follows:

$$\frac{dP}{dt} = u_{Nd}N_d + u_{Ne}N_e + u_{Ni}N_i + (f_p - d_P - l_p)P$$

$$\frac{dD}{dt} = d_p P + R_o - (c_{ed} + m_{ed})ED - (l_d + m_d)D$$

$$\frac{dE}{dt} = c_{ed}ED - m_e E$$

$$\frac{dN_d}{dt} = R_m + m_d D - l_{Nd}N_d - u_{Nd}N_d$$

$$\frac{dN_e}{dt} = m_e E - l_{Ne}N_e - u_{Ne}N_e$$

$$\frac{dN_i}{dt} = m_{ed}ED - l_{Ni}N_i - u_{Ni}N_i.$$

To analyse the long-term effect of earthworms on ecosystem properties, the algebraic expression of the equilibrium stocks of the compartments were calculated as a function of the model parameters. To display the results concisely and to make them more readily comprehensible they are expressed as a function of four expressions that can be interpreted as recycling efficiencies of the different recycling loops: main recycling pathway without earthworms (α_d), earthworm pathway (α_e), nontrophic effect pathway (α_i), both earthworm pathways taken together (α_{e+i}). While we directly give the expressions of these efficiencies, clearly they emerged from algebraic calculations (cf. Table 2) and were then interpreted as recycling efficiencies.

$$\alpha_d = \frac{d_p}{d_p + l_p - f_p}\frac{m_d}{m_d + l_d}\frac{u_{Nd}}{u_{Nd} + l_{Nd}} \qquad \text{eqn 1}$$

Each ratio composing α_d is the fraction of nutrients transmitted between compartments of the main recycling loop without being lost for the ecosystem. Thus, the product of the three ratios is the fraction of nutrients recycled inside the ecosystem. α_e and α_i are defined similarly:

$$\alpha_e = \frac{d_p}{d_p + l_p - f_p}\frac{u_{Ne}}{u_{Ne} + l_{Ne}} \qquad \text{eqn 2}$$

$$\alpha_i = \frac{d_p}{d_p + l_p - f_p}\frac{u_{Ni}}{u_{Ni} + l_{Ni}} \qquad \text{eqn 3}$$

As α_d and α_e, α_i can be interpreted as recycling efficiencies, here from the inorganic compartment to the

Table 2. Equilibrium values

System with earthworms	System without earthworms
$E^* = -\dfrac{(m_d + l_d)\left[D^*(1 - \alpha_d) - \dfrac{R_o}{m_d + l_d} - \dfrac{R_m}{m_d}\alpha_d\right]}{D^*(c_{ed} + m_{ed})(1 - \alpha_{e+i})}$	
$D^* = \dfrac{m_e}{c_{ed}}$	$D^*_{E=0} = \dfrac{\dfrac{R_o}{m_d + l_d} + \dfrac{R_m}{m_d}\alpha_d}{(1 - \alpha_d)}$
$P^* = \dfrac{[(c_{ed} + m_{ed})E^* + (l_d + m_d)]D^* - R_o}{d_p}$	$P^*_{E=0} = \dfrac{(u_{Nd} + l_d)D^*_{E=0} - R_o}{d_p}$
$N^*_e = \dfrac{m_e E^*}{l_{Ne} + u_{Ne}}$	
$N^*_d = \dfrac{R_m + m_d D^*}{l_{Nd} + u_{Nd}}$	$N^*_{d,E=0} = \dfrac{R_m + u_{Nd}D^*_{E=0}}{l_{Nd} + u_{Nd}}$
$N^*_i = \dfrac{m_{ed}E^*D^*}{l_{Ni} + u_{Ni}}$	

detritus compartment, for the two (trophic and non-trophic) earthworm pathways.

$$\alpha_{e+i} = \alpha_e \frac{c_{ed}}{c_{ed} + m_{ed}} + \alpha_i \frac{m_{ed}}{c_{ed} + m_{ed}} \qquad \text{eqn 4}$$

α_{e+i} is the mean of α_e and α_i, weighted by the fluxes of nutrients going through the earthworm trophic and nontrophic pathways. Although α_{e+i} depends on the rates of mineralization due to trophic and nontrophic effects (c_{ed} and m_{ed}), it reflects the recycling efficiency of the two pathways controlled by earthworms.

Results

FEASIBILITY AND BIOLOGICAL MEANING OF THE EQUILIBRIUM

We sought equilibrium properties of the model, requiring determination of cases for which an equilibrium exists. It was shown that: (1) When $f_p - l_p < 0$, the plant compartment leads to a net loss of nutrients, all compartments are bounded and an equilibrium can be attained. (2) When $d_p < f_p - l_p$, the plant compartment can never reach equilibrium because more nitrogen is fixed by symbiotic bacteria than plants can lose. (3) For intermediate values, $0 < f_p - l_p < d_p$, the plant compartment has a net gain of nutrients but the gain is immediately recycled. In this case, equilibrium might be reached depending on the outputs and inputs of nutrients to the detritus and mineral nutrient compartments.

We now focus on situations where equilibrium can be attained. To determine the effect of the different recycling loops, the system must be studied with or without earthworms, and with or without earthworm nontrophic effects. Setting all time derivatives to 0 in the general system, i.e. with earthworms and earthworm nontrophic effect (see above), equilibrium stocks of the compartments (denoted by *) can be expressed as a function of the model parameters (see Table 2). The solutions to the system with earthworms but without their nontrophic effects (hereafter noted with the subscript $m_{ed} = 0$) can be obtained taking the limit of the solution of the general system when m_{ed} goes to 0. In the absence of earthworms, alternative solutions (noted with the subscript $E = 0$) must be calculated (see Table 2). These solutions cannot be obtained by taking the limit of the solutions of the general system when c_{ed} goes to 0.

Using the Routh–Hurwitz criterion (May 1974), the equilibrium found for the system without earthworms was shown to be stable. For the system with earthworms the necessary condition for the stability of the equilibrium is met (all coefficients of the characteristic equation of the Jacobian matrix are positive). Owing to the high number of compartments in the model it was not possible to show algebraically that the sufficient condition for stability (all coefficients of the

first column of the Routh array are positive) is always met. However, numerical simulations made with randomized parameters showed that the equilibrium is always stable.

Finally, at equilibrium, all compartments of the model must be positive in order to be biologically meaningful. It is also biologically sensible to assume that the ecosystem can function without earthworms and thus that $D^*_{E=0}$ is strictly positive. We get (see Table 2):

$$D^*_{E=0} > 0 \Leftrightarrow \alpha_d < 1 \qquad \text{eqn 5}$$

This condition means that the fraction of nutrients coming from the plant compartment and recycled back to this compartment must be smaller than 1. Otherwise, if the considered nutrient is nitrogen and the fixation of atmospheric nitrogen (f_p) is high enough and losses (l_d, l_{Nd}) small enough, the net nitrogen balance is positive whatever the size of the plant compartment. Then, together with the depositions of nitrogen independent of plant biomass the (R_m, R_o) ecosystem accumulates nitrogen and cannot reach equilibrium.

Similarly, we can find the condition for $E^* > 0$ using the expressions of $D^*_{E=0}$, D^* and E^* (cf. Table 2):

$$E^* > 0 \Leftrightarrow (D^*_{E=0} < D^* \text{ and } 1 < \alpha_{e+i}) \text{ or }$$
$$(D^* < D^*_{E=0} \text{ and } \alpha_{e+i} < 1) \qquad \text{eqn 6}$$

with

$$D^*_{E=0} < D^* \Leftrightarrow \frac{R_m}{m_d}\alpha_d + \frac{R_o}{m_d + l_d} < [1 - \alpha_d]D^* \qquad \text{eqn 7}$$

Earthworms can remain in the ecosystem in two circumstances depending on their effect on the detritus compartment (sign of $D^*_{E=0} - D^*$) and the efficiency of the two recycling loops that depend on them (α_{e+1}). At equilibrium, earthworms increase the quantity of detritus ($D^*_{E=0} < D^*$) if and only if the net flux of nutrients to the detritus (in the main recycling loop and due to nutrient inputs to the ecosystem independently of the ecosystem state, R_o and R_m (left-hand side of the inequality 7) does not compensate for the losses (right-hand side of the inequality 7) from the detritus compartment when earthworms are present (D^*). In this case, fluxes through earthworm pathways can only increase the quantity of nutrients remaining inside the ecosystem. Earthworms remain in the ecosystem in two situations (eqn 6). First when they lead to a net loss of nutrients from the detritus compartment through the main recycling loop and when the two earthworm recycling loops lead to a net gain for the ecosystem. Second the reverse of this: a net gain of nutrient through the main recycling loop and a net loss through earthworm recycling loops. This is due to the fact that recycling loops can compensate for each other and that decreasing the detritus compartment

decreases the flux of nutrient in both earthworm pathways. Taken together, in both situations, earthworms are maintained in the ecosystem when they conserve nutrients in the ecosystem.

The first case ($1 < \alpha_{e+1}$) is only possible, due to nutrient fixation by plants (f_p) provided the input of nutrients into the ecosystem compensates for losses: l_{Ne} and l_{Ni} must be small enough and f_p must be higher than l_p (cf. eqns 2–4). This is only possible if nitrogen is considered to be the limiting nutrient and if the biomass of leguminous plants is sufficiently high in the ecosystem. This also holds for the other conditions we found (see below eqns 8 and 9).

EFFECTS OF EARTHWORM ON THE ECOSYSTEM

In terms of the limiting nutrient, primary production (Φ_p) and the production of earthworm biomass (Φ_E) are defined as the sum of all nutrient fluxes entering the earthworm and plant compartments. Supposing $E^*_{m_{ed}=0} > 0$ and comparing the earthworm compartment with and without nontrophic effects, we obtain the following condition:

$$\Phi_E^* > \Phi_{E,m_{ed}=0}^* \Leftrightarrow E^* > E_{m_{ed}=0}^* \Leftrightarrow$$

$$(D_{E=0}^* < D^* \text{ and } \alpha_i < 1 \text{ and } 1 < \alpha_e) \text{ or} \qquad \text{eqn 8}$$

$$(D^* < D_{E=0}^* \text{ and } 1 < \alpha_i \text{ and } \alpha_e < 1)$$

This condition can be interpreted as in eqn 6: nontrophic effects increase earthworm biomass (and the production of earthworm biomass) if they help maintaining nutrients in the ecosystem. This occurs in two situations: when nutrient recycling through the nontrophic earthworm pathway leads to a net decrease in the fraction of nutrient recycled within the ecosystem ($\alpha_i < 1$), and when the earthworm trophic pathway leads to an increase in this fraction ($1 < \alpha_e$); or the reverse. In the first situation, the main recycling loop, without earthworm, results in a net loss of nutrients (see eqn 7) but earthworms increase the detritus compartment (as in eqn 6). Hence, although the nontrophic earthworm pathway is less efficient than the trophic earthworm pathway, the higher the nontrophic earthworm effects the less nutrient is recycled through the inefficient main pathway (without earthworm). In the second situation, the nontrophic earthworm pathway leads to a net increase in the nutrient remaining in the system and nutrients recycled through this pathway are not recycled through the less efficient earthworm trophic pathway.

Comparing primary production with and without nontrophic effects leads to

$$\Phi_P^* > \Phi_{P,m_{ed}=0}^* \Leftrightarrow P^* > P_{m_{ed}=0}^* \Leftrightarrow$$

$$(D_{E=0}^* < D^* \text{ and } \alpha_i < \alpha_e \text{ and } 1 < \alpha_e) \text{ or} \qquad \text{eqn 9}$$

$$(D^* < D_{E=0}^* \text{ and } \alpha_e < \alpha_i \text{ and } \alpha_e < 1)$$

This condition can be again interpreted in terms of nutrient conservation as in eqns 7 and 8. It can be noted that when earthworm nontrophic effects are favourable for the production of earthworm biomass they are also favourable for primary production:

$$\Phi_E^* > \Phi_{E,m_{ed}=0}^* \Rightarrow \Phi_P^* > \Phi_{P,m_{ed}=0}^* \qquad \text{eqn 10}$$

The difference between conditions 8 and 9 is that the effect of the nontrophic pathway on primary production depends on the relative efficiency of the earthworm trophic and nontrophic pathways ($\alpha_i < \alpha_e$ or $\alpha_i > \alpha_e$), while the effect of the nontrophic pathway on the earthworm compartment depends on the net effect of the nontrophic pathway on nutrient conservation ($\alpha_i < 1$ or $\alpha_i > 1$). This is due to the fact that in our model all nutrients recycled in the ecosystem go through the plant compartment. As a consequence, any improvement in the conservation of nutrients inside the ecosystem benefits the plants, while this is not the case for earthworms.

Assuming the system can function without earthworms ($D_{E=0}^* > 0$, eqn 5) we get the condition for which earthworms increase primary production and plant biomass in terms of a limiting nutrient:

$$\Phi_P^* > \Phi_{P,E=0}^* \Leftrightarrow P^* > P_{E=0}^* \Leftrightarrow \alpha_d < \alpha_{e+i} \qquad \text{eqn 11}$$

α_{e+i} and α_d are the respective recycling efficiencies of the two pathways controlled by earthworms and the main pathway (without earthworms). Thus, earthworms increase primary production in terms of a limiting nutrient when the two recycling pathways they control (trophic and nontrophic effects) conserve nutrients inside the ecosystem more efficiently than the main recycling pathway.

Discussion

Our results indicate that: (1) decomposers may increase primary production through their effect on nutrient recycling; (2) both trophic and nontrophic effects of decomposers may increase primary production; (3) trophic and nontrophic effects increase primary production when they increase the conservation of nutrients in the ecosystem. This tends to benefit all compartments; and (4) thus, mineralization of organic matter via the engineering activities of decomposers (nontrophic effects) may also benefit decomposers if it is associated with an increase in nutrient conservation in the ecosystem. The key point is that the increase in plant and earthworm production depends on the efficiency of the different pathways of nutrient recycling, i.e. on the capacity of organisms to recycle the limiting nutrient inside their ecosystem. The long-term, i.e. equilibrium, effect of earthworms on other ecosystem compartments depends on their capacity to limit the losses of nutrients they recycle. This is similar to the conclusion reached regarding the influence of herbivory

on primary production (de Mazancourt *et al.* 1998, 1999), although we also showed that ecosystem engineering activities can influence nutrient recycling efficiency (and not only trophic relations) and can subsequently modify primary production.

Our results also show that the effect of decomposers on primary production depends on inputs and outputs of nutrient they do not control (f_p, l_p, R_o, R_m). Hence, although our work does not focus on nitrogen fixation, the nature of the limiting nutrient (nitrogen vs. other nutrients which cannot be fixed) and the amount of nitrogen fixation (if nitrogen is limiting) clearly determines the possibility of equilibrium (see above 'Feasibility and biological meaning of the equilibrium') and the conditions for an increase in primary production by earthworms (cf. eqns 6, 8 and 9).

The compartment model presented here is very general so that our conclusions should apply to virtually any ecosystem and soil decomposer. Nevertheless, some of our hypotheses and their limitations deserve further discussion. There are four main points. First, there is no direct empirical evidence for the existence of three pools of mineral nutrients. This is the most critical feature of our model because, without these three pools, recycling efficiencies would be the same in the three recycling loops and earthworms could not modify the overall quantity of nutrient in the ecosystem. A priori, these nutrients are chemically identical (although nitrate and ammonium could be represented in different proportions within the three pools). However, mineral nutrients resulting from the different pathways are likely to be distributed differently in the soil layers. This should result in differences in leaching and uptake rates. In particular, inorganic nutrients resulting from earthworm nontrophic effects are released mostly in earthworm casts and thus have specific dynamics due to a partial physical protection linked to cast structure (Blanchart, Bruand & Lavelle 1993; Blanchart *et al.* 1999). It has also been shown that mineral nutrients resulting from the decomposition of earthworm tissue and plant detritus are taken up differently by plants (Whalen *et al.* 1999; Hodge *et al.* 2000). More generally, plants are likely to have evolved root foraging strategies to efficiently exploit sources of nutrients localized in space and time (Sutherland 1990). This could lead to higher rates of nutrient uptake from earthworm casts (Zaller & Arnone 1999) that have often a higher mineral nutrient content than the bulk soil (Lavelle *et al.* 1992; Zaller & Arnone 1999). Consequently, the efficiency of the recycling loops controlled by earthworms may also depend on plant behaviour (Silvertown & Gordon 1989). Another mechanism, not taken into account by the model, is likely to influence the recycling efficiency of earthworm nontrophic effects. Although earthworms increase the overall rate of mineralization, it has been shown that organic matter trapped in fresh earthworm casts has, after a brief pulse of mineralization, a slower rate of mineralization than the organic matter

of the bulk soil (Martin 1991) and is not readily leached.

The three pools of mineral nutrients do not necessarily have to physically exist. Rather, they allowed us to explore the consequences of different leaching and uptake rates in the different recycling pathways and such differences are likely to arise because of the temporal and spatial schedule of earthworm death, cast production, root dynamics and mineralization without earthworms. The decisive factor would then be the level of spatial and temporal synchrony between these processes. Our model does not explicitly examine the mechanisms determining this level of synchrony. However, the uptake and leaching parameters are average parameters that have to be assessed over a relevant spatial and temporal scale. Thus, these parameters take into account the overall level of synchrony at these scales: if there is a high level of synchrony, uptake parameters should be high and leaching parameters should be low.

Second, very simple functions were chosen for nutrient fluxes to keep the model analytically tractable. The donor-controlled function for the absorption of mineral nutrients by plants is not realistic, especially when the biomass of plants is close to zero. However, this may not be an issue at equilibrium for a fully developed vegetation where the root system can be assumed to adjust quickly to maintain a constant rate of nutrient uptake. The dependence of earthworm consumption of organic matter and of their nontrophic mineralization effects on both earthworm and organic matter compartments seems realistic but empirical data are needed to support this hypothesis. Another key assumption is that there is only one limiting nutrient. Although nitrogen is often a limiting nutrient, phosphorous can be limiting in tropical ecosystems, and it might be more realistic to take into account stoichiometric constraints and the relative availability of more than one nutrient (Treseder & Vitousek 2001). In the same vein, earthworms (and other soil decomposers) depend on the quality of soil organic matter and particularly on its nitrogen content. However, a recent study showed that they also depend in some cases on the availability of carbon (Tiunov & Scheu 2004). It would be informative to take into account the possibility of colimitation by carbon and nitrogen, considering the C : N ratio of plant, plant detritus and earthworm compartments as other decomposition models do (Daufresne & Loreau 2001).

Third, the model considers that the long-term properties of an ecosystem are its properties at equilibrium. This is not fully realistic as compartments of all ecosystems are known to be subject to temporal variations. Much of this variation may be due to short-term fluctuations and interactions within compartments that are not taken into account in our model. The compartments of real ecosystems would then vary around some theoretical equilibrium values that would have the same properties as the equilibrium of our differential equations. Many ecosystems are also known to be far

from equilibrium, because they have been disturbed (e.g. fire or land-use changes) too recently to have reached a new equilibrium, or because some nutrients' fluxes change gradually (e.g. long-term increase in the atmospheric deposition of nitrogen). Numerical simulation would be needed to test the robustness of our predictions during such transient phases. This would require the assessment of the model parameters (see below) or at least fixing realistic intervals for them. Such numerical simulations would also allow the assessment of the robustness of our predictions to short-term variability and to test the effect of more realistic functions for nutrient fluxes.

Fourth, our model does not explicitly expose all mechanisms through which nutrient cycling and earthworms interact. In particular, it does not take into account excretion and mucus production. Urea is excreted by earthworms on their body surface and ammonia is excreted through the gut with the casts (Whalen, Parmelee & Subler 2000). Mucus produced by the body surface is incorporated into burrow walls while mucus produced by the intestine is incorporated in the casts. This mucus also contains nitrogen (Whalen *et al.* 2000). Our model does not explicitly account for these fluxes because they originate from earthworm biomass and are delivered in earthworm biogenic structures and not in the decomposing earthworm bodies. These fluxes can be considered as being lumped within the trophic recycling loop (m_e), which only implies that the corresponding leaching and uptake rates (l_{Ne}, u_{Ne}) are averaged along the excretion and earthworm decomposition pathways. Alternatively, taking these fluxes into account only requires adding another recycling loop arising from earthworm biomass. In both cases, the effects of these loops on primary production should depend on the way they increase or decrease the balance of nutrient input/output for the ecosystem. In the same vein, microbial populations are not explicit in the models although they play a critical role in the different recycling pathways. They are probably involved in the assimilation of organic matter in earthworm guts (Barois 1992). Earthworm engineering activities influence microbial populations at different temporal and spatial scales (Chaoui, Zibilske & Ohno 2003; Mora *et al.* 2005) and these populations can sequester nutrients mineralized through earthworm trophic and nontrophic activities. All these processes modify the rapidity and efficiency of nutrient recycling and we consider them to be summarized by the model parameters. Answering specific questions about the influence of microbe–earthworm interactions on plant growth would require taking these processes explicitly into account.

To determine the long-term effect of earthworms on nutrient cycling and primary production, a solution is to compare plots without earthworms and plots that have been invaded by earthworms as in North American forests (Bohlen *et al.* 2004a). Studies have shown that earthworms increased leaching of nitrates (Bohlen

et al. 2004b), but in this case the soils were unlikely to be in equilibrium with earthworm populations that were currently invading the studied forests. A second solution would be to implement long-term field experiments excluding earthworms from some plots (e.g. Bohlen *et al.* 1997) and monitoring all inputs and outputs of nitrates. While this would not allow assessment of our model parameters it would permit the testing of its main prediction: earthworms increase primary production in the long term if and only if they increase the efficiency of nutrient cycling.

To our knowledge, no experiments have lasted more than 3 years (which is probably not enough for soil organic matter to reach a new equilibrium), nor have they monitored all inputs and outputs of nutrients. Given the scarcity of appropriate long-term experiments, it would be interesting to use our model to predict long-term effects of earthworms on plant production using short-term measurements of nutrient fluxes. This implies measuring the uptake and leaching rates of mineral nutrients resulting from the decomposition of plant litter without earthworms (u_{Nd}, l_{Nd}), the decomposition of earthworm dead tissues (u_{Ne}, l_{Ne}) and earthworm nontrophic effects (u_{Ni}, l_{Ni}, in this last case nutrients should be mostly inside earthworm casts). As discussed above, earthworms could decrease leaching rates through the physical protection of nutrients in their casts. They may also increase the absorption rate by plants of the nutrients they help mineralize because they increase the short-term mineralization in localized soil patches (dead earthworms and earthworm casts), and because plants have evolved foraging strategies to exploit such resources. However, earthworms have also been demonstrated to increase leaching through their galleries (Domínguez, Bohlen & Parmelee 2004) and to increase denitrification (Burtelow, Bohlen & Groffman 1998; Yin *et al.* 2003), which also leads to nutrient losses for ecosystems. It is thus not possible to predict the net result of these potential positive and negative effects on the nutrient input/output balance of ecosystems without precise measurements. Such measurements are possible using ^{15}N-labelled nitrogen (Whalen *et al.* 1999; Whalen & Janzen 2002). Here, it would be necessary to mark, in different experimental units and in the presence of a plant but without living earthworms, earthworm dead bodies, soil organic matter and the organic matter contained in earthworm casts. The quantities of labelled nitrogen in the leachates and in the plants would then allow assessment of the three uptake and leaching rates in our model, thereby comparing the recycling efficiency of the three recycling pathways. Measuring these efficiencies would also help assess the relative importance of the different mechanisms invoked to explain earthworm positive effect on plant growth, which has seldom been accomplished (see Blouin's microcosm experiment showing that nitrogen mineralization is not involved in the positive impact of an earthworm species on rice growth; Blouin, Barot & Lavelle 2006).

Different conclusions can be drawn from the different possible outcomes of such measurements. If they show a positive effect of earthworms on the conservation of nutrients inside an ecosystem then our model will permit prediction of the consequent gain in primary production. This predicted gain can be compared with the observed gain to assess the relative importance of nutrient recycling among mechanisms through which earthworms influence plant growth. However, if such measurements show that in most cases earthworms do not improve the efficiency of nutrient cycling, two explanations remain plausible. First, the pervasive positive effect of earthworms on plant growth (respectively 79% and 75% of microcosm experiments involving temperate and tropical earthworms; Brown *et al.* 1999; Scheu 2003) could be an artefact of short-term microcosm experiments (Carpenter 1996). Alternatively, this effect could mainly be due to other mechanisms such as the production of molecules analogous to phytohormones (Tomati, Grappelli & Galli 1998; Pasqualeto Canellas *et al.* 2002). These molecules are released in soils in the presence of earthworms (possibly through the stimulation of certain bacteria), and they do increase plant growth. However, the quantitative impact of such processes has yet to be determined in the field.

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