

# Microbial diversity, producer–decomposer interactions and ecosystem processes: a theoretical model

Michel Loreau

*Laboratoire d'Ecologie, UMR 7625, Ecole Normale Supérieure, 46 Rue d'Ulm, F-75230 Paris Cedex 05, France (loreau@ens.fr)*

Interactions between the diversity of primary producers and that of decomposers—the two key functional groups that form the basis of all ecosystems—might have major consequences on the functioning of depauperate ecosystems. I present a simple ecosystem model in which primary producers (plants) and decomposers (microbes) are linked through material cycling. The model considers a diversity of plant organic compounds and a diversity of microbial species. Nutrient recycling efficiency from organic compounds to decomposers is then the key parameter that controls ecosystem processes (primary productivity, secondary productivity, producer biomass and decomposer biomass). The model predicts that microbial diversity has a positive effect on nutrient recycling efficiency and ecosystem processes through either greater intensity of microbial exploitation of organic compounds or functional niche complementarity, much like in plants. Microbial niche breadth and overlap should not affect ecosystem processes unless they increase the number of organic compounds that are decomposed. In contrast, the model predicts that plant organic compound diversity can only have a negative effect or, at best, no effect on ecosystem processes, at least in a constant environment. This creates a tension between the effects of plant diversity and microbial diversity on ecosystem functioning, which may explain some recent experimental results.

**Keywords:** microbial diversity; plant diversity; nutrient cycling; ecosystem functioning

## 1. INTRODUCTION

The impact of biodiversity loss on the functioning of ecosystems and on their ability to provide ecological services to humans has become a central issue in ecology today. A number of major experiments have recently shown that declining plant diversity may impair such ecosystem properties as plant biomass, primary production and nutrient retention (Tilman *et al.* 1996, 1997a; Hooper & Vitousek 1997; Hector *et al.* 1999). However, few experiments have directly tested the consequences of changing the diversity of ecosystem components other than plants (Naeem *et al.* 1994; Mikola & Setälä 1998; Van der Heijden *et al.* 1998).

Recently, Naeem *et al.* (2000) simultaneously manipulated the diversity of primary producers (algae) and decomposers (bacteria) in aquatic microcosms and found complex interactive effects of algal and bacterial diversity on algal and bacterial biomass production. Both algal and bacterial diversity had significant effects on the number of carbon sources used by bacteria, suggesting nutrient cycling associated with microbial exploitation of organic carbon sources as the link between bacterial diversity and algal production. However, the interpretation of these results is still unclear. Several explanations are possible (Morin 2000) and theory is sorely lacking. Because producers and decomposers are two key functional groups that form the basis of all ecosystems (Harte & Kinzig 1993; Loreau 1998a), interactions between producer diversity and decomposer diversity might have major consequences on the functioning of depauperate ecosystems. Therefore, a theoretical understanding of these interactions is important.

In this paper I present a basic ecosystem model in which primary producers (plants) and decomposers (microbes) are linked through material cycling. The model extends a previous model of producer–decomposer dependency (Loreau 1998a) and considers a diversity of plant organic compounds and a diversity of microbial species. Primary production is assumed to be limited by a nutrient such as nitrogen or phosphorus and decomposers are assumed to be limited by the carbon sources provided by plants. Nutrient immobilization by decomposers and competition for inorganic nutrients between plants and decomposers are known to occur, but at equilibrium the two functional groups must be limited by different limiting factors in order to allow their coexistence and ecosystem persistence (Daufresne & Loreau 2001). Therefore, since I am concerned with the long-term equilibrium behaviour of the model ecosystem, I ignore this complication, which would require a stoichiometrically explicit model. Producer diversity affects decomposers through the diversity of the organic compounds they produce. Therefore, I do not represent plant diversity explicitly, again to avoid unnecessary complications.

## 2. THE MODEL

The model describes the cycle of a nutrient that limits producer growth (figure 1). Accordingly, all compartment sizes and fluxes are measured by nutrient stocks and fluxes. The nutrient cycles between an inorganic pool (of size  $N$ ), a primary producer compartment ( $P$ ) that consumes the nutrient in inorganic form, a set of  $n$  organic compounds produced by plants ( $C_j$ , where  $j = 1, \dots, n$ ) and a set of  $m$  decomposer species ( $D_i$ , where

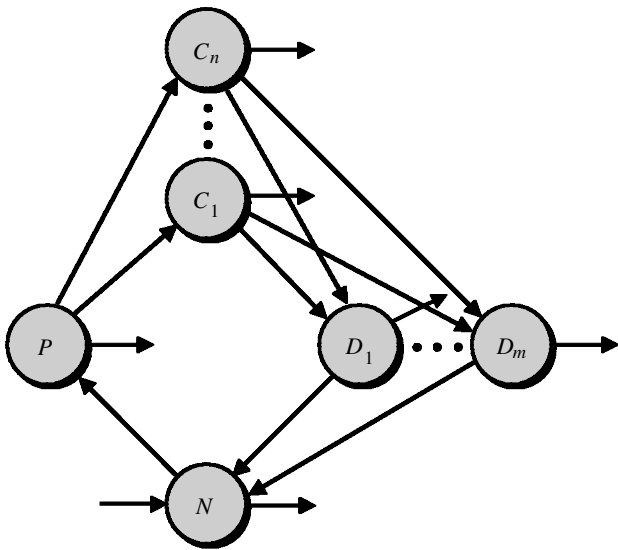


Figure 1. Flow diagram of the model ecosystem. A limiting nutrient cycles between an inorganic pool (of size  $N$ ), a primary producer compartment ( $P$ ) that consumes the nutrient in inorganic form, a set of  $n$  organic compounds produced by plants ( $C_j$ ) and a set of  $m$  decomposer species ( $D_i$ ) that consume the organic compounds and recycle the nutrient in inorganic form.

$i = 1, \dots, m$ ) that consume the organic compounds and recycle the nutrient in inorganic form. The various organic compounds may differ in aspects of chemical quality such as their C:N ratio and, consequently, represent distinct resources for decomposers. The cycle is open to nutrient imports in inorganic form and to nutrient exports from all compartments. The consumption of organic compounds by decomposers is assumed to be donor controlled for the sake of clarity and simplicity. Appendix A relaxes this assumption and analyses a system with Lotka–Volterra, recipient-controlled interactions. The analysis is more complicated and more restricted in that case, but the results are qualitatively similar.

The diagram in figure 1 translates into mathematical equations by setting the time-derivative of compartment size equal to the sum of inflows minus the sum of outflows for each compartment, thus providing the set of equations

$$\frac{dN}{dt} = I - l_N N - f(N)P + \sum_i \mu_{D_i} r_{D_i} D_i, \quad (1)$$

$$\frac{dP}{dt} = f(N)P - r_P P, \quad (2)$$

$$\frac{dC_j}{dt} = p_j \mu_P r_P P - r_{C_j} C_j, \quad (3)$$

and

$$\frac{dD_i}{dt} = \sum_j q_{ji} \mu_{C_j} r_{C_j} C_j - r_{D_i} D_i, \quad (4)$$

where

$$\sum_j p_j = \sum_i q_{ji} = 1. \quad (5)$$

In these equations,  $I$  is the input of inorganic nutrient into the ecosystem,  $l_N$  is the loss rate of inorganic nutrient from the ecosystem,  $f(N)$  is the functional response of primary producers to the availability of inorganic nutrient,  $r_X$  is the turnover rate of any compartment  $X$ ,  $\mu_X$  is the fraction of nutrient released by compartment  $X$  that is recycled within the ecosystem ( $0 \leq \mu_X \leq 1$ ),  $p_j$  is the fraction of nutrient recycled from primary producers in the form of organic compound  $j$  and  $q_{ji}$  is the fraction of nutrient recycled from organic compound  $j$  that is used by decomposer species  $i$ .

### 3. RESULTS

At equilibrium, the time-derivatives in equations (1)–(4) vanish, in other words inflows balance outflows for each compartment. Solving these mass-balance equations provides the equilibrium nutrient stocks, which are denoted by an asterisk:

$$N^* = f^{-1}(r_P), \quad (6)$$

$$P^* = \frac{S_N^*}{r_P \Lambda}, \quad (7)$$

$$C_j^* = \frac{P_j \mu_P S_N^*}{r_{C_j} \Lambda}, \quad (8)$$

and

$$D_i^* = \frac{\mu_P S_N^*}{r_{D_i} \Lambda} \sum_j p_j \mu_{C_j} q_{ji}, \quad (9)$$

where

$$S_N^* = I - l_N N^*, \quad (10)$$

and

$$\Lambda = 1 - \mu_P \sum_i \mu_{D_i} \sum_j p_j \mu_{C_j} q_{ji}, \quad (11)$$

and  $f^{-1}$  denotes the inverse function of  $f$ , the functional response to inorganic nutrient availability.  $S_N^*$  represents the net supply of nutrient in inorganic form at equilibrium, while  $\Lambda$  represents the fraction of nutrient lost from the organic compartments over a complete cycle (Loreau 1998a).

In what follows I assume that producer and decomposer biomasses are proportional to their nutrient stocks after multiplication by a suitable C:N ratio. Similarly, primary productivity and secondary (microbial) productivity are assumed to be proportional to the corresponding nutrient inflows. In order to simplify the analysis and focus on the effects of organic compound diversity and microbial diversity, I further assume that decomposers are equivalent except for the way they use resources, i.e.  $\mu_{D_i} = \mu_D$  and  $r_{D_i} = r_D$  for all species  $i$ .

Primary productivity at equilibrium, i.e.  $\Phi_P^*$ , is then

$$\Phi_P^* = f(N^*)P^* = \frac{S_N^*}{\Lambda}, \quad (12)$$

where the fraction of nutrient lost over a cycle is now

Table 1. *Effects of microbial diversity ( $m$ ) on nutrient recycling efficiency from organic compounds to decomposers ( $\overline{\mu_C}$ ) for the SSC, SDC, G + TO and G – TO scenarios and for increasing values of the rate of nutrient loss from organic compounds ( $l_C$ )*

(Here  $p_j = 1/n$  and  $l_{Cj} = l_C$  for all compounds  $j$  and  $m \leq n$ . The table gives the exact formula for  $\overline{\mu_C}$ , followed by its range of variation in parentheses when  $m$  varies from 1 to  $n$ , with  $n = 20$ .)

	$l_C \rightarrow 0$	$l_C = c/n$	$l_C = c$	$l_C = nc$
SSC	$1/n$ (0.05)	$m/(mn+1)$ (0.05–0.05)	$m/[n(m+1)]$ (0.03–0.05)	$m/[n(m+n)]$ (0.00–0.03)
SDC	$m/n$ (0.05–1.00)	$m/(n+1)$ (0.05–0.95)	$m/(2n)$ (0.03–0.50)	$m/[n(n+1)]$ (0.00–0.05)
G + TO	1 (1.00)	$m/(m+1)$ (0.50–0.95)	$m/(m+n)$ (0.05–0.50)	$m/(m+n^2)$ (0.00–0.05)
G – TO	1 (1.00)	$mn/(mn+1)$ (0.95–1.00)	$m/(m+1)$ (0.50–0.95)	$m/(m+n)$ (0.05–0.50)

$$\Lambda = 1 - \mu_P \mu_D \overline{\mu_C}. \quad (13)$$

Here

$$\overline{\mu_C} = \sum_j p_j \mu_{Cj} \quad (14)$$

is the weighted average fraction of nutrient recycled from organic compounds to decomposers, which measures the nutrient recycling efficiency from organic compounds to decomposers.

Secondary (microbial) productivity, i.e.  $\Phi_D^*$ ; and total decomposer biomass, i.e.  $D^*$ , also simplify to

$$\Phi_D^* = \sum_i \sum_j q_{ji} \mu_{Cj} r_{Cj} C_j^* = \frac{\mu_P \overline{\mu_C} S_N^*}{\Lambda} \quad (15)$$

and

$$D^* = \sum_i D_i^* = \frac{\Phi_D^*}{r_D}, \quad (16)$$

respectively.

It is apparent in equations (7) and (12)–(16) that aggregate ecosystem properties depend on the diversity of organic compounds and decomposers through the single combined parameter  $\overline{\mu_C}$ . Increasing nutrient recycling efficiency within the ecosystem or, equivalently, reducing the average proportion of nutrient lost to the ecosystem contributes to increasing both primary and secondary productivity and producer and decomposer biomasses. Accordingly, one major effect that microbial diversity can have on ecosystem processes, unless each species is a complete generalist able to degrade all organic compounds, is to ensure that all organic compounds are recycled. Any compound  $k$  that is not decomposed by microbes has an associated  $\mu_{Ck} = 0$ , thus driving the average  $\overline{\mu_C}$  down. Note that, in an experimental setting, the same is true for recalcitrant compounds that decompose slowly compared with the time-span of the experiment. Such compounds accumulate and are effectively lost to the ecosystem over the time-scale considered (de Mazancourt *et al.* 1998).

In order to explore how microbial diversity may affect ecosystem processes through nutrient recycling efficiency  $\overline{\mu_C}$  in more detail, let us consider that nutrient is released from organic compound  $j$  through two independent pathways: it may either leave the system at a rate  $l_{Cj}$  or be consumed by decomposer  $i$  at a rate  $c_{ji}$ . Thus,

$$r_{Cj} = l_{Cj} + \sum_i c_{ji} \quad (17)$$

and

$$\mu_{Cj} = \frac{\sum_i c_{ji}}{l_{Cj} + \sum_i c_{ji}}. \quad (18)$$

The outcome depends on the  $c_{ji}$ s, which determine the decomposer niche height (absolute resource-use intensity), niche breadth (degree of generalization) and niche overlap (resource-use similarity between species). I examine four simple scenarios for decomposer niches in which all species have identical niche heights (total consumption rates) and niche breadths (number of compounds used).

- (i) All species are specialized on the same organic compound  $k$  (the SSC scenario): for all  $i$ ,  $c_{ji} = c$  for  $j = k$ , and  $c_{ji} = 0$  for  $j \neq k$ .
- (ii) All species are specialized on different organic compounds (the SDC scenario): for all  $i$ ,  $c_{ji} = c$  for  $j = i$ , and  $c_{ji} = 0$  for  $j \neq i$ .
- (iii) All species are complete generalists using all organic compounds, but there is a trade-off between their degree of generalization and their ability to consume each compound (the G + TO scenario):  $c_{ji} = c/n$  for all  $i$  and  $j$ .
- (iv) All species are complete generalists using all organic compounds and there is no trade-off between generalization and consumption of each compound (the G – TO scenario):  $c_{ji} = c$  for all  $i$  and  $j$ .

These scenarios are not meant to mimic nature, but to examine limiting cases that highlight the effects of different factors. Reality is expected to lie somewhere between the various scenarios. The first two and last two scenarios are limiting cases of minimum and maximum niche breadth, respectively. The SSC and SDC scenarios are limiting cases of maximum and minimum niche overlap, respectively, and G + TO and G – TO contrast scenarios with different niche heights. More concretely, niche breadth might be interpreted as the diversity of enzymes that a microbial species has and that allows it to break down a diversity of organic compounds with different C:N ratios and niche height might be interpreted as a species' potential enzymatic activity.

The effect of microbial diversity on the nutrient recycling efficiency from organic compounds to decomposers is illustrated in table 1 and figure 2 for the different scenarios and for various values of the rate of nutrient

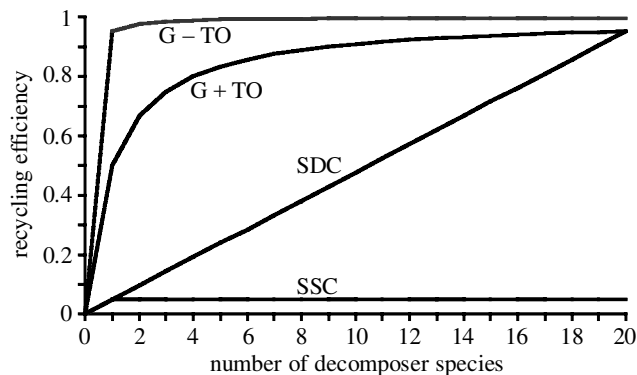


Figure 2. Effects of microbial diversity ( $m$ ) on nutrient recycling efficiency from organic compounds to decomposers ( $\overline{\mu_C}$ ) for the SSC, SDC, G + TO and G – TO scenarios. Here  $p_j = 1/n$  and  $l_{Cj} = c/n$  for all compounds  $j$  and  $m \leq n = 20$ .

loss from organic compounds. A number of results emerge from these comparisons. First, unless the rate of nutrient loss from organic compounds approaches zero, microbial diversity always has a positive effect on nutrient recycling efficiency and, hence, on primary production, secondary production, producer biomass and decomposer biomass. However, the magnitude of this effect is strongly dependent upon the scenario: it is usually greatest under the SDC scenario and intermediate under the G + TO scenario; it is only significant under the G – TO scenario when  $l_C$  is large and is systematically small under the SSC scenario. This is explained easily. Under the SSC scenario, the recycling efficiency from organic compounds to decomposers is strongly constrained by the fact that all species are specialized on the same compound. It cannot exceed the proportion of this compound in total compound production (here 5%), all the other compounds (here 95% of them) being effectively lost to the ecosystem. Under the G – TO scenario, all species consume all compounds; adding more species amounts to increasing the intensity with which each compound is exploited. Because there is no cost to generalization, microbial consumption and, hence, nutrient conservation within the ecosystem, is always high compared with  $l_C$  when this is small; increasing the number of species only makes a difference when  $l_C$  is large. The effect is stronger under the G + TO scenario for a small  $l_C$  because the cost to generalization involved in the trade-off lowers microbial consumption compared with the G – TO scenario; thus, the effect is shifted towards smaller values of  $l_C$ . The effect is usually large under the SDC scenario because the main consequence of increasing microbial diversity under this scenario is to decrease the number of unused compounds, thus improving nutrient conservation in direct proportion to the number of species.

The respective effects of the three niche characteristics can be summarized as follows. As explained above, microbial niche height (absolute resource-use intensity) always has a positive effect on nutrient conservation and, hence, on ecosystem processes, but this effect is only significant when resource use is relatively low compared with the rate of nutrient loss from unconsumed organic compounds. Microbial niche breadth (degree of generalization) has a strong positive effect only to the extent that

it increases the number of compounds used (compare the SSC and G + TO scenarios). However, when all compounds are used it has no effect on nutrient conservation and ecosystem processes (the upper limits of the ranges under the SDC and G + TO scenarios when all compounds are used under both scenarios are identical). The pattern for microbial niche overlap (resource-use similarity between species) is opposite: niche overlap has a strong negative effect to the extent that it reduces the number of compounds used (compare the SSC and SDC scenarios). When all compounds are used, it has no effect on nutrient conservation and ecosystem processes either (identical upper limits of the ranges under the SDC and G + TO scenarios, which also contrast scenarios with extreme values of niche overlap). However, note that niche breadth and overlap may contribute indirectly to enhance ecosystem processes when all compounds are used if they are accompanied by a more intense resource use, as is the case when generalization has no cost (compare the upper limits of the ranges under the SDC and G – TO scenarios).

The same scenarios can also be used to investigate the effect of organic compound diversity (table 2 and figure 3). As long as microbial diversity or generalization is high enough that all compounds can be used, organic compound diversity has no effect on nutrient conservation and ecosystem processes (SDC, G + TO and G – TO scenarios). However, when increasing organic compound diversity means increasing the number of compounds that cannot be used by decomposers, it has a strong negative effect on ecosystem processes (SSC scenario). Thus, the only effect that organic compound diversity can have on ecosystem processes is negative.

#### 4. DISCUSSION

Positive effects of plant species diversity on ecosystem processes have been attributed to two classes of mechanism: functional niche complementarity and selection of extreme trait values (Tilman *et al.* 1997b; Loreau 1998b, 2000). In both cases, biodiversity provides a range of phenotypic trait variation. In the complementarity effect, trait variation then forms the basis for a permanent association of species that enhances collective performance. In the selection effect (also called ‘sampling effect’ or ‘selection probability effect’ in extreme cases of selection; Huston 1997; Tilman *et al.* 1997b), trait variation comes into play only as an initial condition and a selective process then promotes dominance by species with extreme trait values (Loreau 2000).

The same two classes of mechanism operate with microbial diversity. Greater productivity of systems containing a greater diversity of both producers and decomposers is predicted by the increased likelihood that each functional group contains a species that is highly efficient in using resources (Loreau 1998a; Morin 2000). Although this effect was not studied explicitly here, it is implicit in the effect of microbial diversity in the scenarios with complete niche overlap (SSC, G + TO and G – TO scenarios), as well as in the effect of niche height as revealed by a comparison between the G + TO and G – TO scenarios. Adding species with identical niches or increasing niche height amounts to increasing the

Table 2. Effects of organic compound diversity ( $n$ ) on nutrient recycling efficiency from organic compounds to decomposers ( $\overline{\mu}_C$ ) for the SSC, SDC, G + TO and G – TO scenarios and for increasing values of the rate of nutrient loss from organic compounds ( $l_C$ )

(Here  $p_j = 1/n$  and  $l_{Cj} = l_C$  for all compounds  $j$  and  $n \leq m$ . The table gives the exact formula for  $\overline{\mu}_C$ , followed by its range of variation in parentheses when  $n$  varies from 1 to  $m$ , with  $m = 20$ .)

	$l_C \rightarrow 0$	$l_C = c/m$	$l_C = c$	$l_C = mc$
SSC	$1/n$ (1.00–0.05)	$m^2/[n(m+1)]$ (1.00–0.05)	$m/[n(m+1)]$ (0.95–0.05)	$1/(2n)$ (0.50–0.03)
SDC	1 (1.00)	$m/(m+1)$ (0.95)	0.5 (0.50)	$1/(m+1)$ (0.05)
G + TO	1 (1.00)	0.5 (0.50)	$1/(m+1)$ (0.05)	$1/(m^2+1)$ (0.00)
G – TO	1 (1.00)	$m/(m+1)$ (0.95)	0.5 (0.50)	$1/(m+1)$ (0.05)

intensity of microbial exploitation of organic compounds. As a result, decomposers enhance nutrient conservation within the system and, hence, producer and decomposer productivity. Functional niche complementarity occurs in the SDC scenario where niche overlap is zero. The positive effect of microbial diversity is usually greatest in this scenario because increasing microbial diversity decreases the number of unused compounds, which improves nutrient conservation in direct proportion to the number of species.

In the long term, ecosystem processes are governed by the nutrient input–output balance, which itself is determined by nutrient cycling efficiency at the ecosystem level (de Mazancourt *et al.* 1998; Loreau 1998a). This explains why microbial niche breadth and overlap affect them only to the extent that they increase the number of organic compounds that are decomposed. Unused compounds represent nutrient losses to the system and correspondingly decrease nutrient cycling efficiency.

This also explains why a greater organic compound diversity can only have a negative effect or, at best, no effect on ecosystem processes. More organic compounds mean an increased likelihood that some of them will not be consumed by decomposers, at least on the time-scale of an experiment, thus decreasing nutrient cycling efficiency. However, it is conceivable that some organic compounds might be complementary resources for decomposers. In this case, a threshold number of compounds might be necessary in order to ensure microbial growth, a factor that I have not considered in this model and that would contribute to generating a positive effect of organic compound diversity on ecosystem processes.

It is also important to realize that these conclusions apply to constant environments such as those typically found in laboratory experiments. One additional dimension of the role of microbial diversity in natural systems is related to microbial adaptations to spatial and temporal variations in the environment. For many processes that occur under anaerobic conditions in micro-spaces, bacteria live in a dormant state until conditions become favourable. Thus, microbial diversity might be important in maintaining ecosystem processes in the face of spatial and temporal environmental variability, as predicted by the insurance hypothesis (Yachi & Loreau 1999). Organic compound diversity is also likely to have a more positive effect on ecosystem functioning in a longer term perspective in fluctuating natural environments because recalcitrant organic matter may serve as a buffer preventing the definitive loss of nutrients from the ecosystem. Thus, in seasonal terrestrial ecosystems, nutrients bound in recalci-

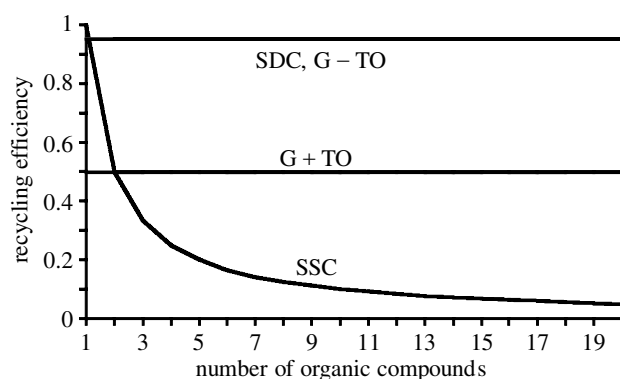


Figure 3. Effects of organic compound diversity ( $n$ ) on nutrient recycling efficiency from organic compounds to decomposers ( $\overline{\mu}_C$ ) for the SSC, SDC, G + TO and G – TO scenarios. Here  $p_j = 1/n$  and  $l_{Cj} = c/m$  for all compounds  $j$  and  $n \leq m = 20$ .

trant soil organic matter, which might otherwise be lost if they were released by decomposition at times when plants are unable to absorb them, are conserved and ultimately released within the ecosystem.

In their experiment, Naeem *et al.* (2000) found a significant positive correlation between microbial diversity and the diversity of organic compounds used, which suggests a scenario close to the SDC scenario with low niche overlap between decomposer species. In this case, my model predicts that microbial diversity should enhance production and biomass in both producers and decomposers at equilibrium. Microbial diversity did have significant effects on these ecosystem processes, but the effects were nonlinear and interacted with those of algal diversity. Producer diversity can have two different effects on ecosystem processes: a direct positive effect due to a better use of inorganic resources, particularly at a low level of diversity, as has been shown experimentally (Tilman *et al.* 1996, 1997a; Hector *et al.* 1999) and theoretically (Tilman *et al.* 1997b; Loreau 1998b) and a negative indirect effect if producer diversity is accompanied by a diversity of organic compounds produced, as revealed above. Since the direct effect is likely to be important at a low diversity and the indirect effect at a high diversity, this might explain the nonlinear dependency of primary production on algal diversity observed in the experiment (Naeem *et al.* 2000).

However, I suspect that part of the explanation for the complex relationship between ecosystem processes, algal diversity and microbial diversity observed in this experiment lies in the fact that the microcosm ecosystems may

not have reached an equilibrium with respect to nutrient cycling. As long as such an equilibrium has not been reached, the nutrient accumulates differently in different compartments, which can lead to large deviations from equilibrium predictions. Another, related factor is competition between producers and decomposers for inorganic nutrient. At equilibrium, this competition should be suppressed because producers and decomposers should be limited by different resources (Daufresne & Loreau 2001), but it can generate significant antagonistic interactions before an equilibrium is reached. Lastly, some microbes may work in consortia in order to break down organic compounds. Synergistic associations might turn small linear changes in diversity into highly nonlinear declines in ecosystem processes.

Deviation from equilibrium conditions may also explain some of the results found by J. Roy, S. Dhillon, J.-L. Guillermin and L. Béguier (unpublished manuscript) in another experiment with terrestrial herbaceous communities. They found that plant functional diversity had significant positive effects on the diversity of carbon sources used by soil bacteria, on microbial production and biomass as well as on nutrient retention within the system, but no significant effect on plant production. Primary production should be correlated with nutrient conservation in the long term, but, given the relatively short duration of the experiment compared with the annual dynamics of these herbaceous communities, non-equilibrium conditions were likely. Although other hypotheses are possible, the transient accumulation of nutrient in microbial biomass seems the simplest hypothesis for accounting for these results. Indeed, the effect of plant functional diversity on soil bacteria had disappeared a few months later (M. Bonkowski, personal communication), although the lack of effect on primary production seemed persistent (J. Roy, personal communication). By focusing on the equilibrium behaviour of a simple model ecosystem, the present model may help not only in providing predictions for nutrient-limited ecosystems in the long term, but also in formulating hypotheses about the factors involved when these predictions are not met.

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## APPENDIX A

This appendix analyses a system that is equivalent to the model shown in equations (1)–(4), but with Lotka–Volterra, recipient-controlled interactions between organic compounds and decomposers. Equations (3) and (4) are now replaced with the following equations:

$$\frac{dC_j}{dt} = p_j \mu_P r_P P - l_{C_j} C_j - \sum_i u_{ji} C_j D_i \quad (\text{A1})$$

and

$$\frac{dD_i}{dt} = \sum_j u_{ji} C_j D_i - r_{D_i} D_i, \quad (\text{A2})$$

where  $l_{C_j}$  is the loss rate of organic compound  $j$  to the external world and  $u_{ji}$  is its consumption rate by decomposer species  $i$ .

An equilibrium is only possible in this system for  $m \leq n$  and there is no explicit solution for the equilibrium for  $m < n$ . Therefore, I concentrate on the case where  $m = n$ . In this case, the equilibrium satisfies

$$N^* = f^{-1}(r_P), \quad (\text{A3})$$

$$P^* = \frac{S_N^*}{r_P \Lambda}, \quad (\text{A4})$$

$$C^* = V^T r_D, \quad (\text{A5})$$

and

$$D^* = VX, \quad (\text{A6})$$

where

$$S_N^* = I - l_N N^* - \sum_i \mu_{D_i} r_{D_i} \sum_j l_{C_j} v_{ij}, \quad (\text{A7})$$

and

$$\Lambda = 1 - \mu_P \sum_i \mu_{D_i} r_{D_i} \sum_j \left( \frac{p_j v_{ij}}{\sum_i r_{D_i} v_{ij}} \right). \quad (\text{A8})$$

Here  $V = (v_{ji})$  is the inverse of matrix  $U = (u_{ji})$ ,  $V^T$  is the transpose of matrix  $V$ , and  $C^* = (C_j^*)$ ,  $D^* = (D_i^*)$ ,  $r_D = (r_{D_i})$  and  $X = (\mu_P r_P P^* p_j / C_j^* - l_{C_j})$  are column vectors.

Although explicit, this solution is difficult to analyse and interpret in general. Consider the simple case  $m = n = 2$ . It is then possible to show that the results are qualitatively similar to those obtained with the equivalent, donor-controlled system in equations (1)–(4). In particular, consider two decomposer species with symmetrical niches and a trade-off between their consumption rates for the two organic compounds such that  $u_{11} = u_{22} = (1 - \alpha/2)u$  and  $u_{12} = u_{21} = (\alpha/2)u$ , where  $\alpha$  measures microbial niche overlap. It is then possible to show that  $S_N^*$  and  $\Lambda$  and, hence, also producer biomass and productivity are independent of  $\alpha$ , just as in the donor-controlled system (comparison between the upper limits of the ranges under the SDC and G + TO scenarios). On the other hand, consider two decomposer species with symmetrical niches but no trade-off between their consumption rates for the two organic compounds such that  $u_{11} = u_{22} = u$  and  $u_{12} = u_{21} = \alpha u$ , where  $\alpha$  again measures microbial niche overlap. In this case, it can be shown that  $S_N^*$  and, hence, producer biomass and productivity increase with  $\alpha$ , again as in the donor-controlled system (comparison between the upper limits of the ranges under the SDC and G – TO scenarios).

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As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.