

REPORT

Feedbacks between nutrient cycling and vegetation predict plant species coexistence and invasion

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Abstract

To investigate the role of species-specific litter decomposability in determining plant community structure, we constructed a theoretical model of the codevelopmental dynamics of soil and vegetation. This model incorporates feedback between vegetation and soil. Vegetation changes the nutrient conditions of soil by affecting mineralization processes; soil, in turn, has an impact on plant community structure. The model shows that species-level traits (decomposability, reproductive and competitive abilities) determine whether litter feedback effects are positive or negative. The feedback determines community-level properties, such as species composition and community stability against invasion. The model predicts that positive feedback may generate multiple alternative steady states of the plant community, which differ in species richness or community composition. In such cases, the realized state is determined by initial abundance of co-occurring species. Further, the model shows that the importance of species-level traits depends on environmental conditions such as system fertility.

Keywords

Decomposition, litter feedback, litter quality, species-level effects on material cycling.

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INTRODUCTION

Nutrients such as nitrogen and phosphorus are essential resources for plants. They can limit growth or reproduction of plants and mediate interspecific competition (Tilman 1982). Therefore, nutrients influence plant community structure. For example, there is a tendency that fast-growing species will be competitive under nutrient-rich conditions, whereas species with high nutrient retention ability will be dominant under nutrient-poor conditions (Berendse *et al.* 1987; Aerts 1999).

Nutrient availability is influenced by plant community composition (Berendse *et al.* 1989; Wedin & Tilman 1990; Nadelhoffer *et al.* 1991; Van Vuuren *et al.* 1993; but see Allen & Hoekstra 1989) because mineralization, a major source of nutrients, may be influenced by plant traits (e.g. litter quality, quantity) as well as by other factors (e.g. soil moisture, temperature, microbial activities, and texture; Jones *et al.* 1999; some of these factors can be also influenced by vegetation, e.g. Hamilton & Frank 2001). One of the general ways in which plant traits influence mineralization processes is alteration of the biochemical composition of litters. Since the biochemical composition of plant litter differs among

species, a litter effect on nutrient availability may be species-specific (Swift *et al.* 1979; Berendse 1990; Van Vuuren *et al.* 1992; Van Vuuren *et al.* 1993; Wedin & Pastor 1993; Aerts & De Caluwe 1997; Köchy & Wilson 1997).

The interactions between vegetation and soil lead to a codevelopmental process (White *et al.* 1988; Wedin & Tilman 1990; Torreta & Takeda 1999). Vegetation changes soil through the alteration of mineralization processes, while soil conditions influence plant community structure by affecting plant growth, reproduction, and competition (Tilman 1982). This implies a litter-mediated interaction between plant species (i.e. litter feedback effects). Litter effect on nutrient availability may reinforce competitive ability of dominant species and stabilize current vegetation (positive feedback) or enhance a potential competitor's advantage and lead to change in vegetation (negative feedback), depending on plant traits such as nutrient-use strategies and competitive abilities (Matson 1990; Wedin & Tilman 1990; Tatenno & Chapin 1997; Van der Putten 1997; Aerts 1999). How does such codevelopment determine stable states for vegetation–soil systems, or community-level properties such as resistance to biological invasion and resilience against perturbations?

Several theoretical studies have investigated the role of litter feedback effects in structuring plant communities (Berendse *et al.* 1989; DeAngelis 1992; Bugmann 1996; Loreau 1998). However, it is still unclear how different feedback effects of multiple species influence community structure. Previous theoretical models that considered interspecific differences in litter quality or quantity have either assumed monoculture communities (Berendse *et al.* 1989; DeAngelis 1992), or have neglected feedback from soil to vegetation because they assumed a fixed species composition (Loreau 1998). Consequently, these models cannot investigate the effects of codevelopmental soil and vegetation processes on plant community composition. Other quantitative models (e.g. FORCLIM by Bugmann 1996) that were developed to simulate patterns of succession are highly complex, and it is difficult to derive a general prediction from them. Also, it remains unknown how the codevelopmental process of soil and vegetation determines community-level properties such as community resistance to biological invasion and resilience against perturbation. To make general predictions about these issues, it is necessary to develop a simple model of soil–vegetation systems that considers dynamic changes in a multispecies community.

Here, we present a mechanistic model of a soil–vegetation system, where plant community composition and soil nutrient conditions interactively shape the whole system. The plant community consists of multiple species, each of which is characterized by species-specific decomposability, competitive ability in local competition (e.g. competition for light), and reproductive ability. Plant community composition is determined by the outcome of interspecific competition influenced by nutrient availability, and this community drives a further change in nutrient availability by affecting the balance between mineralization rates and nutrient uptake rates. With this model, we provide clear insight into how soil and vegetation codevelop to structure the whole ecosystem, and we investigate community-level consequences.

MODEL

A multispecies patch occupancy model (Hastings 1980; Tilman 1994) represents the community dynamics of plant species. A habitat consists of a large number of discrete patches, each of which is empty or occupied by one individual of the competing n plant species. The proportion of patches occupied by species i ($1 \leq i \leq n$), p_i , changes through time, due to inter-patch colonization and within-patch extinction. We assumed that the colonization rate ($c_i N$) increases with increasing inorganic nutrient concentration levels in the soil, N . Each species is characterized by a species-specific reproductive ability (colonization rate per unit of nutrients; c_i), extinction rate (m_i), and within-patch

competitive ability (e.g. competition for light). Species are ranked from the best (species 1) to the poorest competitor (species n), with the assumption that a superior competitor always displaces inferior competitors within a patch (the superior competitor may have higher growth rate or tolerance against shade; Aerts *et al.* 1990; Aerts 1999). The dynamics of the proportion p_i of patches occupied by species i are represented by:

$$dp_i/dt = c_i N p_i \left(1 - \sum_{k=1}^i p_k \right) - m_i p_i - \sum_{k=1}^{i-1} c_k N p_k p_i, \quad (1)$$

where the first term represents colonization, the second term is the loss through local extinction, and the last term is the loss through competitive exclusion.

In this system, nutrient availability may limit the persistence of a plant species. Suppose that there is only one species, i , with nutrient concentrations at a given level, N^* . The equilibrium proportion of patches occupied by species i is given by $p_i^* = 1 - m_i / (c_i N^*)$, suggesting that species i persists if nutrient concentration levels exceed a critical level ($N^* > m_i / c_i \equiv N_{min}^i$). This implies that species with higher mortality rates (m_i) or lower colonization rates c_i (reproductive ability) require higher nutrient levels to persist. In this paper, we refer to this minimum nutrient level as the nutrient requirement level of species i (N_{min}^i).

This model incorporates competition over nutrients, light and space, each of which occurs between individuals at the within-patch or between populations at the whole-habitat scale (see Grace 1990 for the definition of competition between individuals and between populations). At the within-patch scale, we consider competition over light at the individual level and assume that species with competitive advantage for light (e.g. high shade tolerance or high growth rate) always win. At the whole-habitat scale, we consider population-level competition over space and nutrients. Species can exclude other species, either by lowering nutrient concentration to levels where another species cannot keep its population (i.e. competition over nutrients), or by reducing available patches to colonize (i.e. competition over space). Although individuals also potentially compete for both nutrients and light (see Huston & DeAngelis 1994), we assume that individual-level competition is independent of nutrient level and that reproduction rate depends on nutrient level. These simple assumptions realize the situation in which nutrient level influences population-level competitive ability, and thus species composition.

We extend this plant community model by incorporating nutrient recycling processes (Fig. 1), which consist of production and decomposition. Individuals of species i take up a nutrient (b_i) from the nutrient pool (N) during each colonization (production process), and release it into the associated detritus pool (D_i) during each extinction. Once

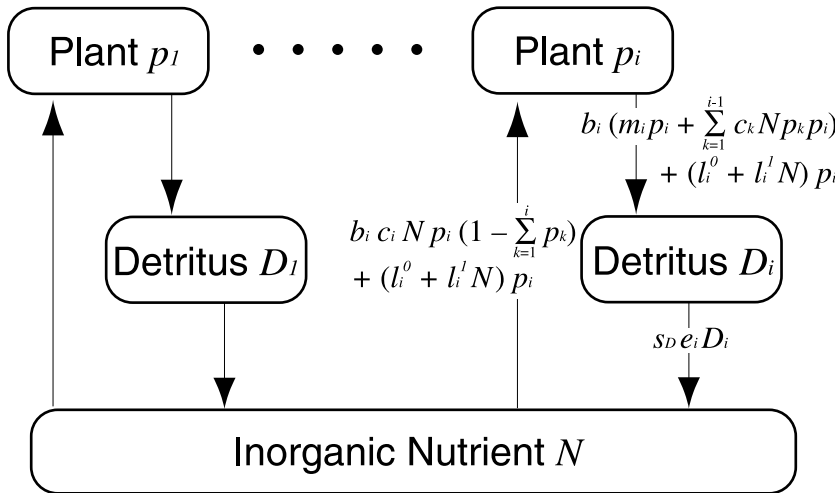


Figure 1 Flow diagram of the model soil-vegetation system. Flows from inorganic nutrient pools (N) to plant compartments (p_i) represent production processes. Such flows consist of two parts: establishment ($b_i c_i N p_i (1 - \sum_{k=1}^i p_k)$), and annual production ($(l_i^0 + l_i^1 N) p_i$). Flows from plant compartments to species-specific detritus pools (D_i) represent two parts of litter production: annual litter production ($(l_i^0 + l_i^1 N) p_i$), and nutrient flow through natural and competitive death of living biomass ($b_i (m_i p_i + \sum_{k=1}^{i-1} c_k N p_k p_i)$). Flows from detritus pools to inorganic nutrient pools represent the decomposition process ($s_D e_i D_i$).

established, an individual plant takes up nutrients at a rate of $l_i^0 + l_i^1 N$ per unit of time (annual production), and releases them at the same rate into the detritus pool (D_i), where l_i^0 and $(l_i^1 N)$ represent production independent of, and in proportion to, nutrient levels, respectively. It is a mechanistic assumption for increasing reproduction with nutrient level that annual production increases with increasing nutrient level, leading to increasing seed production ($c_i N$) (Stephenson 1984; Whigham 1984; Mattila & Kuitunen 2000). Nutrients contained in seeds are neglected for simplicity. Detritus is mineralized at a fixed rate, $s_D e_i$ (decomposition process), where e_i is the species-specific decomposability of species i , and s_D represents the effect of other factors such as temperature, moisture, or micro-organism activities. Although litter quality (decomposability) may in reality be affected by nutrient availability (Aerts & De Caluwe 1997), it is assumed constant for simplicity. It is also assumed that each species' detritus does not change the other species' decomposability (s_D is set to be constant), although it is possible in a real ecosystem when litter content changes soil properties affecting s_D . The diagram in Fig. 1 translates into dynamic equations as follows:

$$dN/dt = s_D \sum_{k=1}^n e_k D_k - \sum_{k=1}^n b_k c_k N p_k \left(1 - \sum_{j=1}^k p_j \right) - \sum_{k=1}^n (l_k^0 + l_k^1 N) p_k \tag{2}$$

$$dD_i/dt = b_i \left(m_i p_i + \sum_{k=1}^{i-1} c_k N p_k p_i \right) + (l_i^0 + l_i^1 N) p_i - s_D e_i D_i. \tag{3}$$

This dynamic system is closed, such that the total amount of nutrients (T_N) is preserved over time, i.e. $\sum_{k=1}^n (b_k p_k + D_k) + N = const \equiv T_N$, where T_N is interpreted as the

fertility of the habitat. To focus on the effects of plant traits on the rate of nutrient cycling and nutrient distribution in the system (living biomass, detritus, and inorganic nutrient), we assume a closed system and a fixed system fertility in this model, although ecosystems are in reality open and the total nutrient that cycles in the system can be partly influenced by vegetation (Matson 1990). Since $N(t)$ is given by:

$$N(t) = T_N - \sum_{k=1}^n (b_k p_k(t) + D_k(t)), \tag{4}$$

the variables of the system are reduced to p_i and D_i .

RESULTS

To investigate potential interspecific interactions within the system, we consider the simplest case of only two species, species 1 (superior competitor) and species 2 (inferior competitor). Although species-specific values of living biomass (b_i), litter quantity (l_i^0, l_i^1), litter quality (e_i), and extinction rate (m_i) can influence nutrient cycling to alter the competitive outcome, we set $b_1 = b_2 = b, l_1^0 = l_2^0 = l_0, l_1^1 = l_2^1 = l_1$, and $m_1 = m_2 = m$ to focus on the effects of litter quality, e_1 and e_2 .

A plant population does not persist if T_N is too small. Establishment of species i in an empty habitat is successful if and only if $(dp_i/dt)/p_i > 0$ for $p_k = 0$ (if k is not i) and $N = T_N$, i.e. $T_N > m/c_i$. Hereafter, we assume that T_N is sufficiently large to satisfy these inequalities for $i = 1, 2$ (i.e. $T_N > m/c_1, T_N > m/c_2$).

Resistance to species invasion

Community resistance to invasion is determined by the competitive and reproductive abilities of both the invading and the invaded species, as well as by the litter quality of the

invaded species. Suppose that a small fraction of species j has entered an equilibrium community of species i . The frequency of the invading species increases (i.e. invasion is successful) when $[(dp_j/dt)/p_j]_{p_i=p_i^*, N=N_i^*} > 0$, where N_i^* and p_i^* represent equilibrium nutrient levels of the community and abundance of invaded species i , respectively. The following results are obtained analytically (without numerical calculations) and robust for all plausible parameter values.

First, consider the conditions for species 1 (the superior competitor) to successfully invade a population of species 2 (the inferior competitor). The invasion succeeds (i.e. $[(dp_1/dt)/p_1]_{p_2=p_2^*, N=N_2^*} > 0$) if and only if the nutrient concentration levels of the invaded community (N_2^*) are higher than the nutrient requirement levels of species 1 ($N_2^* > m/c_1$). If the total amount of nutrients is very small ($T_N < (m/c_1) + b(1 - c_1/c_2)$), then the invasion always fails (Appendix 2). Assuming that T_N is sufficiently large ($T_N > (m/c_1) + b(1 - c_1/c_2)$), we can derive the following conditions for a successful invasion from equations 1, 3, and 4 (Appendix 2):

$$e_2 > \frac{(c_2 - c_1)(bm + l_0 + ml_1/c_1)}{s_D[b_1c_1 + c_2(T_N - b) - (c_2/c_1)m]} \equiv E_2^*. \quad (5.1)$$

If the reproductive rate of species 1 (c_1) is larger than that of species 2 (c_2), then species 1 successfully invades a population of species 2 independently of the decomposability of species 2 (e_2). In the case where $c_1 < c_2$, decomposability does matter; the invasion fails if, and only if, the decomposability of species 2 is sufficiently small ($e_2 < E_2^*$) as to maintain nutrient levels of species 2's population that are lower than the nutrient requirements of species 1.

Second, we consider conditions for species 2 (the inferior competitor) to successfully invade a population of species 1 (the superior competitor). This invasion will succeed if, and only if, nutrient levels in the community (N_1^*) are low ($N_1^* < (c_2/c_1)(m/c_1)$). Noting that N_1^* should be larger than m/c_1 for species 1 to persist (easily derived from the equation $p_1^* = 1 - m/(c_1 N_1^*) > 0$), it follows that $m/c_1 < N^* < (c_2/c_1)(m/c_1)$, implying that the invasion will never succeed if the reproductive ability of species 2 is lower than that of species 1 ($c_2/c_1 < 1$). If the total amount of nutrients is low ($T_N < (mc_2/c_1^2) + b(1 - c_1/c_2)$), then the invasion always succeeds (Appendix 2). When T_N is sufficiently large ($T_N > (m/c_2/c_1^2) + b(1 - c_1/c_2)$), the conditions for a successful invasion are represented by the following inequality (Appendix 2):

$$e_1 < \frac{(c_2 - c_1)(bm + l_0 + (c_2/c_1^2)ml_1)}{s_D[b_1c_1 + c_2(T_N - b) - (c_2/c_1)^2m]} \equiv E_1^*. \quad (5.2)$$

This inequality suggests that when $c_2 > c_1$, the invasion is successful if the decomposability of species 1 is sufficiently small. Low decomposability maintains a low nutrient availability, and therefore lowers the intensity of interspecific competition for space. (Note that the last term of eqn 1 decreases with decreasing N). This facilitates the increase of species 2.

Community composition at competitive equilibrium

There are four possibilities for species composition at equilibrium: no species (F_0 ; $p_1^* = 0, p_2^* = 0$), species 1 alone (F_1 ; $p_1^* > 0, p_2^* = 0$), species 2 alone (F_2 ; $p_1^* = 0, p_2^* > 0$), or the two species coexisting (F_3 ; $p_1^* > 0, p_2^* > 0$). In each case, the abundance of species at equilibrium is given as follows: $(p_1^*, p_2^*) = (0, 0)$ in the case of F_0 ; $(p_1^*, p_2^*) = (1 - m/(c_1 N^*), 0)$ in the case of F_1 ; $(p_1^*, p_2^*) = (0, 1 - m/(c_2 N^*))$ in the case of F_2 ; and $(p_1^*, p_2^*) = (1 - m/(c_1 N^*), m/(c_1 N^*) - (c_1/c_2))$ in the case of F_3 , where N^* is the nutrient concentration level at each equilibrium.

In the following analysis, we focus on the case where $c_1 < c_2$, i.e. where there is a trade-off between reproductive and competitive ability. Such a trade-off would be realized when a species with a higher growth rate is a better competitor within a patch, but higher allocation to growth leads to lower reproduction rate (i.e. a trade-off between growth and reproduction) (El-Kassaby & Barclay 1992; Reekie & Bazzaz 1992; Delph *et al.* 1993; Reekie 1998; but see Tilman 1994 for another mechanism by which the trade-off emerges). No stable equilibrium exists with an abundance of species 2 if $c_1 > c_2$ (populations of species 2 are always invaded by species 1). There is no equilibrium with two species, as may be easily understood by noting that it is required for p_1^* and p_2^* to be positive that $(m/c_1) < N^* < (m/c_1)(c_2/c_1)$. Species composition is influenced by nutrient concentration levels, that is, superior competitors tend to dominate competition over patches (space) when nutrient levels are high, whereas superior competitors with low reproductive abilities do not persist when nutrient levels are low (Kondoh 2001). For clarity, we will refer to species 1 as species C (competitive advantage) and to species 2 as species R (reproductive advantage).

We analysed conditions under which the equilibrium points of species composition ($F_0 - F_3$) are locally stable. We can determine species composition by examining the nutrient concentration level at equilibrium, N^* (Appendix 1). High nutrient levels ($m/c_R/c_C^2 < N^*$) result in a stable equilibrium at which species C alone persists; a stable equilibrium with species R alone exists when nutrient levels are low ($N^* < m/c_C$). At intermediate nutrient levels ($m/c_C < N^* < m/c_R/c_C^2$), there exists an equilibrium with

the two species, although it may not be locally stable. We analytically investigated the conditions of decomposability, e_C and e_R , under which the above-mentioned conditions in nutrient concentration levels are realized.

First, we considered the case in which the total amount of nutrients (T_N) is small ($T_N < (m/c_C)(c_R/c_C) + b(1 - c_C/c_R)$). Here, the system reaches a unique stable state, which is achieved from any initial state. When T_N is extremely small ($m/c_C < T_N < m/c_C + b(1 - c_C/c_R)$), equilibria F_1 and F_3 are both unstable, and species R alone (F_2) persists independently of the decomposability of both species. When T_N is large ($m/c_C + b(1 - c_C/c_R) < T_N < (m/c_C)(c_R/c_C) + b(1 - c_C/c_R)$), the outcome is determined by the decomposability of species R. Species R alone persists if $e_R < E_{R^*}$, and a stable coexistence of the two species is realized if $e_R > E_{R^*}$.

Second, we considered the case in which T_N is sufficiently large ($T_N > (m/c_C)(c_R/c_C) + b(1 - c_C/c_R)$). In this case, the decomposability of both species influences community composition. Furthermore, litter effects may generate multiple stable states, and which stable state is reached depends on the initial state. The stable equilibrium of the dynamic system governed by eqns 1, 3, and 4 is represented by a parameter space of decomposability, e_C and e_R . This consists of several regions, each of which represents possible community composition at a stable equilibrium (see Fig. 2). Basically, these regions were obtained by analytical methods, although some numerical calculations were required to draw the whole picture (see Appendices 1 and 2 for more details). We carried out numerical calculations for many parameter sets, which we chose randomly from a broad range of parameter values as follows: c_C : 0.01–1000, c_R/c_C : 1.01–10.0, b : 0.01–1.0, m : 0.001–1.0, l_1 : 0.0 and 0.01–1000. We set T_N to a fixed value, 1.0, and uptake rate independent of nutrient level (l_0) to zero, because it is reasonable to assume that uptake rate ($(l_0 + l_1 N) p_i$) is zero when nutrient level in the soil is zero. Numerical calculations support that changing parameters do not make qualitative changes in the patterns shown in Fig. 2. If we consider 1 unit time to be 1 year, it is reasonable to expect that these broad ranges of values used in calculations include biologically realistic values. Here, we present the results for $l_0 = l_1 = 0$; we confirmed that the results do not change qualitatively when l_1 is positive. Although there are two possible diagrams (Diagram a and Diagram b), we will not focus on their differences; instead, we shall discuss general characteristics that are apparent in both diagrams. Region Aa emerges in Diagram b but not in Diagram a; numerical calculations have shown that Diagram b is realized when $c_R - c_C$ is sufficiently large.

The necessary and sufficient conditions for local stability at the equilibrium point with species C alone ($p_C^* > 0, p_R^* = 0$) are $e_C > E_{C^*}$, and the conditions for a stable equilibrium point with species R alone ($p_C^* = 0, p_R^* > 0$) are that $e_R < E_{R^*}$. Species R alone persists in region B, while

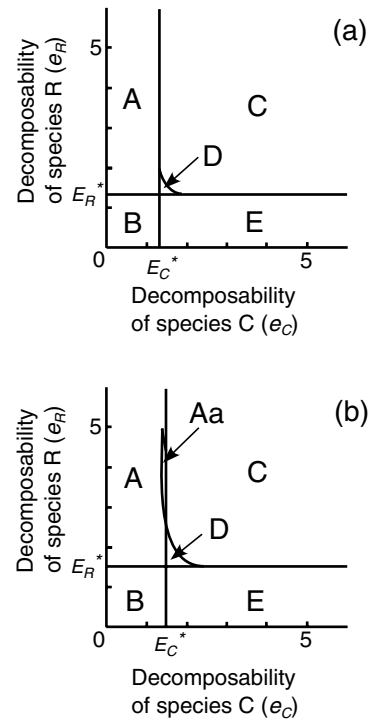


Figure 2 Diagrams of possible species composition of a plant community in a stable state. Five (Diagram a) or six (Diagram b) regions in the parameter space (e_C, e_R) represent the conditions under which each species composition can be realized. Parameters are as follows: (Diagram a) $T_N = 1.0, s_D = 0.004, b = 0.1, l_0 = l_1 = 0.0, m = 0.1, c_1 = 100$ and $c_2 = 200$ or (Diagram b) $c_2 = 230$. In region A, two species coexist in a stable state, whereas coexistence is realized by oscillations in region Aa (Diagram b). In region B, species R persists in monoculture, whereas a monoculture of species C persists in region C. In region D, a monoculture of species C, or a coexistence of the two species, is attained. A monoculture of species C or R is realized in region E.

species C alone persists in region C. When the decomposability of species C is sufficiently low ($e_C < E_{C^*}$) and species R is highly decomposable ($e_R > E_{R^*}$; regions A and Aa in the case of Diagram b), each species can invade the habitat dominated by the other species but cannot exclude it (see the previous section “Resistance to species invasion”). Therefore, the coexistence of two species ($p_C(t), p_R(t) > 0$ for all $t > 0$) is attained in a stable state (region A) or by oscillations (region Aa in the case of Diagram b), for any initial positive abundance. In region D or E, two locally stable equilibria exist, and the realized equilibrium depends on initial conditions (Fig. 3 for region D, Fig. 4 for region E). When the decomposability of species C is high and that of species R is low, there are two equilibria with either species (region E). In region D, the system has two equilibria with a different number of species, that is, the coexistence of two species or species C alone.

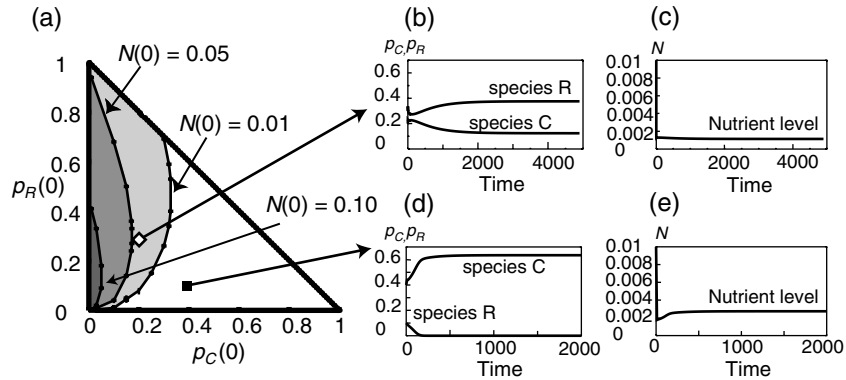


Figure 3 Dependence on initial conditions of the realized stable state of the system: region D. Panel (a) shows a combination of the initial proportion of patches occupied by each species ($p_C(0)$, $p_R(0)$) leading to a coexistence of the two species, or to a monoculture of species C, for different initial nutrient levels ($N(0)$). Note that $p_C(0)$ and $p_R(0)$ satisfy the following inequality: $0 < p_C(0) + p_R(0) \leq 1$. Coexistence of the two species (or the monoculture of species C) is realized for values of $p_C(0)$ and $p_R(0)$ that lie to the left (right) of a curve that corresponds to a particular value of $N(0)$. The decomposability of each species is: $e_C = 1.7$, $e_R = 1.4$. The initial level of detritus is given by $D_1(0) = D_2(0) = (T_N - N(0) - bp_1(0) - bp_2(0))/2$, and other parameters as described in Fig. 2 (a). The curves were derived numerically by iterating calculations for different initial conditions (with steps of 0.01–0.05). (b–e) provide examples of the codevelopment of soil and vegetation, leading to the coexistence of two species (b and c) and the monoculture of species C (d and e). These panels illustrate the dynamics of the proportion of patches occupied by each species ($p_C(t)$ and $p_R(t)$ in b and d) and nutrient levels ($N(t)$ in c and e), which were obtained by numerical calculations. Parameters used are (b–c): $p_C(0) = 0.2$, $p_R(0) = 0.3$, and $N(0) = 0.01$; (d–e): $p_C(0) = 0.4$, $p_R(0) = 0.1$, and $N(0) = 0.01$. Other parameters are described in (a).

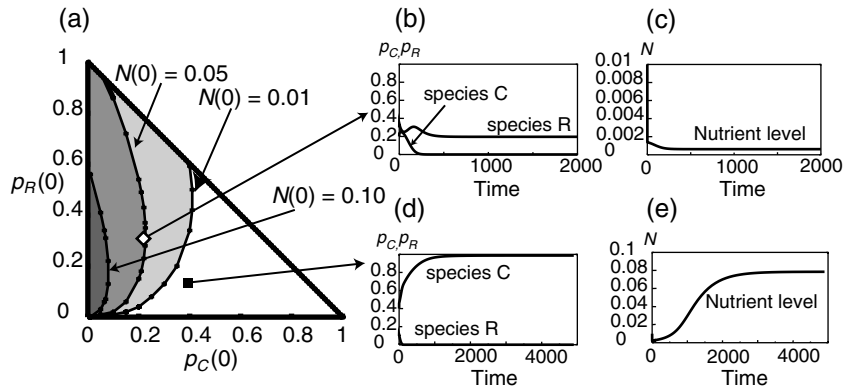


Figure 4 Dependence of the realized stable state of the system on initial conditions: region E. (a) This panel shows a combination of the initial proportion of patches occupied by each species ($p_C(0)$, $p_R(0)$) leading to a monoculture of species R and a monoculture of species C for different initial nutrient levels ($N(0)$). The monoculture of each species is realized for values of $p_C(0)$ and $p_R(0)$ that lie to the left (right) of a curve that corresponds to a particular value of $N(0)$. The decomposability of each species is as follows: $e_C = 3.0$, $e_R = 0.5$. The initial level of detritus is given by $D_1(0) = D_2(0) = (T_N - N(0) - bp_1(0) - bp_2(0))/2$, and other parameters are described in Fig. 2 (a). (b–e) These panels provide examples of soil–vegetation codevelopment leading to a monoculture of species R (b and c) and a monoculture of species C (d and e). These panels illustrate the dynamics of the proportion of patches occupied by each species ($p_C(t)$ and $p_R(t)$ in b and d) and nutrient levels ($N(t)$ in c and e), which were numerically calculated. Parameters used are as follows: (b–c) $p_C(0) = 0.2$, $p_R(0) = 0.3$, and $N(0) = 0.01$; (d–e) $p_C(0) = 0.4$, $p_R(0) = 0.1$, and $N(0) = 0.01$. Other parameters are described in (a).

It is notable that the boundaries separating these regions (E_C^* and E_R^*) are shifted by environmental factors, that is, a larger decomposition efficiency (s_D) or a larger amount of total nutrients in the system (T_N) lowers E_C^* and E_R^* ($\partial E_C^*/\partial s_D < 0$, $\partial E_C^*/\partial T_N < 0$, $\partial E_R^*/\partial s_D < 0$, $\partial E_R^*/\partial T_N < 0$).

Therefore, species composition depends on environmental factors. Suppose that the decomposability of the two species is given by e_c and e_r . When system fertility (T_N) is sufficiently large, E_C^* and E_R^* are small enough such that $e_c > E_C^*$ and $e_r > E_R^*$. Thus, species C grows in a monoculture (region

C). When T_N is sufficiently small, E_C^* and E_R^* are large enough such that $e_c < E_C^*$ and $e_r < E_R^*$, and species R therefore persists alone (region B). Further, multiple equilibria (regions D and E) can be realized only when T_N (and thus E_C^* and E_R^*) are intermediate (e.g. in region E, $e_r < E_R^* < E_C^* < e_c$). The decomposition efficiency (s_D) also has similar effects on species composition.

DISCUSSION

The litter feedback effect of an individual species on nutrient cycling may be either positive, by leading to the nutrient level in which the species is dominant and can prevent other species from invading, or negative, by leading to the nutrient level that facilitates the invasion of competitors. The type of feedback effect depends on the decomposability of the invaded species, the relative competitive ability of the invaded and invading species, and the reproductive abilities of both. For a superior competitor that has low reproductive ability (species C), which is favoured at high nutrient concentration levels, high decomposability provides a positive litter feedback effect, whereas low decomposability leads to negative feedback. In contrast, for an inferior competitor with high reproductive ability (species R), which is favoured at low nutrient concentration levels, high decomposability provides a negative feedback effect, while low decomposability provides positive feedback.

The litter feedback effect, which is influenced by decomposability, affects the competitive outcome and may allow distinct vegetation to emerge under abiotically identical environments. When the litter feedback of both species is positive (species C is highly decomposable and species R is poorly decomposable; region E), an increase in the abundance of either species reinforces the advantages of that species, and the two species therefore do not coexist. Such system dynamics lead to a monoculture of either species, and the one that increases first tends to be dominant. The system always approaches a unique equilibrium for any initial state if N^* is held constant; thus, the founder effect should be a product of litter feedback effects (see Hastings 1980; Tilman 1994). When the litter feedback of both species is negative (species C is poorly decomposable and species R is highly decomposable; regions A and Aa), it acts as a mechanism to generate a minority advantage, and therefore coexistence of the two species is easily attained.

Multiple steady states with different species richness or composition may exist when the litter feedback effect of one species is positive and that of the other species is negative (region D). This implies the possibility that pulse perturbations, such as fire or deforestation, may cause irreversible changes in species richness or composition and nutrient cycling within the system. In some ecosystems, perturbations like fire alter species composition and nutrient cycling

without the loss of nutrients from the system (Mack *et al.* 2001). This situation is similar to one presented in our model (where T_N is constant but vegetation could change), but differs completely from situations predicted by earlier patch-occupancy models without nutrient cycling dynamics (i.e. setting N^* in eqn 1 to a constant value; see Hastings 1980; Tilman 1994). With such a model, the system is predicted to persist (see Stone 1995) against any magnitude of pulse perturbation. However, this no longer holds true if we consider nutrient cycling dynamics, because a perturbation within the system can alter its nutrient cycle, which is an essential determinant of the vegetation.

It is debatable whether different species-level effects on nutrient cycling cause significant differences in ecosystem-level and community-level properties (e.g. vegetation and nutrient cycling). Our model reveals that the importance of species-level traits depends on environmental conditions such as system fertility (T_N). When the fertility of the system is intermediate, species-level traits play a central role in determining nutrient levels and vegetation. Decomposability effects generate minority advantages that lead to species coexistence, or the founder effect that results in multiple alternative equilibria. However, this is not always true. Sufficiently low or sufficiently high system fertility obscures the different roles of species-specific decomposability, because in these cases, decomposability cannot change nutrient levels enough to alter species composition. Instead, the system always reaches a unique equilibrium (species composition) that is determined by T_N . This trend lends support to the hypothesis that system fertility determines vegetation composition, and that individual species have little effect on ecosystem-level properties (Wedin & Tilman 1993).

Species with low nutrient requirements (species R in this model) tend to conserve growth-limiting nutrients within their tissues and produce nutrient-poor litter with relatively low decomposability. In contrast, species that invest much into photosynthetic tissues and have the ability to rapidly convert nutrient uptake into biomass production (species C) tend to produce nutrient-rich, highly decomposable litter, and their nutrient requirements are generally high (Berendse *et al.* 1989; Berendse 1990). These trends might imply a negative correlation between reproductive rate (c_i) and decomposability (e_i). Although the generality of such a correlation is unclear from available empirical studies (Vitousek *et al.* 1994; Aerts & De Caluwe 1997), if such a negative correlation were to exist, then litter feedback effects would tend to be positive in the real world; a large c_i implies low nutrient requirement levels. Species richness could then be maintained at a spatial scale larger than the scale of diffusion of nutrients or detritus. In other words, nutrient concentration levels are heterogeneous over space because of localized litter feedback effects (a high nutrient level around species C, and a low nutrient level around

species R; region E), and each species persists where it performs best (see Tilman & Pacala 1993; Van der Putten 1997).

In summary, we have proposed a hypothesis describing how vegetation and nutrient cycling codevelop and interactively structure ecosystems. Litter feedback effects have the potential to determine community structure, community stability against invasion, and stability of community composition against extrinsic disturbance. In addition, they may generate multiple stable states with different community composition or species richness. Further environmental conditions have influences on the importance of species-level effects on nutrient cycling. These hypotheses should be tested. However, there have been few studies that simultaneously examined the effects of decomposition and nutrient uptake on community properties. Moreover, the time frame of some exceptional experimental studies (Wedin & Tilman 1993) seems too short to examine recycling effects. To test hypotheses on the codevelopment of soil and vegetation, it is necessary to conduct a long-term experiment of multiple species (see Matson 1990), undertaken with precise knowledge of their characteristics, including litter decomposability, under controlled environmental conditions.

APPENDIX 1

We analysed the local stability at the equilibrium points (p_1^* , p_2^* , D_1^* , D_2^*) of a dynamic system governed by eqns 1, 2, and 4. There are four equilibria in regard to plant species composition: $F_0(p_1^* = 0, p_2^* = 0)$, $F_1(p_1^* > 0, p_2^* = 0)$, $F_2(p_1^* = 0, p_2^* > 0)$, and $F_3(p_1^* > 0, p_2^* > 0)$. We calculated the eigenvalues of the Jacobian matrix evaluated at each equilibrium point.

We checked the signs of the eigenvalues explicitly with respect to equilibrium points F_0 – F_2 . Jacobian eigenvalues at F_0 were positive; if $c_1 T_N - m > 0$ or $c_2 T_N - m > 0$, then F_0 is always locally unstable. We obtained the necessary and sufficient conditions for local stability of F_1 , given by:

$$N^* > c_2 m / c_1^2 \quad (\text{A.1})$$

from Jacobian values at F_1 . Similarly, F_2 exists and is locally stable when

$$m / c_2 < N^* < m / c_1. \quad (\text{A.2})$$

Regarding the coexistence equilibrium F_3 , the condition for existence of F_3 ($p_1^* > 0, p_2^* > 0$) is given by:

$$a_1 \equiv m / c_1 < N^* < c_2 m / c_1^2 \equiv a_2. \quad (\text{A.3})$$

Although we determined the local stability of F_3 with the Routh–Hurwitz criterion for its Jacobian matrix (Appendix 2), we could not explicitly convert it to the equivalent condition that N^* should satisfy.

APPENDIX 2

We calculated the nutrient level N^* for each equilibrium. There are four equilibria in regard to plant species composition: $F_0(p_1^* = 0, p_2^* = 0)$, $F_1(p_1^* > 0, p_2^* = 0)$, $F_2(p_1^* = 0, p_2^* > 0)$, and $F_3(p_1^* > 0, p_2^* > 0)$.

For $F_0(p_1^*, p_2^*) = (0, 0)$, $D_1^* = D_2^* = 0$ and then $N^* = T_N$.

For F_j ($j = 1, 2, 3$), by setting the right-hand side of eqns 1 and 3 equal to zero, we solved p_j^* and D_j^* with N^* . Substituting these values into eqn 4 yielded quadratic equations of N^* in each equilibrium as:

$$f_j(N^*) \equiv \alpha_j N^{*2} + \beta_j N^* + \gamma_j = 0, \quad (\text{A.4})$$

where the coefficients $\alpha_j, \beta_j, \gamma_j$ depend on j ($= 1, 2, 3$).

For $j = 1$, these coefficients are given by

$$\begin{aligned} a_1 &= c_1(s_D e_1 + h_1), \\ \beta_1 &= c_1(b(s_D e_1 + m) + l_0 - m h_1 / c_1 - s_D e_1 T_N), \\ \gamma_1 &= -b m (s_D e_1 + m) - l_0 m. \end{aligned}$$

The quadratic eqn A.4 for F_1 has a root satisfying A.1 only when $f_1(a_2) < 0$. This is reduced to the following inequality:

$$\begin{aligned} s_D c_2 \{T_N - b(1 - c_1 / c_2) - c_2 m / c_1^2\} \cdot e_1 \\ > (c_2 - c_1) \cdot (b m + l_0 + c_2 m h_1 / c_1^2). \end{aligned} \quad (\text{A.5})$$

If $T_N > b(1 - c_1 / c_2) + c_2 m / c_1^2$, this is equivalent to $e_1 > E_1^*$, but if $m / c_1 < T_N < b(1 - c_1 / c_2) + c_2 m / c_1^2$, the expression A.5 does not hold and the quadratic equation does not have a root satisfying A.1.

Similarly, for $j = 2$, these coefficients are given by:

$$\begin{aligned} \alpha_2 &= c_2(s_D e_2 + h_1), \\ \beta_2 &= c_2(b(s_D e_2 + m) + l_0 - m h_1 / c_2 - s_D e_2 T_N), \\ \gamma_2 &= -b m (s_D e_2 + m) - l_0 m. \end{aligned}$$

The quadratic eqn A.4 for F_2 has a root satisfying A.2 only when $f_2(a_2) > 0$. This is reduced to the following inequality:

$$\begin{aligned} s_D c_2 \{T_N - b(1 - c_1 / c_2) - m / c_1\} \cdot e_2 \\ < (c_2 - c_1) \cdot (b m + l_0 + m h_1 / c_1). \end{aligned} \quad (\text{A.6})$$

If $T_N > b(1 - c_1 / c_2) + m / c_1$, this is equivalent to $e_2 < E_2^*$, but if $m / c_1 < T_N < b(1 - c_1 / c_2) + m / c_1$, the expression A.6 always holds true and the quadratic equation always has a root satisfying A.2.

For $j = 3$, we obtained coefficients as follows:

$$\begin{aligned} \alpha_3 &= h_1 c_1 c_2 e_2 - c_1^2 e_1 (b c_1 + h_1) + s_D e_1 e_2 c_1 c_2, \\ \beta_3 &= b c_1 c_2 e_2 (m + s_D e_1) - h_1 m c_2 e_2 + m c_2 e_1 (b c_1 + h_1) - b s_D e_1 e_2 c_1^2 \\ &\quad - T_N c_1 c_2 e_1 e_2 s_D + c_1 h_0 (c_2 e_2 - c_1 e_1), \\ \gamma_3 &= -b m^2 c_2 e_2 + m c_2 h_0 (e_1 - e_2). \end{aligned}$$

We obtained the following

$$f_3(a_1) > 0 \Leftrightarrow \text{inequality} \quad (\text{A.6})$$

and

$$f_3(a_2) < 0 \Leftrightarrow \text{inequality} \quad (\text{A.5})$$

Although these expressions imply that N^* satisfies (A.3) in regions A (and Aa) and E, we show that F_3 is locally unstable in region E through the numerical solution of eqn (A.4) and the Routh–Hurwitz criterion for its Jacobian matrix when $l_0 = l_1 = 0$. In regions A and D, F_3 is locally stable whereas F_3 is unstable in region Aa; an attracting limit cycle emerges and the coexistence of the two species is realized by oscillations in some parameters ($c_2 - c_1 \gg 0$, etc.). Pictures obtained by numerical calculations with different parameter values were qualitatively the same.

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