

# An ecosystem organization model explaining diversity at an ecosystem level: Coevolution of primary producer and decomposer

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Ecological complexity of species interactions and habitat heterogeneity creates and maintains biodiversity at a trophic level in an ecosystem. This biodiversity simultaneously serves as raw material on which selective forces for organizing ecosystems operate. As a result of this organization process, differences in structure and functioning of ecosystems (diversity at ecosystem level) are generated. Although understanding diversity at the ecosystem level has attracted great interest, recent theoretical advances toward this aim have not been fully appreciated yet. Following Higashi *et al.* (1993), this report presents a theoretical framework that deals with the organization process of an ecosystem as a consequence of the interactions among its biotic components and their modification of ecological traits. Specifically, the ecosystem organization process of a terrestrial ecosystem is analyzed, including primary producers and decomposers. This model sheds new insight into the differences between temperate and tropical forest ecosystems.

**Key words:** decomposer; diversity at ecosystem level; ecosystem organization; network coevolution; producer.

## INTRODUCTION

The importance of understanding mutual interaction between biodiversity and ecological complexity (i.e. complexity of species interactions and habitat heterogeneity) is now widely recognized and intensive research has emerged based on this topic (e.g. Lawton 1997). Ecological complexity creates and sustains biodiversity at a trophic level in an ecosystem (e.g. diversity of phytoplankton in a freshwater ecosystem, tree diversity in a forest, diversity of decomposers in a soil ecosystem, etc.), while biodiversity in turn increases ecological complexity in a variety of ways.

Biodiversity at a trophic level, together with genetic diversity, serves as raw material on which

selective forces for organizing ecosystems can operate. As a result of the ecosystem organization process, each ecosystem acquires its characteristic structure and functioning. In other words, differences between ecosystem properties are generated (*diversity at ecosystem level*); for example, differences between temperate and tropical forests, and differences between terrestrial and aquatic ecosystems. This diversity at the ecosystem level has attracted ecological and evolutionary interests. For example, Abe and Higashi (1991) proposed a hypothesis that the basic differences between terrestrial and aquatic ecosystems emerged from the fact that terrestrial plants invest more of their primary production in cellulose as cell walls than do aquatic algae. Polis (1999) reviewed the recent advances on this topic; that is, differences between terrestrial and aquatic ecosystems.

Although understanding diversity at the ecosystem level has attracted great interest, recent theoretical advances toward this aim have not been fully appreciated yet. Historically, to describe and predict macroscopic trends in the energy and flux of an ecosystem during its organization process,

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a number of phenomenological and holistic hypotheses or theories have been proposed in terms of various *optimality principles*, such as maximum energy flux (Lotka 1922a,b), power (Odum 1983), maturity (Margalef 1968; Tansky 1976), ascendancy (Ulanowicz 1986), and nutrient cycling (Finn 1982). However, the mechanistic bases for these optimality principles had to wait until Higashi *et al.* (1993), who were the first to attempt to formulate a theory on the mechanistic bases of ecosystem organization.

Higashi *et al.* (1993) considered a model ecosystem that consisting of four aggregated components (plant, dead organic matter, decomposer, and nutrient pool), connected by flows of nutrients to each other. Using this system, they developed a new theoretical method to investigate ecosystem organization that is driven by resource competition among organisms. Their method gave us an intuitive technique with which we could then analyze how a change in the value of an ecosystem component (caused by a succession of species or the (co)evolution of (a) species) alters the network pattern of ecosystem flows and stocks, and how such changes may successively cause a change in the value of another ecosystem component. In terms of the *producer–decomposer matching*, represented as the matching race between the uptake rate of nutrients by plants and the decomposition rate of decomposers, a key concept of *network coevolution* was proposed as a mechanism for self-organization of an ecosystem that builds up the system toward a biologically richer regime.

Loreau (1998) noticed the importance of spatial heterogeneity for ecosystem organization and developed a model of material cycle to explain trends in holistic maximum principles by using a mechanistic approach. In addition to resource competition between organisms in a material cycle (*within-cycle competition*), he stressed that another selective force may operate on an ecosystem in partly contradictory direction to the within-cycle competition; that is, competition between organisms that are involved in spatially distinct cycles (*between-cycle competition*). de Mazancourt *et al.* (1998) and de Mazancourt and Loreau (2000) extended this idea to a more complex model on *grazing optimization*, which can account for the combined effects of within- and between-cycle competition on an ecosystem.

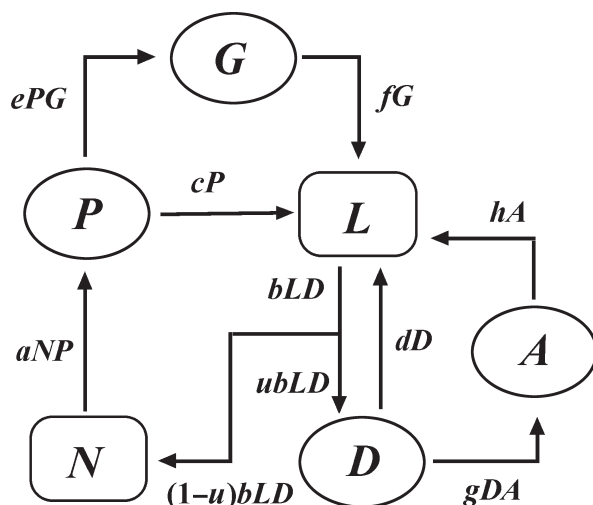


Fig. 1. A model ecosystem consisting of six compartments, which are connected to each other by flows of nutrient transfer.

In the present report, following Higashi *et al.* (1993), we propose a terrestrial ecosystem model that includes producers and decomposers, in which we can calculate explicitly the coevolutionary outcomes of plants and decomposers and their effects on an ecosystem's structure and functioning. The theoretical framework, key concepts and general results obtained using this method are explained and summarized along with our present model. Finally, we show that this model sheds new insights into the differences between temperate and tropical forest ecosystems.

## AN ECOSYSTEM MODEL WITH NUTRIENT CYCLING

Consider the terrestrial ecosystem model depicted in Fig. 1. This consists of six compartments: (i) primary producer ( $P$ ); (ii) litter ( $L$ ); (iii) decomposer ( $D$ ); (iv) nutrient pool ( $N$ ); (v) grazer ( $G$ ); and (vi) consumer of decomposer ( $A$ ), which are all connected by flows of nutrient transfer. The variables  $P$ ,  $L$ ,  $D$ ,  $N$ ,  $G$ , and  $A$  denote the standing stocks in nutrient content of the corresponding compartments.

Each resource exploitation by organisms  $P$ ,  $D$ ,  $G$ , and  $A$  is assumed to be proportional to the stock of the organism and its corresponding resource ( $a$ ,  $b$ ,  $e$ , and  $g$  are the respective coefficients), and each stock loss of the organisms  $P$ ,  $D$ ,  $G$ , and  $A$  is

proportional to its standing crop ( $c$ ,  $d$ ,  $f$ , and  $b$  are the respective coefficients). A fraction  $u$  of the flow  $bLD$  is utilized by the decomposer, the rest  $(1 - u)$  being recycled into the nutrient pool ( $N$ ).

The dynamics of this model are given by the following set of differential equations simply by setting the time derivatives of standing stock equal to the sum of inflows minus the sum of outflows for each compartment in Fig. 1

$$\frac{dP}{dt} = aNP - cP - ePG \quad (1a)$$

$$\frac{dL}{dt} = cP + fG + dD + bA - bLD \quad (1b)$$

$$\frac{dD}{dt} = ubLD - dD - gAD \quad (1c)$$

$$\frac{dN}{dt} = (1 - u)bLD - aNP \quad (1d)$$

$$\frac{dG}{dt} = ePG - fG \quad (1e)$$

$$\frac{dA}{dt} = gDA - bA \quad (1f)$$

## EQUILIBRIUM OF THE ECOSYSTEM

At steady state, the time derivatives in equation 1 vanish. Equating the equations 1a–f as zeros, with conservation of the total nutrient:  $P + L + D + N + G + F + A = \text{Constant} = M$ , provides the equilibrium stocks denoted by the asterisk:

$$P^* = f/e \quad (2a)$$

$$D^* = b/g \quad (2b)$$

$$N^* = \frac{M + c/e + d/g - f/e - b/g}{1 + a/e + (u + g/b)fa/\{(1 - u)be\}} \quad (2c)$$

$$G^* = (aN^* - c)/e \quad (2d)$$

$$L^* = \frac{M + c/e + d/g - f/e - b/g}{1 + ub/g + (1 + e/a)(1 - u)bb/(fg)} \quad (2e)$$

$$A^* = (ubL^* - d)/g \quad (2f)$$

Our numerical simulations assure the stability of the equilibrium over wide ranges of parameters. Hence, we assume that the equilibrium is globally stable.

Parameter dependencies of equilibrium values, which are a basis for the analysis of ecosystem organization in the following sections, can be calculated from equations 2a–f. Because primary production and decomposition are the most essential processes in nutrient cycling, hereafter, we focus on the effects of two parameters: (i) the *nutrient uptake rate of primary producers* ( $a$ ); and (ii) the *decomposition rate of decomposers* ( $b$ ) on an ecosystem's structure and functioning. From equation 2a–f, we can show:

$$\frac{\partial G^*}{\partial a} > 0, \frac{\partial A^*}{\partial a} > 0, \frac{\partial G^*}{\partial b} > 0, \frac{\partial A^*}{\partial b} > 0 \quad (3a)$$

$$\frac{\partial N^*}{\partial a} < 0, \frac{\partial L^*}{\partial a} > 0, \frac{\partial N^*}{\partial b} > 0, \frac{\partial L^*}{\partial b} < 0 \quad (3b)$$

The standing crops of consumers ( $G^*$  and  $A^*$ ) are enhanced with increasing  $a$  or  $b$  (equation 3a), whereas those of producers and decomposers ( $P^*$  and  $D^*$ ) remain unaffected (equations 2a,b). As to non-living parts, the amount of nutrient pool ( $N^*$ ) decreases, whereas that of the dead organic matter ( $L^*$ ) increases with increasing  $a$ , and the contrary holds with increasing  $b$  (equation 3b).

From the aforementioned results of equations 2 and 3, when either  $a$  or  $b$  increases, the total stock of living organisms ( $B = P^* + G^* + D^* + A^*$ ) is enhanced whereas the total stock of non-living parts ( $N^* + L^* = M - B$ ) is reduced, leading to an increase of the ratio  $B/M$ . Furthermore, both the gross primary production ( $aN^*P^*$ ) and the gross decomposition ( $bL^*D^*$ ) are enhanced by increases in either  $a$  or  $b$ . This means that an activation of either of the primary production or the decomposition process enhances both of them and, as a result, the ecosystem changes to one with a higher turnover rate of nutrient cycling with more material allocated to living components. Note that a parameter change in a flow affects not only standing crops *directly* connected by the flow, but also all standing crops and flows through *indirect effects*, as shown by Higashi *et al.* (1993).

## EVOLUTIONARY RESPONSE OF AN ECOSYSTEM COMPONENT

Ecosystem parameters, which determine an ecosystem's properties and are represented by the nutrient uptake rate ( $a$ ) and the decomposition rate ( $b$ ),

have their basis on: (i) physical conditions of the ecosystem; and (ii) physiological traits of organisms that constitute the ecosystem. Thus, these parameter values change (and, as a result, the ecosystem changes) when either physical conditions change or physiological traits of organisms change through ecological succession or genetic (co)evolution. In each ecosystem component of living parts, organisms with different traits compete for resources with each other. Provided that succession proceeds as a result of species invasion and competitive replacement of species, this process may be approximated by a shifting trajectory of steady-state ecosystems. Thus, the argument of genetic evolution can be applied to ecological succession, and the notion of *Evolutionarily Stable Strategy* (ESS; Maynard Smith & Price 1973) is useful for finding the successive outcome of an ecosystem. Therefore, hereafter, we use the word ‘evolution’ and its related terms in evolutionary ecology as including succession. These ideas are the mechanistic bases of the ecosystem organization theory, which was first used by Higashi *et al.* (1993). In the following, we construct a model of an ecosystem functioning along this line.

The nutrient uptake rate ( $a$ ) is assumed to be composed of two factors:  $a = a_0\alpha$ ; that is, the physical factor ( $a_0$ ) and the trait of producers ( $\alpha$ ). Here, we consider a situation in which plants with high photosynthetic efficiency and high rates of growth tend to have a short leaf lifespan and high individual mortality (e.g. Chabot & Hicks 1982; Williams *et al.* 1989). The easiest way to represent this situation would be to introduce a trade-off in plant traits for the nutrient uptake rate ( $\alpha$ ) and the loss rate of primary producers ( $c$ ), which correlates positively with the growth rate of plants. Assuming a non-linear increase in  $c$  with increasing  $\alpha$  as a result of cumulative cost to extremely high value, we insert  $c(\alpha) = c_0 + c_1\alpha^2/2$  as the simplest function for the loss rate,  $c$ .

The same assumption can be applied to the decomposition rate ( $b$ ):  $b = b_0\beta$ , in which  $b_0$  is the physical factor and  $\beta$  is the trait of decomposers. Similarly, a trade-off in the decomposer’s traits for the decomposition rate ( $\beta$ ) and the its death rate ( $d$ ) is assumed following the trade-off in plant traits ( $\alpha$ ) and ( $c$ ), as  $d(\beta) = d_0 + d_1\beta^2/2$ .

From equation 1a, the per capita growth rate of the plant standing crop is  $aN - c - eG$ . Therefore,

the *fitness* of a producer (here, *producer* refers to a mutant or single species) with trait value  $\alpha$  in the population that is dominated by producers with an identical trait value  $\alpha^*$ , is given as:

$$W_p = a_0\alpha N^* - (c_0 + c_1\alpha^2/2) - eG^* \quad (4)$$

where  $N^*$  and  $G^*$  are equilibrium values represented by equations 2c and 2d, in which  $a = a_0\alpha^*$ . Likewise, from equation 1c, the fitness of a decomposer with  $\beta$  in the population that is dominated by decomposers with an identical trait value  $\beta^*$ , is given as:

$$W_D = b_0\beta L^* - (d_0 + d_1\beta^2/2) - gA^* \quad (5)$$

where  $L^*$  and  $A^*$  are equilibrium values represented by equations 2e and 2f, in which  $b = b_0\beta^*$ .

An ESS is defined as a value of trait  $\alpha$  such that once the organism with  $\alpha^*$  prevails, an organism with any value  $\alpha$  other than  $\alpha^*$  cannot invade the population. The ESS values  $\alpha^*$  and  $\beta^*$  should satisfy the condition that  $W_p$ , as a function of  $\alpha$ , takes its maximum value at  $\alpha = \alpha^*$ ;  $\left. \frac{\partial W_p}{\partial \alpha} \right|_{\alpha=\alpha^*} = 0$

and that  $W_D$ , as a function of  $\beta$ , takes its maximum value at  $\beta = \beta^*$ ;  $\left. \frac{\partial W_D}{\partial \beta} \right|_{\beta=\beta^*} = 0$ , respectively

(Maynard Smith 1982). This leads to the following two equations:

$$a_0N^* = c_1\alpha^* \quad (6)$$

$$b_0L^* = d_1\beta^* \quad (7)$$

Inserting  $a = a_0\alpha^*$  and  $b = b_0\beta$  in equation 2c and applying it to equation 6, we have a quadratic equation for  $\alpha^*$ :

$$\left\{ 1 + \left( u + \frac{g}{b_0\beta} \right) \frac{2f}{(1-u)b} \right\} \alpha^{*2} + 2 \frac{e}{a_0} \alpha^* - \left( \frac{2emg + ed_1\beta^2}{c_1g} \right) = 0 \quad (8)$$

where

$$m = M + \frac{c_0}{e} + \frac{d_0}{g} - \frac{f}{e} - \frac{b}{g} \quad (9)$$

Equation 8 is explicitly solved with respect to  $\alpha^*$  as a function of  $\beta$ :

$$\alpha^*(\beta) = \frac{-\frac{e}{a_0} + \sqrt{\left(\frac{e}{a_0}\right)^2 + r\left(\frac{2emg + ed_1\beta^2}{c_1g}\right)}}{r} \quad (10)$$

where  $r = \left\{1 + \left(u + \frac{g}{b_0\beta}\right)\frac{2f}{(1-u)b}\right\}$

Similarly, putting  $b = b_0\beta^*$  and  $a = a_0\alpha$  in equation 2e and applying it to equation 7, we have a quadratic equation for  $\beta^*$ :

$$\left\{1 + \left(1 + \frac{e}{a_0\alpha}\right)\left(\frac{(1-u)2b}{uf}\right)\right\}\beta^{*2} + 2\frac{g}{ub_0}\beta^* - \left(\frac{2emg + gc_1\alpha^2}{d_1e}\right) = 0 \quad (11)$$

which is explicitly solved with respect to  $\beta^*$  as a function of  $\alpha$ :

$$\beta^*(\alpha) = \frac{-\frac{g}{ub_0} + \sqrt{\left(\frac{g}{ub_0}\right)^2 + s\left(\frac{2emg + gc_1\alpha^2}{d_1e}\right)}}{s} \quad (12)$$

where  $s = 1 + \left(1 + \frac{e}{a_0\alpha}\right)\left(\frac{(1-u)2b}{uf}\right)$

Equation 10 represents the evolutionary stable response of plants through evolution or succession when decomposers do not undergo evolution or ecological succession. From equations 8 and 10, we can see that  $\alpha^*$  is an increasing function of  $\beta$  where  $\alpha^*$  is proportional to  $\sqrt{\beta}$  when  $\beta$  is small and increases linearly with  $\beta$  when  $\beta$  is large. This means that the evolutionary stable response, thus the primary productivity of the ecosystem, is enhanced as the response of the decomposer is enhanced. The same logic holds for  $\beta^*$  as a function of  $\alpha$ . The functions  $\alpha^*(\beta)$  and  $\beta^*(\alpha)$  can be illustrated in  $(\alpha, \beta)$  space, as shown in Fig. 2.

### ECOSYSTEM ORGANIZATION PROCESS

Three topics that are related to ecosystem organization: (i) autonomous ecosystem development; (ii) diversity at ecosystem level; and (iii) ecosystem

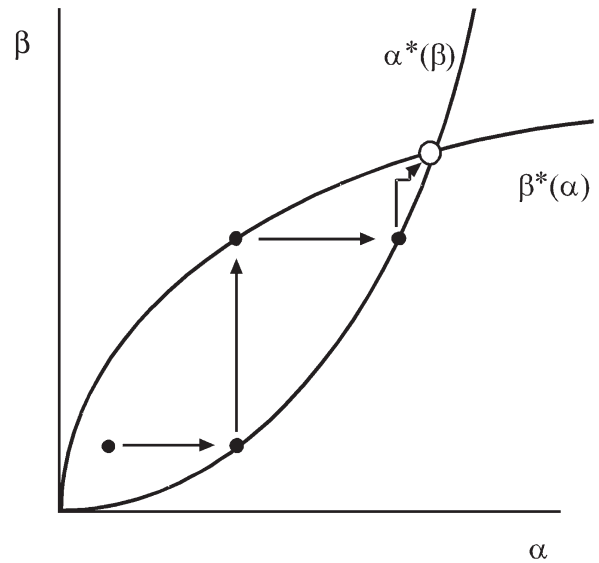


Fig. 2. Starting from small values of traits for the nutrient uptake rate ( $\alpha$ ) and for the decomposition rate ( $\beta$ ), the system approaches a coevolutionary stable state (CSS), which is the intersection of two ESS curves,  $\alpha^*(\beta)$  and  $\beta^*(\alpha)$ .

transition due to environmental changes, are explained using this model.

### Autonomous ecosystem development to a richer regime

Autonomous ecosystem development to a richer regime in a constant environment can be understood mechanistically.

Assume that an ecosystem begins with plants having small  $\alpha$  and decomposers having small  $\beta$ . This ecosystem is *poor* in the sense that the total stock of living organisms ( $B = P^* + G^* + D^* + A^*$ ), the gross primary production ( $aN^*P^*$ ), and the gross decomposition ( $bL^*D^*$ ) are all small in amount. As shown in Fig. 2,  $\alpha$  evolves to  $\alpha^*(\beta)$  if evolution of the plant trait occurs. If evolution of the decomposer trait occurs afterwards,  $\beta$  evolves to  $\beta^*[\alpha^*(\beta)]$ . Comparing slopes of linear approximation for  $\alpha^*(\beta)$  and  $\beta^*(\alpha)$ , we can show that the graphs of  $\alpha^*(\beta)$  and  $\beta^*(\alpha)$  intersect at a point, which represents a *Coevolutionary Stable State* (CSS; Roughgarden 1983; Matsuda & Namba 1989). The alternate evolution of plants and decomposers finally moves the system to this CSS. As is shown by the arguments in the previous section, as  $\alpha^*(\beta)$  and  $\beta^*(\alpha)$  increases, the total stock of living



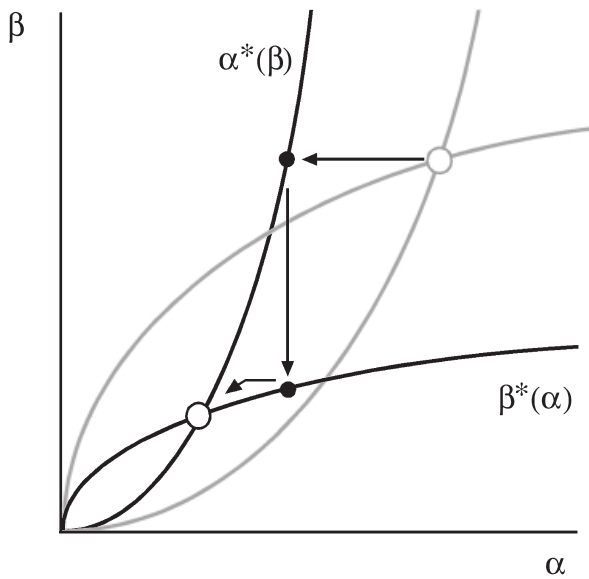


Fig. 3. When environmental conditions change drastically, evolutionarily stable strategy (ESS) curves change so that the system at a coevolutionary stable state (CSS) (intersection of two gray ESS curves) moves to a new CSS (intersection of two black ESS curves), which correspond to the new environment.

organisms ( $B$ ), the gross primary production ( $aN^*P^*$ ), and the gross decomposition ( $bL^*D^*$ ) are enhanced through the increase in the nutrient uptake rate ( $a^*$ ) and the decomposition rate ( $b^*$ ). Thus, the ecosystem develops to a *richer* regime.

We propose that the trait of an organism (plant or decomposer) evolves at a higher level when the two traits coevolve rather than when only one trait evolves. This fact emerges from properties of the functions  $\alpha^*(\beta)$  and  $\beta^*(\alpha)$ ; the optimal plant trait increases when the decomposer trait increases and vice versa; that is, the two compartments mutually facilitate one another, leading to a richer ecosystem. This process of *mutual facilitation* between primary producers and decomposers has been named *flow matching* by Higashi *et al.* (1993).

### Diversity at ecosystem level

The differences between ecosystems in different environmental conditions (i.e. diversity at ecosystem level) can be understood as the result of ecosystem organization in different environmental conditions.

Ecosystems in different environmental conditions could be driven to different coevolutionary goals (CSS). Referring to the model proposed by

us in this report, equations 10 and 12 show that an increase in either of the physical factors  $a_0$  or  $b_0$  enhances both  $\alpha^*$  and  $\beta^*$ ; hence, the values at the CSS, which are represented by the intersection of the ESS curves  $\alpha^*(\beta)$  and  $\beta^*(\alpha)$ , are also enhanced (see Fig. 3). Thus, an ecosystem develops to a richer regime when its physical condition is physiologically more favorable. A difference in one physical condition of a compartment in the ecosystem brings about changes in the traits of other compartments through networks of material flows. This repercussion effect is a general feature of ecosystem organization (*network coevolution perspective* described by Higashi *et al.* 1993).

### Ecosystem transition due to environmental change

When environmental conditions change, an ecosystem at a CSS can be destabilized. Then the ecosystem responds to this change by *reorganization* and transits to a new CSS.

Environmental conditions may change over ecological and geological time scales. Assume that an ecosystem staying at a CSS suffers a drastic environmental change, such as a severe temperature decline. In the model we propose here, for simplicity, we assume only  $a_0$  drastically decreases from a physiologically favorable condition  $a_{01}$  to a less favorable condition  $a_{02}$  ( $a_{01} > a_{02}$ ). Figure 3 shows two sets of curves representing  $\alpha^*(\beta)$  and  $\beta^*(\alpha)$ ; gray ones corresponding to  $a_{01}$  and black ones to  $a_{02}$ . As is seen easily from equations 10 and 12, the new CSS is located below and to the left of the previous ESS, as shown in Fig. 3.

Ecosystem reorganization proceeds in three steps. Here, we show an alternate evolution scenario, as indicated by the arrows in Fig. 3. First, the nutrient uptake rate of producers  $a = a_0\alpha$  decreases as a direct physiological response to the environmental change in  $a_0$ . In the second step, producers respond evolutionarily to the decrease in physical condition  $a_0$  by reducing the trait value  $\alpha^*(\beta)$  from the point indicated by the circle on the previous CSS to the point on the new  $\alpha^*(\beta)$ . Third, decomposers respond evolutionarily by reducing the trait value  $\beta$  to the point on the new  $\beta^*[\alpha^*(\beta)]$ . These alternate evolutionary responses by producers and decomposers in the third step continue until the state converges to the new CSS. A more complicated scenario of ecosystem

reorganization is possible; however, neither of the traits  $\alpha^*(\beta)$ ,  $\beta^*(\alpha)$  increases during its trajectory. Thus, the ecosystem shrinks to a *poor* structure during its reorganization process.

## DISCUSSION

So far, a theoretical framework to deal with the organization process of an ecosystem has been explained along a model ecosystem (equations 1a–f). The theoretical procedure developed by Higashi *et al.* (1993) and extended in the present paper is summarized in the following six steps:

1. Build an ecosystem model and find its steady state structure in terms of stocks and flows at equilibrium (which corresponds to equations 1 and 2 in the model we propose).
2. Relate physical conditions and/or traits of organisms that affect ecosystem functioning with parameters of ecosystem functioning [e.g. corresponding to the relationship between nutrient uptake rate ( $a$ ) and the physical factor ( $a_0$ ), the organism's trait ( $\alpha$ ):  $a = a_0\alpha$ ].
3. Build a fitness function for each organism and apply the evolutionary dynamics method to each ecosystem component to find its ESS response (which corresponds to equations 4–12).
4. Apply the network coevolution concept (mutual facilitation in a flow network through indirect effects) to the ecosystem components to find CSS.
5. Translate the (co)evolutionary responses of species into changes in ecosystem parameters by the relationships constructed in step 2.
6. Calculate the changes in ecosystem structure and functioning at its steady state by the equations constructed in step 1 (which correspond to equations 2 and 3).

The essence of this method is to: (i) connect ecosystem structure and functioning with its physical environment and traits of organisms; then (ii) find the ecosystem organization as a consequence of competitive replacement of organisms in each ecosystem component, to which theories of evolutionary dynamics is applicable.

The model developed so far is a conceptual one. It provides mechanistic bases on how an ecosystem organization proceeds dynamically in constant and

changing environments and reveals mechanistic bases for various maximum principles (see Loreau 1998 for further discussion on this topic). Model assumptions such as choice of compartments, functions of flows, choice of evolving traits and modes of trade-offs are made rather simple, aiming at convenience for explaining the method. Thus, understanding specific biodiversity at the ecosystem level requires a more specified model. However, even the results obtained from this simple model give us useful insights for such a purpose. We show an example in the following.

Compared with temperate forest ecosystems, tropical forest ecosystems are characterized by their high productivity and rich standing stock of aboveground trees, high nutrient circulation rate, and poor stock in belowground nutrient pool (e.g. Kohyama *et al.* 1999). Traditionally, the high productivity of a tropical forest used to be explained mainly as the outcome of its rich physical conditions, such as high light intensity and temperature.

The network coevolution perspective, however, postulates a new scenario for forest ecosystem development. Mutual facilitation of aboveground producers and belowground decomposers through coevolution could have enhanced the ecosystem organization. As a result, it might have: (i) elevated the physiological activities of producers and decomposers more than the levels solely expected from their physiological conditions, such as temperature; and (ii) magnified the differences in ecosystem structure between temperate and tropical ecosystems.

We should note that mutual facilitation cannot be well driven if either biodiversity (e.g. species richness) of producers or decomposers is not supplied sufficiently. For example, if the decomposer cannot change its trait  $\beta$  in response to an increase in the producer's increment in  $\alpha$ , the evolution of producer cannot further increase its  $\alpha$  even if its own biodiversity is supplied sufficiently. This constraint on ecosystem development sheds insights into the role of biodiversity at a trophic level as *fuel* for ecosystem development. The differences in biodiversity of decomposers between temperate and tropics might have played a key role in generating the differences in the aboveground ecosystem structure and functioning between temperate and tropics.

Another useful frontier to which to apply this theoretical framework is *ecology of invasions* (Kalar

& Lodge 2001). Network coevolution approach will give insights into problems such as under what conditions an alien species succeeds to invade an ecosystem and how the effect of invasion spreads and reorganizes its ecosystem structure.

## ACKNOWLEDGEMENTS

This work is a product of the USA–UK–JAPAN Cooperative Research on the Relationship Between Biodiversity and Ecological Complexity, which is partly supported by the Ministry of Education, Culture, Sports, Science and Technology. We thank Drs S. Levin, C. Godfray and J. Lawton, the organizers of the USA and UK research groups, and the former organizer of the UK research group, for their valuable help in carrying out this project. We are grateful to Dr R. Ishii for his valuable comments in improving this manuscript.

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