Ecosystem Configurations Consequent on the Maximum Respiration Hypothesis [*]

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Abstract

The Maximum Respiration Hypothesis (MRH) asserts that matured ecosystems organize their configuration to maximize community respiration. Hence the object of the hypothesis is not individual living organisms but the whole ecosystem. In this paper we use two types of ecosystem models to show how the MRH works in ecosystems. The first is a simple theoretical model that consists of two compartments: a producer and a decomposer. The main results of this first model are as follows. (1) The model presents the community structure which is consistent with the MRH. (2) The dual solution (respiration values) presents the scarcities of different types of matter and energy in an ecosystem with maximal respiration. They operate as similar indicators to the inverse of buffer capacity. (3) The model, when extended to include two types of decomposers, can show the conditions of the coexistence and the competitive exclusion of components. Even if two biological components are strongly overlapping in their ecological niches, a slight differentiation of the ratio of matter exchanges can permit the coexistence. The competition and the coexistence are regulated by the imperative shown by the MRH. The second model is a simulation model for a hypothetical grassland ecosystem which consists of 19 biological components, and 15 kinds of matter and energy. The model includes a grazer system and a decomposer system. The main results are as follows. (1) The ecosystem configuration for biomass production, consumption, egestion, nutrient production, and respiration is presented under the MRH. It especially shows the dominance of the decomposer system. (2) Interspecific substitution guided by respiration values cause an increase in community respiration. If an inferior component undergoes a mutation to increase its production of net respiration value, the component may dominate its competitor and contribute to the increase in the community respiration. This means that the MRH can predict the working of natural selection from the macroscopic point of view.

1 Introduction

The beauty of ecosystems is due to the inconceivable number of facets that appear as we approach them for scientific analysis. One of important tasks of ecology is undoubtedly to specify the

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inherent principle which regulates functions and tendencies behind the glitter of the facets. The purpose of this paper is to present a hypothesis on the macroscopic tendency by which ecosystem configuration is organized, and to construct analytical and simulation models which are consistent with the hypothesis. This will make it possible to reveal a part of the secret of the beauty.

The fundamental hypothesis is that ecosystems tend to organize their biological configuration to maximize the total community respiration, measured in energy wasted. In other words, species which contribute to increasing the total community respiration can survive in matured ecosystems. We call it the Maximum Respiration Hypothesis (abbreviated as MRH).

The MRH is intended to describe the macroscopic aspects of ecosystem development. This type of hypothesis for ecosystems was originated by Lotka (1922). Lotka stated in that short article that natural selection operates on the living organisms which contribute to enlarging the total energy flux through ecosystem, and named it the Law of Maximum Energy Flux. Since then, many macroscopic hypotheses for ecosystems have been presented. Herendeen (1991) pointed out that the common attribute of these hypotheses is the existence of system-wide indicators and quantities. It is, however, preferable to define macro hypotheses for ecosystems as those which utilise an *aggregated* system-wide indicator, such as the total energy flux in Lotka's law.

The early stage of the development of Lotka's law started with investigating energy flows in ecosystems. Lotka's Law was rediscovered by Odum and Pinkerton (1955) and Odum(1983), and they presented the Maximum Power Principle, in which they stated that the power generated by the energy flow through ecosystem is maximized. The Energy Storage Maximizing Hypothesis presented by Hannon (1976 and 1979) stated that at the steady state condition, the amount of total energy flow for maintenance and operation per unit of total energy stored in the system is a minimum, and the total stored energy is a maximum.

The macroscopic hypotheses of ecosystems also show how the energy flow through ecosystems is connected to the organizational attributes of ecosystems. The hypothesis which placed emphasis on these organizational attributes was presented by Ulanowicz (1980 and 1986). In his theory, ascendency plays the role of a macroscopic indicator, which directly represents the organizational order or maturity of an ecosystem network.

Some authors have tried to place the macroscopic hypotheses of ecosystems in the context of the laws of thermodynamics. With respect to this aspect, the theory presented by Kay (1983), Kay and Schneider (1992) and Schneider and Kay (1993) is notable. They have reformulated the second law of thermodyanmics for nonequilibrium systems and have presented the macroscopic hypotheses of ecosystems by deduction. The hypothesis states that as ecosystems develop or mature they should increase their total dissipation, and should develop more complex structures with greater diversity and more hierarchical levels to encourage energy degradation. The other theory in this stream was presented by Jørgensen (1992) and Jørgensen and Mejer (1979). This theory, named the Ecological Law of Thermodynamics, states that ecosystems attempt to maximize the exergy embedded in their structure and to develop toward the organization with the highest efficiency. These theories are seen as an attempt to integrate the energy flow aspect and the organizational aspect of the macroscopic hypotheses of ecosystems with the second law of thermodynamics. (see also Ulanowicz and Hannon 1987)

The MRH is closely related to Kay and Schneider's theory. The community respiration is the major pathway through which fixed solar energy is degraded and dissipated as the result of its utilization. However, there is a difference between Kay and Schneider's theory and the MRH. Although Kay and Schneider's theory asserts that the highly organized structure of ecosystems is consequent on the increase of energy degradation, it seems that they beforehand integrate attributes of organization and the structure of ecosystems into their macroscopic hypothesis. This characteristic of Kay and Schneider's theory may be due to the fact that they do not present a structural ecosystem model embodying the hypothesis. On the other hand, the MRH directs its attention towards how the attributes of ecosystem structure are organized in consequence of the hypothesis. In other words, the purpose of applying Kay and Schneider's theory to ecosystem analysis is to prove the effectiveness of the restated second law of thermodynamics. On the other hand, the MRH has no general theory from which the hypothesis is deducted. The MRH is simply a synthetic hypothesis of observations that have been presented in the realm of ecology.

A general proposition is not always effective when we analyse a special fields of science with a special purpose. There is also a difference between the contents of the two theories. Kay and Schneider's theory regards evapotranspiration and respiration as the indifferent pathways of energy degradation for ecosystems. However, from the view point of the MRH, the whole ecosystem has to try to minimize evapotranspiration and to maximize the community respiration in consequence of the maximized fixation of solar energy. The evapotranspiration is only a cost for the ecosystem development. The consequences of this difference should be empirically tested from many aspects.

The models in this paper are classified into linear input-output models. Because of the complexity of ecosystem networks, it is necessary to construct an appropriate mathematical model to analyze the network (see Field, Wulff and Mann 1989). Hannon(1973) first applied the input-output model to ecosystems analysis, and many works have since been published in this field (see Hannon 1976, Finn 1976, Hannon 1979, Constanza 1980, Herendeen 1981, Constanza and Herendeen 1984, Constanza and Hannon 1989, Hannon 1991). The model in this paper is a linear programming model to embody the maximization of the community respiration. In the realm of economics, models of this type are called von Neumann models (see von Neumann 1945 and Morishima 1969). Constanza and Neill (1984) used this type of model, and they implemented resource minimization as an integrated indicator. They stated that the objective function was consistent with Hannon's Energy Storage Maximizing Hypothesis.

In this paper we use two types of ecosystem models to show how the MRH works in ecosystems. The first is a simple theoretical model that consists of two compartments: a producer and a decomposer. The main results of this first model are as follows. (1) The model presents the community structure which is consistent with the MRH. (2) The dual solution (respiration values) presents the scarcities of different types of matter and energy in an ecosystem with maximal respiration. They operate as similar indicators to the inverse of buffer capacity. (3) The model, when extended to include two types of decomposers, can show the conditions of the coexistence and the competitive exclusion of components. Even if two biological components are strongly overlapping in their ecological niches, a slight differentiation of the ratio of matter exchanges can permit the coexistence. The competition and the coexistence are regulated by the imperative shown by the MRH.

The second model is a simulation model for a hypothetical grassland ecosystem which consists of 19 biological components, and 15 kinds of matter and energy. The model includes a grazer system and a decomposer system. The main results are as follows. (1) The ecosystem configuration for biomass production, consumption, egestion, nutrient production, and respiration is presented under the MRH. It especially shows the dominance of the decomposer system. (2) Interspecific substitution guided by respiration values cause an increase in community respiration. If an inferior component undergoes a mutation to increase its production of net respiration value, the component may dominate its competitor and contribute to the increase in the community respiration. This means that the MRH can predict the working of natural selection from the macroscopic point of view.

2 Maximum Respiration in Steady State

The Maximum Respiration Hypothesis (MRH) asserts that matured ecosystems organize their configuration to maximize community respiration. Hence the object of the hypothesis is not individual living organisms but the whole ecosystem. The MRH has two aspects; one is to maximize the community production and the other is to maximize the community respiration. Hence the MRH does not only mean the latter under given community production, for greater production is also a necessary condition for greater respiration.

The maximum respiration does not uniformly regulate all stages of ecological succession. We have to make a distinction between the developing stage and the matured stage of ecological succession. The growth, that is the accumulation of the total biomass of the community, is dominant in the developing stage. Denote the community respiration as R, the accumulated biomass as $\triangle B$ and the total production as P. This means that $\triangle B = P - R$ is relatively large in the developing stage. In other words, P/R is noticeably greater than 1. On the other hand, the P/R approaches 1 in the matured stage (see Cooke 1967, Kira and Shidei 1967, E.P.Odum 1969, Smith 1980). In this stage, the production reaches its maximal level subject to the given abiotic environment, and community respiration reaches its maximal level subject to production. It is important to see that this matured stage of ecological succession is an steady state, which means that all scale or quantitative indicators are maintained invariably, and fluctuations, if possible, are restricted within a small range. This does not mean, however, that the MRH has no effect on the developing stage of ecological succession. The developing stage should be organized to attain the configuration of maximum respiration as early as possible. Therefore, the MRH requires both steady state models and dynamic models of ecosystem development.

One thing remains to be mentioned. It is possible for many reasons that the maximal level of respiration attained in the developing stage is greater than that in the matured stage, for instance as observed in Cooke (1967). In most cases, these situations in the developing stage are accompanied by a higher production level than that in the matured stage. This situation seems to be mainly caused by the initial endowment of nutrients. Hence the ecosystem utilizes these nutrients before moving into the matured stage, in which ecosystem organizes closed nutrient cycles and sustains the steady state. The fluctuation of abiotic environment may cause that situation in a short time span.

3 Producer-Decomposer Model

The ecosystem configuration given by the MRH can show the optimal scale of each population in an ecosystem. The optimality is not for the populations but for the holistic ecosystem. If a population cannot maintain a positive scale in the configuration that realizes the maximum community respiration, then the species cannot increase the vitality of the ecosystem and therefore cannot survive. This may be caused by competitive exclusion. On the other hand, two different species on similar ecological niches can coexist in the configuration. These phenomena will be explained by the theoretical model presented in this section.

Since all the models used in this paper are linear programming models we can specify dual solutions which show how scarce each matter or service (like pollination activity of insects) is in the ecosystem. These dual configurations give the respiration value for each matter or service. The respiration value shows that if one unit of that matter or service is imported (exported) then that amount of the community respiration will increase (decrease). Therefore it operates as a similar indicator to the inverse of buffer capacity presented by Jϕrgensen and Mejer (1977), Jϕrgensen and Mejer (1979) and Jϕrgensen (1992). Moreover the respiration value system can evaluate the contribution level of each species. This aspect will be intensively examined by the simulation model in the next section.

3.1 Model Structure

We present in this section the simplest model of ecosystem to show the functions of the MRH stated above. More complex aspects of ecosystems will be treated in the simulation model in the next section. This simple model consists of two biological components: a producer and a decomposer, representing autotrophs and heterotrophs respectively. The solar radiation impinging on the ecosystem is a unique energy inflow. The nutrient being considered in the model is also unique. The producer inputs solar radiation and nutrient to output net production (= plant biomass) and respiration (= wasted heat). The decomposer inputs the plant biomass to output nutrient, decomposer biomass and respiration. We intentionally do not incorporate the components that decompose the decomposer biomass. Hence the decomposer biomass represents the type of matter that is difficult to decompose in a short period.

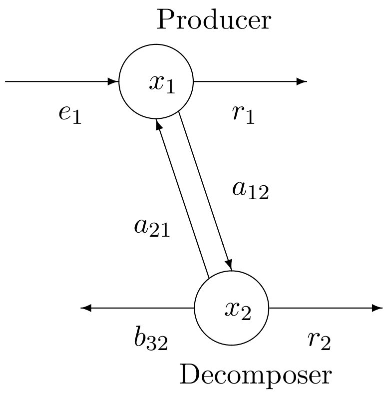

Figure 1: Producer-Decomposer Model

The input of solar energy and the respiration are measured in calories. Both plant biomass and decomposer biomass are measured in grams of dry matter weight. The nutrient is measured in grams of a chemical element, for instance, nitrogen (N).

We assume that the production and the decomposition are synchronized for every period, e.g., a year or a month. It means that the production and the decomposition are repeated steadily every period, and the temporal interelations are not changed over time. Let x_1 be the amount of plant biomass produced in a period. Since the ecosystem is in a steady state, a suffix for specifying the period is unnecessary. The amounts of solar energy and the nutrient required for one unit production are denoted by $e_1(>0)$ and $a_{21}(>0)$ respectively. The amount of respiration generated by one unit of production is denoted by $r_1(>0)$. The amount of nutrient produced in a period is denoted by x_2. Let $a_{12}(>0)$ be the plant biomass required for one unit production of the nutrient. $b_{32}(>0)$ and $r_2(>0)$ are respectively the decomposer biomass and the amount of respiration jointly produced by one unit production of the nutrient. Thus x_1 and x_2 represent the activity levels of the producer and the decomposer respectively. Since this is a linear model all coefficients are constant and do not depend on the activity levels of components. Substitution between factors is assumed to be impossible for both input and output. The structure of this ecosystem is shown in Figure 1.

3.2 Maximum Respiration Configuration

First we have to confirm that these coefficients do not violate the First Law of Thermodynamics. We assume that both the plant biomass and the decomposer biomass store usable energy, and the nutrient does not. Let p_1, p_3 be the stored energy for one unit plant biomass and the decomposer biomass respectively. Both of these are measured in calories. Because of the first law, the following equations must be fulfilled for each component.

$$e_1 = p_1 + r_1 \tag{1}$$

$$p_1 a_{12} = p_3 b_{32} + r_2 \tag{2}$$

The left hand side of (1) is input energy for one unit of production, and the right hand side is the sum of net production in terms of energy and the respiration as wasted heat for one unit of production. All coefficients in this equation are measured in calories. The left hand side of (2) shows the amount of assimilation in terms of the energy that is required for one unit of the nutrient production by the decomposer. The right hand side is the sum of the decomposer biomass in terms of energy ($p_3 b_{32}$) and the respiration for one unit of the nutrient production. Since p_1, p_3 are measurable, these equations represent the constraints imposed on coefficients by the first law.

The steady state configuration (x_1, x_2) has to fulfill these inequalities.

$$e_1 x_1 \leq E \tag{3}$$

$$a_{12} x_2 \leq x_1 \tag{4}$$

$$a_{21} x_1 \leq x_2 \tag{5}$$

$$0 \leq b_{32} x_2 \tag{6}$$

$$x_1, x_2 \geq 0, \tag{7}$$

(3) represents the condition for the solar energy, where E is the upper limit of usable solar radiation for the producer. E is, however, not the amount of solar radiation which directly impinges on the ecosystem. In other words, let the direct energy of the solar radiation be S and the efficiency of the producer for the fixation of S be q ($\simeq 0.02$), then, the following equation holds.

$$E = qS$$

Thus the producer can actually use up to E. (4) shows that the demand by the decomposer for plant biomass ($a_{12} x_2$) cannot exceed its supply (x_1). (5) shows that the demand by the producer for the nutrient ($a_{21} x_1$) cannot exceed its supply (x_2). This inequality means that there is no inflow from the outside, and no outflow of the nutrients from the ecosystem. Strictly speaking, since the model includes indecomposable matter, the absolute scarcity of the nutrient may arise and then the steady state will be impossible to achieve. We assume, however, for simplicity that the nutrient is a nitrogen compound, and the decomposer can work like a nitrogen-fixing bacteria and the amount of the fixation is just equal to the amount of the stored nutrient in the decomposer biomass. (6) shows that there is no component which requires the decomposer biomass ($b_{32} x_2$), because the left hand side is zero. (7) is the non negative condition for the activity levels of components.

Two dimensional vectors of the form (x_1, x_2) which satisfy the above inequalities are called feasible solutions. The optimal configuration of the ecosystem is determined among the feasible solutions. First of all, it is necessary to show that at least one feasible solution actually exists under the given structural coefficients. The condition which ensures the existence of feasible solutions is as follows.

$$a_{12} a_{21} \leq 1 \tag{8}$$

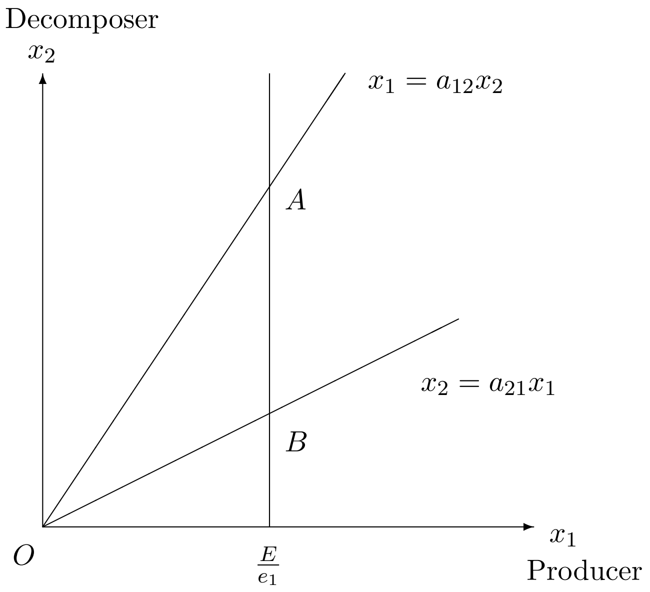

Figure 2: Feasible Solution

This condition means that the amount of plant biomass which is indirectly required to produce one unit of plant biomass itself has to be less than or equal to one. If this condition cannot be satisfied, the ecosystem cannot sustain the steady state and will continuously shrink in scale. Let us assume that this condition which ensures net production within the ecosystem is satisfied in every model used in this paper.

In Figure 2, the set of feasible solutions of (x_1, x_2) is depicted by the inside of the triangle OAB. This figure shows the case that (8) holds with a strict inequality.

The MRH states that the ecosystem configuration is given in such a way as to maximize the community respiration of the ecosystem. In other words, the configuration (x_1, x_2) that maximizes $R \equiv r_1x_1 + r_2x_2$ becomes the ecosystem configuration in the steady state. Since $r_1, r_2 > 0$, in this case only point A satisfies the requirement of the MRH.

There is no difference between A and B in that energy E is exhausted by the ecosystem at both. The major difference is in the activity level of the decomposer. The point A represents where the decomposer decomposes all the plant biomass, and the nutrient is supplied in excess. On the other hand, the point B is where the activity level of the decomposer is restricted regarding the level of decomposition to supply just the nutrient which is required by the producer, and the plant biomass is supplied in excess. Since we can observe tendencies of the biomass with stored energy in ecosystems to be completely decomposed in most cases, our result from the MRH is consistent with this observation of real ecosystems.

3.3 Attributes of Dual Solution

Next we investigate the dual problem, and the solution of this problem. The dual problem can give an evaluation vector for types of matter and energy which is consistent with the maximum respiration solution. The dual problem and the original maximum respiration problem can be considered as two sides of the same coin. Let s_0, s_1, s_2, s_3 be the values for one unit of the energy resource, the biomass of the producer, the nutrient, and the biomass of the decomposer respectively. The units of these values are also calories per unit of each factor. Then the dual problem can be constructed as specified by the linear programming theory as follows.

$$min. \qquad s_0 E$$

$$s.t.$$

$$s_0 e_1 + s_2 a_{21} \geq s_1 + r_1 \tag{9}$$

$$s_1 a_{12} \geq s_2 + s_3 b_{32} + r_2 \tag{10}$$

$$s_0, s_1, s_2, s_3 \geq 0$$

As shown in the above system, the problem maximizing respiration heat has its own dual problem which minimizes the value of the waste heat of the energy resource. As the duality theorem of linear programming states, the maximized objective function in the original problem is equal to the minimized objective function of the dual problem, i.e., in the optimized solutions,

$$R \equiv r_1 x_1 + r_2 x_2 = s_0 E, \tag{11}$$

(see Gale 1960).

Each value of s_0, s_1, s_2, s_3 means the increased (decreased) quantity of the total wasted heat R caused by one unit increase (decrease) of each type of matter (see Dorfman, Samuelson, and Sollow, 1958). Hence we call them the respiration values of the types of matter. In other words, s_0 in the minimized solution means the proportion of the increase in the amount of the community respiration R to the increase in the input of one unit of usable solar energy, thus, $s_0 = \triangle R / \triangle E$. In order to investigate the other values s_1, s_2, s_3, let us define the marginal increase in inflows of corresponding types of matter to be $\triangle d_1, \triangle d_2, \triangle d_3$, then the following equations hold.

$$s_i = \frac{\triangle R}{\triangle d_i} \qquad i = 1, 2, 3.$$

Therefore, each value $s_i, i = 0, 1, 2, 3$ can be interpreted as intensity of the contribution of each type of matter to the increase in the community respiration. We can understand that if a type of matter is excessively produced in an optimal configuration, then the value of the matter has to be zero. This is because since the matter is excessively supplied, additional supply cannot contribute to increase in the community respiration.

We have to notice that the inverse of the value $1/s_i$ is similar to the ecological buffer capacity introduced by Jϕrgensen and Mejer (1977) and Jϕrgensen (1992). In this case, R is the state variable and d_is the forcing function.

Next, multiply (3) $\sim$ (6) by $s_i, i = 0, 1, 2, 3$ respectively and sum these inequalities. We have,

$$s_0 e_1 x_1 + s_1 a_{12} x_2 + s_2 a_{21} x_1 - s_1 x_1 - s_2 x_2 - s_3 b_{32} x_2 \leq s_0 E, \tag{12}$$

where the equality sign holds in the case that (3) $\sim$ (6) hold as equality. Then multiply (9) and (10) by x_1, x_2 respectively and sum these inequalities. We have,

$$r_1 x_1 + r_2 x_2 \leq s_0 e_1 x_1 + s_1 a_{12} x_2 + s_2 a_{21} x_1 - s_1 x_1 - s_2 x_2 - s_3 b_{32} x_2, \tag{13}$$

where the equality sign holds in the case that (9) and (10) hold as equality. Since (11) is fulfilled in the optimal solutions and the left hand side of (12) is equal to the right hand side of (13), the above two inequalities have to be fulfilled with the equality sign. This shows that since (5) and (6) hold with the inequality sign even in the optimal solution (the optimal solution is given at A), the multipliers have to be zero, i.e., $s_2 = s_3 = 0$. This means that the nutrient and the decomposer biomass are excessively supplied in the optimal solution. On the other hand, because $x_1, x_2 > 0$, (9) and (10) are fulfilled with the equality sign in the optimal solution. Therefore we have,

$$s_0 e_1 = s_1 + r_1 \tag{14}$$

$$s_1 a_{12} = r_2 \tag{15}$$

Subtracting (14) from (1) we get,

$$(1 - s_0) e_1 = p_1 - s_1.$$

And also, subtracting (15) from (2), we get,

$$(p_1 - s_1) a_{12} = p_3 b_{32}.$$

Therefore,

$$(1 - s_0) e_1 a_{12} = (p_1 - s_1) a_{12} = p_3 b_{32}.$$

Since $p_3 b_{32} > 0$, finally, we get,

$$1 > s_0 (> 0), \tag{16}$$

$$p_1 > s_1. \tag{17}$$

(16) means that the one unit increase of solar energy must correspond to a lesser increase of the total waste heat ($\triangle R / \triangle E < 1$). (17) means that the respiration value of the biomass of the producer is strictly less than its stored energy. Let us pay attention to (16). We can paraphrase the meaning as being that a portion of solar energy is accumulated in biomass, which cannot be decomposed within this ecosystem. In other words, the decomposer biomass is indecomposable in this model.

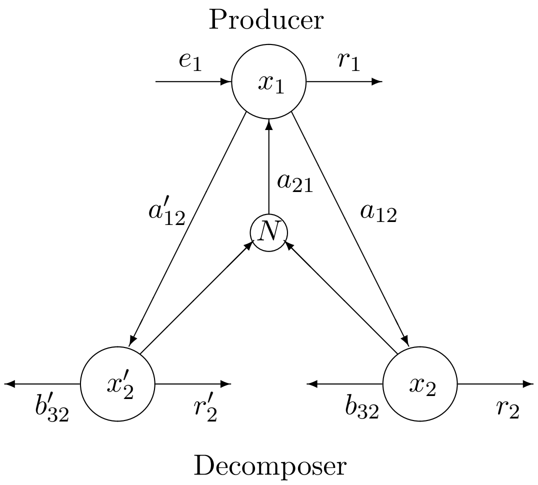

Figure 3: Extended Model

3.4 Competitive Exclusion and Coexistence of Two Decomposers

Next, we extend this model to include two types of decomposers, one of which is the same as the previous one. Although the matter types of the input and output are identical for both decomposers, the proportions of the types of matter are different. This means that the ecological niches of these decomposers are not identical but strongly overlapping. This situation is expressed in Figure 3.

In this figure the coefficients related to the new decomposer are denoted by attaching a prime mark ($'$). The nutrient which is produced by these two types of decomposers is pooled and denoted by N. It means that the nutrients produced by the two decomposers are completely interchangeable.

The primary problem which we have to investigate in this extended model is to determine the ecosystem configuration given under the MRH. We are especially interested in the conditions under which one decomposer excludes the other decomposer, or both decomposers coexist.

First, let us specify the equations which show that activities of every component cannot violate the conservation law of energy. (1), (2) also hold in this model. The equation for the activity of new decomposer is as follows.

$$p_1 a'_{12} = p_3 b'_{32} + r'_2 \tag{18}$$

Then the maximum respiration problem for this model is described as follows.

$$max. \qquad r_1 x_1 + r_2 x_2 + r'_2 x'_2$$

$s.t.$

$$e_1 x_1 \leq E \tag{19}$$

$$a_{12} x_2 + a'_{12} x'_2 \leq x_1 \tag{20}$$

$$a_{21}x_1 \leq x_2 + x'_2 \tag{21}$$

$$0 \leq b_{32}x_2 + b'_{32}x'_2 \tag{22}$$

$$x_1, x_2, x'_2 \geq 0$$

Furthermore, the dual problem of this original problem is as follows.

$$min. \qquad s_0E$$

s.t.

$$s_0e_1 + s_2a_{21} \geq s_1 + r_1 \tag{23}$$

$$s_1a_{12} \geq s_2 + s_3b_{32} + r_2 \tag{24}$$

$$s_1a'_{12} \geq s_2 + s_3b'_{32} + r'_2 \tag{25}$$

$$s_0, s_1, s_2, s_3 \geq 0$$

Let us investigate the optimal configuration of the maximum respiration problem. First we have to tackle the conditions of the net productivity. In the case of a unique decomposer, (8) describes that condition. The problem in this case is whether or not the condition is fulfilled by the other decomposer. Thus we investigate two cases.

(*Case I*) **The two decomposers are both productive.**

In other words, (8) and the following condition are satisfied simultaneously.

$$a'_{12}a_{21} \leq 1 \tag{26}$$

In this case, since the solar energy is fully used, the activity level of the producer x_1 is E/e_1 and the activity levels of the decomposers are determined so as to completely decompose the plant biomass. Therefore the maximal solution depends on the comparison of the slopes of the following equations.

$$\frac{E}{e_1} = a_{12}x_2 + a'_{12}x'_2,$$

$$R - \frac{r_1E}{e_1} = r_2x_2 + r'_2x'_2,$$

where R denotes the value of the objective function in the maximum respiration problem. Therefore, the maximum solution depends upon the following equation.

$$\frac{r'_2}{a'_{12}} > \frac{r_2}{a_{12}} \tag{27}$$

If this condition holds, then $x_2 = 0, x'_2 > 0$ is the solution. Contrarily, if this equation holds strict inverse inequality, then $x_2 > 0, x'_2 = 0$; and if with equality, then the two decomposers are equivalent. (27) means that owing to the input of one unit plant biomass the new decomposer produces more respiration waste heat than the other. In other words, the new decomposer stores comparatively less energy as biomass. It means that the decomposer which most effectively produces waste heat contributes most to maximizing the ecosystem respiration. After the exclusion of one decomposer, the situation of the waste heat values is equivalent to the previous case for the unique decomposer.

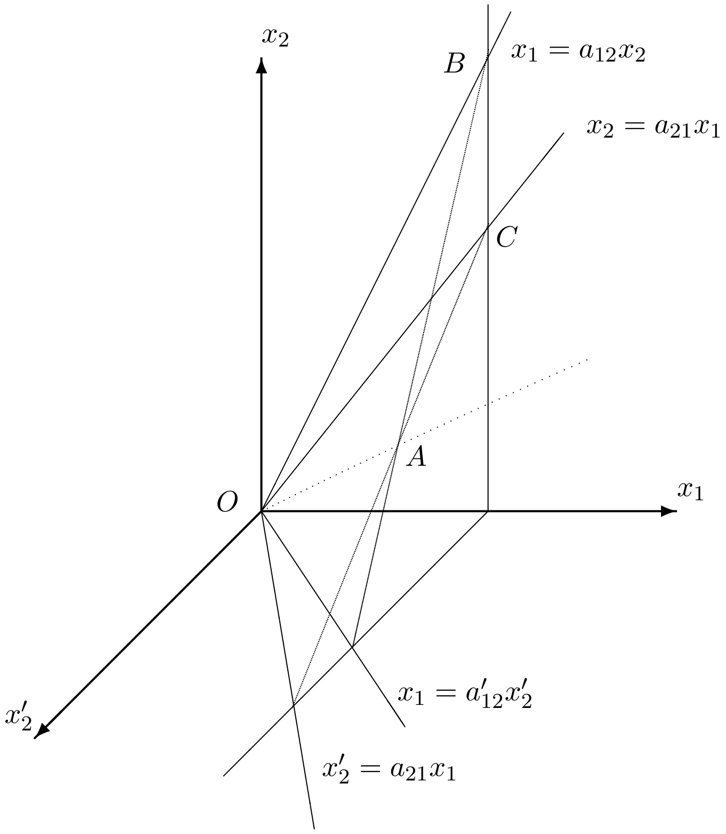

Figure 4: Feasible Area of Extended Model

(*Case II*) **The new decomposer is not productive.**

In this case, although (8) holds, the condition (26) for the new decomposer does not hold. This means that the ecosystem cannot be sustained by only the new decomposer. If the new decomposer cannot maintain (27) then it loses any positive meaning of existence in this ecosystem. In fact, if the following strict inequality holds then the new decomposer is excluded from the ecosystem.

$$\frac{r_2'}{a_{12}'} < \frac{r_2}{a_{12}}$$

Now the situation is equivalent to that of the one decomposer model.

Therefore our main concern is the case that (27) holds. In this case, although the new decomposer has an insufficient productivity for the nutrient in the ecosystem, it has a higher output of wasted heat per one unit input of the biomass. The feasible area is shown in Figure 4 and is the polyhedral cone whose vertex is the point O and whose bottom triangle is ABC. This figure illustrates the case that (8) holds with the strict inequality sign. Since (27) holds, the configuration of the maximum respiration is given at the point A, which is translated from the point B by the participation of the new decomposer. At the point A, the activity level of the original decomposer is lower than that at the point B because of the positive activity of the new decomposer. We can paraphrase it as follows. At the point B, the solar energy E is fully utilized and the production level of the producer biomass and the nutrient is at a maximum. The important problem is in the excess nutrient production. This excess production does not contribute to the increase of the waste heat. Therefore, since the new decomposer has higher productivity for respiration, the excess nutrient should be absorbed by the positive activity of the new decomposer which is less productive in nutrients, and the activity leads to the high productivity of the community respiration in the ecosystem.

Let us inquire into the characteristics of the dual solutions. We can easily ensure that (16) holds. Moreover, since both of the two decomposers have positive activity levels, (24) and (25) hold with the equality sign. Thus both sides of these equations divided by a_{12} and a'_{12} bring the following equation.

$$\frac{s_2}{a_{12}} + \frac{r_2}{a_{12}} = \frac{s_2}{a'_{12}} + \frac{r'_2}{a'_{12}}.$$

Hence,

$$(\frac{1}{a_{12}} - \frac{1}{a'_{12}})s_2 = \frac{r'_2}{a_{12}} + \frac{r_2}{a_{12}}.$$

Since (8) holds and (26) does not hold, $a_{12} < a'_{12}$ has to hold. Thus the left hand side of the above equation is positive. On the other hand, the higher productivity of waste heat of the new decomposer means that (27) holds. Therefore,

$$s_2 > 0.$$

Thus the nutrient which does not store energy also has a positive respiration value.

3.5 Stability Ensured by Evolution

Although in the previous section we explored the characteristics of ecosystem configurations under the MRH, we did not inquire into the stability, which is ensured by the tendencies to converge to the configuration. For example, in Figure 4, the problem is why point A is selected, in other words, what is the direct motivation to translate the configuration to A, if the ecosystem is initially in a situation such as B. Since B is a feasible solution, the ecosystem is sustainable at that point. The difference is that B is less efficient on the production of waste heat.

If the ecosystem is ruled only by the principle of survival for each individual, it is impossible for the ecosystem to translate the equilibrium configuration from B to A. The reason is that in the translation the original decomposer must shrink its activity level without self interest. It is as if a kind of altruism works in the behavior of the decomposer. Furthermore, as far as we accept the MRH, this altruistic situation frequently happens under the more generalized situation where ecosystem consists of many kinds of producers, consumers and decomposers.

In order to solve this problem, we have to explore the ramifications of the ecosystem's tendency to maximize the community respiration again. If an ecosystem is in an early stage of ecological succession, the ecosystem needs to accumulate a large amount of biomass. This means that a portion of energy taken in from outside will not be transformed into waste heat. The ecosystem we have been discussing, however, is in the matured stage of ecological succession in which the ecosystem is liberated from the tendency to change indicators of the ecosystem scale.

	Hervivore		Carnivore		Microbivore		Saprovore	
	A/C	P/A	A/C	P/A	A/C	P/A	A/C	P/A
Microorganisms	—	—	—	—	—	—	—	0.40
Invertebrates	0.40	0.40	0.80	0.30	0.30	0.40	0.20	0.40
Vertebrate (Homeotherms)	0.50	0.02	0.80	0.02	—	—	—	—
Vertebrate (Heterotherms)	0.50	0.10	0.80	0.10	—	—	—	—

Table 1: Assimilation and production efficiency used in Heal and MacLean (1975). Consumption (C), Assimilation (A), Production (P).

Our inquiry into the working of the MRH shows that the ecosystem in the matured stage tends to reorganize the configuration to maximize the community respiration.

The point we have to clarify is that the maximization of the community respiration means that the ecosystem tends to fully consume the energy of solar radiation. In other words, the ecosystem tends to maximize the efficiency of the utilization of the energy, which is not a result of the accumulation of biomass. The low efficiency of energy usage in the matured stage has to be identical with the vulnerability of the ecosystem. The vulnerability means the lack of vitality to recover from a perturbation, and weakness against competitive ecosystems. The vulnerable ecosystem will die out in the process of the natural selection. This means that the natural selection does not operate on individuals but on holistic ecosystems.

The working of natural selection for an ecosystem generates the individuals which have hereditary motivations such that they cooperate with the existence of the ecosystem even if they sacrifice their increase of populations. Thus, the individual has two kinds of hereditary factors. The one is acquired by optimality as an individual, and the other is by the motivation to sustain the whole ecosystem to which it belongs. In other words, we can say every living organism has its social life. Therefore, the stability of the ecosystem configuration under the MRH is ensured by evolution.

4 Simulation Model for a Grassland Ecosystem

Although a simple model as used in the last section is tractable for analyzing the theory incorporated in the model, we sometimes have difficulty seeing the connection with the actual object treated in the model. Therefore we present in this section a simulation model for a grassland ecosystem and show how the MRH works in the model. It is generally very difficult to assemble coefficients that can construct a holistic ecosystem for a simulation. The coefficients of our model in this section are based upon those estimated for a hypothetical grassland ecosystem in Heal and MacLean (1975). Table 1 shows the efficiency of the secondary productivity for that community used in Heal and MacLean's grassland model. Consumption (C), assimilation (A), production (P) in Heal and MacLean's model are measured in unit of calories per m^{2}year. These coefficients and the intercomponents' consumption efficiency C_n/P_{n-1} ($n, n-1$ denote trophic levels) make it possible for Heal and MacLean's model to determine an ecosystem configuration.

components			energy and materials		
No.		name	No.		name
		Producer	1	S	Solar Energy
1	P	Plant	2	N	Nutrient
		Grazer System	3	H_u	Humus
2	H_a	Herbivore (Homeothermal Vertebrate)	4	P_v	Plant Biomass (Vertebrate)
3	H_b	Herbivore (Heterothermal Vertebrate)			
4	H_c	Herbivore (Invertebrate)	5	P_i	Plant Biomass (Invertebrate)
5	C_{ga}	Carnivore (Homeothermal Vertebrate)			
6	C_{gb}	Carnivore (Heterothermal Vertebrate)	6	B_{pv}	Herbivorous Biomass (Vertebrate)
7	C_{gc}	Carnivore (Invertebrate)			
		Decomposer System	7	B_{pi}	Herbivorous Biomass (Invertebrate)
8	M_{fc}	Microorganisms (Carnivorous Faeces)			
9	S_{fc}	Saprovore (Carnivorous Faeces)	8	B_c	Carnivorous Biomass
10	M_{fo}	Microorganisms (General Faeces)	9	B_s	Saprovorous Biomass
11	S_{fo}	Saprovore (General Faeces)	10	B_m	Microbivorous Biomass
12	M_p	Microorganisms (Dead Plant Matter)	11	M	Microorganism Biomass
13	S_p	Saprovore (Dead Plant Matter)	12	F_c	Faeces(Carnivore)
14	M_a	Microorganisms (Dead Animal Matter)	13	F_o	Faeces(General)
15	S_a	Saprovore (Dead Animal Matter)	14	D_p	Dead Plant Matter
16	I_m	Microbivore	15	D_a	Dead Animal Matter
17	C_{sa}	Carnivore (Homeothermal Vertebrate)		R	Respiration
18	C_{sb}	Carnivore (Heterothermal Vertebrate)			
19	C_{sc}	Carnivore (Invertebrate)			

Table 2: Components and Matters of a Grassland Ecosystem Model

Our simulation is performed without giving the trophic efficiency. Instead, we incorporate the MRH into the model and determine the ecosystem configuration.

4.1 Model Structure

Our simulation model consists of 19 components, the solar energy, respiration and 14 materials. These factors are listed in Table 2. The notable differences with the Heal and MacLean's model are as follows. (1) Nutrient and humus are introduced in our model. The nutrient is supposed to be a nitrogen compound. Humus represents matter that are difficult to decompose in the ecosystem. (2) Carnivores are assembled in one trophic level. (3) Dead organic matter (DOM) is divided into two kinds of faeces, dead plant matter and dead animal matter. (4) Corresponding to this extension, microorganisms and saprovores are disaggregated as components who assimilate these types of matter. The main reason for this aggregation is that since we explicitly introduce the function of nutrient recycling, we have to consider the difference of the amount of stored nutrient in materials. Although our model does not introduce the other matter resources than the nutrient, e.g., water, carbon, etc., the extension of this model to include these types of matter is not difficult. Moreover, the model does not incorporate the non matter factors, e.g., pollination service by insects, in this stage of development of our research. This restricts the working of our model as we will see in the other part of this paper.

The interrelation of components is depicted in Figure 5, where circles represent components and rectangles represent matter pools. Respiration is not included in this diagram.

Now let us specify the coefficients of the model. All types of matter are measured in calories stored except for the nutrients, which are measured in grams. We assume that one unit of the nutrient is equal to the amount of the nutrient element stored in one unit of plant biomass. A/C's and P/A's in Heal and Maclean's Table 1 present the ratio $C : E : P : R$ for all heterotrophic components, where $E = C - A$ is egestion and $R = A - P$ is respiration. The coefficients of all heterotrophic components in our model are basically inherited and are adjusted as $C = 1$ for each component. Since the ratio $C : E : P : R$ satisfies $C = E + P + R = 1$, it is unnecessary to show equations corresponding to (1) and (2) in the producer-decomposer model.

Coefficients used in this model are listed in Table 3. Each column represents the coefficients for the corresponding component. Zero factors are expressed by "—". All coefficients of the heterotrophic components show the required or produced amount for one unit of consumption of the column components. The required quantity is expressed by a positive number and the produced quantity by a negative number. If a type of matter is required and produced by a component simultaneously, the amount is expressed by the required quantity subtracted by the produced quantity.

Some specific extensions have been done for constructing Table 3 compared with Heal and MacLean's model. Let us show them briefly.

We assume that the photosynthetic efficiency of the plant is 2 %. Hence 50 units of solar energy are required to fix one unit of energy. We also assume that 40 % of gross production is used by respiration of the plant. The column coefficients for the plant are expressed for one unit of gross production. This means that one unit of activity of the plant is expressed by one unit of the gross production. The ratio of using the net primary production is equivalent to Heal and MacLean's model.

For the heterotrophic components, as mentioned previously, the activity levels are measured in units of consumption. The first thing to be explained is that the amount of biomass production by these components is written in two places in the same column, one is corresponding to biomass, the other is dead animal matter. This is a device to enable excessively supplied animal biomass to be included in the DOM as the dead animal matter. Hence when we check the energy balance of the input and the output for each component, we have to exclude the quantity of dead animal matter.

We assume that every heterotrophic component produces nutrient. In order to deal consistently with nutrient production we had to specify a balance equation including the nutrient for each component, as we have done for the energy flow. However this makes the model excessively complex. Thus we estimate the coefficients for nutrient production by means of the following guidelines. (1) The major producers of the nutrient in this ecosystem are decomposers (microorganisms and saprovores). (2) Microorganisms produce more nutrient per unit consumption than saprovores. (3) Decomposers who consume faeces of carnivores have the highest efficiency

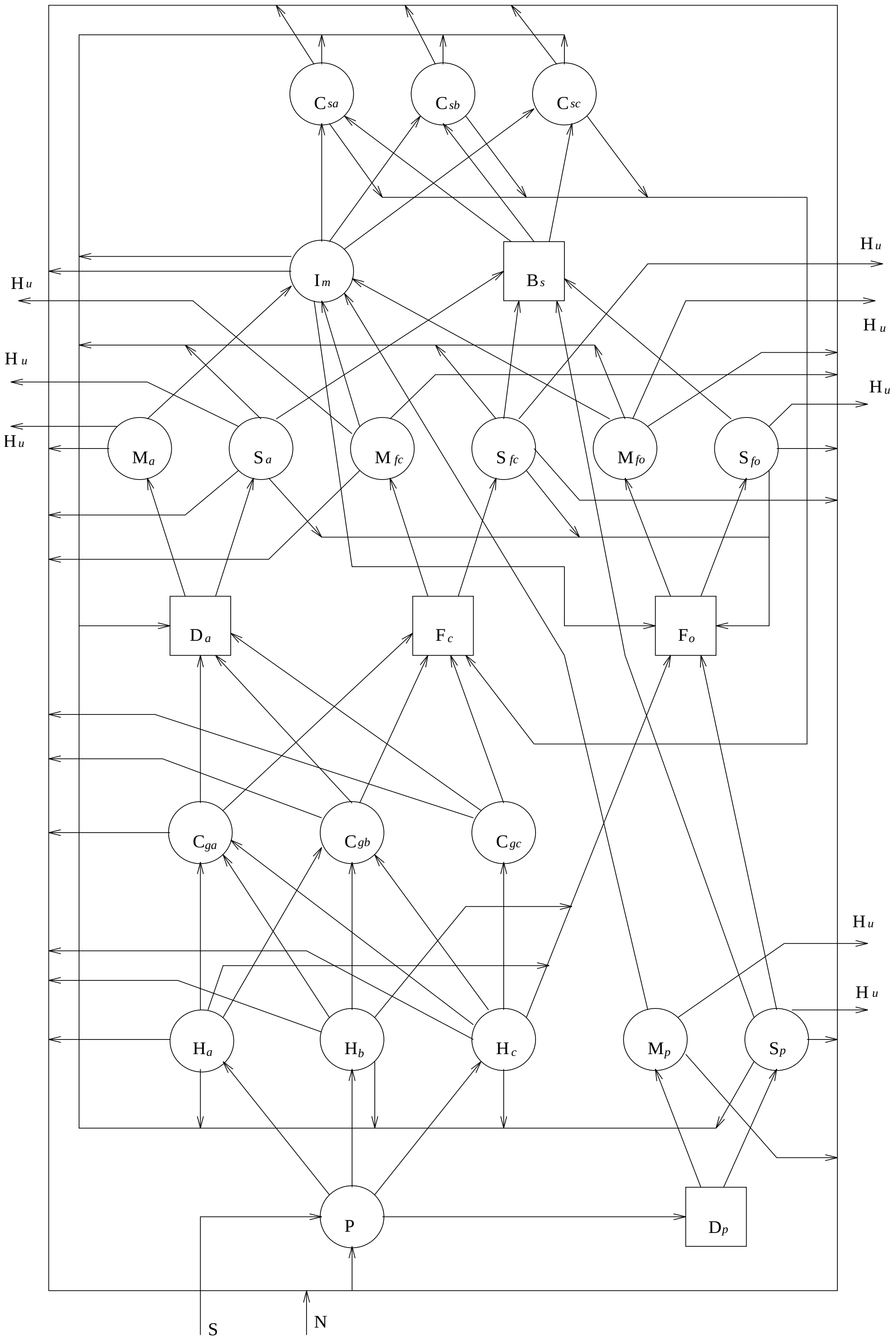

Figure 5: Interrelation of Components

No.		P	H_a	H_b	H_c	C_{ga}	C_{gb}	C_{gc}	M_{fc}	S_{fc}	M_{fo}	S_{fo}	M_p	S_p	M_a	S_a	I_m	C_{sa}	C_{sb}	C_{sc}
1	S	50.000	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	N	0.600	-0.060	-0.030	-0.010	-0.200	-0.100	-0.050	-2.400	-1.800	-0.800	-0.400	-0.300	-0.100	-0.400	-0.200	-0.100	-0.200	-0.100	-0.050
3	H_u	—	—	—	—	—	—	—	-0.008	-0.016	-0.016	-0.032	-0.040	-0.080	-0.032	-0.064	—	—	—	—
4	P_v	-0.150	1.000	1.000	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5	P_i	-0.024	—	—	1.000	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6	B_{pv}	—	-0.010	-0.050	—	0.800	0.700	—	—	—	—	—	—	—	—	—	—	—	—	—
7	B_{pi}	—	—	—	-0.160	0.200	0.300	1.000	—	—	—	—	—	—	—	—	—	—	—	—
8	B_c	—	—	—	—	-0.016	-0.080	-0.240	—	—	—	—	—	—	—	—	—	-0.016	-0.080	-0.240
9	B_s	—	—	—	—	—	—	—	—	-0.080	—	-0.080	—	-0.080	—	-0.080	—	0.500	0.600	0.700
10	B_m	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	-0.120	0.500	0.400	0.300
11	M	—	—	—	—	—	—	—	-0.392	—	-0.384	—	-0.360	—	-0.368	—	1.000	—	—	—
12	F_c	—	—	—	—	-0.200	-0.200	-0.200	1.000	1.000	—	—	—	—	—	—	—	-0.200	-0.200	-0.200
13	F_o	—	-0.500	-0.500	-0.600	—	—	—	—	-0.784	1.000	0.232	—	-0.720	—	-0.736	-0.700	—	—	—
14	D_p	-0.426	—	—	—	—	—	—	—	—	—	—	1.000	1.000	—	—	—	—	—	—
15	D_a	—	-0.010	-0.050	-0.160	0.984	0.920	0.760	—	-0.080	—	-0.080	—	-0.080	1.000	0.920	-0.120	0.984	0.920	0.760
16	R	-0.400	-0.490	-0.450	-0.240	-0.784	-0.720	-0.560	-0.600	-0.120	-0.600	-0.120	-0.600	-0.120	-0.600	-0.120	-0.180	-0.784	-0.720	-0.560

Table 3: Coefficients for types of matter and energy

for nutrient production. The efficiency decreases in order of decomposers of general faeces, decomposers of dead animal matter, and decomposers of dead plant matter. (4) The efficiency of carnivores is higher that that of herbivores. (5) The level of nutrient production reflects to a certain extent the amount of respiration.

We assume that humus is produced as a byproduct by decomposers, and it stores energy. Compared with Heal and MacLean's model, a certain proportion of energy stored in the faeces of saprovores is transferred to the humus. In the case of microorganisms, a certain proportion of the energy stored in biomass is transferred to the humus. The proportions are assumed to be 2%, 4%, 8% and 10% for the decomposers of carnivorous faeces, general faeces, the dead animal matter and the dead plant matter respectively.

4.2 Specification of the Maximum Respiration Problem

Let $a_{ij}, i = 1, 2, \ldots, 15; j = 1, 2, \ldots, 19$ be factors of ith row and jth column in Table 3 except for the 16th row for respiration. The activity level of the jth component is x_j, where $j = 1, 2, \ldots, 19$ and the amount of respiration is r_j, where $j = 1, 2, \ldots, 19$. The amount of the ith matter imported from outside the ecosystem is d_i, where $i = 1, 2, \ldots, 15$. Solar energy d_1 must be positive. Then the maximum respiration problem is specified as follows.

$$Max. \qquad \sum_{j=1}^{19} r_j x_j$$

$$s.t.$$

$$\sum_{j=1}^{19} a_{ij} x_j \leq d_i \qquad i = 1, 2, \ldots, 15 \tag{28}$$

$$x_j \geq 0, \quad j = 1, 2, \ldots, 19 \tag{29}$$

The objective function $\sum_{j=1}^{19} r_j x_j$ represents the community respiration under the configuration $(x_1, x_2, \ldots, x_{19})$. The left hand side of the inequality (28) shows the net inputs for types of matter that cannot exceed the imports. (29) is the non negativity condition.

Next we have to specify the dual problem. Let the respiration values for types of matter be $s_i, i = 1, 2, \ldots, 15$, which are measured in calories. Then the dual problem is as follows.

$$Min. \qquad \sum_{i=1}^{15} s_i d_i$$

$$s.t.$$

$$\sum_{i=1}^{15} s_i a_{ij} \geq r_j \qquad j = 1, 2, \ldots, 19 \tag{30}$$

$$s_i \geq 0, \quad i = 1, 2, \ldots, 15 \tag{31}$$

The objective function of this dual problem is the total respiration value of imported energy and types of matter.

Let us reconfirm simple corollaries of the duality theorem of linear programming theory. Multiply both sides of (28) by $s_i, i = 1, 2, \ldots, 15$ respectively. The sum of these inequalities is,

$$\sum_{i=1}^{15}\sum_{j=1}^{19} s_i a_{ij} x_j \leq \sum_{i=1}^{15} s_i d_i. \tag{32}$$

Then multiply both sides of (30) by $x_j, j = 1, 2, \ldots, 19$. The sum of these inequalities is,

$$\sum_{i=1}^{15}\sum_{j=1}^{19} s_i a_{ij} x_j \geq \sum_{j=1}^{19} r_j x_j. \tag{33}$$

On the other hand, the duality theorem ensures that the maximal objective function is equivalent to the minimal objective function, i.e.,

$$\sum_{j=1}^{19} r_j x_j = \sum_{i=1}^{15} s_i d_i,$$

in optimal solutions. This means that the lefthand sides of (32) and (33) are equivalent. Therefore, for the optimal configurations, $x_j, j = 1, 2, \ldots, 19$ and $s_i, i = 1, 2, \ldots, 15$, the following statements are fulfilled.

(I) if ith equation in (28) holds with a strict inequality sign, then $s_i = 0$.

(II) if jth equation in (29) holds with a strict inequality sign, then $x_j = 0$.

The corollary (I) has appeared in the last section, and (II) will appear in this section.

4.3 Community Structure and Dominance of Decomposer System

We have to specify $d_i, i = 1, 2, \ldots, 15$ to solve the problem. We assume $d_i = 0, i = 2, \ldots, 15$, that is, the ecosystem is closed except for solar energy. As shown in the previous section, respiration values represent how the community respiration changes as a result of marginal changes in matter inflow. This assumption aims to avoid unnecessary complexity for the analysis. As for the nutrients, we previously assumed a closed situation in the producer-decomposer model. This assumption for the nutrients has the same meaning, that is, the decomposers can work as a nutrient (nitrogen) fixing bacteria and the amount of the fixation just balances the amount of nutrients fixed in total humus produced.

d_1, which is the solar energy impinging on the ecosystem, is assumed to be 8333.333 units in a year. If the plants fix the energy, the net primary production amounts to 100 units and the gross production amounts to 166.6667 units.

The maximum community respiration of this problem was 158.3951. The optimal configuration of components, and the other results are summarized in Table 4. The first notable attribute of the results is that six components cannot survive in this hypothetical ecosystem, in other words they have zero activity levels. This can be explained by the *Competitive Exclusion Principle.* Every component of zero activity has a strong interspecific competitor. The competitors of homeothermal vertebrates are heterothermal vertebrates. The competitors of microorganisms are saprovores. The differentiation between competitors given by the model

No.		Configuration	Production	Egestion	Humus	Nutrient	Respiration
1	P	166.6667	100.0000	0.0000	0.0000	0.0000	66.6667
2	H_a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
3	H_b	25.0000	1.2500	12.5000	0.0000	0.7500	11.2500
4	H_c	4.0000	0.6400	2.4000	0.0000	0.0400	0.9600
5	C_{ga}	1.5625	0.0250	0.3125	0.0000	0.3125	1.2250
6	C_{gb}	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
7	C_{gc}	0.3275	0.0786	0.0655	0.0000	0.0164	0.1834
8	M_{fc}	2.8820	1.1297	0.0000	0.0231	6.9168	1.7292
9	S_{fc}	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
10	M_{fo}	83.8608	32.2025	0.0000	1.3418	67.0886	50.3165
11	S_{fo}	32.6663	2.6133	0.0000	1.0453	13.0665	3.9200
12	M_p	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
13	S_p	71.0000	5.6800	51.1200	5.6800	7.1000	8.5200
14	M_a	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
15	S_a	2.8353	0.2268	2.0868	0.1815	0.5671	0.3402
16	I_m	33.3323	3.9999	23.3326	0.0000	3.3332	5.9998
17	C_{sa}	1.2194	0.0195	0.2439	0.0000	0.2439	0.9560
18	C_{sb}	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
19	C_{sc}	11.3006	2.7122	2.2601	0.0000	0.5650	6.3284

Table 4: Results of the Maximum Respiration Problem

specification is very small. This means that this hypothetical model cannot provide sufficient niche differentiation for the components. This is caused by the simplicity of the model, especially in that it incorporates only 15 types of matter that connect components. We are neglecting all non-matter factors that play important roles in actual ecosystems, for instance, the assistance of pollination by animals. Moreover, the differentiation of matter is also very weak. In actual ecosystems, one biological component provides many kinds of matter and there can be different predators for each matter. Thus more types of matter should be incorporated to this model to improve it. In the next subsection we show that a small change of the niche for a component causes the change of survival conditions for its competitor.

The gross production is 166.6667 as we expected. This means that the plant fully utilizes solar energy under the given efficiency. The plant respiration is 66.6667 and the net primary production is 100. Thus if heterotrophic components utilize this production and convert it into respiration heat then the community respiration amounts to 166.6667. The maximum respiration, however, is 158.3951. The difference 8.2716 is just equal to the total of humus production, which is accumulated in the ecosystem. The indecomposable matter in the ecosystem appears only as humus.

The construction ratios of the grazer system and the decomposer system are summarized in Table 5. The ratios show the domination of the decomposer system, which is also shown in Heal and MacLean (1975). This is regarded as a general attribute of ecosystems.

From the viewpoint of individual components, the activity levels of the decomposer for

	Consumption	Production	Nutrient	Respiration
Grazer system	30.9(11.4)	2.0(3.9)	1.1(1.1)	13.6(14.9)
Decomposer system	239.1(88.6)	48.6(96.1)	98.9(98.9)	78.1(85.1)

Table 5: Structure of the two systems (%)

general faeces, especially the microorganisms, are very high. The microorganisms for general faeces make up 63.67% of the secondary production, 67.09% of the nutrient production, and 54.85% of the total respiration by heterotrophic components. This shows the crucial role of matter recycling in the ecosystem.

The activity levels of carnivores are very low. The total production by carnivores amounts to 2.8353, which makes up 5.61% of the secondary production. This means that carnivores have no stable position in this ecosystem.

4.4 Respiration Values and Interspecific Substitution

Since there is no imported matter and energy other than solar energy impinging on the ecosystem, the objective function of the dual problem represents the respiration value of the solar energy to be minimized. The minimized solution is 158.3951, which is equal to the maximum community respiration according to the imperative of the duality theorem from linear programming theory.

The system of respiration values for types of matter and energy and the value loss of components are shown in Table 6.

First let us examine the respiration values. The reason that the humus and the carnivorous biomass are valueless is that these are excessively produced in the ecosystem. The humus is absolutely excessively produced. There is no predator of carnivorous biomass in this hypothetical ecosystem. We treat the carnivorous biomass as dead animal matter, so that the biomass is finally decomposed in the ecosystem.

The value of solar energy means that one unit of increase in solar energy causes a 0.019 increase in the community respiration. Since the efficiency of fixation of solar energy by the plant is 2%, if the energy is completely utilized, the value has to be 0.02. The difference means that types of matter with stored energy are accumulated in the ecosystem.

The positive values of the nutrient show the scarcity of that matter in the ecosystem. The respiration value means that if one unit of additional nutrient inflows from outside the ecosystem, the community respiration increases by 0.14989. The interpretation of this fact is a little complex. Since the gross production of the plant is restricted by solar energy, the increase of nutrient inflow does not affect the gross production. Thus the increase of community respiration means that the community configuration is reconstructed to decrease the humus production by the sacrifice of nutrient production.

Since the other types of matter are measured in the same unit as the respiration, direct comparisons of values are meaningful. Carnivorous faeces embody the highest respiration value.

Respiration Value No.			Value Loss No.		
1	S	0.01901	1	P	—
2	N	0.14989	2	H_a	0.000034
3	H_u	—	3	H_b	—
4	P_v	1.08888	4	H_c	—
5	P_i	1.11363	5	C_{ga}	—
6	B_{pv}	0.02284	6	C_{gb}	0.008923
7	B_{pi}	0.02005	7	C_{gc}	—
8	B_c	—	8	M_{fc}	—
9	B_s	0.01671	9	S_{fc}	0.020573
10	B_m	0.02785	10	M_{fo}	—
11	M	1.13938	11	S_{fo}	—
12	F_c	1.40636	12	M_p	0.001766
13	F_o	1.15743	13	S_p	—
14	D_p	1.05691	14	M_a	0.011170
15	D_a	1.09042	15	S_a	—
			16	I_m	—
			17	C_{sa}	—
			18	C_{sb}	0.008087
			19	C_{sc}	—

Table 6: Respiration Values for types of matter and energy and Value Losses for Components

This is because decomposers produce nutrients from the carnivorous faeces with the highest efficiency. As a whole, the respiration values related to the decomposer system are higher than those of the grazer system.

Next we examine the value balance for each component. The value losses in Table 6 are the total respiration value of produced types of matter and respiration subtracted by the total value of input types of matter and energy. Six components suffer from value loss, and the others are in balance. The value loss components just correspond to those which cannot survive in the ecosystem, in other words, these activity levels in the problem of the maximum community respiration are zero, as shown in Table 4. We can expect this from the corollary (II) in the subsection of the problem specification.

All value losses are measured in terms of energy for one unit of activity level, which is equal to one unit of consumption in terms of energy. Therefore, the value losses of the above six components are comparable and we can regard them as the rate of value loss for each component. From this viewpoint, the component with the largest value loss is the saprovore for carnivorous faeces and conversely the component with the smallest value loss is the homeothermal herbivorous vertebrate. The smallest value loss means that if the input-output structure or the environment for the component changes slightly, it is highly possible that the component becomes a contributor for the maximization of the community respiration, and has a positive activity level. In other words, the niche of the component is strongly overlapping with its competitor.

	N	P_v	B_{pv}	F_o	D_a	R
Coefficients	-0.06	1.00	-0.01	-0.50	-0.01	-0.49
Values	0.149886	1.088875	0.022837	1.157432	1.090417	1.00
Valued coefficients	-0.008993	1.088875	-0.000228	-0.578716	-0.010904	-0.49

Table 7: Coefficients of the input-output structure for the homeothermal herbivorous vertebrate

The changes of the input-output structure for component can be interpreted in different ways. For instance, the dominant individuals in the component are substituted by their mutants which have a slightly different input-output structure. Furthermore it may possible that an evolutionary change is caused within the component in a long period.

Let us examine how the interspecific substitution occurs for the homeothermal herbivorous vertebrate and what it causes for the ecosystem configuration and the community respiration. The coefficients of structure for this component are presented in the first row of Table 7. Now let us assume that the ratio of the biomass production decreases by 0.002. This does not only mean the decrease of input factors, but the overall changes of the input-output factors, for we fix the consumption as one unit when we specify coefficients. The biomass production amounts to 0.008. Since the energy is conserved, there has to be an increase in production of the other factors. Two directions are possible. (1) As the result of the increase in the activity, both nutrient production and respiration production tend to increase. (2) As the result of the increase of consumption, respiration and nutrients increase with the same ratio as the consumption, the biomass production does not increase noticeably, instead there is an increase in faeces production.

First let us assume the direction (1). The respiration increases by 0.002 and becomes 0.492 instead of a decrease in biomass by 0.002. Moreover we assume that the nutrient production slightly increases up to 0.062. Then multiplying those differences by the corresponding respiration values we have a value increase of products by 0.000073. There is no change in the total input value. This means that this change of the structure for the homeothermal herbivorous vertebrate causes the production of value added instead of the value loss. Furthermore both the maximal community respiration and the respiration values are inconsistent with the existence of this new component. Hence we have to solve the new maximum respiration problem. The results are shown in (1) column of Table 8. Since the maximum respiration for the original problem is 158.3951, the maximum respiration for this problem increases by 0.0009. Moreover the homeothermal herbivorous vertebrate has a positive activity level in this solution instead of the zero activity level of the heterothermal herbivorous vertebrate which is the closest competitor. The result shows that the mutation of a weaker component guided by the respiration values causes the increase of the community respiration and get a stronger position compared to the competitor. The community respiration acts as an indicator to direct the evolution.

Next let us assume direction (2), i.e., the faeces production increases by 0.002 instead of a decrease of the biomass production by 0.002. This increases the value added by 0.000088 for the

No.		(1)	(2)
	Total respiration	158.3960	158.3964
1	P	166.6667	166.6667
2	H_a	25.0000	25.0000
3	H_b	0.0000	0.0000
4	H_c	4.0000	4.0000
5	C_{ga}	0.2500	0.2500
6	C_{gb}	0.0000	0.0000
7	C_{gc}	0.5900	0.5900
8	M_{fc}	2.6696	2.6696
9	S_{fc}	0.0000	0.0000
10	M_{fo}	83.8491	83.9268
11	S_{fo}	32.6006	32.5581
12	M_p	0.0000	0.0000
13	S_p	71.0000	71.0000
14	M_a	0.0000	0.0000
15	S_a	2.8821	2.8780
16	I_m	33.2445	33.2744
17	C_{sa}	1.1848	1.2029
18	C_{sb}	0.0000	0.0000
19	C_{sc}	11.3232	11.3049

Table 8: Result of the interspecific substitution

homeothermal herbivorous vertebrate. This value added is greater than that in direction (1). We have a similar result to direction (1) as shown in Table 8. That the community respiration is greater than in direction (1) reflects the greater change of the input-output structure measured in respiration values.

Finally we are required to make some remarks on how the respiration values actually work in ecosystems. As shown in the above analysis, the respiration values are exchanged as if they were information in ecosystems. The information is generated not for each component but for the macroscopic structure of the ecosystem. Moreover, biological components in ecosystems have to be able to perceive the information. The generation and exchange of the information are not performed by the same modes as are used by human beings. Allelopathy may represent this information exchange. The MRH is inevitably accompanied by this secondary hypothesis on the information exchange in ecosystem.

5 Concluding Remarks

We have been trying to show the potential of the MRH for the analysis of ecosystems. We have used a simple theoretical model of an ecosystem and a simulation model of a hypothetical grassland ecosystem. Extensions for two directions are required. First, we have to construct dynamic models that are consistent with the MRH. This extension is not difficult. We can expect that the dynamic models will provide information about the theory of ecological succession. Second, we are required to construct an ecosystem model to analyze an actual ecosystem, introducing complete data for the ecosystem. This may enable us to establish strategic policies for recovering the endangered ecosystems.

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