DYNAMICS OF COMPETITIVE SYSTEMS WITH A SINGLE COMMON LIMITING FACTOR

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Abstract. The concept of limiting factors (or regulating factors) succeeded in formulating the well-known principle of competitive exclusion. This paper shows that the concept of limiting factors is helpful not only to formulate the competitive exclusion principle, but also to obtain other ecological insights. To this end, by focusing on a specific community structure, we study the dynamics of Kolmogorov equations and show that it is possible to derive an ecologically insightful result only from the information about interactions between species and limiting factors. Furthermore, we find that the derived result is a generalization of the preceding work by Shigesada, Kawasaki, and Teramoto (1984), who examined a certain Lotka-Volterra equation in a different context.

1. **Introduction.** The dynamics of ecological systems is often modeled by the following system of ordinary differential equations:

$$\dot{x}_i = x_i g_i(x_1, x_2, \ldots, x_n), \quad i = 1, 2, \ldots, n \tag{1}$$

with the initial values in

$$\mathbb{R}_+^n := \{(x_1, x_2, \ldots, x_n) \in \mathbb{R}^n : x_i \geq 0 \text{ for all } i\}.$$

Here $\dot{x}_i = dx_i/dt$ and x_i denotes the population size of species i. The function g_i denotes the (per capita) growth rate of species i. This system is called the ecological system of Kolmogorov type. The well-known ecological system of Lotka-Volterra type is a special case of Eq. (1). If we are interested in competitive systems,

$$(\partial g_i / \partial x_j)(x_1, x_2, \ldots, x_n) \leq 0 \tag{2}$$

is assumed for every $i, j \in \{1, 2, \ldots, n\}$ with $i \neq j$ and $(x_1, x_2, \ldots, x_n) \in \mathbb{R}_+^n$. Eq.(2) with the strict inequality implies that the growth rate of species i is suppressed by species j. Under this general assumption system (1) has been studied in the literature. For instance, the theory of monotone dynamical systems succeeded to characterize the dynamical properties of system (1) with (2) (e.g., see [4, 16]). However, the assumption (2) is too general to further obtain ecologically insightful results. Therefore, in this paper, as a way of further restricting system (1) with (2), we focus on the concept of *limiting factors* (or *regulating factors*) introduced by Levin [9].

The concept of limiting factors was introduced to generalize the concept of resources. Consider system (1) with

$$
\begin{array}{rcl}
g_i(x_1, x_2, \ldots, x_n) & = & u_i(z_1, z_2, \ldots, z_k), \quad i = 1, 2, \ldots, n, \\
z_j & = & r_j(x_1, x_2, \ldots, x_n), \quad j = 1, 2, \ldots, k.
\end{array}
\tag{3}
$$

The system has k limiting factors in the sense that the growth rates g_i are regulated by k factors, whose amounts are denoted by $z_1, z_2, \ldots, z_k$. Each factor is potentially dependent of the population sizes. In practical problems, $z_1, z_2, \ldots, z_k$ are the amounts of nutrients, the densities of natural enemies and so on. In addition to (3), we may assume that

$$
(\partial u_i / \partial z_j)(z_1, z_2, \ldots, z_k) \geq 0 \quad \text{and} \quad (\partial r_j / \partial x_i)(x_1, x_2, \ldots, x_n) \leq 0
\tag{4}
$$

for all $i \in \{1, 2, \ldots, n\}$, $j \in \{1, 2, \ldots, k\}$, $(x_1, x_2, \ldots, x_n) \in \mathbb{R}_+^n$, and $(z_1, z_2, \ldots, z_k) \in \mathbb{R}^k$. This assumption is biologically reasonable if z_i (or z_i plus a constant) denotes the amount of a nutrient or $-z_i$ (or $-z_i$ plus a constant) denotes the population size of a natural enemy. With the framework (3), the preceding works [3, 11] succeeded to mathematically formulate the competitive exclusion principle that the number of coexisting species, n, cannot exceed the number of limiting factors, k (see also [1, 2]).

The introduction of the concept of limiting factors enhances the resolution of viewing competitive systems. The condition (2) only determines the interaction between species. But the condition (3) with (4) determines the interaction between species and a limiting factor. Each species is indirectly connected with competitors through limiting factors. It is clear that (3) with (4) implies (2). Therefore, competition between species is more finely described by (3) with (4). As the preceding works of competitive exclusion, this extent of specification of community structure might be enough to obtain some ecologically insightful results from (1). In order to support this expectation, we focus on the specific community structure shown in Fig. 1 (iii). The structure is a combination of two extreme cases (i) and (ii): (i) each species has its own limiting factor; (ii) all species share a single limiting factor. Both extreme cases are simple and their dynamics are known (see section 2). By focusing on this specific community structure, we show that the concept of limiting factors is helpful not only to formulate the competitive exclusion principle, but also to obtain other ecological insights.
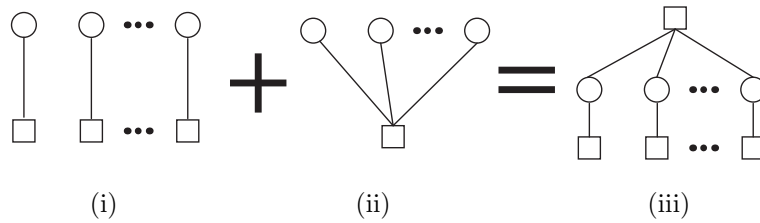

FIGURE 1. Community structures visualized with limiting factors. A species and a limiting factor are represented by a circle and a square, respectively. An edge between a circle and a square implies that the population growth of the corresponding species is regulated by the corresponding limiting factor.

The next section examines the dynamics of the extreme cases (i) and (ii) and mathematically formulates the system shown in Fig. 1 (iii). The result is used in the subsequent sections. Section 3 includes main results of this paper. We examine the equilibrium points of our system. Then we reveal some characteristic properties of our system due to its community structure. Section 3 also includes the result of global stability. These results are reviewed within the framework of Lotka-Volterra equations. The final section includes conclusions.

2. **Prerequisite.** In order to formulate our system shown in Fig. 1 (iii), we further specify the community structure with directed graphs as shown in Fig. 2. An arrow from node A to node B implies that the amount of A influences the amount of B. Denote by y_i the amount of the liming factor connected only to species i. y_i is called
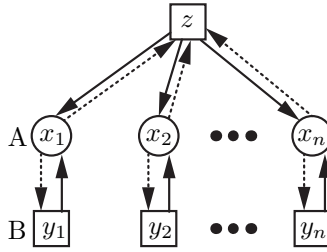

FIGURE 2. A community structure specified with directed graphs. The dashed arrow from A to B implies that the amount of B is suppressed by A. The solid arrow from B to A implies that the amount of A is enhanced by B. Under the assumption (4) every arrow directed to a circle (resp. square) is solid (resp. dashed).

the *species-specific limiting factor* since it regulates only the population growth of species i. Since only x_i influences y_i, we have

$$y_i = r_i(x_i), \quad i = 1, 2, \ldots, n. \tag{5}$$

Similarly, denote by z the amount of the limiting factor shared by all species. z is called the *common liming factor* since it regulates all species growth rates. Since all $x_1, x_2, \ldots, x_n$ influence z, we have

$$z = s(x_1, x_2, \ldots, x_n). \tag{6}$$

Since species i is regulated by the limiting factors y_i and z, we have

$$g_i(x_1, x_2, \ldots, x_n) = u_i(y_i, z), \quad i = 1, 2, \ldots, n. \tag{7}$$

In order to normalize the amounts of the limiting factors, we assume

$$s(0, 0, \ldots, 0) = 0, \quad r_i(0) = 0, \quad i = 1, 2, \ldots, n. \tag{8}$$

This is not assumed in the preceding works of competitive exclusion principle [3, 11] but is necessary in our work to specify the situation that some limiting factor is absent. In our case, the condition (4) becomes the condition that

$$\begin{aligned} (\partial u_i/\partial y_i)(y_i, z) > 0, \quad (\partial u_i/\partial z)(y_i, z) > 0, \\ (\partial r_i/\partial x_i)(x_i) < 0, \quad (\partial s/\partial x_i)(x_1, x_2, \ldots, x_n) < 0 \end{aligned} \tag{9}$$

for all $i \in \{1, 2, \ldots, n\}$, $(y_i, z) \in \mathbb{R}^2$ and $(x_1, x_2, \ldots, x_n) \in \mathbb{R}^n_+$.

If the common limiting factor z is removed (see Fig. 1 (i)), our system is reduced to

$$\dot{x}_i = x_i u_i(r_i(x_i), 0), \quad i = 1, 2, \ldots, n,$$

where every species is isolated with each other. Since (9) is assumed, it is natural to assume that

$$u_i(0,0) > 0, \quad i = 1, 2, \ldots, n. \tag{10}$$

Otherwise, all species go extinct even with the common limiting factor z. Furthermore, if $u_i(r_i(x_i), 0) > 0$ for all $x_i > 0$, then x_i increases unboundedly when x_i is initially positive. Therefore, it is natural to assume that

$$\exists K_i > 0 : \ u_i(r_i(K_i), 0) = 0, \quad i = 1, 2, \ldots, n, \tag{11}$$

where K_i should be unique. Under these assumptions, if the common limiting factor z is removed, our system equilibrates at the globally asymptotically stable equilibrium point $(K_1, K_2, \ldots, K_n)$.

On the other hand, if all species-specific limiting factors y_i are removed (see Fig. 1 (ii)), our system is reduced to

$$\dot{x}_i = u_i(0, s(x_1, x_2, \ldots, x_n)), \quad i = 1, 2, \ldots, n. \tag{12}$$

Let $\mathbf{e}_i$, $i = 1, 2, \ldots, n$, be the standard bases of $\mathbb{R}^n$. If $u_i(0, s(x_i \mathbf{e}_i)) > 0$ for all $x_i > 0$, then x_i increases unboundedly when all species but species i is absent (i.e., when only x_i is initially positive). Therefore, it is natural to assume that

$$\exists L_i > 0 : \ u_i(0, s(L_i \mathbf{e}_i)) = 0, \quad i = 1, 2, \ldots, n, \tag{13}$$

where L_i should be unique. Denote $z_i^* = s(L_i \mathbf{e}_i)$. Then z_i^* is the critical value of the common limiting factor with which species i equilibrates in absence of y_i. Under these assumptions, system (12) is studied in [3] and the following result of global competitive exclusion is obtained.

Theorem 2.1 ([3, Theorem D1]). *Suppose that the inequalities*

$$z_1^* < z_2^* < \cdots < z_n^* \tag{14}$$

hold. Then every solution to (12) *satisfies*

$$\lim_{t \to \infty} x_1(t) = L_1, \quad \lim_{t \to \infty} x_i(t) = 0, \quad i = 2, 3, \ldots, n$$

if $(x_1(0), x_2(0), \ldots, x_n(0)) \in \mathbb{R}_+^n$ *and* $x_1(0) > 0$.

This theorem shows that competitive exclusion occurs due to competition via the common limiting factor z and only the best competitor (species 1) can survive. If species 1 is removed from the system, then only species 2, which is the second best competitor, can survive. That is, the outcome is completely determined by the amount of z_i^*, at which species i equilibrates without y_i. This result is known as an R^* rule, which states that the dominant species suppresses resources to a lower level than any other competing species, or a P^* rule, which states that the dominant species withstands the higher predator density than any other species [8].

In the subsequent sections, we study system (1) satisfying all assumptions mentioned above except (11), which is not necessary to derive mathematical results below. The system is summarized as system (1) satisfying

(H): There exist smooth functions $u_i : \mathbb{R}^2 \to \mathbb{R}$, $r_i : \mathbb{R}_+ \to \mathbb{R}$, $i = 1, 2, \ldots, n$, and $s : \mathbb{R}_+^n \to \mathbb{R}$ such that the conditions (5), (6), (7), (8), (9), (10), and (13) are fulfilled.

3. **Equilibria and stability.** In this section, we investigate the equilibrium points of system (1) satisfying **(H)**. The investigation is helped with the concept of saturated equilibrium points. Especially, this concept helps to consider uniqueness of asymptotically stable equilibrium points. In the following subsections, we introduce the concept of saturated equilibrium points and recall that the concept is equivalent to a certain nonlinear complementarity problem. Then using a general result of nonlinear complementarity problems, we show that our system has a unique saturated equilibrium point and reveal its characteristic property. A global stability problem and an application to an affine case are finally addressed.

3.1. **Saturated equilibrium points and nonlinear complementarity problems.** For (column) vectors $\mathbf{x} = (x_i)$ and $\mathbf{y} = (y_i)$ in $\mathbb{R}^n$, $\mathbf{x} \geq \mathbf{y}$ implies that $x_i \geq y_i$ for all i, and $\mathbf{x}^\top$ denotes the transpose of the vector $\mathbf{x}$. The transpose of a matrix A is denoted by $A^\top$. Define $\mathrm{supp}(\mathbf{x}) := \{i : x_i > 0\}$. Saturated equilibrium points introduced in [6, 7] and nonlinear complementarity problems are defined as follows.

Definition 3.1 (saturated equilibrium point). An equilibrium point $\mathbf{x}^* \geq \mathbf{0}$ of system (1) is said to be *saturated* (resp. *strictly saturated*) if $g_i(\mathbf{x}^*) \leq 0$ for all i (resp. $g_i(\mathbf{x}^*) < 0$ for all $i \notin \mathrm{supp}(\mathbf{x}^*)$).

Definition 3.2 (nonlinear complementarity problem). For the function $G : \mathbb{R}^n \to \mathbb{R}^n$, the problem of finding $\mathbf{x}$ satisfying

$$\mathbf{x} \geq \mathbf{0}, \quad G(\mathbf{x}) \geq \mathbf{0}, \quad \mathbf{x}^\top G(\mathbf{x}) = 0$$

is called the *nonlinear complementary problem* with respect to G and is denoted by $\mathrm{NCP}(G)$.

Let $\mathbf{x}^* = (x_i^*)$ be an equilibrium point of system (1). Then

$$x_i^* = 0 \quad i \notin \mathrm{supp}(\mathbf{x}^*) \quad \text{and} \quad g_i(\mathbf{x}^*) = 0 \quad i \in \mathrm{supp}(\mathbf{x}^*).$$

By definition, any positive equilibrium point $\mathbf{x}^*$ is saturated. Suppose that $\mathbf{x}^*$ is not positive. Then the growth rates of all missing species are nonpositive at $\mathbf{x}^*$. Thus any missing species cannot increase their population sizes around a saturated equilibrium point. In this sense, a saturated equilibrium point is invulnerable to species invasion.

It is straightforward to show that the problem of finding a saturated equilibrium point of system (1) is equivalent to solving the nonlinear complementarity problem $\mathrm{NCP}(-G)$ with $G = (g_1, g_2, \ldots, g_n)^\top$. This equivalence was pointed out in [17, 18].

3.2. **Uniqueness of saturated equilibrium points.** Using a known result on NCP, we examine uniqueness of saturated equilibrium points of our system. The following class of functions is important to ensure uniqueness of solutions to NCP.

Definition 3.3 (P-functions). Let $D \subset \mathbb{R}^n$. $G = (g_1, g_2, \ldots, g_n)^\top : D \to \mathbb{R}^n$ is said to be a *P-function* if $\mathbf{x}, \mathbf{y} \in D$ and $\mathbf{x} \neq \mathbf{y}$ implies

$$\max_{1 \leq i \leq n} (x_i - y_i)(g_i(\mathbf{x}) - g_i(\mathbf{y})) > 0.$$

The following theorem is fundamental to show that our system has a unique saturated equilibrium point.

Theorem 3.4 ([13, Theorem 2.3]). *If $G : \mathbb{R}_+^n \to \mathbb{R}^n$ is a P-function, then $\mathrm{NCP}(G)$ has at most one solution.*

Using this theorem, we prove that our system has a unique saturated equilibrium point. To this end, we introduce two important classes of matrices.

Definition 3.5 (VL-stable matrix)**.** An $n \times n$ matrix A is said to be *VL-stable* if there exists a positive diagonal matrix D such that $DA + A^\top D$ is negative definite, i.e., there exist positive numbers $d_1, d_2, \ldots, d_n$ such that

$$\sum_{i=1}^n \sum_{j=1}^n d_i a_{ij} x_i x_j < 0$$

for all $\mathbf{x} \neq \mathbf{0}$.

Definition 3.6 (P-matrix)**.** An $n \times n$ matrix A is said to be a *P-matrix* if $\mathbf{x} \neq \mathbf{0}$ implies

$$\max_{1 \leq i \leq n} x_i (A\mathbf{x})_i > 0.$$

By the well-known Liapunov theorem, A is stable if it is VL-stable. A VL-stable matrix is also called a *dissipative* matrix [14] and S_w-matrix [19] (see also [10, Definition 4.4']). The following theorem shows the well-known relevance of the class of VL-stable matrices to those of P-matrices.

Theorem 3.7 (e.g, [20, Theorem 2])**.** *If A is VL-stable, then $-A$ is a P-matrix.*

Let $D_{\mathbf{x}} G(\mathbf{x})$ be the Jacobi matrix of G evaluated at $\mathbf{x}$. The following theorem provides a sufficient condition that a given function G is a P-function.

Theorem 3.8 ([12, Theorem 5.2])**.** *Let D be a rectangular region of $\mathbb{R}^n$ and $G : D \to \mathbb{R}^n$ be differentiable. If $D_{\mathbf{x}} G(\mathbf{x})$ is a P-matrix at every $\mathbf{x} \in D$, then G is a P-function.*

Application of Theorems 3.7 and 3.8 to the growth rate function $G = (g_1, g_2, \ldots, g_n)^\top$ of system (1) leads to the following theorem.

Theorem 3.9. *System* (1) *satisfying* **(H)** *has a unique saturated equilibrium point. If the saturated equilibrium point is positive, it is (locally) asymptotically stable.*

Proof. If a given matrix A is of the form $A = -\mathrm{diag}(\mathbf{q}) - \mathbf{v}\mathbf{w}^\top$ with positive vectors $\mathbf{q} = (q_i)$, $\mathbf{v} = (v_i)$ and $\mathbf{w} = (w_i) \in \mathbb{R}^n$, then A is VL-stable. In fact, with the diagonal matrix $D = \mathrm{diag}(w_1/v_1, \ldots, w_n/v_n)$,

$$\mathbf{x}^\top (DA + A^\top D)\mathbf{x} = -2 \left\{ (\mathbf{w}^\top \mathbf{x})^2 + q_1 \frac{w_1}{v_1} x_1^2 + \cdots + q_n \frac{w_n}{v_n} x_n^2 \right\} < 0$$

holds for every $\mathbf{x} \neq \mathbf{0}$. This implies that A is VL-stable. Since the Jacobi matrix of G is

$$D_{\mathbf{x}} G = \mathrm{diag}\left(\frac{\partial u_1}{\partial y_1} \frac{dr_1}{dx_1}, \ldots, \frac{\partial u_n}{\partial y_n} \frac{dr_n}{dx_n} \right) + \begin{pmatrix} \dfrac{\partial u_1}{\partial z} \\ \vdots \\ \dfrac{\partial u_n}{\partial z} \end{pmatrix} \begin{pmatrix} \dfrac{\partial s}{\partial x_1}, \ldots, \dfrac{\partial s}{\partial x_n} \end{pmatrix},$$

$(\partial u_i / \partial y_i)(dr_i / dx_i) < 0$, $\partial u_i / \partial z > 0$, and $\partial s / \partial x_i < 0$, the matrix $D_{\mathbf{x}} G(\mathbf{x})$ is VL-stable irrespective of $\mathbf{x} \in \mathbb{R}_+^n$. Thus Theorems 3.7 and 3.8 show that $-G$ is a P-function on $\mathbb{R}_+^n$ and Theorem 3.4 ensures that system (1) satisfying **(H)** has at most one saturated equilibrium point. Existence of the saturated equilibrium point

is ensured if system (1) satisfying **(H)** is dissipative, i.e., there exists a compact forward invariant set that attracts every point in $\mathbb{R}_+^n$ [5, Theorem 2]. The dissipativity follows since

$$
\begin{aligned}
\dot{x}_i &= x_i u_i(r_i(x_i), s(x_1, x_2, \ldots, x_n)) \\
&\leq x_i u_i(r_i(0), s(x_i \mathbf{e}_i)) = x_i u_i(0, s(x_i \mathbf{e}_i)) < 0
\end{aligned}
$$

for all $x_i \geq 0$ sufficiently large.

Let $\mathbf{x}^* = (x_i^*)$ be the positive saturated equilibrium point. The Jacobi matrix $J = (\partial \dot{x}_i / \partial x_j)$ of system (1) evaluated at $\mathbf{x}^*$ is of the form

$$
\frac{\partial \dot{x}_i}{\partial x_j} = x_i^* \frac{\partial g_i}{\partial x_j}(\mathbf{x}^*).
$$

In the same way as above, we see that J is VL-stable, thus it is stable. Therefore, $\mathbf{x}^*$ is asymptotically stable. □

Note that the result of this theorem applies to every subsystem of (1) satisfying **(H)**. Therefore, every boundary equilibrium point $\hat{\mathbf{x}}$ is asymptotically stable within the subsystem $\{\mathbf{x} \in \mathbb{R}_+^n : x_i = 0 \ \forall i \notin \mathrm{supp}(\hat{\mathbf{x}})\}$. Furthermore, if the boundary equilibrium point $\hat{\mathbf{x}}$ is strictly saturated, then it is asymptotically stable in the full system since $g_i(\hat{\mathbf{x}})$, $i \notin \mathrm{supp}(\hat{\mathbf{x}})$, is a transversal eigenvalue (see [6, 7]).

3.3. **Equilibrium structure.** We examine the characteristic property of the saturated equilibrium point, at which our system is likely to equilibrate.

Theorem 3.10. *Let $\mathbf{x}^* = (x_i^*)$ be the saturated equilibrium point of system (1) satisfying **(H)**. If (14) is satisfied, then there exists a $k \geq 1$ such that $\mathrm{supp}(\mathbf{x}^*) = \{1, 2, \ldots, k\}$.*

Proof. Let $k = \max \mathrm{supp}(\mathbf{x}^*)$. Suppose that $\mathrm{supp}(\mathbf{x}^*) = \{1, 2, \ldots, k\}$ does not hold. Then there exists $l < k$ such that $x_l^* = 0$. Let $z^* = s(\mathbf{x}^*)$. Since $x_k^* > 0$, we have $u_k(r_k(x_k^*), z^*) = 0$. Recall that z_i^* is the constant satisfying $u_i(0, z_i^*) = 0$. If $z_k^* \geq z^*$, then the monotonicity assumption implies $0 = u_k(r_k(x_k^*), z^*) < u_k(0, z^*) \leq u_k(0, z_k) = 0$. This is a contradiction. Thus $z_k^* < z^*$. Then, by the monotonicity assumption, we have $u_l(0, z^*) > u_l(0, z_k^*) > u_l(0, z_l^*) = 0$. This implies that $\mathbf{x}^*$ is not saturated. This is a contradiction. Thus $x_l^* > 0$ for all $l < k$. □

Note that, using the method proposed by Shigesada, Kawasaki, and Teramoto [15], the index k can be calculated from the parameters if $G = (g_1, g_2, \ldots, g_n)^\top$ is an affine function (see Section 3.5).

Theorem 3.10 shows that the rank determined by the competition through the common limiting factor z is still important even with the species-specific limiting factors y_i. Because of the sign pattern of $\mathbf{x}^*$, invasion of high rank species could lead to extinction of low rank species. For instance, consider a three-species system with $\mathbf{x}^* = (+, +, 0)$ and suppose that the system is at the equilibrium $(0, 0, +)$. Then the theorem suggests that the invasions of species 1 and 2 succeed and lead to the extinction of species 3. Furthermore, the theorem suggests that an endangered species cannot be saved by improving the relation to its species-specific limiting factor. In fact, at the saturated equilibrium point $\mathbf{x}^*$, an extinct species i satisfies $g_i(\mathbf{x}^*) = u_i(0, s(\mathbf{x}^*)) \leq 0$, which does not increase by improving the relation to y_i. Thus such an improvement does not change the stability of $\mathbf{x}^*$. For instance,

consider the case where

$$u_i(y_i, z) = b_i(1 + y_i) + a_i z, \quad b_i > 0, \ a_i > 0$$
$$y_i = -x_i/K_i, \quad K_i > 0.$$

Then, in absence of the common limiting factor z, species i with larger K_i is more abundant. However, if the common limiting factor z is present, then increasing K_i does not help to save species i since $z_i^* = -b_i/a_i$ does not depend on K_i. The index k

Theorem 3.11. *Let $\hat{\mathbf{x}} = (\hat{x}_i)$ and $\check{\mathbf{x}} = (\check{x}_i)$ be distinct equilibrium ponts of system* (1) *satisfying* **(H)**. *If $\emptyset \neq \operatorname{supp}(\hat{\mathbf{x}}) \subset \operatorname{supp}(\check{\mathbf{x}})$, then $\hat{z} = s(\hat{\mathbf{x}}) > \check{z} = s(\check{\mathbf{x}})$ and $\hat{x}_i > \check{x}_i$ for all $i \in \operatorname{supp}(\hat{\mathbf{x}})$.*

Proof. Since $\hat{\mathbf{x}}$ and $\check{\mathbf{x}}$ are distinct equilibrium points, $\operatorname{supp}(\hat{\mathbf{x}}) \neq \operatorname{supp}(\check{\mathbf{x}})$ holds. Otherwise, the subsystem $\{\mathbf{x} \in \mathbb{R}_+^n : x_i = 0 \ \forall i \notin \operatorname{supp}(\hat{\mathbf{x}}) = \operatorname{supp}(\check{\mathbf{x}})\}$ has two saturated equilibrium points.

Let $\hat{z} = s(\hat{\mathbf{x}})$, $\hat{y}_i = r_i(\hat{x}_i)$, $\check{z} = s(\check{\mathbf{x}})$, and $\check{y}_i = r_i(\check{x}_i)$. Suppose that $\hat{z} \leq \check{z}$. Then for every $i \in \operatorname{supp}(\hat{\mathbf{x}})$, $0 = u_i(\hat{y}_i, \hat{z}) \leq u_i(\hat{y}_i, \check{z})$. Thus $\hat{y}_i \geq \check{y}_i$ holds. Otherwise $u_i(\check{y}_i, \check{z}) = 0$ does not hold. Therefore, for every $i \in \operatorname{supp}(\hat{\mathbf{x}})$, we have $\hat{y}_i \geq \check{y}_i$, which implies $\hat{x}_i \leq \check{x}_i$. Then $\hat{z} = s(\hat{\mathbf{x}}) > s(\check{\mathbf{x}}) = \check{z}$ (note that $\operatorname{supp}(\hat{\mathbf{x}}) \subset \operatorname{supp}(\check{\mathbf{x}})$, $\operatorname{supp}(\hat{\mathbf{x}}) \neq \operatorname{supp}(\check{\mathbf{x}})$). Thus we have a contradiction. Therefore, $\hat{z} > \check{z}$.

Let $i \in \operatorname{supp}(\hat{\mathbf{x}})$. Since $0 = u_i(\hat{y}_i, \hat{z}) > u_i(\hat{y}_i, \check{z})$, we have $\hat{y}_i = r_i(\hat{x}_i) < \check{y}_i = r_i(\check{x}_i)$, which implies $\hat{x}_i > \check{x}_i$. $\qquad\square$

This theorem implies that after successful invasion of new species, the amount of the common limiting factor z decreases and the population sizes of preexisting species decrease.

3.4. **Global stability.** To study the global stability of system (1), we introduce the following class of functions: $G : \mathbb{R}_+^n \to \mathbb{R}^n$ is said to be a *strongly monotone* function on $\mathbb{R}_+^n$ if there exists a constant $K > 0$ such that

$$(\mathbf{x} - \mathbf{y})^\top (G(\mathbf{x}) - G(\mathbf{y})) \geq K(\mathbf{x} - \mathbf{y})^\top (\mathbf{x} - \mathbf{y})$$

for all $\mathbf{x}, \mathbf{y} \in \mathbb{R}_+^n$. The usefulness of this class of functions in the study of ecological systems was noticed by Takeuchi and Adachi [18, Theorem 8]. A subtle generalization of their result leads to the following theorem.

Theorem 3.12. *Let $\mathbf{x}^*$ be a unique saturated equilibrium point of system* (1). *If there exists a positive diagonal matrix $D = \operatorname{diag}(d_1, \ldots, d_n)$ such that $-DG$ is strongly monotone on $\mathbb{R}_+^n$, then $\mathbf{x}^*$ is globally asymptotically stable in $\Omega = \{\mathbf{x} = (x_1, \ldots, x_n)^\top \in \mathbb{R}_+^n : x_i > 0 \ \forall i \in \operatorname{supp}(\mathbf{x}^*)\}$.*

Proof. Let $V(\mathbf{x}) = \sum_{i=1}^n d_i(x_i^* \log x_i - x_i)$. This is the standard Liapunov function proposed by Volterra. It is defined for all $\mathbf{x} \in \Omega$. The global maximum is attained at $\mathbf{x} = \mathbf{x}^*$. Then there exists a positive number $K > 0$ such that

$$\begin{aligned}
\dot{V}(\mathbf{x}) &= \sum_{i=1}^n d_i \left(x_i^* \frac{\dot{x}_i}{x_i} - \dot{x}_i \right) \\
&= \sum_{i=1}^n d_i(x_i^* - x_i) g_i(\mathbf{x}) \\
&= \sum_{i=1}^n (x_i - x_i^*)(-d_i g_i(\mathbf{x}) + d_i g_i(\mathbf{x}^*)) + \sum_{i=1}^n d_i(x_i^* - x_i) g_i(\mathbf{x}^*)
\end{aligned}$$

$$\geq \quad K(\mathbf{x} - \mathbf{x}^*)^\top (\mathbf{x} - \mathbf{x}^*) - \sum_{i \notin \mathrm{supp}(\mathbf{x}^*)} d_i x_i g_i(\mathbf{x}^*).$$

The first term is positive for $\mathbf{x} \neq \mathbf{x}^*$ and the second term is nonpositive since $\mathbf{x}^*$ is saturated. Thus $\mathbf{x}^*$ is globally asymptotically stable in Ω. $\qquad \square$

It is not clear under what conditions the theorem is applicable to system (1) satisfying (**H**). However, the next subsection shows that it is sufficient to assume that G is an affine function.

3.5. **Affine cases.** Suppose that $G = (g_1, g_2, \ldots, g_n)^\top$ is an affine function, i.e., there exist a vector $\mathbf{b} = (b_i)$ and an $n \times n$ matrix $A = (a_{ij})$ such that $G(\mathbf{x}) = \mathbf{b} + A\mathbf{x}$. Then system (1) is reduced to the Lotka-Volterra equation

$$\dot{x}_i = x_i(b_i + (A\mathbf{x})_i), \quad i = 1, 2, \ldots, n. \tag{15}$$

The following theorem reveals the condition that the vector $\mathbf{b}$ and the matrix A have to satisfy if (**H**) is assumed.

Theorem 3.13. *Suppose that $G(\mathbf{x}) = \mathbf{b} + A\mathbf{x}$. Then* (**H**) *is satisfied if and only if* $\mathbf{b} > \mathbf{0}$ *and there exist constant vectors* $\mathbf{q}, \mathbf{v}, \mathbf{w} \in \mathbb{R}^n$ *such that*

$$A = -\mathrm{diag}(\mathbf{q}) - \mathbf{v}\mathbf{w}^\top, \quad \mathbf{q} > \mathbf{0}, \ \mathbf{v} > \mathbf{0}, \ \mathbf{w} > \mathbf{0}. \tag{16}$$

Proof. Suppose that (**H**) is satisfied. Eqs (8) and (10) imply $\mathbf{b} > \mathbf{0}$. Since $D_\mathbf{x}G(\mathbf{x}) = A$ holds for all $\mathbf{x} \in \mathbb{R}_+^n$, as shown in Theorem 3.9, there exist vector-valued functions $\mathbf{q}(\mathbf{x}) = (q_i(x_i))$, $\mathbf{v} = (v_i(\mathbf{x}))$, $\mathbf{w} = (w_i(\mathbf{x}))$ such that

$$A = -\mathrm{diag}(\mathbf{q}(\mathbf{x})) - \mathbf{v}(\mathbf{x})\mathbf{w}(\mathbf{x})^\top$$

for all $\mathbf{x} \in \mathbb{R}_+^n$. By (9), $\mathbf{q}(\mathbf{x})$, $\mathbf{v}(\mathbf{x})$, and $\mathbf{w}(\mathbf{x})$ are positive for all $\mathbf{x} \in \mathbb{R}_+^n$, and thus $a_{ij} < 0$ for all i, j. Since $a_{ii} = -q_i(x_i) - v_i(\mathbf{x})w_i(\mathbf{x})$ and $a_{ij} = -v_i(\mathbf{x})w_j(\mathbf{x})$ for $i \neq j$, we have

$$\frac{a_{ii} + q_i(x_i)}{a_{ji}} = \frac{a_{ij}}{a_{jj} + q_j(x_j)} = \frac{v_i(\mathbf{x})}{v_j(\mathbf{x})}$$

and

$$\frac{a_{ii} + q_i(x_i)}{a_{ij}} = \frac{a_{ji}}{a_{jj} + q_j(x_j)} = \frac{w_i(\mathbf{x})}{w_j(\mathbf{x})}.$$

These equalities imply that every $q_i(x_i)$ is constant and

$$v_j(\mathbf{x}) = \frac{a_{j1}}{a_{11} + c}v_1(\mathbf{x}) \quad \text{and} \quad w_i(\mathbf{x}) = \frac{a_{1i}}{a_{11} + c}w_1(\mathbf{x}),$$

where $c = q_1(x_1)$. Thus

$$\mathbf{v}(\mathbf{x})\mathbf{w}(\mathbf{x})^\top = \frac{v_1(\mathbf{x})w_1(\mathbf{x})}{(a_{11} + c)^2} \ (a_{11}, \ldots, a_{n1}) \begin{pmatrix} a_{11} \\ \vdots \\ a_{1n} \end{pmatrix},$$

where $v_1(\mathbf{x})w_1(\mathbf{x}) > 0$ is constant since $\mathbf{v}(\mathbf{x})\mathbf{w}(\mathbf{x})^\top = -A - \mathrm{diag}(\mathbf{q}(\mathbf{x}))$ is constant. Thus (16) follows.

Suppose that $\mathbf{b} > \mathbf{0}$ and A is of the form (16). Then it is clear that $u_i(y_i, z) = b_i + q_i y_i + v_i z$, $r_i(x_i) = -x_i$ and $s(\mathbf{x}) = -\mathbf{w}^\top \mathbf{x}$ fulfill the condition (**H**). $\qquad \square$

It is straightforward to show that for $G(\mathbf{x}) = \mathbf{b} + A\mathbf{x}$ with the matrix A of the form (16), the function $-DG(\mathbf{x})$ with $D = \mathrm{diag}(w_1/v_1, \ldots, w_n/v_n)$ is strongly monotone on $\mathbb{R}_+^n$.

The Lotka-Volterra equation (15) with (16) is studied by Shigesada, Kawasaki, and Teramoto [15] in a different context without the concept of limiting factors. They examined the effects of interference competition on stability of ecosystems. Theorem 3.13 shows that their results can be reviewed with the concept of limiting factors. We see that their mathematical results can be covered by Theorems 3.9, 3.10, 3.11, and 3.12.

4. **Conclusion.** In order to reveal the value of the concept of limiting factors, we studied a competitive system with a specific community structure that is visible with limiting factors (see Fig. 2). The general theory of competitive exclusion only predicts that competitive exclusion does not always occur in such a community since the number of limiting factors exceeds the number of species. However, our result shows that if interactions between species and limiting factors are specified, more informative prediction is available. Theorem 3.9 shows stable coexistence is realized at a unique saturated equilibrium point $\mathbf{x}^*$. Therefore, the number of positive components of $\mathbf{x}^*$ tells us how many species can coexist. Theorem 3.10 shows that the species composition of the realized stable community is dependent on the rank determined by the competition through the common limiting factor. A higher rank species has priority of persistence over other lower rank species. Thus invasion of high rank species could lead to extinction of low rank species. Theorem 3.11 shows that the amount of the common limiting factor changes directionally as successful invasion of new species occurs. These results are strengthened by the global stability analysis in Theorem 3.12. Theorem 3.13 reveals that the preceding work by Shigesada, Kawasaki, and Teramoto [15], who studies the dynamics of a certain Lotka-Volterra equation, can be reviewed with the concept of limiting factors. Their main results are covered by our general results on the equation of Kolmogorov type. These results suggest that the specification of competitive systems with the concept of limiting factors is sufficiently specific to obtain ecological insights and is sufficiently general to include Lotka-Volterra equations as a special case.

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