Interaction Strength Is Key to Persistence of Complex Mutualistic Networks

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The relationship between stability of complex ecosystems and the interactions among species has always been a basic research focus in ecology. In this paper, we rigorously prove two facts about mutualistic ecological networks based on the Lotka–Volterra model of n-species. First, we prove that the dominant eigenvalue of the mutualistic interaction matrix will monotonically increase to infinity as any one of its off-diagonal elements increases to infinity, coinciding with the discoveries by ecologists via simulations. Second, we show that the persistence of mutualistic networks is equivalent to the stability of their interaction matrix. These two results together reveal the fact that the persistence of large mutualistic ecosystems can be guaranteed with proper interaction strengths, though they will eventually be destroyed as the interaction strength between any two species increases.

1. Introduction

Since May's work 40 years ago [1] the study of the stability of large complex ecological networks [2–8] has attracted much attention. Various features of ecosystems are connected with their stability, including species diversity [3], the system architecture [4, 5], the strength of interactions among species [6], and also the interaction types [7, 8].

As a basic class of ecosystems, mutualistic systems have been investigated by ecologists and mathematicians [9–11]. It has been verified by using the mutualistic Lotka–Volterra model that the persistence of mutualistic networks can be guaranteed by the stability of their interaction matrix [10, 11]. Here, persistence is one type of stability, related to two features: the system possesses a feasible (positive) equilibrium point, and the equilibrium point is stable (which means all

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species have a constant positive abundance across time) [12]. But beyond that, how the interaction strength among species affects the persistence of mutualistic ecosystems is still unclear. Very recently, it has been shown by simulations that increasing interaction strength between species could increase the maximum real part of eigenvalues of the interaction matrix [12]. One important implication of this result is that the persistence of mutualistic ecosystems might be destroyed when the interaction strength increases.

In this paper, we will rigorously prove that the dominant eigenvalue (a real eigenvalue that is larger than the real part of any other eigenvalue) of the mutualistic interaction matrix will monotonically increase to infinity as any one of its off-diagonal elements increases to infinity, thus mathematically justifying the interesting observation of [12]. In addition, under a weaker assumption that one intrinsic growth rate is positive, we further prove that the existence of a globally asymptotically stable equilibrium point in R_+^n (open positive half-plane), which defines the persistence, is equivalent to the stability of the mutualistic interaction matrix. These results distinctly indicate the fact that the proper interaction strength will guarantee the coexistence of species, while too strong an interaction strength is detrimental to the persistence of mutualistic ecosystems.

The rest of this paper is organized as follows: the model of mutualistic ecological networks and the main results are described in Section 2, and Section 3 gives some concluding remarks.

2. Main Results

Consider the following nonlinear Lotka–Volterra population dynamics with a linear functional response [7, 8, 12]:

$$\dot{x}_i = x_i\left(r_i + a_{ii}x_i + \sum_{j\neq i} a_{ij}x_j\right), \quad i = 1, \ldots, n, \tag{1}$$

where n is the number of species of the ecosystem, x_i is the abundance of species i, r_i is the intrinsic growth rate of i, a_{ii} is the density-dependent self regulation, and a_{ij} is the interaction coefficient of i with species j. Let $x = (x_1, \ldots, x_n)^T$, $A = \left[a_{ij}\right]$, $1 \leq i, j \leq n$, and $r = (r_1, \ldots, r_n)^T$, then equation (1) can be rewritten in the following form:

$$\begin{pmatrix} x_1 & & \\ & \ddots & \\ & & x_n \end{pmatrix}(Ax + r). \tag{2}$$

For mutualistic networks, equation (2) satisfies $a_{ii} < 0$, $a_{ij} \geq 0 (i \neq j)$, and $r \geq 0$ with at least one r_i positive. Other than that, we commonly assume that the ecological network is strongly connected; that is, for any two species i and j, there exists a direct interaction path of finite length from i to j. The strong connectivity means the interaction matrix A is an irreducible matrix, which will be shown by a preliminary lemma in Appendix A.

To begin with, we first present some basic mathematical definitions, while all preliminary lemmas are given in Appendix A. Let $A = [a_{ij}] \in R^{n\times n}$. A is called a non-negative (positive) matrix, denoted by $A \geq (>) 0$, if $a_{ij} \geq (>) 0$. Let $B \in R^{n\times n}$; if $A - B \geq (>) 0$, then it is denoted $A \geq (>) B$. Let $|A| = [|a_{ij}|]$; if $A \geq 0$, then $A = |A|$. A is called a Z-matrix, denoted by $A \in Z_n$, if $a_{ij} \leq 0$ $(i \neq j)$ and an M-matrix if $A \in Z_n$ and $-A$ is stable, that is, all eigenvalues of $-A$ possess negative real parts. A is called an irreducible matrix if $(I + |A|)^{n-1} > 0$. $\rho(A) \equiv \max\{|\lambda| : \lambda$ is an eigenvalue of $A\}$ is called the spectral radius of A; $d(A)$, which is an algebraically simple real eigenvalue of A and larger than the real part of any other eigenvalue, is called the dominant eigenvalue of A, if it exists.

Suppose $f : R^{n\times n} \to R$. If for any two matrices $\alpha, \beta \in R^{n\times n}$, with $\alpha \geq \beta$ and $\alpha \neq \beta$, one has $f(\alpha) \geq f(\beta)$, then it is said that $f(X)$ is monotonically increasing along with $X \in R^{n\times n}$. Furthermore, if the inequality holds strictly, it is said that $f(X)$ is strictly monotonically increasing along with X.

For the interaction matrix A of the mutualistic network in equation (2), the simulation discoveries in [12] imply that the maximum real part of eigenvalues decreases along with the increasing interaction strength. Here, we prove the following conclusion.

Theorem 1. Let $A = [a_{ij}]$ and $a_{ij} \geq 0$ $(i \neq j)$. If A is irreducible, then for any matrix $B = [b_{ij}] \geq 0$, the following conclusions hold:

1. $A + B$ has a dominant eigenvalue $d(A + B)$.
2. $d(A + B) \geq d(A)$, and $d(A + B) > d(A)$ if $B \neq 0$.
3. $d(A + B) \to \infty$, as $\|B\| \to \infty$.

Proof. It is easy to verify that $A + B$ is irreducible and the off-diagonal elements are all non-negative. Then conclusion 1 holds by Lemma 4. As for conclusion 2, it is easy to know by the proof of Lemma 4 that there exists $\gamma > 1$ such that $\gamma I + A$ is irreducible and non-negative, and $d(A) = \rho(\gamma I + A) - \gamma$. Then by Lemma 5, $\gamma I + A + B$ is still irreducible and non-negative, and $d(A + B) = \rho(\gamma I + A + B) - \gamma$. Thus, it only remains to prove $\rho(\gamma I + A + B) > \rho(\gamma I + A)$, which can be obtained from Lemma 5 directly. Since $A + B$ is still irreducible with its off-diagonal elements non-negative, conclusion 2 actually indicates that $d(A + B)$ is strictly monotonically increasing along with B.

Now we prove conclusion 3. When $\|B\| \to \infty$, there is at least one element b_{ij} of B that satisfies $b_{ij} \to \infty$. Since $d(A + B) = \rho(\gamma I + A + B) - \gamma$, and because of the monotone increase of $d(A + B)$ along with B as indicated by conclusion 2, we know that to prove conclusion 3, it only remains to prove that for any given $1 \le i, j \le n$, $\rho(\gamma I + A + B) \to \infty$, when $b_{ij} \to \infty$.

Now, since $\gamma I + A + B$ is irreducible and non-negative, by Lemma 3, we know that for any $b_{ij} \ge 0$, there exists a positive vector $x(b_{ij}) = (x_1(b_{ij}), \ldots, x_n(b_{ij}))^T$, such that

$$(\gamma I + A + B)x(b_{ij}) = \rho(\gamma I + A + B)x(b_{ij}). \tag{3}$$

If $i = j$, then

$$(\gamma + a_{ii} + b_{ii}) + \sum_{k \ne i} (a_{ik} + b_{ik}) \frac{x_k(b_{ij})}{x_i(b_{ij})} = \rho(\gamma I + A + B). \tag{4}$$

Since the second term of the left side of equation (4) is always non-negative, it follows that $\rho(\gamma I + A + B) \to \infty$ as $b_{ii} \to \infty$.

If $i \ne j$, by conclusion 2, $\rho(\gamma I + A + B)$ increases strictly monotonically along with b_{ij}. If conclusion 3 does not hold, then $\rho(\gamma I + A + B)$ is monotonically increasing with an upper bound, and hence a real number c exists such that

$$\lim_{b_{ij} \to \infty} \rho(\gamma I + A + B) = c. \tag{5}$$

By equation (3), $\rho(\gamma I + A + B)$ is the eigenvalue of $\gamma I + A + B$. Thus

$$(\gamma I + A + B)^{n-1} x(b_{ij}) = (\rho(\gamma I + A + B))^{n-1} x(b_{ij}). \tag{6}$$

Denote $(\gamma I + A + B)^{n-1} = [s_{ij}] \in R^{n \times n}$. By equations (3) and (6), we have

$$\begin{gathered}(\gamma + a_{ii} + b_{ii}) + (a_{ij} + b_{ij}) \frac{x_j(b_{ij})}{x_i(b_{ij})} + \sum_{k \ne i,j} (a_{ik} + b_{ik}) \frac{x_k(b_{ij})}{x_i(b_{ij})} = \\ \rho(\gamma I + A + B),\end{gathered} \tag{7}$$

and

$$s_{jj} + s_{ji}\frac{x_i(b_{ij})}{x_j(b_{ij})} + \sum_{k\neq i,j} s_{jk}\frac{x_k(b_{ij})}{x_j(b_{ij})} = \left(\rho(\gamma I + A + B)\right)^{n-1}. \tag{8}$$

It is easy to observe that every part of the left side of equation (7) is non-negative, thus from equation (5), we can get

$$\frac{x_j(b_{ij})}{x_i(b_{ij})} \to 0, \text{ as } b_{ij} \to \infty,$$

which implies

$$\frac{x_i(b_{ij})}{x_j(b_{ij})} \to \infty, \text{ as } b_{ij} \to \infty. \tag{9}$$

Moreover, it is obvious that $(\gamma - 1)I + A + B$ is irreducible, which implies

$$(\gamma I + A + B)^{n-1} > 0.$$

By direct calculations, it can be easily checked that s_{ji} is positive and monotonically nondecreasing along with b_{ij}. It can be known from equation (9) that when $b_{ij} \to \infty$, the left side of equation (8) will tend to infinity, while the right side tends to $c^{n-1} < \infty$, which is a contradiction. Thus

$$\rho(\gamma I + A + B) \to \infty,$$

as $b_{ij} \to \infty$ $(i \neq j)$. This completes the proof of conclusion 3. □

Corollary 1. For the mutualistic system of equation (2), there exists a dominant eigenvalue $d(A)$ for its interaction matrix A. Moreover, for any given $1 \leq i, j \leq n$, $d(A)$ is monotonically increasing along with a_{ij}, and $d(A) \to \infty$, as $a_{ij} \to \infty$.

Proof. The first part holds by letting $B = 0$ in Lemma 1, and the second part holds by letting $B \geq 0$ and $B \neq 0$. □

Theorem 1 and Corollary 1 indicate that when the mutualistic strength lies within an appropriate level, the interaction matrix will stay stable, while too strong an interaction strength will destroy the stability of the mutualistic matrix. Now we present an example to illustrate part of the results of Theorem 1 and Corollary 1.

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Example 1. Let

$$A = \begin{pmatrix} -2 & a & 0 \\ 0 & -3 & b \\ c & 0 & -4 \end{pmatrix}$$

where a, b, c are all positive real numbers. It can be checked that A is irreducible, whose characteristic polynomial is

$$f(\lambda) \triangleq \det(\lambda I - A) = \lambda^3 + 9\lambda^2 + 26\lambda + 24 - abc.$$

When $a < 2$, $b < 3$, $c < 4$, the Gerschgorin disk theorem states that all eigenvalues of A possess negative real parts. If $abc = 24$, then 0 is an eigenvalue of A, since $f(0) = 24 - abc$. While $abc > 24$, it holds that $f(0) < 0$, $f\left(\sqrt[3]{abc - 24}\right) > 0$, and by continuity, $f(\lambda) = 0$ has a positive root, meaning A has a positive eigenvalue.

In mathematics, a matrix is said to be stable if all of its eigenvalues have negative real parts, which means that the states of the corresponding continuous-time linear systems will tend to the equilibrium point under the action of the matrix. Theorem 1 indicates that the stability of the mutualistic interaction matrix will be destroyed as the strength between any two species increases, since at least one of its eigenvalues will eventually be positive. However, since equation (2) possesses a nonlinear structure, it is far from obvious how its stability can be affected by the stability of the interaction matrix. This will be answered by the following theorem.

Theorem 2. Equation (2) possesses a globally asymptotically stable equilibrium point in R_+^n if and only if A is stable.

Proof. Sufficiency: Suppose A is stable. For equation (2), it is easy to see that the only possible positive equilibrium point is the solution of the equation $Ax + r = 0$. Suppose

$$A\overline{x} + r = 0, \tag{10}$$

then $\overline{x} = -A^{-1}r$. Since $-A$ is a Z-matrix and A is stable, then $-A$ is an M-matrix, and hence $-A^{-1} \geq 0$ by Lemma 8, implying

$$\overline{x} = -A^{-1}r \geq 0.$$

To prove the positivity of $\overline{x}$, one only needs to prove that no entry in $\overline{x}$ is 0. If not, suppose $\overline{x} = (\overline{x}_1, \ldots, \overline{x}_n)$, $N = \{1, 2, \ldots, n\}$ and $D = \{i \mid \overline{x_i} = 0, i \in N\}$; then both D and $\overline{D} = N - D$ are nonempty. By the strong connectivity of equation (2), there exist $i \in \overline{D}$ and $j \in D$ satisfying $a_{ji} > 0$. Thus, one has

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$$\sum_{k=1}^{n} a_{jk}\overline{x}_k = a_{jj}\times 0 + \sum_{k\neq j} a_{jk}\overline{x}_k \geq a_{ji}\overline{x}_i > 0,$$

which contradicts equation (10) since $r \geq 0$. Therefore, $\overline{x}$ is the unique positive equilibrium point.

Next, we prove $\overline{x}$ is globally asymptotically stable in R_+^n. Since $-A$ is an M-matrix, by Lemma 9, there exists a positive diagonal matrix $D = \mathrm{diag}(d_1, \ldots, d_n)$, such that $DA + A^T D$ is negative definite. Construct the following Lyapunov function [10]:

$$V(x) = \sum_{i=1}^{n} d_i \int_{\overline{x}_i}^{x_i} \left(1 - \frac{\overline{x}_i}{x}\right) dx,$$

then $V(\overline{x}) = 0$, and $V(x) > 0$ when $x \in R_+^n - \{\overline{x}\}$. Since $A\overline{x} + r = 0$, the derivative of $V(x)$ about t along the trajectory of equation (2) is

$$\begin{aligned}
&\frac{dV(x)}{dt} = \sum_{i=1}^{n} d_i\left(1 - \frac{\overline{x}_i}{x_i}\right)\dot{x}_i = \\
&\sum_{i=1}^{n} d_i\left(1 - \frac{\overline{x}_i}{x_i}\right) x_i\left(-a_{ii}x_i + \sum_{j\neq i} a_{ij}x_j + r_i\right) = \\
&\sum_{i=1}^{n} d_i(x_i - \overline{x}_i)\left(-a_{ii}(x_i - \overline{x}_i) + \sum_{j\neq i} a_{ij}(x_j - \overline{x}_j)\right) = \\
&\frac{1}{2}(x - \overline{x})^T (DA + A^T D)(x - \overline{x}) < 0, \quad x \in \mathbb{R}_+^n - \{\overline{x}\}.
\end{aligned}$$

In addition, it is easy to check that $V(x) \to \infty$ as $x_i \to 0$ or ∞ for any $i = 1, \ldots, n$, and the global stability of equilibrium in R_+^n is obtained by the Lyapunov theorem (Barbashin–Krasovskii theorem, see [13]).

Necessity: Suppose $\overline{x} = (\overline{x}_1, \ldots, \overline{x}_n)$ is the globally asymptotically stable positive equilibrium point. Then $\overline{x}$ is the solution of the equation $Ax + r = 0$, and thus the Jacobian of equation (2) at $\overline{x}$ is $\overline{X}A$ as in equation (11), where $\overline{X} = \mathrm{diag}(\overline{x}_1, \ldots, \overline{x}_n)$ is the diagonal matrix with diagonal entries taking values $\overline{x}$ and other entries taking values 0:

$$\begin{pmatrix}
a_{11}\overline{x}_1 + r_1 + \sum_{j=1}^{n} a_{1j}\overline{x}_j \cdots & a_{1i}\overline{x}_1 & \cdots & a_{1n}\overline{x} \\
\vdots & \vdots & & \vdots \\
a_{i1}\overline{x}_i & \cdots a_{ii}\overline{x}_i + r_i + \sum_{j=1}^{n} a_{ij}\overline{x}_j \cdots & & a_{in}\overline{x}_i \\
\vdots & \vdots & & \vdots \\
a_{n1}\overline{x}_n & \cdots \quad a_{ni}\overline{x}_n & & \cdots a_{nn}\overline{x}_n + r_n + \sum_{j=1}^{n} a_{nj}\overline{x}_j
\end{pmatrix} \triangleq \overline{X}A. \tag{11}$$

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Since $\overline{x}$ is asymptotically stable, by Lemma 10, no eigenvalue of $\overline{X}A$ has a positive real part. Now, we prove that all eigenvalues of $\overline{X}A$ have negative real parts. If not, suppose there is at least one eigenvalue of $\overline{X}A$ whose real part is 0. It is easy to see that all the off-diagonal entries of $\overline{X}A$ are non-negative, and $\overline{X}A$ is irreducible, thus by Lemma 4, 0 is the dominant eigenvalue of $\overline{X}A$ and hence an eigenvalue of A. Next, we will show that 0 is also the dominant eigenvalue of A.

By Lemma 4, A has a dominant eigenvalue $\lambda = d(A)$. If 0 is not the dominant eigenvalue of A, then $\lambda > 0$ and 0 is the dominant eigenvalue of $A - \lambda I$, and thus the eigenvalue of $\overline{X}(A - \lambda I)$. Suppose $\overline{x}_m = \min\{\overline{x}_1, \ldots, \overline{x}_n\}$; then $\overline{X} = \overline{x}_m I + \overline{X}^c$, where $\overline{X}^c = \overline{X} - \overline{x}_m I \geq 0$. Thus by Lemma 6,

$$\begin{aligned} d\left(\overline{X}(A - \lambda I)\right) &= d\left(\overline{X}A - \lambda \overline{x}_m I - \lambda \overline{X}^c\right) \leq d\left(\overline{X}A - \lambda \overline{x}_m I\right) \\ &= d\left(\overline{X}A\right) - \lambda \overline{x}_m < d\left(\overline{X}A\right) = 0, \end{aligned}$$

which contradicts the fact that 0 is the eigenvalue of $\overline{X}(A - \lambda I)$. Therefore, 0 is the dominant eigenvalue of A.

Now, denote $t = \max_{1 \leq i \leq n} |a_{ii}|$; then $tI + A$ is a non-negative and irreducible matrix and t is the dominant eigenvalue of $tI + A$, since $t + \lambda(A)$ is an eigenvalue of $tI + A$, with $\lambda(A)$ being any eigenvalue of A. By Lemma 3, $t = \rho(tI + A)$ and there is a positive vector y such that $y^T(tI + A) = ty^T$. Thus, $y^T A = 0$. Since $r \geq 0$ and at least one entry is positive, then

$$y^T(A\overline{x} + r) = y^T A\overline{x} + y^T r = y^T r > 0,$$

which contradicts $A\overline{x} + r = 0$. Thus, all eigenvalues of $\overline{X}A$ have negative real parts. Notice that $-\overline{X}A$ is a Z-matrix, which implies $-\overline{X}A$ is an M-matrix, and by Lemma 7, $-\overline{X}^{-1}(-\overline{X}A) = A$ is stable. This completes the proof. □

Theorem 2 indicates the persistence of the mutualistic system in equation (2) is equivalent to the stability of its interaction matrix. In [11], the equivalence between the existence of the positive equilibrium point and the stability of the mutualistic interaction matrix was proved with the assumption that $r_i > 0$, $i = 1, \ldots, n$. Here, we carry out the proof under a weaker assumption that at least one intrinsic growth rate is supposed to be positive. In [10], it has been proved that if equation (2) has a positive equilibrium point, and if the interaction matrix is stable, then the positive equilibrium point is globally asymptotically stable in R_+^n. In Theorem 2, we also strictly prove that the global stability of the positive equilibrium point implies the stability of the interaction matrix. Since Corollary 1 indicates that the increase of the interaction strength between any two species will eventually destroy the stability of the interaction matrix, then Theorem 2 shows that it also destroys the existence of the globally asymptotically stable positive equilibrium point, or persistence, of equation (2).

3. Conclusion

It is known that the properties of one large complex system can be essentially determined by the interactions among the components. In this paper, we have theoretically investigated how the interaction strength determines the persistence of complex mutualistic networks. We proved that increasing the interaction strength between any two species will finally destroy the stability of the mutualistic interaction matrix, which is equivalent to the persistence of mutualistic networks. On the other hand, our results also indicate that the proper mutualistic interaction strength can ensure the persistence of mutualistic networks.

After that, our results may demonstrate their own potential value in two ways. First, since mutualism or cooperation ubiquitously exists in nature, it is necessary to probe strategies to eliminate the instability of mutualistic ecosystems by reducing or transforming mutualistic interactions. Other than that, as a typical complex system, ecosystems provide some insights into the study of properties of many other complex systems, such as biological systems, economic systems, social systems, and others. Our results uncover the role of positive interactions on ecosystems with specific mutualistic structure, which may stimulate more theoretical explorations of systems with different richer interaction types in the future.

Appendix

A. Preliminary Lemmas

Lemma 1. [14] Suppose G is a directed graph and A is its interaction matrix. Then G is strongly connected if and only if A is irreducible.

Lemma 2. [14] Let $A,\ B \in R^{n\times n}$; if $|A| \le B$, then $\rho(A) \le \rho(|A|) \le \rho(B)$.

Lemma 3. [14] Suppose A is a positive or an irreducible and non-negative matrix. Then

1. $\rho(A) > 0$.
2. $\rho(A)$ is an eigenvalue of A.
3. There are two positive vectors x, y such that $Ax = \rho(A)x$ and $y^T A = \rho(A)y^T$.
4. $\rho(A)$ is an algebraically simple eigenvalue of A; that is, the algebraic multiplicity of $\rho(A)$ is 1.

Lemma 4. Let $A = \left[a_{ij}\right]$ and suppose $a_{ij} \geq 0$ $(i \neq j)$. If A is irreducible, then A has an algebraically simple real eigenvalue $d\left(A\right)$, called a dominant eigenvalue, which satisfies $d\left(A\right) > \mathrm{Re}(\lambda_i)$ for every other eigenvalue λ_i of A.

Proof. Since A is irreducible and $a_{ij} \geq 0(i \neq j)$, it is easy to see that there exists $\gamma > 1$ (such as $\gamma = \max_{0 \leq i \leq n}\left|a_{ii}\right| + 1$) such that $\gamma I + A \geq 0$ and is irreducible. Then by Lemma 3, $\rho\left(\gamma I + A\right)$ is a positive eigenvalue of $\gamma I + A$ with algebraic multiplicity 1. For each eigenvalue $\lambda_i\left(A\right)$ of A, $\gamma + \lambda_i\left(A\right)$ is an eigenvalue of $\gamma I + A$. Denote $d\left(A\right) = \rho\left(\gamma I + A\right) - \gamma$; then $d\left(A\right)$ is an eigenvalue of A with algebraic multiplicity 1 and is larger than the real part of any other eigenvalue of A by the definition of $\rho\left(\gamma I + A\right)$. □

Lemma 5. Let $A = \left[a_{ij}\right]$ be irreducible and non-negative. Then $A + B$ is irreducible whenever $B \in R^{n\times n}$ is non-negative, and $\rho\left(A + B\right) > \rho\left(A\right)$ whenever $B \geq 0$ and $B \neq 0$.

Proof. Since A is irreducible and non-negative, then for any $B \geq 0$,

$$\left(I + A + B\right)^{n-1} = \left(I + A\right)^{n-1} + \binom{n-1}{n-2}$$
$$\left(I + A\right)^{n-2}B + \cdots + B^{n-1} \geq \left(I + A\right)^{n-1} > 0,$$

where the relation $M \geq N$ between two matrices M and N means $M - N \geq 0$. Thus, $A + B$ is irreducible by definition.

For the second part, by Theorem 8.1.18 in [14], it holds that

$$\rho\left(A + B\right) \geq \rho\left(A\right).$$

By Lemma 3, there exists a positive vector x such that

$$\left(A + B\right)x = \rho\left(A + B\right)x. \tag{A.1}$$

For $B \geq 0$ and $B \neq 0$, if $\rho\left(A + B\right) = \rho\left(A\right)$, then

$$\rho\left(A + B\right)x = \rho\left(A\right)x = Ax < Ax + Bx = \left(A + B\right)x, \tag{A.2}$$

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since $\rho(A)$ is also an eigenvalue of A. But equation (A.2) contradicts equation (A.1), thus

$$\rho(A+B) > \rho(A). \square$$

Lemma 6. Suppose A is described as in Lemma 4; then for any $B \geq 0$ and $B \neq 0$, it holds that $d(A+B) > d(A)$.

Proof. It is easy to see that there exists $\gamma > 1$, such that $\gamma I + A$ is irreducible and non-negative; then by Lemmas 3–5 we get $d(A+B) = \rho(\gamma I + A + B) - \gamma$ for $B \geq 0$. Again by Lemma 5 we have $\rho(\gamma \mathrm{I} + A + B) > \rho(\gamma I + A)$ for $B \geq 0$ and $B \neq 0$, thus $d(A+B) > d(A)$. $\square$

Lemma 7. Suppose A is an M-matrix; then for all positive diagonal matrices D, $-DA$ is stable.

Proof. Since A is an M-matrix, then by Lemma 8, $A \in Z_n$ is nonsingular and $A^{-1} \geq 0$. Thus, for any positive diagonal matrix D, it holds that $DA \in Z_n$, and that

$$(DA)^{-1} = A^{-1} D^{-1} \geq 0.$$

Then by Lemma 8, DA is an M-matrix, and thus $-DA$ is stable by definition. $\square$

Lemma 8. [14] Suppose $A \in Z_n$; then A is an M-matrix if and only if A is nonsingular and $A^{-1} \geq 0$.

Lemma 9. [14] If $-A$ is an M-matrix, there exist positive diagonal matrices D, such that $DA + A^T D$ is negative definite.

Lemma 10. [13] Let $x = \overline{x}$ be an equilibrium point for the nonlinear system

$$\dot{x} = f(x)$$

where $f : D \to R^n$ is continuously differentiable and D is a neighborhood of $\overline{x}$. Let

$$A = \frac{\partial f}{\partial x}(x)\,|_{x=\overline{x}}\,.$$

Then

1. $\overline{x}$ is asymptotically stable if $\mathrm{Re}(\lambda_i) < 0$ for all eigenvalues of A.
2. $\overline{x}$ is unstable if $\mathrm{Re}(\lambda_i) > 0$ for one or more of the eigenvalues of A.

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