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Effective competition determines the global stability of model ecosystems

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Abstract We investigate the stability of Lotka-Volterra (LV) models constituted by two groups of species such as plants and animals in terms of the intragroup effective competition matrix, which allows separating the equilibrium equations of the two groups. In matrix analysis, the effective competition matrix represents the Schur complement of the species interaction matrix. It has been previously shown that the main eigenvalue of this effective competition matrix strongly influences the structural stability of the model ecosystem. Here, we show that the spectral properties of the effective competition matrix also strongly influence the dynamical stability of the model ecosystem. In particular, a necessary condition for diagonal stability of the full system, which guarantees global stability, is that the effective competition matrix is diagonally stable, which means that intergroup interactions must be weaker than intra-group competition in appropriate units. For mutualistic or competitive interactions, diagonal stability of the effective competition is a sufficient condition for global stability if the inter-group interactions are suitably correlated, in the sense that the biomass that each species provides to (removes from) the other group must be proportional to the biomass that it receives from (is removed by) it. For a non-LV mutualistic system with saturating interactions, we show that the diagonal stability of the corresponding LV system close to the fixed point is a sufficient condition for global stability.

Introduction

More than 60 years after the pioneering work by Robert MacArthur (1955), and 40 years after the landmark paper by Robert May (1972), the stability of model ecosystems is still intensely debated (McCann 2000; Ives and Carpenter 2007). In this paper, we propose that the apparent contradiction between stability and complexity in model ecosystems can be in part reconciled by focusing on structural stability i.e. the stability of an equilibrium point with respect to variations in parameters.

In this paper, we consider model ecosystems that consist of two groups of species that we denominate plants and animals, characterized by intragroup competition and intergroup interactions of predatory, competitive or mutualistic nature. For such systems, the effective competition matrix (Bastolla et al. 2005) allows separating the equilibrium equations of the two groups of species and to analytically predict their structural stability (Bastolla et al. 2005, Bastolla et al. 2009, Pascual-García and Bastolla 2017). The effective competition represents the competition between species in the same group that arises both from their direct competition and from the dynamics of species in the other

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group, and is related to a previous theory by Chesson 1994). If some species or resources of the ecosystem are unknown, we interpret the direct competition matrix as an effective competition matrix that takes into account the dynamics of the unknown species. In this case, it is important to investigate how the stability properties of the full system map into the properties of the effective competition matrix. Here, we show that there is a deep relationship between the effective competition matrix of a single group and the global stability of the complete system.

The paper is organized as follows. We start by discussing the concept of global stability and its implications. A sufficient condition for global stability of a Lotka-Volterra system is that the matrix A describing ecological interactions is diagonally stable (Goh 1977; Berman and Hershkowitz, 1983). As we discuss in the first section, this condition means that there must be abundance units in which the interaction matrix is positive definite (with the sign convention that we adopt; with the usual convention, the interaction matrix must be negative definite). This guarantees the existence of a Lyapunov function.

In the section "Effective competition and global stability", we discuss the relationship between the global stability of two-group system and the diagonal stability of the effective competition matrix C that allows separating the equilibrium equations of the two groups. We first show that, if the interaction matrix A is diagonally symmetric, diagonal stability of the effective competition matrices is a necessary and sufficient condition for diagonal stability of the interaction matrix A. Consequently, the stability analysis can be performed on each sub-system, much in the same way in which the effective competition between consumers derived from the dynamics of resources allows analyzing global stability in MacArthur's theory (MacArthur 1970; Chesson 1990). If A is not symmetric, diagonal stability of the effective competition matrix C is a necessary condition for diagonal stability of A, but it must be complemented with additional conditions on the antisymmetric part of the interactions to become a sufficient condition. In the "Conclusions and perspectives" section we examine mutualistic systems. In this case, the effective competition parameter may become negative if the mutualistic interactions are strong with respect to intragroup competition, implying unbounded population growth. To avoid this unrealistic behaviour, we have to model mutualistic interactions that saturate when the abundances of mutualistic partners increase, as proposed by Holland et al. (2002). For such a non-linear model, we can still define linearized Lotka-Volterra equations close to an equilibrium point. The corresponding effective mutualistic interactions are much smaller than the interactions that would be observed in the absence of saturation,

which enhances global stability. Therefore, the observation that Lotka-Volterra mutualistic systems becomes rapidly unstable when the number of species increases, as repeatedly reported in the literature (May 1974; Bascompte et al. 2006; Allesina and Tang 2012), does not mean by itself that mutualistic interactions destabilize model ecosystems.

We present the conclusions in the "Conclusions and perspectives" section . We propose that, for globally stable interaction matrices, the question of dynamical stability has to be substituted with the more general question of the space of the intrinsic growth rate parameters that give raise to feasible equilibria. This question is equivalent to structural stability.

Global stability for a Lotka-Volterra system

We consider in most of this paper Lotka-Volterra systems of n species, in which the growth rates of each species i in the model ecosystem is a linear function of the abundance of all other species, namely, the standard Lotka-Volterra equations

$$dN_i/dt = N_i \left(r_i - \sum_k A_{ik} N_k \right). \tag{1}$$

The parameter r_i is the intrinsic growth rate of species i, and it is positive if species i is a primary producer and negative otherwise, and A_{ik} is the interaction matrix. Note that the matrix A appears in the above equation with a negative sign with respect to the usual definition i.e. the interaction matrix A would be denoted as $-A$ in the usual formulation. We use this convention because in this way the interaction matrix A and the effective competition matrix (see below) have the same sign, and we can pass from one framework to the other without having to change sign.

We are interested in the unique fixed point at which all n species are present with non-zero equilibrium biomasses N_i^*. This equilibrium is locally stable if all equilibrium biomasses are positive, $N_i^* > 0$, and if all eigenvalues of the community matrix with elements $J_{ik} = -N_i^* A_{ik}$ have negative real part. A stronger condition is global stability, which guarantees that the coexistence fixed point is stable for an arbitrarily large perturbation of the abundances i.e. any configuration with initial positive abundances for all species always returns to the same fixed equilibrium, hence no species can get extinct starting from positive abundance. Goh (1977) has shown that sufficient conditions for global stability of the coexistence fixed point are that (1) all equilibrium biomasses are positive (feasibility) and (2) there exists a diagonal matrix D with real and positive

elements such that the symmetric matrix $DA + A^T D$ is positive definite.[1]

$$Q = DA + A^T D \succ 0 \tag{2}$$

Matrices A satisfying this condition are variedly referred in the literature as being diagonally stable or Volterra-Lyapunov stable (VL-stable). In what follows, we will use the former notation. A matrix M is said to be positive definite if its symmetric part $M^S = \frac{1}{2}\left(M + M^T\right)$ has all positive eigenvalues. Note that, if one uses the usual convention for the sign of the matrix A, then diagonal stability is equivalent to negative definiteness of the matrix DA.

The feasibility of the equilibrium depends on the intrinsic growth rates r_i: The equilibrium is feasible if and only if the r_i are such that all equilibrium abundances are positive, $N_i^* = \sum_j A_{ij}^{-1} r_j > 0 \; \forall i$. Therefore, when the intrinsic growth rates r_i provide feasibility dynamical stability is guaranteed as well, and the volume of this space of growth rates can be taken as a measure of the structural stability of the model ecosystem.

When the coexistence fixed point is not feasible and A is diagonally stable, there will be at least one maximal subset Ω_p of $p < n$ species such that the fixed point restricted to these p species is feasible i.e. $\delta_i \left(\sum_j A_{ij} N_j^* \delta_j - r_i\right) = 0 \; \forall i$, where $\delta_i = 1$ if $i \in \Omega_p$ and 0 otherwise and $N_i^* > 0$, and no feasible equilibrium exists if another species is added. Since the fixed point $N_i^* \delta_i$ is globally stable, the time evolution of the system will converge to one of the maximal feasible fixed points determined by the intrinsic growth rates, and all other species go extinct.

Diagonal stability and changes of units

Here, we show that the condition of diagonal stability is equivalent to requiring that there are units of abundance such that the interaction matrix is positive definite. Imagine that we change the units of abundances for all species, for instance from number of individuals to biomasses. We

write such a change of units as $N_k' = d_k N_k$ (in the example, the factor d_k represents the average biomass of an individual of species k), or $N' = DN$ in matrix notation, where D is a diagonal matrix with diagonal entries $d_1, \ldots, d_k$. Under such change of units, the interaction matrix A, which has units of inverse abundance times inverse time, changes to $\overline{A}_{ik} = A_{ik}/d_k$, or $\overline{A} = A D^{-1}$ in matrix notation, since in this way the dynamical Eq. 1 are left invariant: $(1/N_i)dN_i/dt = (1/N_i')dN_i'/dt = r_i - \sum_k A_{ik} N_k = r_i - \sum_k \overline{A}_{ik} N_k'$. In this paper, we denote by an overline a matrix multiplied from the right by the diagonal matrix D^{-1}, $\overline{M} = M (D)^{-1}$, which we interpret as the matrix expressed in the units defined by D.

If we multiply both sides of Eq. 2 times D^{-1}, we get

$$Q' = D^{-1} Q D^{-1} = A D^{-1} + \left(A D^{-1}\right)^T \succ 0. \tag{3}$$

Clearly Q' will be positive definite if and only if Q is positive definite[2]. Since Q' is the symmetric part of the matrix $\overline{A} = A D^{-1}$, Eq. 3 tells us that the system will be diagonally stable if and only if there are units in which the interaction matrix $\overline{A}$ is positive definite. In other words, the condition of diagonal stability is invariant under changes of units, and it is therefore the ecologically relevant condition, while the condition that a matrix is positive definite is not invariant under changes of units since the matrix DA may be positive definite while A is not (see below for one example). In the following, we will express the diagonal stability condition in the equivalent form Eq. 3 and we will interpret the matrix $\overline{A} = AD^{-1}$ as the interaction matrix expressed in the new units.

We can get another equivalent condition by multiplying Eq. 2 both on the right and the left times $D^{-1/2}$, obtaining

$$Q'' = D^{-1/2} Q D^{-1/2} = D^{1/2}AD^{-1/2} + D^{-1/2}A^T D^{1/2} \succ 0. \tag{4}$$

The matrix $A_D = D^{1/2} A D^{-1/2}$ is said to be related to A by diagonal similarity, which preserves the eigenvalues and is an equivalence relationship amongst matrices. The global stability condition Eq. 2 may be equivalently stated by saying that the system will be globally stable if and only if A is diagonally similar to a positive definite matrix A_D.

Effective competition

We now consider an ecosystem composed of two guilds of species, which we designate as P and A (plants and

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[1]We describe here the main notation used in this paper. A matrix M is said to be positive definite (the term Hermitian positive is more frequently used in the mathematical literature), which we write as $M \succ 0$, when its symmetric part $M^S \equiv \frac{1}{2}\left(M + M^T\right)$ has all positive eigenvalues, where M^T is the transposed matrix. This implies that $\langle x, Mx \rangle$ is positive for all possible vectors $x \neq 0$, where $\langle x, y \rangle$ indicates the scalar product. We denote by $M^a \equiv \frac{1}{2}\left(M - M^T\right)$ the antisymmetric part of matrix M. We also use the short notation $M^{-T} \equiv \left(M^T\right)^{-1} \equiv \left(M^{-1}\right)^T$. We denote by $\overline{M} \equiv MD^{-1}$ the matrix M multiplied by the right times the diagonal matrix $(D)^{-1}$, which we interpret as the matrix M in the abundance units defined by D (see below).

[2]In fact, it holds $\langle x, D^{-1}QD^{-1}x \rangle = \langle (D^{-1}x), Q(D^{-1}x) \rangle$; therefore, Q' is positive definite if and only if Q is such.

animals, although we can also interpret them as two groups of competing species of the same kind). The interaction matrix is

$$A = \begin{pmatrix} B_P & \Gamma_P \\ \Gamma_A & B_A \end{pmatrix}, \tag{5}$$

where B_P and B_A are the direct competition matrices between species in groups P and A, and Γ_P (Γ_A) describes how the growth rates of species in group P (A) are affected by the abundances of species in group A (P), with components being negative for mutualistic interactions or predation of A over P, positive for competitive interactions or predation of P over A, with the sign convention that we have adopted for A. For this system, we can write down the fixed point equations separately for species in each group as

$$\begin{aligned} C_P N_P^* &= R_P, \\ C_A N_A^* &= R_A, \end{aligned} \tag{6}$$

where C_P and C_A are the effective competition matrices, defined as (Bastolla 2005)

$$C_P = B_P - \Gamma_P (B_A)^{-1} \Gamma_A, \qquad C_A = B_A - \Gamma_A (B_P)^{-1} \Gamma_P. \tag{7}$$

and R_A and R_P are the effective productivity vectors for species in guild A and P, respectively, defined as (Bastolla 2005)

$$R_P = r_P - \Gamma_P (B_A)^{-1} r_A, \qquad R_A = r_A - \Gamma_A (B_P)^{-1} r_P. \tag{8}$$

The effective competition matrices incorporate in a single matrix the effects of the indirect interaction between species of the same group mediated through species in the other group. Eq. 6 make clear that, by using effective productivities/competitions, the two guilds can be decoupled as if they were two isolated, purely competitive systems. We also define matrices that act on both guilds as

$$B = \begin{pmatrix} B_P & 0 \\ 0 & B_A \end{pmatrix}; \quad \Gamma = \begin{pmatrix} 0 & \Gamma_P \\ \Gamma_A & 0 \end{pmatrix};$$
$$C = \begin{pmatrix} C_P & 0 \\ 0 & C_A \end{pmatrix} = B - \Gamma B^{-1} \Gamma. \tag{9}$$

Effective competition and global stability

For diagonally symmetric interaction matrices, diagonal stability of the effective competition and of the full interaction matrix are equivalent

In matrix theory, the effective competition matrix C_A corresponds to the *Schur complement* (Horn and Johnson 1985;

Zhang 2005) of the matrix B_P in the interaction matrix A (analogously with C_P). An important result of the theory of the Schur complement is that if a matrix A partitioned like in Eq. 5 is symmetric, then it is positive definite (thus, the corresponding LV system is globally stable) if and only if both B_P and its Schur complement C_A are positive definite (see Horn and Johnson (1985) Theorem 7.7.6 pag.472, pag. 34 in Zhang (2005) and Boyd and Vandenberghe (2004)).

This result is directly generalized to diagonal stability. We use the notation $\overline{B_P} = B_P (D_P)^{-1}$, $\overline{B_A} = B_A (D_A)^{-1}$, $\overline{\Gamma_P} = \Gamma_P (D_A)^{-1}$, $\overline{\Gamma_A} = \Gamma_A (D_P)^{-1}$. We have

$$\begin{aligned} \overline{\Gamma_A (B_P)^{-1} \Gamma_P} &= \Gamma_A (D_P)^{-1} D_P (B_P)^{-1} \Gamma_P (D_A)^{-1} \\ &= \overline{\Gamma_A} \left(\overline{B_P}\right)^{-1} \overline{\Gamma_P}, \end{aligned}$$

so that the diagonally transformed effective competition is equal to the effective competition of the diagonally transformed matrices $\overline{B}$ and $\overline{\Gamma}$. In general, since we will only consider products of matrices that have homogeneous units, the product of matrices multiplied by the right times $(D)^{-1}$ will be equal to the same product of matrices, each one multiplied by the right times $(D)^{-1}$. The theorem of the Schur complement then states that, if the matrix $\overline{A}$ is symmetric (i.e. if the interaction matrix is diagonally symmetric), then it is positive definite if and only if both $\overline{B}$ and $\overline{C}$ are positive definite i.e. if they are diagonally stable.

If the interaction matrix $\overline{A}$ is not symmetric, then it is positive definite if and only if its symmetric part $\overline{A}^S$ is positive definite. This matrix can be written as

$$\overline{A}^S = \begin{pmatrix} \left(\overline{B_P}\right)^S & \frac{1}{2}\left(\overline{\Gamma}_P + \overline{\Gamma}_A^T\right) \\ \frac{1}{2}\left(\overline{\Gamma}_P + \overline{\Gamma}_A^T\right)^T & \left(\overline{B_A}\right)^S \end{pmatrix}, \tag{10}$$

and it is positive definite if and only if both the symmetric part of $\overline{B_P}$ and its Schur complement in $\overline{A}^S$, denoted as $\overline{S_A}$, are such, yielding the following necessary and sufficient condition:

$$\begin{aligned} \overline{A}^S \succ 0 \;\leftrightarrow\; &\overline{B_P} \succ 0, \; \overline{S_A} = \left(\overline{B_A}\right)^S \\ &-\frac{1}{4}\left(\overline{\Gamma}_P + \overline{\Gamma}_A^T\right)^T \left(\overline{B}_P^S\right)^{-1} \left(\overline{\Gamma}_P + \overline{\Gamma}_A^T\right) \succ 0 \end{aligned} \tag{11}$$

This condition is necessary and sufficient for diagonal stability of the matrix $\overline{A}$. If $\overline{A}$ is symmetric, the matrix $\overline{S_A}$ coincides with the symmetric part of the effective competition matrix $\left(\overline{C_A}\right)^S$ and the above condition is equivalent to diagonal stability of the effective competition matrix. Although this is not true in the general case, there is still a strong relationship between the diagonal stability of the

effective competition matrix and the diagonal stability of the interaction matrix, as we discuss below.

Diagonal stability of the effective competition is a necessary condition for diagonal stability of the whole system

We now assume that the direct competition matrices $\overline{B_A}$ and $\overline{B_P}$ are positive definite. The computation reported in Appendix A proves the following condition, which, together with $\overline{B_P} \succ 0$, is necessary and sufficient for positive definiteness of the interaction matrix $\overline{A}$:

$$\overline{A} \succ 0 \leftrightarrow \overline{B_P} \succ 0, \overline{S_A} \succ 0 \leftrightarrow$$
$$\left(\overline{C_A}\right)^S - \overline{E_P}^T \left(\overline{B_P}^S\right)^{-1} \overline{E_P} \succ 0 \qquad (12)$$

$$\overline{E_P} = \frac{1}{2}\left[\overline{B_P}^T \left(\overline{B_P}\right)^{-1} \overline{\Gamma_P} - \overline{\Gamma_A}^T\right]. \qquad (13)$$

The same result can be obtained from the necessary and sufficient condition for positivity of the effective competition matrix $\overline{C_A}$ i.e.

$$\overline{C_A} \succ 0 \leftrightarrow \overline{S_A} + \overline{E_P}^T \left(\overline{B_P}^S\right)^{-1} \overline{E_P} \succ 0 \qquad (14)$$

(for the proof, see Appendix B).

If the matrix $\overline{A}$ is symmetric, then $\overline{B_P}^T = \overline{B_P}$, $\overline{\Gamma_A}^T = \overline{\Gamma_P}$ and the matrix $\overline{E_P}$ vanishes identically, confirming that a symmetric interaction matrix is diagonally stable if and only if the corresponding direct and effective competition matrices are diagonally stable.

Since the symmetric matrix $\overline{E_P}^T \left(\overline{B_P}^S\right)^{-1} \overline{E_P}$ is clearly positive semi-definite [3], it is immediate to see from Eq. 12 that positivity of the effective competition matrix $\overline{C_A}$ is a necessary condition for positivity of the interaction matrix $\overline{A}$ [4].

An equivalent and slightly more direct proof of this statement may be also found in the supplementary material of Bastolla et al. (2009). However, in the same supplementary material, the proof of the corresponding sufficient condition is wrong, and in fact the sufficient condition does not have the generality stated there, as we show in the following.

Thus, necessary condition for diagonal stability of the interaction matrix is that the effective competition matrix is diagonally positive. This condition implies that all eigenvalues of the effective competition matrix must have positive real parts, a necessary condition that is easier to test numerically [5].

Sufficient conditions for diagonal stability

If $\overline{E_P}$ is not zero, positivity of $\overline{C_A}$ may not be sufficient for positivity of $\overline{A}$. Nevertheless, we can obtain a sufficient condition by using additional degrees of freedom of the diagonal matrix D, but we have to take care that $\overline{C}$ and $\overline{B}$ remain positive definite. The simplest way to impose these conditions consists in using the diagonal matrix $D' = d^2 D$, with d constant in each block, $d_{ii} = d_A$ if $i \in$ A and $d_{ii} = d_P$ if $i \in$ P, and D such that the four competition matrices $\overline{B_A}$, $\overline{B_P}$, $\overline{C_A}$ and $\overline{C_P}$ are positive definite. With the above choice, the matrix d commutes with the competition matrices and it does not modify them. However, d does modify the interguild interaction terms Γ, and it can be used to make them more symmetric, thus reducing $\overline{E_P}$. Note that the conditions obtained in this way are only sufficient, since they only exploit one out of $n-1$ degrees of freedom of the diagonal matrix D'. If they fail, it is still possible that a more general sufficient condition is found with d not constant in each block.

We denote the new interaction matrix as $\overline{\overline{A}} \equiv \overline{A} d^{-2}$, where the double overline indicates that the matrix is expressed in different units from those used for $\overline{C_A}$ and $\overline{C_P}$. This matrix is positive definite if and only if the matrix $\overline{A}(z)$ is such, with $z = d_P/d_A$ and

$$\overline{A}(z) = d\overline{A}d^{-1} = \begin{pmatrix} \overline{B_P} & z\overline{\Gamma_P} \\ \frac{1}{z}\overline{\Gamma_A} & \overline{B_A} \end{pmatrix}. \qquad (15)$$

Two species

For the simple example of two groups constituted by one species each, B_A, B_P, Γ_P and Γ_A are scalar quantities and $D_A = D_P = 1$. In this case, positivity of the effective competition $C_A = B_A - \Gamma_A (B_P)^{-1} \Gamma_P > 0$ is not sufficient for positivity definiteness of A. If Γ_A and Γ_P have the same sign (competitive or mutualistic interactions) and we choose $z \equiv d_P/d_A = \sqrt{\Gamma_A/\Gamma_P}$ the matrix $A(z)$ becomes symmetric, and it is positive definite if and only if its determinant is positive i.e. if $C_A > 0$. Instead, if Γ_A and Γ_P have

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[3] In fact, $\left\langle x, \overline{E_P}^T \left(\overline{B_P}^S\right)^{-1} \overline{E_P} x \right\rangle = \left\langle (\overline{E_P} x), \left(\overline{B_P}^S\right)^{-1} (\overline{E_P} x) \right\rangle \geq 0$ by the hypothesis that $\overline{B_P}$ is positive definite.

[4] In fact, Eq. 12 involves a symmetric matrix, and it can be rewritten as $\left\langle x, \left(\overline{C_A}\right)^S x \right\rangle > \left\langle x, \overline{E_P}^T \left(\overline{B_P}^S\right)^{-1} \overline{E_P} x \right\rangle \geq 0.$

[5] In fact, in the complex field the condition of positive definiteness can be written as $x^*(M + M^T)x > 0 \forall x \neq 0$, where x^* denotes the conjugate transpose of x. In particular, if x is a right eigenvector with eigenvalue λ, it holds $Mx = \lambda x x^*M = \lambda^* x^*$, thus the above condition implies that $(\lambda + \lambda^*)(x^* x) > 0$ and $(\lambda + \lambda^*) > 0$ since $(x^* x)$ is positive by definition i.e. all eigenvalues of M must have positive real part.

different sign (predatory interactions), the choice $z = \sqrt{|\Gamma_A/\Gamma_P|}$ cancels the off-diagonal elements of the symmetric part of $A(z)$, so that $B_A > 0$ and $B_P > 0$ are necessary and sufficient both for the positivity of the effective competition and for the diagonal stability of A. This proves that for two species systems the diagonal stability of the effective competition matrix is a necessary and sufficient condition for the diagonal stability of the full interaction matrix, which is related to the known result that for two species local stability implies global stability (Goh 1977).

Many species: off-diagonal matrix

We can follow a similar procedure for the general case where there is more than one species in each guild. We assume that $\overline{B_P} \succ 0$. If $\overline{S_A}$ defined in Eq. 12 is positive definite then the system is globally stable. Alternatively, if there is at least one eigenvector v^0 such that $\overline{S_A} v^0 = \lambda v^0$ with $\lambda < 0$, we consider the eigenvector v^0 corresponding to the most negative λ. In this case, we rescale the interaction matrix with a diagonal matrix d constant in each group, in such a way that the second term of Eq. 12, $\left\langle v^0, \overline{\overline{E_P}}^T \left(\overline{B_P}^S\right)^{-1} \overline{\overline{E_P}} v^0 \right\rangle$, computed over the vector v^0, is minimized. Here, $\overline{\overline{E_P}} = \frac{1}{2}\left[z\overline{B_P}^T \overline{B_P}^{-1} \overline{\Gamma_P} - \frac{1}{z}\overline{\Gamma_A}^T \right]$ is the off-diagonal matrix defined in Eq. 13 and rescaled with d, and the optimal value of $z \equiv d_P/d_A$ is given by

$$z = \left(\frac{\left\langle \overline{\Gamma_A}^T v^0, \left(\overline{B_P}^S\right)^{-1} \overline{\Gamma_A}^T v^0 \right\rangle}{\left\langle \left(\overline{B_P}^T \overline{B_P}^{-1} \overline{\Gamma_P}\right) v^0, \left(\overline{B_P}^S\right)^{-1} \left(\overline{B_P}^T \overline{B_P}^{-1} \overline{\Gamma_P}\right) v^0 \right\rangle} \right)^{1/4},$$

which generalizes the two-species result. After rescaling the intergroup interactions, we have to test whether the rescaled symmetric matrix $\overline{\overline{S_A}} = (\overline{C_A})^S - \overline{\overline{E_P}}^T \left(\overline{B_P}^S\right)^{-1} \overline{\overline{E_P}}$ is positive definite. The matrix element that we minimize is non-negative and it can be cancelled if and only if the vector v^0 satisfies the following generalized eigenvector equation:

$$\overline{B_P}^T \overline{B_P}^{-1} \overline{\Gamma_P} v^0 = \frac{1}{z^2} \overline{\Gamma_A}^T v^0 \tag{16}$$

If this relation does not hold, we cannot exclude that $\left\langle v^0, \overline{\overline{S_A}} v^0 \right\rangle$ is negative even if $\overline{C_A}$ is positive definite. This possibility suggests that the diagonal positivity of the effective competition matrix C_A is not a sufficient condition for global stability, but it must be supplemented by the condition that the intergroup interaction matrices Γ_A^T and Γ_P are correlated as dictated by Eq. 16 (for mutualistic or competitive interactions), which states that the growth rate gained

by a species of group P through the interaction with a distribution of abundances v^0 in group A is proportional to the growth rate that the same species provides to the group A (and analogous interpretation for competitive interactions). For predatory interactions, Eq. 16 does not hold, since Γ_P and Γ_A have opposite sign. Nevertheless,

$$\overline{B_P}^T \overline{B_P}^{-1} \overline{\Gamma_P} v^0 = -\frac{1}{z^2} \overline{\Gamma_A}^T v^0 \tag{17}$$

guarantees that $\left\langle v^0, \overline{\overline{S_A}} v^0 \right\rangle = \left\langle v^0, \overline{B_A} v^0 \right\rangle > 0$. Once again, this relation is not sufficient for diagonal stability, since other eigenvectors have to be tested for positivity but, since v^0 is the eigenvector with most negative eigenvalue for the non-rescaled matrix $\overline{S_A}$, it strongly suggests that the system is diagonally stable. Note that Eq. 17 also requires that the intergroup interactions are correlated.

Many species: principal components

A sufficient condition of diagonal stability can be obtained by rewriting the necessary and sufficient condition Eq. 11 into units specified by the scalar $z = d_P/d_A$. We get

$$\overline{\overline{S_A}}(z) = b_A \left[I_A - \frac{1}{4} M_A(z) \right] b_A \succ 0$$

$$\leftrightarrow I_A - \frac{1}{4} M_A(z) \succ 0 \tag{18}$$

$$M_A(z) = \left(z \tilde{\Gamma}_P^T \tilde{\Gamma}_P + \frac{1}{z} \tilde{\Gamma}_A \tilde{\Gamma}_A^T + \tilde{\Gamma}_A \tilde{\Gamma}_P + \tilde{\Gamma}_P^T \tilde{\Gamma}_A^T \right)$$

where I_A is the identity matrix, $b_A = \left(\overline{B_A}^S\right)^{1/2}$ and $b_P = \left(\overline{B_P}^S\right)^{1/2}$ are the square roots of the direct competition matrices, and $\tilde{\Gamma}_A = (b_A)^{-1} \overline{\Gamma_A} (b_P)^{-1}$, $\tilde{\Gamma}_P = (b_P)^{-1} \overline{\Gamma_P} (b_A)^{-1}$ are competition-rescaled interguild interaction matrices. The Schur matrix $\overline{\overline{S_A}}(z)$ is positive definite if and only if $\lambda_{\max}(M_A(z)) < 4$, where $\lambda_{\max}$ denotes the maximum eigenvalue and $M_A(z)$ is the symmetric matrix in round brackets.

We first consider mutualistic or competitive interactions for which the signs of the matrices Γ_A and Γ_P are the same. Since the maximum eigenvalue of a sum of matrices is not larger than the sum of the maximum eigenvalues, and the maximum eigenvalue of the product of matrices is not larger than the product of their maximum singular values, it holds

$$\lambda_{\max}(M_A(z)) \leq z \lambda_{\max}\left(\tilde{\Gamma}_A \tilde{\Gamma}_A^T\right) + \frac{1}{z} \lambda_{\max}\left(\tilde{\Gamma}_P^T \tilde{\Gamma}_P\right)$$

$$+ 2\lambda_{\max}\left(\tilde{\Gamma}_A \tilde{\Gamma}_P\right)$$

$$\leq 4 \sigma_{\max}\left(\tilde{\Gamma}_A\right) \sigma_{\max}\left(\tilde{\Gamma}_P\right) \tag{19}$$

where we denote by $\sigma_{\max}(M)$ the maximum singular value of matrix M i.e. $\sigma_{\max}^2(M) = \lambda_{\max}(M^T M)$, and we have

chosen the value of z that minimizes Eq. 19 i.e. $z = \sigma_{\max}\left(\tilde{\Gamma}_P\right)/\sigma_{\max}\left(\tilde{\Gamma}_A\right)$. Since $\lambda_{\max}\left(M_A(z)\right) < 4$ is sufficient for fulfilling Eq. 19, the above equation shows that sufficient condition for diagonal stability of A and consequently global stability is that the direct competition matrices B_A and B_P are diagonally stable, and moreover, the main singular values of the rescaled interaction matrices satisfy

$$\overline{\overline{S_A}}(z) \succ 0 \leftrightarrow \overline{B_A} \succ 0, \overline{B_P} \succ 0,$$
$$\sigma_{\max}\left(\tilde{\Gamma}_P\right)\sigma_{\max}\left(\tilde{\Gamma}_A\right) < 1. \tag{20}$$

If the direct competition matrix B_P is diagonally symmetric (i.e. if $\overline{B_P}$ is symmetric), the effective competition matrix simplifies to

$$\left(\overline{C_A}\right)^S = b_A\left[I_A - \frac{1}{2}\left(\tilde{\Gamma}_A\tilde{\Gamma}_P + \tilde{\Gamma}_P^T\tilde{\Gamma}_A^T\right)\right]b_A, \tag{21}$$

and the necessary and sufficient condition for the positivity of the effective competition is $\lambda_{\max}\left(\tilde{\Gamma}_A\tilde{\Gamma}_P\right) < 1$, which is weaker than Eq. 20. However, the two conditions coincide in the important special case in which the main singular vectors u and v of the interaction matrices $\tilde{\Gamma}_A$ and $\tilde{\Gamma}_P^T$ are collinear i.e. $\tilde{\Gamma}_A u = \sigma_{\max}v$ and $\tilde{\Gamma}_P v = \sigma_{\max}u$. In this case, the main principal vector u satisfies $\left(\tilde{\Gamma}_P\tilde{\Gamma}_A + \tilde{\Gamma}_A^T\tilde{\Gamma}_P^T\right)u = 2\sigma_{\max}^2 u$, so that Eq. 20 is in this case also necessary condition for diagonal stability of C_A. Thus, we have shown that, if B_P is diagonally symmetric and positive and if the main singular vectors of the rescaled interaction matrices coincide, then A is diagonally stable if and only if C_A is diagonally stable. Note that the collinearity condition for competitive and mutualistic systems implies that the vector v satisfies $\tilde{\Gamma}_P v = \tilde{\Gamma}_A^T v$, which in turn implies Eq. 16 (here $z = 1$, since we have chosen the optimal value of the scale factor z, and $\overline{B_P}^T\overline{B_P}^{-1} = I_P$ since B_P is assumed to be diagonally symmetric), supporting the view that the sufficient condition requires a balance between between the intergroup interactions Γ_P and Γ_A^T.

For predatory systems, $(\Gamma_A)_{ik} \geq 0$ and $(\Gamma_P)_{ki} \leq 0$ have opposite sign. If we assume that $\left\langle x, \tilde{\Gamma}_A\tilde{\Gamma}_P x\right\rangle \leq 0 \,\forall x$, then the effective competition is positive definite, $\left\langle x, \left(\overline{C_A}\right)^S x\right\rangle > 0 \,\forall x$, and the sufficient condition for diagonal stability is $\langle x, M_A(z)x\rangle < 4$ that can be written as $\sqrt{\left\langle x, \tilde{\Gamma}_P^T\tilde{\Gamma}_P x\right\rangle\left\langle x, \tilde{\Gamma}_A\tilde{\Gamma}_A^T x\right\rangle} < 2 - \left\langle x, \tilde{\Gamma}_A\tilde{\Gamma}_P x\right\rangle \,\forall x$ and it is weaker than the corresponding sufficient condition for mutualistic or competitive systems. Note that also in this

case the collinearity between principal vectors favours stability. Collinearity can be written as $\tilde{\Gamma}_A u = \sigma v$ and $\tilde{\Gamma}_P v = -\sigma u$ (note the minus sign), which corresponds to Eq. 17, and it implies that $M_A(z)u = 0$ so that $\left\langle u, \overline{\overline{S_A}}(z)u\right\rangle > 0$ and $\left\langle u, \left(\overline{C_A}\right)^S u\right\rangle > 0$. Thus, we conjecture that, for predatory systems whose principal vectors of the interaction matrices are collinear, diagonal stability of the direct competition matrix B_A is sufficient both for diagonal stability of the effective competition matrix C_A and for diagonal stability of the complete system.

Global stability of mutualistic systems

In Lotka-Volterra mutualistic systems, if the strength of mutualistic interactions overcomes a threshold, the main eigenvalue of the effective competition matrix becomes negative, implying that the typical interspecific competition is negative and the system is dynamically unstable. The larger is the system, the smaller the mutualistic interaction strength at which this instability arises (Bascompte et al. 2006). However, this instability is an artefact of the LV model in which the mutualistic growth rates, which are proportional to abundances, can increase without bounds. In a realistic model of mutualism, the growth rates should be modelled through functional responses that saturate (Holland et al. 2002; Holland et al. 2006). One possible model is given by the following dynamical equations (Bastolla et al. 2009)

$$\frac{1}{N_i^P}\frac{dN_i^P}{dt} = r_i^P - \sum_{j\in P}(B_P)_{ij}N_j^P + \sum_{k\in A}\frac{(\Gamma_P)_{ik}N_k^A}{1 + h_i^P\sum_{l\in A}(\Gamma_P)_{il}N_l^A} \tag{22}$$

and analogous for species in the group A, with $(\Gamma_P)_{ik} \geq 0$. The non-linear terms that limit the growth rates lead to the existence of additional fixed points with respect to the linear functional response with $h_i^P \equiv 0$. Depending on whether the quantity

$$Y_i = h_i^P\sum_{l\in A}(\Gamma_P)_{il}N_l^* \tag{23}$$

is small or large at the equilibrium point, the species i is said to be at a weak or strong mutualistic fix point. Approximate solutions of the fixed point equations can be easily obtained in the limits $Y_i \ll 1$ and $Y_i \gg 1$. For a simple system with only two mutualistic species, all combinations of coexistence fixed points exist and it can be shown that the two-species system has a stable coexistence fixed point for all combinations of parameters that guarantee feasibility (Holland et al. 2002)

The dynamical stability analysis of this non-linear system can be performed linearizing the dynamical equations close to the fixed point N_i^*. This produces Lotka-Volterra equations with parameters

$$
\left(B_P^{LV}\right)_{ij} = (B_P)_{ij} \quad \left(\Gamma_P^{LV}\right)_{ik} = \frac{(\Gamma_P)_{ik}}{(1 + Y_i)^2}
$$

$$
r_i^{LV} = r_i + \frac{1}{h_i}\left(\frac{Y_i}{1 + Y_i}\right)^2 \tag{24}
$$

It is clear from Eq. 24 that the effective Lotka-Volterra mutualistic interactions become very small at the strong mutualistic fixed point $Y_i \gg 1$. This favours both the local stability of the fixed point, which is guaranteed if the community matrix $-N_i^* A_{ij}^{LV}$ has all eigenvalues with negative real part, and the global stability of the linearized dynamical system, which is guaranteed if the interaction matrix of the Lotka-Volterra system, A_{ij}^{LV}, is diagonally stable.

Therefore, recent papers that rediscovered that randomly drawn Lotka-Volterra mutualistic interactions become locally unstable for smaller number of species than competitive interactions (Allesina and Tang 2012) do not imply that mutualism is detrimental for species coexistence, if saturation of mutualistic interactions is taken into account.

We now consider the global stability of Eq. 22. We omit the superscripts P and A for simplicity of notation. We note that the derivative of the growth rate can be written as

$$
\frac{1}{N_i}\frac{dN_i}{dt} \equiv f_i(N) = f_i^{LV}(N)\frac{(Y_i - Y_i^*)^2}{(1 + Y_i)(1 + Y_i^*)^2}
$$

$$
\equiv f_i^{LV}(N) + g_i(N)
$$

where Y_i is given by Eq. 23, Y_i^* is the same at the fixed point N_k^*, and $g_i(N)$, the correction of the time derivative with respect to the LV system, is always negative, it is a second order function of the deviation from fixed point abundances, $\delta N_k \equiv (N_k - N_k^*)$, and it vanishes for $h = 0$. The Lyapunov function proposed by Goh for the LV system is $L = \sum_i \left[(N_i - N_i^*) - N_i^* \log(N_i/N_i^*)\right]$, and its time derivative is $\dot{L} = \sum_i \delta N_i \left(f_i^{LV}(N) + g_i(N)\right)$, whence it appears that the correction term is stabilizing when $\delta N_i > 0$ but destabilizing in the opposite case. Each term of $\dot{L}$ satisfies the inequality

$$
\delta N_i \left(f_i^{LV}(N) + g_i(N)\right) \leq \begin{cases} \delta N_i f_i^{LV}(N) & \text{if } \delta N_i \geq 0 \\ \delta N_i f_i^{LV}(N, \Gamma = 0) & \text{if } \delta N_i \leq 0 \end{cases}
$$

where $f_i^{LV}(N, \Gamma = 0)$ is the LV growth rate computed when the mutualistic strength vanishes i.e. it is the purely competitive growth rate. More compactly, $\delta N_i \left(f_i^{LV}(N) + g_i(N)\right) \leq \max\left(\delta N_i f_i^{LV}(N), \delta N_i f_i^{LV}(N, \Gamma = 0)\right)$, from which it follows

$$
\dot{L} \leq \max\left(-\left(\delta N, A^{LV}\delta N\right), -\left(\delta N, B^{LV}\delta N\right)\right) \tag{25}
$$

where A^{LV} is the interaction matrix of the LV system and B^{LV} is its competitive part. Thus, if the corresponding LV system is diagonally stable, the mutualistic system is globally stable as well.

Conclusions and perspectives

This paper is motivated by the benefits of the condition of global stability for improving the analytic understanding of model ecological systems with respect to the condition of local stability, which also includes small attraction basins that guarantee coexistence only in a small neighbourhood of the equilibrium abundances, or even limit cycles or other complex coexistence conditions. Although global stability is not a necessary condition for the coexistence of a model ecosystem, simulations of Lotka-Volterra systems often converge to globally stable fixed points. Global stability is a useful mathematical concept because, if it holds, structural stability is strongly related with the maintainance of feasibility under perturbations of the intrinsic growth rates, as we will discuss in another paper. It is worth to mention that the concept of permanence (Hofbauer and Sigmund 1998) allows for the advantages of global stability without assuming the existence of an equilibrium point. A dynamical system is said to be permanent if the boundary of the positive cone is repelling. Permanence is equivalent to persistence of all species despite rare large perturbations, while local stability is equivalent to persistence despite frequent small perturbations. Advantages and disadvantages of these definitions are discussed in Schreiber (2006). In this context, structural stability corresponds to robust permanence, i.e. the dynamical system remains permanent for sufficiently small perturbations of the parameters (Schreiber 2000).

Here, we discussed diagonal stability, which is a sufficient condition for global stability, in the framework of the effective competition matrix, which allows reducing the fixed point of a system with two groups of interacting species into two smaller systems of effectively competing species. It is interesting to note that diagonal stability is a more intrinsic condition than positivity, since it is invariant under the multiplication times a positive diagonal matrix, which we interpret as a change of abundance units, while positivity is not. Under this interpretation, positivity is a too strict condition for global stability, since it depends on the units adopted, while global stability is an intrinsic property independent of the units. We have shown that the effective

competition matrix also maps the stability properties of the two effective systems into those of the complete system. In particular, diagonal stability of the effective competition matrix is a necessary and sufficient condition for diagonal stability of the complete interaction matrix A if this matrix is diagonally symmetric, and it is a necessary condition for diagonal stability in general.

The general sufficient condition for global stability is related but apparently it is stronger. We could not determine whether diagonal stability of the effective competition matrix is sufficient for diagonal stability of the complete interaction matrix in general, neither we could find a counterexample, but we provide here sufficient conditions for global stability in two specific cases: (1) The effective competition matrix is diagonally stable and the abundance vector v^0 corresponding to the minimum eigenvalue of $S_A = C_A - E_P^T (B_P^S)^{-1} E_P$ is well balanced, in the sense specified by Eq. 16. This has the qualitative meaning that, when the distribution of animal abundances is given by v^0, the mutualistic biomass that each species provides to the plants, $\Gamma_P v^0$, is proportional to the input of biomass that it receives from them, $\left(\overline{\Gamma_A}\right)^T v^0$ (multiplied times the matrix $\overline{B_P}\left(\overline{B_P}\right)^{-T}$), and corresponding interpretation for competitive interactions. This condition is not sufficient in general, but the positivity of $\overline{\overline{S_A}}(z)$ can be tested numerically, since we can explicitly compute the parameter z that minimizes the off-diagonal term over the vector v^0. (2) The main singular values of the competition-rescaled interaction matrices must be small, $\sigma_{max}\left(\tilde{\Gamma}_P\right) \sigma_{max}\left(\tilde{\Gamma}_A\right) < 1$. This condition is stronger than the positivity of the effective competition matrix C_A, but the two conditions coincide if the direct competition matrices B_P and B_A are diagonally symmetric and the main singular vectors of the rescaled intergroup interaction matrices are collinear, which implies a balance condition equivalent to Eq. 16.

We expect that the collinearity of interactions in the two directions applies in many situations, since the strengths of the interaction of a species i with species of the other group in both directions are proportional to their number of links in the ecological network. Thus, we expect that, for a broad range of models, diagonal stability of the effective competition matrix is a sufficient condition for global stability.

In our opinion, the concept of global stability is quite relevant in the framework of the debate on the stability-complexity relationship. In the seminal work by May (1972) and its sequels, the stability-complexity relationship is examined assuming that the equilibrium is feasible, which requires choosing the growth rates r_i in such a way that all equilibrium biomasses are positive, and estimating the conditional probability that it is stable given that it is feasible. On the other hand, if the interaction matrix satisfies the conditions discussed in the present work, then the equilibrium will be automatically stable if it is feasible. If the equilibrium is not feasible, there will be a maximum subset of species, determined by the growth rates and not by the initial conditions, that can coexist in a globally stable equilibrium. Therefore, if the interaction matrix is diagonally stable, then the question on stability reduces to the question on the growth rate parameters that allow feasible equilibria, since all of these feasible equilibria will be globally stable due to the diagonal stability of the interaction matrix. This is consistent with a general result by Smith and Waltman, who showed that, if a mild uniform dissipative condition is met, the property that a locally asymptotically stable steady state is globally attracting is an open condition in the parameters, therefore small perturbations of the parameters conserve global stability.

Since the growth rates change due to changes in environmental conditions or biological changes in the species that constitute the ecosystem, this perspective requires to shift the focus from the dynamical stability of the equilibrium formed under a particular set of growth rates, a trivial question if the interaction matrix is diagonally stable, to the structural stability of the model ecosystem, meaning by this the volume of the space of growth rates that give rise to feasible equilibria under a given diagonally stable interaction matrix. We think that this approach, complementary to the classical approach to study the stability of the equilibrium given that it is feasible, is biologically relevant. We have proposed in previous works how to analytically estimate the structural stability of an interaction matrix A, which is naturally related with the effective competition matrix.

Appendix A: Conditions for diagonal stability of A

Theorem *the interaction matrix $\overline{A} = AD$ is positive definite; hence, the matrix A describes a globally stable system, if and only if the matrix*

$$H = \begin{pmatrix} \left(\overline{B_P}\right)^S & \overline{E_P} \\ \overline{E_P}^T & \left(\overline{C_A}\right)^S \end{pmatrix} \qquad (26)$$

is positive definite, where $\overline{C_A} = \overline{B_A} - \overline{\Gamma_A}\left(\overline{B_P}\right)^{-1}\overline{\Gamma_P}$, and $\overline{E_P} = \frac{1}{2}\overline{B_P}^T\left(\left(\overline{B_P}\right)^{-1}\overline{\Gamma_P} - \left(\overline{B_P}\right)^{-T}\overline{\Gamma_A}\right)$. We denote the

symmetric part of a matrix by the superscript s, $\left(\overline{C_A}\right)^S = \frac{1}{2}\left(\overline{C_A} + \overline{C_A}^T\right)$, *and denote* B^{-T} *as a shortcome of* $\left(B^T\right)^{-1}$ *or, equivalently,* $\left(B^{-1}\right)^T$.

Proof The block effective competition matrix C_A corresponds to the Schur complement of B_P in the matrix A. One can go from A to a matrix containing C_A in a diagonal block by means of the Aitken's block diagonalization formula (Zhang 2005). This corresponds to

$$A = \begin{pmatrix} B_P & -\Gamma_P \\ -\Gamma_A & B_A \end{pmatrix}$$

$$= \begin{pmatrix} I_P & 0 \\ -\Gamma_A (B_P)^{-1} & I_A \end{pmatrix} \begin{pmatrix} B_P & 0 \\ 0 & C_A \end{pmatrix} \begin{pmatrix} I_P & -(B_P)^{-1}\Gamma_P \\ 0 & I_A \end{pmatrix}$$

$$\equiv LCU, \tag{27}$$

where L and U correspond to the lower and upper triangular matrices of the Aitken's transform, respectively, and C is the matrix with diagonal blocks equal to B_P and C_A. Next, we substitute this expression for A in the condition for diagonal stability, obtaining

$$Q' = \frac{1}{2}\left(AD + DA^T\right) = \frac{1}{2}\left[LCUD + DU^TC^TL^T\right] \succ 0. \tag{28}$$

We now apply a congruence by U^{-1} to get the matrix H

$$H = U^{-T}Q'U^{-1} = \frac{1}{2}\left[\left(U^{-T}L\right)CD + DC^T\left(U^{-T}L\right)^T\right]$$

$$= \begin{pmatrix} \overline{B_P}^S & \overline{E_P} \\ \overline{E_P}^T & \overline{C_A}^S \end{pmatrix}, \tag{29}$$

with $\overline{E_P}$ given by Eq. 13 in the main text. Thus, A will be diagonally stable if and only if there is a positive diagonal matrix D such that H in Eq. 29 is positive definite. □

From this calculation and from Theorem 7.7.6 in Horn and Johnson (1985), we see that the interaction matrix $\overline{A}$ will be positive definite if and only if the following holds:

$$\overline{C_A}^S - \overline{E_P}^T\left(\overline{B_P}^S\right)^{-1}\overline{E_P} \succ 0. \tag{30}$$

Appendix B: Conditions for positivity of C

We prove here that the effective competition matrix C_A is positive definite if and only if it holds

$$(B_A)^S - (\Gamma)_A^S\left(B_P^S\right)^{-1}(\Gamma)_P^S + E_A^T\left(B_P^S\right)^{-1}E_A$$

$$= S_A + E_A^T\left(B_P^S\right)^{-1}E_A \succ 0 \tag{31}$$

where S_A is given by Eq. 11 and E_A is given by Eq. 13 in the main text. We denote by superscripts S and a

the symmetric and antisymmetric part, respectively, and we use the block notation where B is the matrix whose diagonal blocks are B_P and B_A, and Γ is a matrix whose off-diagonal blocks are Γ_P and Γ_A, respectively. With this notation, we can compactly write $C = B - \Gamma B^{-1}\Gamma$. The computation is based on expressing the matrix B^{-1} as the sum of its symmetric part, $\left(B^{-1}\right)^S = B^{-T}B^SB^{-1} = \left(B^S\right)^{-1} + \left(B^{-T}B^a\right)\left(B^S\right)^{-1}\left(B^aB^{-1}\right)$ and antisymmetric part $\left(B^{-1}\right)^a = -B^{-T}B^aB^{-1}$.

$$-(C)^S + (B)^S = \frac{1}{2}\left[\Gamma(B)^{-1}\Gamma + \Gamma^T(B)^{-T}\Gamma^T\right]$$

$$= \frac{1}{2}\left[\left(\Gamma^S + \Gamma^a\right)\left(\left(B^{-1}\right)^S + \left(B^{-1}\right)^a\right)\right]$$

$$\left(\Gamma^S + \Gamma^a\right)$$

$$+ \left(\Gamma^S - \Gamma^a\right)\left(\left(B^{-1}\right)^S - \left(B^{-1}\right)^a\right)$$

$$\left(\Gamma^S - \Gamma^a\right)\Big]$$

$$\sim \Gamma^S\left(B^{-1}\right)^S\Gamma^S + \Gamma^a\left(B^{-1}\right)^S\Gamma^a + 2\Gamma^a$$

$$\left(B^{-1}\right)^a\Gamma^S$$

$$= \Gamma^S\left(B^S\right)^{-1}\Gamma^S + \Gamma^S$$

$$\left(B^{-T}B^a\left(B^S\right)^{-1}B^aB^{-1}\right)\Gamma^S$$

$$+ \Gamma^a\left(B^{-T}B^SB^{-1}\right)\Gamma^a - 2\Gamma^a$$

$$\left(B^{-T}B^aB^{-1}\right)\Gamma^S$$

$$= \Gamma^S\left(B^S\right)^{-1}\Gamma^S$$

$$- \left(B^aB^{-1}\Gamma^S - B^SB^{-1}\Gamma^a\right)^T\left(B^S\right)^{-1}$$

$$\left(B^aB^{-1}\Gamma^S - B^SB^{-1}\Gamma^a\right)$$

$$= \Gamma^S\left(B^S\right)^{-1}\Gamma^S + E^T\left(B^S\right)^{-1}E \tag{32}$$

where $M \sim N$ indicates that $\langle x, Mx \rangle = \langle x, Nx \rangle$ (i.e. we eliminate asymmetric components, such as $\Gamma^SB^{-T}B^aB^{-1}\Gamma^S$ or $\Gamma^a\left(B^S\right)^{-1}\Gamma^a$). This proves Eq. 31 above.

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