

Coexistence in MacArthur-style consumer–resource models

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Abstract

The nature of and conditions for permanent coexistence of consumers and resources are characterized in a family of models that generalize MacArthur's consumer–resource model. The generalization is of the resource dynamics, which need not be of Lotka–Volterra form but are subject only to certain restrictions loose enough to admit many resource dynamics of biological interest. For any such model, (1) if there is an interior equilibrium, then it is globally attracting, else some boundary equilibrium is globally attracting—thus permanent coexistence is coexistence at a globally attracting equilibrium; (2) there is an interior equilibrium if and only if for any species, the equilibrium approached in the absence of that species and the presence of the others is invulnerable by that species—thus permanent coexistence is equivalent to mutual invulnerability; (3) for resources without direct interactions, the conditions for permanent coexistence of the consumers admit an instructive formulation in terms of regression statistics. The significance and limitations of the models and results are discussed.

Introduction

Thirty years ago, MacArthur proposed a model of consumers that compete with each other by harvesting common resources (MacArthur and Levins, 1967; MacArthur, 1969; MacArthur, 1970). MacArthur’s consumer–resource model has strongly influenced thinking about consumptive competition ever since (Yodzis, 1989, sec. 5.2.1). In this article, I unite and extend ideas of MacArthur, Case and Casten (1979), Chesson (1990), Goh (1977), and others to characterize the nature of and conditions for permanent coexistence of consumers and resources in a family of models that generalize MacArthur’s. The generalization is of the resource dynamics. MacArthur supposed the resource dynamics were of Lotka–Volterra form, and subsequent researchers have typically done likewise. Here, I suppose the resource dynamics are subject only to certain restrictions loose enough to admit many resource dynamics of biological interest, and I show all such resource dynamics have similar implications.

I first present the models, then a sequence of results, and finally a discussion of the significance and limitations of the models and results. Throughout, I emphasize biological interpretations and relegate mathematical formalities to an appendix.

Models

Definitions

Table I is a glossary of my notation. In MacArthur’s models and the generalizations in this article, each consumer species is regulated by its resource harvest, which is linear in the resource densities, relative to its maintenance requirement:

$$\frac{dC_\gamma}{dt} = C_\gamma \frac{1}{(e_C)_\gamma} \left(\sum_{\rho=1}^{n_R} (e_R)_\rho u_{\gamma\rho} R_\rho - m_\gamma \right), \quad (1)$$

where C_γ is the density of consumer species γ , $1 \leq \gamma \leq n_C$; R_ρ is the density of resource species ρ , $1 \leq \rho \leq n_R$; per unit time, a unit of consumer species γ harvests (utilizes) $u_{\gamma\rho} R_\rho$ units of resource species ρ ; multiplication by $(e_R)_\rho$ converts units of resource species ρ into units of

a single currency, here known as energy, common across the resources; per unit time, a unit of consumer species γ must harvest energy m_γ to maintain itself; and multiplication by $1/(e_C)_\gamma$ converts units of energy into units of consumer species γ . Each resource species is subject to a growth function, which may involve not only self-regulation but also interactions with other resource species, and to mortality by consumption:

$$\frac{dR_\rho}{dt} = R_\rho \left(G_\rho[R_1, \dots, R_{n_R}] - \sum_{\gamma=1}^{n_C} u_{\gamma\rho} C_\gamma \right), \quad (2)$$

where G_ρ is the growth function of resource species ρ , a smooth function of the resource densities. Equations (1) and (2), subject to the restrictions specified below, define the family of what I term MacArthur-style consumer–resource models.

In MacArthur’s original model, each growth function involves logistic self-regulation only:

$$G_\rho[R_\rho] = r_\rho \left(1 - \frac{R_\rho}{k_\rho} \right), \quad (3)$$

where r_ρ and k_ρ are the intrinsic rate of increase and carrying capacity of resource species ρ . Given (3), (1) and (2) are of Lotka–Volterra form. Schoener (1974) proposed a variant for resources supplied from outside the system:

$$G_\rho[R_\rho] = \frac{s_\rho}{R_\rho} - d_\rho, \quad (4)$$

where s_ρ and d_ρ are the total supply rate and per-capita decay rate of resource species ρ . Given (4), (1) and (2) are not of Lotka–Volterra form. (See also Wilson and Turelli, 1986.) More generally, combinations of internal regulation and external supply might be interesting.

In MacArthur’s original model and Schoener’s variant, the resources interact only indirectly, by apparent competition (Holt, 1977). An extended model, introduced by MacArthur (1970), admits Lotka–Volterra competition, mutualism, and predation:

$$G_\rho[R_1, \dots, R_{n_R}] = r_\rho \left(1 - \frac{1}{k_\rho} \sum_{\sigma=1}^{n_R} d_{\rho\sigma} R_\sigma \right), \quad (5)$$

where r_ρ and k_ρ are as in (3), $d_{\rho\rho} = 1$, and $d_{\rho\sigma}$ is the direct effect of resource species σ on resource species ρ relative to the direct effect of resource species ρ on itself. More generally, non-logistic self-regulation and non-Lotka–Volterra direct interactions might be interesting.

Restrictions

Vector and matrix notation will be useful. Let $\vec{\mathbf{C}}$, $\vec{\mathbf{R}}$, $\vec{\mathbf{m}}$, and $\vec{\mathbf{G}}$ be the column vectors of all C_γ , R_ρ , m_γ , and G_ρ , respectively, let \mathbf{C} , \mathbf{R} , \mathbf{e}_R , and \mathbf{e}_C^{-1} be the diagonal matrices of all C_γ , R_ρ , $(e_R)_\rho$, and $1/(e_C)_\gamma$, respectively, and let \mathbf{u} be the matrix of all $u_{\gamma\rho}$. In this notation, (1) and (2) become

$$\frac{d\vec{\mathbf{C}}}{dt} = \mathbf{C} \mathbf{e}_C^{-1} (\mathbf{u} \mathbf{e}_R \vec{\mathbf{R}} - \vec{\mathbf{m}}) \quad \text{and} \quad \frac{d\vec{\mathbf{R}}}{dt} = \mathbf{R} (\vec{\mathbf{G}}[\vec{\mathbf{R}}] - \mathbf{u}^t \vec{\mathbf{C}}),$$

where \mathbf{u}^t is the transpose of \mathbf{u} . A vector will be termed feasible if every element is nonnegative, interior if every element is positive, and boundary if feasible but not interior.

In the absence of restrictions on the growth functions of the resources, complicated behaviors are possible. However, restrictions on the growth functions are of dubious value if they exclude most resource dynamics of biological interest. Happily, there are restrictions tight enough to exclude complicated behaviors but loose enough to admit many resource dynamics of biological interest. We suppose

Restriction 1a: There is a constant b_R such that for any feasible $\vec{\mathbf{R}}$ with $\|\mathbf{e}_R \vec{\mathbf{R}}\| > b_R$,
 $\vec{\mathbf{R}}^t \mathbf{e}_R \vec{\mathbf{G}}[\vec{\mathbf{R}}] < 0$,

where $\|\mathbf{e}_R \vec{\mathbf{R}}\| = \sum_\rho (e_R)_\rho R_\rho$. (For Schoener’s variant (4), $\vec{\mathbf{R}}$ should be not merely feasible but interior. This technicality is suppressed in what follows.) We also suppose

Restriction 1b: For any $\vec{\mathbf{R}}^{(1)}$ and feasible $\vec{\mathbf{R}}^{(2)}$, $(\vec{\mathbf{R}}^{(1)})^t \mathbf{e}_R \mathbf{J}_G[\vec{\mathbf{R}}^{(2)}] \vec{\mathbf{R}}^{(1)} \leq 0$, with equality if and only if $\vec{\mathbf{R}}^{(1)} = \vec{\mathbf{0}}$,

where \mathbf{J}_G is the Jacobian matrix of $\vec{\mathbf{G}}$ (the element in row ρ and column σ is $\partial G_\rho / \partial R_\sigma$). (Equivalently, for any feasible $\vec{\mathbf{R}}^{(2)}$, the quadratic form $\vec{\mathbf{R}}^{(1)} \mapsto (\vec{\mathbf{R}}^{(1)})^t \mathbf{e}_R \mathbf{J}_G[\vec{\mathbf{R}}^{(2)}] \vec{\mathbf{R}}^{(1)}$ is negative definite.) For resources without direct interactions, Restrictions 1b and 1a amount to the restriction that

for any ρ , $G_\rho[R_\rho]$ decreases and becomes negative as R_ρ increases. This holds for MacArthur's original model (3) and Schoener's variant (4), and more generally, it is plausible for biotic resources, except perhaps at low resource densities; Allee effects with extinction thresholds (Yodzis, 1989, sec. 2.1) are discussed under "Results" below. For MacArthur's extended model (5), Restriction 1b implies Restriction 1a and holds if the direct interactions are weak enough; for example, it is sufficient, although not necessary, that for any ρ , $\sum_{\sigma \neq \rho} |d_{\rho\sigma}| < 1$.

Restrictions 1a and 1b can be interpreted in terms of energy. In the absence of the consumers, the total energy in the system is $\|\mathbf{e}_R \vec{\mathbf{R}}\| = \sum_\rho (e_R)_\rho R_\rho$, and its time derivative is $\sum_\rho (e_R)_\rho R_\rho G_\rho[\vec{\mathbf{R}}] = \vec{\mathbf{R}}^t \mathbf{e}_R \vec{\mathbf{G}}[\vec{\mathbf{R}}]$. Thus according to Restriction 1a, starting from high enough energy, the system loses energy. Moreover,

$$\vec{\mathbf{G}}[\vec{\mathbf{R}}] = \vec{\mathbf{G}}[\vec{\mathbf{0}}] + \left(\int_0^1 \mathbf{J}_G[s\vec{\mathbf{R}}] ds \right) \vec{\mathbf{R}}$$

(by the mean-value theorem (Lang, 1998, Theorem XIII.4.2); the integral is over the line segment from $\vec{\mathbf{0}}$ to $\vec{\mathbf{R}}$). The first term comprises the growth rates in the absence of interactions, not only between but also within species, and the second term comprises the effects of interactions on the growth rates. The time derivative of the total energy in the system is

$$\vec{\mathbf{R}}^t \mathbf{e}_R \vec{\mathbf{G}}[\vec{\mathbf{R}}] = \vec{\mathbf{R}}^t \mathbf{e}_R \vec{\mathbf{G}}[\vec{\mathbf{0}}] + \int_0^1 \left(\vec{\mathbf{R}}^t \mathbf{e}_R \mathbf{J}_G[s\vec{\mathbf{R}}] \vec{\mathbf{R}} \right) ds.$$

Subject to Restriction 1b, the integrand is negative, hence the integral is negative, unless $\vec{\mathbf{R}} = \vec{\mathbf{0}}$. Thus according to Restriction 1b, the net effect of interactions is to dissipate energy. It is the *net* effect that is decisive; mutualism is admissible, but it must not dominate. For logistic self-regulation and Lotka–Volterra direct interactions, Restriction 1b implies Restriction 1a and was known to Volterra, who termed such systems dissipative (Volterra, 1927, sec. II.7); another term is Volterra–Lyapunov stable (Hofbauer and Sigmund, 1998, sec. 15.3). Subject to Restrictions 1a and 1b, there is a globally attracting equilibrium of the resources (Appendix, Corollary 1, for $n_C = 0$), that is, there is a feasible $\vec{\mathbf{R}}^*$ such that starting from any interior state, $\vec{\mathbf{R}}$ approaches $\vec{\mathbf{R}}^*$, in the absence of the consumers.

To exclude degenerate cases, which are mathematically possible but biologically improbable, it is appropriate to restrict the utilization coefficients and maintenance requirements of the consumers. For any subsystem, consisting of consumer species $\gamma_1, \gamma_2, \dots, \gamma_{\tilde{n}_C}$ and resource species $\rho_1, \rho_2, \dots, \rho_{\tilde{n}_R}$, let $\tilde{\mathbf{C}}, \tilde{\mathbf{R}}, \tilde{\mathbf{u}}, \tilde{\mathbf{e}}_R$, and $\tilde{\mathbf{m}}$ be the corresponding subvectors and submatrices of $\vec{\mathbf{C}}, \vec{\mathbf{R}}, \mathbf{u}, \mathbf{e}_R$, and $\vec{\mathbf{m}}$, respectively. We suppose

Restriction 2a: If $\tilde{n}_C > \tilde{n}_R$, then for any $\tilde{\mathbf{R}}, \tilde{\mathbf{u}}\tilde{\mathbf{e}}_R\tilde{\mathbf{R}} \neq \tilde{\mathbf{m}}$.

This is generic, in that if $\tilde{n}_C > \tilde{n}_R$, then the system of \tilde{n}_C equations $\tilde{\mathbf{u}}\tilde{\mathbf{e}}_R\tilde{\mathbf{R}} = \tilde{\mathbf{m}}$ in the \tilde{n}_R unknowns $\tilde{\mathbf{R}}$ is overdetermined (Yodzis, 1989, sec. 5.2.1). We also suppose

Restriction 2b: If $\tilde{n}_C \leq \tilde{n}_R$, then for any $\tilde{\mathbf{C}} \neq \vec{\mathbf{0}}, \tilde{\mathbf{u}}^t\tilde{\mathbf{C}} \neq \vec{\mathbf{0}}$.

This is generic, in that $\tilde{\mathbf{u}}^t\tilde{\mathbf{C}}$ is a linear combination of the rows of $\tilde{\mathbf{u}}$, and if $\tilde{n}_C \leq \tilde{n}_R$, then \tilde{n}_C feasible \tilde{n}_R -dimensional vectors picked at random are almost surely linearly independent.

Results

Nature of coexistence

For any MacArthur-style consumer–resource model,

Result 1: If there is an interior equilibrium, then it is globally attracting, else some boundary equilibrium is globally attracting (Appendix, Corollary 1).

For MacArthur’s original model (3), this result was obtained by Case and Casten (1979).

Thus an equilibrium is approached. There are no attracting limit cycles or more complicated attractors, as there may be for even one consumer species and one resource species if the resource harvest of the consumer is nonlinear in the resource density (Yodzis, 1989, sec. 4.2.1.3), a possibility reconsidered under “Discussion” below. Moreover, the same equilibrium is approached starting from any interior state. There is no segregation of interior states into alternative basins

of attraction, as there may be for even two Lotka–Volterra competitors (Hofbauer and Sigmund, 1998, sec. 3.3).

(Naturally, species modeled using a MacArthur-style consumer–resource model may be subject to stochastic fluctuations, perhaps to extinction. By permanent coexistence, I mean a deterministic tendency toward coexistence, according to the ecology represented in a model.)

If the resources were subject to Allee effects with extinction thresholds (Yodzis, 1989, sec. 2.1), then an interior equilibrium would not be globally attracting. For resources without direct interactions, if the density of a resource fell below the extinction threshold of that resource, then some boundary equilibrium lacking that resource would be approached.

Conditions for coexistence

For any MacArthur-style consumer–resource model, an equilibrium with consumer and resource densities \vec{C}^{**} and \vec{R}^{**} is approached starting from any interior state. \vec{C}^{**} is interior only if $\mathbf{u e}_R \vec{R}^{**} = \vec{m}$, hence by Restriction 2a, $n_C \leq n_R$. Thus $n_C \leq n_R$ is necessary for permanent coexistence; this is the “competitive exclusion principle” (Armstrong and McGehee, 1980) in this context.

Necessary and sufficient conditions for permanent coexistence are given by

Result 2: There is an interior equilibrium if and only if for any species, the equilibrium approached in the absence of that species and the presence of the others is invasible by that species (Appendix, Corollary 2).

The latter property has been termed mutual invasibility (Yodzis, 1989, sec. 5.2.2). Thus in MacArthur-style consumer–resource models, permanent coexistence is equivalent to mutual invasibility. These properties are not equivalent in every smooth deterministic ecological model (Armstrong and McGehee, 1980).

The equilibrium approached when a species is removed need not admit all the other species. For example, removal of a resource species may engender extinction of some consumer species.

What matters is whether the species that is removed can invade the species that permanently coexist in its absence.

For resources without direct interactions, the conditions for permanent coexistence of the consumers admit an instructive formulation in terms of regression statistics. Regarding each column of \mathbf{u} (corresponding to a resource species) as a datum, consider the multiple regression of one row of \mathbf{u} (corresponding to a consumer species) on the others, where the $(n_C - 1)$ -dimensional regression hyperplane passes through the origin, and the regression is weighted using characteristics of the resources and consumers. Specifically, letting \mathbf{u}_γ be row γ of \mathbf{u} , termed the utilization function of consumer species γ , and $\mathbf{u}_{\bar{\gamma}}$ the remainder of \mathbf{u} , the regression model is

$$\mathbf{u}_\gamma = \mathbf{b}_\gamma \mathbf{u}_{\bar{\gamma}} + \mathbf{e}_\gamma,$$

where $\mathbf{b}_\gamma = (b_{\gamma 1}, \dots, b_{\gamma(\gamma-1)}, b_{\gamma(\gamma+1)}, \dots, b_{\gamma n_C})$ comprises the partial regression coefficients, and $\mathbf{e}_\gamma = (e_{\gamma 1}, \dots, e_{\gamma n_R})$ comprises the residual errors. Assuming $\bar{\mathbf{R}}^*$ (the globally attracting equilibrium of the resources in the absence of the consumers) and $\bar{\mathbf{R}}^{**}$ are interior and $n_C \leq n_R$, the weight of resource species ρ is

$$w_\rho = \frac{(e_R)_\rho (R_\rho^* - R_\rho^{**})}{G_\rho [R_\rho^{**}]} \quad (6)$$

if $R_\rho^{**} \neq R_\rho^*$, else resource species ρ should be ignored in what follows; by Restriction 1b, $w_\rho > 0$.

The weighted least squares partial regression coefficients are

$$\mathbf{b}_\gamma = \mathbf{u}_\gamma \mathbf{w} \mathbf{u}_{\bar{\gamma}}^\dagger (\mathbf{u}_{\bar{\gamma}} \mathbf{w} \mathbf{u}_{\bar{\gamma}}^\dagger)^{-1} \quad (7)$$

(Seber, 1977, sec. 3.6), where \mathbf{w} is the diagonal matrix of all w_ρ . The formulation also involves the column vector

$$\bar{\mathbf{h}}^* = \mathbf{u} \mathbf{e}_R \bar{\mathbf{R}}^* - \bar{\mathbf{m}}, \quad (8)$$

which comprises the net energy harvests of the consumers when the consumer densities are negligible and the resource densities are equilibrial.

Result 3: For resources without direct interactions, assuming \vec{R}^* and \vec{R}^{**} are interior and $n_C \leq n_R$, \vec{C}^{**} is interior if and only if for any γ ,

$$h_\gamma^* > \sum_{\substack{\delta=1 \\ \delta \neq \gamma}}^{n_C} b_{\gamma\delta} h_\delta^* \quad (9)$$

(Appendix, Proposition 2).

For MacArthur's original model (3) with two consumer species, this result was obtained by Chesson (1990), who recommended exploration of the multi-consumer case.

Chesson's insight was that permanent coexistence of the consumers depends on the degree of linear independence of their utilization functions, a notion that can be made precise in terms of regression statistics. For two consumer species, linear dependence of the utilization functions means the pairs $(u_{1\rho}, u_{2\rho})$ lie on a line passing through the origin. The coefficient of determination $r^2 = b_{12}b_{21}$, which is between 0 and 1, measures the scatter of the pairs around the regression line. The smaller r^2 is, the farther from linear dependence the utilization functions are. As Chesson showed, \vec{C}^{**} is interior if and only if $s r < h_1^*/h_2^* < s/r$, where the scale factor $s = \sqrt{(\sum_\rho u_{1\rho} w_\rho u_{1\rho} / \sum_\rho u_{2\rho} w_\rho u_{2\rho})}$ measures the relative magnitudes of the utilization functions. In terms of the regression coefficients, these conditions are $h_1^* > b_{12}h_2^*$ and $h_2^* > b_{21}h_1^*$. These generalize to (9) for any number of consumer species. Unless the resource dynamics are of Lotka–Volterra form, the regression statistics depend on \vec{C}^{**} , hence the value of the formulation is not computational but conceptual.

For example, (6) discloses characteristics of the resources and consumers relevant to permanent coexistence of the consumers. The factor $(e_R)_\rho$ is the energy per unit of resource species ρ . Greater values indicate more benefit to the consumers per unit of resource harvested. The factor $R_\rho^* - R_\rho^{**}$ is the effect of consumption on the standing crop of resource species ρ at equilibrium. Greater values indicate more units of resource harvested. The factor $1/G_\rho[R_\rho^{**}] = 1/\sum_\gamma u_{\gamma\rho} C_\gamma^{**}$ is the time it takes the consumers to harvest the standing crop of resource species ρ at equilibrium. Greater values indicate more resilience to consumption.

Result 3 can be extended to resources with direct interactions, but the formalism becomes difficult to interpret. The weight matrix becomes

$$\mathbf{w} = -\mathbf{e}_R \left(\int_0^1 \mathbf{J}_G[(1-s)\vec{\mathbf{R}}^* + s\vec{\mathbf{R}}^{**}] ds \right)^{-1}$$

(the integral is over the line segment from $\vec{\mathbf{R}}^*$ to $\vec{\mathbf{R}}^{**}$), which is positive definite but generally not symmetric. In regression analysis, a weight matrix that is not symmetric is enigmatic.

Discussion

As models of ecological communities, or merely of consumptive competition, MacArthur-style consumer–resource models are limited in several ways. For example, the resources are substitutable (Yodzis, 1989, sec. 5.4.2.1)—every resource supplies the consumers with the same thing, here known as energy; the functional responses (Taylor, 1984, ch. 8) are linear—a unit of consumer species γ harvests resource species ρ at the rate $u_{\gamma\rho}R_\rho$, which is linear in the density of resource species ρ ; and the system is spatiotemporally homogeneous—effectively, the system is a well stirred chemostat. Despite their limitations, understanding these models is valuable. They serve as reference points for understanding more complicated models. MacArthur’s original model (3), as elucidated by MacArthur, Case, Casten, Chesson, Goh, and others, served as a reference point in the development of the results in this article. Given Schoener’s variant (4) and MacArthur’s extended model (5), a natural question is, to what extent do results that hold for MacArthur’s original model also hold for these models? According to the results presented here, every MacArthur-style model has similar implications.

Moreover, the limitations may be relatively insignificant for many species. For example, resources may be nearly substitutable for generalist consumers, functional responses may be approximately linear over naturally occurring ranges of resource density, and spatiotemporal heterogeneity may perturb rather than negate processes and patterns that prevail in its absence (Chesson,

2000). These issues remain in need of research, both experimental and theoretical. For example, in consumer–resource models with nonlinear functional responses, permanent but nonequilibrium coexistence is possible (Yodzis, 1989, sec. 4.2.1.3), in contrast with Result 1 for MacArthur-style models. Indeed, with suitably chosen nonlinear functional responses, permanent but nonequilibrium coexistence is possible for any number of consumer species and one resource species (Armstrong and McGehee, 1980). However, complicated attractors do not immediately appear when nonlinearity is introduced into functional responses of MacArthur-style models. The globally attracting equilibrium asserted by Result 1 is structurally stable with respect to perturbations from linearity. What is needed is an investigation of the bifurcations that ensue as, for example, processing times per unit of resource harvested increase, to characterize the ecological conditions for various dynamical behaviors.

Such investigations will probably require different approaches. MacArthur-style consumer–resource models are simple enough that the results in this article hold for arbitrary n_C and n_R and were obtained without numerical analyses. Understanding more complicated models may well require numerical analyses and algebraic analyses restricted to small n_C and n_R .

Appendix

In what follows, two lemmas, two propositions, and two corollaries are stated and proved. Lemmas 1 and 2 are used to prove Proposition 1, which is used to prove Corollaries 1 and 2. Results 1, 2 and 3 in the main text correspond to Corollaries 1 and 2 and Proposition 2, respectively.

Notation: $n_N = n_C + n_R$,

$$\vec{\mathbf{N}} = \begin{pmatrix} \vec{\mathbf{C}} \\ \vec{\mathbf{R}} \end{pmatrix}, \quad \dot{\vec{\mathbf{N}}} = \frac{d\vec{\mathbf{N}}}{dt}, \quad \mathbf{N} = \begin{pmatrix} \mathbf{C} & \mathbf{0} \\ \mathbf{0} & \mathbf{R} \end{pmatrix}, \quad \vec{\mathbf{F}}[\vec{\mathbf{N}}] = \begin{pmatrix} \mathbf{e}_C^{-1}(\mathbf{u} \mathbf{e}_R \vec{\mathbf{R}} - \vec{\mathbf{m}}) \\ \vec{\mathbf{G}}[\vec{\mathbf{R}}] - \mathbf{u}^t \vec{\mathbf{C}} \end{pmatrix},$$

$$\mathbf{e}_N = \begin{pmatrix} \mathbf{e}_C & \mathbf{0} \\ \mathbf{0} & \mathbf{e}_R \end{pmatrix}, \quad \mathbf{J}_F[\vec{\mathbf{N}}] = \begin{pmatrix} \mathbf{0} & \mathbf{e}_C^{-1} \mathbf{u} \mathbf{e}_R \\ -\mathbf{u}^t & \mathbf{J}_G[\vec{\mathbf{R}}] \end{pmatrix}.$$

Lemma 1: The feasible solutions of $\dot{\vec{\mathbf{N}}} = \mathbf{N} \vec{\mathbf{F}}[\vec{\mathbf{N}}]$ are uniformly bounded.

Proof: Let $E = \|\mathbf{e}_N \vec{\mathbf{N}}\| = \sum_{\lambda} e_{\lambda} N_{\lambda}$, hence

$$\dot{E} = \sum_{\lambda=1}^{n_N} e_{\lambda} N_{\lambda} F_{\lambda}[\vec{\mathbf{N}}] = \vec{\mathbf{N}}^t \mathbf{e}_N \vec{\mathbf{F}}[\vec{\mathbf{N}}] = -\vec{\mathbf{C}}^t \vec{\mathbf{m}} + \vec{\mathbf{R}}^t \mathbf{e}_R \vec{\mathbf{G}}[\vec{\mathbf{R}}].$$

If $\|\mathbf{e}_R \vec{\mathbf{R}}\| > b_R$, then $\vec{\mathbf{R}}^t \mathbf{e}_R \vec{\mathbf{G}}[\vec{\mathbf{R}}] < 0$ (Restriction 1a), hence $\dot{E} < 0$. On the compact set $\{\text{feasible } \vec{\mathbf{R}} \mid \|\mathbf{e}_R \vec{\mathbf{R}}\| \leq b_R\}$, the continuous function $\vec{\mathbf{R}} \mapsto \vec{\mathbf{R}}^t \mathbf{e}_R \vec{\mathbf{G}}[\vec{\mathbf{R}}]$ attains a maximum M .

Let $b_C = M \max((e_C)_{\delta}) / \min(m_{\delta})$. If $\|\mathbf{e}_C \vec{\mathbf{C}}\| > b_C$, then

$$\begin{aligned} \vec{\mathbf{C}}^t \vec{\mathbf{m}} &= \sum_{\gamma=1}^{n_C} C_{\gamma} m_{\gamma} \geq \min(m_{\delta}) \sum_{\gamma=1}^{n_C} C_{\gamma} \geq \frac{\min(m_{\delta})}{\max((e_C)_{\delta})} \sum_{\gamma=1}^{n_C} (e_C)_{\gamma} C_{\gamma} \\ &= \frac{\min(m_{\delta})}{\max((e_C)_{\delta})} \|\mathbf{e}_C \vec{\mathbf{C}}\| > \frac{\min(m_{\delta})}{\max((e_C)_{\delta})} b_C = M, \end{aligned}$$

hence $\dot{E} < 0$. Let $b_N = b_R + b_C$. If $E > b_N$, then $\|\mathbf{e}_R \vec{\mathbf{R}}\| > b_R$ or $\|\mathbf{e}_C \vec{\mathbf{C}}\| > b_C$, hence $\dot{E} < 0$.

Therefore $\limsup_{t \rightarrow \infty} E \leq b_N$. Let $b = b_N / \min(e_{\lambda})$. For any λ ,

$$N_{\lambda} \leq \frac{1}{\min(e_{\mu})} \sum_{\mu=1}^{n_N} e_{\mu} N_{\mu} = \frac{1}{\min(e_{\mu})} E.$$

Therefore

$$\limsup_{t \rightarrow \infty} N_{\lambda} \leq \frac{1}{\min(e_{\mu})} \limsup_{t \rightarrow \infty} E \leq \frac{1}{\min(e_{\mu})} b_N = b.$$

Thus b is a uniform bound on the feasible solutions. ■

Lemma 2: For any $\vec{\mathbf{N}}^{(1)}$ and feasible $\vec{\mathbf{N}}^{(2)}$, $(\vec{\mathbf{N}}^{(1)})^t \mathbf{e}_N \mathbf{J}_F[\vec{\mathbf{N}}^{(2)}] \vec{\mathbf{N}}^{(1)} \leq 0$, with equality if and only if $\vec{\mathbf{R}}^{(1)} = \vec{\mathbf{0}}$.

Proof: Observe that

$$\begin{aligned} (\vec{\mathbf{N}}^{(1)})^t \mathbf{e}_N \mathbf{J}_F[\vec{\mathbf{N}}^{(2)}] \vec{\mathbf{N}}^{(1)} &= \begin{pmatrix} (\vec{\mathbf{C}}^{(1)})^t & (\vec{\mathbf{R}}^{(1)})^t \end{pmatrix} \begin{pmatrix} \mathbf{0} & \mathbf{u} \mathbf{e}_R \\ -\mathbf{e}_R \mathbf{u}^t & \mathbf{e}_R \mathbf{J}_G[\vec{\mathbf{R}}^{(2)}] \end{pmatrix} \begin{pmatrix} \vec{\mathbf{C}}^{(1)} \\ \vec{\mathbf{R}}^{(1)} \end{pmatrix} \\ &= (\vec{\mathbf{C}}^{(1)})^t \mathbf{u} \mathbf{e}_R \vec{\mathbf{R}}^{(1)} - (\vec{\mathbf{R}}^{(1)})^t \mathbf{e}_R \mathbf{u}^t \vec{\mathbf{C}}^{(1)} + (\vec{\mathbf{R}}^{(1)})^t \mathbf{e}_R \mathbf{J}_G[\vec{\mathbf{R}}^{(2)}] \vec{\mathbf{R}}^{(1)}. \end{aligned}$$

$(\vec{\mathbf{R}}^{(1)})^t \mathbf{e}_R \mathbf{u}^t \vec{\mathbf{C}}^{(1)}$ is the transpose of $(\vec{\mathbf{C}}^{(1)})^t \mathbf{u} \mathbf{e}_R \vec{\mathbf{R}}^{(1)}$, and these are scalars, hence they are equal, and the first two terms cancel out. Thus the lemma reduces to Restriction 1b. ■

Definition: A feasible equilibrium $\vec{\mathbf{N}}^*$ of $\dot{\vec{\mathbf{N}}} = \mathbf{N} \vec{\mathbf{F}}[\vec{\mathbf{N}}]$ is saturated if $-\vec{\mathbf{F}}[\vec{\mathbf{N}}^*]$ is feasible (Hofbauer and Sigmund, 1998, sec. 13.4), that is, an interior equilibrium is saturated, and a boundary equilibrium is saturated unless it is invisable by a species it lacks.

Proposition 1: There is exactly one saturated equilibrium of $\dot{\vec{\mathbf{N}}} = \mathbf{N} \vec{\mathbf{F}}[\vec{\mathbf{N}}]$, which is globally attracting.

Proof: By Lemma 1 and general theory (essentially, the Brouwer fixed point theorem), there is at least one saturated equilibrium (Hofbauer and Sigmund, 1998, Exercise 13.4.4). As we will see, a saturated equilibrium is globally attracting, hence there is at most one.

The following proof that a saturated equilibrium is globally attracting was inspired by Case and Casten (1979) and Goh (1977). Given a saturated equilibrium $\vec{\mathbf{N}}^*$, let

$$L[\vec{\mathbf{N}}; \vec{\mathbf{N}}^*] = \sum_{\lambda \in \text{spt}(\vec{\mathbf{N}}^*)} e_\lambda \left(N_\lambda - N_\lambda^* - N_\lambda^* \ln \left[\frac{N_\lambda}{N_\lambda^*} \right] \right) + \sum_{\lambda \notin \text{spt}(\vec{\mathbf{N}}^*)} e_\lambda N_\lambda,$$

where $\text{spt}(\vec{\mathbf{N}}^*) = \{\lambda \mid N_\lambda^* \neq 0\}$ is the support of $\vec{\mathbf{N}}^*$. L is well defined on $\{\text{feasible } \vec{\mathbf{N}} \mid \text{spt}(\vec{\mathbf{N}}) \supseteq \text{spt}(\vec{\mathbf{N}}^*)\}$. As we will see, L is a Lyapunov function on this domain. This means L has two properties. The first is that L has a unique global minimum at $\vec{\mathbf{N}}^*$. To see this, observe that L is a sum of independent terms, hence L is minimal if and only if every summand is minimal. Given $n^* > 0$, let $\ell[n; n^*] = n - n^* - n^* \ln[n/n^*]$. ℓ is well defined for any $n > 0$. $d\ell/dn = (n - n^*)/n$, which is zero if $n = n^*$, negative if $n < n^*$, and positive if $n > n^*$, hence ℓ has a unique global minimum at n^* . Because $e_\lambda > 0$, the summand $e_\lambda \ell[N_\lambda; N_\lambda^*]$ has a unique global minimum at N_λ^* . Likewise, the summand $e_\lambda N_\lambda$ has a unique global minimum at $N_\lambda^* = 0$. Thus L has a unique global minimum at $\vec{\mathbf{N}}^*$.

The second property of L is that L is nonincreasing along any feasible solution. To see this, observe that

$$\begin{aligned}
\dot{L} &= \sum_{\lambda \in \text{spt}(\vec{\mathbf{N}}^*)} e_\lambda \frac{N_\lambda - N_\lambda^*}{N_\lambda} \dot{N}_\lambda + \sum_{\lambda \notin \text{spt}(\vec{\mathbf{N}}^*)} e_\lambda \dot{N}_\lambda \\
&= \sum_{\lambda=1}^{n_N} e_\lambda (N_\lambda - N_\lambda^*) F_\lambda[\vec{\mathbf{N}}] \\
&= (\vec{\mathbf{N}} - \vec{\mathbf{N}}^*)^\dagger \mathbf{e}_N \vec{\mathbf{F}}[\vec{\mathbf{N}}] \\
&= (\vec{\mathbf{N}} - \vec{\mathbf{N}}^*)^\dagger \mathbf{e}_N \left(\vec{\mathbf{F}}[\vec{\mathbf{N}}^*] + \left(\int_0^1 \mathbf{J}_F[(1-s)\vec{\mathbf{N}}^* + s\vec{\mathbf{N}}] ds \right) (\vec{\mathbf{N}} - \vec{\mathbf{N}}^*) \right) \tag{A1}
\end{aligned}$$

$$= (\vec{\mathbf{N}} - \vec{\mathbf{N}}^*)^\dagger \mathbf{e}_N \vec{\mathbf{F}}[\vec{\mathbf{N}}^*] + \int_0^1 \left((\vec{\mathbf{N}} - \vec{\mathbf{N}}^*)^\dagger \mathbf{e}_N \mathbf{J}_F[(1-s)\vec{\mathbf{N}}^* + s\vec{\mathbf{N}}] (\vec{\mathbf{N}} - \vec{\mathbf{N}}^*) \right) ds. \tag{A2}$$

Equation (A1) is by the mean-value theorem (Lang, 1998, Theorem XIII.4.2). In (A2), the first term is nonpositive because $\vec{\mathbf{N}}^*$ is a saturated equilibrium, and the second term is nonpositive by Lemma 2. Thus L is nonincreasing along any feasible solution, so L is a Lyapunov function.

By Lyapunov theory, every interior solution approaches an invariant set A on which L is constant (Hofbauer and Sigmund, 1998, Theorem 2.6.1). For any $\vec{\mathbf{N}} \in A$, \dot{L} vanishes. Each term in (A2) is nonpositive, hence each term vanishes. Vanishing of the first term implies $C_\gamma - C_\gamma^* = 0$ for any γ such that $(\mathbf{u} \mathbf{e}_R \vec{\mathbf{R}}^*)_\gamma - m_\gamma \neq 0$. By Lemma 2, vanishing of the second term implies vanishing of the integrand for any value of the integration variable. As in the proof of Lemma 2, this implies $\vec{\mathbf{R}} - \vec{\mathbf{R}}^* = \vec{\mathbf{0}}$. Therefore $\vec{\mathbf{N}}$ is of the form

$$\begin{pmatrix} \vec{\mathbf{C}}^* + \Delta \vec{\mathbf{C}} \\ \vec{\mathbf{R}}^* \end{pmatrix},$$

where $\Delta C_\gamma = 0$ for any γ such that $(\mathbf{u} \mathbf{e}_R \vec{\mathbf{R}}^*)_\gamma \neq m_\gamma$. This implies $\dot{\vec{\mathbf{R}}} = \mathbf{R}(\vec{\mathbf{G}}[\vec{\mathbf{R}}] - \mathbf{u}^\dagger \vec{\mathbf{C}})$ amounts to $\vec{\mathbf{0}} = \mathbf{R}^*(\vec{\mathbf{G}}[\vec{\mathbf{R}}^*] - \mathbf{u}^\dagger(\vec{\mathbf{C}}^* + \Delta \vec{\mathbf{C}}))$, which reduces to $\mathbf{R}^* \mathbf{u}^\dagger \Delta \vec{\mathbf{C}} = \vec{\mathbf{0}}$, because $\vec{\mathbf{N}}^*$ is an equilibrium. For the subsystem consisting of the consumer species in $\text{spt}(\Delta \vec{\mathbf{C}})$ and the resource species in $\text{spt}(\vec{\mathbf{R}}^*)$, let \tilde{n}_C , \tilde{n}_R , $\Delta \vec{\mathbf{C}}$, $\vec{\mathbf{R}}^*$, $\tilde{\mathbf{u}}$, $\tilde{\mathbf{e}}_R$, and $\tilde{\mathbf{m}}$ be the corresponding numbers, vectors, and matrices. $\gamma \in \text{spt}(\Delta \vec{\mathbf{C}})$ implies $(\mathbf{u} \mathbf{e}_R \vec{\mathbf{R}}^*)_\gamma = m_\gamma$. Therefore $\tilde{\mathbf{u}} \tilde{\mathbf{e}}_R \vec{\mathbf{R}}^* = \tilde{\mathbf{m}}$, hence $\tilde{n}_C \leq \tilde{n}_R$ (Restriction 2a). $\mathbf{R}^* \mathbf{u}^\dagger \Delta \vec{\mathbf{C}} = \vec{\mathbf{0}}$ implies $\tilde{\mathbf{u}}^\dagger \Delta \vec{\mathbf{C}} = \vec{\mathbf{0}}$, hence $\Delta \vec{\mathbf{C}} = \vec{\mathbf{0}}$ (Restriction 2b), that is, $\tilde{n}_C = 0$. Therefore $\Delta \vec{\mathbf{C}} = \vec{\mathbf{0}}$, hence $\vec{\mathbf{N}} = \vec{\mathbf{N}}^*$. Thus $A = \{\vec{\mathbf{N}}^*\}$, so every interior solution approaches $\vec{\mathbf{N}}^*$. ■

Corollary 1: If there is an interior equilibrium of $\dot{\vec{N}} = \mathbf{N}\vec{F}[\vec{N}]$, then it is globally attracting, else some boundary equilibrium is globally attracting.

Proof: If there is an interior equilibrium, then it is saturated, hence globally attracting. Otherwise, because there must be one saturated equilibrium, some boundary equilibrium is saturated, hence globally attracting. ■

Corollary 2: There is an interior equilibrium of $\dot{\vec{N}} = \mathbf{N}\vec{F}[\vec{N}]$ if and only if for any species, the equilibrium approached in the absence of that species and the presence of the others is invulnerable by that species.

Proof: Suppose there is an interior equilibrium. It is saturated, hence because there must be at most one saturated equilibrium, no boundary equilibrium is saturated. In the absence of, say, species 1, some boundary equilibrium is approached. It is saturated with respect to the other species. Thus it is invulnerable by species 1, else it would be saturated with respect to all the species.

Conversely, suppose mutual invulnerability, and suppose some boundary equilibrium lacks, say, species 1. If it is the equilibrium approached in the absence of species 1, then it is invulnerable by species 1. Otherwise, another boundary equilibrium is saturated with respect to the other species, hence because there must be at most one equilibrium saturated with respect to the other species, the first equilibrium is not saturated with respect to the other species. In either case, the boundary equilibrium is not saturated with respect to all the species. Thus no boundary equilibrium is saturated, hence because there must be at least one saturated equilibrium, there is an interior equilibrium. ■

Proposition 2: Let $(\vec{0}, \vec{R}^*)^t$ and $(\vec{C}^{**}, \vec{R}^{**})^t$ be the globally attracting equilibria of $\dot{\vec{N}} = \mathbf{N}\vec{F}[\vec{N}]$ in the absence and presence of the consumers. For resources without direct interactions, assuming \vec{R}^* and \vec{R}^{**} are interior and $n_C \leq n_R$, \vec{C}^{**} is interior if and only if for any γ ,

$$h_\gamma^* > \sum_{\substack{\delta=1 \\ \delta \neq \gamma}}^{n_C} b_{\gamma\delta} h_\delta^*,$$

where b_γ and \vec{h}^* are defined by (7) and (8).

Proof: Let $\mathbf{a} = \mathbf{u}\mathbf{w}\mathbf{u}^\dagger$, where \mathbf{w} is defined by (6). \mathbf{w} is positive definite (Harville, 1997, Lemma 14.2.1), and \mathbf{u} is of full row rank ($n_C \leq n_R$ and Restriction 2b), hence \mathbf{a} is positive definite (Harville, 1997, Theorem 14.2.9). Therefore \mathbf{a} is invertible, and \mathbf{a}^{-1} is positive definite (Harville, 1997, Corollary 14.2.11). Let $\vec{\mathbf{h}}^{**} = \mathbf{u}\mathbf{e}_R\vec{\mathbf{R}}^{**} - \vec{\mathbf{m}}$. $(\vec{\mathbf{C}}^{**}, \vec{\mathbf{R}}^{**})^\dagger$ is saturated, hence $-\vec{\mathbf{h}}^{**}$ is feasible.

$\vec{\mathbf{C}}^{**}$ is interior if and only if $\mathbf{a}^{-1}\vec{\mathbf{h}}^*$ is interior. To see this, observe that because $\vec{\mathbf{R}}^{**}$ is interior, $\vec{\mathbf{G}}[\vec{\mathbf{R}}^{**}] = \mathbf{u}^\dagger\vec{\mathbf{C}}^{**}$. Therefore by (6), $\mathbf{w}\mathbf{u}^\dagger\vec{\mathbf{C}}^{**} = \mathbf{e}_R(\vec{\mathbf{R}}^* - \vec{\mathbf{R}}^{**})$, hence $\mathbf{a}\vec{\mathbf{C}}^{**} = \mathbf{u}\mathbf{e}_R(\vec{\mathbf{R}}^* - \vec{\mathbf{R}}^{**})$. Therefore by (8), $\mathbf{a}\vec{\mathbf{C}}^{**} = \vec{\mathbf{h}}^* - \vec{\mathbf{h}}^{**}$, hence $\mathbf{a}^{-1}\vec{\mathbf{h}}^* = \vec{\mathbf{C}}^{**} + \mathbf{a}^{-1}\vec{\mathbf{h}}^{**}$. If $\vec{\mathbf{h}}^{**} = \vec{\mathbf{0}}$, then $\mathbf{a}^{-1}\vec{\mathbf{h}}^* = \vec{\mathbf{C}}^{**}$, and the conclusion holds. If $\vec{\mathbf{h}}^{**} \neq \vec{\mathbf{0}}$, then $\vec{\mathbf{C}}^{**}$ is not interior. Because \mathbf{a}^{-1} is positive definite, $(\vec{\mathbf{h}}^{**})^\dagger\mathbf{a}^{-1}\vec{\mathbf{h}}^{**} > 0$. Because $-\vec{\mathbf{h}}^{**}$ is feasible, there is a γ such that $h_\gamma^{**} < 0$ and $(\mathbf{a}^{-1}\vec{\mathbf{h}}^{**})_\gamma < 0$. $h_\gamma^{**} < 0$ implies $C_\gamma^{**} = 0$. Therefore $(\mathbf{a}^{-1}\vec{\mathbf{h}}^*)_\gamma = (\mathbf{a}^{-1}\vec{\mathbf{h}}^{**})_\gamma < 0$, hence $\mathbf{a}^{-1}\vec{\mathbf{h}}^*$ is not interior.

Moreover, $(\mathbf{a}^{-1}\vec{\mathbf{h}}^*)_\gamma > 0$ if and only if $h_\gamma^* > \sum_{\delta \neq \gamma} \mathbf{b}_{\gamma\delta} h_\delta^*$. It suffices to show this for $\gamma = n_C$; the argument for $\gamma < n_C$ is analogous. Observe that $(\mathbf{a}^{-1}\vec{\mathbf{h}}^*)_{n_C} = \sum_{\delta} (\mathbf{a}^{-1})_{n_C\delta} h_\delta^*$. Because \mathbf{a}^{-1} is positive definite, the diagonal element $(\mathbf{a}^{-1})_{n_C n_C}$ is positive (Harville, 1997, Corollary 14.2.13). Therefore $(\mathbf{a}^{-1}\vec{\mathbf{h}}^*)_{n_C} > 0$ if and only if

$$h_{n_C}^* > \sum_{\delta=1}^{n_C-1} -\frac{(\mathbf{a}^{-1})_{n_C\delta}}{(\mathbf{a}^{-1})_{n_C n_C}} h_\delta^*.$$

Thus it suffices to show

$$\mathbf{b}_{n_C\delta} = -\frac{(\mathbf{a}^{-1})_{n_C\delta}}{(\mathbf{a}^{-1})_{n_C n_C}}.$$

Let $\mathbf{a}_{\overline{\gamma\gamma}}$ be the matrix obtained by deleting row γ and column γ from \mathbf{a} and $\mathbf{a}_{\gamma\overline{\gamma}}$ the row vector obtained by deleting column γ from row γ of \mathbf{a} . In this notation, (7) becomes $\mathbf{b}_\gamma = \mathbf{a}_{\gamma\overline{\gamma}}\mathbf{a}_{\overline{\gamma\gamma}}^{-1}$.

Therefore $\mathbf{b}_{n_C\delta} = \sum_{\varepsilon < n_C} a_{n_C\varepsilon}(\mathbf{a}_{\overline{n_C n_C}}^{-1})_{\varepsilon\delta}$. Thus it suffices to show

$$-\frac{(\mathbf{a}^{-1})_{n_C\delta}}{(\mathbf{a}^{-1})_{n_C n_C}} = \sum_{\varepsilon=1}^{n_C-1} a_{n_C\varepsilon}(\mathbf{a}_{\overline{n_C n_C}}^{-1})_{\varepsilon\delta}.$$

By the standard formula for an element of an inverse (Harville, 1997, Corollary 13.5.4),

$$(\mathbf{a}^{-1})_{n_C\delta} = \frac{(-1)^{n_C+\delta} |\mathbf{a}_{\overline{\delta n_C}}|}{|\mathbf{a}|}, \quad (\mathbf{a}^{-1})_{n_C n_C} = \frac{|\mathbf{a}_{\overline{n_C n_C}}|}{|\mathbf{a}|},$$

and

$$(\mathbf{a}_{\overline{n_C n_C}}^{-1})_{\varepsilon\delta} = \frac{(-1)^{\varepsilon+\delta} |(\mathbf{a}_{\overline{n_C n_C}})_{\overline{\delta\varepsilon}}|}{|\mathbf{a}_{\overline{n_C n_C}}|},$$

where $|\cdot|$ denotes determinant, $\mathbf{a}_{\overline{\delta n_C}}$ is the matrix obtained by deleting row δ and column n_C from \mathbf{a} , and $(\mathbf{a}_{\overline{n_C n_C}})_{\overline{\delta\varepsilon}}$ is the matrix obtained by deleting row δ and column ε from $\mathbf{a}_{\overline{n_C n_C}}$. After substituting, cancelling, and rearranging, the desired equation is

$$|\mathbf{a}_{\overline{\delta n_C}}| = \sum_{\varepsilon=1}^{n_C-1} (-1)^{(n_C-1)+\varepsilon} a_{n_C\varepsilon} |(\mathbf{a}_{\overline{n_C n_C}})_{\overline{\delta\varepsilon}}|.$$

$a_{n_C\varepsilon}$ is the element in row $n_C - 1$ and column ε of $\mathbf{a}_{\overline{\delta n_C}}$, and $(\mathbf{a}_{\overline{n_C n_C}})_{\overline{\delta\varepsilon}} = (\mathbf{a}_{\overline{\delta n_C}})_{\overline{(n_C-1)\varepsilon}}$, the matrix obtained by deleting row $n_C - 1$ and column ε from $\mathbf{a}_{\overline{\delta n_C}}$. Thus the desired equation amounts to the standard formula for the determinant of $\mathbf{a}_{\overline{\delta n_C}}$ by expansion along row $n_C - 1$ (Harville, 1997, Theorem 13.5.1). ■

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notation	definition
C_γ	density of consumer species γ
$d_{\rho\sigma}$	Lotka–Volterra coefficient in MacArthur’s extended model (5)
$(e_C)_\gamma$	energy per unit of consumer species γ
$(e_R)_\rho$	energy per unit of resource species ρ
G_ρ	growth function of resource species ρ
\mathbf{J}_G	Jacobian matrix of $\vec{\mathbf{G}}$
m_γ	maintenance requirement of consumer species γ
n_C	number of consumer species in system
n_R	number of resource species in system
R_ρ	density of resource species ρ
$u_{\gamma\rho}$	utilization coefficient of consumer species γ for resource species ρ

Table I: Glossary of notation. A notation is glossed if it is defined in the main text (not the appendix) and used in the main text outside the context in which it is defined. Typically, an upper-case Latin letter denotes a variable, and a lower-case Latin letter denotes a parameter. Consumer species are indexed (from 1 to n_C) by γ or δ , and resource species are indexed (from 1 to n_R) by ρ or σ . A bold letter with an arrow denotes the column vector of all instances of the plain letter (e.g., $\vec{\mathbf{C}}$ is the n_C -dimensional column vector of all C_γ). A bold letter without an arrow denotes the matrix of all instances of the plain letter (e.g., \mathbf{C} is the n_C -by- n_C diagonal matrix of all C_γ , and \mathbf{u} is the n_C -by- n_R matrix of all $u_{\gamma\rho}$). The superscript ^t denotes transpose, and the superscript * denotes equilibrium.