The Minimum Environmental Perturbation Principle

Online Appendices

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Appendix A: Interpretations of MacArthur's Minimization Principle

MacArthur developed an interpretation of the minimization principle for the consumer resource model with non-interacting resources, under the assumption that all species have the same requirements $m_i = m$ and the same total harvesting ability $\sum_{\alpha=1}^{M} c_{i\alpha} = c$ (MacArthur 1970). This same constraint has been discussed recently in the context of microbial ecology (Posfai et al. 2017), where it has been shown to give rise to non-generic behavior in highly diverse communities (Cui et al. 2019). In this scenario, MacArthur's objective function from eq. (4) in the main text can be written as:

$$Q(\mathbf{N}) = \frac{1}{2} \sum_{\alpha \in \mathbf{M}^*} \frac{K_\alpha}{r_\alpha} w_\alpha \left[\frac{r_\alpha}{K_\alpha} \left(K_\alpha - \frac{m}{c w_\alpha} \right) - \sum_j c_{j\alpha} N_j \right]^2 + \frac{m}{c} \left(\sum_{\alpha \notin \mathbf{M}^*} c_{j\alpha} \right) \sum_j N_j \qquad \text{(A1)}$$

where $\mathbf{M}^*$ is the set of resources where $r_\alpha \geq \sum_j c_{j\alpha} N_j$, which can stably avoid extinction at the current consumer population size.

When all the resource types survive, the final term in this expression simplifies (since there are no resource labels α that are not in $\mathbf{M}^*$), and the remaining part takes on the straightforward physical meaning proposed by MacArthur. $\frac{r_\alpha}{K_\alpha} \left(K_\alpha - \frac{m}{c w_\alpha} \right)$ is the production rate of resource α when the abundance R_α is at the minimum value that supports consumer growth. The objective function is a weighted sum of squared differences between this "available production" and the community's total harvest rate $\sum_j c_{j\alpha} N_j$. These ecological dynamics can thus be conceived of as an algorithm for performing a least-squares fit of the harvest rate (with positive free parameters N_j) to the available production.

But if any resources go extinct in the steady state, this interpretation is no longer valid. Now some terms end up disappearing from the first sum, with corresponding modifications to the final term, which has no clear biological meaning. Even in this case, however, a revised explanation by Gatto (1990) still applies. In this reading, no constraints on m_i or $c_{i\alpha}$ are required, and one instead directly interprets the two terms that already appeared in the original expression for Q in eq. (5) The first term, which he calls the "unutilized productivity" U, is a weighted sum of squared

differences between the maximal resource production rate r_α and the current consumption rate:

$$U = \frac{1}{2} \sum_{\alpha \in \mathbf{M}^*} r_\alpha^{-1} K_\alpha w_\alpha \left(r_\alpha - \sum_j c_{j\alpha} N_j \right)^2. \tag{A2}$$

While Gatto (1990) does not comment on the restriction of the sum to the surviving resources, this interpretation of U is compatible with the restriction. If a resource is extinct, it is reasonable to say that none of its (nonexistent) potential productivity is unutilized. The second term is the "basal energy consumption" B which is the total consumption of nutritional value by the community required to maintain the current population sizes:

$$B = \sum_j m_j N_j. \tag{A3}$$

This term is not affected by resource extinction, and the interpretation remains valid.

The full expression for Q in eq. (4) can also be rearranged in a different way, which sets the stage for the present work. To obtain this form, we first note that the local equilibrium abundance $\bar{R}_\alpha$ of resource α at fixed consumer population sizes N_i are given by

$$\bar{R}_\alpha(\mathbf{N}) = \max \left[0, K_\alpha \left(1 - r_\alpha^{-1} \sum_i N_i c_{i\alpha} \right) \right]. \tag{A4}$$

This expression comes from the fact that there are two solutions to $dR_\alpha/dt = 0$, one where $R_\alpha = 0$ and one given by the second term in the brackets. Since resource abundances must be positive, we are required to take $R_\alpha = 0$ if the nonzero solution turns out to be negative. If the nonzero solution is positive, then the $R_\alpha = 0$ solution is unstable to the addition of a small amount of resource α. This consideration fully accounts for resource extinction, and so eq. (4) simplifies to

$$Q(\mathbf{N}) = -\frac{1}{2} \sum_\alpha \frac{w_\alpha r_\alpha}{K_\alpha} [K_\alpha - \bar{R}_\alpha(\mathbf{N})]^2 - \sum_i N_i \left(\sum_\alpha w_\alpha c_{i\alpha} \bar{R}_\alpha(\mathbf{N}) - m_i \right) \tag{A5}$$

where the sums are no longer restricted. The first term now measures the difference between the local equilibrium resource concentrations $\bar{R}_\alpha(\mathbf{N})$ and the carrying capacities K_α, while the second term measures the total rate of biomass production. This form of $Q(\mathbf{N})$ also makes it easier to see that MacArthur's minimization principle is the Lagrange dual of MEPP (Boyd and Vandenberghe 2004). The first term is clearly minus the objective function d defined in eq. (14)

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of the main text, and the second term is the sum of the Lagrange multipliers times the active constraints g_i, with R_α replaced by $\bar{R}_\alpha(\mathbf{N})$ in both terms.

Appendix B: Derivation of Minimum Environmental Perturbation Principle

In this Appendix, we justify the three mathematical results required for the derivation of MEPP in the main text:

- that the impact vectors are related to the gradients of the growth rates by eq. (8) whenever the environmentally mediated interactions between species are symmetric

- that this same symmetry implies that the rescaled supply vector h_α/b_α can be written as the (negative) gradient of some function d, as done in eq. (13)

- that the unconstrained minimum of d coincides with the supply point of the resource dynamics.

We also explain how an extended version of MEPP can be obtained for asymmetric models by using a modified supply vector.

Implications of symmetric interactions

In this section we deal with the first two points in the list, concerning the consequences of symmetric interactions. To quantify the interactions between two species, we compute the effect of a small change in the abundance of the first species on the growth rate of the second. We introduce a scale factor a_i that can depend on the environmental state, and measure abundances as $a_i N_i$. Since the growth rates directly depend only on the resource abundances, we need to imagine making the perturbation and then holding all the population sizes fixed until the environment relaxes to its new equilibrium state $\bar{\mathbf{R}}(\mathbf{N})$. Thus we define the interaction matrix α_{ij}

as:

$$\alpha_{ij} = -\frac{dg_i}{d(a_j N_j)} = -\sum_\alpha \frac{\partial g_i}{\partial R_\alpha} \frac{\partial \bar{R}_\alpha}{\partial (a_j N_j)}. \tag{B1}$$

Now we can compute $\frac{\partial \bar{R}_\alpha}{\partial (a_j N_j)}$ by implicit differentiation of the local steady-state equation for the environment:

$$0 = h_\alpha + \sum_i N_i q_{i\alpha} \tag{B2}$$

To facilitate the derivation, we write the impact vector as:

$$q_{i\alpha} = -a_i \sum_\beta b^i_{\alpha\beta} \frac{\partial g_i}{\partial R_\beta}. \tag{B3}$$

for some functions $b^i_{\alpha\beta}(\mathbf{R})$ and $a_i(\mathbf{R})$. This does not impose any additional assumptions on the form of $q_{i\alpha}$, as long as $\frac{\partial g_i}{\partial R_\beta} \neq 0$. If the partial derivative does vanish, as in the case of essential resources examined in Appendix C, a limiting procedure has to be taken to apply these results, as will be explained in the context of that example.

If we now further assume that the $b^i_{\alpha\beta}$ are invertible, we can multiply by $(b^j)^{-1}$ and obtain:

$$0 = \sum_\beta (b^j)^{-1}_{\alpha\beta} h_\beta - \sum_{i\beta\gamma} N_i a_i (b^j)^{-1}_{\alpha\beta} b^i_{\beta\gamma} \frac{\partial g_i}{\partial R_\gamma}. \tag{B4}$$

Taking the derivative of both sides with respect to $a_j N_j$ gives:

$$0 = \sum_\lambda \frac{\partial}{\partial R_\lambda} \left(\sum_\beta (b^j)^{-1}_{\alpha\beta} h_\beta \right) \frac{\partial \bar{R}_\lambda}{\partial (a_j N_j)} - \sum_{i\beta\gamma\lambda} N_i a_i (b^j)^{-1}_{\alpha\beta} b^i_{\beta\gamma} \frac{\partial^2 g_i}{\partial R_\lambda \partial R_\gamma} \frac{\partial \bar{R}_\lambda}{\partial (a_j N_j)} - \frac{\partial g_j}{\partial R_\alpha} \tag{B5}$$

$$= -\sum_\lambda A^j_{\alpha\lambda} \frac{\partial \bar{R}_\lambda}{\partial (a_j N_j)} - \frac{\partial g_j}{\partial R_\alpha} \tag{B6}$$

where

$$A^j_{\alpha\lambda} = -\frac{\partial}{\partial R_\lambda} \left(\sum_\beta (b^j)^{-1}_{\alpha\beta} h_\beta \right) + \sum_{i\beta\gamma} N_i a_i (b^j)^{-1}_{\alpha\beta} b^i_{\beta\gamma} \frac{\partial^2 g_i}{\partial R_\lambda \partial R_\gamma}. \tag{B7}$$

Now, further assuming that this matrix is invertible, we obtain:

$$\frac{\partial \bar{R}_\alpha}{\partial (a_j N_j)} = -\sum_\beta (A^j)^{-1}_{\alpha\beta} \frac{\partial g_j}{\partial R_\beta}. \tag{B8}$$

Finally, inserting this into the definition of the interaction matrix yields

$$\alpha_{ij} = \sum_{\alpha\beta}(A^j)_{\alpha\beta}^{-1}\frac{\partial g_i}{\partial R_\alpha}\frac{\partial g_j}{\partial R_\beta}. \tag{B9}$$

With this expression in hand, we can proceed to investigate the implications of symmetry ($\alpha_{ij} = \alpha_{ji}$), by looking for conditions under which

$$\sum_{\alpha\beta}(A^j)_{\alpha\beta}^{-1}\frac{\partial g_i}{\partial R_\alpha}\frac{\partial g_j}{\partial R_\beta} = \sum_{\alpha\beta}(A^i)_{\alpha\beta}^{-1}\frac{\partial g_j}{\partial R_\alpha}\frac{\partial g_i}{\partial R_\beta}. \tag{B10}$$

Inspection of this equation reveals two important conditions. The first is that $A_{\alpha\beta}^j$ is the same for all j. Going back to the definition of $A_{\alpha\beta}^j$ in eq. (B7), we find that this is true if and only if $b_{\alpha\beta}^j$ is the same for all j. In this case, the definition simplifies to

$$A_{\alpha\lambda} = -\frac{\partial}{\partial R_\lambda}\left(\sum_\beta b_{\alpha\beta}^{-1}h_\beta\right) + \sum_i N_i a_i\frac{\partial^2 g_i}{\partial R_\lambda \partial R_\alpha}. \tag{B11}$$

The second condition is that $A_{\alpha\beta}$ must itself be symmetric. The second term in eq. (B11) is always symmetric, so we can focus on the first. Symmetry of this term means that

$$\frac{\partial}{\partial R_\lambda}\left(\sum_\beta b_{\alpha\beta}^{-1}h_\beta\right) = \frac{\partial}{\partial R_\alpha}\left(\sum_\beta b_{\lambda\beta}^{-1}h_\beta\right). \tag{B12}$$

For this to be satisfied in a generic model, $b_{\alpha\beta}$ must be diagonal ($b_{\alpha\beta} = b_\alpha\delta_{\alpha\beta}$). (If $b_{\alpha\beta}$ is not diagonal, very specific correlations between the **R**-dependence of $b_{\alpha\beta}^{-1}$ and the h_α would be required to satisfy the condition.) This, combined with eq. (B3), yields eq. (8) of the main text:

$$q_{i\alpha} = -a_i b_\alpha\frac{\partial g_i}{\partial R_\alpha} \tag{B13}$$

The symmetry requirement can now be written as:

$$\frac{\partial}{\partial R_\lambda}\frac{h_\alpha}{b_\alpha} = \frac{\partial}{\partial R_\alpha}\frac{h_\lambda}{b_\lambda}, \tag{B14}$$

Eq. (B14) is sufficient to guarantee that $\frac{h_\alpha}{b_\alpha}$ can be written as a gradient of some function, as claimed in eq. (13) of the main text:

$$\frac{\partial d}{\partial R_\alpha} = -\frac{h_\alpha}{b_\alpha}. \tag{B15}$$

In this case, $A_{\alpha\beta}$ further simplifies to:

$$A_{\alpha\lambda} = \frac{\partial^2 d}{\partial R_\lambda \partial R_\alpha} + \sum_i N_i a_i \frac{\partial^2 g_i}{\partial R_\lambda \partial R_\alpha}. \tag{B16}$$

Thus we obtain the first two of the three key results listed at the beginning of this Appendix.

We can restate these corollaries of interaction symmetry in a particularly useful way by returning to the dynamical equations. The preceding arguments show that the environmentally mediated interactions between species in a generic niche model described by eqs. (6-7) are symmetric if and only if the dynamics can be rewritten as:

$$\frac{dN_i}{dt} = N_i g_i(\mathbf{R}) \tag{B17}$$

$$\frac{dR_\alpha}{dt} = -b_\alpha \left[\frac{\partial d}{\partial R_\alpha} + \sum_i a_i N_i \frac{\partial g_i}{\partial R_\alpha} \right] \tag{B18}$$

for some functions $b_\alpha(\mathbf{R})$ and $a_i(\mathbf{R})$.

In two of our examples, $A_{\alpha\beta}^j$ is not invertible. To define symmetry in these cases, we add a small additional self-limitation term $-\epsilon R_\alpha^2$ to h_α, and then evaluate α_{ij}/α_{ji} in the limit $\epsilon \to 0$. If this ratio converges to 1, we consider the interactions to be symmetric.

Supply point as unconstrained minimum

In the main text, we made the assumption that $b_\alpha > 0$, and that the supply point $\mathbf{R}^0$ is a stable fixed point of the intrinsic environmental dynamics $\frac{dR_\alpha}{dt} = h_\alpha(\mathbf{R})$. We evaluate the stability of the fixed point in the usual way, by computing the Jacobian $\frac{\partial h_\alpha}{\partial R_\beta}$. The equilibrium point is stable if and only if this matrix is negative definite, so that the dynamics tend to resist small perturbations from equilibrium. Now from the definition of d in eq. (13) we have

$$\frac{\partial h_\alpha}{\partial R_\beta} = -\frac{\partial^2 d}{\partial R_\beta \partial R_\alpha} b_\alpha - \frac{\partial d}{\partial R_\alpha} \frac{\partial b_\alpha}{\partial R_\beta} \tag{B19}$$

where the second term vanishes at the supply point $\mathbf{R}^0$ since $h_\alpha = -b_\alpha \frac{\partial d}{\partial R_\alpha} = 0$ there. From the remaining term and the fact that $b_\alpha > 0$, standard results on D-stability (cf. Hogben 2013) yield that the Hessian $\frac{\partial^2 d}{\partial R_\beta \partial R_\alpha}$ is positive definite whenever $\partial h_\alpha/\partial R_\beta$ is negative definite. Thus we arrive

at the result stated in the main text, that the supply point $\mathbf{R}^0$ is an unconstrained local minimum of d.

Extended MEPP for arbitrary niche models

Here we show how to obtain and use a minimization principle for models with asymmetric interactions between species, where the impact vector and growth rate cannot be related by an equation of the form of eq. (13). We do this by constructing a symmetric model that shares the same stable equilibrium point $\bar{\mathbf{N}}, \bar{\mathbf{R}}$. The parameters of this model will depend on the location of the equilibrium point, requiring an iterative method of estimating and updating the equilibrium point in order to function as a practical algorithm.

We start by decomposing the impact vector into a part $q_{i\alpha}^S = b_\alpha(\mathbf{R})a_i(\mathbf{R})\partial g_i/\partial R_\alpha$ corresponding to a convenient reference model with symmetric interactions, and a part $q_{i\alpha}^A$ that contains the rest of the impact:

$$q_{i\alpha} = q_{i\alpha}^S + q_{i\alpha}^A \tag{B20}$$

This can clearly be done for any $q_{i\alpha}$, without loss of generality. Substituting in to the general equation for the resource dynamics (7), we obtain

$$\frac{dR_\alpha}{dt} = h_\alpha(\mathbf{R}) + \sum_i N_i q_{i\alpha}^A(\mathbf{R}) - \sum_i N_i a_i b_\alpha \frac{\partial g_i}{\partial R_\alpha}. \tag{B21}$$

We now construct our new symmetric model by freezing the asymmetric part of the impact $\sum_i N_i q_{i\alpha}^A(\mathbf{R})$ at its equilibrium value $\sum_i \bar{N}_i q_{i\alpha}^A(\bar{\mathbf{R}})$, and regarding it as part of the supply. The resource dynamics for this new model are given by

$$\frac{dR_\alpha}{dt} = -b_\alpha \left[-\frac{\tilde{h}_\alpha}{b_\alpha} + \sum_i N_i a_i b_\alpha \frac{\partial g_i}{\partial R_\alpha} \right] \tag{B22}$$

with

$$\tilde{h}_\alpha(\mathbf{R}) = h_\alpha(\mathbf{R}) + \sum_i \bar{N}_i q_{i\alpha}^A(\bar{\mathbf{R}}). \tag{B23}$$

By construction, this new model has the same equilibrium state as the original model, and it is nearly of the form of eq. (B18) that guarantees the applicability of MEPP. The remaining step is to write $-\tilde{h}_\alpha / b_\alpha$ as the gradient of a function $d(\mathbf{R})$. For models with direct interactions among resources, where h_α depends on R_β with $\beta \neq \alpha$, it is possible that $-\tilde{h}_\alpha / b_\alpha$ contains a curl, with the result that no such d exists. In that case, we would also have to decompose h_α into two parts, freezing the part that produces the curl at its equilibrium value. But in the present work we focus on cases where h_α is a function of R_α alone, and in particular on the important case of externally supplied resources $h_\alpha = \tau^{-1}(R_\alpha^0 - R_\alpha)$. For this form of the supply, we can write

$$\frac{dR_\alpha}{dt} = -b_\alpha \left[\frac{\partial d(\tilde{\mathbf{R}}^0, \mathbf{R})}{\partial R_\alpha} + \sum_i N_i a_i b_\alpha \frac{\partial g_i}{\partial R_\alpha} \right] \tag{B24}$$

where d is the same function that would have been obtained in the true symmetric model with $q_{i\alpha}^A = 0$, but with modified supply point

$$\tilde{R}_\alpha^0(\bar{\mathbf{N}}, \bar{\mathbf{R}}) = R_\alpha^0 + \tau \sum_i \bar{N}_i q_{i\alpha}^A(\bar{\mathbf{R}}). \tag{B25}$$

The modification is always equal to the asymmetric part of the impact from all the organisms over one chemostat turnover time τ.

As noted in the main text, the difficulty of practically implementing the extended version of MEPP is that computing the effective supply point via eq. (B25) requires prior knowledge of the equilibrium state $\bar{\mathbf{N}}, \bar{\mathbf{R}}$. This problem of minimizing an objective function whose parameters depend on the solution arises frequently in Machine Learning, in the context of fitting models with latent variables (Mehta et al. 2019a). It can be solved with a simple iterative approach, called Expectation Maximization (EM), where one starts by guessing the values of these parameters, then minimizes the function, and then updates the estimates using the new solution. For the case of externally supplied resources, the algorithm can be straightforwardly written as a discrete-time dynamical system describing the evolution of a vector $\mathbf{r}^0(t)$ which represents the effective supply point calculated using the current estimate $\mathbf{n}(t), \mathbf{r}(t)$ of the equilibrium state $\bar{\mathbf{N}}, \bar{\mathbf{R}}$. The parameter

t represents the number of iterations. With these definitions, the algorithm is:

While $||\mathbf{r}^0(t) - \mathbf{r}^0(t-1)|| > \epsilon$:

$$r_\alpha^0(t) \leftarrow R_\alpha^0 + \tau \sum_i n_i(t) q_{i\alpha}^A(\mathbf{r}(t))$$

$$\mathbf{r}(t+1) \leftarrow \underset{\mathbf{R}}{\text{argmin}}\, d(\mathbf{r}^0(t), \mathbf{R}) \text{ subject to } g_i(\mathbf{R}) \leq 0 \text{ for all } i$$

$$n_i(t+1) \leftarrow \frac{\lambda_i}{a_i} \text{ where } \lambda_i \text{ is the KKT multiplier corresponding to the constraint } g_i(\mathbf{R}) \leq 0$$

$$t \leftarrow t+1 \tag{B26}$$

where ϵ is a small number that controls the precision of the numerical solution.

We can evaluate the stability of the fixed point $r_\alpha^0 = \tilde{R}_\alpha^0$, by initializing the system at $r_\alpha^0(0) = \tilde{R}_\alpha^0 + \epsilon_\alpha$ for some small perturbation ϵ_α. After the first iteration, the effective supply point has updated to

$$r_\alpha^0(1) = \tilde{R}_\alpha^0 + \sum_\beta \left(\sum_\gamma \frac{\partial r_\alpha^0(t)}{\partial r_\gamma(t)} \frac{\partial r_\gamma(t)}{\partial r_\beta^0(t-1)} + \sum_j \frac{\partial r_\alpha^0(t)}{\partial n_j(t)} \frac{\partial n_j(t)}{\partial r_\beta^0(t-1)} \right) \epsilon_\beta \tag{B27}$$

where the derivatives

$$\frac{\partial r_\alpha^0(t)}{\partial r_\gamma(t)} = \tau \sum_i n_i(t) \frac{\partial q_{i\alpha}^A}{\partial R_\gamma} \tag{B28}$$

$$\frac{\partial r_\alpha^0(t)}{\partial n_j(t)} = \tau q_{j\alpha}^A \tag{B29}$$

come from differentiating the first step in the algorithm with respect to the components of the equilibrium estimate $\mathbf{n}, \mathbf{r}$, and the other two derivatives measure how the new estimate of the equilibrium point depends on the previous estimate of the supply point (via the minimization in step 2). The change in the estimate of the effective supply point over this first iteration is thus:

$$\delta r_\alpha^0 = r_\alpha^0(1) - r_\alpha^0(0) = \sum_\beta J_{\alpha\beta} \epsilon_\beta \tag{B30}$$

where the Jacobian is

$$J_{\alpha\beta} = \sum_\gamma \frac{\partial r_\alpha^0(t)}{\partial r_\gamma(t)} \frac{\partial r_\gamma(t)}{\partial r_\beta^0(t-1)} + \sum_j \frac{\partial r_\alpha^0(t)}{\partial n_j(t)} \frac{\partial n_j(t)}{\partial r_\beta^0(t-1)} - \delta_{\alpha\beta}. \tag{B31}$$

From eq. (B30), we see that the algorithm is stable near the fixed point if and only if the real parts of all the eigenvalues of $J_{\alpha\beta}$ are negative.
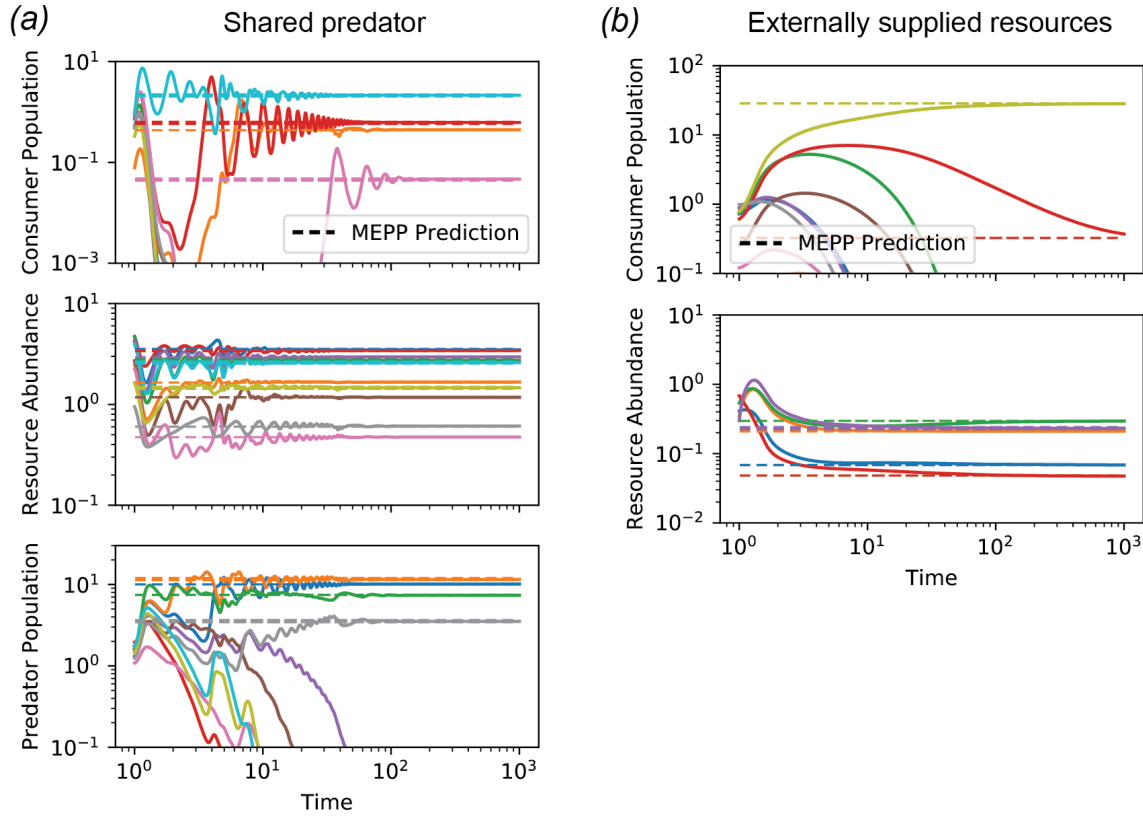
Figure C1: **Additional simulations with symmetric interactions.** Simulations of the second two models from fig. 2 with larger numbers of species and resources, compared with the predictions of MEPP for the uninvadable equilibrium state. Consumer abundances are obtained from the Lagrange multipliers that enforce the constraints during optimization. See Appendix D for all simulation parameters.

Appendix C: Analysis of specific models

In this Appendix, we show in detail how to obtain the objective function d and the auxiliary functions b_α and a_i for each of the seven models analyzed here. We do this by following the first two steps of the procedure outlined in the main text, which are copied here for reference:

1. Find b_α and a_i by comparing the impact vectors with the derivative of the growth rates using $q_{i\alpha}(\mathbf{R}) = -a_i(\mathbf{R}) b_\alpha(\mathbf{R}) \frac{\partial g_i}{\partial R_\alpha}$.

2. Compute d from b_α and the supply vector using $\frac{\partial d}{\partial R_\alpha} = -\frac{h_\alpha(\mathbf{R})}{b_\alpha(\mathbf{R})}$.

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We also provide explicit expressions for the effective pairwise interaction matrix α_{ij}, using eq. (B7) and (B9) from Appendix B above.

Noninteracting resources

We begin with the dynamical equations

$$\frac{dN_i}{dt} = e_i N_i \left[\sum_\alpha w_\alpha c_{i\alpha} R_\alpha - m_i \right] \tag{C1}$$

$$\frac{dR_\alpha}{dt} = \frac{r_\alpha}{K_\alpha} R_\alpha (K_\alpha - R_\alpha) - \sum_i N_i c_{i\alpha} R_\alpha. \tag{C2}$$

Comparing with the general niche theory scheme of eq. (6-7), we identify

$$g_i(\mathbf{R}) = e_i \left[\sum_\alpha w_\alpha c_{i\alpha} R_\alpha - m_i \right] \tag{C3}$$

$$q_{i\alpha}(\mathbf{R}) = -c_{i\alpha} R_\alpha \tag{C4}$$

$$h_\alpha(\mathbf{R}) = \frac{r_\alpha}{K_\alpha} R_\alpha (K_\alpha - R_\alpha), \tag{C5}$$

as also given in table **??**. The gradient of the growth rate is

$$\frac{\partial g_i}{\partial R_\alpha} = e_i w_\alpha c_{i\alpha}. \tag{C6}$$

Now we can follow Step 1 from the list above, comparing this to the impact vector to obtain

$$a_i = e_i^{-1} \tag{C7}$$

$$b_\alpha = \frac{R_\alpha}{w_\alpha}. \tag{C8}$$

Step 2 now yields the expression for d:

$$\frac{\partial d}{\partial R_\alpha} = -\frac{r_\alpha w_\alpha}{K_\alpha} (K_\alpha - R_\alpha). \tag{C9}$$

Integrating this expression, we find

$$d = \frac{1}{2} \sum_\alpha \frac{r_\alpha w_\alpha}{K_\alpha} (K_\alpha - R_\alpha)^2 \tag{C10}$$

which is equivalent to eq. (14) in the main text.

We are not quite finished, however, because the minimization of this expression for d subject to $g_i \leq 0$ can produce negative values of $\bar{R}_\alpha$. Physically, we know that the resource abundances cannot be negative numbers, and the original dynamical equation (C2) ensures that R_α never becomes negative as long as the initial conditions are positive. But this constraint is lost when we divide by $b_\alpha = R_\alpha/w_\alpha$ in the derivation of the KKT conditions. To address this issue, one must impose $R_\alpha \geq 0$ as an additional set of explicit constraints when performing the optimization. This problem occurs for most models with self-renewing resources, and can always be resolved by adding additional constraints in this way.

The effective pairwise interaction α_{ij} between species i and j in this model were shown by MacArthur (1970) to be equal to the overlap between consumption vectors $c_{i\alpha}$ and $c_{j\alpha}$. We can also see this from our general formulas, using eq. (B7) and (B9) to compute:

$$A^j_{\alpha\beta} = \frac{r_\alpha w_\alpha}{K_\alpha}\delta_{\alpha\beta} \tag{C11}$$

$$\alpha_{ij} = \sum_{\alpha\beta}(A^j)^{-1}_{\alpha\beta}\frac{\partial g_i}{\partial R_\alpha}\frac{\partial g_j}{\partial R_\beta} = \sum_\alpha \frac{w_\alpha K_\alpha}{r_\alpha}e_i e_j c_{i\alpha}c_{j\alpha}. \tag{C12}$$

Interacting self-regulation

We begin with the dynamical equations

$$\frac{dN_i}{dt} = e_i N_i\left[\sum_\alpha w_\alpha c_{i\alpha}R_\alpha - m_i\right] \tag{C13}$$

$$\frac{dR_\alpha}{dt} = r_\alpha R_\alpha\left(1 - \sum_\beta a_\beta R_\beta\right) - \sum_i N_i c_{i\alpha}R_\alpha. \tag{C14}$$

Comparing with the general niche theory scheme of eq. (6-7), we make the same identifications as for noninteracting resources, but with a modified supply vector:

$$g_i(\mathbf{R}) = e_i \left[\sum_\alpha w_\alpha c_{i\alpha} R_\alpha - m_i \right] \tag{C15}$$

$$q_{i\alpha}(\mathbf{R}) = -c_{i\alpha} R_\alpha \tag{C16}$$

$$h_\alpha(\mathbf{R}) = r_\alpha R_\alpha \left(1 - \sum_\beta a_\beta R_\beta \right). \tag{C17}$$

Since g_i and $q_{i\alpha}$ are unchanged, we have the same expressions for a_i and b_α:

$$a_i = e_i^{-1} \tag{C18}$$

$$b_\alpha = \frac{R_\alpha}{w_\alpha}. \tag{C19}$$

Step 2 now yields the expression for d:

$$\frac{\partial d}{\partial R_\alpha} = -r_\alpha w_\alpha \left(1 - \sum_\beta a_\beta R_\beta \right). \tag{C20}$$

For generic a_β and w_α, there is no function d that satisfies this expression, because the second derivatives of the function would be:

$$\frac{\partial^2 d}{\partial R_\beta \partial R_\alpha} = -r_\alpha w_\alpha a_\beta \neq \frac{\partial^2 d}{\partial R_\alpha \partial R_\beta}. \tag{C21}$$

This means that the model is generically not symmetric. But if we set $w_\alpha = w a_\alpha$ and $r_\alpha = r$ as described in the main text, we find that

$$d = \frac{wr}{2} \left(1 - \sum_\alpha a_\alpha R_\alpha \right)^2 \tag{C22}$$

satisfies the equation.

In this case the effective pairwise interactions α_{ij} are ill-defined, because many sets of resource concentrations can satisfy $dR_\alpha/dt = 0$ for the same set of species abundances. But we can still evaluate symmetry by adding a small self-limitation term $-\epsilon R_\alpha^2$ to h_α, and then taking the limit as $\epsilon \to 0$. Using the modified h_α, we obtain (see eq. B7):

$$A_{\alpha\beta}^j = w_\alpha (r_\alpha a_\beta + \epsilon \delta_{\alpha\beta}). \tag{C23}$$

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Then, using the Sherman-Morrison formula (Bartlett 1951), we find

$$(A^j)^{-1}_{\alpha\beta} = \epsilon^{-1} w_\beta^{-1} \left(\delta_{\alpha\beta} - \frac{r_\alpha a_\beta}{\sum_\gamma a_\gamma r_\gamma} \right). \tag{C24}$$

Inserting this into eq. (B9), we find:

$$\alpha_{ij} = \sum_{\alpha\beta} (A^j)^{-1}_{\alpha\beta} \frac{\partial g_i}{\partial R_\alpha} \frac{\partial g_j}{\partial R_\beta} = \epsilon^{-1} \sum_{\alpha\beta} \left(w_\alpha \delta_{\alpha\beta} - \frac{r_\alpha w_\alpha a_\beta}{\sum_\gamma a_\gamma r_\gamma} \right) e_i e_j c_{i\alpha} c_{j\beta}. \tag{C25}$$

We see that $\alpha_{ij}/\alpha_{ij} = 1$ for all ϵ, including $\epsilon \to 0$, when $r_\alpha = r$ for all α and $w_\alpha = wa_\alpha$. The

divergence of α_{ij} in this limit is reflected in the long transient of highly volatile dynamics in fig.

??.

Shared predators

We begin with the dynamical equations

$$\frac{dN_i}{dt} = e_i N_i \left[\sum_\alpha w_\alpha c_{i\alpha} R_\alpha - m_i \right] - \sum_a p_{ia} P_a N_i \tag{C26}$$

$$\frac{dR_\alpha}{dt} = \frac{r_\alpha}{K_\alpha} R_\alpha (K_\alpha - R_\alpha) - \sum_i N_i c_{i\alpha} R_\alpha \tag{C27}$$

$$\frac{dP_a}{dt} = \sum_i \eta_i p_{ia} N_i P_a - u_a P_a \tag{C28}$$

To situate this model within the general niche theory scheme of eq. (6-7), we must treat the preda-

tors as additional environmental factors, along with the resources. We denote the impact and

supply vectors for the resources by $q_{i\alpha}^R$ and h_α^R, and the corresponding vectors for the predators

by q_{ia}^P and h_a^p. We obtain:

$$g_i(\mathbf{R}, \mathbf{P}) = e_i \left[\sum_\alpha w_\alpha c_{i\alpha} R_\alpha - m_i \right] - \sum_a p_{ia} P_a \tag{C29}$$

$$q_{i\alpha}^R(\mathbf{R}) = -c_{i\alpha} R_\alpha \tag{C30}$$

$$q_{ia}^P(\mathbf{P}) = \eta_i p_{ia} P_a \tag{C31}$$

$$h_\alpha^R(\mathbf{R}) = \frac{r_\alpha}{K_\alpha} R_\alpha (K_\alpha - R_\alpha) \tag{C32}$$

$$h_a^P(\mathbf{P}) = -u_a P_a. \tag{C33}$$

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Following Step 1 from the general procedure with $q_{i\alpha}^R$ as the impact vector yields the same results for a_i and b_α as the previous two cases, while using q_{ia}^P yields:

$$a_i = \frac{\eta_i}{e_0} \tag{C34}$$

$$b_a^P = e_0 P_a \tag{C35}$$

for an arbitrary constant e_0. We have added a superscript to b_a^P, because there is a separate set of these functions for the predators and for the resources. The scaling factor a_i, however, is only indexed by the species label, and must be the same for both the predator and the resource impacts. This means that Step 1 of the general procedure outlined above can only be satisfied if

$$e_i = \frac{e_0}{\eta_i} \tag{C36}$$

which is the requirement for symmetric interactions stated in the main text.

Under this assumption, we can apply Step 2 to obtain expressions for the derivatives of d:

$$\frac{\partial d}{\partial R_\alpha} = -\frac{r_\alpha}{K_\alpha} w_\alpha (K_\alpha - R_\alpha) \tag{C37}$$

$$\frac{\partial d}{\partial P_a} = \frac{u_a}{e_0}. \tag{C38}$$

Integrating these expressions, we obtain:

$$d = \frac{1}{2} \sum_\alpha \frac{r_\alpha}{K_\alpha} w_\alpha (K_\alpha - R_\alpha)^2 + \frac{1}{e_0} \sum_a u_a P_a \tag{C39}$$

as reported in the main text.

This model also has an ill-defined interaction matrix, because a range of equilibrium predator abundances are compatible with any given set of prey abundances. Following the procedure outlined above, we add a small additional self-limitation term $-\epsilon P_a^2$ to the predator supply vector h_a^P. Using eq. (B7) and keeping track of the contributions of the predators and the resources, we find (for general η_i):

$$A_{\alpha\beta}^j = \frac{r_\alpha w_\alpha}{K_\alpha} \delta_{\alpha\beta} \tag{C40}$$

$$A_{ab}^j = \epsilon \frac{1}{\eta_j e_j} \delta_{ab}. \tag{C41}$$

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Note that we are finally using the j superscript on A_{ab}^{j}. The full matrix is thus completely diagonal, with these two diagonal blocks, and the inverse is readily obtained, yielding:

$$\alpha_{ij} = \sum_{\alpha\beta} (A^j)_{\alpha\beta}^{-1} \frac{\partial g_i}{\partial R_\alpha} \frac{\partial g_j}{\partial R_\beta} = \sum_{\alpha} \frac{w_\alpha K_\alpha}{r_\alpha} e_i e_j c_{i\alpha} c_{j\alpha} + \epsilon^{-1} \sum_a \eta_j e_j p_{ia} p_{ja}. \tag{C42}$$

To have $\alpha_{ij}/\alpha_{ji} = 1$ for any ϵ, including $\epsilon \to 0$, we need $\eta_j e_j = e_0$ for some constant e_0, as claimed above.

Externally supplied resources

We begin with the dynamical equations

$$\frac{dN_i}{dt} = e_i N_i \left[\sum_\alpha w_\alpha c_{i\alpha} R_\alpha - m_i \right] - \tau^{-1} N_i \tag{C43}$$

$$\frac{dR_\alpha}{dt} = \tau^{-1}(R_\alpha^0 - R_\alpha) - \sum_i N_i c_{i\alpha} R_\alpha. \tag{C44}$$

Comparing with the general niche theory scheme of eq. (6-7), we identify

$$g_i(\mathbf{R}) = e_i \left[\sum_\alpha w_\alpha c_{i\alpha} R_\alpha - m_i \right] - \tau^{-1} \tag{C45}$$

$$q_{i\alpha}(\mathbf{R}) = -c_{i\alpha} R_\alpha \tag{C46}$$

$$h_\alpha(\mathbf{R}) = \tau^{-1}(R_\alpha^0 - R_\alpha), \tag{C47}$$

which is the same as for the original consumer resource model (1-2), except for the supply vector. We thus obtain the same conversion factors:

$$a_i = e_i^{-1} \tag{C48}$$

$$b_\alpha = \frac{R_\alpha}{w_\alpha}. \tag{C49}$$

Step 2 now yields the expression for d:

$$\frac{\partial d}{\partial R_\alpha} = -\tau^{-1} w_\alpha \frac{R_\alpha^0 - R_\alpha}{R_\alpha} \tag{C50}$$

Integrating this expression, we find

$$d = \tau^{-1} \sum_\alpha w_\alpha \left[R_\alpha^0 \ln \frac{R_\alpha^0}{R_\alpha} - (R_\alpha^0 - R_\alpha) \right]. \tag{C51}$$

which is eq. (**??**) in the main text. Note that this expression diverges as $R_\alpha \to 0$, so there is no need to explicitly impose the resource feasibility constraints.

For this model, we can straightforwardly compute the interactions using eq. (B7) and (B9):

$$A^j_{\alpha\beta} = \frac{\tau^{-1} w_\alpha R^0_\alpha}{\bar{R}^2_\alpha} \delta_{\alpha\beta} \tag{C52}$$

$$\alpha_{ij} = \sum_{\alpha\beta} (A^j)^{-1}_{\alpha\beta} \frac{\partial g_i}{\partial R_\alpha} \frac{\partial g_j}{\partial R_\beta} = \tau \sum_\alpha \frac{w_\alpha \bar{R}^2_\alpha}{R^0_\alpha} e_i e_j c_{i\alpha} c_{j\alpha}. \tag{C53}$$

Note that in this case the strength of the interaction depends directly on the equilibrium resource abundances $\bar{R}_\alpha$.

Microbial consumer resource model

We begin with the dynamical equations

$$\frac{dN_i}{dt} = e_i N_i \left[\sum_\alpha (1 - l_\alpha) w_\alpha c_{i\alpha} R_\alpha - m_i \right] \tag{C54}$$

$$\frac{dR_\alpha}{dt} = \tau^{-1} (R^0_\alpha - R_\alpha) - \sum_i N_i c_{i\alpha} R_\alpha + \sum_{i\beta} N_i D_{\alpha\beta} l_\beta \frac{w_\beta}{w_\alpha} c_{i\beta} R_\beta. \tag{C55}$$

Comparing with the general niche theory scheme of eq. (6-7), we identify

$$g_i(\mathbf{R}) = e_i \left[\sum_\alpha (1 - l_\alpha) w_\alpha c_{i\alpha} R_\alpha - m_i \right] \tag{C56}$$

$$q_{i\alpha}(\mathbf{R}) = -c_{i\alpha} R_\alpha + \sum_\beta D_{\alpha\beta} l_\beta \frac{w_\beta}{w_\alpha} c_{i\beta} R_\beta \tag{C57}$$

$$h_\alpha(\mathbf{R}) = \tau^{-1} (R^0_\alpha - R_\alpha). \tag{C58}$$

As noted in the main text, the generation of byproducts breaks the symmetry of interactions between consumers, and so we must use the extended form of MEPP discussed above at the end of Appendix B. In this case, the symmetric reference model has an impact vector $q^S_{i\alpha}$ identical to that of an ordinary consumer-resource model, and $q^A_{i\alpha}$ encodes byproduct generation:

$$q^S_{i\alpha} = -c_{i\alpha} R_\alpha \tag{C59}$$

$$q^A_{i\alpha} = \sum_\beta D_{\alpha\beta} l_\beta \frac{w_\beta}{w_\alpha} c_{i\beta} R_\beta. \tag{C60}$$

We thus see that this model shares an equilibrium state with a pure competition model of the form (C43-C44), but with a modified supply vector

$$\tilde{h}_\alpha = \tau^{-1}(R_\alpha^0 - R_\alpha) + \sum_{i\beta} \bar{N}_i D_{\alpha\beta} l_\beta \frac{w_\beta}{w_\alpha} c_{i\beta} \bar{R}_\beta \tag{C61}$$

and modified resource weights

$$\tilde{w}_\alpha = w_\alpha(1 - l_\alpha). \tag{C62}$$

The change to the supply vector is equivalent to a shift of the supply point from R_α^0 to

$$\tilde{R}_\alpha^0 = R_\alpha^0 + \tau \sum_{i\beta} \bar{N}_i D_{\alpha\beta} l_\beta \frac{w_\beta}{w_\alpha} c_{i\beta} \bar{R}_\beta, \tag{C63}$$

which accounts for the total quantity of byproducts generated by all consumers over one chemostat turnover time τ.

We can therefore use the same objective function obtained for the pure competition model in eq. (24), but with these modified formulas for the weights w_α and the supply point $\tilde{R}_\alpha^0$.

To compute the interactions in the original model, we need to write the full impact vector $q_{i\alpha}$ in the form of eq. (B3). We find:

$$a_i = e_i^{-1} \tag{C64}$$

$$b_{\alpha\beta}^i = \left(\delta_{\alpha\beta} - D_{\alpha\beta} l_\beta \frac{w_\beta}{w_\alpha}\right) \tilde{w}_\beta^{-1} R_\beta = \tilde{b}_{\alpha\beta} \tilde{w}_\beta^{-1} R_\beta \tag{C65}$$

where

$$\tilde{b}_{\alpha\beta} = \delta_{\alpha\beta} - D_{\alpha\beta} l_\beta \frac{w_\beta}{w_\alpha}. \tag{C66}$$

Using eq. (B7), we thus obtain:

$$A_{\alpha\beta}^j = \frac{\tau^{-1}\tilde{w}_\alpha}{\bar{R}_\alpha} \left(\tilde{b}_{\alpha\beta}^{-1} - \frac{\delta_{\alpha\beta}}{\bar{R}_\alpha} \sum_\gamma \tilde{b}_{\alpha\gamma}^{-1}(R_\gamma^0 - \bar{R}_\gamma)\right) = \frac{\tau^{-1}\tilde{w}_\alpha}{\bar{R}_\alpha} W_{\alpha\beta} \tag{C67}$$

where

$$W_{\alpha\beta} = \tilde{b}_{\alpha\beta}^{-1} - \frac{\delta_{\alpha\beta}}{\bar{R}_\alpha} \sum_\gamma \tilde{b}_{\alpha\gamma}^{-1}(R_\gamma^0 - \bar{R}_\gamma). \tag{C68}$$

Plugging in to eq. (B9), we have:

$$\alpha_{ij} = \sum_{\alpha\beta} (A^j)^{-1}_{\alpha\beta} \frac{\partial g_i}{\partial R_\alpha} \frac{\partial g_j}{\partial R_\beta} = \tau \sum_{\alpha\beta} \tilde{w}_\alpha \bar{R}_\alpha W^{-1}_{\alpha\beta} e_i e_j c_{i\alpha} c_{j\beta}. \tag{C69}$$

Note that the factor of $\bar{R}_\alpha$ in the final expression generically breaks the symmetry even in special cases where $W_{\alpha\beta}$ is symmetric. Note also that $W_{\alpha\beta}$ is fully determined by the intrinsic properties of the resources, encoding the information about the structure of the universal metabolic byproduct network.

Alternative crossfeeding model

A different model of microbial resource exchange that has recently been proposed and analyzed is (Butler and O'Dwyer 2018, 2020):

$$\frac{dN_i}{dt} = N_i \left[\sum_\alpha (c_{i\alpha} R_\alpha - P_{i\alpha}) - m_i \right] \tag{C70}$$

$$\frac{dR_\alpha}{dt} = \tau^{-1}(R^0_\alpha - R_\alpha) - \sum_i N_i c_{i\alpha} R_\alpha + \sum_i N_i P_{i\alpha}. \tag{C71}$$

Comparing with the general niche theory scheme of eq. (6-7), we identify

$$g_i(\mathbf{R}) = \sum_\alpha (c_{i\alpha} R_\alpha - P_{i\alpha}) - m_i \tag{C72}$$

$$q_{i\alpha}(\mathbf{R}) = -c_{i\alpha} R_\alpha + P_{i\alpha} \tag{C73}$$

$$h_\alpha(\mathbf{R}) = \tau^{-1}(R^0_\alpha - R_\alpha). \tag{C74}$$

In general, there is no way of casting $q_{i\alpha}$ into the form required by eq. (8), even when the matrix $P_{i\alpha}$ is square and symmetric. This means that the effective pairwise interactions are not symmetric, as will be confirmed explicitly below. But we can still use the extended form of MEPP discussed above. We obtain results similar to the MiCRM, but with a simpler asymmetric component $q^A_{i\alpha}$:

$$q^S_{i\alpha} = -c_{i\alpha} R_\alpha \tag{C75}$$

$$q^A_{i\alpha} = P_{i\alpha}. \tag{C76}$$

We thus see that this model shares an equilibrium state with a pure competition model of the form (C43-C44), but with a modified supply vector

$$\tilde{h}_\alpha = \tau^{-1}(R_\alpha^0 - R_\alpha) + \sum_i \bar{N}_i P_{i\alpha}. \tag{C77}$$

The change to the supply vector is equivalent to a shift of the supply point from R_α^0 to

$$\tilde{R}_\alpha^0 = R_\alpha^0 + \tau \sum_i \bar{N}_i P_{i\alpha}, \tag{C78}$$

which accounts for the total quantity of byproducts generated by all consumers over one chemostat turnover time τ.

This model is known to exhibit both stable and unstable fixed points, depending on the parameters, and explicit stability criteria were previously derived for the case where $c_{i\alpha} = c\delta_{i\alpha}$ and the mortality rates m_i and supply rates $\tau^{-1}R_\alpha^0$ are tuned such that the equilibrium population sizes $\bar{N}_i = N$ and resource abundances $\bar{R}_\alpha = R$ take on equal pre-specified values (Butler and O'Dwyer 2018). The limit is also taken where $\tau^{-1} \to 0$ at fixed $\tau^{-1}R_\alpha^0$, so that all resource depletion comes from consumption. Under these conditions, one can readily use eq. (B31) to evaluate the stability of the EM algorithm introduced at the end of Appendix B. We find that the elements of this Jacobian are given by:

$$J_{ij} = \frac{P_{ij}}{cR} - \delta_{ij} \tag{C79}$$

where the resources α have been re-indexed in terms of the species i that specializes in each one. For symmetric P_{ij}, Butler and O'Dwyer (2018) showed that the fixed point is stable under the original dynamics if and only if all the eigenvalues of P_{ij} are less than cr. This is equivalent to the stability condition for the EM algorithm, that the eigenvalues of J_{ij} must all be negative.

Liebig's Law

We begin with the dynamical equations

$$\frac{dN_i}{dt} = N_i \left[\min_\beta \left(\left\{ \frac{\mu_{i\beta} R_\beta}{k_{i\beta} + R_\beta} \right\} \right) - m_i \right] \tag{C80}$$

$$\frac{dR_\alpha}{dt} = \tau^{-1}(R_\alpha^0 - R_\alpha) - \sum_i N_i v_{\alpha i} \min_\beta \left(\left\{ \frac{\mu_{i\beta} R_\beta}{k_{i\beta} + R_\beta} \right\} \right). \tag{C81}$$

Comparing with the general niche theory scheme of eq. (6-7), we identify

$$g_i(\mathbf{R}) = \min_\beta \left(\left\{ \frac{\mu_{i\beta} R_\beta}{k_{i\beta} + R_\beta} \right\} \right) \tag{C82}$$

$$q_{i\alpha}(\mathbf{R}) = -v_{\alpha i} \min_\beta \left(\left\{ \frac{\mu_{i\beta} R_\beta}{k_{i\beta} + R_\beta} \right\} \right) \tag{C83}$$

$$h_\alpha(\mathbf{R}) = \tau^{-1}(R_\alpha^0 - R_\alpha). \tag{C84}$$

Note that we have slightly changed the definition of g_i, so that now $dN_i/dt = N_i(g_i - m_i)$. This significantly simplifies the expressions in the derivation of the effective interaction matrix below. Since m_i is a constant, this has no effect on the key MEPP equation involving $\partial g_i/\partial R_\alpha$.

As noted in the main text, the consumption of resources that are not currently limiting growth breaks the symmetry of the interactions between consumers, and so we must use the extended form of MEPP discussed above at the end of Appendix B. In this case, the symmetric reference model has an impact vector $q_{i\alpha}^S$ that only depletes the limiting nutrient, and $q_{i\alpha}^A$ encodes the consumption of non-limiting nutrients. To write explicit expressions for these quantities, it is convenient to denote the index of the limiting resource by β_i, so that $\min_\beta \left(\left\{ \frac{\mu_{i\beta} R_\beta}{k_{i\beta} + R_\beta} \right\} \right) = \frac{\mu_{i\beta_i} R_{\beta_i}}{k_{i\beta_i} + R_{\beta_i}}$. Then we have

$$q_{i\alpha}^S = -v_{\beta_i i} \delta_{\alpha\beta_i} \frac{\mu_{i\beta_i} R_{\beta_i}}{k_{i\beta_i} + R_{\beta_i}} \tag{C85}$$

$$q_{i\alpha}^A = -v_{\alpha i}(1 - \delta_{\alpha\beta_i}) \frac{\mu_{i\beta_i} R_{\beta_i}}{k_{i\beta_i} + R_{\beta_i}}. \tag{C86}$$

We obtain a_i and b_α by comparing $q_{i\alpha}^S$ with the gradient of the growth rate

$$\frac{\partial g_i}{\partial R_\alpha} = \delta_{\alpha\beta_i} \frac{\mu_{i\beta_i} k_{i\beta_i}}{(k_{i\beta_i} + R_{\beta_i})^2} \tag{C87}$$

to find

$$a_i = k_{i\beta_i} + R_{\beta_i} \tag{C88}$$

$$b_{\beta_i} = \frac{\nu_{\beta_i i}}{k_{i\beta_i}} R_{\beta_i}. \tag{C89}$$

The competitive exclusion principle guarantees that there is at most one consumer species i limited by each resource α, which allows us to unambiguously index the functions b_α in this way. Aside from the strange indexing, this is the same b_α as in all the other resource competition models discussed so far, with effective resource weights

$$w_{\beta_i} = \frac{k_{i\beta_i}}{\nu_{\beta_i i}}. \tag{C90}$$

We thus obtain an expression for d that is identical to the case of substitutable resources, but with a modified supply point:

$$\frac{\partial d}{\partial R_\alpha} = \frac{\tilde{h}_\alpha}{b_\alpha} = -\frac{\tau^{-1} w_\alpha (\tilde{R}^0_\alpha - R_\alpha)}{R_\alpha} \tag{C91}$$

where the effective supply point is

$$\tilde{R}^0_\alpha = R^0_\alpha - \tau \sum_{i, \alpha \neq \beta_i} \bar{N}_i \nu_{\alpha i} \frac{\mu_{i\beta_i} R_{\beta_i}}{k_{i\beta_i} + R_{\beta_i}} \tag{C92}$$

with the second term accounting for the total consumption of resource α over a chemostat turnover time by organisms that are limited by some other resource ($\beta_i \neq \alpha$).

Note that the weights w_α in eq. (C90) are only defined for resources that are limiting for some species. Resources that are not limiting for any species are not subject to any constraints in the optimization, and always reach the effective supply point regardless of the values of the weights. The weights can therefore be set arbitrarily for these resources, for example by taking them all to equal 1.

To compute the interactions in the original model, we again need to write the full impact vector $q_{i\alpha}$ in the form of eq. (B3), with $q_{i\alpha} = a_i \sum_\beta b^i_{\alpha\beta} \partial g_i / \partial R_\beta$. Doing this directly involves division by zero. To proceed, we note that

$$\min_\beta \left(\left\{ \frac{\mu_{i\beta} R_\beta}{k_{i\beta} + R_\beta} \right\} \right) = \lim_{n \to \infty} \left[\sum_\beta \left(\frac{\mu_{i\beta} R_\beta}{k_{i\beta} + R_\beta} \right)^{-n} \right]^{-1/n}. \tag{C93}$$

We can therefore perform the computations for finite n, and then take the limit. First, we define:

$$\delta^n_{\alpha\gamma_i} \equiv \left(\frac{\mu_{i\alpha}R_\alpha}{k_{i\alpha}+R_\alpha}\right)^n \sum_\gamma \left(\frac{\mu_{i\gamma}R_\gamma}{k_{i\gamma}+R_\gamma}\right)^{-n} \tag{C94}$$

which converges to $\delta_{\alpha\gamma_i}$ in the limit $n \to \infty$, where γ_i is the index of the most limiting resource for species i. We thus find:

$$a_i = 1 \tag{C95}$$

$$b^i_{\alpha\beta} = \delta_{\alpha\beta}\frac{\nu_{\alpha i}R_\alpha(k_{i\alpha}+R_\alpha)}{k_{i\alpha}\delta^n_{\alpha\gamma_i}} \tag{C96}$$

$$\frac{\partial g_i}{\partial R_\alpha} = \delta^n_{\alpha\gamma_i}g_i\frac{k_{i\alpha}}{R_\alpha(k_{i\alpha}+R_\alpha)} \tag{C97}$$

$$\frac{\partial^2 g_i}{\partial R_\alpha \partial R_\beta} = \frac{\delta^n_{\alpha\gamma_i}g_i k_{i\alpha}}{R_\alpha(k_{i\alpha}+R_\alpha)}\left(\frac{\delta^n_{\beta\gamma_i}k_{i\beta}}{R_\beta(k_{i\beta}+R_\beta)}-\delta_{\alpha\beta}\frac{k_{i\alpha}+2R_\alpha}{R_\alpha(k_{i\alpha}+R_\alpha)}\right). \tag{C98}$$

Note that this is the first time we have need of the second term involving the second derivatives of g_i in eq. (B7), since g_i is no longer linear in the resource abundances. We thus obtain:

$$A^j_{\alpha\beta} = \delta^n_{\alpha\gamma_j}\delta_{\alpha\beta}\frac{\tau^{-1}k_{j\alpha}}{\nu_{\alpha j}}\frac{R^0_\alpha(k_{j\alpha}+2R_\alpha)-R^2_\alpha}{R^2_\alpha(k_{j\alpha}+R_\alpha)} + \sum_i N_i \frac{k_{j\alpha}\delta^n_{\alpha\gamma_j}\nu_{i\alpha}g_i}{\nu_{\alpha j}R_\alpha(k_{j\alpha}+R_\alpha)}\left(\frac{\delta^n_{\beta\gamma_i}k_{i\beta}}{R_\beta(k_{i\beta}+R_\beta)}-\delta_{\alpha\beta}\frac{k_{i\alpha}+2R_\alpha}{R_\alpha(k_{i\alpha}+R_\alpha)}\right). \tag{C99}$$

Again, without loss of generality, we can reindex the species by their limiting resource at equilibrium, so that $N_\alpha = N_i$ when $\gamma_i = \alpha$. If no species is limited by a given resource β, we introduce a fictitious species with $N_\beta = 0$. We find:

$$A^\gamma_{\alpha\beta} = \frac{k_{\gamma\alpha}\delta^n_{\alpha\gamma}}{\nu_{\alpha\gamma}R_\alpha(k_{\gamma\alpha}+R_\alpha)}W^\gamma_{\alpha\beta} \tag{C100}$$

where

$$W^\gamma_{\alpha\beta} = \delta_{\alpha\beta}\frac{1}{R_\alpha}\left(\tau^{-1}[R^0_\alpha(k_{\gamma\alpha}+2R_\alpha)-R^2_\alpha]-\sum_\lambda N_\lambda\nu_{\lambda\alpha}g_\lambda(k_{\lambda\alpha}+2R_\alpha)\right)$$
$$+\sum_\lambda \delta^n_{\beta\lambda}N_\lambda\frac{\nu_{\lambda\alpha}g_\lambda k_{\lambda\beta}}{R_\beta(k_{\lambda\beta}+R_\beta)}. \tag{C101}$$

Plugging in to eq. (B9), we have:

$$\alpha_{\lambda\gamma} = \sum_{\alpha\beta}(A^\gamma)^{-1}_{\alpha\beta}\frac{\partial g_\lambda}{\partial R_\alpha}\frac{\partial g_\gamma}{\partial R_\beta}$$
$$= \sum_{\alpha\beta}(W^\gamma)^{-1}_{\alpha\beta}\delta^n_{\alpha\lambda}\frac{k_{\lambda\alpha}g_\lambda g_\gamma}{R_\alpha(k_{\lambda\alpha}+R_\alpha)}. \tag{C102}$$

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Finally, taking the limit $n \to \infty$, and replacing N_α, R_α with the equilibrium values $\bar{N}_\alpha, \bar{R}_\alpha$, we conclude:

$$\alpha_{ij} = \sum_\beta (W^j)^{-1}_{\alpha_i \beta} \frac{\nu_{\beta j} k_{i\alpha_i} g_i g_j}{\bar{R}_{\alpha_i}(k_{i\alpha_i} + \bar{R}_{\alpha_i})} \tag{C103}$$

where again α_i is the resource limiting the growth of species i, respectively, with

$$W^j_{\alpha\beta} = \delta_{\alpha\beta} \frac{1}{\bar{R}_\alpha} \left(\tau^{-1}[R^0_\alpha(k_{j\alpha} + 2\bar{R}_\alpha) - \bar{R}^2_\alpha] - \sum_\gamma \bar{N}_\gamma \nu_{\gamma\alpha} g_\gamma (k_{\gamma\alpha} + 2\bar{R}_\alpha) \right) + \bar{N}_\beta \frac{\nu_{\beta\alpha} g_\beta k_{\beta\beta}}{\bar{R}_\beta(k_{\beta\beta} + \bar{R}_\beta)}. \tag{C104}$$

Interactively essential resources

Another model not discussed in the main text due to space constraints, but of interest to some readers, is the following scenario of interactively essential resources, with growth rate governed by the product of all the incoming nutrient fluxes, each following Michaelis-Menten kinetics:

$$\frac{dN_i}{dt} = e_i N_i \left[\prod_\alpha \frac{\mu_{i\alpha} R_\alpha}{k_{i\alpha} + R_\alpha} - m_i \right] \tag{C105}$$

$$\frac{dR_\alpha}{dt} = \tau^{-1}(R^0_\alpha - R_\alpha) - \sum_i N_i \frac{\mu_{i\alpha} R_\alpha}{k_{i\alpha} + R_\alpha}. \tag{C106}$$

Comparing with the general niche theory scheme of eq. (6-7), we identify

$$g_i(\mathbf{R}) = e_i \prod_\alpha \frac{\mu_{i\alpha} R_\alpha}{k_{i\alpha} + R_\alpha} \tag{C107}$$

$$q_{i\alpha}(\mathbf{R}) = -\frac{\mu_{i\alpha} R_\alpha}{k_{i\alpha} + R_\alpha} \tag{C108}$$

$$h_\alpha(\mathbf{R}) = \tau^{-1}(R^0_\alpha - R_\alpha). \tag{C109}$$

As in the previous section, we have altered the definition of g_i, so that now $dN_i/dt = N_i(g_i - m_i)$, which again significantly simplifies the notation in the derivations. The gradient of the growth rate is

$$\frac{\partial g_i}{\partial R_\alpha} = \frac{k_{i\alpha} g_i}{R_\alpha(k_{i\alpha} + R_\alpha)}. \tag{C110}$$

In general, there are no functions a_i and b_α that relate this gradient to the impact vector in the way required by Step 1 of the MEPP procedure. But if the low-density specific consumption rate

$\mu_{i\alpha}/k_{i\alpha}$ is the same for all species i, so that we can define $w_\alpha = k_{i\alpha}/\mu_{i\alpha}$ with the left-hand side independent of i, we obtain:

$$b_\alpha = \frac{R_\alpha^2}{w_\alpha} \tag{C111}$$

$$a_i = \frac{1}{g_i}. \tag{C112}$$

The resulting expression for d is:

$$\frac{\partial d}{\partial R_\alpha} = -\frac{\tau^{-1} w_\alpha (R_\alpha^0 - R_\alpha)}{R_\alpha^2}. \tag{C113}$$

Integrating this, we obtain a weighted KL divergence between the inverse resource concentrations and the inverse supply point:

$$d(\mathbf{R}^0, \mathbf{R}) = \tau^{-1} \sum_\alpha R_\alpha^0 w_\alpha \left[\frac{1}{R_\alpha^0} \ln \frac{1/R_\alpha^0}{1/R_\alpha} - \left(\frac{1}{R_\alpha^0} - \frac{1}{R_\alpha} \right) \right]. \tag{C114}$$

To compute the effective pairwise interactions, we use eq. (B7) to obtain:

$$A_{\alpha\beta}^j = \frac{\tau^{-1} k_{j\alpha}}{R_\alpha \mu_{j\alpha}} W_{\alpha\beta} \tag{C115}$$

with

$$W_{\alpha\beta} = \delta_{\alpha\beta} \frac{2R_\alpha^0 - \bar{R}_\alpha}{\bar{R}_\alpha^2} + \tau \sum_i \frac{\bar{N}_i \mu_{i\alpha} [k_{i\beta}(1 - \delta_{\alpha\beta}) + 2\bar{R}_\beta \delta_{\alpha\beta}]}{\bar{R}_\beta (k_{i\alpha} + \bar{R}_\alpha)(k_{i\beta} + \bar{R}_\beta)}. \tag{C116}$$

We thus find

$$\alpha_{ij} = \sum_{\alpha\beta} (A^j)_{\alpha\beta}^{-1} \frac{\partial g_i}{\partial R_\alpha} \frac{\partial g_j}{\partial R_\beta} = \tau \sum_{\alpha\beta} W_{\alpha\beta}^{-1} \frac{k_{i\alpha} \mu_{j\beta}}{\bar{R}_\alpha (k_{i\alpha} + \bar{R}_\alpha)(k_{i\beta} + \bar{R}_\beta)} g_i g_j. \tag{C117}$$

We see that this matrix is symmetric only if $k_{i\alpha} = w_\alpha \mu_{i\alpha}$ for some w_α independent of i, as claimed above.

Type II functional response

We begin with the dynamical equations

$$\frac{dN_i}{dt} = e_i N_i \left[\sum_\alpha \frac{c_{i\alpha} R_\alpha}{1 + \sum_\beta \frac{c_{i\beta} R_\beta}{J_{i\beta}}} - m_i \right] - \tau^{-1} N_i \tag{C118}$$

$$\frac{dR_\alpha}{dt} = \tau^{-1}(R_\alpha^0 - R_\alpha) - \sum_i N_i \frac{c_{i\alpha} R_\alpha}{1 + \sum_\beta \frac{c_{i\beta} R_\beta}{J_{i\beta}}}. \tag{C119}$$

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Comparing with the general niche theory scheme of eq. (6-7), we identify

$$g_i(\mathbf{R}) = e_i \left[\sum_\alpha \frac{c_{i\alpha} R_\alpha}{1 + \sum_\beta \frac{c_{i\beta} R_\beta}{J_{i\beta}}} - m_i \right] - \tau^{-1} \tag{C120}$$

$$q_{i\alpha}(\mathbf{R}) = -\frac{c_{i\alpha} R_\alpha}{1 + \sum_\beta \frac{c_{i\beta} R_\beta}{J_{i\beta}}} \tag{C121}$$

$$h_\alpha(\mathbf{R}) = \tau^{-1}(R_\alpha^0 - R_\alpha). \tag{C122}$$

The gradient of the growth rate is

$$\frac{\partial g_i}{\partial R_\alpha} = e_i \frac{\left(1 + \sum_\beta \frac{c_{i\beta} R_\beta}{J_{i\beta}}\right) c_{i\alpha} - \sum_\beta c_{i\beta} R_\beta \frac{c_{i\alpha}}{J_{i\alpha}}}{\left(1 + \sum_\beta \frac{c_{i\beta} R_\beta}{J_{i\beta}}\right)^2}. \tag{C123}$$

In general, there are no functions a_i and b_α that relate this gradient to the impact vector in the way required by Step 1 of the MEPP procedure. But if the maximum uptake rates $J_{i\alpha}$ of a given consumer i are the same for all resource types α, the gradient simplifies to

$$\frac{\partial g_i}{\partial R_\alpha} = e_i \frac{c_{i\alpha}}{\left(1 + \sum_\beta \frac{c_{i\beta} R_\beta}{J_{i\beta}}\right)^2}. \tag{C124}$$

Now this can be related to $q_{i\alpha}$ in the required way, yielding

$$a_i = \frac{1 + \sum_\beta \frac{c_{i\beta} R_\beta}{J_{i\beta}}}{e_i} \tag{C125}$$

$$b_\alpha = R_\alpha. \tag{C126}$$

Since h_α and b_α are the same as for the original model with externally supplied resources and linear functional response (with $w_\alpha = 1$, because we did not need the weight parameters to fit the data of interest), the objective function is also the same. The only consequences of introducing the saturating growth law are to modify the constraint region $g_i \leq 0$ and to change the conversion factor a_i required for extracting the species abundances from the Lagrange multipliers.

To compute the pairwise interactions for the general model, we note that if the $J_{i\alpha}$ are not the same for all α, then casting the impact vector into the form of eq. (B3) requires $b_{\alpha\beta}^i$ to be

dependent on the species index i:

$$b^i_{\alpha\beta} = \delta_{\alpha\beta} \frac{R_\alpha}{1 + \sum_\beta c_{i\beta} R_\beta \left(\frac{1}{J_{i\beta}} - \frac{1}{J_{i\alpha}} \right)}. \tag{C127}$$

For this model, we also need the second derivatives of the growth rate:

$$\frac{\partial^2 g_i}{\partial R_\alpha \partial R_\beta} = e_i c_{i\alpha} \frac{2 \sum_\gamma \frac{c_{i\gamma} c_{i\beta} R_\gamma}{J_{i\alpha} J_{i\beta}} - \left(1 + \sum_\gamma \frac{c_{i\gamma} R_\gamma}{J_{i\gamma}} \right) c_{i\beta} \left(\frac{1}{J_{i\beta}} + \frac{1}{J_{i\alpha}} \right)}{\left(1 + \sum_\gamma \frac{c_{i\gamma} R_\gamma}{J_{i\gamma}} \right)^3}. \tag{C128}$$

Putting it all together using eq. (B7) and (B9), we obtain

$$A^j_{\alpha\beta} = \frac{\tau^{-1}}{\bar{R}_\alpha} \left[R^0_\alpha \frac{1 + \sum_\gamma c_{j\gamma} \bar{R}_\gamma \left(\frac{1}{J_{i\gamma}} - \frac{1}{J_{i\alpha}} \right)}{\bar{R}_\alpha} \delta_{\alpha\beta} - (R^0_\alpha - \bar{R}_\alpha) c_{j\beta} \left(\frac{1}{J_{i\beta}} - \frac{1}{J_{i\alpha}} \right) \right]$$

$$+ \sum_i \bar{N}_i c_{i\alpha} \frac{1 + \sum_\beta c_{j\beta} \bar{R}_\beta \left(\frac{1}{J_{j\beta}} - \frac{1}{J_{j\alpha}} \right)}{1 + \sum_\beta c_{i\beta} \bar{R}_\beta \left(\frac{1}{J_{i\beta}} - \frac{1}{J_{i\alpha}} \right)} \frac{2 \sum_\gamma \frac{c_{i\gamma} c_{i\beta} \bar{R}_\gamma}{J_{i\alpha} J_{i\beta}} - \left(1 + \sum_\gamma \frac{c_{i\gamma} R_\gamma}{J_{i\gamma}} \right) c_{i\beta} \left(\frac{1}{J_{i\beta}} + \frac{1}{J_{i\alpha}} \right)}{\left(1 + \sum_\gamma \frac{c_{i\gamma} \bar{R}_\gamma}{J_{i\gamma}} \right)^2} \tag{C129}$$

$$\alpha_{ij} = \sum_{\alpha\beta} (A^j)^{-1}_{\alpha\beta} \frac{\partial g_i}{\partial R_\alpha} \frac{\partial g_j}{\partial R_\beta} = \sum_\alpha (A^j)^{-1}_{\alpha\beta} \frac{e_i e_j c_{i\alpha} c_{j\beta}}{\left(1 + \sum_\gamma \frac{c_{i\gamma} \bar{R}_\gamma}{J_{i\gamma}} \right)^2 \left(1 + \sum_\gamma \frac{c_{j\gamma} \bar{R}_\gamma}{J_{j\gamma}} \right)^2}. \tag{C130}$$

Note that when $J_{i\alpha} = J_i$ is independent of α, the first expression simplifies to

$$A^j_{\alpha\beta} = \frac{\tau^{-1} R^0_\alpha}{\bar{R}^2_\alpha} \delta_{\alpha\beta} - 2 \sum_i \frac{\bar{N}_i c_{i\alpha} c_{i\beta}}{J_i \left(1 + \sum_\gamma \frac{c_{i\gamma} \bar{R}_\gamma}{J_i} \right)^2} \tag{C131}$$

which is symmetric and independent of j, thus giving rise to symmetric interactions via eq. (B9).

Appendix D: Simulation details

All simulations and data analysis were performed in Python using the Scipy scientific computing package (Jones et al. 2001–). Data and scripts (in Jupyter notebooks) to generate the figures can be downloaded from https://github.com/Emergent-Behaviors-in-Biology/mepp.

The equations parameter values for all simulations are as follows. Note that for the simulations with more than two resources, parameter values were randomly sampled. The symbol $\mathcal{U}(a, b)$ will represent a uniform probability distribution over the interval $[a, b]$, and $\mathcal{D}(\alpha)$ a Dirichlet distribution with concentration parameters all equal to α.

- **Figure 2**

  - (a) eq. (1-2), $c_{1\alpha} = (0.5, 0.3)$, $c_{2\alpha} = (0.4, 0.6)$, $K_\alpha = (4.8, 2.85)$, $r_1 = r_2 = m_1 = m_2 = e_1 = e_2 = w_1 = w_2 = 1$

  - (b) eq. (15-16), $c_{1\alpha} = (0.5, 0.3)$, $c_{2\alpha} = (0.4, 0.6)$, $m_i = (0.2, 0.22)$, $w_i = (0.2, 0.15)$, $e_1 = e_2 = 1$

  - (c) eq. (18-20), $c_{11} = 0.5$, $c_{21} = 0.4$, $p_{11} = 0.3$, $p_{21} = 0.6$, $K_1 = 4$, $m_i = (1, 0.5)$, $u_1 = 0.5$, $r_1 = w_1 = e_1 = e_2 = 1$

  - (d) eq. (22-23), $c_{1\alpha} = (0.5, 0.3)$, $c_{2\alpha} = (0.4, 0.6)$, $R_\alpha^0 = (4.8, 2.5)$, $m_1 = m_2 = 0$, $e_1 = e_2 = w_1 = w_2 = \tau = 1$

  - (e) eq. (1-2), $S = 10$, $M = 10$, $c_{i\alpha} \sim \mathcal{U}(0,1)$, $K_\alpha \sim \mathcal{U}(5,6)$, $r_\alpha \sim \mathcal{U}(1,2)$, $m_i \sim \mathcal{U}(1,2)$, $w_\alpha \sim \mathcal{U}(1,2)$, $e_i = 1$

  - (f) eq. (15-16), $S = 10$, $M = 15$, $c_{i\alpha} \sim \mathcal{U}(0,1)$, $m_i \sim \mathcal{U}(0.033, 0.066)$, $w_\alpha \sim \mathcal{U}(0.05, 0.1)$, $e_i = 1$

- **Figure 3**

  - (b) eq. (25-26), $c_{1\alpha} = (0.5, 0.3)$, $c_{2\alpha} = (0.4, 0.6)$, $D_{\alpha 1} = (0, 1)$, $D_{\alpha 2} = (1, 0)$, $R_\alpha^0 = (4.5, 0.9)$, $l_1 = l_2 = 0.5$, $m_1 = m_2 = w_1 = w_2 = e_1 = e_2 = \tau = 1$

  - (c) eq. (25-26) $S = 10$, $M = 5$, $c_{i\alpha} \sim \mathcal{U}(0,1)$, $D_{\alpha\beta} \sim \mathcal{D}(10)$, $R_\alpha^0 \sim \mathcal{U}(0,10)$, $l_\alpha \sim \mathcal{U}(0,1)$, $m_i \sim \mathcal{U}(1,2)$, $w_\alpha \sim \mathcal{U}(1,2)$, $e_i = \tau = 1$

  - (e) eq. (28-29), $\mu_{1\alpha} = (6, 9)$, $\mu_{2\alpha} = (8, 5)$, $k_{1\alpha} = k_{2\alpha} = (10, 10)$, $v_{1\alpha} = (1, 0.7)$, $v_{2\alpha} = (0.7, 1)$, $R_\alpha^0 = (4.3, 4)$, $\tau = m_1 = m_2 = 1$

  - (f) eq. (28-29), $S = 10$, $M = 3$, $\mu_{i\alpha} \sim \mathcal{U}(0, 30)$, $k_{i\alpha} \sim \mathcal{U}(28.5, 31.5)$, $R_\alpha^0 \sim \mathcal{U}(20, 21)$, $\tau = m_i = 1$. The $v_{\alpha i}$ are generated by first sampling $\tilde{v}_{\alpha i} \sim (k_{i\alpha}/\mu_{i\alpha})^{-1} + \mathcal{U}(0, 0.1)$, in order to increase the odds of finding stable consortia, and then normalizing with $v_{\alpha i} = \frac{\tilde{v}_{\alpha i}}{\sum_\beta \tilde{v}_{\beta i}}$.

- **Figure 4**: In panel (*b*) an additional term $-\tau^{-1} N_i$ was added to eq. (30) in the simulations, to account for the dilution of consumers. This was not required for the fitting in panel

(a), because the growth rates were measured using the change in population size between dilutions.

- **Figure 5**: The same additional term $-\tau^{-1}N_i$ was added to eq. (30) for the purpose of computing the ZNGI's.

- **Figure A1**

  - (a) eq. (18-20), $S = 10$, $M_R = 10$, $M_P = 10$, $c_{i\alpha} \sim \mathcal{U}(0,1)$, $p_{ia} \sim \mathcal{U}(0,1)$, $m_i \sim \mathcal{U}(1,2)$, $u_a \sim \mathcal{U}(1,2)$, $w_\alpha \sim \mathcal{U}(1,2)$, $r_\alpha \sim \mathcal{U}(1,2)$, $K_\alpha \sim \mathcal{U}(0,5)$, $e_i = 1$

  - (b) eq. (22-23), $S = 9$, $M = 5$, $c_{i\alpha} \sim \mathcal{U}(0,1)$, $w_\alpha \sim \mathcal{U}(1,2)$, $R_\alpha^0 \sim \mathcal{U}(1,7)$, $\tau = e_i = 1$

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