Tilman diagrams

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This is a short tutorial summarizing the math underlying Tilman diagrams [3] using a model with mass-action consumption terms. We will cover sketching consumer nullclines in a space spanned up by resources, impact vectors establishing the existence of a steady state, and Routh-Horwitz criteria testing the stability of the steady state.

1 Nullclines

Consider the following model with two resources, R_i, and two consumers, N_i,

$$
\begin{aligned}
\frac{\mathrm{d}R_1}{\mathrm{d}t} &= f_1(R_1) - c_{11}N_1R_1 - c_{21}N_2R_1 \\
\frac{\mathrm{d}R_2}{\mathrm{d}t} &= f_2(R_2) - c_{12}N_1R_2 - c_{22}N_2R_2 \\
\frac{\mathrm{d}N_1}{\mathrm{d}t} &= c_{11}N_1R_1 + c_{12}N_1R_2 - \delta_1N_1 \\
\frac{\mathrm{d}N_2}{\mathrm{d}t} &= c_{21}N_2R_1 + c_{22}N_2R_2 - \delta_2N_2
\end{aligned}
$$

where the production of the resources could be logistic growth, a source death model, or anything else, e.g.,

$$f_i(R_i) = r_iR_i(1 - R_i/K_i) \quad \text{or} \quad f_i(R_i) = s_i - d_iR_i \ ,$$

where the latter has carrying capacities defined as $K_i = s_i/d_i$. This is a phenomenological model with "additive" resources, mass action consumption, and no parameters for the conversion of resource into consumer.

In a Tilman diagram one draws the consumer nullclines in the space spanned up by the resources. We therefore ignore the $\mathrm{d}R_i/\mathrm{d}t$ equations and solve the nullclines from the consumer equations:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = 0 \quad \leftrightarrow \quad N_1 = 0 \quad \text{or} \quad R_2 = \frac{\delta_1}{c_{12}} - \frac{c_{11}}{c_{12}}\,R_1 = R^*_{12} - \frac{c_{11}}{c_{12}}\,R_1$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = 0 \quad \leftrightarrow \quad N_2 = 0 \quad \text{or} \quad R_2 = \frac{\delta_2}{c_{22}} - \frac{c_{21}}{c_{22}}\,R_1 = R^*_{22} - \frac{c_{21}}{c_{22}}\,R_1$$

where R^*_{12} is the minimum density of the second resource required for growth of the first consumer, and R^*_{22} is the minimum density of the second resource required for growth of the second consumer. These are straight lines with slopes $-\frac{c_{11}}{c_{12}}$ and $-\frac{c_{21}}{c_{22}}$, respectively (see Fig. 1a). The consumers expand above their nullcline, and a steady state is only possible if these nullclines intersect. The location of this intersection point $(\bar{R}_1, \bar{R}_2)$ can be computed by solving $R_1 = \frac{\delta_1}{c_{11}} - \frac{c_{12}}{c_{11}}R_2$ from $\mathrm{d}N_1/\mathrm{d}t = 0$ and substituting that into $\mathrm{d}N_2/\mathrm{d}t = 0$, i.e., $\bar{R}_2 = \frac{c_{21}\delta_1/c_{11} - \delta_2}{c_{12}c_{12}/c_{11} - c_{22}}$, and then computing $\bar{R}_1$ using this expression for $\bar{R}_2$. Note that the steady states of the resources are determined by the parameters of the consumers only.

One can add more consumers to this diagram because the consumer equations are independent from each other, i.e., for a third consumer species the nullcline would be $R_2 = \frac{\delta_3}{c_{32}} - \frac{c_{31}}{c_{32}}\,R_1$ (see Fig. 1b). The three nullclines in Fig. 1b intersect in three points, of which only the intersection where $\mathrm{d}N_1/\mathrm{d}t = \mathrm{d}N_2/\mathrm{d}t = 0$ (marked as $(\bar{R}_1, \bar{R}_2)_{12}$) can be a steady state. The other two points are either located above the $\mathrm{d}N_1/\mathrm{d}t = 0$ nullcline, or above the $\mathrm{d}N_2/\mathrm{d}t = 0$ nullcline, implying that N_1 or

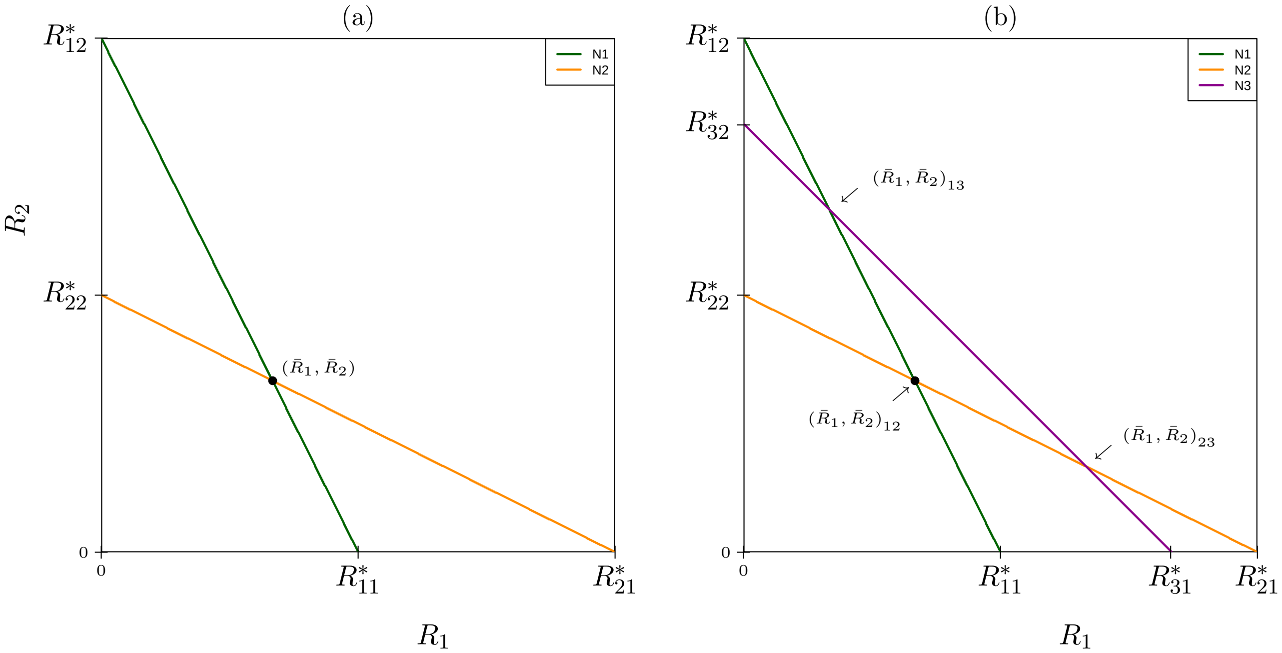

Figure 1: Tilman diagrams with two (a) or three consumers (b). Because each consumer nullcline is independent of the resource equations and the other consumer equations, one can plot many consumer nullclines in a single diagram. The nullclines intersect the axes at the minimum resource densities required for growth of the consumer, i.e., they all run from R^*_{i2} on the vertical axis to R^*_{i1} on the horizontal axis. Two nullclines can only intersect when each consumers specializes on a particular resource, i.e., if $R^*_{i2} < R^*_{j2}$ then it is required that $R^*_{j1} < R^*_{i1}$ for any pair i and j. Finally note that generically one only expects intersections between pairs of nullclines (see Panel b), i.e., maximally two consumers can be maintained at steady state on these two resources. This figure was made with the model `TilmanLV.R`

N_2 is expanding in these points. Finally, note that an intersection point can only be a steady state when the production of the resources, $f_1(R_1)$ and $f_2(R_2)$, allow for the required resource densities, $(\bar{R}_1, \bar{R}_2)$. To test this one can plot the point where both resources are at their carrying capacity, and this point should be located above an intersection point for it to be a potential steady state. To know the carrying capacity, one needs to specify the growth functions of the resources, however.

2 Impact vectors

The fact that the nullclines intersect in Fig. 1a tells us that $\mathrm{d}N_1/\mathrm{d}t = \mathrm{d}N_2/\mathrm{d}t = 0$ at these resource densities, but does not guarantee that this intersection corresponds to a steady state where also $\mathrm{d}R_1/\mathrm{d}t = \mathrm{d}R_2/\mathrm{d}t = 0$. A first requirement is that the carrying capacities of the resources (denoted by the circle in Fig. 2a), have to be located above the intersection point, otherwise the required resource densities are larger than their maximal densities. However, this still does not guarantee that $\mathrm{d}R_1/\mathrm{d}t = \mathrm{d}R_2/\mathrm{d}t = 0$ in the intersection point. Finally, even if this were a steady state, the diagram would fail to inform us about the stability of that state. Tilman [3] developed two procedures to test for (1) the existence of the steady state, and (2) its stability.

To address whether or not the intersection point $(\bar{R}_1, \bar{R}_2)$ corresponds to a steady state Tilman studied the local change of the resource densities by depicting the vectors reflecting the local consumption rates, and the local growth of the resources, R_1 and R_2. These vectors should be able to add up to zero such that $\mathrm{d}R_1/\mathrm{d}t = \mathrm{d}R_2/\mathrm{d}t = 0$ in the intersection point. The impact of the first consumer

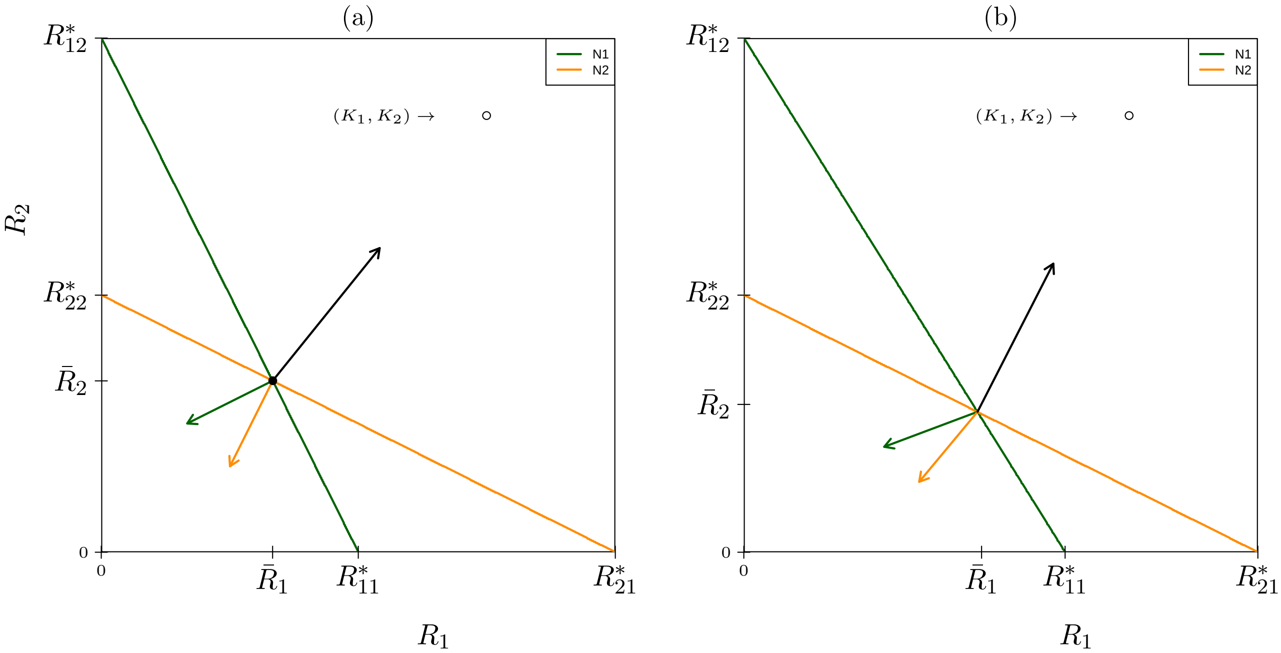

Figure 2: Tilman diagrams with impact vectors. The colored vectors depict the local impact of the consumers on the resources, i.e., the green arrow is a vector $-\binom{c_{11}\bar{R}_1}{c_{12}\bar{R}_2}N_1$ reflecting the local consumption of the first consumer, and similarly the orange arrow is the vector $-\binom{c_{21}\bar{R}_1}{c_{22}\bar{R}_2}N_2$. The black vector is the local growth of the resources, $\binom{f_1(\bar{R}_1)}{f_2(\bar{R}_2)}$, for which we here define $f_1(R_1) = s_1 - d_1R_1$ and $f_2(R_2) = s_2 - d_2R_2$. Since in Panel (a) the direction of the black resource production vector falls between the two colored consumption vector, the three vectors can add up to zero (for appropriate values of N_1 and N_2), and allow $\mathrm{d}R_1/\mathrm{d}t = \mathrm{d}R_2/\mathrm{d}t = 0$. In Panel (b) we have decreased c_{11}, which increases R_{11}^*, and changes the location of the intersection point, $(\bar{R}_1, \bar{R}_2)$, and the direction of the local vectors such that the black growth vector can no longer be balanced by the two consumption vectors. The open circles denote the carrying capacities of the resources, and because the two resources have similar dynamics, the black vectors point in the direction of these open circles. This figure was made with the model `TilmanLV.R`

on the resources is taken from its consumption terms, i.e., $c_{11}N_1R_1$ and $c_{12}N_1R_2$, and hence would be the green vector $-\binom{c_{11}\bar{R}_1}{c_{12}\bar{R}_2}\bar{N}_1$ pointing left and downwards from the point $(\bar{R}_1, \bar{R}_2)$, where we have chosen an arbitrary length because $\bar{N}_1$ is unknown. Similarly, the impact of second consumer on the resources is the orange vector $-\binom{c_{21}\bar{R}_1}{c_{22}\bar{R}_2}\bar{N}_2$, pointing left and downwards, and of arbitrary length. The black vector in Fig. 2 reflects the local growth of the resources, $\binom{f_1(\bar{R}_1)}{f_2(\bar{R}_2)}$, and points in the opposite direction (i.e., to the right and upwards). (If the growth rates of the resources have identical time scales this vector points towards the steady state of the resources in the absence of consumers, i.e., the open circles in Fig. 2 [3]). Since the length of the consumption vectors depends on the consumer densities, the three vectors in Fig. 2a can sum up to zero for appropriate values of the consumers, which allows the intersection point to be a steady state. After decreasing the niche specialization, by decreasing c_{11} in Fig. 2b, this is no longer possible because the direction of the black growth vector is no longer in between the two consumption vectors. Summarizing, the conditions for two consumers to co-exist in steady state with two resources are stronger than the minimum requirements on the R^* values delivering intersection points (see Fig. 1), their specialization on a single resource has to be even stronger.

3 Stability

To study the stability of the steady state of these models Tilman [3] computed the the largest eigenvalue of the Jacobian of the 4-dimensional system. This was feasible because this Jacobi matrix contains many zero elements. For instance, the Jacobian of a model with resources maintained by a source, i.e., $f_i(R_i) = s_i - d_i R_i$, can be written as

$$J = \begin{pmatrix} \partial_{R_1} R_1' & \dots & \partial_{N_2} R_1' \\ \vdots & \ddots & \\ \partial_{R_1} N_2' & \dots & \partial_{N_2} N_2' \end{pmatrix} = \begin{pmatrix} -d_1 - c_{11}\bar{N}_1 - c_{21}\bar{N}_2 & 0 & -c_{11}\bar{R}_1 & -c_{21}\bar{R}_1 \\ 0 & -d_2 - c_{12}\bar{N}_1 - c_{22}\bar{N}_2 & -c_{12}\bar{R}_2 & -c_{22}\bar{R}_2 \\ c_{11}\bar{N}_1 & c_{12}\bar{N}_1 & c_{11}\bar{R}_1 + c_{12}\bar{R}_2 - \delta_1 & 0 \\ c_{21}\bar{N}_2 & c_{22}\bar{N}_2 & 0 & c_{21}\bar{R}_1 + c_{22}\bar{R}_2 - \delta_2 \end{pmatrix}$$

where the two $\partial_{R_j} R_i'$ elements are zero because the resource equations do not contain the other resource, and the two $\partial_{N_j} N_i'$ elements are zero because the consumer equations do not contain the other consumer. Because the two diagonal $\partial_{N_i} N_i' = c_{ii}\bar{R}_i + c_{ij}\bar{R}_j - \delta_i$ elements correspond to the *per capita* growth rates of the consumers, which is zero at steady state, this Jacobian can be simplified into a matrix with the same structure of signs and zeros,

$$J = \begin{pmatrix} -\rho_1 & 0 & -\gamma_{11} & -\gamma_{21} \\ 0 & -\rho_2 & -\gamma_{12} & -\gamma_{22} \\ \phi_{11} & \phi_{12} & 0 & 0 \\ \phi_{21} & \phi_{22} & 0 & 0 \end{pmatrix} ,$$

where ρ_i elements define the feedback of the resources onto themselves, the γ_{ij} elements define the *per capita* amounts of resources consumed, and the ϕ_{ij} terms define the contribution of resources to the growth of the consumer populations at steady state [3]. The trace of this matrix, $-(\rho_1 + \rho_2)$, is negative. The characteristic equation of this Jacobi matrix can be obtained with Mathematica, and is defined as

$$\lambda^4 + a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0 = 0 ,$$

where

$$a_3 = \rho_1 + \rho_2 , \quad a_2 = \phi_{11}\gamma_{11} + \phi_{21}\gamma_{12} + \phi_{12}\gamma_{21} + \phi_{22}\gamma_{22} + \rho_1\rho_2 ,$$

$$a_1 = \phi_{12}\rho_1\gamma_{21} + \phi_{22}\rho_1\gamma_{22} + \phi_{11}\gamma_{11}\rho_2 + \phi_{21}\gamma_{12}\rho_2 \quad \text{and}$$

$$a_0 = (\gamma_{11}\gamma_{22} - \gamma_{12}\gamma_{21})(\phi_{11}\phi_{22} - \phi_{12}\phi_{21}) .$$

The steady state will be stable when all four solutions of the eigenvalues in the characteristic equation are negative. Fortunately, there is a general method to test this without having to solve this fourth-order polynomial. This is the so-called Routh-Horwitz stability criterion on the n coefficients, a_i, of an n^{th} order polynomial [1, 3]. One of the Routh-Horwitz criteria is that all parameters, a_i, in the characteristic equation should be positive (or all negative, as one can multiply the equation with -1). Thanks to the many zeros in the Jacobi matrix we here have a simple situation where $a_3 > 0, a_2 > 0, a_1 > 0$, and only a_0 can be negative. Hence testing $a_0 > 0$ is sufficient to establish the stability of the steady state at which the four species co-exist.

We have seen above that this 4-dimensional steady state can only be present when the two consumers have a sufficiently different diet (see Fig. 2a). Therefore consider a case where consumer one specializes on resource one, and consumer two on resource two, i.e., $c_{11} > c_{12}$ and $c_{22} > c_{21}$. Checking the sign of the first term of the a_0 equation we see that

$$(\gamma_{11}\gamma_{22} - \gamma_{12}\gamma_{21}) = (c_{11}\bar{R}_1 c_{22}\bar{R}_2 - c_{12}\bar{R}_2 c_{21}\bar{R}_1) > 0 \quad \leftrightarrow \quad c_{11}c_{22} - c_{12}c_{21} > 0 ,$$

which is true because we consider the case where $c_{11}c_{22} > c_{12}c_{21}$. For the same reason we observe for the second term of the a_0 equation

$$(\phi_{11}\phi_{22} - \phi_{12}\phi_{21}) = (c_{11}\bar{N}_1 c_{22}\bar{N}_2 - c_{12}\bar{N}_1 c_{21}\bar{N}_2) > 0 \quad \leftrightarrow \quad c_{11}c_{22} - c_{12}c_{21} > 0 .$$

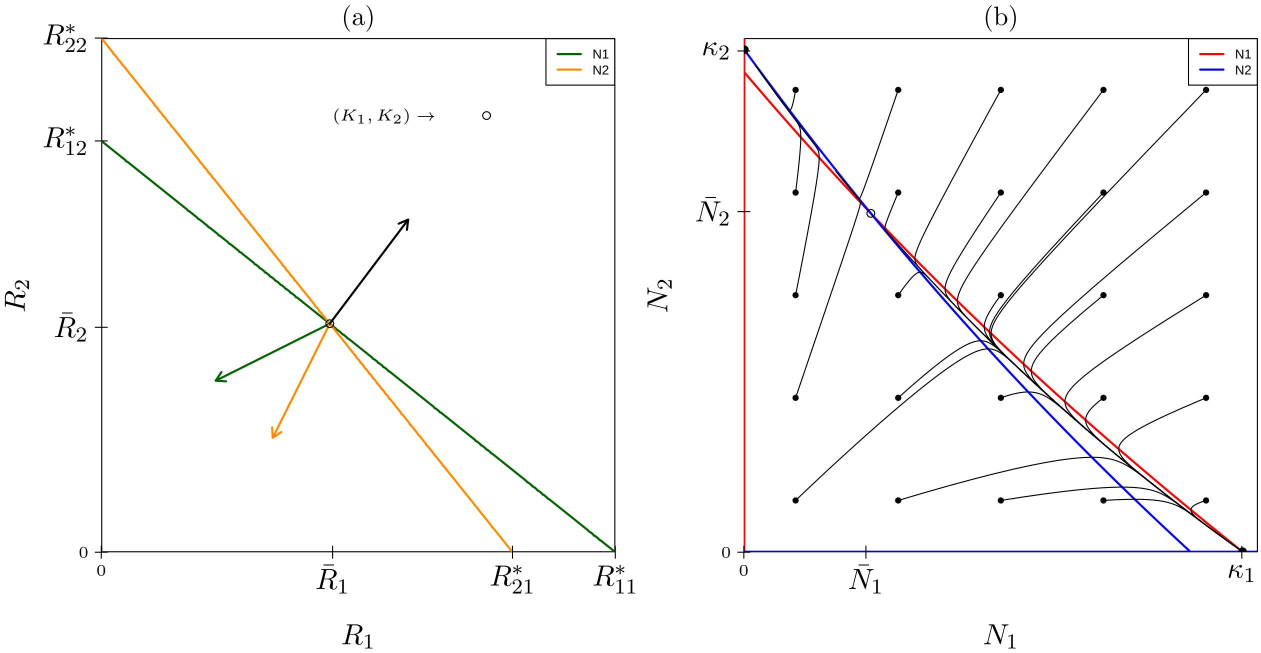

Figure 3: An unstable steady state. In the Tilman diagram in Panel (a) the colored vectors depict the local impact of the consumers on the resources, and the black vector reflects the local growth of the resources (as in Fig. 2). Since the direction of the black resource production vector falls between the two colored consumption vectors, the three vectors can add up to zero, allowing this point to be a steady state where $\mathrm{d}R_1/\mathrm{d}t = \mathrm{d}R_2/\mathrm{d}t = 0$ (like in Fig. 2a). However, because each species benefits most from the resource it consumes the least, i.e., $c_{11} > c_{21}$ but $\alpha_{11} < \alpha_{21}$ and $c_{12} < c_{22}$ but $\alpha_{21} > \alpha_{22}$, this steady state corresponds to a saddle point. In Panel (b) we study the same system by making the quasi steady state assumption, $\mathrm{d}R_1/\mathrm{d}t = \mathrm{d}R_2/\mathrm{d}t = 0$, and depict a phase space spanned up by the two consumers. This confirms that the non-trivial point is a saddle point and that the two "carrying capacities", κ_1 and κ_2, of the consumers form two stable points on the horizontal and vertical axis, respectively. The black lines in Panel (b) are trajectories, starting at the regularly spaced bullets, together forming a phase portrait. This figure was made with the model `TilmanLV.R`.

Since both terms are positive we conclude that $a_0 > 0$ which fulfills this Routh-Horwitz criterion Thus the steady state is expected to be stable. We conclude that if these two consumers have sufficiently different niches, i.e., when their nullclines intersect, and the production vector can balance the consumption vectors (see Fig. 2a), the 4-dimensional steady state is expected to be stable.

Although we here considered the case where the resources are maintained by a source, little changes when we define replicating resources by replacing $f_i(R_i) = r_j R_j(1 - R_j/K_j)$, because (1) the Tilman diagram remains the same, and (2) in the Jacobian only the upper two diagonal elements change into

$$\rho_1 = r_1 - \frac{2r_1}{K_1}\bar{R}_1 - c_{11}\bar{N}_1 - c_{21}\bar{N}_2 \quad \text{and} \quad \rho_2 = r_2 - \frac{2r_2}{K_2}\bar{R}_2 - c_{11}\bar{N}_1 - c_{21}\bar{N}_2 \ ,$$

both of which should remain negative. Hence, the Routh-Horwitz criteria remain the same and the steady state should be stable.

3.1 Resource requirements

In the model considered above the two resources were equally nutritious for both consumers. We will see below that steady states can become unstable when species eat most of their least nutritious resource. Let us therefore introduce four conversion factors, α_{ij}, defining the contribution of the amount of resource consumed, $c_{ij}R_i$, to the growth of the consumers,

$$\begin{aligned}\frac{\mathrm{d}N_1}{\mathrm{d}t} &= \alpha_{11}c_{11}N_1R_1 + \alpha_{12}c_{12}N_1R_2 - \delta_1 N_1 \ , \\ \frac{\mathrm{d}N_2}{\mathrm{d}t} &= \alpha_{21}c_{21}N_2R_1 + \alpha_{22}c_{22}N_2R_2 - \delta_2 N_2 \ .\end{aligned}$$

We obtain an Jacobian that is quite similar to the one derived above, as only the four $\partial_R N'$ elements change:

$$\begin{pmatrix}\partial_{R_1}N_1' & \partial_{R_2}N_1' \\ \partial_{R_1}N_2' & \partial_{R_2}N_2'\end{pmatrix} = \begin{pmatrix}\alpha_{11}c_{11}\bar{N}_1 & \alpha_{12}c_{12}\bar{N}_1 \\ \alpha_{21}c_{21}\bar{N}_2 & \alpha_{22}c_{22}\bar{N}_2\end{pmatrix} = \begin{pmatrix}\phi_{11} & \phi_{12} \\ \phi_{21} & \phi_{22}\end{pmatrix} \ .$$

The full Jacobian therefore has the same signs and zeros as the previous matrix, which means that the same $a_0 > 0$ criterion remains a sufficient condition for stability.

Again consider a case where consumer one specializes on resource one, and consumer two on resource two, i.e., $c_{11} > c_{12}$ and $c_{22} > c_{21}$. Like above the first term of the $a_0 > 0$ criterion, $\gamma_{11}\gamma_{22} > \gamma_{12}\gamma_{21}$, remains satisfied. However, the sign of the second term will only be positive when,

$$\phi_{11}\phi_{22} - \phi_{12}\phi_{21} = \alpha_{11}c_{11}\bar{N}_1\alpha_{22}c_{22}\bar{N}_2 - \alpha_{12}c_{12}\bar{N}_1\alpha_{21}c_{21}\bar{N}_2 > 0 \quad \leftrightarrow \quad \alpha_{11}c_{11}\alpha_{22}c_{22} - \alpha_{12}c_{12}\alpha_{21}c_{21} > 0 \ ,$$

which fails to be true when the conversion rates, α_{ij}, are not concordant with the consumption rates, c_{ij}. For instance, if species one (that consumes most of resource one) would benefit most of resource two, i.e., if $\alpha_{11} < \alpha_{12}$, and if species two would benefit most of resource one, i.e., if $\alpha_{22} < \alpha_{21}$, this term can become negative. Whenever $\phi_{11}\phi_{22} - \phi_{12}\phi_{21} < 0$ (and $\gamma_{11}\gamma_{22} - \gamma_{12}\gamma_{21} > 0$), the Routh-Horwitz criterion $a_0 > 0$ fails, and the steady state is expected to be unstable (see Fig. 3a).

Interestingly, we see that both consumers need to be restricted most by the resource they eat most, and that the condition $a_0 > 0$ has the biological interpretation that the species can co-exist when they evolve consumption rates reflecting their resource requirements, i.e., when the ϕ_{ij} terms concur with the γ_{ij} terms [2, 3]. Intuitively, one can understand that it is destabilizing when a consumer hardly consumes the resource it is mostly limited by (as an increase in the resource density would hardly increase its birth rate). This destabilizes the steady state and leads to the "founder controlled" situations where the initial condition determines which of the consumers survives (see Fig. 3b).

Finally, similar to deriving a graphical Jacobian from a local vector field, one can sometimes estimate the relative sizes of the ϕ_{ij} terms from a Tilman diagram. In Fig. 1a we can see that $\partial_{R_1}N_1' = \phi_{11} > \partial_{R_2}N_1' = \phi_{12}$ because a small step to the right lands at a larger distance from the $\mathrm{d}N_1/\mathrm{d}t = 0$ nullcline than a small step to the top. Similarly, one can see that $\partial_{R_1}N_2 = \phi_{22} > \partial_{R_2}N_2' = \phi_{21}$, which together provides us with the Routh-Horwitz criterion, $\phi_{11}\phi_{22} - \phi_{12}\phi_{21} > 0$, and tells us that the steady state should be stable. In Fig. 3a this is just the other way around, i.e., $\phi_{11}\phi_{22} < \phi_{12}\phi_{21}$. A simple rule of thumb would be therefore be that the $\mathrm{d}N_1/\mathrm{d}t = 0$ nullcline needs to be steep, whereas the $\mathrm{d}N_2/\mathrm{d}t = 0$ nullcline should be flat (if R_1 is on the horizontal axis, and N_1 specializes on R_1).

References

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