OLM 9.3. The Tilman model: Full analysis

We have argued that robust coexistence of competitors requires differentiation both in the impact and in the sensitivity vectors (TBox 9.3, p.184). The idea was demonstrated in Tilman's resource competition model (Figure 9.11, p.181) in which the consumption vectors are considered a kind of proxy for the impact vectors. We stated that the impact and the consumption vectors would be identical (up to a factor) *if* the consumption vector were independent of the resource point. Unfortunately, that condition is never met, so we owe the Reader a serious analysis. Here we calculate the true impact vector in Tilman's model and discuss, why the consumption vector is still a good proxy.

We study Tilman's model, as defined in TBox 9.2 (p.182), but we take the dependence of consumption vectors on resource concentration (cf. functional response, TBox 6.3, p.108) into account. The lack of such a dependence is just impossible: it would mean that the consumer would be able to maintain its consumption at arbitrarily low resource concentrations. However, this dependence is not necessarily relevant in all considerations. The more detailed version of Tilman's model in the Appendix of Tilman (1982) accounts for the dependence, but the graphical considerations throughout the book rely on fixed resource equilibrium points, making the dependence inconsequential.

First we determine the relationship between consumption and impact vectors, then consider its implication for the robustness of coexistence. Finally, we repeat the calculation specifically for the Holling Type I functional response for comparison with the analysis in TBox 6.4 (p. 111) for a single resource.

Consumption and impact: the general case

According to Eq. (9.25)[1] in TBox 9.3 (p.185), the impact vector $\boldsymbol{I}_i$ of species *i* is defined as the derivative of the vector of equilibrium resource concentrations with respect to the density of species *i*:

$$\boldsymbol{I}_i = \frac{\partial \boldsymbol{R}}{\partial N_i} = \begin{pmatrix} \frac{\partial R_1}{\partial N_i} \\ \frac{\partial R_2}{\partial N_i} \end{pmatrix}. \qquad (9.3.1)$$

[1] Equation in the format (9.25) is an equation in Chapter 9 of the printed book. Equation in the format of (9.3.1) is an equation in OLM 9.3.

Here we focus on resources, so we do not write script *R*. We find it useful to write vectors in the column form to comply with the matrix-multiplication formalism. In order to determine the impact vectors we should know the dependence of equilibrium resource concentrations on consumer densities.

We can write Eq. (9.16) (p.182) as

$$\boldsymbol{R} = \widehat{\boldsymbol{R}} - \frac{1}{\alpha}\left[\boldsymbol{c}_1(\boldsymbol{R})N_1 + \boldsymbol{c}_2(\boldsymbol{R})N_2\right]. \tag{9.3.2}$$

We have explicitly spelled out the dependence of the consumption vectors on resource concentrations here. Because of this dependence, the equation determines $\boldsymbol{R}$ only implicitly. As the functions $\boldsymbol{c}_i(\boldsymbol{R})$ (i.e., the functional responses) are unspecified, we can aim only at local results through linearization (TBox 1.1, p.9). For infinitesimal change in densities we can write

$$d\boldsymbol{R} = -\frac{1}{\alpha}\left[\boldsymbol{c}_1 dN_1 + \boldsymbol{c}_2 dN_2 + \left(N_1\frac{\partial \boldsymbol{c}_1}{\partial \boldsymbol{R}} + N_2\frac{\partial \boldsymbol{c}_2}{\partial \boldsymbol{R}}\right)d\boldsymbol{R}\right]. \tag{9.3.3}$$

Here we have taken into account that, for example, the term $\boldsymbol{c}_1(\boldsymbol{R})N_1$ depends on N_1 not only directly, but also through $\boldsymbol{R}$**.** We applied the derivative matrix notation

$$\frac{\partial \boldsymbol{c}_i}{\partial \boldsymbol{R}} = \begin{pmatrix} \frac{\partial c_{i1}}{\partial R_1} & \frac{\partial c_{i1}}{\partial R_2} \\ \frac{\partial c_{i2}}{\partial R_1} & \frac{\partial c_{i2}}{\partial R_2} \end{pmatrix}, \tag{9.3.4}$$

which was already used in the book for the definition of the generalised competition matrix (Eq.(9.22), p.185). In words, the partial derivative of a vector with respect to another vector is the matrix of the partials of the elements of the first vector with respect to the elements of the second vector.

Reordering Eq. (9.3.3) leads to

$$\underbrace{\left[\mathbf{1} + \frac{1}{\alpha}\left(N_1\frac{\partial \boldsymbol{c}_1}{\partial \boldsymbol{R}} + N_2\frac{\partial \boldsymbol{c}_2}{\partial \boldsymbol{R}}\right)\right]}_{\boldsymbol{M}} d\boldsymbol{R} = -\frac{1}{\alpha}(\boldsymbol{c}_1 dN_1 + \boldsymbol{c}_2 dN_2), \tag{9.3.5}$$

where $\mathbf{1}$ denotes the identity matrix

$$\mathbf{1} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}. \tag{9.3.6}$$

(Almost every author – including us in OLM 4.2 – denote the identity matrix by $\boldsymbol{I}$. We have chosen a rarely used notation – strictly limited to this OLM – to avoid notational conflict with the impact vector $\boldsymbol{I}_i$.) Introducing the matrix

$$\boldsymbol{M} = \mathbf{1} + \frac{1}{\alpha}\left(N_1\frac{\partial \boldsymbol{c}_1}{\partial \boldsymbol{R}} + N_2\frac{\partial \boldsymbol{c}_2}{\partial \boldsymbol{R}}\right) \tag{9.3.7}$$

for the left-hand side of Eq. (9.3.5), we can solve that equation for $d\boldsymbol{R}$ as a function of dN_1 and dN_2:

$$d\boldsymbol{R} = -\frac{1}{\alpha}\boldsymbol{M}^{-1}\boldsymbol{c}_1 dN_1 - \frac{1}{\alpha}\boldsymbol{M}^{-1}\boldsymbol{c}_2 dN_2 = \boldsymbol{I}_1 dN_1 + \boldsymbol{I}_2 dN_2. \qquad (9.3.8)$$

Here we have found that the impact vectors of the two populations (as defined by Eq. (9.3.1)) are

$$\boldsymbol{I}_1 = \frac{\partial \boldsymbol{R}}{\partial N_1} = -\frac{1}{\alpha}\boldsymbol{M}^{-1}\boldsymbol{c}_1 \quad \text{and} \quad \boldsymbol{I}_2 = \frac{\partial \boldsymbol{R}}{\partial N_2} = -\frac{1}{\alpha}\boldsymbol{M}^{-1}\boldsymbol{c}_2. \qquad (9.3.9)$$

Note that a positive consumption has a negative impact on the resource level.

That is, we just learned that the impact vectors can be calculated from the consumption vectors by multiplication with a matrix that is common for the two species. Consequently, similarity of the consumption vectors translates to similarity of the impact vectors, and *vice versa*. This is why we do not cheat when using the consumption vectors as proxies for impact vectors in discussing the relation between robustness and dissimilarity.

Robustness of coexistence

In TBox 9.3 we connected robustness to dissimilarity of the impact as well as of the sensitivity vectors. Here we revisit the issue in terms of consumption – rather than of impact – vectors.

Unfortunately, we have to start by confessing a sign mistake in the (first print of) the book. Eq. (9.26), determining the competition matrix in terms of impacts and sensitivities, reads correctly as

$$\boldsymbol{a} = -\tilde{\boldsymbol{S}} \cdot \tilde{\boldsymbol{I}}. \qquad (9.3.10)$$

The – sign, which is missing from the book, is a consequence of our sign convention for the competition matrix in Eqs. (9.22) and (9.24). In compliance with the usual notation in competitive Lotka-Volterra equations (Eqs. (9.1) and (9.2) in TBox 9.1, p.171), a positive element of the competition matrix a_{ij} describes a negative effect on population growth. Fortunately, the next formula, Eq. (9.27) in the book (p.185) is correct. It is because the determinant of a 2x2 matrix remains the same with all its elements multiplied by -1.

In Eq. (9.3.10) matrix $\tilde{\boldsymbol{S}}$ is composed of the sensitivity vectors as its rows, while matrix $\tilde{\boldsymbol{I}}$ is composed of the impact vectors as its columns. We are interested in the latter. It can be expressed as

$$\tilde{\boldsymbol{I}} = -\frac{1}{\alpha}\boldsymbol{M}^{-1}\tilde{\boldsymbol{c}}, \qquad (9.3.11)$$

where matrix $\tilde{\boldsymbol{c}}$ is composed of the consumption vectors as its columns. Think about it carefully: it is a direct rewriting of Eq. (9.3.9).

Then the competition matrix reads

$$\boldsymbol{a} = -\tilde{\boldsymbol{S}} \cdot \tilde{\boldsymbol{I}} = \frac{1}{\alpha}\tilde{\boldsymbol{S}}\boldsymbol{M}^{-1}\tilde{\boldsymbol{c}}. \qquad (9.3.12)$$

The negative sign has disappeared: positive consumption and positive sensitivity result in a negative effect, i.e., in positive competition. Then, from Eq. (9.27) we arrive to our final result in relation to robustness:

$$\det \boldsymbol{a} = \det \tilde{\boldsymbol{S}} \det \tilde{\boldsymbol{I}} = \frac{\det \tilde{\boldsymbol{S}} \det \tilde{\boldsymbol{c}}}{\alpha \det \boldsymbol{M}}. \qquad (9.3.13)$$

Here we used the fact that the determinant of the inverse matrix is the reciprocal of the original determinant.

We learned in TBox 9.3 (p.184) that the robustness of coexistence is lost if $\det \boldsymbol{a} \approx 0$. Eq. (9.27) translates this condition to either $\det \tilde{\boldsymbol{S}} \approx 0$ or $\det \tilde{\boldsymbol{I}} \approx 0$. That is, either similarity in the sensitivity vectors, or similarity in the consumption vectors destroys the robustness of coexistence. With Eq. (9.3.13) we can say the same upon replacing impact vectors with consumption vectors. That is, robustness is destroyed both by similar sensitivity vectors, and by similar consumption vectors. This is just the conclusion we arrived at studying Figure 9.11. The figure would not change essentially by taking the resource dependence of the consumption vectors into account.

Well, $\det \boldsymbol{M} \approx 0$ in the denominator of Eq. (9.3.13) would ruin our conclusion. However, it will never happen in a realistic situation. According to Eq. (9.3.9), it would mean that impacts become somehow extraordinarily sensitive to consumptions just to magically compensate similarity in consumptions.

Special case: Holling Type I functional response

Throughout the TBoxes of the book we have used sometimes Holling Type I, sometimes Type II functional responses (TBox 6.3) – or left the shape of the functional response curve arbitrary: whichever was the simplest, or the most insightful in the specific context. Here we allow ourselves the luxury of considering our topic in different ways in this respect.

If we are interested only in the system's response to small perturbations, we can rely on linearizations and the exact shapes of the functions are irrelevant. This is why we were able to discuss robustness of coexistence in a model-independent way in TBox 9.3. We could discuss robustness in Tilman's model without specifying the functional response above. This type of result is strictly local, i.e., its validity is restricted to small neighbourhoods within the parameter space.

On the other hand, we determined the impact of a single species on a single resource in TBox 6.4 with the assumption of Holling I. This is why our result for impact Eq.(9.3.9) is not directly comparable to the corresponding single-resource result Eq.(6.34). To make the comparison feasible, here we recalculate the two-resource case with Holling I. (Appendix of Tilman, 1982 introduces a Holling Type II dependence, but it would be too complicated for our purposes.)

The functional response to several resources is not trivial to determine, because the uptake of one resource may depend on the availability of the other, see e.g. Morozov and Petrovskii (2013). The possibility of cross-dependence was allowed in our notation above: both components of $\boldsymbol{c}_i$ could depend on both N_1 and N_2. Here, however, we neglect the possibility of interaction and assume Holling Type I functional responses with respect to both resources, independently from one another.

With these assumptions the consumption vectors read as

$$\boldsymbol{c}_i = \begin{pmatrix} \beta_{i1}R_1 \\ \beta_{i2}R_2 \end{pmatrix} = \underbrace{\begin{pmatrix} \beta_{i1} & 0 \\ 0 & \beta_{i2} \end{pmatrix}}_{\boldsymbol{\beta}_i} \begin{pmatrix} R_1 \\ R_2 \end{pmatrix} = \boldsymbol{\beta}_i \boldsymbol{R}, \qquad (9.3.14)$$

from which we can write

$$\frac{\partial \boldsymbol{c}_i}{\partial \boldsymbol{R}} = \boldsymbol{\beta}_i. \qquad (9.3.15)$$

Here β_{ij} is the β parameter (Eq. (6.14) of TBox 6.3) of species *i* with respect to resource *j*. They are collected into matrix $\boldsymbol{\beta}_i$. The diagonal nature of this matrix reflects the non-interference between consumptions of the two resources. Then matrix $\boldsymbol{M}$ follows as

$$\boldsymbol{M} = \boldsymbol{1} + \frac{1}{\alpha}(N_1\boldsymbol{\beta}_1 + N_2\boldsymbol{\beta}_2) =$$

$$= \begin{pmatrix} 1 + \frac{1}{\alpha}(N_1\beta_{11} + N_2\beta_{21}) & 0 \\ 0 & 1 + \frac{1}{\alpha}(N_1\beta_{12} + N_2\beta_{22}) \end{pmatrix}. \qquad (9.3.16)$$

The inverse of a diagonal matrix can be calculated by just taking the reciprocals of the diagonal elements:

$$\boldsymbol{M}^{-1} = \begin{pmatrix} \frac{\alpha}{\alpha + N_1\beta_{11} + N_2\beta_{21}} & 0 \\ 0 & \frac{\alpha}{\alpha + N_1\beta_{12} + N_2\beta_{22}} \end{pmatrix} \qquad (9.3.17)$$

(Rule 2.24, in Otto & Day, 2007 p. 235). From Eq. (9.3.9) the impact vectors become

$$\boldsymbol{I}_i = -\frac{1}{\alpha}\boldsymbol{M}^{-1}\boldsymbol{c}_i = -\begin{pmatrix} \frac{\beta_{i1}R_1}{\alpha+N_1\beta_{11}+N_2\beta_{21}} \\ \frac{\beta_{i2}R_2}{\alpha+N_1\beta_{12}+N_2\beta_{22}} \end{pmatrix}. \tag{9.3.18}$$

Here we would be inclined to compare this result to the single-resource one, Eq. (6.34). Unfortunately, we expressed the impacts in terms of the actual resource concentrations R_i, while the unloaded concentrations $\hat{R}_i$ were used in Eq. (6.34). To see the connection, we have to figure out the relationship between the loaded and the unloaded concentrations.

To this end we rewrite Eq. (9.3.2) with the Holling Type I functional response:

$$\boldsymbol{R} = \widehat{\boldsymbol{R}} - \frac{1}{\alpha}(N_1\boldsymbol{\beta}_1\boldsymbol{R} + N_2\boldsymbol{\beta}_2\boldsymbol{R}) = \widehat{\boldsymbol{R}} - \frac{1}{\alpha}(N_1\boldsymbol{\beta}_1 + N_2\boldsymbol{\beta}_2)\boldsymbol{R}, \tag{9.3.19}$$

from which, using Eq. (9.3.16),

$$\boldsymbol{M}\boldsymbol{R} = \widehat{\boldsymbol{R}} \tag{9.3.20}$$

and

$$\boldsymbol{R} = \begin{pmatrix} R_1 \\ R_2 \end{pmatrix} = \boldsymbol{M}^{-1}\widehat{\boldsymbol{R}} = \begin{pmatrix} \frac{\alpha\hat{R}_1}{\alpha+N_1\beta_{11}+N_2\beta_{21}} \\ \frac{\alpha\hat{R}_2}{\alpha+N_1\beta_{12}+N_2\beta_{22}} \end{pmatrix} \tag{9.3.21}$$

follows. This is the generalisation of Eq. (6.31) for two species and two resources. Both of them are typical non-local results, because the loaded concentrations need not be close to the unloaded ones. It was just impossible to calculate such a relationship without specifying the functional response curve. As we opted for a linear functional response, we have a linear relationship between $\widehat{\boldsymbol{R}}$ and $\boldsymbol{R}$.

Combining Eq. (9.3.21) with Eqs. (9.3.9) and (9.3.14) leads to

$$\boldsymbol{I}_i = -\frac{1}{\alpha}\boldsymbol{M}^{-1}\boldsymbol{c}_i = -\frac{1}{\alpha}\boldsymbol{M}^{-1}\boldsymbol{\beta}_i\boldsymbol{R} = -\frac{1}{\alpha}\boldsymbol{M}^{-1}\boldsymbol{\beta}_i\boldsymbol{M}^{-1}\widehat{\boldsymbol{R}} =$$

$$= -\begin{pmatrix} \frac{\alpha\beta_{i1}\hat{R}_1}{(\alpha+N_1\beta_{11}+N_2\beta_{21})^2} \\ \frac{\alpha\beta_{i2}\hat{R}_2}{(\alpha+N_1\beta_{12}+N_2\beta_{22})^2} \end{pmatrix}. \tag{9.3.22}$$

(We multiply diagonal matrices by multiplying their corresponding elements in the diagonals.)

At this point we can declare victory: one can easily recognize the correspondence between this result and the single-species, single-resource case of Eq. (6.34) on p.112.

Outlook: connection between impact and sensitivity

Thus far we have considered sensitivity and impact as independent descriptors of a species. However, they are often related. It is meaningful to assume that a species has impact on and sensitivity to the kind of food that is consumed by the species. Put another way, while the impact is related to the functional response of the species, the sensitivity is the gradient vector of the numerical response function $r(\boldsymbol{R})$. On the other hand, the numerical and the functional responses are often related (TBox 6.3). See more on the relationship between impact and sensitivity in TBox 10.2 (p. 210) and OLM 9.1.

For Tilman's model, a more mechanistic representation (e.g. appendix of Tilman 1982) connects both impact and sensitivity (numerical and functional response) to resource consumption. Schreiber and Tobiason (2003) discuss the evolution of resource use in such a context using the adaptive dynamics methodology (TBox 10.6, p.227). Depending on the relation between the two resources, evolution may branch, resulting in the emergence of two coexisting specialists.

See also Kleinhesselink and Adler (2015) for a related niche-sensitivity analysis of Tilman's model; correspondence with these authors was instrumental in writing this OLM.

References

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