OLM 9.1. *K* or r_0?

In TBox 9.1 (TBE, p.171), we derived two conditions for coexistence in the competitive Lotka-Volterra model: one in terms of r_0s, and another in term of *K*s. These conditions are mathematically equivalent and equally valid. By considering the two arms of feed-back loops separately, we discuss the formal and intuitive difference between the two formulations.

We learnt that robust coexistence (mutual invasibility) requires lowered interspecific competition relative to intraspecific one. Specifically, Eqs. (9.6) and (9.7) provide two conditions for coexistence:

$$\frac{a_{12}}{a_{22}} < \frac{r_{01}}{r_{02}} < \frac{a_{11}}{a_{21}} \qquad (9.1.1)$$

and

$$\frac{a_{12}}{a_{11}} < \frac{K_1}{K_2} < \frac{a_{22}}{a_{21}}. \qquad (9.1.2)$$

They are equivalent, because

$$K_i = \frac{r_{0i}}{a_{ii}}, \qquad (9.1.3)$$

by definition. Observe, that e.g., a_{12} is divided by a_{22} in Eq. (9.1.1), but divided by a_{11} in Eq. (9.1.2). So the difference between the two conditions is, whether we compare the interspecific competition to the intraspecific one either within the first, or within the second species.

To understand this difference in more detail we express the competition coefficients via the impact and sensitivity vectors

$$a_{ij} = -\boldsymbol{S}_i \cdot \boldsymbol{I}_j \qquad (9.1.4)$$

(Eq. (9.24) in TBox 9.3, p.185). Here the impact vector $\boldsymbol{I}_j$ represents the per capita impact of species *j* on the vector of regulating variables; sensitivity vector $\boldsymbol{S}_i$ represents the sensitivity of species *i* towards the same variables. The competitive effect of species *j* on species *i* is determined by the impact of species *j* and the sensitivity of species *i* (Figure 9.14, p.184).

First we rewrite the coexistence condition Eq.(9.1.1) in terms of impacts and sensitivities:

$$\frac{\boldsymbol{S}_1 \cdot \boldsymbol{I}_2}{\boldsymbol{S}_2 \cdot \boldsymbol{I}_2} = \frac{a_{12}}{a_{22}} < \frac{r_{01}}{r_{02}} < \frac{a_{11}}{a_{21}} = \frac{\boldsymbol{S}_1 \cdot \boldsymbol{I}_1}{\boldsymbol{S}_2 \cdot \boldsymbol{I}_1} \qquad (9.1.5)$$

and see that the numerators differ from the corresponding denominators in sensitivity. If the sensitivities of the populations are the same for the two species, i.e., $\boldsymbol{S}_1 = \boldsymbol{S}_2 = \boldsymbol{S}$, it is

$$1 = \frac{\boldsymbol{S}\cdot\boldsymbol{I}_2}{\boldsymbol{S}\cdot\boldsymbol{I}_2} = \frac{a_{12}}{a_{22}} < \frac{r_{01}}{r_{02}} < \frac{a_{11}}{a_{21}} = \frac{\boldsymbol{S}\cdot\boldsymbol{I}_1}{\boldsymbol{S}\cdot\boldsymbol{I}_1} = 1 \qquad (9.1.6)$$

that follows. Therefore only the special case of equal r_0 values allows coexistence, a neutral one (Figure 9.2.c, p.173). Otherwise the species with larger r_0 excludes the other one, irrespective of the size of the difference.

This result is easy to understand in intuitive terms. Equal sensitivities means that the two populations depend on the regulating variables in the same way. Therefore, regulation does not affect the difference between their growth rates. Difference in the growth rates, r_i-s, is just the difference between the initial growth rates, r_{0i}-s; the latter difference determines the outcome of competition unequivocally. In this case it does not matter whether the impacts are different, or not. Even if the two species affects the environment differently, they still react to an environmental change in the same way.

In contrast, the numerator and the denominator differ in the impact in case of (9.1.2).

$$\frac{\boldsymbol{S}_1\cdot\boldsymbol{I}_2}{\boldsymbol{S}_1\cdot\boldsymbol{I}_1} = \frac{a_{12}}{a_{11}} < \frac{K_1}{K_2} < \frac{a_{22}}{a_{21}} = \frac{\boldsymbol{S}_2\cdot\boldsymbol{I}_2}{\boldsymbol{S}_2\cdot\boldsymbol{I}_1}. \qquad (9.1.7)$$

For equal impacts ($\boldsymbol{I}_1 = \boldsymbol{I}_2 = \boldsymbol{I}$)

$$1 = \frac{\boldsymbol{S}_1\cdot\boldsymbol{I}}{\boldsymbol{S}_1\cdot\boldsymbol{I}} = \frac{a_{12}}{a_{11}} < \frac{K_1}{K_2} < \frac{a_{22}}{a_{21}} = \frac{\boldsymbol{S}_2\cdot\boldsymbol{I}}{\boldsymbol{S}_2\cdot\boldsymbol{I}} = 1. \qquad (9.1.8)$$

In this case equality of the *K*s is the requirement for neutral coexistence; otherwise the species with higher *K* excludes the other one. When the impacts are the same the sum of the two population sizes determines the environment, therefore the principle of *K*-maximization (Ch7.1.2, p.124) is applicable.

In line with TBox 9.3 (p.185) we saw that either identical impact vectors or identical sensitivity vectors lead to competitive exclusion generically. If the regulations of two species are very similar, then both their sensitivities and their impacts become similar at the same time. In this case both of the arguments above applicable: the winner can be picked up either on basis of the r_{0i}-s or on the basis of *K* values with the same result (Figure 7.5.a, p.126).

This OLM and TBox 9.1 were motivated by an early paper of John Vandermeer who already discussed the existence and meanings of the two different forms of the coexistence condition (Eq.(9.1.1) and Eq.(9.1.2)) in the context of the Lotka - Volterra model. To our knowledge it was the first paper that clearly showed (Figure 9.1.1) that the coexistence range is shrinking with increasing similarity either of the a_{ij}/a_{ii} or of the a_{ij}/a_{jj} ratios (Vandermeer 1975).

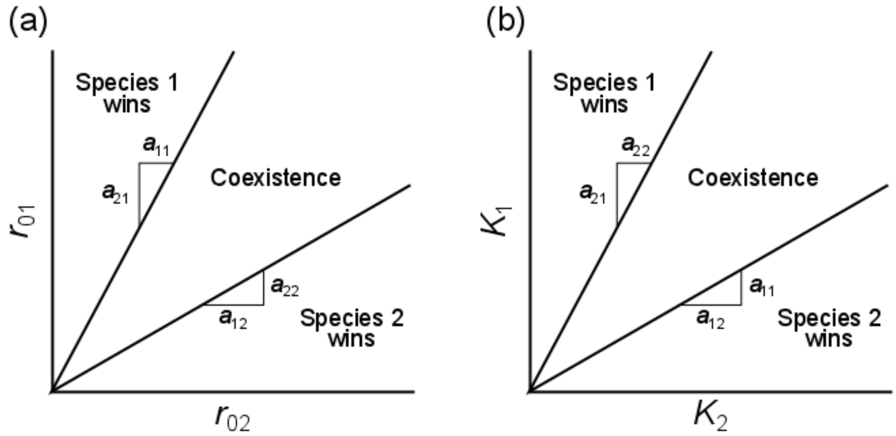

Figure 9.1.1: Robustness of coexistence depends on the relative strength of intra- and interspecific competition (after Vandermeer 1975)

a) The equation of the upper line is $r_{01} = \frac{a_{11}}{a_{21}} r_{02}$ of lower line is $r_{01} = \frac{a_{12}}{a_{22}} r_{02}$ (cf. Eq.(9.1.1). b) The equation of the upper line is $K_1 = \frac{a_{22}}{a_{21}} K_2$ of lower line is $K_1 = \frac{a_{12}}{a_{11}} K_2$ (cf. Eq.(9.1.2). Notice, that the areas within the lines increase in both cases when the values of a_{ii} are larger and of the a_{ij} are smaller.

He also concluded that ecological equivalence of two competitors may have two different meanings: either the "received effects" or the "imposed effects" of the competitors may be the same for both species (Vandermeer 1975, p. 255). Here we showed that he had been right: the equivalence of either the sensitivities or the impacts of the competitors makes coexistence impossible, thus in this sense makes the competitors ecologically equivalent. Expressing the same in terms of niches: the equivalence of either arm of the feed-back loop makes the niches of the competitors equal and leads to competitive exclusion.

Another issue that is worth mentioning here, is the problem of the so called “equalizing mechanisms” (Warning, p.173). While it is true that exactly equal r_0 values allow neutral coexistence of competitors, nearly equal r_0 values do not. As we showed implicitly by a model example in TBox 10.6 (p.227), competition and selection increases the difference between impacts and between sensitivities of the competitors. However, it is unclear what kind of process might diminish the difference between their r_0 values.

The traditional controversies over *r*, *K* selection were briefly touched upon in Note 8.1 (p.165). These controversies have no direct relationships to the issues discussed here. As we stressed also in the note, we should analyse each problem on a solid theoretical basis, instead of via conflicting over-interpretations of over-simplified models, like the logistic formula.

References

Vandermeer, J.H. (1975). Interspecific competition: a new approach to the classical theory. *Science*, 188(4185): 253-55.