OLM 7.1. The equilibrium resource density with fluctuating growth rates

Ch7Excl has shown that competition for a single resource in a constant environment leads to the exclusion of all other populations by the one which attains zero growth rate at the lowest resource density. In such a situation each of the competing variants can be characterized by the resource density at which its growth rate (r) is zero. Following Tilman's terminology, this is called the R^* value of the species with respect to that specific resource. In this OLM we compare the equilibrium resource density in a constant environment to the average resource density $\bar{R}$ at which the average growth rate is zero in case of fluctuating resource supply rates.

If the growth rate is a linear function of resource density, then $\bar{R}$ is equal to the R^* measured in a constant environment, since if

$$r(R) = a + bR \ , \tag{7.1.1}$$

then

$$\overline{r(R)} = \overline{a + bR} = a + b\bar{R} = r(\bar{R}) \tag{7.1.2}$$

That is, $\overline{r(R)} = 0$, if $r(\bar{R}) = 0$, and this equals to R^*, which is, by definition, the resource concentration at which the value of the $r(R)$ function is zero. Let us analyse the case in which the growth rate is a saturating function of resource density (Figure 7.1.1). Draw the tangent of the $r(R)$ function, $L(R)$, at the R^* point! We have seen earlier that if the $L(R)$ linear function would specify the dependence of the growth rate on resource density, then R^* and $\bar{R}$ would be equal. Since $L(R)$ is larger than $r(R)$ everywhere except for a single point, its average will also be larger, i.e., $\overline{r(R)} < \overline{L(R)} = L(\bar{R})$. Thus, for $\overline{r(R)} <= 0$ to hold $L(\bar{R})$ must be larger than zero, and since $L(R)$ is an increasing function, the average resource density $R^{*\prime}$ at which the average growth rate of the population equals zero under fluctuation will satisfy $\bar{R} = R^{*\prime} > R^*$.

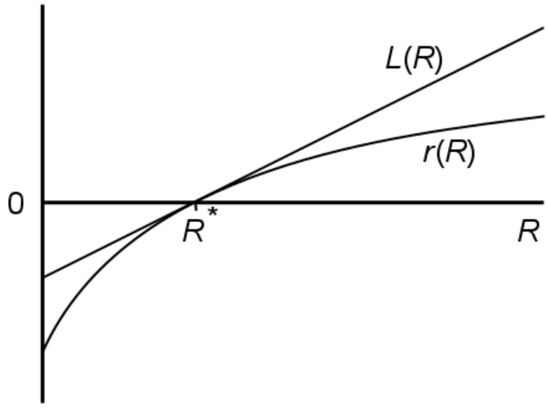

Figure 7.1.1: R^* in a fluctuating environment

In case of a saturating Holling Type II functional response the growth rate $r(R)$ is a concave function of resource density. R^* is the equilibrium resource density attained at a constant supply rate. The tangent $L(R)$ fitted to the functional response function at this point runs higher than the functional response curve itself at any resource density apart from R^*. Therefore, if resource density fluctuates, then the average resource density $R^{*\prime}$ at which the average growth rate of the population equals zero will be higher than R^* (after Armstrong and McGehee 1980).

We can come to the same conclusion by applying Taylor series approximation (Taylor series expansion, Otto and Day 2007, p. 100) to the expected value of the $r(R)$ function:

$$\overline{r(R)} \approx r(\bar{R}) - \frac{\partial^2 r}{\partial R^2}\frac{\sigma^2(R)}{2}, \qquad (7.1.3)$$

where $\sigma^2(R)$ is the variance of resource density. In the linear case the second derivative (and the higher derivatives occurring in more accurate approximations) is zero, returning Eq. (7.1.2). The speed of the increase (i.e., the first derivative) of a concave function is decreasing, so its second derivative is negative. Thus, $\overline{r(R)} < r(\bar{R})$, and the difference is larger with larger fluctuations (larger variance) of the resource density. Holling Type III functional responses are convex at low resource densities and concave later. In such cases it is the shape of the $r(R)$ function in the vicinity of the R^* that matters, provided that the fluctuations are not too large. At higher $R^{*\prime}$ values the function is already concave, and the above considerations apply.

Reference

Armstrong, R.A. and McGehee, R. (1980). Competitive exclusion. *American naturalist*: 151-70.
Otto, S.P. and Day, T. (2007). *A Biologist's Guide to Mathematical Modeling in Ecology and Evolution*. Princeton and Oxford, Princeton University Press.