

## OLM10.7. Coexistence in fluctuating environments: relative nonlinearity and storage effect

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The effect of environmental fluctuations on competitive exclusion and coexistence is an essential problem of ecology. The main point made by Chesson & Huntly (1997) was that fluctuations do not alleviate competitive exclusion and allow for coexistence universally. Instead, there are specific mechanisms through which environmental fluctuations can help dissimilar species to coexist. Chesson (1994) classified these mechanisms into two classes: “relative nonlinearity” and the “storage effect”. The topic was discussed shortly in Ch7.4.1 and Tbox10.4. Here we elaborate on it more thoroughly.

We know that at most as many species can coexist as the number of regulating variables. Specifically, as many consumer species can coexist as the number of resources in the case of equilibrium resource competition. For simplicity therefore, let us consider just a single resource and ask the question when environmental variability (only temporal, not spatial) will promote the coexistence of multiple species on a single resource (e.g., Fox, 2013).

Let us denote the resource by  $R$ ; its dynamics in time is given by some underlying equation we are not concerned with. Let us now imagine two consumers with abundances  $N_1$  and  $N_2$ . Denote their per capita growth rates by  $r_1$  and  $r_2$ , they can be written in the linear and additive case as

$$r_i = S_i R - u_i, \quad (10.7.1)$$

where  $S_i$  is the growth species  $i$  achieves on a unit of resource, and  $u_i$  is a density-independent loss rate.

### No fluctuations

Imagine that there are no environmental fluctuations for the moment. For coexistence, we need  $r_1 = r_2 = 0$  simultaneously, or

$$S_1 R - u_1 = 0, \quad (10.7.2)$$

$$S_2 R - u_2 = 0, \quad (10.7.3)$$

or

$$R^* = \frac{u_1}{S_1}, \quad (10.7.4)$$

$$R^* = \frac{u_2}{S_2}, \quad (10.7.5)$$

which can only be simultaneously satisfied if  $u_1/S_1$  is exactly equal to  $u_2/S_2$ . Therefore, even if coexistence happens, it is fragile to altering the model parameters, and in general, the species with the lower  $R^*$  wins.

## Fluctuating resource and mortalities

Let us now introduce fluctuations in  $R$  and in the loss rate  $u_i$  (season-dependent loss rate). The fluctuations are stochastically bounded. For fluctuating dynamics, the equilibrium conditions  $r_1 = r_2 = 0$  are replaced by the requirement that the long-term average growth rates must be zero:  $\bar{r}_1 = \bar{r}_2 = 0$ , where the overbar denotes time average. The conditions now read

$$S_1 \bar{R} - \bar{u}_1 = 0, \quad (10.7.6)$$

$$S_2 \bar{R} - \bar{u}_2 = 0, \quad (10.7.7)$$

or

$$\bar{R} = \frac{\bar{u}_1}{S_1}, \quad (10.7.8)$$

$$\bar{R} = \frac{\bar{u}_2}{S_2}, \quad (10.7.9)$$

which still cannot be satisfied simultaneously, unless  $\bar{u}_1/S_1 = \bar{u}_2/S_2$ . The species with the lower equilibrium  $\bar{R}$  wins. Fluctuations actually play no role at all in coexistence: if we simply replace the fluctuating mortalities  $u_i$  and  $R$  with  $\bar{u}_i$  and  $\bar{R}$ , we get the exact same long-term dynamics. Noise in this model is exactly that: just noise.<sup>1</sup>

## Nonlinear response to a fluctuating resource

Here we assume that the loss rates and  $R$  fluctuate, but the per capita growth rates of the species are slightly different:

$$r_1 = S_1 R - u_1, \quad (10.7.10)$$

$$r_2 = S_2 R^2 - u_2, \quad (10.7.11)$$

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<sup>1</sup> Huston (1979) argues that fluctuations in this model do actually slow down competitive exclusion, but his result was obtained because, instead of comparing the fluctuating model with its time average, he compared it with a different parameterization not corresponding to those means.

That is, one of the species has a nonlinear response to the resource. The long-term “equilibrium” conditions are  $\bar{r}_1 = \bar{r}_2 = 0$ . Using the fact that  $\overline{R^2} = \bar{R}^2 + \text{Var}(R)$ , where  $\text{Var}(R)$  is the variance of  $R$ , we get

$$S_1 \bar{R} - \bar{u}_1 = 0, \quad (10.7.12)$$

$$S_2 (\bar{R}^2 + \text{Var}(R)) - \bar{u}_2 = 0. \quad (10.7.13)$$

Due to the nonlinear averaging, a new quantity,  $\text{Var}(R)$  emerged, which means that we have two equations for two unknowns (as opposed to just one, as in the previous examples). In other words, now we have two different regulating variables. Therefore, coexistence of two species becomes possible.

One can interpret this result as species 1 “consuming” the mean, and species 2 “consuming” the variance of the resource. Because species 2’s growth depends quadratically on the resource, it performs relatively worse for average levels of  $R$  but gets a disproportionate advantage when  $R$  is high. Then it can coexist with species 1 even if species 1 performs better under “normal” circumstances, i.e. when  $R$  is close to its mean. Since extraordinarily high  $R$  values are followed by an outbreak of species 2, it will consume the resource, thus lowering it to a level where species 1 performs better. Thus, quite literally, species 1 consumes the mean, and species 2 consumes the variance.

A few remarks are in order. First, because there are two independent quantities (i.e., regulating variables) in Eqs. (10.7.12-13),  $\bar{R}$  and  $\text{Var}(R)$ , at most two species can coexist. Second, if we introduced a third/fourth/etc. species whose growth rates depended on  $R^3$ ,  $R^4$ , and so on, then the skewness, kurtosis, and other higher moments of  $R$  would also become independent regulating variables which in principle allow for the coexistence of as many species as many different moments are included in the equations. Third, these are only necessary, but not sufficient conditions for coexistence: for instance, the second moment is strictly positive, and so if the equilibrium equations can only be satisfied with a negative  $\text{Var}(R)$ , there will be no feasible coexistence equilibrium. Even if all equations are satisfied and the solutions are feasible, stability of the equilibrium has to be ascertained. The point being made here is that the above argument is sufficient to establish that coexistence of multiple species on a single resource is in principle possible. Stability can be assessed via other methods; for instance by performing mutual invasibility analysis, à la Chesson (1994).

## Generalization

The example above can be generalized by writing the growth rates as

$$r_i = E_i - C_i(R), \quad (10.7.14)$$

where  $E_i$  is referred to as environmental response, and  $C_i$  is the competitive response of species  $i$ . For instance,  $E_i$  could measure the birth rate as a function of temperature (which is a function of time), and  $C_i$  could be any monotonically decreasing function of the resource (because high resource levels imply low competition, and vice versa). The average growth rate of a species is then

$$\bar{r}_i = \bar{E}_i - \overline{C_i(R)}. \quad (10.7.15)$$

Due to averaging over the nonlinear functions  $C_i(R)$ , higher moments will show up as extra variables, potentially allowing for coexistence. Chesson's (1994) trick for evaluating this average is to approximate  $C_i(R)$  quadratically in  $R$ :

$$C_i(R) \approx C_i(R^*) + \phi_i(R - R^*) + \psi_i(R - R^*)^2. \quad (10.7.16)$$

This will mean that only the first and second moments will show up in the equations. Therefore, at most two species will be able to coexist under this approximation.

This coexistence mechanism was first discussed by Levins (1979) (see also Kisdi & Meszéna, 1993), and later was coined relative nonlinearity by Chesson (1994). The rationale behind this terminology is as follows. First: if  $C_i$  is a linear function of  $R$ , no fluctuation-mediated coexistence is possible — nonlinearity is a strict requirement. Second, imagine that two species have the exact same nonlinear response to  $R$ , denoted  $C = C_1 = C_2$ . The equilibrium equations then read

$$\bar{E}_1 - \overline{C(R)} = 0, \quad (10.7.17)$$

$$\bar{E}_2 - \overline{C(R)} = 0, \quad (10.7.18)$$

which – regardless of the shape of  $C(R)$  – could only be simultaneously satisfied if  $\bar{E}_1 = \bar{E}_2$ . In other words, it is not enough to have a nonlinear response to  $R$ : the two species have to possess differently shaped nonlinear responses. Their responses need to be nonlinear relative to each other.

## Coupled fluctuations in the resource and the birth rates

Let us now go back to the original model, but assume that both  $R$  and  $S_i$  fluctuate. We use the fact that  $\overline{AB} = \bar{A}\bar{B} + \text{Cov}(A, B)$ , where  $\text{Cov}(A, B)$  means the covariance between  $A$  and  $B$ . Then the average growth rates will now read

$$\bar{r}_i = \bar{S}_i\bar{R} + \text{Cov}(S_i, R) - \bar{u}_i. \quad (10.7.19)$$

The situation is just like before: every covariance term is a new variable, allowing for a long-term coexistence solution of the equilibrium equations. Intuitively: one species may be the superior competitor on average (higher  $\bar{S}_i\bar{R} - u_i$ ), but suffer from a negative, or less positive, covariance between its  $S_i$  and  $R$  than the other species, meaning it grows worst (low  $S_i$ ) whenever  $R$  is high. TBox 10.4 discusses the relation to temporal niche segregation.

For a detailed discussion of Chesson's coexistence theory, see Barabás et al. (2018).

## References

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