# Notes on Masel model

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Masel (2014) proposes a reorganization of the classic $r$-$K$ model of density-dependent selection into one with three conceptually independent quantities $r$, $K$, and additionally $c$ for competitive ability, separated from the concept of "parsimoniousness of resource use" $K$. The population dynamics equation is

$$\frac{dN_i}{dt} = r_i N_i \left( 1 - \frac{1}{c_i} \sum_j \frac{c_j N_j}{K_j} \right).$$

This is the selection gradient for that model:

$$S \begin{pmatrix} r_0 \\ c_0 \\ K_0 \end{pmatrix} = \begin{pmatrix} \frac{K_0 - \hat{X}_0}{K_0} \\ \frac{\hat{X}_0 r_0}{K_0 c_0} \\ 0 \end{pmatrix} = \begin{pmatrix} 0 \\ \frac{r_0}{c_0} \\ 0 \end{pmatrix}$$

Separating the traditional $K$ into a "cooperation" trait $K$ and a "competition" trait $c$, the classical result that selection focuses entirely on $K$ and ignores $r$ becomes a focus entirely on $c$ and none on either $K$ or $r$.

I notice, though, that the neutrality of $r$ depends on the fact that the generally nontrivial selection on $r$ is neutralized by the density dependence exactly balancing out the density-independent growth. Symbolically, this is because $r$ is multiplied across both terms of the population dynamics. If those two coefficients might be different, then selection on the two of them may not cancel out. Here we break that into two values, $r$ and $s$:

$$\frac{dX_0}{dt} = X_0 \left( r_0 - \frac{X_0 s_0}{K_0} \right)$$

$$S \begin{pmatrix} r_0 \\ s_0 \\ c_0 \\ K_0 \end{pmatrix} = \begin{pmatrix} 1 \\ -\frac{\hat{X}_0}{K_0} \\ \frac{\hat{X}_0 s_0}{K_0 c_0} \\ 0 \end{pmatrix} = \begin{pmatrix} 1 \\ -\frac{r_0}{s_0} \\ \frac{r_0}{c_0} \\ 0 \end{pmatrix}$$

In this case, we confirm that selection favors increase in density-independent growth $r$, at constant intensity 1, and decrease in the impact of density on growth, $s$, at intensity $-r/s$. If we constrain $s = r$ then these two "pressures" or tropisms cancel out.

If we constrain $s$ to $r$ in a more general way, by making both functions of a real-valued parameter $u$, we find a (slightly garbled) relationship:

$$S\begin{pmatrix} u_0 \\ c_0 \\ K_0 \end{pmatrix} = \begin{pmatrix} \frac{K_0 D[0](r)(u_1) - \hat{X}_0 D[0](s)(u_1)}{K_0} \\ \frac{\hat{X}_0 \lim_{u_1 \to u_0} s(u_1)}{K_0 c_0} \\ 0 \end{pmatrix} = \begin{pmatrix} -\frac{r(u_0) D[0](s)(u_1)}{s(u_0)} + D[0]\left(r\right)\left(u_1\right) \\ \frac{\lim_{u_1 \to u_0} s(u_1) r(u_0)}{c_0 s(u_0)} \\ 0 \end{pmatrix}$$

That is, the net selection on $u$ is $(r'(u)s(u) - r(u)s'(u))/s(u)$.

Q:

- What's the simplest way to model $r$ selection? G functions with slow population dynamics?
- Eq 4, Grimes: $\frac{dN_i}{N_i dt} = b_i(1 - D + \frac{c_i}{\bar{c}})(1 - D) - \mu_i$
  - triangle of selected patterns: tolerators ($\mu$), high-density competitors ($rc$), low-density colonizers ($r$)
  - project $b, K, \mu$ to $r, K$

# Bibliography

Masel, Joanna. 2014. "Eco-Evolutionary 'Fitness' in 3 Dimensions: Absolute Growth, Absolute Efficiency, and Relative Competitiveness."