Sebastian J. Schreiber, Reinhard Bürger, and Daniel I. Bolnick. 2011. The community effects of phenotypic and genetic variation within a predator population. *Ecology* 92:1582–1593.

Appendix B: Coexistence equilibria and their stability

The purpose of this section is twofold. First, we calculate the equilibrium abundances of the coexistence equilibria, i.e., those with all three species present, if the predator trait value $\bar{x}$ is given, and we derive a univariate transcendental equation from which the actual equilibrium values $\hat{\bar{x}}$ can be computed. To this end, we introduce compound parameters and a proper scaling for the predator trait that simplify the presentation considerably. It follows that existence and location of these equilibria depend only on six compound parameters instead of the fourteen parameters $(K_i, e_i, \alpha_i, \tau_i, r_i, \theta_i, d, \sigma)$ of the full model. Second, we prove that for sufficiently low heritabilities, trajectories always converge to an equilibrium.

We exclude the trivial case $\theta_1 = \theta_2$ when (1c) and (2) show that $\bar{x} = \theta_1 = \theta_2$ gives the only equilibrium value. Because we can choose the origin of the predator trait arbitrary, we assume $\theta = \theta_2 = -\theta_1 > 0$. In addition, we suppose $\sigma > 0$.

Because (2) demonstrates that $d\overline{W}/d\bar{x} < 0$ if $\bar{x} < -\theta$ and $d\overline{W}/d\bar{x} > 0$ if $\bar{x} > \theta$, admissible equilibrium values $\bar{x}$ always lie in the interval $[-\theta, \theta]$. However, it is possible that $d\overline{W}/d\bar{x} = 0$ has no solution in $[-\theta, \theta]$.

B.1. Determining the equilibria

To compute the equilibria of (1), we start be choosing an arbitrary but fixed value $\bar{x}$. Then the stationary points of the three-dimensional system (1a) and (1b) can be calculated explicitly. As is easily checked with *Mathematica*, seven solutions are obtained. There are four solutions, where the predator is missing at equilibrium, i.e., $P = 0$. At these, none of the preys, one prey, or both are present. If a prey species is present, it is at carrying capacity.

There are two solutions, where one of the preys is absent and the predator coexists with the other prey species. If prey 2 is absent, then the prey and predator abundances at equilibrium are

$$\hat{N}_1 = \exp\left[\frac{(\bar{x} + \theta)^2}{2(\sigma^2 + \tau_1^2)}\right] \frac{d\sqrt{\sigma^2 + \tau_1^2}}{e_1 \alpha_1 \tau_1}, \quad \hat{N}_2 = 0, \tag{B.1a}$$

$$\hat{P} = \exp\left[\frac{(\bar{x} + \theta)^2}{2(\sigma^2 + \tau_1^2)}\right] \frac{r_1\sqrt{\sigma^2 + \tau_1^2}}{\alpha_1 \tau_1}\left(1 - \frac{\hat{N}_1}{K_1}\right). \tag{B.1b}$$

If $\bar{x} = -\theta$, then the exponential term becomes unity; cf. (3). If prey 1 is absent, analogous expressions for the equilibrium abundances are obtained.

To represent the final and most interesting solution, yielding equilibria at which all three species coexist, we introduce the compound parameters

$$\beta_i = \frac{K_i e_i \alpha_i \tau_i \sigma^2}{d(\sigma^2 + \tau_i^2)^{3/2}} \,, \ \ \rho_1 = r_1 \frac{K_2 e_2 \alpha_2^2 \tau_2^2 (\sigma^2 + \tau_1^2)}{\sigma^2 (\sigma^2 + \tau_2^2)} \,, \ \ \rho_2 = r_2 \frac{K_1 e_1 \alpha_1^2 \tau_1^2 (\sigma^2 + \tau_2^2)}{\sigma^2 (\sigma^2 + \tau_1^2)} \,, \tag{B.2a}$$

$$t_i = \tau_i/\sigma \,, \ \ O = \theta/\sigma \,, \tag{B.2b}$$

where $i = 1, 2$, and the scaled trait variable

$$z = \bar{x}/\sigma \,. \tag{B.2c}$$

Thus, we are measuring the quantitative trait x in units of σ.

If we write

$$X_1 = \exp\left[\frac{(z+O)^2}{2(1+t_1^2)}\right] \ \ \text{and} \ \ X_2 = \exp\left[\frac{(z-O)^2}{2(1+t_2^2)}\right] \,, \tag{B.3}$$

the equilibrium abundances become

$$\hat{N}_1 = \frac{X_1 K_1}{\beta_1} \frac{X_1 \rho_1 \beta_1 (1+t_2^2) + X_2^2 \rho_2 - X_2 \rho_2 \beta_2 (1+t_2^2)}{X_1^2 \rho_1 (1+t_1^2) + X_2^2 \rho_2 (1+t_2^2)} \,, \tag{B.4a}$$

$$\hat{N}_2 = \frac{X_2 K_2}{\beta_2} \frac{X_2 \rho_2 \beta_2 (1+t_1^2) + X_1^2 \rho_1 - X_1 \rho_1 \beta_1 (1+t_1^2)}{X_1^2 \rho_1 (1+t_1^2) + X_2^2 \rho_2 (1+t_2^2)} \,, \tag{B.4b}$$

$$\hat{P} = \frac{\rho_1 \rho_2 X_1 X_2}{d\alpha_1 \alpha_2 \beta_1 \beta_2 t_1 t_2 \sqrt{1+t_1^2}\sqrt{1+t_2^2}} \frac{X_1 \beta_2 (1+t_2^2) + X_2 \beta_1 (1+t_1^2) - X_1 X_2}{X_1^2 \rho_1 (1+t_1^2) + X_2^2 \rho_2 (1+t_2^2)} \,. \tag{B.4c}$$

Substituting (B.4) into the differential equation (1c) for the evolution of the mean phenotype, we find that the equilibrium values $\hat{z}$ are the zeros of the transcendental function

$$\psi(z) = \rho f(\beta_1, t_1, t_2, O, z) + f(\beta_2, t_2, t_1, -O, z) \,, \tag{B.5}$$

where

$$\rho = \rho_1/\rho_2 \tag{B.6}$$

and

$$f(\beta, t_1, t_2, O, z) = X_1^2 (O - z) - X_1 \beta [O(2 + t_1^2 + t_2^2) - z(t_1^2 - t_2^2)] \,. \tag{B.7}$$

Thus, we have reduced the problem of finding coexistence equilibria of (1) to solving the univariate equation (B.5). Analytically, this is impossible, but numerically it is easy. A solution $\hat{z}$

of (B.5) gives rise to an equilibrium of the full model (1) if and only if the resulting values N_1, N_2, and P, as determined from (B.4), are all positive.

It is remarkable that the equilibrium values $\hat{\bar{x}}$, hence the number of coexistence equilibria, can be determined from the six compound parameters β_1, β_2, t_1, t_2, ρ, and O instead of the 13 parameters of the full model (K_i, e_i, α_i, τ_i, r_i, d, θ, σ).

For completeness, we note that

$$\psi(z) = \frac{\sigma}{d}[\rho X_1(1 + t_2^2) + X_2(1 + t_1^2)]\frac{d\overline{W}}{d\bar{x}}(\bar{x}). \tag{B.8}$$

This confirms that ψ and $\frac{d\overline{W}}{d\bar{x}}$ have the same zeros, but shows that the curvature of $\overline{W}$ cannot be simply obtained by differentiating ψ.

A simple sufficient condition ensuring that at least one solution $\bar{x} \in (-\theta, \theta)$ exists is

$$\max\left\{\beta_1(1 + t_1^2), \beta_2(1 + t_2^2)\right\} \leq 1. \tag{B.9}$$

Then $\psi(-O) > 0$ and $\psi(O) < 0$. Hence, there exists an odd number of zeros in $(-O, O)$.

More generally, the condition $A_1 A_2 > 0$ ensures the existence of at least one equilibrium value z. Here,

$$A_1 = \rho\beta_1(1 + t_2^2)\exp\left[\frac{2O^2}{1 + t_1^2}\right] + 1 - \beta_2(1 + t_2^2)\,, \ \ A_2 = \beta_2(1 + t_1^2)\exp\left[\frac{2O^2}{1 + t_2^2}\right] + \rho(1 - \beta_1(1 + t_1^2))\,. \tag{B.10}$$

The assertion follows from $\psi(O) = -2OA_1$ and $\psi(-O) = 2OA_2$. Plots suggest that $A_1 A_2 > 0$ is actually necessary and sufficient. Clearly, $A_1 A_2 > 0$ gives explicit bounds for, e.g., ρ, but this requires to consider several cases. The condition $A_1 A_2 > 0$ is violated if $\beta_2 \gg \beta_1\rho$ or $\beta_2 \ll \beta_1\rho$, i.e., if there is great asymmetry.

Finally, we show that alternative equilibria with all species present arise only when there is sufficient resource differentiation. Let ψ be as above and assume $t_1 = t_2 = t$ and $O = 0$. Then we have

$$\psi'(z) = -\exp\left(\frac{z^2}{1 + t^2}\right)(1 + \rho)\frac{1 + t^2 + 2z^2}{1 + t^2} < 0 \tag{B.11}$$

for every $z \in \mathbb{R}$. By continuity, $\psi'(z) < 0$ for every $z \in \mathbb{R}$ holds if O is sufficiently small and also if $t_1 \approx t_2$. (One can calculate the first-order perturbation terms but they are a bit complicated.) Therefore, ψ is strictly monotone on $[-O, O]$, hence there can exist at most one equilibrium at which all species coexist.

B.2.   Fitness minima and disruptive selection

We prove that there is selection for increased variation at equilibria at which $\overline{W}$ is minimized. This shows that such equilibria are indeed under disruptive selection. Hence, the trait variance should evolve to higher values if the whole distribution of genetic effects were allowed to evolve. If $\tau_1 = \tau_2$, a simple explicit criterion is obtained for disruptive selection to act.

To demonstrate our assertion, we proceed as follows. We calculate the first derivative of $\overline{W}$ with respect to σ^2, transform the resulting expression to the compound variables (B.2), and evaluate at equilibrium, i.e., we substitute (B.4) and $\rho_1 = \rho\rho_2$, where ρ is calculated from (B.5). Now employ $t_1 = t_2 = t$ to obtain

$$\left.\frac{\partial \overline{W}}{\partial \sigma^2}\right|_{z=\hat{z}} = \frac{d(O^2 - t^2 - \hat{z}^2 - 1)}{2\sigma^2(1+t^2)^2}, \tag{B.12}$$

where $\hat{z}$ is the equilibrium trait value, i.e., a solution of (B.5). (If $\tau_1 \neq \tau_2$, the resulting expression is (proportional to) a complicated cubic polynomial in $\hat{z}$.) An analogous procedure shows that

$$\left.\frac{\partial^2 \overline{W}}{\partial \bar{x}^2}\right|_{z=\hat{z}} = \frac{d(O^2 - t^2 - \hat{z}^2 - 1)}{\sigma^2(1+t^2)^2}, \tag{B.13}$$

i.e., these derivatives always differ by a factor of two (this is also true if $\tau_1 \neq \tau_2$). Thus, at fitness minima (with respect to $\bar{x}$) there is selection for increased variance (and vice versa).

In terms of the original coordinates, we obtain that there is selection for increased variance at an equilibrium if and only if

$$\hat{\bar{x}}^2 < \theta^2 - \tau^2 - \sigma^2, \tag{B.14}$$

which necessarily requires $\theta^2 > \tau^2 + \sigma^2$ or, equivalently, $O^2 > t^2 + 1$. As a consequence, if there are multiple equilibria, then equilibria close to the boundary (so that the predator specializes on one of the preys) are under stabilizing selection, whereas equilibria closer to $\bar{x} = 0$ may be under disruptive selection. It seems difficult to obtain simple conditions for ESS or CSS.

B.3.   Convergence

To show that solutions converge to equilibria whenever σ_G^2 is sufficient small, we first observe that if $\sigma_G^2 = 0$, then $\bar{x}$ remains stationary and the dynamics of (1a)-(1b) correspond to the classical Lotka-Volterra dynamics of two prey species with a common predator. Takeuchi and

Adachi (1983) have studied these dynamics in great detail and have shown (cf. Theorem 6 with $\alpha = \beta = 0$) that the solutions of these equations converge to a unique stable equilibrium whenever all species are initially present. This globally stable equilibrium is given by (B.4) whenever it is feasible (i.e. $\hat{N}_1, \hat{N}_2$ and $\hat{P}$ are positive), otherwise it is given by the boundary equilibrium $(N_1, N_2, P) = (\hat{N}_1, 0, \hat{P}_1)$, $(N_1, N_2, P) = (0, \hat{N}_2, \hat{P}_2)$, or $(N_1, N_2, P) = (K_1, K_2, 0)$ which is locally asymptotically stable. Let $(\hat{N}_1(\bar{x}), \hat{N}_2(\bar{x}), \hat{P}(\bar{x}))$ denote this globally stable equilibrium for (1a)-(1b) as a function of $\bar{x}$. Without loss of generality, we assume that $\theta_1 = -\theta$ and $\theta_2 = -\theta_2$. The graph of this function, $\mathcal{E} = \{(\hat{N}_1(\bar{x}), \hat{N}_2(\bar{x}), \hat{P}(\bar{x}), \bar{x}) : \bar{x} \in [-\theta, \theta]\}$, defines a piece-wise smooth, one dimensional manifold homeomorphic to $[-\theta, \theta]$ that is a global attractor for the dynamics of (1a)-(1b) when $\sigma_G^2 = 0$, i.e., all solutions with all species initially present converge to $\mathcal{E}$. Geometric singular perturbation theory (see, e.g., Hek (2010) for a nice review) implies that if each of the equilibria in $\mathcal{E}$ are linearly stable for the corresponding ecological dynamics, then for $\sigma_G^2 > 0$ sufficiently small, there is a one dimensional manifold $\tilde{\mathcal{E}}$ homeomorphic to $[-\theta, \theta]$ "near" $\mathcal{E}$ that is a global attractor for the dynamics of (1a)-(1b). Moreover for $\sigma^2 > 0$ sufficiently small, solutions with all species initially present are asymptotically in "phase" with solutions lying in $\tilde{\mathcal{E}}$, and the dynamics on $\tilde{\mathcal{E}}$ for $\sigma_G^2 > 0$ are topological conjugate to the dynamics of

$$\frac{d\bar{x}}{dt} = \frac{d\overline{W}}{d\bar{x}}(\bar{x}, \hat{N}_1(\bar{x}), \hat{N}_2(\bar{x}))$$

on the interval $[-\theta, \theta]$. Hence, for $\sigma_G^2 > 0$ sufficiently small, solutions with all species initially present converge to equilibria of the form $(\bar{x}, N_1, N_2, P) = (\hat{\bar{x}}, \hat{N}_1(\bar{x}), \hat{N}_2(\bar{x}))$ where $\hat{\bar{x}}$ satisfies $\frac{d\overline{W}}{d\bar{x}}(\hat{\bar{x}}, \hat{N}_1(\bar{x}), \hat{N}_2(\bar{x})) = 0$. We conclude by noting that for these Lotka-Volterra equations, the assumption that each of the equilibria in $\mathcal{E}$ are linearly stable for the corresponding ecological dynamics is satisfied whenever all points of $\mathcal{E}$ are feasible (i.e. $\hat{N}_i(\bar{x}) > 0$ and $\hat{P}(\bar{x}) > 0$ for all $\bar{x} \in [-\theta, \theta]$). However, even when this restriction is violated, numerical simulations suggest that dynamics converge to an equilibrium for $\sigma^2 > 0$ sufficiently small.

REFERENCES

G. Hek. Geometric singular perturbation theory in biological practice. *Journal of Mathematical Biology*, 60(3):347–386, 2010.

L. Perko. *Differential Equations and Dynamical Systems*, volume 7 of *Texts in Applied Mathematics*. Springer Verlag, New York, 1996.

Y. Takeuchi and N. Adachi. Existence and bifurcation of stable equilibrium in two-prey, one-predator communities. *Bulletin of Mathematical Biology*, 45(6):877–900, 1983.