Ecological Archives **E091-106-A2**

Orr Spiegel and Ran Nathan. 2010. Incorporating density dependence into the directed-dispersal hypothesis. ***Ecology*** **91:1538–1548.**

Appendix B. Analytical model for the DrD paradox (the quadratic version).

Consider the same model described in Appendix A (presented here for the case of $R = 1$), modified to demonstrate nonlinear habitat response. Hence, equation (A.6) is replaced by

$$\omega = \beta - \alpha\delta^2 . \tag{B.1}$$

Consequently, survival function and fitness of the RD and the DrD strategy in the two habitats will change. The net fitness function will now be

$$\Delta F = (\beta_1 - \alpha_1 N^2 \Omega^2) N H_1 \Omega + \frac{(N - NH_1\Omega)}{(1-H_1)^2}\left(\beta_2 - \frac{\alpha_2 (N - NH_1\Omega)^2}{(1-H_1)^2}\right)$$
$$- N(H_1\beta_1 - H_1\alpha_1 N^2 + \beta_2 - \alpha_2 N^2 - H_1\beta_2 + H_1\alpha_2 N^2) \tag{B.2}$$

Here the net fitness gain is a third-order polynomial function of Ω with three following solutions (Ω_a, Ω_b, Ω_c) for DrD levels that lead to no fitness gain ($\Delta F = 0$):

$$\Omega_a = 1$$

$$\Omega_{\mathrm{b,c}} = \frac{Q \pm \sqrt{-(H_1 - 1)^2 W}}{3N(\alpha_1 - 2H_1\alpha_1 + H_1^{\,2}\alpha_1 - \alpha_2 H_1^{\,2})}$$

where

$$Q = 2N\alpha_1 H_1 - NH_1^{\,2}\alpha_1 + NH_1^{\,2}\alpha_2 - 3N\alpha_2 H_1 - N\alpha_1$$

$$W = 4\alpha_2\beta_2 H_1^{\,2} + 4\alpha_2\beta_1 H_1^{\,2} + 4\alpha_1\beta_2 H_1^{\,2} + 3\alpha_2^{\,2} N^2 H_1^{\,2} - 4\alpha_1\beta_1 H_1^{\,2} + 3\alpha_1^{\,2} N^2 H_1^{\,2} - 6\alpha_1\alpha_2 N^2 H_1^{\,2}$$
$$+ 6\alpha_1\alpha_2 N^2 H_1 + 8\alpha_1\beta_1 H_1 - 8\alpha_1\beta_2 H_1 - 6\alpha_1^{\,2} N^2 H_1 + 3\alpha_1^{\,2} N^2 + 4\alpha_1\beta_2 - 12\alpha_1\alpha_2 N^2 - 4\alpha_1\beta_1$$

One of the solutions $\Omega_{b,c}$ is in the negative range of Ω, which is biologically irrelevant. The other solution is within Ω biologically defined range (but not above Ω upper threshold) according to the numeric values of the parameters N, α_1, β_1, α_2, β_2, and H_1.

The net fitness gain function (*ΔF*) for this model has two vertex points

$$\Omega^* = \frac{3NH_1\alpha_2 \pm (H_1 - 1)\sqrt{(-3Q)}}{3N[H_1^{\,2}(\alpha_2 - \alpha_1) + \alpha_1(2H_1 - 1)]} \ . \qquad \text{(B.3)}$$

Where Q is

$$\alpha_1\beta_1H_1^{\,2} - \alpha_2\beta_2H_1^{\,2} + \alpha_2\beta_1H_1^{\,2} + \alpha_1\beta_2H_1^{\,2} - 2\alpha_1\beta_2H_1 + 2\alpha_1\beta_1H_1 + \alpha_1\beta_1 + \alpha_1\beta_2 - 3\alpha_1\alpha_2N^2 \ .$$

Unavoidably, One of the *Ω** solution is in the negative range of the *Ω* parameter, and therefore undefined.

Results

To demonstrate a numerical solution to this nonlinear model and the net fitness gain (*ΔF*) as a function of the DrD level, *Ω*, we use an arbitrarily chosen set of values for the model parameters. Note that the values of *α* cannot correspond to the linear model as it is now limited to the range $0<\alpha<1/\delta^2$ instead of $0<\alpha<1/\delta$. The results are similar to those of the linear model, where for each parameter set, the fitness gain rises to a maximum at Ω^*, and then drops off as *Ω* increases (Fig. B1).

The combined effect of the density-dependent suitability ratio and the density-independent suitability ratio (*β* ratio) on Ω^* shows an asymptotic pattern (Fig. B2). As in the linear model the effect of *β* ratio is significantly stronger in the lower range, but it reaches saturation in an asymptote at the value of *Ω**= 6.1 for this specific example, or of

$$\Omega^*\Big|_{\beta_1=1,\beta_2=0} = \frac{-3NH_1\alpha_2 \pm \sqrt{3[(H_1-1)^2(H_1^{\,2}\alpha_1 - \alpha_2H_1^{\,2} - 2H_1\alpha_1 + 3\alpha_1\alpha_2N^2 + \alpha_1)]}}{3N(\alpha_1 - 2H_1\alpha_1 + H_1^{\,2}\alpha_1 - \alpha_2H_1^{\,2})}$$

for the general case. When density-independent suitability ratio approaches its maximal limit the asymptote is

$$\lim_{\alpha_2\to 1/N}(\Omega^*) = \frac{3NH_1 \pm \dfrac{H_1}{N}\sqrt{3(\beta_2-\beta_1)(H_1-1)^2}}{3H_1^{\,2}} \ .$$

Fig. B1.

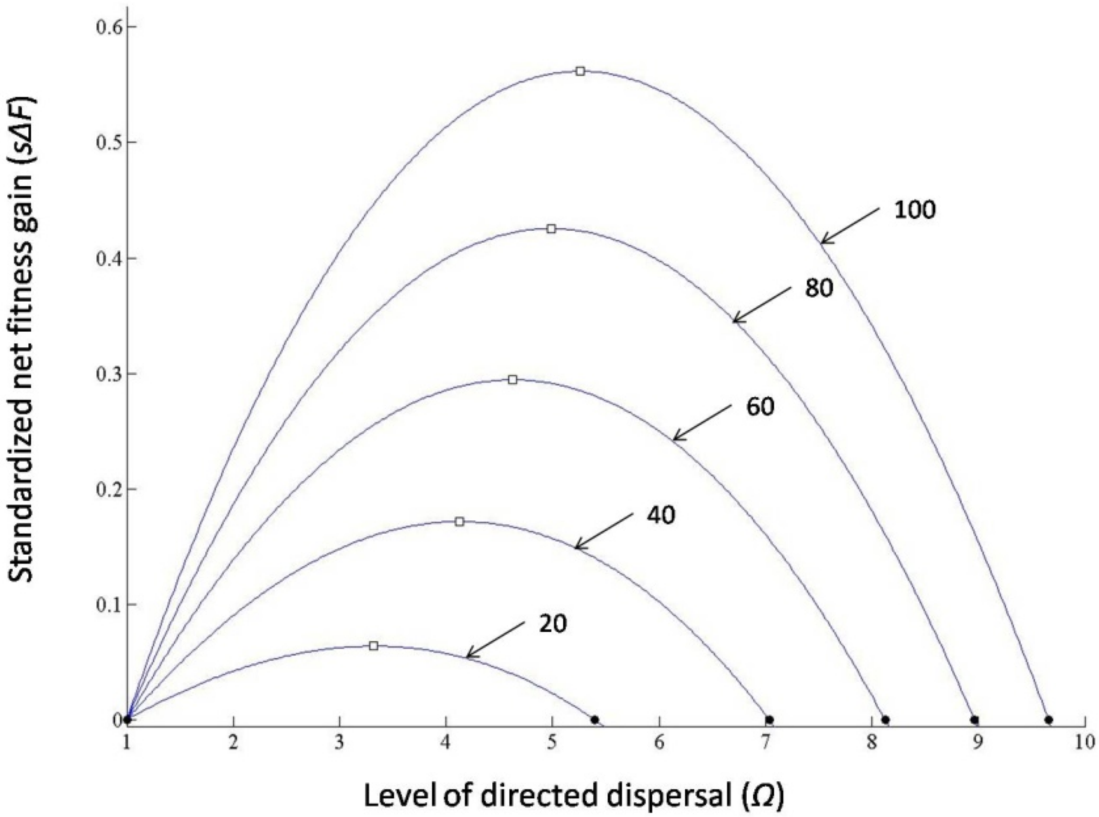

FIG. B1. Results of the analytical nonlinear model describing the effect of DrD level (Ω) on expected fitness gain of DrD strategy in comparison with random dispersal ($s\Delta F$; standardized by fecundity). Each line represents a model solution using a different ratio of density-dependent suitability between the two simulated habitats (i.e., α_2/α_1 ratio; values noted with arrows). A higher ratio represents a stronger difference between habitats, hence a higher fitness gain for a given Ω, along with a wider range of positive fitness gain values. Points of maximum fitness gain (Ω^*) and zero fitness gain (Ω_a, Ω_b) are marked (empty squares and solid circles, respectively). Other parameters were set as follows: $N = 1000$, $H_1 = 0.1$, $\alpha_1 = 9*10^{-9}$, $\beta_1 = 1$, $\beta_2 = 1$.

Fig. B2.

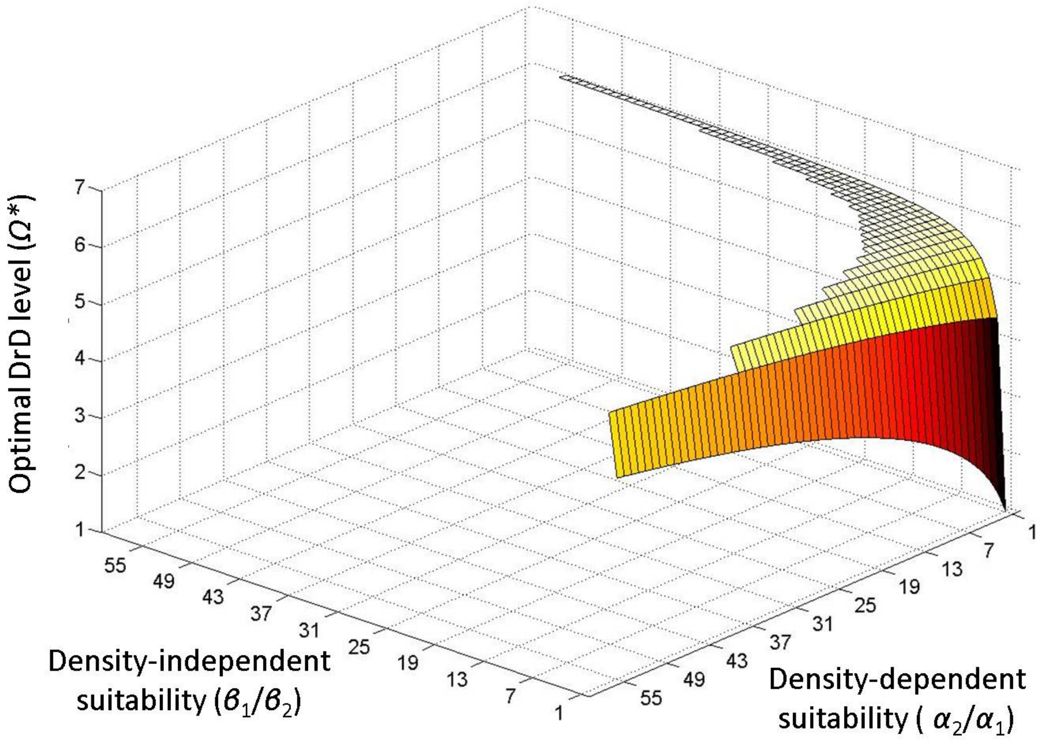

Fig. B2. The effect of differences in habitat suitability on DrD levels (Ω*) maximizing the net fitness gain for nonlinear habitat response. Increasing values in both horizontal axes indicate increasing differences between habitats, either in density-independent suitability (β ratio: β_1/β_2) or in their density-dependent suitability (α ratio: α_2/α_1). The Ω* value rises fast with the increase in the density-independent suitability ratio until it reaches an asymptote at Ω*= *6.1*. The asymptote of high density-dependent suitability is not reachable within the parameters definition range. Other parameters were set as follows: $N = 1000$, $H_1 = 0.1$, $\beta_1 = 1$, $\alpha_1 = 9*10^{-9}$.