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

Appendix A. Analytical model for the DrD paradox (a linear version).

Consider a region with a population of a single plant species and two habitats differing in their suitability for establishment of this plant. To assess the adaptive value of directed dispersal (DrD) towards the favorable habitat (where survival probability is higher), relatively to random dispersal (RD), we calculated the expected difference in fitness (i.e., the difference in the expected number of surviving offspring). We subtracted the total expected fitness of the RD strategy in both habitats from the total expected fitness of the DrD strategy in both habitats. The expected net fitness gain of the DrD over the RD strategy, ΔF, is thus

$$\Delta F = \left(F_{DrD1} + F_{DrD2}\right) - \left(F_{RD1} + F_{RD2}\right) \tag{A.1}$$

where F_{DrD} and F_{RD} are, respectively, the expected fitness of the DrD and RD strategies; subscripts 1 and 2 denote the favorable and unfavorable habitats. Equation (A.1) can be solved analytically by incorporating the fraction of seeds dispersed to each habitat by each strategy and calculating seed-survival probability given the resulting seed density in each habitat and the habitat basic properties. The model follows neutrality assumptions where all individuals in the population are identical in fecundity and dispersal strategy. Also the seeds are assumed to arrive at an unoccupied area, thus density effects respond to seed densities only.

Calculating Fitness for the RD strategy:

The proportion of seeds expected to arrive at each habitat under the RD strategy is equivalent to proportional area of each habitat. The number of seeds dispersed by this strategy (n_{RD}) to the two habitats is thus

$$n_{RD1} = NH_1 \tag{A.2}$$

and

$$n_{RD2} = N(1 - H_1) = N - NH_1, \tag{A.3}$$

where N is the total fecundity of all plants, assumed to be constant across individuals and habitats (hence N can be view as a product of number of plants and number of seeds per plant). H_1 is the proportion of the favorable habitat from the total area. In the main text we assume, for simplicity, that the total area of the region (R) equals one spatial unit (e.g., one square kilometer); in this appendix, we develop the general case in which seed density in each habitat (δ_{RD1} and δ_{RD2}) is calculated by dividing seed number at each habitat (equation A.2 and A.3) by the corresponding habitat area, thus

$$\delta_{RD1} = \frac{n_{RD1}}{RH_1} = \frac{N}{R} \tag{A.4}$$

and

$$\delta_{RD2} = \frac{n_{RD2}}{R(1 - H_1)} = \frac{N - NH_1}{R(1 - H_1)} = \frac{N}{R}\ . \tag{A.5}$$

Thus, the density of dispersed seeds under the RD strategy is identical for the two habitats, as expected under random dispersal.

The negative effect of seed density on seed survival can be expressed linearly as

$$\omega = \beta - \alpha\delta \tag{A.6}$$

where ω is the proportion of surviving seeds, α and β are two distinct habitat properties affecting seed survival independently of the dispersal strategy. The parameter α determines habitat density-dependent suitability and the parameter β determines habitat density-independent suitability (see main text for details on both parameters). Equation (A.6) is restricted to the biologically relevant parameter range of $0<\omega<1$, which in turn limits the parameters in both habitats and for both dispersal strategies (RD and DrD) to the range $0<\beta<1$ and $0<\alpha<1/\delta$ (i.e., $0<\alpha< R/N$).The proportion of surviving seeds in each habitat is calculated by substituting equation (A.4) and equation (A.5) into equation (A.6), thus

$$\omega_{1RD} = \beta_1 - \alpha_1 \frac{N}{R} \quad (A.7)$$

and

$$\omega_{2RD} = \beta_2 - \alpha_2 \frac{N}{R}. \quad (A.8)$$

To calculate the total fitness of the RD strategy, we multiply the survival probabilities (equations A.7 and A.8) by the corresponding number of seeds dispersed to each habitat (equations 2A and 3A), and sum the number of surviving seeds in the two habitats combined:

$$F_{RD} = F_{RD1} + F_{RD2} = n_{RD1}\omega_1 + n_{RD2}\omega_2 =$$

$$((\beta_1 - \alpha_1 \frac{N}{R})H_1 + \left(\beta_2 - \alpha_2 \frac{N}{R}\right)(1 - H_1))N. \quad (A.9)$$

Calculating Fitness for the DrD strategy:

The proportion of seeds expected to disperse to the favorable habitat under DrD strategy is Ω-folds higher than the proportion expected by the RD strategy (see text for details and further explanation of this parameter). Recalling that $1 \leq \Omega \leq 1/H_1$, the number of seeds dispersed by plants exhibiting the DrD strategy (n_{DrD}) to the two habitats is thus

$$n_{DrD1} = NH_1\Omega \quad (A.10)$$

and

$$n_{DrD2} = N - NH_1\Omega. \quad (A.11)$$

For the DrD strategy, the resulting seed densities (δ_{DrD1} and δ_{DrD2}) in the two habitats, calculated using the same procedure described for the RD strategy, are

$$\delta_{DrD1} = \frac{n_{DrD1}}{RH_1} = \frac{N}{R}\Omega \quad (A.12)$$

and

$$\delta_{DrD2} = \frac{n_{DrD2}}{R(1 - H_1)} = \frac{N}{R}\frac{(1 - H_1\Omega)}{(1 - H_1)}. \quad (A.13)$$

Notice that as long as Ω is greater than 1 the term $(1-H_1\Omega)/(1-H_1)$ in equation (A.13) is always smaller than δ_{DrD1} in equation (A.12). Thus, unlike the RD strategy in which seed densities in both habitats are equal, the DrD strategy (Ω>1) necessitates that seed densities in the favorable habitat will be higher than those in the unfavorable habitat.

Applying the same linear density-dependent seed survival function equation (A.6) as for RD strategy above, we obtain

$$\omega_{1DrD} = \beta_1 - \alpha_1 \Omega \frac{N}{R} \tag{A.14}$$

and

$$\omega_{2DrD} = \beta_2 - \frac{\alpha_2(1-H_1\Omega)}{R(1-H_1)} . \tag{A.15}$$

The total fitness of the DrD strategy can be calculated equivalently to equation (A.9) using equations (A.10), (A.11), (A.14) and (A.15):

$$F_{DrD} = F_{DrD1} + F_{DrD2} = n_{DrD1}\omega_1 + n_{DrD2}\omega_2 =$$

$$N((\beta_1 - \alpha_1 \Omega \frac{N}{R})H_1\Omega + \left(\beta_2 - \frac{\alpha_2 N(1-H_1\Omega)}{R(1-H_1)}\right)(1-H_1\Omega)) . \tag{A.16}$$

Comparing the adaptive value of the two strategies and finding the optimal DrD level

The net fitness gain of the DrD strategy in comparison to the RD strategy is calculated by solving equation (A.1), using values from equations (A.9) and (A.16), thus

$$\Delta F = (\beta_1 - \alpha_1 \Omega \frac{N}{R})NH_1\Omega + \left(\beta_2 - \frac{\alpha_2(N-NH_1\Omega)}{R(1-H_1)}\right)(N-NH_1\Omega)$$

$$-(\beta_1 - \alpha_1 \frac{N}{R})NH_1 - \left(\beta_2 - \alpha_2 \frac{N}{R}\right)(N-NH_1) . \tag{A.17}$$

Since N, α_1, β_1, α_2, β_2, R and H_1 are set parameters, the net fitness gain is a second-order polynomial function of Ω with two following solutions (Ω_a, Ω_b) for DrD levels that lead to no fitness gain (ΔF= 0):

$$\Omega_a = 1$$

and

$$\Omega_b = \frac{\left[R(1-H_1)(\beta_2-\beta_1)+N(\alpha_1-H_1(\alpha_1-\alpha_2)-2\alpha_2)\right]}{N\left[H_1(\alpha_1-\alpha_2)-\alpha_1\right]}.$$

Because the first and second terms in equation (A.17) imply a negative coefficient of Ω^2, this function should have one vertex (maximum) point, reflecting the highest possible fitness gain for the optimal value of DrD level. To determine this maximum point, we calculated the first and second derivative of equation (A.17) and obtained the value of Ω at $\Delta F'$=0. Because the first derivative is

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

$$= \frac{NH_1[(1-H_1)(2\alpha_1 N\Omega - \beta_1 R + \beta_2 R) + 2\alpha_2 N(H_1\Omega - 1)]}{R(1-H_1)}$$

and the second derivative is always negative

$$\Delta F'' = -2\alpha_1\frac{N^2}{R}H_1 - \frac{2\alpha_2 N^2 H_1^2}{R(1-H_1)},$$

the vertex point is the maximum point of that function. The value of Ω at the maximum of the net fitness gain function (i.e., the optimal DrD level Ω^*) is

$$\Omega^* = \frac{[(1-H_1)(\beta_1 R-\beta_2 R)+2N\alpha_2]}{2N(\alpha_1-H_1\alpha_1+H_1\alpha_2)}. \qquad \text{(A.18)}$$

This value approaches an asymptote as the difference in habitat suitability increases from zero. When the density-dependent suitability of the unfavorable habitat deteriorates, (i.e., when α_2 increases to its upper limit R/N), the value of Ω^* reaches the limit of

$$\lim_{\alpha_2\to 1/N}(\Omega^*) = \frac{2+R(1-H_1)(\beta_1-\beta_2)}{2H_1}$$

Thus, for β ratio=1, the limit of Ω^* is $1/H_1$ and for high β-ratio the asymptote approaches the value of Ω^{*}= 1+R(1- H_1)/H_1. When the difference between habitats in their density-independent suitability is at its most extreme (i.e., when β_1= 1 and β_2= 0,) Ω^{*} has the value

$$\Omega^{*}\Big|_{\beta_1=1,\beta_2=0} = \frac{R(H_1-1)-2N\alpha_2}{2N(\alpha_1 H_1-\alpha_2 H_1-\alpha_1)}\,.$$

Yet, since Ω^{*} is constrained to 1/H_1, this asymptote may fall out of range for many possible value combinations of the parameters. For instance, when α ratio equals 1, this expression is always above the 1\H_1 maximum value.