Ecological Archives **E091-106-A4**

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

Appendix D. The effect of variation in the DrD level on mutant establishment.

Many dispersal systems are characterized by inherent stochasticity. This may be caused by environmental factors that change habitat suitability in time (Bleher and Bohning-Gaese 2001, Schupp et al. 2002), or by spatiotemporal fluctuations in dispersers abundance and behavior (Herrera 1998, Bleher and Bohning-Gaese 2001). The magnitude and frequency of these changes may influence the spatiotemporal *consistency* of DrD levels experienced by a certain plant species. Because variation in DrD levels around a given mean value may increase the conflict with density-dependent mortality on the one hand, but limit the DrD advantage on the other hand, we predict that the invasion of the DrD mutant will be negatively affected by increasing variance in DrD levels among mutants.

To test this prediction, we incorporate the effect of variation in DrD levels into the simulation model by simulating population dynamics associated with a DrD mutant invasion for Ω values sampled from eight normal distributions. All distributions have similar mean of $\Omega = 5$ (the analytically calculated optimal value for used parameters), but they differ in their standard deviations, with values of σ_{Ω}= 0, ⅓, ⅔, 1, 1⅓, 1⅔, 2 and 2⅓ used. These σ_{Ω} intervals allow Ω to fluctuate through all of its biologically-constrained range (i.e., 1 to $1/H_1 = 10$). Fifty values were sampled from each Ω distribution, each used for 100 model runs, making for 40,000 model runs in total. Means and SE of the sampled Ω values are presented in Fig. D1: A.

The results show that increasing σ_{Ω} negatively affects the invasion process (Fig. D1: B,C, and D). We use linear regression to quantify indices response to increasing σ_{Ω} values. All three indices (the final number of mutant individuals, the number of generations required to the mutant establishment and the mutant population persistence) show strong (R^2= 0.98, 0.63 and

0.81, respectively), significant ($P = 0.0001$, 0.02 and 0.002, respectively) responses. Yet, when considering the magnitude of the effect, (i.e., the slopes of the regressions) it is clear that the negative effect is important for the final mutant population only. An increase in one standard deviation unit in Ω leads to a decrease of 99.6 individuals in the mutant population, but only to a change of 0.3 generations and of 0.03 in the persistence ratio which can be considered as biologically unimportant. This difference between the former index and the latter two indices reflects the difference in their response of establishment process to the mutant DrD level. While mutant population size is negatively affected when Ω differs from Ω^* towards both ends (Fig. 3A), the other two indices have monotonic response to Ω (Fig. 3C, E). Runs with low Ω values (where mutant advantage over the RD wild type is minimized) lead to slow establishments and low persistence ratios, but this may be partially balanced by runs with high Ω values where establishment is fast and with high persistence rations (Fig. 3C, E). this balancing effect is not true when considering mutant population size where high Ω also decrease population size.

In addition to the effect of variation in DrD level on the general trend, high σ_Ω values entail a high frequency of model runs with extreme Ω values and therefore less predictable results, as can be seen with the obvious trend of increase in the error bars, representing less uniform results for Ω values drawn from the same distribution.

Overall, increasing variation in DrD levels negatively affects establishment process, suggesting that both consistency and amplitude of DrD levels are important aspects of dispersal service directing seeds to favorable establishment sites.

LITERATURE CITED

Bleher, B., and K. Bohning-Gaese. 2001. Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. Oecologia 129:385–394.

Herrera, C. M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. Ecological Monographs 68:511–538.

Schupp, E. W., T. Milleron, and S. E. Russo. 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. Pages 19–33 *in* D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed dispersal and frugivory: ecology, evolution and conservation. CAB International, Oxfordshire, UK.

Fig. D1.

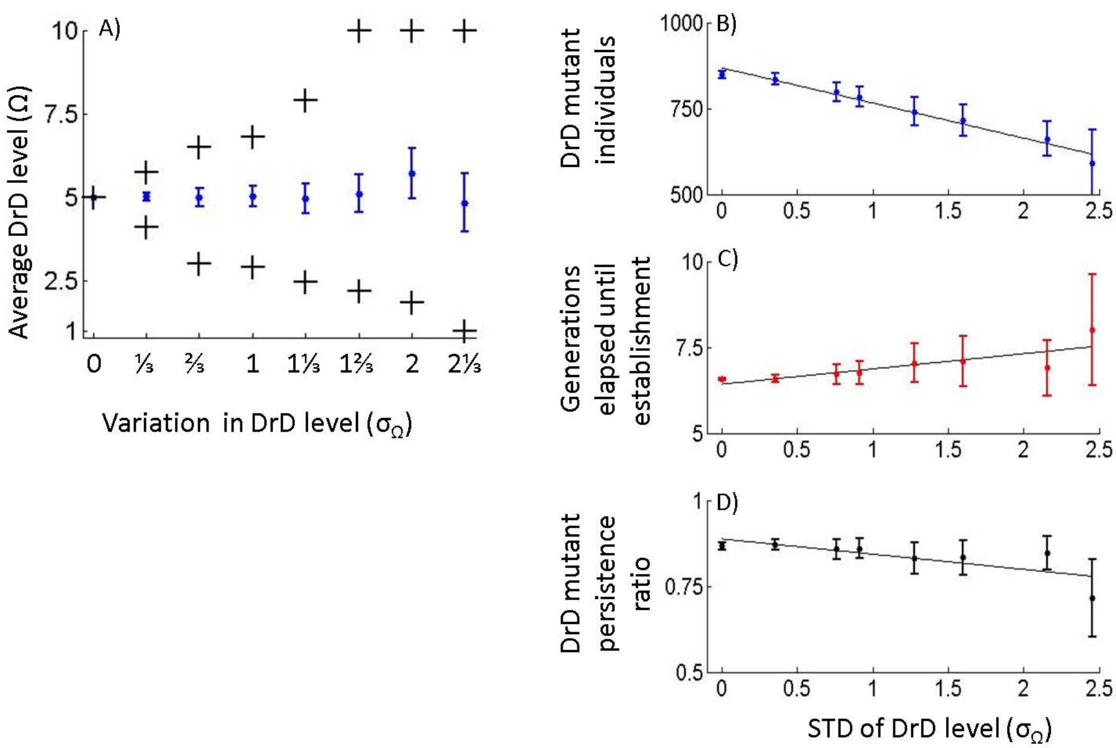

FIG. D1. Simulation results showing the effect of the variation in DrD level (σ_Ω) on the invasion process of the DrD mutants into a RD population. (A) Means of the fifty Ω values sampled from each of the eight normal distributions, all with mean Ω value of 5 and increasing standard deviation. Minimum and maximum sampled values are also presented ('+' symbols). The right column presents the effects on the three indices: (B) Mutant final population size, (C) the number of generations elapsed until establishment and (D) the proportion of model runs in which the mutant population persisted throughout the simulation. The lines are linear regression trend lines with R^2= 0.98, 0.63 and 0.81; P = 0.001, 0.02, and 0.002, respectively. Error bars represent ±1 SE. all other parameters correspond to Fig 4.