

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

Appendix C. Simulation model of a DrD mutant invasion in a random-dispersal (RD) population.

The following simulation model is designed to explore the temporal dynamics of the invasion process of a particular DrD strategy in a RD population and vice versa. This spatially implicit model simulates the invasion process over 100 successive nonoverlapping generations. In Appendix D we also incorporate variation in the level of Ω to demonstrate that variance in Ω levels will negatively affect the invasion process of a DrD mutant.

As with the analytical model, we simulate a region with two habitats differing in their suitability for establishment. Here, a single DrD mutant is introduced into an initial finite population of wild-type randomly dispersed (RD) individuals. DrD mutants do not differ from RD individuals in their fecundity or in any other aspect except their dispersal strategy: while RD individuals disperse seeds randomly between habitats, according to their areal proportion, DrD mutants direct a Ω -fold higher proportion of the seeds to the favorable habitat.

We assume nonoverlapping generations (e.g., annual plants) with all individuals simultaneously dispersing 10 seeds before dying (thus all sites are unoccupied and free for seed deposition). Each dispersed seed is deposited in a site, potentially becoming an adult plant in the next generation. For each generation, seeds of all plants are pooled (both strategies combined) and assigned to the two habitats using a uniform random variable with appropriate proportions for each strategy. For instance, the probability of a seed dispersed from a DrD mutant plant to arrive to the favorable habitat is $\Omega \cdot H_1$.

While the analytical model assumes homogenous habitats with no restriction on the number of established plants, the simulation models assumes that each habitat type consists of

a finite number of sites, each might be occupied by a single plant. We make this assumption to limit habitat maximal occupancy, preventing an artificial overflow caused by the stochastic nature of the seed arrival and survival randomizations (see below). We arbitrarily use a total number of 1000 sites in the simulated landscape, all initially occupied (i.e., the initial population size is 1000 individuals and frequency of mutants is 0.1% of the population).

Following the dispersal (arrival) stage, habitat-specific density-independent suitability determines seed-to-adult survival probability. Thus, irrespective of seed arrival during dispersal phase, and although usually dispersed seeds will arrive to most sites in both habitats, the proportion of sites considered as occupied (a seed arrives and survives to maturity) depends on the habitat quality. Note that the parameters α and β of the analytical model are slightly modified to allow for spatial consideration: the density-dependent suitability (α) represents the relative density of sites in the habitat (thus the favorable habitat has more than H_1 sites). The density-independent suitability (β) represents the probability of a seed surviving to maturity. Altogether, surviving seeds of the two types (DrD and RD) in the two habitats constitute the population of the following generation.

Three indices are used to quantify the effect of the DrD level and its increasing variation on the invasion process: (1) the mutant population size (number of individuals at the end of the simulation); (2) the number of generations until an invading DrD mutant is established. Establishment is defined as when the mutants constitute >10% of the population. This threshold is much higher than the initial condition of the simulation (0.1%) and, above the threshold, extinction was extremely unlikely. Yet, the threshold is still sufficiently low to document establishment when DrD does not dominate the population, which was a common result for many combinations of the parameters. (3) The persistence ratio of the mutant population, defined as the proportion of model runs in which mutants did not go extinct after 100 generations. For each set of parameter values, we averaged the results over 100 model

runs.

Results

In general, the results of the simulation model agree with those of the analytical model, further highlighting the trade-off depicted by the DrD paradox. Yet, by observing also the dynamic of the invasion process, the simulation adds the temporal effects of the DrD level on establishment, and shows that some properties of the process are actually facilitated by high DrD levels and not by intermediate levels as expected.

Typical model runs illustrate that mutant frequency increases both in the favorable (Fig. C1, upper row) and the unfavorable (Fig. C1, middle row) habitats, rapidly reaching a steady level after 10–50 generations, and then fluctuating gently. In high DrD levels (Fig. C1, right column), the final proportions of DrD mutants reflect the balance between their higher success in the favorable habitat (Fig. C1C), and the higher success of RD individuals in the unfavorable habitat (Fig. C1F), mostly due to shortage of mutant seeds allocated to this habitat. Moreover, the RD population that dominates the unfavorable habitat produces a constant seed flux to the favorable habitat, and may prevent mutants from completely overtaking it (Fig. C1C).

The initial population size affects the proportion of model runs where mutants go extinct (smaller mutant proportions increase likelihood of stochastic extinction during the first generations). This may slightly change the quantitative value of the mutant persistence ratio index, but has no qualitative effect on our main findings described below. The results are insensitive, however, to the number of sites in the simulated landscape. When the initial population does not occupy all sites, the population expands during the first 2–3 generations, and the process shows exactly the same dynamics once all sites are occupied. Similarly, the initial location of mutants has no effect as seed allocation among the habitats as it is

determined by the dispersal strategy and not by the location of the mother plant (i.e., no dispersal barrier between habitats).

According to the simulation model, intermediate levels of DrD are likely to maximize fitness. Increasing DrD level adds to mutant population at the lower range of Ω but has an opposite effect at the higher range (Fig. 3A for α ratio = 6, 8 and also Fig. 3B for $\Omega = 1, 10$). These negative effects of high levels of DrD arise mainly from seed shortage in the unfavorable habitat that is not compensated for by a higher success in the favorable habitat. However, the time required to establish (for the model runs during which mutants did not become extinct) shows a different pattern in which the invasion process is faster for the higher DrD levels of the invading mutant and not for intermediate DrD levels (Fig. 3C). In addition, mutant persistence ratio in the population increases with Ω (Fig. 3E). The data for α ratio equals 1 (i.e., when the two habitats do not differ in their quality) is absent for generations until establishment (Fig. 3C) and zero for individual number (Fig. 3A) and persistence (Fig. 3E). This is because the mutant has no advantage over the RD wild types in this situation and randomly goes extinct (being one out of many in the population of first generation).

When inter-habitat differences increase, DrD is expected to be more beneficial because mutant advantage is maximized. Indeed, for a given Ω value, increasing α ratio facilitates invasion, increases the final mutant population size (Fig. 3A), and minimizes both time till establishment (Fig. 3C) and the chances for the mutant to go extinct (Fig. 3E). Although the density-dependent suitability ratio presented here increases by equal intervals (excluding the first value of α ratio = 1), differences in all three indices are not equally spaced, reflecting interaction between DrD levels and habitat properties. This is pronounced for the second index in particular where, for instance, above α ratio = 4 and $\Omega = 5$ establishment is quickly achieved by directing a significant fraction of the seeds to the favorable habitat. Thus, further increase in the habitat suitability or in the DrD level does not contribute to faster establishment.

DrD level of the invaded population also influences its persistence and the invasion dynamics. An invaded population with an optimal DrD level ($\Omega^* = 5$) is completely resistant to invasion by DrD mutant of any Ω , including a RD mutant (hence the line $\Omega = 5$ is missing in the right column of Fig. 3). When the invaded population has a DrD value close to optimal it is invaded by fewer mutants (Fig. 3B), invasion takes a longer time (Fig. 3D) and occurs in a smaller proportion of cases (Fig. 3F). Moreover, an invaded population with a high DrD level can be easily invaded by a DrD mutant with low Ω , which directs enough seeds to establish in the nonfavorable habitat. Similarly, populations with low DrD levels are easily invaded by mutants with high DrD levels. This mechanism of unbalanced seed allocation between habitats at extreme DrD levels contributes also to shorter establishment times of the mutant invading the population (Fig. 3D), and to a higher probability of persistence (Fig. 3E).

To conclude, the results of the simulation model support the prediction that the DrD level plays an important role in determining the temporal dynamics of the invasion process. As predicted, the final number of DrD mutants invading a RD population, and the resistance of a DrD population to invading RD individuals, are maximized in *intermediate* DrD levels suggesting an evolutionary stable strategy (ESS). Nevertheless, *high* DrD levels can facilitate both the likelihood and the duration of a DrD mutant establishment process in a RD population. This result was not expected intuitively from the analytical model, and arises from a rapid establishment in the favorable habitat first, and then in the entire population.

Fig. C1

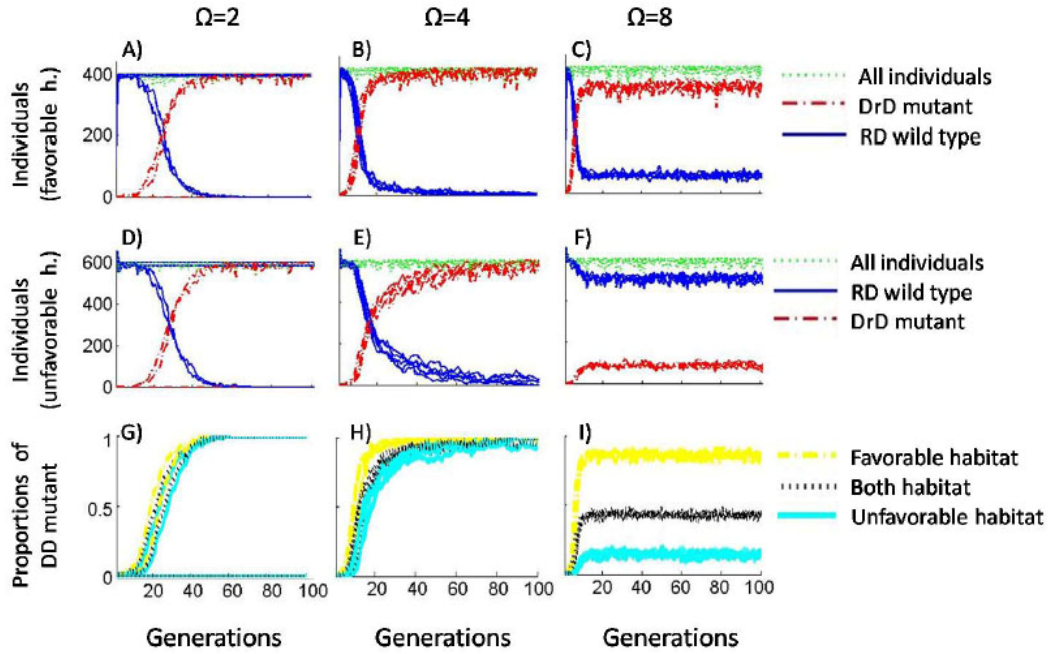


FIG. C1. Examples of the invasion process of a single directly-dispersed (DrD) mutant into a population of randomly-dispersed (RD) wild type individuals, illustrated by five simulation runs for three DrD levels ($\Omega = 2, 4$ and 8 ; left, middle and right columns, respectively). The first (A, B, and C) and the second (D, E, and F) rows show number of individuals in the favorable and unfavorable habitats, respectively. The third row (G, H, and I) shows the proportion of the DrD mutant in the entire population. For low DrD levels ($\Omega = 2$), the mutant establishes in the population only in two out of five runs. In addition, when establishment did occur, it took longer than for intermediate DrD levels ($\Omega = 4$), where the DrD mutant established in all five runs. For high DrD levels ($\Omega = 8$), the DrD mutant established in all five runs, mainly due to its dominance in the favorable habitat only (C), but was almost absent from the unfavorable habitat (F), and hence only 50% of the population (I). Parameters were set as follows: $N = 1000$, $H = 0.1$, $\alpha_1 = 6$, $\alpha_2 = 1$, $\beta_1 = 1$, $\beta_2 = 1$. Analytically calculated optimal Ω for these value is $\Omega^* = 4$.

