

## Exercise 4: Structured populations

### Part 1: Plants with seed bank

Consider a population of annual plants with the following life cycle: Seeds are produced at the end of summer, after which all adult plants die. A proportion of the seeds survives winter and some of these seeds then germinate in the following spring. Some of the seeds that don't germinate survive another winter and may germinate in the spring following this second winter. No seeds germinate after more than two winters.

4.1 Justify the model

$$N_{t+2} = \alpha\sigma f N_{t+1} + \beta(1 - \alpha)\sigma^2 f N_t \quad (1)$$

and interpret the parameters biologically. Write the model as a Leslie matrix. Derive the life-time reproductive success. What is the minimum value of  $f$  for which the population can grow in the long term?

4.2 Assume that each plant has a fixed amount of resources available for seed production and that these resources are distributed evenly among its seeds. Further, assume that a seed's probability to survive winter is proportional to the resources it contains, but of course at most one. Based on this information, write down the equation for this trade-off between  $f$  and  $\sigma$ . How should the plant invest its resources, i.e. what strategy will evolve? Speculate what will happen in a more realistic model where the survival probability approaches 1 asymptotically?

### Part 2: Seed dispersal model

A population of plants grows on three patches, *west*, *central*, and *east*. In each generation, each plant individual produces  $b$  seeds, of which a fraction  $d$  disperse and  $1 - d$  remain on the parental patch. Of the dispersing seeds, a fraction  $f$  disperse west and  $1 - f$  disperse east. Dispersal is only between neighboring patches and seeds that disperse west from the *west* patch, or east from the *east* patch, land on infertile ground and die. After seed dispersal, the parents die and all seeds that have landed on one of the patches grow into adult plants.

4.3 Draw a flow diagram of the model and construct the transition matrix. What is the long-term growth rate? What are the sensitivities for the model parameters  $b$ ,  $d$ , and  $f$ ? If the parameters could evolve, in which direction should we expect them to evolve?

4.4 What is the long-term distribution of plants across the three patches? What are the reproductive values of the plants in each patch? Discuss the biological intuition behind these results.

4.5 Assume now that dispersal with probability  $d_w$  is initially entirely from west to east ( $f_w = 0$ ), following the prevalent wind direction. A mutant with an additional mode of dispersal then arises, for example through sticky seeds that are transported by animals. Mutant seeds are dispersed via this mode with probability  $d_a$  (they are still wind-dispersed with probability  $d_w$ ) and they can be dispersed in both directions ( $f_a > 0$ ). Under which conditions will such a mutant be able to grow and dominate the population? Discuss the general case and the case where animals have non-directional dispersal  $f_a = 1/2$ . For a given fixed wind dispersal probability  $d_w$ , determine the optimal rate of animal dispersal  $d_a$ .