*Supplementary material to:*

**Appendix 3: The Perron-Frobenius Theorem**

*From:*

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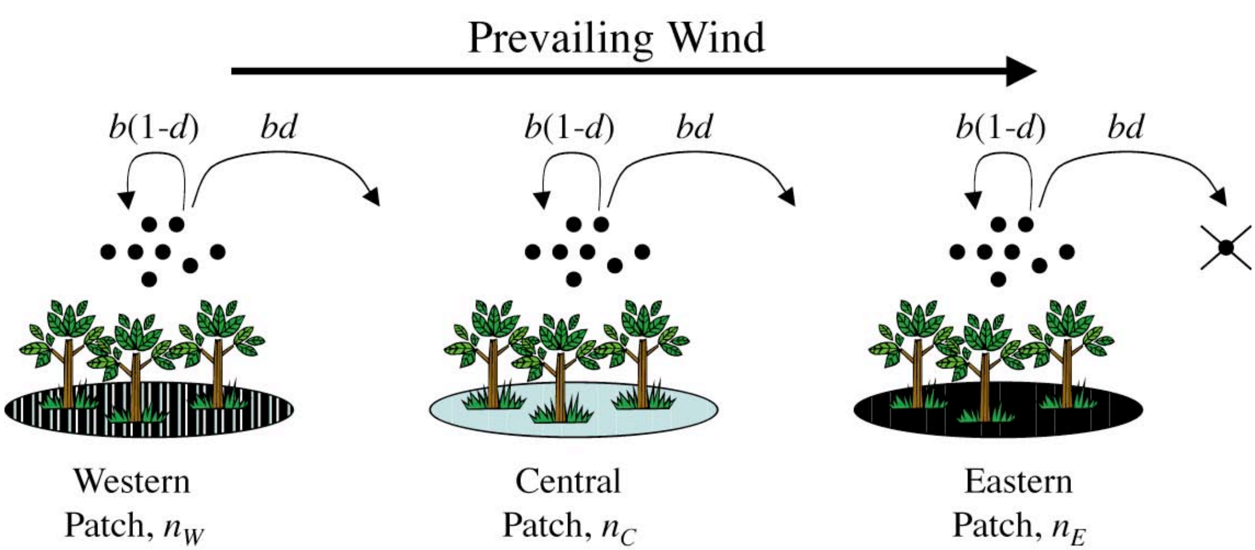
## Supplementary Material A3.1: Seed dispersal among patches

Here we explore a model of seed dispersal and use this model to illustrate the Perron-Frobenius theorem (Appendix 3). Consider a population of annual plants that live in three distinct patches (Figure A3.1.1). Let's suppose that the species has wind-dispersed seeds and that there is a prevailing direction to the wind such that seeds either remain on the same patch or disperse from west to east (Figure A3.1.1). We want to construct a model to predict the dynamics of the population size in each patch.

**Figure A3.1.1: A schematic of a three-patch plant population.**




Consider the western patch. Each plant is assumed to produce *b* seeds every year. A proportion *d* disperses and gets blown eastward to the central patch. Therefore, the number of plants in the western patch next year will be

$$n_W(t+1) = n_W(t)b(1-d), \tag{A3.1.1a}$$

where $n_W(t)$, $n_C(t)$, and $n_E(t)$ are the number of plants in the western, central, and eastern patch in year *t*. Similarly, the number of plants in the central patch in year *t* + 1 will be the sum of those seeds that immigrated from the western patch, plus those seeds that were produced in the central patch and did not disperse:

$$n_C(t+1) = n_W(t)bd + n_C(t)b(1-d). \tag{A3.1.1b}$$

Finally, the number of seeds in the eastern patch next year will be the sum of those that immigrated from the central patch, plus those that were produced in the eastern patch and remained there:

$$n_E(t+1) = n_C(t)bd + n_E(t)b(1-d). \tag{A3.1.1c}$$

Equations (A3.1.1a-c) can be written in matrix notation as

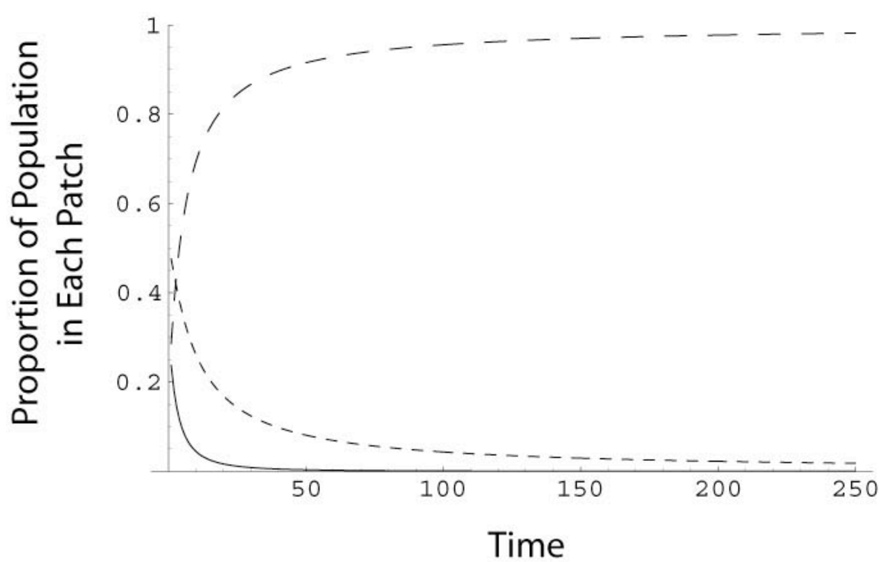
$$\begin{pmatrix} n_W(t+1) \\ n_C(t+1) \\ n_E(t+1) \end{pmatrix} = \begin{pmatrix} b(1-d) & 0 & 0 \\ bd & b(1-d) & 0 \\ 0 & bd & b(1-d) \end{pmatrix} \begin{pmatrix} n_W(t) \\ n_C(t) \\ n_E(t) \end{pmatrix}. \tag{A3.1.2}$$

The transition matrix in system (A3.1.2) is lower triangular, and we therefore know that its eigenvalues are the diagonal elements, $b\,(1-d)$ repeated thrice (Rule P2.26). Nevertheless, let's apply the Perron-Frobenius Theorem (Appendix 3) to this example to get a better feeling for how it can be used. First let's check whether the transition matrix is primitive, by raising the transition matrix to the $3^2 - 2(3) + 2 = 5^{\text{th}}$ power (Appendix 3). Doing so shows that the transition matrix is not primitive because some of the resulting entries are zero. Next, we can follow the recipe of Appendix 3 to check if the matrix is irreducible. We first add the $3 \times 3$ identity matrix to it, and then raise this to the $n - 1 = 2^{\text{nd}}$ power. The resulting matrix also has entries that are zero, so the matrix is not irreducible either.

Let's stop for a moment and try to understand these findings. A matrix is irreducible if all classes can be reached from all other classes in a finite number of time steps. An examination of Figure A3.1.5 reveals why the current transition matrix is not irreducible. Due to the prevailing wind, seeds in the eastern patch can never move to the central patch or to the western patch. Furthermore, seeds from the central patch can never reach the western patch either.

The Perron-Frobenius Theorem (Appendix 3) tells us to expect that there might be multiple real leading eigenvalues when the transition matrix is reducible. In fact, we know that this is true, because all three eigenvalues equal $b(1-d)$. The Perron-Frobenius Theorem also tells us that some of the elements of the dominant (right) eigenvector might be zero. In other words, the proportion of the population in some classes might go to zero at the stable class distribution. As you can show (Problem A3.1.1), the dominant right eigenvector is (0,0,1), indicating the 100% of the population will be found in the eastern patch once the stable class distribution is reached. This makes intuitive sense. Although the population size in each patch might be growing indefinitely (provided that $b(1-d)>1$), the prevailing wind will cause the proportion of the total population found in the eastern patch to keep increasing up to 1, while the proportion found in the other patches will decrease to 0 (Figure A3.1.2).

**Figure A3.1.2: Proportions of plants in different patches.** The proportions found in the western patch (solid line), central patch (dotted line), and eastern patch (dashed line) are graphed over time.




The complete lack of flow of seeds from east to west is not very realistic. We can easily revise our model to allow for some movement in both directions. If a fraction of all dispersing seeds from each patch, $f$, goes east and a fraction, $1-f$ goes west, then the revised transition matrix becomes

$$\mathbf{M} = \begin{pmatrix} b(1-d) & bd(1-f) & 0 \\ bdf & b(1-d) & bd(1-f) \\ 0 & bdf & b(1-d) \end{pmatrix}. \qquad \text{(A3.1.3)}$$

□

We leave it as an exercise to demonstrate that the transition matrix (A3.1.3) is now both irreducible and primitive (see Problem A3.1.2). From this fact, we can conclude that plants will eventually be present on all of the islands, no matter which patch is initially inhabited (this is explored in Problem 10.1).

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### Supplementary Problems

**Problem A3.1.1:** Using the transition matrix (10.13) in the seed dispersal model,

$$\begin{pmatrix} b(1-d) & 0 & 0 \\ bd & b(1-d) & 0 \\ 0 & bd & b(1-d) \end{pmatrix},$$

show that one eigenvector of this matrix points in the direction (0, 0, 1) and that there are no other non-zero eigenvectors.

**Problem A3.1.2:** Using the transition matrix (10.14) in the seed dispersal model,

$$\begin{pmatrix} b(1-d) & bd(1-f) & 0 \\ bdf & b(1-d) & bd(1-f) \\ 0 & bdf & b(1-d) \end{pmatrix},$$

and the definitions in Appendix 3: (a) show that the matrix is irreducible, (b) show that the matrix is primitive, (c) use your results from (a) and (b) and the Perron-Frobenius theorem to say what you can infer about the eigenvalues and eigenvectors of this matrix. [Hint: to show that a matrix is primitive, you can stop powering up $\mathbf{M}$ whenever all elements of $\mathbf{M}^i$ are positive; you don't need to go all the way up to $\mathbf{M}^{n^2-2n+2}$ (see Recipe A3.2).]