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Mathematical Tools for Biology

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Begin with a easy (but significant) example

We study the expansion of natural forest in a fallow plot

· State 1 (denoted h) consists on herbs or pioneer species

· State 2 (denoted a) corresponds to presence of shrubs

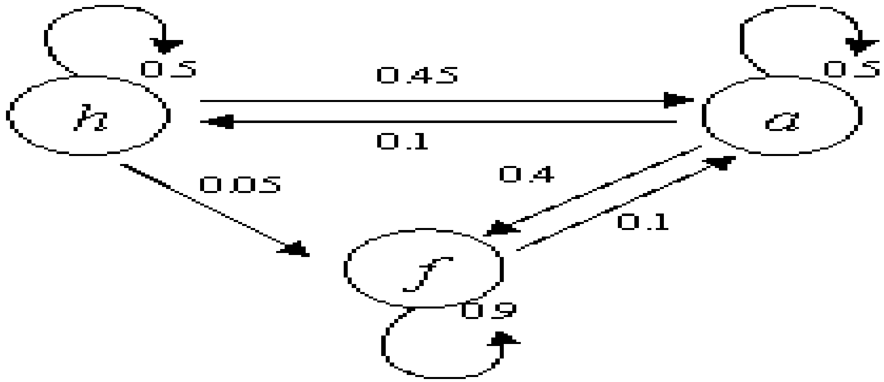
· State 3 (denoted f) corresponds to large trees (forest)

Let p_{ij} the proportion of plot in state i that are passed to state j

$$P = (p_{ij})_{i,j=1,2,3} = \begin{array}{c} \\ \\ \\ \end{array} \begin{array}{ccc} h & a & f \end{array}$$

$$P = (p_{ij})_{i,j=1,2,3} = \begin{pmatrix} 0,5 & 0,45 & 0,05 \\ 0,1 & 0,5 & 0,4 \\ 0 & 0,1 & 0,9 \end{pmatrix} \begin{array}{c} h \\ a \\ f \end{array}$$

Diagram points-and-arrows



If $\pi_0(h)$ is the probability of being in state h at time $t = 0$, we can compute (for example) the probability of a trajectory h, h, a, f, f :

$$\begin{aligned} P \quad & (X_0 = h, X_1 = h, X_2 = a, X_3 = f, X_4 = f) \\ = \quad & \pi_0(h) P(X_1 = h / X_0 = h) P(X_2 = a / X_1 = h) P(X_3 = f / X_2 = a) P(X_4 = f \\ = \quad & \pi_0(h) p_{hh} p_{ha} p_{af} p_{ff} = \pi_0(h)(0,5)(0,45)(0,4)(0,9) = 0,081 \pi_0(h). \end{aligned}$$

Evolution of the distribution of states over time

S	h	a	f
π_0	$\pi_0(h)$	$\pi_0(a)$	$\pi_0(f)$

S	h	a	f
π_1	$\pi_1(h)$	$\pi_1(a)$	$\pi_1(f)$

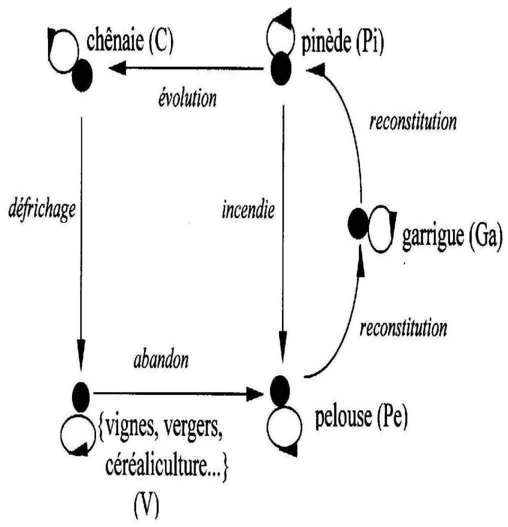
The probability $\pi_1(h)$ is given by

$P(X_1 = h/X_0 = h)P(X_0 = h)+P(X_1 = h/X_0 = a)P(X_0 = a)+P(X_1 = h/X_0$

Thus $\pi_1(h) = 0,5 \cdot \pi_0(h) + 0,1 \cdot \pi_0(a) + 0 \cdot \pi_0(f)$is the scalar product of π_0 with thefirst column of $\mathbb{P}$. Thus

$$(\pi_1(h), \pi_1(a), \pi_1(f)) = (\pi_0(h), \pi_0(a), \pi_0(f)) \begin{pmatrix} 0,5 & 0,45 & 0,05 \\ 0,1 & 0,5 & 0,4 \\ 0 & 0,1 & 0,9 \end{pmatrix}.$$

Example of a Mediterranean Ecosystem



$$P = \begin{pmatrix} 0,8 & 0,2 & 0 & 0 & 0 \\ 0 & 0,7 & 0,3 & 0 & 0 \\ 0 & 0 & 0,4 & 0,6 & 0 \\ 0 & 0 & 0 & 0,2 & 0,8 \\ 0,1 & 0 & 0,25 & 0 & 0,65 \end{pmatrix}$$

Chenaie=oak, pinède=pine forest, guarrigue=scrubland, pelouse=lawn, verger=orchard

Question : what is the long term behaviour of this ecosystem ?

Limiting distribution

Given π_0, on can compute easily π_1 as $\pi_1 = \pi_0 P$

Similarly $\pi_2 = \pi_1 P$ thus $\pi_2 = \pi_1 P = (\pi_0 P)P = \pi_0(PP) = \pi_0 P^2$

in general, $\pi_k = \pi_0 P^k$

Question : what is the limit, if it exists, $\lim_{k\to\infty} \pi_0 P^k$?

$$P^{40} = \begin{pmatrix} 0,17520 & 0,11680 & 0,20437 & 0,15327 & 0,35034 \\ 0,17517 & 0,11680 & 0,20438 & 0,15328 & 0,35035 \\ 0,17551 & 0,11678 & 0,20438 & 0,15328 & 0,35037 \\ 0,17517 & 0,11678 & 0,20438 & 0,15328 & 0,35037 \\ 0,17518 & 0,11678 & 0,20437 & 0,15328 & 0,36036 \end{pmatrix}.$$

The Perron-Frobenius Theorem

A *stochastic matrix* is a *primitive matrix* if one of its power is strictly positive.

Théorème 1 *Any primitive stochastic matrix* $\mathbb{P}$ *has a strictly positive left eigenvector,* $\pi^\infty > 0$ *such that for all stochastic* π_0

$$\lim_{k \to +\infty} \pi_0 P^k = \pi^\infty.$$

For any Markov chain, if the transition matrix is primitive, there exists a stationary distribution which is the limit of the dynamic, whatever the initial distribution.