Notes on Life-Cycle Diagrams, the Characteristic Equation, and Reproductive Value

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Videos

1. The Z-Transformed Life Cycle

1 Introduction

These notes violate the ten-papers spirit of this class somewhat, but the topic is important enough that it warrants its own set of notes and videos. There isn't a single paper with which to associate this topic, but the authoratative source is obviously Caswell (2001).

2 The Life-Cycle Graph

A life-cycle graph is a digraph (or directed graph) composed two things: (1) nodes, which represent the states (ages, stages, subgroups, localities, etc.) and (2) edges, which represent transitions between states. Figure 1 presents a simple age-structured life cycle with five ages and reproduction in age classes 2-5.

3 The Z-Transformed Life-Cycle

Caswell (2001) introduces the concept of the Z-transform of the life cycle to population biology. The Z-transform is essentially a discrete-time version of the more familiar Laplace transform and is equivalent to the probability generating function in discrete probability theory. With it, we map a function of discrete time into a function of a complex variable z^{-1}. This is the equivalent of transforming a sequence of real numbers into a frequency-domain representation.

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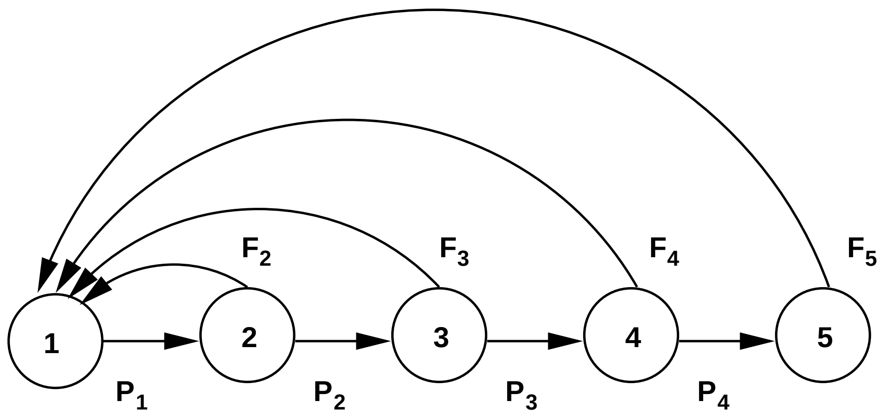

Figure 1: Life cycle diagram with five age classes.

For our purposes, the Z-transford can be thought of simply as a means of transforming the system of linear equations that the life cycle graph represents into a form that has convenient mathematical properties. Caswell (2001) provides a readable introduction to the subject that applies to very general life cycle graphs. Here we will concentrate on one special case of graphs: those that all must pass through a common stage. This will always be the case for age-structured renewal phenomena since every individual must pass through the first stage. That is, everyone is born. For some phenomena, this will not necessarily be the case, but because our focus is age-structured human life cycles, we will not deal with them.

An *arc* between stage j and stage i is simply a directed edge starting at j and ending at i in the life cycle graph. Define a *loop transmission* as the product of the coefficients of the arcs of the ith loop in the life cycle group. Following Caswell, we denote the ith loop transmission $L^{(i)}$.

The Z-transform of the life cycle simply involves multiplying each arc in the life cycle graph by the inverse of the dominant eigenvalue of the associated projection matrix, λ^{-1}. Each of these arcs represents a coefficient a_{ij} from the projection matrix $\boldsymbol{A}$, so we are just replacing these a_{ij} in the original graph with $a_{ij}\lambda^{-1}$ in the Z-transformed graph.

One of the mathematical conveniences that follows from the Z-transform is the ability to reduce the life cycle. Caswell (2001, p. 179) lists a number of important reductions that are possible for the Z-transformed life cycle graph.

Once we have transformed our life cycle graph, we can write down the discrete-time characteristic equation simply by collecting the various loops, $L^{(i)}$. For the special case of a life cycle where all loops must pass through a common loop (i.e., newborns), the characteristic equation is simply

$$1 = \sum_i L^{(i)}. \tag{1}$$

The Z-transformed version of the life cycle first introduced in figure 1 is shown in figure 2. We can see that there are four loops:

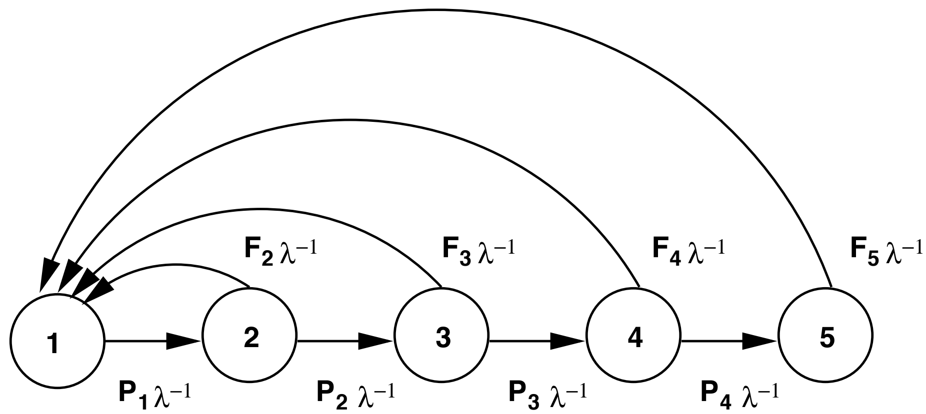

Figure 2: The z-transformed life cycle of the life cycle presented in figure 1.

$$\begin{aligned}
L^{(2)} &= P_1 F_2 \lambda^{-2} \\
L^{(3)} &= P_1 P_2 F_3 \lambda^{-3} \\
L^{(4)} &= P_1 P_2 P_3 F_4 \lambda^{-4} \\
L^{(5)} &= P_1 P_2 P_3 P_4 F_5 \lambda^{-5}
\end{aligned} \tag{2}$$

Having collected the loops from the Z-transformed life cycle, we use equation 1 to write out the characteristic equation:

$$1 = P_1 F_2 \lambda^{-2} + P_1 P_2 F_3 \lambda^{-3} + P_1 P_2 P_3 F_4 \lambda^{-4} + P_1 P_2 P_3 P_4 F_5 \lambda^{-5}.$$

We can now simplify this to arrive at a general characteristic equation for the age-structured population in discrete time:

$$1 = \sum_{i=1}^{\beta} F_i \lambda^{-i} \left(\prod_{j=1}^{i-1} P_j \right) \tag{3}$$

where β is the age of last reproduction. The analogy to the characteristic equation in continuous time is clear when we consider that $\lambda = e^r$ and $l(x) = \prod_{j=1}^{x-1} P_j$ and that F_i is the discrete-time equivalent of ASFR $m(x)$ for $i = x$.

3.1 The Stable Age Distribution

Let $T_{1x}^{(i)}$ denote the ith path from stage 1 to stage x. For the age-classified life cycle, the stable age distribution is simply:

$$
\begin{aligned}
u_1 &= 1 \\
u_x &= \sum_i T_{1x}^{(i)} \;\; x > 1
\end{aligned} \tag{4}
$$

Caswell (2001) provides formulae for life cycles where not all loops pass through a common first stage. For our 5-age-class life cycle, the stable age distribution is thus:

$$
\begin{aligned}
u_1 &= 1 \\
u_2 &= P_1\lambda^{-1} \\
u_3 &= P_1P_2\lambda^{-2} \\
u_4 &= P_1P_2P_3\lambda^{-3} \\
u_5 &= P_1P_2P_3P_4\lambda^{-4}
\end{aligned} \tag{5}
$$

3.2 Reproductive Value

We can also calculate reproductive value directly from the transformed life-cycle graph. The matrix of k left eigenvectors for the $k \times k$ projection matrix is the inverse of the matrix of of right eigenvectors. The left eigenvectors are also the right eigenvectors of the transpose of the Leslie matrix, $\boldsymbol{A}^T$. To calculate reproductive value from the transposed life cycle graph, we need to tanspose the life cycle graph so that we are enumerating the transmission paths from age class x to age class 1. Again, following Caswell's notation, define $\tilde{T}_{1x}$ as the transposed loop transmission from stage x to stage to stage 1.

$$
\begin{aligned}
v_1 &= 1 \\
v_2 &= F_2\lambda^{-1} + P_2F_3\lambda^{-2} + P_2P_3F_4\lambda^{-3} + P_2P_3P_4F_5\lambda^{-4} \\
v_3 &= F_3\lambda^{-1} + P_3F_4\lambda^{-2} + P_3P_4F_5\lambda^{-3} \\
v_4 &= F_4\lambda^{-1} + P_4F_5\lambda^{-2} \\
v_5 &= F_5\lambda^{-1}
\end{aligned} \tag{6}
$$

References

Caswell, H. (2001). *Matrix population models: Formulation and analysis* (2nd ed.). Sunderland, MA: Sinauer.