Mathematical Techniques in Evolution and Ecology

General solutions and transformations – One-variable models (part I)

Based on Chapter 6 in Otto and Day (2007)

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Outline

Goals

- To describe methods for obtaining general solutions for models with one variable
- To describe transformation methods for simplifying models

Concepts

- Transformation
- Affine models
- Brute force iteration
- Separation of variables

Motivation

For a small fraction of models, it is possible to go beyond identifying equilibria and their stability by finding the **general solution** of the equations.

Definition: General solution

An explicit description of the state of the system for all future points in time that depends only on the *parameters*, the *initial state*, and the amount of *time that has passed*.

Example: Exponential growth in discrete time

The recursion equation $n(t+1) = R\,n(t)$ can be iterated by hand to obtain the general solution

$$n(t) + R^t\,n(0), \tag{1}$$

where R is the parameter, $n(0)$ the initial state, and t the amount of time passed.

Transformations

Finding a solution by iteration rarely works – the model must have a particularly simple form, where the variable is multiplied by the same constant factor each generation to obtain the value of the variable in the next generation.

For linear models, we will learn more general methods with some hope to find a general solution for models that are hard or impossible to solve by iteration. The key to many techniques is to use a **transformation**.

Definition: Transformation

A transformation **rewrites the dynamical equations of a model in terms of a new set of variables**, which is chosen to *simplify the equations* or to *provide more biological insight* than the original set of variables.

Examples:

- In unit 3, we made a transformation when rewriting the equations in terms of absolute numbers n_A and n_a of alleles A and a as equations in terms of the relative frequency $p_A = n_A/(n_A + n_a)$ of A.
- In unit 5, we assessed the stability of an equilibrium by studying the displacement of a system from the equilibrium at time t, $\epsilon(t) = n(t) - \hat{n}$.

Which transformation should you use? Different transformations work best in different situations. Finding one that works often needs a combination of experience and trial and error. We start by introducing a transformation that works for **linear models in discrete time**.

Linear models in discrete time

With only one variable in discrete time, there are two types of linear models we need to solve:

- (1) Those of the form of the exponential growth model, where a process acts independently on every individual on a per-captia basis:

$$n(t+1) = R\,n(t). \tag{2}$$

- (2) Those that involve an additional constant that describes a constant input or outflow from the system that does not depend on the current state:

$$n(t+1) = R\,n(t) + m \tag{3}$$

We have seen an example of the second kind with the model of squirrels on campus, where m was the constant input of squirrels from the Arboretum, and $R = (1+b)(1-d)$ was the reproductive factor, i.e. the net effect of birth and death through cyclists.

Models of the second kind are called **affine models**.

Definition: Affine model

An **affine model** depends *linearly on the variables* and contains *a constant term* representing any *input or outflow* to the system.

We can still try to use **"brute force iteration"** for an affine model: That means solving the recursion equation(s) by *repeatedly plugging in the recursion equation for the value of the variable in the previous step*.

Exercise:

Use brute force iteration to find a general solution to the model described by Eq. (3).

Often, brute force iteration results in a "mess" and does not always work.

Tranformation of an affine model

A much more promising and general approach is to apply a tranformation. Fortunately, in the case of linear models in discrete time, there is a procedure that always works (see Recipe 6.1).

Recipe 6.1: Solving a linear discrete-time model with a constant term

Affine recursions of the form $n(t+1) = \rho\, n(t) + c$ can be solved as follows:

- (1) Solve for the equilibrium $\hat{n}$. Here, $\hat{n} = c/(1-\rho)$.
- (2) Define a *new variable* $\delta(t)$ as the *distance of the system from the equilibrium*, $\delta(t) = n(t) - \hat{n}$. Reversing this equation implies that $n(t) = \delta(t) + \hat{n}$.

- (3) The recursion equation for the transformed variable is $\delta(t+1) = \rho\,\delta(t)$ (see Remark 1 below for a proof).
- (4) The general solution for the distance to the equilibrium can be found by iteration: $\delta(t) = \rho^t\,\delta(0)$.
- (5) The general solution for the original variable is found by using the result from (4) in $n(t) = \delta(t) + \hat{n}$, which results in

$$n(t) = \rho^t\,\delta(0) + \hat{n}$$

Rewriting $\delta(0)$ in terms of $n(0)$, i.e. $\delta(0) = n(0) - \hat{n}$, gives the general solution of interest:

$$n(t) = \rho^t\,(n(0) - \hat{n}) + \hat{n} = \rho^t\,n(0) + (1 - \rho^t)\,\hat{n}. \tag{4}$$

Remark 1: To prove step (3), use the recursion equation for $n(t+1)$ to write the recursion equation for $\delta(t+1)$:

$$\delta(t+1) = n\,(t+1) - \hat{n} = \rho\, n\,(t) + c - \hat{n}.$$

Replacing $n(t)$ by $\delta(t) + \hat{n}$ gives

$$\delta(t+1) = \rho\,\delta\,(t) + \rho\,\hat{n} + c - \hat{n}.$$

Plugging in the formula for the equilibrium, $\hat{n} = c/(1-\rho)$, causes the last three terms to equal zero.

Remark 2: As Recipe 6.1 always works for affine recursions with one variable, steps (2) to (4) can be skipped, and the result in Eq. (4) from step (5) can be used directly after having identified $\hat{n}$ and ρ.

Exercise

Find a general solution for the (female) squirrels-on-campus example introduced in unit 1, using Recipe 6.1. Start from the discrete-time recursion equation

$$n(t+1) = (1+b)\,(1-d)\,n\,(t) + m,$$

where b is the number of offspring per mother, d is the proportion of squirrels dying, and m a constant number of squirrels immigrating from the Arboretum each time step. As a first step, identify R and c.