Supplementary material to:

Chapter 5: Equilibria and Stability Analyses – One Variable Models

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Supplementary Material 5.1: Further issues in perturbation analysis

Here we discuss problems that can arise when carrying out a perturbation analysis and how to circumvent some of these. More detailed information and suggestions can be found in Hinch (1991) and Simmonds and Mann (1988).

As mentioned in Primer 1, the Taylor series does not always converge, meaning that the terms involving ζ^i might not tend towards zero for high values of i. If the Taylor series for the equation of interest does not converge, then a perturbation analysis can give an incorrect approximation. If possible, you should check whether successive terms in the Taylor series are indeed smaller. Plus it is good, as a general policy, to check your approximate solution against numerical solutions to the equation of interest.

Even when higher-order terms in the Taylor series do converge, it might be impossible to evaluate $f(\zeta)$ at $\zeta = 0$. This problem arises when the leading-order term (i.e., the term that has the largest magnitude) is a term like $1/\zeta^k$, which blows up as ζ goes to zero. In this case, you can try multiplying $f(\zeta)$ by ζ^k and then proceeding with a regular perturbation analysis.

In other cases, a good approximation might require that the solution, $\hat{n}$, be written in terms of non-integer powers of ζ. For example, let's reconsider the diploid model of natural selection with mutation. Equation (5.32) gives the approximate equilibrium obtained by replacing $\hat{p}$ with $\hat{p}_0 + \hat{p}_1\,\zeta + \hat{p}_2\,\zeta^2 + \ldots$ in the equilibrium condition and following the steps outlined in Recipe 5.4 and Box 5.1. But what if allele A is perfectly dominant and $h = 0$? The approximation $\hat{p} \approx 1 - \dfrac{\mu}{h\,s}$ then becomes undefined.

What went wrong in the perturbation analysis? When $h = 0$, the zeroth order term in the Taylor series is perfectly well behaved and equals zero when $\hat{p}_0 = 0$ and $\hat{p}_0 = 1$. These are the only two equilibria in the model without mutation when allele A is dominant, because the third potential equilibrium given by (5.4) becomes one. Assuming that individuals carrying allele A are more fit, the equilibrium of interest is near $\hat{p}_0 = 1$.

When we calculate the linear order term in the Taylor series, $\frac{\mathrm{d}f(0)}{\mathrm{d}\zeta}$, however, we get $\tilde{\mu}$. This cannot be made to equal zero whenever mutations are present. Why has this problem arisen? One possibility is that a good approximation for $\hat{p}$ requires terms of order ζ^k for some power, k, between 0 and 1. Because we do not account for such non-integer terms, we end up with a linear-order term in our Taylor series that does not equal zero.

In cases like this, there are methods to determine the appropriate value of k, although these techniques are beyond the scope of this book (Hinch 1991; Simmonds and Mann 1988). In this example, if we include square-root terms in our series using $k = 1/2$, we can obtain an excellent approximation for the equilibrium. Including square-root terms, we can replace $\hat{p}$ with $\hat{p}_0 + \hat{p}_{1/2}\,\zeta^{1/2} + \hat{p}_1\,\zeta + \hat{p}_{3/2}\,\zeta^{3/2} + \hat{p}_2\,\zeta^2 + \ldots$ in the equilibrium condition. It is awkward to work with fractional powers, however, so we next replace ζ with δ^2 to get a function, $f(\delta)$, which should equal zero at the equilibrium. We then proceed through the steps of Recipe 5.4 as in a regular perturbation analysis.

The zeroth order term in the Taylor series with respect to δ is zero if either $\hat{p}_0 = 0$ and $\hat{p}_0 = 1$. Again, we are interested in the equilibrium near $\hat{p}_0 = 1$. The linear-order term in the Taylor series turns out to be zero already at $\hat{p}_0 = 1$. We must then consider the second-order term in the Taylor series with respect to δ. For this term to equal zero, it must be the case that $\tilde{\mu} - \hat{p}_{1/2}^2\, s = 0$, which is satisfied when $\hat{p}_{1/2} = \pm\sqrt{\frac{\tilde{\mu}}{s}}$. Thus, an approximation for the equilibrium is

$\hat{p} \approx \hat{p}_0 + \hat{p}_{1/2}\,\zeta^{1/2} = 1 \pm \sqrt{\frac{\tilde{\mu}}{s}}\,\zeta^{1/2}$. Replacing $\tilde{\mu}\zeta$ with the original parameter, μ, and focusing on the root that lies between zero and one, we get the approximate allele frequency, $\hat{p} \approx 1 - \sqrt{\frac{\mu}{s}}$.

This provides an excellent approximation for the allele frequency at mutation-selection balance when mutations are recessive as long as the mutation rate is small enough ($\mu << 1$ and $\mu << s$). Furthermore, this approximate solution corresponds to the exact equilibrium in the model when reverse mutations are absent, $\nu = 0$ (Problem 5.5).

Another complication that can arise in a perturbation analysis is that it does not always identify all solutions to an equation. We illustrate this potential problem using the discrete-time logistic model, modified to allow harvesting of the population at some constant rate, θ:

$$n(t+1) = n(t) + rn(t)\left(1 - \frac{n(t)}{K}\right) - \theta. \tag{S5.1.1}$$

Let's suppose that we want to know the equilibria when the carrying capacity is very large. We can handle this using a perturbation analysis by defining $\zeta = 1/K$ to be a small parameter and re-writing the model as

$$n(t+1) = n(t) + rn(t)\big(1 - \zeta\, n(t)\big) - \theta. \tag{S5.1.2}$$

The equilibrium condition for equation (S5.1.2) is:

$$0 = r\,\hat{n}\,\big(1 - \zeta\,\hat{n}\big) - \theta. \tag{S5.1.3}$$

The nice thing about this example is that we can solve (S5.1.3) for $\hat{n}$ using the quadratic formula (Rule A1.10) to get two exact solutions:

$$\hat{n} = \frac{-r + \sqrt{r^2 - 4r\zeta\theta}}{-2r\zeta} \text{ and } \hat{n} = \frac{-r - \sqrt{r^2 - 4r\zeta\theta}}{-2r\zeta} \tag{S5.1.4}$$

which we can compare with the approximation obtained using a perturbation analysis.

Performing a perturbation analysis of (S5.1.3), we get the linear approximation:

$$\hat{n} \approx \frac{\theta}{r} + \left(\frac{\theta}{r}\right)^2 \zeta \tag{S5.1.5}$$

(see Problem S5.1). At this point, we've stumbled upon a conundrum. There are two exact solutions (S5.1.4), yet we have only identified one solution in the approximation. What happened to the second equilibrium in the perturbation analysis? Even more disturbing, if the population sustains itself at the carrying capacity in the absence of harvesting (θ = 0), the equilibrium is *K*, or $1/\zeta$ in the current notation, whereas (S5.1.5) predicts $\hat{n} = 0$.

Looking at the case where harvesting is absent provides a clue about what went wrong. For the equilibrium, $\hat{n}$, to be near *K* requires that we have a term proportional to $K = 1/\zeta$ in our expansion for $\hat{n}$. But the expansion (5.1.1) that we assume for $\hat{n}$ in a regular perturbation analysis does not include a term proportional to $1/\zeta$. We can revise the perturbation analysis by defining $\hat{n} = \hat{n}_{-1}\frac{1}{\zeta} + \hat{n}_0 + \hat{n}_1\,\zeta + \hat{n}_2\,\zeta^2 + \hat{n}_3\,\zeta^3 + \ldots$. Using this definition for $\hat{n}$ rather than (5.1.1), a perturbation analysis identifies a second approximate equilibrium besides (S5.1.5):

$$\hat{n} \approx \frac{1}{\zeta} - \frac{\theta}{r} - \left(\frac{\theta}{r}\right)^2 \zeta. \tag{S5.1.6}$$

If we perform a Taylor series of the exact solution (S5.1.4) with respect to ζ near $\zeta = 0$, we also get the approximations (S5.1.5) and (S5.1.6). This provides an excellent check in this example, although the exact solution will typically not be known.

There is an underlying reason why the perturbation analysis runs into difficulties in the logistic model with harvesting. The equilibrium condition (S5.1.3) has a different number of solutions when ζ is zero (one solution at $\hat{n} = \theta/r$) than when ζ is not zero (two solutions given by (5.1.4)). If both solutions to the equilibrium condition had the form assumed by (5.1.1), this would imply that there are always two solutions to the equilibrium condition even as ζ decreases towards zero. The fact that one solution involves $1/\zeta$, however, allows the second solution to disappear (by marching off to infinity) when ζ goes to zero.

As in this example, techniques exist to generalize perturbation analyses so that they can identify all solutions to equations such as (S5.1.3) that have a different number of roots when a parameter is absent than when it is small. The method is known as a *singular perturbation analysis* (as opposed to the *regular perturbation analysis* described in Box 5.1) and is described in more depth in several texts on perturbation methods (Hinch 1991; Simmonds and Mann 1988).

Supplementary Problems

Problem S5.1: Perform a perturbation analysis to find an approximation for the equilibrium of the logistic model with harvesting of θ individuals per generation given by equation (5.4.1). The equilibrium condition for this model is:

$$0 = r\,\hat{n}\left(1 - \varepsilon\,\hat{n}\right) - \theta,$$

where $\varepsilon = 1/K$ is assumed to be small. (a) First use the expansion $\hat{n} = \hat{n}_0 + \hat{n}_1\,\varepsilon$ in the perturbation analysis to find an approximation for $\hat{n}$ that is accurate to linear order in ε. (b) Next, use the expansion $\hat{n} = \hat{n}_{-1}\,\frac{1}{\varepsilon} + \hat{n}_0 + \hat{n}_1\,\varepsilon$ in the perturbation analysis. You should identify only one solution in (a) but two solutions in (b). Show your work and then check your results against (S5.1.5) and (S5.1.6). Although the exact equilibria can be calculated in this example using the quadratic formula (Rule A1.10), it is worthwhile practicing perturbation methods on examples like this where you can check your answers.

References:

Hinch, E. J. 1991. Perturbation methods. Cambridge University Press, Cambridge ; New York.

Simmonds, J. G., and J. E. Mann. 1988. A First Look at Perturbation Theory. Dover Publications, Mineola, NY.