Mathematical Techniques in Evolution and Ecology

Equilibria and stability analysis – One-variable models (part II)

Based on Chapter 5 in Otto and Day (2007)

Spring Quarter 2015

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Approximations

When mathematical analysis of a model becomes complicated or even impossible to conduct, we basically have two (non-exclusive) choices:

1. Resort to numerical and simulation techniques using computers
2. Seek approximations that hopefully allow us to proceed the analytical treatment

For option 2, it is often necessary to focus on cases where some parameter values are either very small or very large. Here, we learn how to use such restrictions on the magnitude of the parameter values to

- approximate values for equilibria and
- perform approximate stability analysis

Approximating equilibria (perturbation analysis)

Here, we describe a method based on the Taylor series for finding an approximate solution for an equilibrium $\hat{n}$. The method is called perturbation analysis. A **perturbation analysis** identifies an *approximate solution to an equation by assuming that a parameter is small*.

This is a very important and general method that can be used to approximate the solution to any equation of interest. Here, we apply it to solve the equilibrium condition.

Recall that for a one-dimensional discrete-time model, the equilibrium condition is of the form

$$\hat{n} = \text{function of } \hat{n},$$

and for a continuous-time model, it is of the form

$$0 = \text{function of } \hat{n}.$$

Theoretical basis (summary of Box 5.1 in OD2007)

- Start from the equation you wish to solve, e.g. $\hat{n}$ = function of $\hat{n}$, but for which you cannot obtain an exact solution.
- Bring all of the terms in the equation to one side, so that it has the form "stuff" = 0.
- Identify a (set of) parameter(s) that you are willing to assume is small.
  - If it is a single parameter, replace it by e.g. ζ.
  - If there are multiple parameters, write each as some constant times ζ.

- The key is to write $\hat{n}$ as a sum of terms (i.e. as a series) as follows:

$$\hat{n} = \hat{n}_0 + \hat{n}_1\,\zeta + \hat{n}_2\,\zeta^2 + \hat{n}_3\,\zeta^3 + \cdots. \tag{1}$$

- We have just written the unknown solution $\hat{n}$ as a Taylor series with respect to ζ around $\zeta = 0$, where $\hat{n}_i$ represents $1/i!\left(d^i\,\hat{n}\big/d\,\zeta^i\right)\,|_{\zeta=0}$. To see this, remind yourself of the general expression of a Taylor series in P1_FunctionsAndApproximations.pdf.
- Plug Eq. (1) into the equation that we wish to solve, "stuff" = 0. To emphasise that “stuff” depends on ζ, we write this equation as $f(\zeta) = 0$. The goal is to solve this equation for the $\hat{n}_i$ needed to obtain a sufficiently accurate approximation for $\hat{n}$.

- For the method to work, we must be able to solve the original equation "stuff" = 0 for the case where $\zeta = 0$, i.e. solve $f(0) = 0$ for $\hat{n}_0$. If even this is impossible, we are stuck and need to reconsider our choice of what parameter(s) are small.
- How do we find the $\hat{n}_i$ terms needed in Eq. (1)? Surely, we cannot find the derivatives $\left(d^i \hat{n} / d\zeta^i\right) |_{\zeta=0}$ because we do not know $\hat{n}$. The crux is that we take the Taylor series of the equation we want to solve, $f(\zeta)$:

$$f(\zeta) = f(0) + \frac{d f(\zeta)}{d\zeta} |_{\zeta=0} \zeta + \frac{d^2 f(\zeta)}{d\zeta^2} |_{\zeta=0} \zeta^2 + \frac{d^3 f(\zeta)}{d\zeta^3} |_{\zeta=0} \zeta^3 + \cdots. \quad (2)$$

- A perfect approximation would cause each term in this sum to be zero (recall that we want to solve $f(\zeta) = 0$). Our goal is therefore to find the values $\hat{n}_i$ that cause each term in Eq. (2) to equal zero.

- We set $\left(d^i f(\zeta) / d\zeta^i\right) |_{\zeta=0}$ to zero for i, starting with $i = 0$ up to the order that is needed for the desired level of accuracy.
  - We already know that $\hat{n}_0$ causes the first term to equal zero, $f(0) = 0$, because this is the solution when $\zeta = 0$.
  - We then move to the next term, plugging our result for $\hat{n}_0$ into $\left(d f(\zeta) / d\zeta\right) |_{\zeta=0}$, setting this to zero, and solving $\hat{n}_1$.
  - This can be repeated for ever, but in practice we often focus on the first two terms in Eq. (1).

Recipe 5.4 below summarises these steps.

Recipe 5.4: Finding an approximate equilibrium

Suppose we have an equilibrium condition for $\hat{n}$, and we wish to find an approximate solution for $\hat{n}$ under the assumption that some parameter is small.

- (1) Identify a parameter that you can assume is small, and write it as ζ. If you want several parameters to be small, replace each by a constant times ζ.
- (2) Plug $\hat{n} = \hat{n}_0 + \hat{n}_1 + \hat{n}_2 + \hat{n}_3 + \cdots$ into the equation that you wish to solve, and write this equation with all terms on the same side as $f(\zeta) = 0$.
- (3) Calculate $\left(d^i f(\zeta) / d\zeta^i\right) |_{\zeta=0}$ for $i = 0$ up to the order desired. The zeroth derivative is jsut the function evaluated at zero, $f(0)$.

- (4) Starting with $i = 0$, solve $\left(d^i f(\zeta) / d\zeta^i\right) |_{\zeta=0} = 0$ for any $\hat{n}_i$ that it contains. Repeat for higher values of i, plugging in any $\hat{n}_i$ that have already been determined. Repeat this until you have obtained a sufficiently accurate estimate of $\hat{n}$.
- (5) Once you have determined the $\hat{n}_i$ for $i = 0$ to some order k, plug these values into Eq. (1) to obtain an approximation to $\hat{n}$ that is accurate to order ζ^k. To interpret the result, rewrite ζ in terms of the original parameter(s) by reversing Step (1).

Example 1: Approximate solution to a transcendental equation

Let us find an approximate solution to the transcendental equation

$$e^{\alpha \hat{n}} + \hat{n} = 5 \tag{3}$$

using Recipe 5.4.

- (1) There is only one parameter, α, which we assume to be small and hence replace by ζ.
- (2) Plugging in Eq. (1) and moving all terms to the right gives

$$f(\zeta) = e^{\zeta\left(\hat{n}_0 + \hat{n}_1\,\zeta + \hat{n}_2\,\zeta^2 + \hat{n}_3\,\zeta^3 + \cdots\right)} + \left(\hat{n}_0 + \hat{n}_1\,\zeta + \hat{n}_2\,\zeta^2 + \hat{n}_3\,\zeta^3 + \cdot\cdot\cdot\right) - 5 = 0. \tag{4}$$

- (3) The first three derivatives in the Taylor series in Eq. (2), evaluated at $\zeta = 0$, are $f(0) = 1 + \hat{n}_0 - 5 = \hat{n}_0 - 4$, $(d f(\zeta)/d\zeta)\,|_{\zeta=0} = \hat{n}_0 + \hat{n}_1$, and $\left(d^2 f(\zeta)\big/ d\zeta^2\right)|_{\zeta=0} = \hat{n}_0^2 + 2\,\hat{n}_1 + 2\,\hat{n}_2$.

- (4) For $i = 0$, we solve $f(0) = \hat{n} - 4 = 0$ for $\hat{n}_0$, which gives $\hat{n}_0 = 4$. Proceeding with $i = 1$, we solve $\hat{n}_0 + \hat{n}_1 = 4 + \hat{n}_1 = 0$ for $\hat{n}_1$, which gives $\hat{n}_1 = -4$. For $i = 2$, we solve $\hat{n}_0^2 + 2\,\hat{n}_1 + 2\,\hat{n}_2 = 4^2 + 2\,(-4) + 2\,\hat{n}_2 = 0$ for $\hat{n}_2$, which yields $\hat{n}_2 = -4$. We could go on, but choose to stop here.
- (5) Plugging the solutions from Step (4) into Eq. (1), to the level of accuracy chosen here, we obtain $\hat{n} \approx 4 - 4\,\zeta - 4\,\zeta^2$, which is $\hat{n} \approx 4 - 4\,\alpha - 4\,\alpha^2$ in terms of the original parameter.
- As a check, we solve $e^{\alpha\,\hat{n}} + \hat{n} = 5$ with $\alpha = 0.01$ numerically using *Mathematica* to obtain $\hat{n} \approx 3.95961$. Using our approximation, we obtain $\hat{n} \approx 4 - 4 \times 0.01 - 4 \times (0.01)^2 = 3.9596$, which is a good match! Even if we only use the first two terms, we still get very close: $\hat{n} \approx 4 - 4 \times 0.01 = 3.96$

Remark to step (3): The first and second derivatives of $f(\zeta)$ are as follows:

$$\frac{d f(\zeta)}{d\zeta} = e^{\zeta(\hat{n}_0+\hat{n}_1\zeta+\hat{n}_2\zeta^2+\hat{n}_2\zeta^2+\cdots)}\left[1\left(\hat{n}_0+\hat{n}_1\zeta+\hat{n}_2\zeta^2+\hat{n}_2\zeta^2+\cdots\right)+\zeta\left(\hat{n}_1+2\hat{n}_2\zeta+3\hat{n}_3\zeta^2+\cdots\right)\right]+ \hat{n}_1+2\hat{n}_2\zeta+3\hat{n}_3\zeta^2+\cdots \tag{5}$$

$$\frac{d^2 f(\zeta)}{d\zeta^2} = e^{\zeta(\hat{n}_0+\hat{n}_1\zeta+\hat{n}_2\zeta^2+\hat{n}_2\zeta^2+\cdots)}\left[1\left(\hat{n}_0+\hat{n}_1\zeta+\hat{n}_2\zeta^2+\hat{n}_2\zeta^2+\cdots\right)+\zeta\left(\hat{n}_1+2\hat{n}_2\zeta+3\hat{n}_3\zeta^2+\cdots\right)\right]\times \left[1\left(\hat{n}_0+\hat{n}_1\zeta+\hat{n}_2\zeta^2+\hat{n}_2\zeta^2+\cdots\right)+\zeta\left(\hat{n}_1+2\hat{n}_2\zeta+3\hat{n}_3\zeta^2+\cdots\right)\right]+ e^{\zeta(\hat{n}_0+\hat{n}_1\zeta+\hat{n}_2\zeta^2+\hat{n}_2\zeta^2+\cdots)}\times \left[\left(\hat{n}_1+2\hat{n}_2\zeta+3\hat{n}_3\zeta^2+\cdots\right)+\left(\hat{n}_1+4\hat{n}_2\zeta+6\hat{n}_3\zeta^2+\cdots\right)\right]+ 2\hat{n}_2+6\hat{n}_3\zeta^2+\cdots \tag{6}$$

In practice, a software capable of doing symbolic calculation such as *Mathematica*, *Maple,* or *Matlab* comes in handy here.

Example 2: Discrete-time diploid model of natural selection with mutation

In the diploid model of selection, we have so far ignored mutation. Let us assume that alleles *A* mutate to *a* at a rate *u* per generation, and alleles *a* mutate to allele *A* at a rate *v* per generation. Further, assume that mutation happens during the production of gametes, so that we have the following life cycle:

$$\text{gametes }(t) \xrightarrow{\text{union of gametes}} \text{diploid juveniles }(t) \xrightarrow{\text{viability selection}}$$
$$\text{diploid adults }(t) \xrightarrow{\text{gamete production and mutation}} \text{gametes }(t+1) \longrightarrow \cdots$$

As seen in previous units, the frequency of *A* after selection is

$$p' = \frac{p(t)^2 W_{AA} + p(t)(1 - p(t)) W_{Aa}}{p(t)^2 W_{AA} + 2\,p(t)(1 - p(t)) W_{Aa} + (1 - p(t))^2 W_{aa}}. \quad (7)$$

Then, mutation changes the frequency, so that in the next generation of gametes, we have

$$p(t+1) = (1 - u)\,p' + v(1 - p'). \quad (8)$$

We obtain the equilibrium condition by plugging p' from Eq. (7) into Eq. (8) and setting $p(t+1) = p(t) = \hat{p}$. The result is a complicated cubic polynomial in $\hat{p}$, which we do not show here. Therefore, a perturbation analysis is the way to go.

- (1) Assume that both mutation rates are small and replace u and v by $\tilde{u}\,\zeta$ and $\tilde{v}\,\zeta$, respectively. We will find an approximate solution up to the order ζ.

- (2) Replace $\hat{p}$ by $\hat{p}_0 + \hat{p}_1 \zeta + \hat{p}_2 \zeta^2 + \cdots$ in the equilibrium condition and write this condition in the form $f(\zeta) = 0$.
- (3) Calculate the terms $\left(d^i f(\zeta) \big/ d\zeta^i\right) \mid_{\zeta=0}$ for $i = 0, 1, 2$, to construct the Taylor series of $f(\zeta)$ with respect to ζ around $\zeta = 0$.
- (4) Starting with $i = 0$, we set $f(0) = 0$ and solve for $\hat{p}_0$, which yields the three equilibria we have seen before for the case without mutation: $\hat{p}_0 = 0$, $\hat{p}_0 = 1$, and $\hat{p}_0 = (W_{\text{aa}} - W_{\text{Aa}}) / (W_{\text{AA}} - 2\, W_{\text{Aa}} + W_{\text{aa}})$. Let us focus on $\hat{p}_0 = 1$, and parametrise fitnesses as $W_{\text{AA}} = 1$, $W_{\text{Aa}} = 1 - h\, s$, and $W_{\text{aa}} = 1 - s$, where $0 < s < 1$ and $0 < h < 1$. This corresponds to directional selection in favour of A, i.e. without mutation, A is guaranteed to fix.
  Moving on to $i = 1$, we find $(d f(\zeta) / d\zeta) \mid_{\zeta=0} = h\, s\, \hat{p}_1 + \tilde{u}$. Setting this to 0 and solving for $\hat{p}_1$, we find $\hat{p}_1 = -\tilde{u} \big/ (h\, s)$.

- (5) Gathering terms and replacing $\tilde{u}$ by u/ζ, we find

$$\hat{p} = \hat{p}_0 + \hat{p}_1 \zeta + O(\zeta^2) = 1 + \left(-\frac{\tilde{u}}{h\,s}\right)\zeta + O(\zeta^2) \approx 1 - \frac{u}{h\,s},$$
$$\hat{q} = 1 - \hat{q} \approx \frac{u}{h\,s}. \tag{9}$$

This equilbrium is known as the **mutation–selection balance**. It is a classic result in evolutionary biology going back to Haldane (1927). To first order in ζ, the result is independent of the back-mutation rate v. This makes sense, given that we did a perturbation analysis of the equilibrium where A is fixed.

Remark: The calculations involved in finding approximation (9) are more involved and it is advisable to use a software like *Mathematica* to carry them out. Below, you find the code (see “Calculations for Example 2”).

Stability analysis when the equilibrium is known by approximation

If we can identify an equilibrium only approximately, we can still determine whether it is stable or unstable. The approach is analogous to the case where we know the equilibrium exactly, except that we cannot evaluate the decisive quantities $\lambda = (d f(n) / d n)\,|_{n=\hat{n}}$ (for a discrete-time model) or $r = (d f(n) / d n)\,|_{n=\hat{n}}$ (for a continuous-time model) exactly at the equilibrium.

- Let us assume that we found an approximation to the equilibrium $\hat{n}$ of the form $\hat{n} = \hat{n}_0 + \hat{n}_1\,\zeta + \hat{n}_1\,\zeta + \hat{n}_3\,\zeta^3 + \cdots$, as described above.

- We can substitute this for $\hat{n}$ in the expression for λ (or r) above:

$$\lambda = \frac{df(n)}{dn} \mid_{n=\hat{n}} = \lambda(\zeta) = \frac{df(n)}{dn} \mid_{n=\hat{n}_0+\hat{n}_1\zeta+\hat{n}_1\zeta+\hat{n}_3\zeta^3+\cdots} \tag{10}$$

- To emphasise that λ (or r) is now a function of the small parameter ζ, we write $\lambda(\zeta)$ (or $r(\zeta)$). **Important:** When computing the derivative $df(n)/dn$, you must not forget to replace the original parameter(s) by ζ (or $c\,\zeta$).
- The key idea now is to write $\lambda(\zeta)$ as a Taylor series in ζ around $\zeta = 0$:

$$\lambda(\zeta) = \lambda(0) + \left(\frac{d\lambda(\zeta)}{d\zeta} \mid_{\zeta=0}\right)\zeta + \frac{1}{2!}\left(\frac{d^2\lambda(\zeta)}{d\zeta^2} \mid_{\zeta=0}\right)\zeta^2 + \frac{1}{3!}\left(\frac{d^3\lambda(\zeta)}{d\zeta^3} \mid_{\zeta=0}\right)\zeta^3 + \cdots. \tag{11}$$

- Note that Eq. (11) depends on the terms $\hat{n}_i$ (cf. Eq. 10), of which we do not know all. However, we know them up to the order of ζ we decided we wanted our approximation to be good. That is sufficient for Eq. (11). In essence, if we want an approximation that is exact up to and including the order of ζ^k, we need all terms $\hat{n}_i$ for $i = 0, 1, \ldots, k$.

Remark: Eq. (11) provides an imortant qualitative insight: Recall that if the magnitude of λ is above 1 the equilibrium is unstable, and if it is below 1 it is stable. Now, if $|\lambda(0)|$ is *not* close to 1, i.e. if in the absence of the parameter of interest, the equilibrium is “clearly” unstable or stable, the higher-order terms in Eq. (11) will not change this much. Hence, in this case, the stability properties remain unchanged in the presence of a small ζ. If, however, $|\lambda(0)|$ *is* close to 1, then a small term proportional to ζ chan tip the balance between stability and instability!

Example: Natural selection and mutation continued

Let us come back to the diploid model of natural selection with mutation as introduced above. We still focus on the equilibrium close to fixation of allele *A*. We found a first-order approximation in ζ to that equilibrium as

$$\hat{p} \approx 1 - \frac{\tilde{u}}{h\,s}\zeta. \tag{12}$$

This is what we are going to substitute for $\hat{p}$ in $\lambda = (df(p)/dp)\,|_{p=\hat{p}}$. In other words, the derivative must be taken of Eq. (8), and then evaluated at $\hat{p} = 1 - \tilde{u}/(h\,s)\,\zeta$. Doing this in *Mathematica*, we obtain a relatively complicated function $\lambda(\zeta)$ not shown here (but see below).

Next, we expand this function $\lambda(\zeta)$ as a Taylor series in ζ around $\zeta = 0$. Doing so, we obtain $\lambda_0 = W_{Aa} / W_{AA} = 1 - h\,s$, which corresponds to what we know from the last unit, where we looked into the case without mutation. Because we assumed $0 < s < 1$ and $0 < h < 1$, $|\lambda_0| < 1$ always, and the equilibrium $\hat{p} = 1$ is always stable in the absence of mutation (i.e. if $\zeta = 0$). Again, no surprise.

Looking into the second term of the Taylor series of $\lambda(\zeta)$ around $\zeta = 0$, we find

$$\left(\frac{d\lambda(\zeta)}{d\zeta}\,|_{\zeta=0}\right)\zeta = \left(\left(5 - \frac{2}{h} - 3\,h\,s\right)\mu + (-1 + h\,s)\,v\right)\zeta. \tag{13}$$

We see immediately that Eq. (13) is small if ζ is small. Therefore, adding this term to $\lambda_0 = 1 - h\,s$ will not make a difference as long as ζ is small, and the stability properties of the perturbed equilibrium $\hat{p} = 1 - u/(h\,s)$ are identical to those of the unperturbed equilibrium $\hat{p} = 1$.

Concluding message

The methods described for finding equilibria and determining their stability are very important, but have two main limitations.

1. They only describe the behaviour of the model *at or near equilibria*. In the next unit, we will look into methods for **finding general solutions to models with one variable**.
2. The methods described in this unit have been *limited to models involving a single variable*. In future units, we will look into **finding equilibria and determining stability for models with more than one variable**.

Problems

1. [Problem 5.14 in OD2007] Consider a variant of the logistic model with immigration, as given by the following recursion equation:

$$n(t+1) = (1+r)\, e^{-\alpha\, n(t)}\, n(t) + m \tag{14}$$

If you build the equilibrium condition, you will notice that you cannot find an explicit solution for the equilibrium $\hat{n}$. Instead, use a perturbation analysis to find a linear approximation for the equilibrium population size, assuming that migration is weak. Further, assume that the population would go extinct in the complete absence of migration (i.e., $\hat{n}_0 = 0$). Use this approximation to show that $\hat{n}$ becomes positive when migration is present, as long as the growth rate r is negative.

Initialisation cells

In[21]:=
```
f[ξ_] := n0 + n1 ξ + n2 ξ^2 + n3 ξ^3
```

In[22]:=
```
D[ⅇ^(ξ f[ξ]) + f[ξ] - 5, {ξ, 1}] /. {ξ → 0}
D[ⅇ^(ξ f[ξ]) + f[ξ] - 5, {ξ, 2}] /. {ξ → 0}
```

Out[22]= $n0 + n1$

Out[23]= $n0^2 + 2\,n1 + 2\,n2$

In[24]:=
```
NSolve[Exp[α n] + n == 5 /. {α → 0.01}, n]
```

NSolve::ifun : Inverse functions are being used by NSolve, so some solutions may not be found; use Reduce for complete solution information. ≫

Out[24]= {{n → 3.95961}}

In[25]:= $4 - 4 \times 0.01 - 4 \times 0.01^2$

Out[25]= 3.9596

In[26]:=
```
4 - 4 * 0.01
```

Out[26]= 3.96

Calculations for Example 2

In[27]:=
```
pPrime := (p^2 WAA + p (1 - p) WAa)/(p^2 WAA + 2 p (1 - p) WAa + (1 - p)^2 Waa)
```

In[28]:=
```
pRec := (1 - u) pPrime + v (1 - pPrime)
```

```
pRec
```

$$\frac{(1-u)\left((1-p)\,p\,\mathrm{WAa}+p^2\,\mathrm{WAA}\right)}{(1-p)^2\,\mathrm{Waa}+2\,(1-p)\,p\,\mathrm{WAa}+p^2\,\mathrm{WAA}}+v\left(1-\frac{(1-p)\,p\,\mathrm{WAa}+p^2\,\mathrm{WAA}}{(1-p)^2\,\mathrm{Waa}+2\,(1-p)\,p\,\mathrm{WAa}+p^2\,\mathrm{WAA}}\right)$$

In[29]:=
```
pRecSubst = pRec /. {u → μ ξ, v → ν ξ}
```

Out[29]= $$\frac{\left((1-p)\,p\,\mathrm{WAa}+p^2\,\mathrm{WAA}\right)(1-\xi\,\mu)}{(1-p)^2\,\mathrm{Waa}+2\,(1-p)\,p\,\mathrm{WAa}+p^2\,\mathrm{WAA}}+\left(1-\frac{(1-p)\,p\,\mathrm{WAa}+p^2\,\mathrm{WAA}}{(1-p)^2\,\mathrm{Waa}+2\,(1-p)\,p\,\mathrm{WAa}+p^2\,\mathrm{WAA}}\right)\xi\,\nu$$

In[30]:=
```
equilCond = Simplify[pRecSubst - p == 0 /. {p → pHat}];
```

In[31]:=
```
pHatAF[ξ_] := pHat0 + pHat1 ξ + pHat2 ξ^2
```

```
equilCond
```

$$\left(\mathrm{pHat}^3\,(\mathrm{Waa}-2\,\mathrm{WAa}+\mathrm{WAA})-\mathrm{Waa}\,\xi\,\nu+\mathrm{pHat}\,(\mathrm{Waa}+\mathrm{WAa}\,(-1+\xi\,(\mu-\nu))+2\,\mathrm{Waa}\,\xi\,\nu)-\mathrm{pHat}^2\,(\mathrm{WAA}-\mathrm{WAA}\,\xi\,\mu+\mathrm{WAa}\,(-3+\xi\,\mu-\xi\,\nu)+\mathrm{Waa}\,(2+\xi\,\nu))\right)\Big/\left((-1+\mathrm{pHat})^2\,\mathrm{Waa}+\mathrm{pHat}\,(-2\,(-1+\mathrm{pHat})\,\mathrm{WAa}+\mathrm{pHat}\,\mathrm{WAA})\right)=0$$

In[32]:=
```
equilCondSubst = FullSimplify[equilCond /. {pHat → pHatAF[ξ]}]
```

Out[32]= $$\Big((\mathrm{Waa}-2\,\mathrm{WAa}+\mathrm{WAA})\,(\mathrm{pHat0}+\xi\,(\mathrm{pHat1}+\mathrm{pHat2}\,\xi))^3-\mathrm{Waa}\,\xi\,\nu+(\mathrm{pHat0}+\xi\,(\mathrm{pHat1}+\mathrm{pHat2}\,\xi))\,(\mathrm{Waa}+\mathrm{WAa}\,(-1+\xi\,(\mu-\nu))+2\,\mathrm{Waa}\,\xi\,\nu)-(\mathrm{pHat0}+\xi\,(\mathrm{pHat1}+\mathrm{pHat2}\,\xi))^2\,(2\,\mathrm{Waa}-3\,\mathrm{WAa}+\mathrm{WAA}+(\mathrm{WAa}-\mathrm{WAA})\,\xi\,\mu+(\mathrm{Waa}-\mathrm{WAa})\,\xi\,\nu)\Big)\Big/\Big(\mathrm{Waa}\,(-1+\mathrm{pHat0}+\xi\,(\mathrm{pHat1}+\mathrm{pHat2}\,\xi))^2+(\mathrm{pHat0}+\xi\,(\mathrm{pHat1}+\mathrm{pHat2}\,\xi))\,(-2\,\mathrm{WAa}\,(-1+\mathrm{pHat0}+\xi\,(\mathrm{pHat1}+\mathrm{pHat2}\,\xi))+\mathrm{WAA}\,(\mathrm{pHat0}+\xi\,(\mathrm{pHat1}+\mathrm{pHat2}\,\xi)))\Big)=0$$

In[33]:=
```
equilCondSubstFunc := ((Waa - 2 WAa + WAA) (pHat0 + ξ (pHat1 + pHat2 ξ))^3 -
    Waa ξ ν + (pHat0 + ξ (pHat1 + pHat2 ξ)) (Waa + WAa (-1 + ξ (μ - ν)) + 2 Waa ξ ν) -
    (pHat0 + ξ (pHat1 + pHat2 ξ))^2 (2 Waa - 3 WAa + WAA + (WAa - WAA) ξ μ + (Waa - WAa) ξ ν)) /
  (Waa (-1 + pHat0 + ξ (pHat1 + pHat2 ξ))^2 + (pHat0 + ξ (pHat1 + pHat2 ξ))
      (-2 WAa (-1 + pHat0 + ξ (pHat1 + pHat2 ξ)) + WAA (pHat0 + ξ (pHat1 + pHat2 ξ))))
```

```
Simplify[Series[equilCondSubstFunc, {ζ, 0, 2}]]
```

```
((-1 + pHat0) pHat0 ((-1 + pHat0) Waa + WAa - 2 pHat0 WAa + pHat0 WAA)) /
   ((-1 + pHat0)^2 Waa + pHat0 (-2 (-1 + pHat0) WAa + pHat0 WAA)) +
  ((-2 (-1 + pHat0) pHat0 pHat1 ((-1 + pHat0) Waa + WAa - 2 pHat0 WAa + pHat0 WAA)^2 +
        ((-1 + pHat0)^2 Waa + pHat0 (-2 (-1 + pHat0) WAa + pHat0 WAA))
         (pHat1 Waa - pHat1 WAa - 2 pHat0 pHat1 (2 Waa - 3 WAa + WAA) +
            3 pHat0^2 pHat1 (Waa - 2 WAa + WAA) + pHat0 WAa μ - Waa ν + 2 pHat0 Waa ν -
            pHat0 WAa ν + pHat0^2 (WAA μ - Waa ν + WAa (-μ + ν)))) ζ) /
   ((-1 + pHat0)^2 Waa + pHat0 (-2 (-1 + pHat0) WAa + pHat0 WAA))^2 +
  ((((-1 + pHat0) pHat0 ((-1 + pHat0) Waa + WAa - 2 pHat0 WAa + pHat0 WAA)
              (4 pHat1^2 ((-1 + pHat0) Waa + WAa - 2 pHat0 WAa + pHat0 WAA)^2 - ((-1 + pHat0)^2
                    Waa + pHat0 (-2 (-1 + pHat0) WAa + pHat0 WAA)) (pHat1^2 (Waa - 2 WAa +
                       WAA) + 2 pHat2 ((-1 + pHat0) Waa + WAa - 2 pHat0 WAa + pHat0 WAA)))) /
          ((-1 + pHat0)^2 Waa + pHat0 (-2 (-1 + pHat0) WAa + pHat0 WAA)) -
        2 pHat1 ((-1 + pHat0) Waa + WAa - 2 pHat0 WAa + pHat0 WAA)
          (pHat1 Waa - pHat1 WAa - 2 pHat0 pHat1 (2 Waa - 3 WAa + WAA) +
            3 pHat0^2 pHat1 (Waa - 2 WAa + WAA) + pHat0 WAa μ - Waa ν +
            2 pHat0 Waa ν - pHat0 WAa ν + pHat0^2 (WAA μ - Waa ν + WAa (-μ + ν))) +
        ((-1 + pHat0)^2 Waa + pHat0 (-2 (-1 + pHat0) WAa + pHat0 WAA))
          (pHat2 Waa - pHat2 WAa - (pHat1^2 + 2 pHat0 pHat2) (2 Waa - 3 WAa + WAA) +
            3 pHat0 (pHat1^2 + pHat0 pHat2) (Waa - 2 WAa + WAA) + pHat1 WAa μ +
            2 pHat1 Waa ν - pHat1 WAa ν + 2 pHat0 pHat1 (WAA μ - Waa ν + WAa (-μ + ν)))) ζ^2) /
   ((-1 + pHat0)^2 Waa + pHat0 (-2 (-1 + pHat0) WAa + pHat0 WAA))^2 +
  O[ζ]^3
```

In[34]:=
```
f0 = Simplify[D[equilCondSubstFunc, {ζ, 0}]] /. {ζ → 0}
```

Out[34]=
```
(pHat0 (Waa - WAa) - pHat0^2 (2 Waa - 3 WAa + WAA) + pHat0^3 (Waa - 2 WAa + WAA)) /
  ((-1 + pHat0)^2 Waa + pHat0 (-2 (-1 + pHat0) WAa + pHat0 WAA))
```

In[35]:=
```
Simplify[Solve[f0 == 0, pHat0]]
```

Out[35]=
```
{{pHat0 → 0}, {pHat0 → 1}, {pHat0 → (Waa - WAa)/(Waa - 2 WAa + WAA)}}
```

In[36]:=
```
pHat0Sol = 1
```

Out[36]=
```
1
```

In[37]:=
```
rulesW := {WAA → 1, WAa → 1 - h s, Waa → 1 - s}
```

In[38]:=
```
Deriv1 = Simplify[D[equilCondSubstFunc, {ζ, 1}]] /. {ζ → 0}
```

Out[38]=
```
(-2 pHat1 ((-1 + pHat0) Waa - (-1 + 2 pHat0) WAa + pHat0 WAA)
      (pHat0 (Waa - WAa) - pHat0^2 (2 Waa - 3 WAa + WAA) + pHat0^3 (Waa - 2 WAa + WAA)) +
    ((-1 + pHat0)^2 Waa + pHat0 (-2 (-1 + pHat0) WAa + pHat0 WAA)) (pHat1 (Waa - WAa) -
        2 pHat0 pHat1 (2 Waa - 3 WAa + WAA) + 3 pHat0^2 pHat1 (Waa - 2 WAa + WAA) -
        Waa ν + pHat0 (WAa (μ - ν) + 2 Waa ν) + pHat0^2 (WAA μ - Waa ν + WAa (-μ + ν)))) /
  ((-1 + pHat0)^2 Waa + pHat0 (-2 (-1 + pHat0) WAa + pHat0 WAA))^2
```

In[39]:=
```
Deriv1Subst = Simplify[Deriv1 /. {pHat0 → pHat0Sol} /. rulesW]
```

Out[39]=
```
h pHat1 s + μ
```

In[40]:= **pHat1Sol = Solve[Deriv1Subst == 0, pHat1]**

Out[40]= $\left\{\left\{\text{pHat1} \to -\frac{\mu}{h\, s}\right\}\right\}$

In[41]:= **pRec**

Out[41]= $$\frac{(1-u)\,\left((1-p)\,p\,WAa+p^2\,WAA\right)}{(1-p)^2\,Waa+2\,(1-p)\,p\,WAa+p^2\,WAA}+v\left(1-\frac{(1-p)\,p\,WAa+p^2\,WAA}{(1-p)^2\,Waa+2\,(1-p)\,p\,WAa+p^2\,WAA}\right)$$

In[50]:= **pRecSubst**

Out[50]= $$\frac{\left((1-p)\,p\,WAa+p^2\,WAA\right)\,(1-\zeta\,\mu)}{(1-p)^2\,Waa+2\,(1-p)\,p\,WAa+p^2\,WAA}+\left(1-\frac{(1-p)\,p\,WAa+p^2\,WAA}{(1-p)^2\,Waa+2\,(1-p)\,p\,WAa+p^2\,WAA}\right)\zeta\,\nu$$

In[62]:= **pRecSubst**

Out[62]= $$\frac{\left((1-p)\,p\,WAa+p^2\,WAA\right)\,(1-\zeta\,\mu)}{(1-p)^2\,Waa+2\,(1-p)\,p\,WAa+p^2\,WAA}+\left(1-\frac{(1-p)\,p\,WAa+p^2\,WAA}{(1-p)^2\,Waa+2\,(1-p)\,p\,WAa+p^2\,WAA}\right)\zeta\,\nu$$

In[74]:= **λImpl = FullSimplify[D[pRecSubst, {p, 1}] /. {p → 1 - μ / (h s) ζ}]**

Out[74]= $$-\left(\left(h^2\,s^2\,\left(h^2\,s^2\,WAa\,WAA+2\,h\,s\,(Waa-WAa)\,WAA\,\zeta\,\mu+(Waa\,(WAa-2\,WAA)+WAa\,WAA)\,\zeta^2\,\mu^2\right)\,(-1+\zeta\,(\mu+\nu))\right)\Big/\left(h^2\,s^2\,WAA+2\,h\,s\,(WAa-WAA)\,\zeta\,\mu+(Waa-2\,WAa+WAA)\,\zeta^2\,\mu^2\right)^2\right)$$

In[75]:= **λ0 = Simplify[λImpl /. {ζ → 0}]**

Out[75]= $$\frac{WAa}{WAA}$$

In[81]:= **λ0 /. rulesW**

Out[81]= $1-h\,s$

In[76]:= **Deriv1λ = Simplify[D[λImpl, {ζ, 1}] /. {ζ → 0}]**

Out[76]= $$\frac{-4\,WAa^2\,\mu+2\,Waa\,WAA\,\mu-WAa\,WAA\,((-2+h\,s)\,\mu+h\,s\,\nu)}{h\,s\,WAA^2}$$

In[77]:= **Deriv1λExpl = Simplify[D[λImpl /. rulesW, {ζ, 1}] /. {ζ → 0}]**

Out[77]= $$\left(5-\frac{2}{h}-3\,h\,s\right)\mu+(-1+h\,s)\,\nu$$

In[78]:= **λApprox = λ0 + Deriv1λ ζ /. rulesW**

Out[78]= $$1-h\,s+\frac{1}{h\,s}\zeta\left(2\,(1-s)\,\mu-4\,(1-h\,s)^2\,\mu-(1-h\,s)\,((-2+h\,s)\,\mu+h\,s\,\nu)\right)$$

In[79]:= **Collect[λApprox, {μ, ν}]**

Out[79]= $$1-h\,s+\left(\frac{2\,(1-s)\,\zeta}{h\,s}-\frac{4\,(1-h\,s)^2\,\zeta}{h\,s}+\frac{(-2+h\,s)\,(-1+h\,s)\,\zeta}{h\,s}\right)\mu+(-1+h\,s)\,\zeta\,\nu$$

In[80]:= **FullSimplify**$$\left[\left(\frac{2\,(1-s)\,\zeta}{h\,s}-\frac{4\,(1-h\,s)^2\,\zeta}{h\,s}+\frac{(-2+h\,s)\,(-1+h\,s)\,\zeta}{h\,s}\right)\mu+(-1+h\,s)\,\zeta\,\nu\right]$$

Out[80]= $$\zeta\left(\left(5-\frac{2}{h}-3\,h\,s\right)\mu+(-1+h\,s)\,\nu\right)$$

Obviously, this is small if ζ is small, and hence irrelevant relative to $\lambda_0 = 1 - h\,s$.