Unstable oscillations and spatial structure: the Nicholson-Bailey model

Level 2 module in "Modelling course in population and evolutionary biology"

(701-1418-00 SS)

Module author: Sebastian Bonhoeffer

Course director: Sebastian Bonhoeffer
Theoretical Biology
Institute of Integrative Biology
ETH Zürich

1   Introduction

In the 1930s Nicholson and Bailey[a] proposed a simple discrete-time model for the population dynamics of insect hosts and their parasitoids that has since become one of the classical models of population biology. Parasitoids, such as parasitic wasps, lay eggs into their hosts and thus the completion of the parasitoid life cycle requires that their hosts be killed. Parasitoids resemble parasites as they grow inside a host, but also resemble predators in that they are obligate killers of their host. The Nicholson-Bailey model is a two-dimensional system of difference equations given by

$$H_{t+1} = RH_t e^{-aP_t} \tag{1}$$
$$P_{t+1} = cH_t(1 - e^{-aP_t}) \tag{2}$$

---

[a](i) Bailey, Victor Albert, born in Alexandria, Egypt, 18 December 1895; died in Geneva, Switzerland, 7 December 1964. Education Queen's College Oxford (B.A. 1919; D.Philosophy 1923). Demonstrator in physics at Oxford University 1924-25. Associate Professor of physics at Sydney University 1926-36; Professor of experimental physics 1936-53; Research Professor 1952-60. Worked for the WHO at the end of his career. (ii) Nicholson, Alexander John (England-Australia 1895-1969, population biologist, entomologist, and science administrator. Worked on mimicry and animal population regulation. President of the Royal Society of Australia.
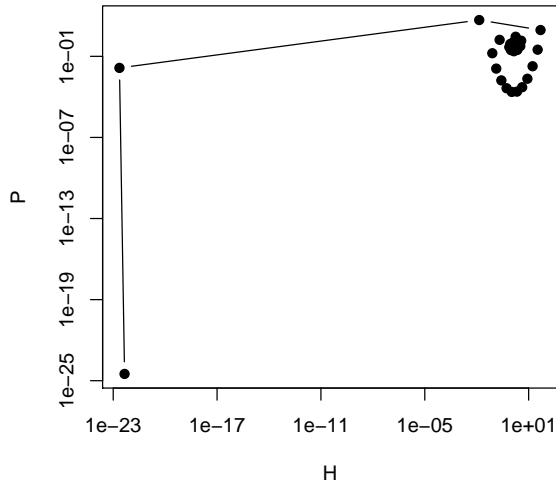
Figure 1: Phase diagram of the Nicholson-Bailey model. Starting from a value near the equilibrium the trajectory spirals outwards until the population crashes (i.e. reaches extremely low values, such that realistically all individuals in the population die). Thus the Nicholson-Bailey model is an example for an unstable oscillation. Parameters used for the simulation are $R = 2$ and $c = a = 1$. The initial conditions were $P_0 = log(R)/a + 0.3$ and $H_0 = \frac{R}{R-1}\frac{\log(R)}{ac} + 0.3$.

Here H_t and P_t represent the densities of the host and parasitoid population at year t. R is the number of offspring of an unparasitized host surviving to the next year. Assuming random encounter between hosts and parasitoids the probability that a host escapes parasitism can be approximated by e^{-aP_t}, where a is a proportionality constant. Similarly, the probability to become infected is then given by $(1 - e^{-aP_t})$. Finally, the parameter c describes the number of parasitoids that hatch from an infected host.

The equilibrium of the Nicholson-Bailey model is obtained by setting $H_{t+1} = H_t$ and $P_{t+1} = P_t$ and is given by

$$P = \frac{\log(R)}{a} \qquad \text{and} \qquad H = \frac{R}{R-1}\frac{\log(R)}{ac} \qquad (3)$$

However, this equilibrium is unstable[b]. The simulation of the Nicholson-Bailey model (see figure 1) shows that that the dynamics are characterized by oscillations of increasing amplitude until the population crashes.

---

[b]The stability of difference equations can be determined mathematically in a procedure similar to the mathematical stability analysis for differential equations as discussed in section 1.2.5 of the reader to "Ecology and Evolution II: Populations". As for differential equations one needs to determine the eigenvalues of the Jacobian (which in discrete time is often called the "next-generation matrix"). In contrast to differential equations, where the stability depends on whether the largest eigenvalue is larger or smaller than zero, for difference equations the stability depends on whether the largest eigenvalue is larger or smaller than 1.

1.1 Tips to develop an R script for the simple Nicholson-Bailey model

Write a function that iterates the Nicholson-Bailey model. A simple example for a function that iterates a difference equation would be

```
model <- function(time) {
        param1 <- 2
        param2 <- 1
        population <- 1
                cc <- data.frame(time=0,pop=population)
        for (t in c(1:time)) {
            population <- population*param1 + param2
            cc <- rbind(cc,c(t,population))
        }
        cc
}



### Run the model
out  <- model(10)
### Plot the model
plot(out$time,out$population,xlab="time",ylab="population size")
```

Modify the above model to obtain the Nicholson-Bailey model and then plot the time course and phase diagram of the Nicholson-Bailey model. Try out different parameters.

2 Spatial Nicholson-Bailey model

Although host-parasitoid interactions are often characterized by very strong fluctuations from year to year, unlike in the simple Nicholson-Bailey model, they typically do not lead to the complete extinction of either the host or the parasitoid. One important factor neglected in the Nicholson-Bailey model is space. Space can be neglected if the populations can be considered to be well mixed. However, this may often not be justified. Both the interactions between species and the dispersal of offspring may be local.

The Nicholson-Bailey model can be extended to incorporate space. To this end we consider a spatial grid on which the Nicholson-Bailey dynamics take place. At each site (i, j) in the grid the dynamics are (more or less) given by the simple Nicholson-Bailey model of the previous section, but in addition we allow that hosts and parasitoids disperse to all immediately neighbouring sites (with dispersal rates d_h and d_p). Mathematically, the spatial model is thus given by the following equations

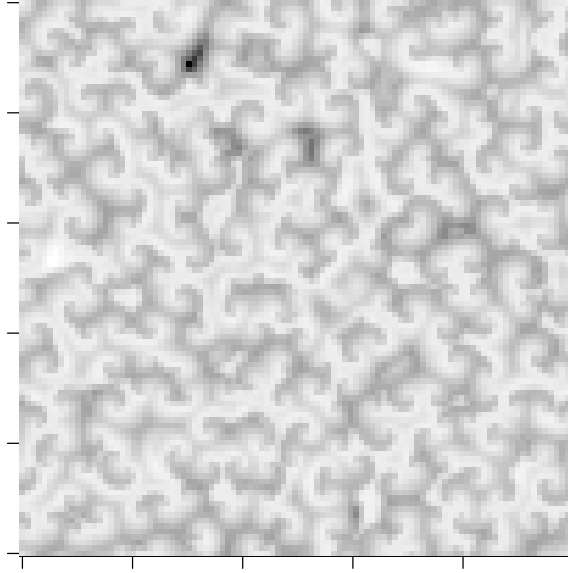$$H_{i,j}(t+1) \quad = \quad R H_{i,j}^{\star}(t) e^{-a P_{i,j}^{\star}(t)} \tag{4}$$

Figure 2: Simulation of the spatial Nicholson-Bailey model. Depending on the dispersal rates of hosts and parasitoids, d_p and d_h, parasitoids and hosts can coexist indefinitely. The plot shows the logarithm of the host density (as levels of gray) on a quadratic grid. The graph corresponds to a 100×100 lattice.

$$P_{i,j}(t+1) = cH_{i,j}^{\star}(t)(1 - e^{-aP_{i,j}^{\star}(t)}) \tag{5}$$

(where the time dependence is no longer indicated by a subscript but by brackets.) Here

$$H_{i,j}^{\star}(t) = (1 - d_h)H_{i,j} + d_h/8 \sum H_{k,l}(t) \tag{6}$$

$$P_{i,j}^{\star}(t) = (1 - d_p)P_{i,j} + d_p/8 \sum P_{k,l}(t) \tag{7}$$

where the sum is over all 8 neighbouring fields (i.e. $(i-1, j-1), \ldots, (i+1, j+1)$).

Importantly, it can be shown (see figure 2) that in the spatial Nicholson-Bailey model hosts and parasitoids can coexist indefinitely (in contrast to the non-spatial model).

2.1 Tips to develop the spatial extension of the Nicholson-Bailey model

- Define h and p as matrices in R. To create matrices look up

```
help(matrix)
```

in R. The matrix indices correspond to points on a two dimensional lattice. Hence $h_{i,j}$ would be the density of hosts at lattice point (i, j).

- Multiplication of $h*p$ in R results in a new matrix, say m, which is given by $m_{i,j} = h_{i,j}*p_{i,j}$. Note that this is different from normal matrix multiplication, but is very convenient for programming. Hence, you can update the entire playing field in a single line:

```
hn <- r* h * exp(-a p)
```

where h and p are matrices, a and r are numbers, and hn is the updated matrix of host densities.

- Implement host and parasitoid dispersal. Use periodic boundary conditions such that hosts or parasitoids that exit on one side of the quadratic "playing field" enter again on the opposite side. This is important because otherwise parasitoids or hosts are lost from the field. Notice that one can conveniently change the order of indices in a matrix in R. The command

```
h[c(2:10,1),]
```

for example shifts the rows 2 to 10 one up and places the first row last. The command

```
h[,c(2:10,1)]
```

does the same for columns. I recommend testing that dispersal equations (eqs 6 and 7) work independently.

- Use R-functions `image()` or `persp()` to plot the matrices containing the host and parasitoid densities.

3 Exercises

3.1 Basic exercises

Eb1. Why does the simple Nicholson-Bailey model show unstable oscillations? How could it be stabilized? Try to implement realistic biological factors to achieve this. See the footnote[c] for some possible stabilizing factors or experiment with your own ideas.

Eb2. How does the spatial dispersal rate of hosts and parasitoids affect the population dynamics of the spatial model and why? Determine the probability of coexistence or extinction for different combinations of the two dispersal rates and plot the results in a 2D plot of the parameter space (i.e. in a coordinate system with axes corresponding to the two parameters). In the regime of stable coexistence, plot the host and parasitoid densities as a function of the two parameters. (You may also experiment with changing R, a or c).

Eb3. Given the instability of the system, initial conditions can greatly influence the outcome even in the spatial model. Try out different initial conditions. Hint: use the `runif()` function to generate random initial values for the population sizes in each cell. Alternatively, you can start the system with non-zero populations in just one or a few cells (as in *Hassel et al*). Investigate Exercise Eb2 with both alternatives.

---

[c]Some possible stabilizing factors: self-limitation in the host or the parasitoid (see the module on logistic difference equation), constant immigration from the neighbourhood, sanctuary for a part of the host population, etc.

3.2 Advanced/additional exercises

Ea1. Implement extinction in the models. Introduce a cut-off value below which the population density is set to zero. This can be done in both the simple and the spatial model. Hints for the latter: logical operations on matrices (e.g. `h<cutoff`) produce a matrix of logical values; multiplication with logical values behaves as if `TRUE=1` and `FALSE=0`.

Ea2. Vary lattice size and boundary conditions, and test their effect on the probability of coexistence. How is the stable size of the global population in the spatial model related to the (unstable) equilibrium point in the non-spatial system?

Ea3. Does the order of dispersal and reproduction matter?

Ea4. What would happen if either the hosts or the parasitoids spread equally over the entire space?

Ea5. Introduce "long-lived" parasitoids (i.e. a fraction surviving even in the absence of hosts in the lattice cell) and show how it affects the stability of the system.

Ea6. Introduce self-limitation in the host or other stabilizing factors and show how it affects the spatial dynamics.

Ea7. Measure the correlation between the dynamics at two sites as a function of their distance. How strong is the spatial correlation and how does that depend on the parameters controlling parasitoid and host dispersal? A lattice can be regarded as an infinite two-dimensional surface, if the correlation length is smaller than half of the side length of the lattice. Check whether this criterion is fulfilled for the parameters that you use. Hint: measuring all pairwise correlations between the cells of the lattice may require a lot of computer time. Experiment with a small lattice first. *(Note: this exercise is difficult and computationally intensive.)*

Ea8. Can parasitoids facilitate the coexistence of competing hosts? Introduce two host types and either one parasitoid type affecting both hosts or two parasitoid types specialized to the two hosts. Hint: to be able to simulate the system without parasitoids, introduce logistic self-limitation in the hosts.