Ecological Dynamics - Chapter 2

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Exercise 1:

The growth of the population of bacteria is exponential, so the number of individuals in the population at time t can be find by the equation of geometric growth:

$$X(t) = X(0)exp(rt) \qquad \text{where r is the growth parameter} \qquad (1)$$

We know that the population of bacteria grows by a factor 12 in 8 hours so $X(t = 8) = 12X(0)$
First we want to calculate r, so we transform equation (1):

$$r = \frac{ln(X(t)) - ln(X(0))}{t}$$

Then at t $t = 8$ hours, $r = \dfrac{ln(12X(0) - ln(X(0))}{8}$

$$\Rightarrow r = \frac{ln(12)}{8} \approx 0.31$$

With this r value, the time required for the population to grow by a factor of a million is:

$$t = \frac{ln(10^6)}{r} \approx 44.48 \text{ hours}$$

Exercise 2: the discrete logistic model

We consider the discrete logistic model defined by:

$$n_{t+1} = bn_t(1 - cn_t)$$

We assume that $c \approx 0.001$ and $b = 3.1 \pm 0.8$. We investigate the dynamics of the system in relation with the different possible values that b can take in its defined range.

R script:

```r
# parameters:
c <- 0.001
b <- seq(3.1-0.8, 3.1+0.8, 0.4)

tmax <- 30
t <- 0:tmax

# initial values:
n <- rep(NA, length(t))
n[1] <- 2

# model plot:
par(mfrow = c(2,3))
for(p in 1:length(b)){
  for(i in 2:length(t)){
    n[i] <- b[p] * n[i-1] * ( 1 - c * n[i-1] )
  }
  plot(t,n, type = "l", col = 'blue', ylim = c(0,1000))
}
```

Results:

According to the numerical solutions for this model (Figures 1, and **??**), the system has two equilibrium states: one zero equilibrium that is unstable, and one non-zero equilibrium which is stable or unstable depending on the b value:

- if $2.3 \leq b < b_o$ with $2.9 < b_o < 3.1$, the system settles at n^* after an exponential growth and damped fluctuations. The non-zero equilibrium state is then stable.

- if $b_o < b < b_c$ with $3.5 < b_c < 3.7$, the equilibrium state of the system is unstable, but is characterized by stable limit cycles, which are cycles of fluctuations with stable period and stable shape regardless of the initial conditions.

- if $b_c < b \leq 3.9$, the equilibrium state is unstable, and characterized by chaotic fluctuations, which are irregular fluctuations sensitively dependent on initial conditions.
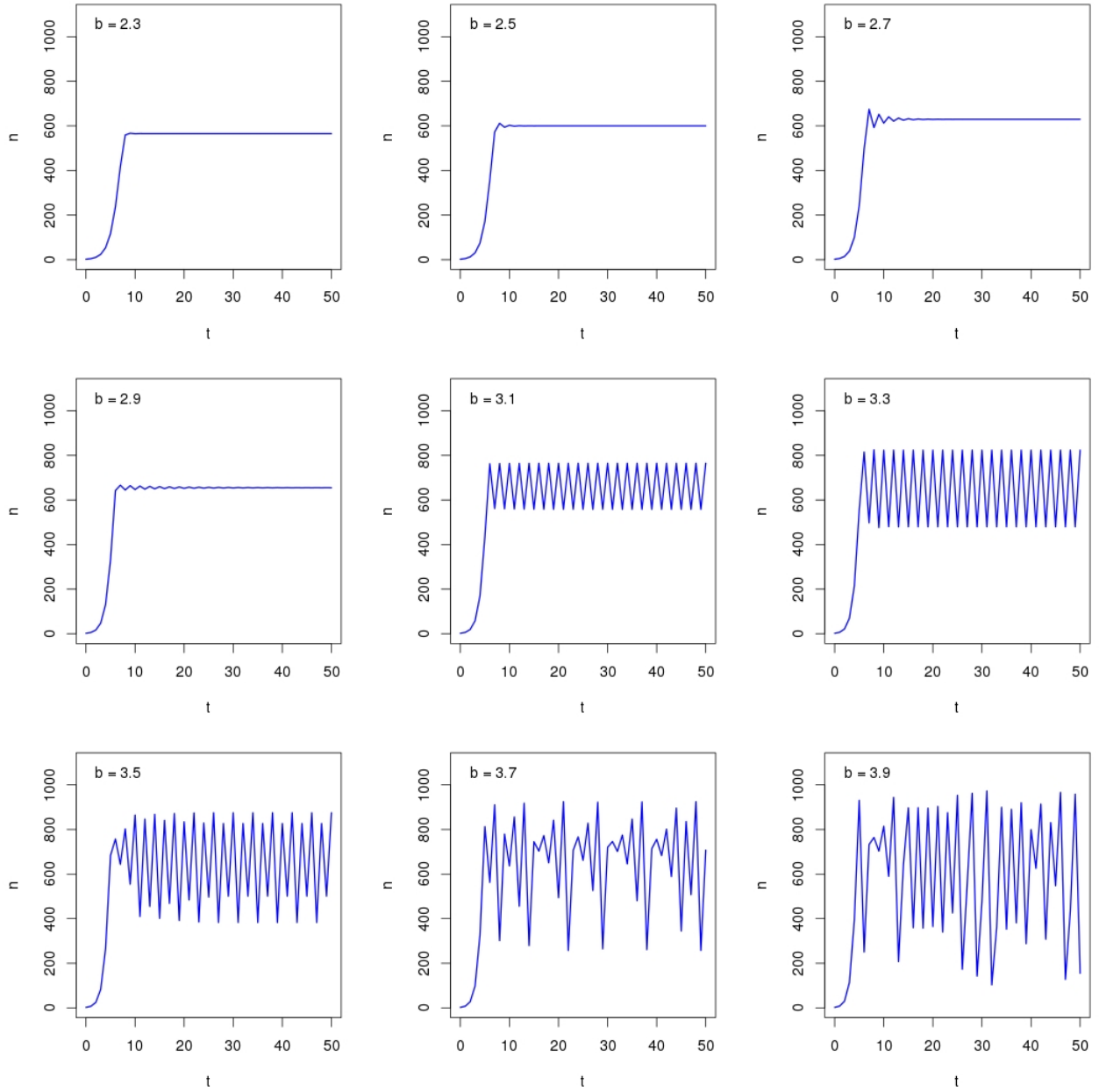
Figure 1: Numerical solutions for the discrete logistic model with the same parameter $c = 0.001$ and initial population $n(0) = 2$, but different values of b between 2.3 and 3.9.
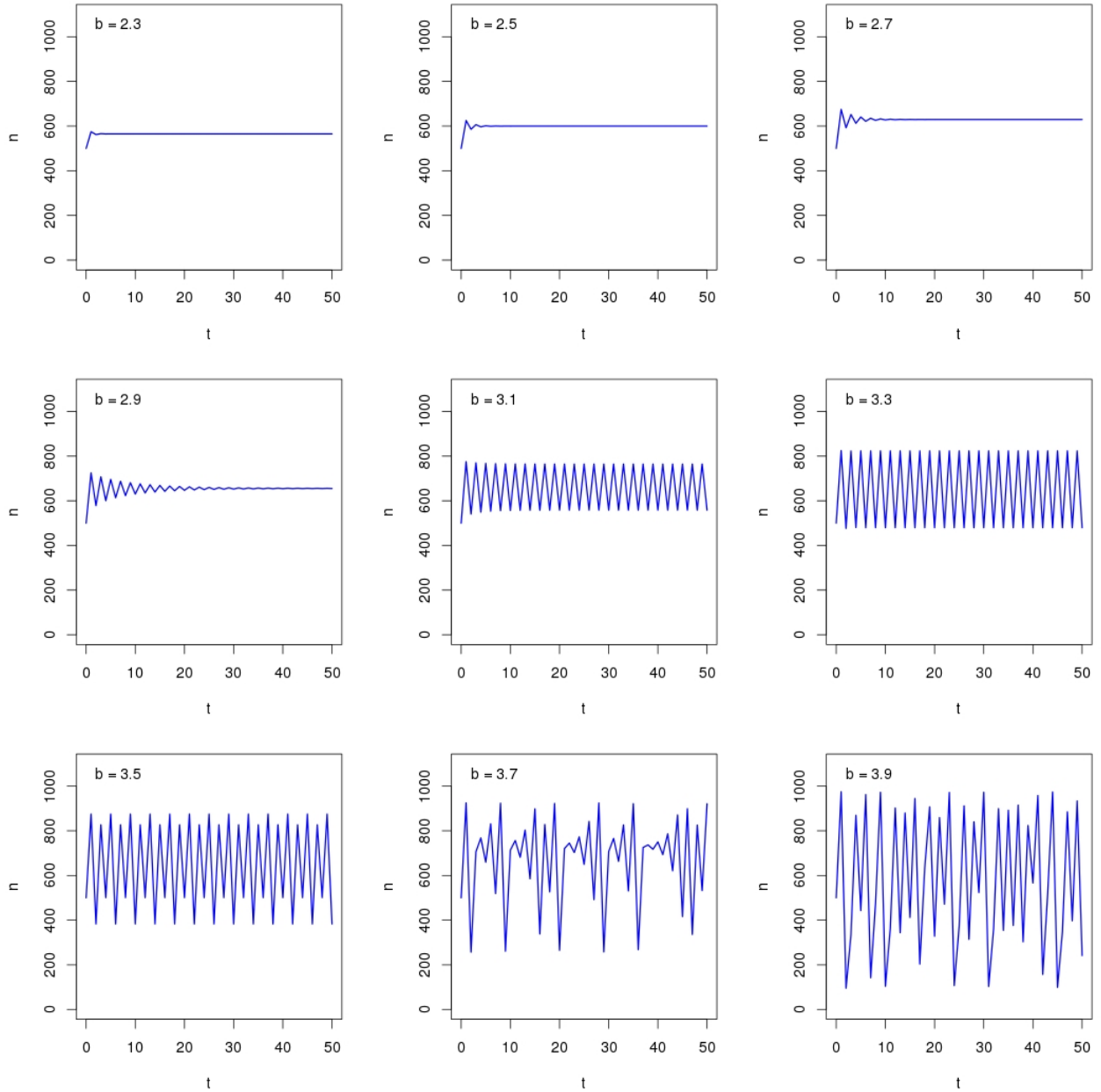
Figure 2: Numerical solutions for the discrete logistic model with the same parameter $c = 0.001$ and initial population $n(0) = 500$, but different values of b between 2.3 and 3.9.

Exercise 3: Lake with two inflow rivers

We want to describe the dynamics of the pollutant stock in a lake that has two inflow rivers. One of the river discharges R_p m³ day⁻¹ of water with a pollutant concentration q_{in} kg m⁻³. The second river doesn't content any pollutant and has a flow of R_c m³ day⁻¹.

We assume that the volume V of the lake is constant, which implies that both inflow and outflow are equal:

$$R_p + R_c = R_{out}$$

First, we consider the balance equation for pollutant concentration in the lake:

$$\frac{dq}{dt} = \frac{1}{V}(R_p q_{in} - (R_p + R_c)q)$$

$$\Rightarrow \frac{dq}{dt} = \frac{R_p + R_c}{V}\left(\frac{R_p q_{in}}{R_p + R_c} - q\right) \tag{1}$$

Then, we transform equation (1) to get the balance equation of the pollutant stock Q in the lake (where $Q = qV$):

$$\frac{dQ}{dt} = \frac{R_p + R_c}{V}\left(\frac{R_p q_{in} V}{R_p + R_c} - Q\right)$$

$$\Rightarrow \frac{dQ}{dt} = D(Q_\infty - Q) \tag{2}$$

where

$$Q_\infty \equiv \frac{R_p q_{in} V}{R_p + R_c} \quad \text{and} \quad D \equiv \frac{R_p + R_c}{V}$$

If the system reaches its equilibrium state $Q*$, then $\dfrac{dQ^*}{dt} = 0$

$$\Rightarrow D(Q_\infty - Q^*) = 0 \qquad \Rightarrow Q^* = Q_\infty$$

Now, we want to investigate the long-term effect of the clean river input on the pollutant stock in the lake. To do that, we first rewrite the balance equation of the pollutant stock without considering the second river inflow:

$$\frac{dQ}{dt} = \frac{R_p}{V}(q_{in}V - Q)$$

Then, we find the equilibrium state of this equation, defined by Q_w^*:

$$\frac{dQ_w^*}{dt} = \frac{R_p}{V}(q_{in}V - Q_w^*) = 0 \qquad \Rightarrow \quad Q_w^* = q_{in}V$$

If we consider back the river inflow of clean water, we know that on the long-term, the pollutant stock is:

$$Q^* = Q_\infty = \frac{R_p q_{in} V}{R_p + R_c}$$

Since $q_{in}V$ is equal Q_w^*, which is the equilibrium state of the pollutant stock in a similar lake without clean water inflow, we see that

$$Q^* = \frac{R_p}{R_p + R_c}Q_w^*$$

So, we conclude that the clean river input reduces the long-term pollutant stock by a factor $\dfrac{R_p}{R_p + R_c}$.

Exercise 4: continuous-time, logistic equation

The objective is to find back the continuous-time, logistic equation from different cases of population dynamics.

Case 1: closed population

We consider a closed population with $N(t)$ individuals, a constant per-capita fecundity β_0, and a per-capita mortality of the form $\delta = \delta_0 + \delta_1 N$. Then the population dynamics are described by:

$$
\begin{aligned}
\frac{dN}{dt} &= \beta_0 N - (\delta_0 + \delta_1 N)N \\
&= (\beta_0 - \delta_0 - \delta_1 N)N \\
&= \left(r - \frac{r\delta_1}{r} N \right)N \qquad \text{where} \quad r \equiv (\beta_0 - \delta_0)
\end{aligned}
$$

$$
\Rightarrow \quad \frac{dN}{dt} = rN\left(1 - \frac{N}{K} \right) \qquad \text{where} \quad K \equiv \frac{r}{\delta_1}
$$

Case 2: population with emigration but no immigration

We consider now a population of $N(t)$ individuals with constant per-capita fecundity and mortality rates β and δ. Each individual of the population has a probability $\epsilon N \Delta t$ of emigrating during a short interval Δt. Then the population dynamics are described by:

$$
\begin{aligned}
\frac{dN}{dt} &= (\beta - \delta)N - \epsilon N^2 \\
&= N(\beta - \delta - \epsilon N) \\
&= N\left((\beta - \delta) - \frac{(\beta - \delta)\epsilon}{\beta - \delta} N \right) \\
&= (\beta - \delta)N\left(1 - \frac{\epsilon}{\beta - \delta} N \right)
\end{aligned}
$$

$$
\Rightarrow \quad \frac{dN}{dt} = rN\left(1 - \frac{N}{K} \right)
$$

where

$$
r \equiv \beta - \delta \qquad \text{and} \qquad K \equiv \frac{r}{\epsilon}
$$

Exercise 5: Population model considering predation

Acccording to Ludwig, Jones, and Holling (1978), the dynamic equation of a population of the North American spruce budworm predated by birds is:

$$
\frac{dN}{dt} = rN\left(1 - \frac{N}{K} \right) - \frac{\beta N^2}{\alpha^2 + N^2}
$$

We investigate the equilibrium state(s) N^* of this equation, when $\dfrac{dN^*}{dt} = 0$:

$$rN^*\left(1 - \frac{N^*}{K}\right) - \frac{\beta N^{*2}}{\alpha^2 + N^{*2}} = 0$$

$$rN^*\left(1 - \frac{N^*}{K}\right) = \frac{\beta N^{*2}}{\alpha^2 + N^{*2}}$$

$$rN^*\left(1 - \frac{N^*}{K}\right)(\alpha^2 + N^{*2}) = \beta N^{*2}$$

$$r\left(1 - \frac{N^*}{K}\right)(\alpha^2 + N^{*2}) = \beta N^*$$

$$-\frac{r}{K}N^{*3} + rN^{*2} + \left(-\beta - \frac{r\alpha^2}{K}\right)N^* + r\alpha^2 = 0$$

This is a cubic equation which has either one or three roots. Considering non-zero parameters, N^* must be different from zero to fulfill the equation. So the dynamic equation has either one or three non-zero equilibrium states.

We now study the stability of these equilibrium states, and we consider $n(t)$ that describes small deviations from an particular equilibrium:

$$n(t) = N(t) - N^*$$

With $\dfrac{dn}{dt} = G(N)$ where $G(N) = \dfrac{dN}{dt}$, we approximate $\dfrac{dn}{dt}$ using Taylor's theorem:

$$\frac{dn}{dt} = G(n + N^*) \approx G(N^*) + n\left(\frac{dG}{dN}\right)_{N=N^*}$$

$$\frac{dn}{dt} \approx \lambda n \qquad \text{where} \quad \lambda \equiv \left(\frac{dG}{dN}\right)_{N=N^*}$$

This equation corresponds to the equation for the exponential growth or decline with the solution $x(t) = x(0)e^{\lambda t}$. So the equilibrium is stable if $\lambda < 0$, and unstable if $\lambda > 0$.

Exercise 6: the 'mussel' model

We consider a population of mussels whose dynamics in a fluctuating environment are described by the following discrete-time model:

$$X_{t+1} = I_t + SX_t$$

where I_t corresponds to recruitment and only occur every second year:

$$I_t = \begin{cases} 2I & \text{if t is even} \\ 0 & \text{if t is odd.} \end{cases}$$

When this model reaches its equilibrium state, then $X_t = X_{t-2}$.
So, if t is even:

$$
\begin{aligned}
X_t &= I_{t-1} + SX_{t-1} \\
&= SX_{t-1} \qquad \text{where} \quad X_{t-1} = 2I + SX_{t-2} \\
\Rightarrow X_t &= S(2I + SX_t) \\
\Rightarrow X_t &= \frac{2IS}{1 - S^2}
\end{aligned}
$$

If t is odd:

$$
\begin{aligned}
X_t &= 2I + SX_{t-1} \qquad \text{where} \quad X_{t-1} = SX_{t-2} \\
\Rightarrow X_t &= 2I + S^2 X_t \\
\Rightarrow X_t &= \frac{2I}{1 - S^2}
\end{aligned}
$$

So we proved that after any transient dynamics, the system ultimately executes two-year cycles defined by:

$$
X_t = \begin{cases}
\dfrac{2IS}{1 - S^2} & \text{if t is even} \\[3ex]
\dfrac{2I}{1 - S^2} & \text{if t is odd.}
\end{cases}
$$

Numerical solutions:

According to the dynamic equation of the 'mussel' model, the year-to-year survival rate is the parameter that controls the time needed to reach the equilibrium state:
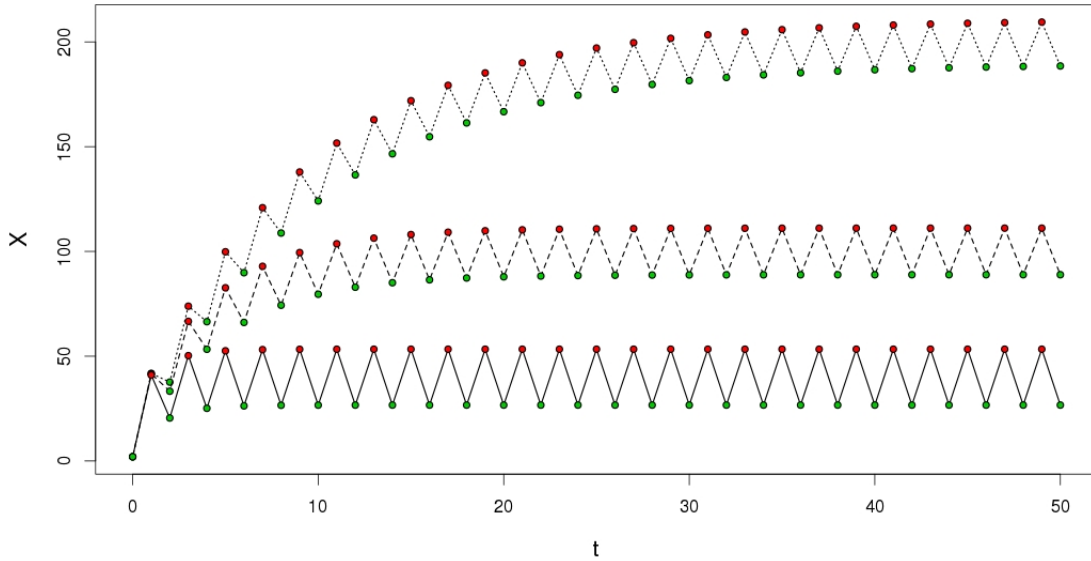

Figure 3: Numerical solutions for the 'mussel' model in a fluctuating environment, with the same initial population $X(0) = 2$, and recruitment parameter $I = 20$, but different values of the year-to-year survival rate: $S = 0.5$ (solid line), 0.8 (long dashes), 0.9 (short dashes) ; green, and red points give even, odd years respectively.

R script:

```
library(gtools)

# Parameters:
I <-20
S <- 0.9

t <- 0:50
X <- rep(NA,51)

# initial values:
X[1] <- 2

# model run:
for (i in 2:length(t)){
    if (even(t)[i] == T){
        X[i] <- S*X[i-1]
    } else {
        X[i] <- 2*I + S*X[i-1]
    }
}
```

Project: continuous-time logistic model

We consider a closed population whose dynamics is described by the continuous-time logistic model:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

First, we want to understand the effect of the parameters r and K, and the initial population $N(0)$ on the system behaviour, testing different values of them. Then we will investigate the model with a carrying capacity K varying sinusoidally in time.

Case 1: with K constant

R script:

```r
# continuous-time logistic model:
G <- function(N){
  r*N * (1-N/K)
}

# Runga-Kutta 4 :
RG4 <- function(N){
  k1 <- dt* G( N )
  k2 <- dt* G( N + k1/2 )
  k3 <- dt* G( N + k2/2 )
  k4 <- dt* G( N + k3 )
  N + (k1 + 2*k2 + 2*k3 + k4)/6
}

# Parameters:
  ## growth rate:
  r <- 0.4
  ## carrying capacity:
  K <- 300

# Intitial population:
  N0 <- 5

  dt <- 0.02

# Run:
  t <- seq(0, 40, dt)
  N <- rep(NA, length(t))
  N[1] <- N0

  for (i in 2:length(t)){
    # Approximation by RK4:
    N[i] <- RG4( N[i-1], t[i-1] )
  }

# Model plot:
  plot(t, N, type='l')
```

Results:

Testing different values of the initial population $N(0)$ with the same parameter values (Figure 3a) show that any $N(0)$ lead the system to the same equilibrium which is equal to K. So this equilibrium is globally stable. The larger the difference is between $N(0)$ and the equilibrium K, the longer is the time taken to reach this equilibrium.

The figure 3b shows that the growth rate r has an effect on the time taken to reach the equilibrium state. The population grows more rapidly and reach K more rapidly, if the growth rate is high.

Changing the constant carrying capacity K primarily changes the population size at the equilibrium state (Figure 3c. However, since changing the K value but keeping the same initial population modifies the difference between $N(0)$ and K, it also has an effect on the time taken to reach the equilibrium state.
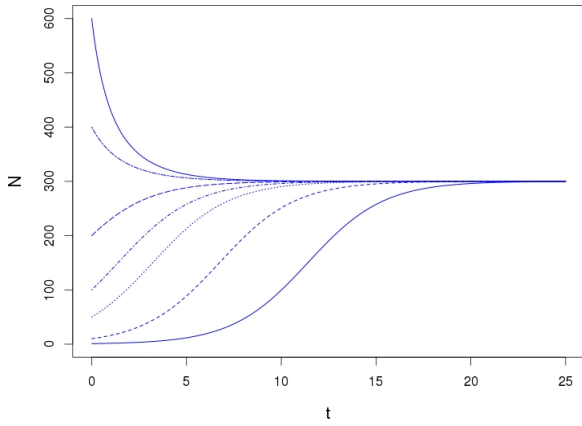
(a) With the same parameters $K = 300$, and $r = 0.4$, but different values of the initial population: $N(0) = 1$, 10, 50, 100, 200, 400, or 600.
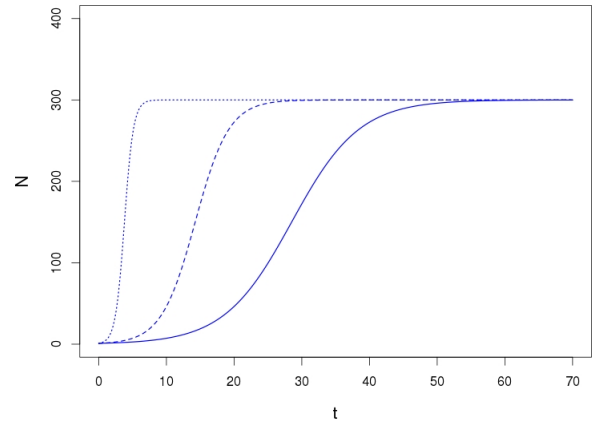
(b) With the same initial population $N(0) = 1$, and carrying capacity $K = 300$, but different growth rates: $r = 0.2$, 0.4, or 1.5.
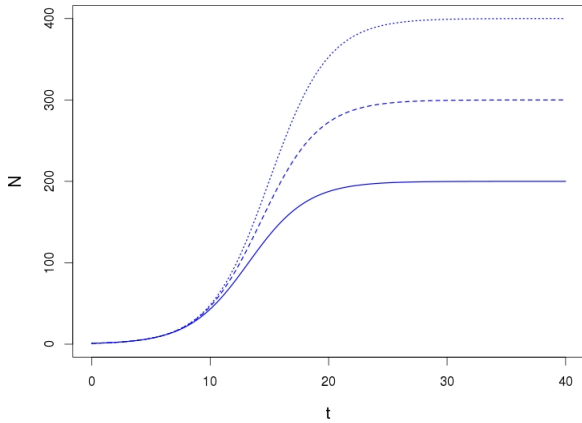
(c) With the same initial population $N(0) = 1$, and growth rate $r = 0.4$, but different carrying capacities: $K = 100$, 200, or 300.

Figure 4: Numerical solutions of the continuous-time logistic model, investigating the effects of the initial population $N(0)$ (a), the carrying capacity K (b), and the growth rate r (c) on the evolution of the system.

Case 2: with K varying sinusoidally in time

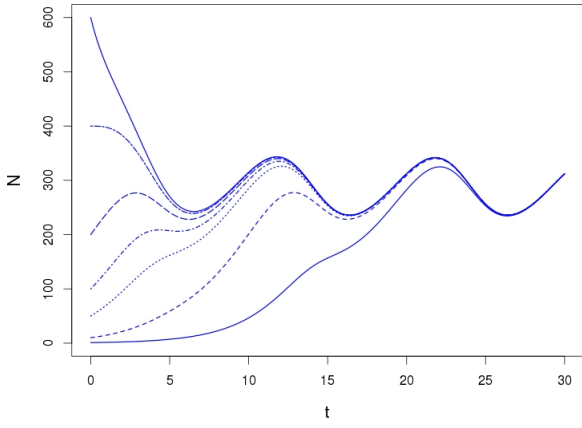We consider now a carrying capacity defined by the equation:

$$K(t) = K_0 + K_1 cos\left(\frac{2\pi t}{t_p}\right)$$

And we investigate the effects of K_0, K_1, and t_p, where K_1 is always positive and smaller than K_0.

R script:

```r
# the carrying capacity K varies sinusoidally with time:
K <- function(t){
  K0 + K1 * cos(2*pi*t/tp)
}
# model becomes:
G <- function(N,t){
  r*N * (1-N/K(t))
}

# Runga-Kutta 4 :
RG4 <- function(N, t){
  k1 <- dt* G( N, t )
  k2 <- dt* G( N + k1/2, t )
  k3 <- dt* G( N + k2/2, t )
  k4 <- dt* G( N + k3, t )
  N + (k1 + 2*k2 + 2*k3 + k4)/6
}

# Parameters:
  ## growth rate:
  r <- 0.4
  ## carrying capacity:
  K0 <- 200
  K1 <- 50
  tp <- 10

# Intitial population:
  N0 <- 5

  dt <- 0.02

# Run:
  t <- seq(0, 40, dt)
  N <- rep(NA, length(t))
  N[1] <- N0

  for (i in 2:length(t)){
    # Approximation by RK4:
    N[i] <- RG4( N[i-1], t[i-1] )
  }

# Model plot:
  plot(t, N, type='l')
```
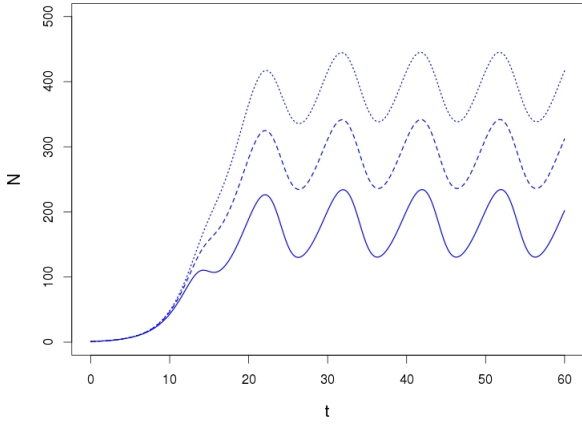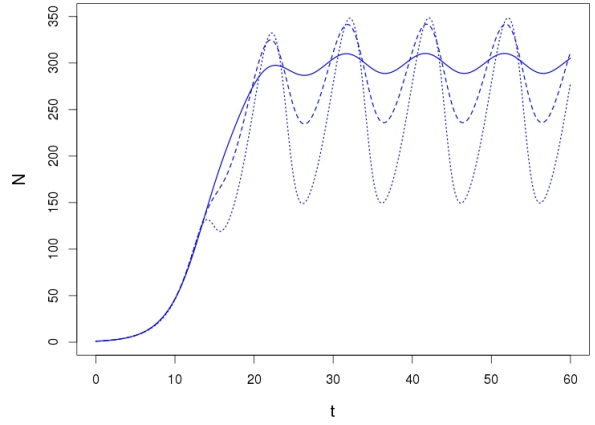
(a) With $r = 0.4$, $K_0 = 300$, $K_1 = 100$, $t_p = 10$, and $N(0) = 1, 10, 50, 100, 200, 400,$ or 600.
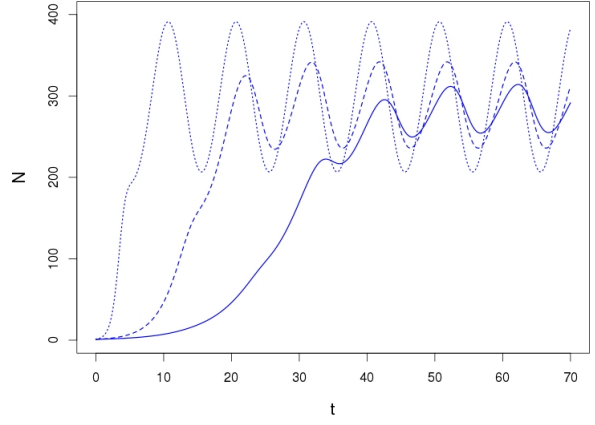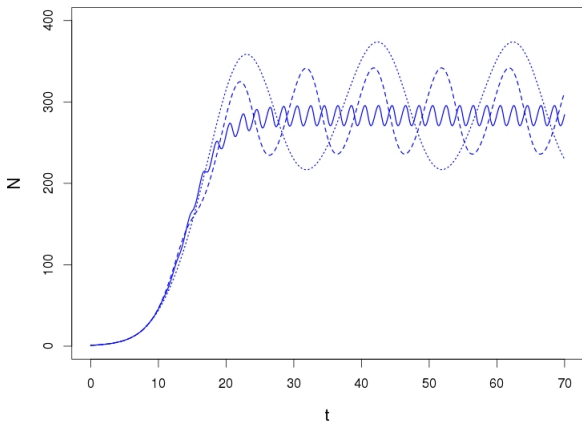
(b) With $N(0) = 1$, $K_0 = 300$, $K_1 = 100$, $t_p = 10$, and $r = 0.2$ (solid line), 0.4 (long dashes), 1.5 (short dashes).

(c) With $N(0) = 1$, $r = 0.4$, $K_1 = 100$, $t_p = 10$, and $K_0 = 200$ (solid line), 300 (long dashes), 400 (short dashes).

(d) With $N(0) = 1$, $r = 0.4$, $K_0 = 300$, $t_p = 10$, and $K_1 = 20$ (solid line), 100 (long dashes), 200 (short dashes).

(e) With $N(0) = 1$, $r = 0.4$, $K_0 = 300$, $K_1 = 100$, and $t_p = 2$ (solid line), 10 (long dashes), 20 (short dashes).

Figure 5: Numerical solutions of the continuous-time logistic model, with the carrying capacity K varrying sinusoidally with time: $K = K_0 + K_1 cos\left(\dfrac{2\pi t}{t_p}\right)$.

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The numerical solutions of the continuous-time model, with a capacity K varrying sinusoidally with time, show that the system reaches after a variable length of time an equilibrium state which is defined by oscillations with constant amplitude and the same period as the carrying capacity variations.

With the numerical solutions of the figure 4a, we find back the assumption that the time needed to the system to settle at the equilibrium state depends on the distance of $N(0)$ from this equilibrium state. The system more rapidly settles down to oscillations with constant amplitudes, if the initial population $N(0)$ is closer to the K_0 value.

With larger values of the growth rate r, the system still reaches the equilibrium state more rapidly (Figure 4b). But at equilibrium, we observe that the amplitude of the oscillations are larger with larger values of r.

If we only change the value of K_0, we change the average population size at the equilibrium state and we change the time the system required to settle at oscillations with constant amplitude (Figure 4c).

By changing K_1 which modifies the amplitude of the K variations, we mainly change the amplitude of the population oscillations at the equilibrium state (Figure 4d). However, this does not change the minimum and maximum values of these oscillations in the same proportion: when K_1 is increased, the maximum value of the stable oscillations increases far less than the minimum value decreases.

The figure 4e shows that changing the period t_p not only affects the period of the population variations at the equilibrium state, but also affects the amplitude of these variations: the longer the period t_p, the larger the amplitude.