Evolutionary Dynamics Exercise 1

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This solution PDF is written in R markdown.

```r
sessionInfo()
```

```
## R version 4.4.1 (2024-06-14)
## Platform: x86_64-pc-linux-gnu
## Running under: Ubuntu 20.04.6 LTS
##
## Matrix products: default
## BLAS:   /usr/lib/x86_64-linux-gnu/openblas-pthread/libblas.so.3
## LAPACK: /usr/lib/x86_64-linux-gnu/openblas-pthread/liblapack.so.3;  LAPACK version 3.9.0
##
## locale:
##  [1] LC_CTYPE=en_US.UTF-8       LC_NUMERIC=C
##  [3] LC_TIME=en_US.UTF-8        LC_COLLATE=en_US.UTF-8
##  [5] LC_MONETARY=en_US.UTF-8    LC_MESSAGES=en_US.UTF-8
##  [7] LC_PAPER=en_US.UTF-8       LC_NAME=C
##  [9] LC_ADDRESS=C               LC_TELEPHONE=C
## [11] LC_MEASUREMENT=en_US.UTF-8 LC_IDENTIFICATION=C
##
## time zone: Europe/Zurich
## tzcode source: system (glibc)
##
## attached base packages:
## [1] stats     graphics  grDevices datasets  utils     methods   base
##
## loaded via a namespace (and not attached):
##  [1] compiler_4.4.1    fastmap_1.2.0     cli_3.6.3         htmltools_0.5.8.1
##  [5] tools_4.4.1       yaml_2.3.10       rmarkdown_2.28    knitr_1.48
##  [9] xfun_0.47         digest_0.6.37     rlang_1.1.4       renv_1.0.7
## [13] evaluate_1.0.0
```

```r
library(foreach)
library(ggplot2)
```

Problem 1: Discrete time

Suppose you have a difference equation $x_{t+1} = f(x_t)$ of a discrete time model with

$$f(x) = 5x^2(1-x).$$

(a) Determine the equilibrium points x^* of the system.

At equilibrium points we have $x_{t+1} = x_t = x^*$, which means

$$\begin{aligned} x^* - 5{x^*}^2(1-x^*) &= 0 \\ 5{x^*}^3 - 5{x^*}^2 + x^* &= 0 \\ x^*(5{x^*}^2 - 5x^* + 1) &= 0 \end{aligned}$$

Solving the equation gives solutions:

$$x_1^* = 0, \qquad x_2^* = \frac{1}{2} - \frac{1}{2\sqrt{5}} \qquad x_3^* = \frac{1}{2} + \frac{1}{2\sqrt{5}}$$

(b) Which of the equilibrium points x^* are stable?

For an equilibrium to be stable we need to have the absolute value of the derivative of $|f'(x^*)| < 1$.

$$f(x) = 5x^2(1-x) = -5x^3 + 5x^2 f'(x) = -15x^2 + 10x$$

Plug in $x_1^* = 0$, $x_2^* = \frac{1}{2} - \frac{1}{2\sqrt{5}}$, $x_3^* = \frac{1}{2} + \frac{1}{2\sqrt{5}}$, we have

$$\begin{aligned} |f'(x_1^*)| &= 0 < 1 && \text{(stable)} \\ |f'(x_2^*)| &= \frac{1}{2} + \frac{\sqrt{5}}{2} > 1 && \text{(unstable)} \\ |f'(x_3^*)| &= \frac{\sqrt{5}}{2} - \frac{1}{2} < 1 && \text{(stable)} \end{aligned}$$

Problem 2: Continuous time

Consider the case:

$$\frac{dx(t)}{dt} = f(x) = 3x(x-1)(x-2).$$

(a) Determine the equilibrium points x^* of the system.

At the equilibrium, we have

$$\frac{dx^*(t)}{dt} = f(x^*) = 3x^*(x^*-1)(x^*-2) = 0$$

which yields:

$$x_1^* = 0, \qquad x_2^* = 1, \qquad x_3^* = 2$$

(b) Which of the equiliubrium points x^* are stable?

$$f'(x^*) = 3(x^* - 1)(x^* - 2) + 3x^*(x^* - 2) + 3x^*(x^* - 1)$$

Plug in $x_1^* = 0$, $x_2^* = 1$, $x_3^* = 2$, we have

$$\begin{aligned} f'(x_1^*) &= 6 > 0 \qquad \text{(unstable)} \\ f'(x_2^*) &= -3 < 0 \qquad \text{(stable)} \\ f'(x_3^*) &= 6 < 0 \qquad \text{(unstable)} \end{aligned}$$

Problem 3: Logistic difference equation

In a discrete time model for population growth, the value x (number of cells divided by the maximum number supported by the habitat) at time $t + 1$ is calculated from the value at time t according to the difference equation:

$$x_{t+1} = rx_t(1 - x_t)$$

(a) Determine the equilibrium points x^* of the system.

At equilibrium we have $x_{t+1} = x_t = x^*$, which means:

$$\begin{aligned} x^* &= rx^*(1 - x^*) \\ x^*(rx^* - (r - 1)) &= 0 \end{aligned}$$

Solving the equation gives:

$$x_1^* = 0, \qquad x_2^* = \frac{r-1}{r}$$

(b) Are the equilibrium points table for $r = 0.9$, $r = 1.9$, $r = 2.9$?

As $f(x) = rx(1 - x)$, we have:

$$f'(x) = r - 2rx$$

Plug in $x_1^* = 0$, $x_2^* = \frac{r-1}{r}$ with different r values into the equation, we have:

(1) $r = 0.9$

With $r = 0.9$, $x_2^* = \frac{0.9-1}{0.9} = \frac{-1}{9}$.

$$\begin{aligned} |f'(x_1^*)| &= |f'(0)| = 0.9 < 1 && \text{(stable)} \\ |f'(x_2^*)| &= \left|f'\left(\frac{1}{9}\right)\right| = \left|\frac{9}{10} + 2 \cdot \frac{9}{10} \cdot \frac{1}{9}\right| = \frac{11}{10} > 1 && \text{(unstable)} \end{aligned}$$

(2) $r = 1.9$

With $r = 1.9$, $x_2^* = \frac{1.9-1}{1.9} = \frac{9}{19}$.

$$
\begin{aligned}
|f'(x_1^*)| &= |f'(0)| = 1.9 > 1 && \text{(unstable)} \\
|f'(x_2^*)| &= \left|f'\left(\frac{9}{19}\right)\right| = \left|\frac{19}{10} - 2 \cdot \frac{19}{10} \cdot \frac{9}{19}\right| = \frac{1}{10} < 1 && \text{(stable)}
\end{aligned}
$$

(3) $r = 2.9$

With $r = 2.9$, $x_2^* = \frac{2.9-1}{2.9} = \frac{19}{29}$.

$$
\begin{aligned}
|f'(x_1^*)| &= |f'(0)| = 2.9 > 1 && \text{(unstable)} \\
|f'(x_2^*)| &= \left|f'\left(\frac{19}{29}\right)\right| = \left|\frac{29}{10} - 2 \cdot \frac{29}{10} \cdot \frac{19}{29}\right| = \frac{9}{10} < 1 && \text{(stable)}
\end{aligned}
$$

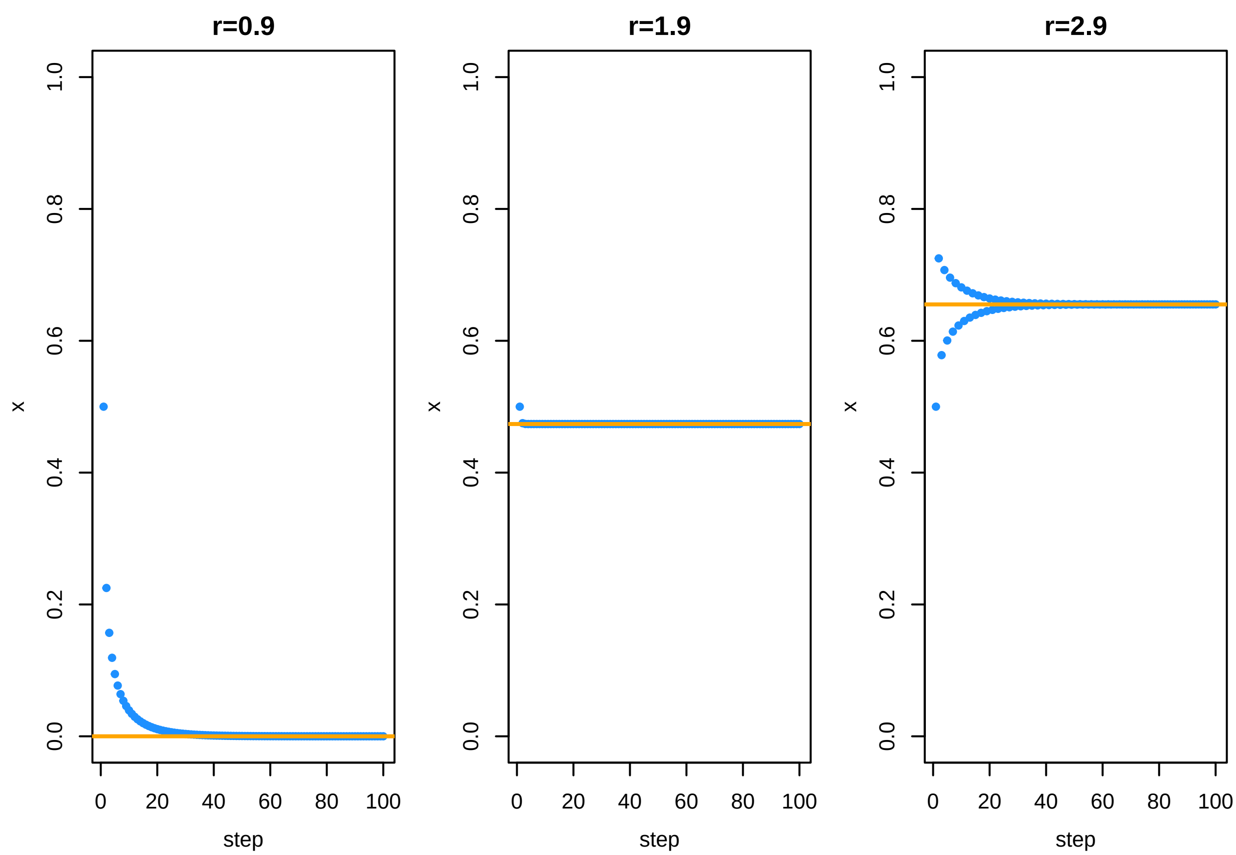
(c) Confirm this by numerically iterating the difference equation

```r
sim_diffeq <- function(ini, r, steps=100) {
  x <- rep(0, steps)
  x[1] <- ini
  foreach (i=2:steps) %do% {
    x[i] <- r * x[i - 1] * (1 - x[i - 1])
  }
  return(x)
}
```

```r
sim1 <- sim_diffeq(0.5, 0.9)
sim2 <- sim_diffeq(0.5, 1.9)
sim3 <- sim_diffeq(0.5, 2.9)
```

```r
par(mar = c(4, 4, 2, 0.5))
par(mgp = c(2.5, 1, 0))
# par(cex.lab = 1.25)
par(mfrow=c(1,3))
plot(sim1,
     xlab = "step",
     ylab = "x",
     main = "r=0.9",
     col = "dodgerblue",
     pch = 20,
     ylim = c(0,1)
)
abline(h = 0, col = "orange", lwd=2)

plot(sim2,
     xlab = "step",
     ylab = "x",
     main = "r=1.9",
     col = "dodgerblue",
```

```
      pch = 20,
      ylim = c(0,1)
)
abline(h = 9/19, col = "orange", lwd=2)

plot(sim3,
      xlab = "step",
      ylab = "x",
      main = "r=2.9",
      col = "dodgerblue",
      pch = 20,
      ylim = c(0,1)
)
abline(h = 19/29, col = "orange", lwd=2)
```

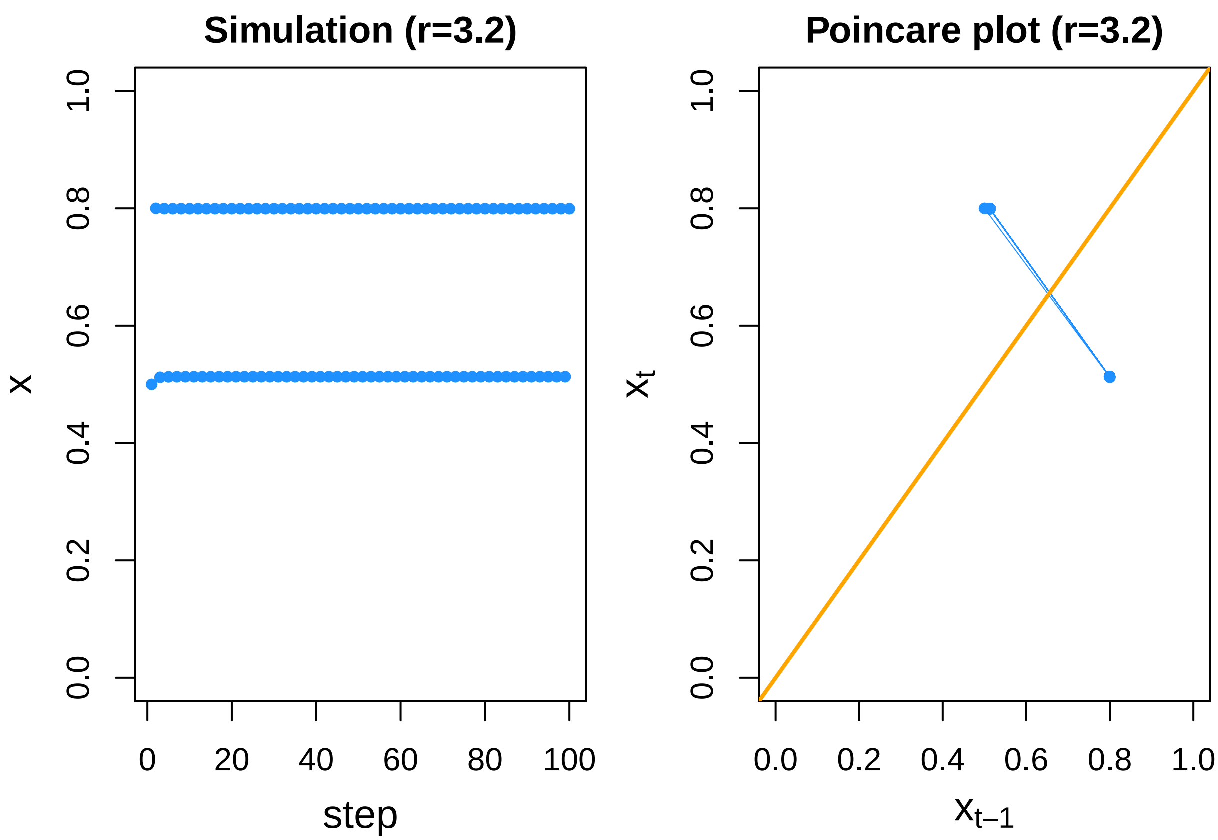


(d) Examine the stability and behavior for $r = 3.2$.

The system approaches permanent oscillation between two values (can be computed using the same technique used in previous sections).

```
par(mar = c(4, 4, 2, 0.5))
par(mgp = c(2.5, 1, 0))
par(cex.lab = 1.25)
par(mfrow=c(1,2))
```

```r
sim4 <- sim_diffeq(0.5, 3.2)

xstm1 <- sim4[-length(sim4)]
xst <- sim4[-1]

plot(sim4,
     xlab = "step",
     ylab = "x",
     main = "Simulation (r=3.2)",
     col = "dodgerblue",
     pch = 20,
     ylim = c(0,1)
)

# Poincare
plot(xstm1,
     xst,
     xlab = expression(x[t-1]),
     ylab = expression(x[t]),
     main = "Poincare plot (r=3.2)",
     col = "dodgerblue",
     pch = 20,
     xlim = c(0,1),
     ylim = c(0,1)
)
lines(xstm1, xst, col = "dodgerblue", lwd=0.5)
abline(b = 1, a = 0, col = "orange", lwd =2)
```

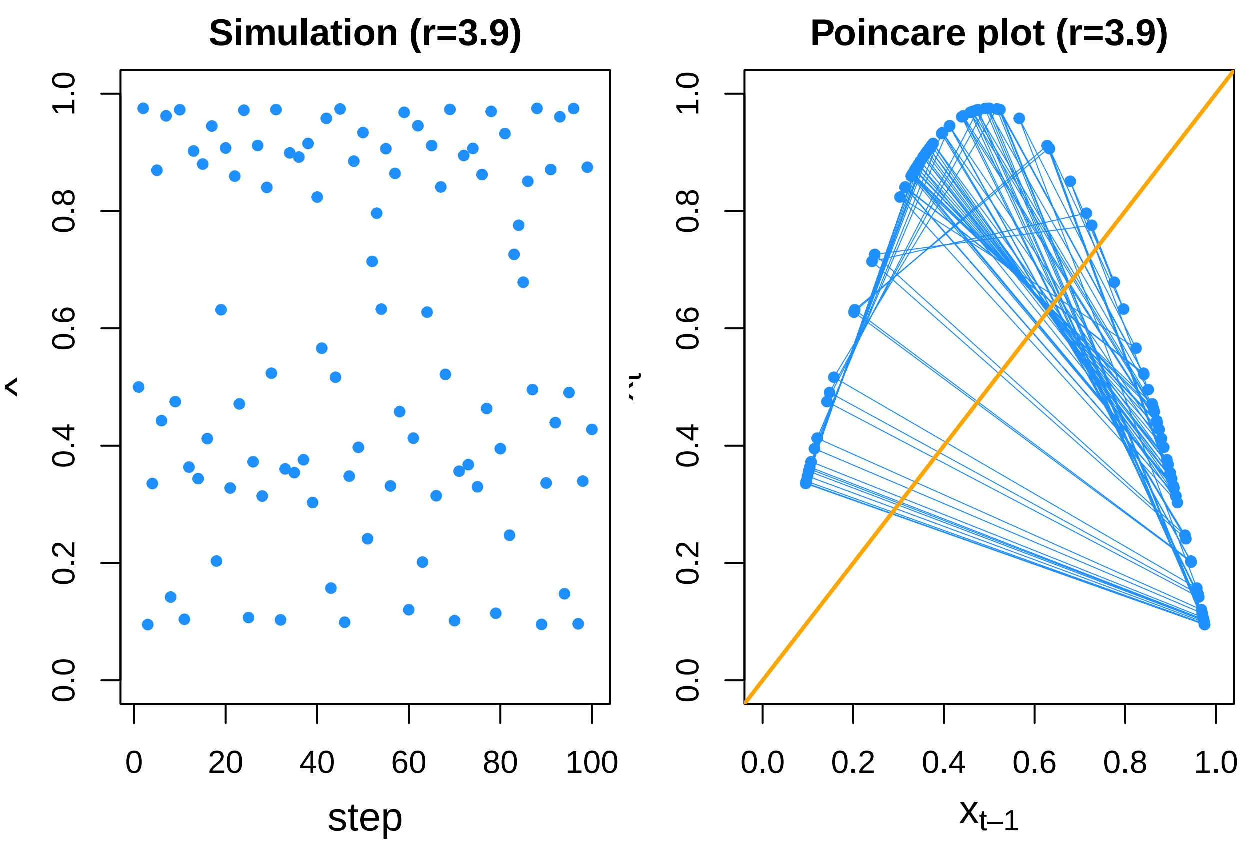


(e) What happens for $r = 3.9$?

The system exhibits chaotic behavior.

```
par(mar = c(4, 3, 2, 0.5))
par(mgp = c(2.5, 1, 0))
par(cex.lab = 1.25)
par(mfrow=c(1,2))

sim4 <- sim_diffeq(0.5, 3.9)

xstm1 <- sim4[-length(sim4)]
xst <- sim4[-1]

plot(sim4,
     xlab = "step",
     ylab = "x",
     main = "Simulation (r=3.9)",
     col = "dodgerblue",
     pch = 20,
     ylim = c(0,1)
)

# Poincare
plot(xstm1,
```

```
    xst,
    xlab = expression(x[t-1]),
    ylab = expression(x[t]),
    main = "Poincare plot (r=3.9)",
    col = "dodgerblue",
    pch = 20,
    xlim = c(0,1),
    ylim = c(0,1)
)
lines(xstm1, xst, col = "dodgerblue", lwd=0.5)
abline(b = 1, a = 0, col = "orange", lwd =2)
```



(r) Describe what happens for $r > 4$. Is the model still biologically plausible?

Beyond r = 4, almost all initial values eventually leave the interval [0,1] and diverge. It is not biologically plausible.

Problem 4: Logistic growth in continuous time

The logistic model for population growth is:

$$\frac{dx(t)}{dt} = \lambda x(t) \left(1 - \frac{x(t)}{K}\right)$$

(a) Show the solution of logistic growth by direct integral

$$x(t) = \frac{Kx_0 e^{\lambda t}}{K + x_0(e^{\lambda t} - 1)}$$

This is a very basic linear differential equation exercise.

$$\begin{aligned}
\int \frac{dx(t)}{x(t)\left(1 - \frac{x(t)}{K}\right)} &= \int \lambda dt \\
\int \frac{dx(t)}{x(t)} + \int \frac{dx(t)}{K - x(t)} &= \int \lambda dt \\
\ln|x(t)| - \ln|K - x(t)| &= \lambda t + C \\
\ln\left|\frac{K - x(t)}{x(t)}\right| &= -(\lambda t + C) \\
\left|\frac{K - x(t)}{x(t)}\right| &= e^{-(\lambda t + C)} \\
\frac{K - x(t)}{x(t)} &= C_0 \cdot e^{-\lambda t}
\end{aligned}$$

Rewrite the equation we get:

$$x(t) = \frac{K}{1 + C_0 e^{-\lambda t}}$$

To get the final form, we need to replace C_0 with some expression with x_0, which is the initial condition of the population at $t = 0$:

$$\frac{K - x_0}{x_0} = C_0$$

Plug it back to the equation, we have:

$$\begin{aligned}
x(t) &= \frac{K}{1 + \frac{K - x_0}{x_0} e^{-\lambda t}} \\
&= \frac{Kx_0 e^{\lambda t}}{K + x_0(e^{\lambda t} - 1)}
\end{aligned}$$

(b) Find the equilibrium points of the systems and discuss their stability

At equilibrium points we have $\frac{dx(t)}{dt} = f(x) = 0$, i.e.:

$$f(x^*) = \lambda x^* \left(1 - \frac{x^*}{K}\right) = 0 \Longrightarrow x_1^* = 0, \quad x_2^* = K$$

$$f'(x) = \lambda\left(1 - \frac{x}{K}\right) - \frac{\lambda x}{K} = \lambda\left(1 - \frac{2x}{K}\right)$$

At equilibrium points, we have

$$f'(x_1^*) = f'(0) = \lambda$$
$$f'(x_2^*) = f'(K) = -\lambda$$

Interestingly, we will then only have one of the two equilibrium points to be stable. If $\lambda > 0$, then $x_1^* = 1$ is unstable and $x_2^* = K$ is stable; while if $\lambda < 0$ we have the exact opposite.

(c) Demostrate the results above for $K = 3$ and a series of time points.

```
logistic_sim <- function (ini, lambda, K, steps=100) {
  x <- rep(0, steps)
  x[1] <- ini
  foreach (i=2:steps) %do% {
    x[i] <- lambda * x[i-1] * (1 - (x[i-1])/K) + x[i-1]
  }
  return(x)
}
```

```
par(mar = c(4, 3, 2, 0.5))
par(mgp = c(2.5, 1, 0))
par(cex.lab = 1.25)
par(mfrow=c(1,2))

x_logistic_1 <- logistic_sim(
  0.8,
  lambda = -1,
  K = 1
)

x_logistic_2 <- logistic_sim(
  0.01,
  lambda = 1,
  K = 1
)

plot(x_logistic_1,
     xlab = "step",
     ylab = "x",
     main = "lambda=-1, K=1",
     col = "dodgerblue",
     pch = 20,
     ylim = c(0,1)
)
abline(h = 0, col = "orange", lwd=2)

plot(x_logistic_2,
     xlab = "step",
     ylab = "x",
     main = "lambda=1, K=1",
     col = "dodgerblue",
     pch = 20,
     ylim = c(0,1)
```

```
)
abline(h = 1, col = "orange", lwd=2)
```