Exercise 1: Growth models in 1D

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Course: BIO-341 *Systèmes dynamiques en biologie*

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Note that this document is primarily aimed at being consulted as a Jupyter notebook, the PDF rendering being not optimal.

[1]:
```
import numpy as np
import matplotlib.pyplot as plt
from ipywidgets import interact
```

1 Growth models in 1D

1.1 Linear model for population growth

Consider a population of N birds with birth and death rates n and m. Arrival of new individuals through migrations occurs at rate $a > 0$. This can be translated into the simple model:

$$\frac{dN}{dt} = F(N) = (n - m)N + a \tag{1}$$

1) Write down what type of equation this is, e.g. first order, second order, linear, non-linear, etc.

> The equation is a linear first order ODE.

2) Solve this equation analytically using the Ansatz: $N(t) = Ae^{\lambda t} + B$. Express A, B and λ in function of the rates and the population size $N_0 = N(t = 0)$; explicitly write the solution $N(t)$.

> Differentiating the Ansatz gives: $\frac{dN}{dt} = A\lambda e^{\lambda t}$
> If the Ansatz is a solution of the differential equation, then $\frac{dN}{dt}$ is also equal to $(n - m)N + a$, so:
> $$A\lambda e^{\lambda t} = k(Ae^{\lambda t} + B) + a, \text{ with } k = (n - m)$$
> By separating terms which depends on time and terms which are time-independent, we can deduce that $kB + a = 0 \Rightarrow B = -\frac{a}{k}$. In addition, by comparison of the left-hand side and right-hand side it follows that $\lambda = k$.
> To find A, use the initial conditions in the equation: $N(t = 0) = N_0 = A - \frac{a}{k} \Rightarrow A = N_0 + \frac{a}{k}$. Finally, $N(t) = (N_0 + \frac{a}{k})e^{kt} - \frac{a}{k}$.

3) Solve the equation using an alternative method, such as the separation of variables.

Solving an equation like $\frac{dN}{dt} = kN$ is trivial, so we seek for a change of variable that could get rid of the $+a$ term in the original equation. Taking $N = u - \frac{a}{k} \Rightarrow u = N + \frac{a}{k}$ we have:
$dN = du$, since a and k are two constants.
$\frac{du}{dt} = ku \Rightarrow u = u_0 e^{kt}$
Then, you can substitute back: $N(t) = (N_0 + \frac{a}{k})e^{kt} - \frac{a}{k}$ where $u_0 = N_0 + \frac{a}{k}$ is found with the initial conditions.

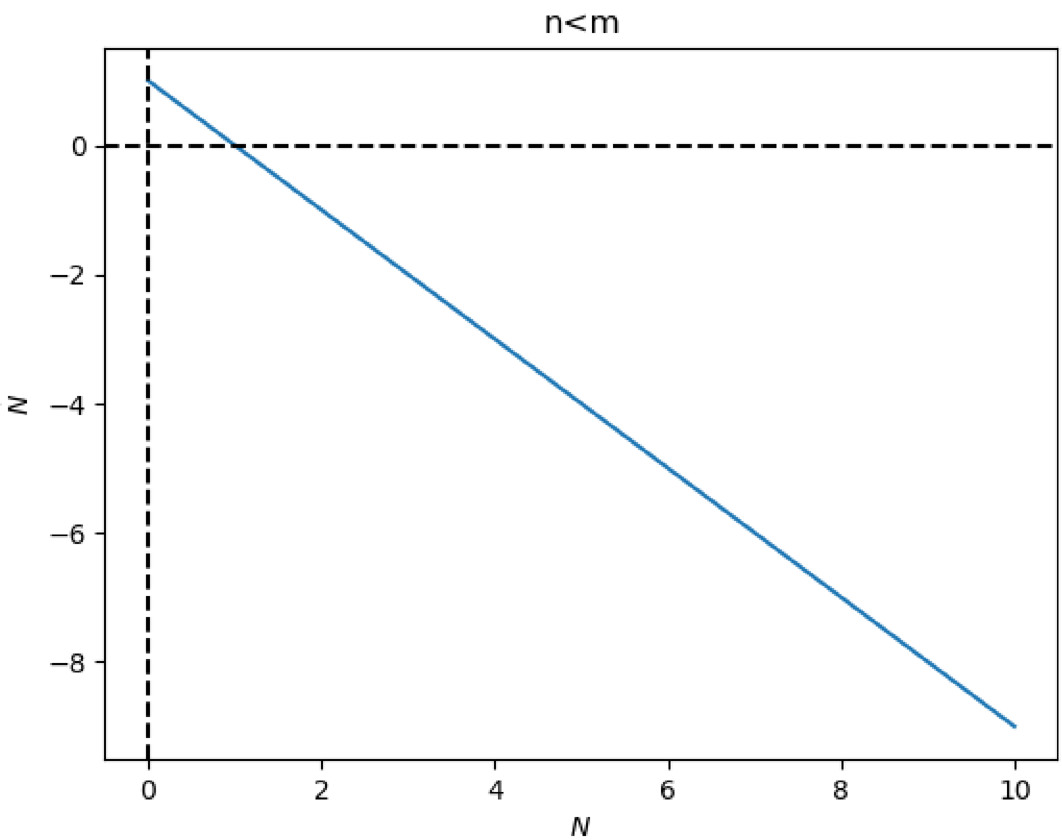
Another way to solve this equation is by a direct separation of variables.
$\int_{N_0}^{N} \frac{dM}{kM+a} = \int_0^t d\tau \Rightarrow \frac{1}{k}\ln(kM+a)\Big|_{N_0}^{N} = t \Rightarrow \ln(\frac{kN+a}{kN_0+a}) = kt \Rightarrow N(t) = (N_0 + \frac{a}{k})e^{kt} - \frac{a}{k}$

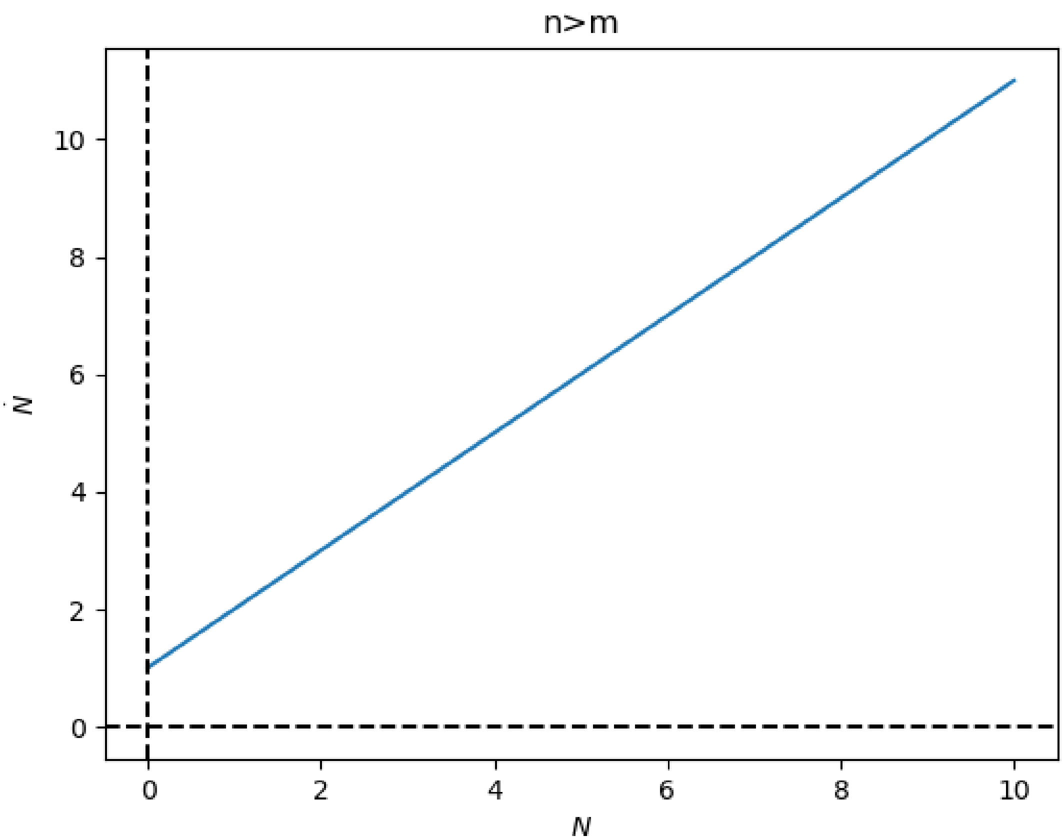
4) Qualitative analysis

1) Draw $F(N)$ in function of N for the two cases (i) $n < m$ and (ii) $n > m$. *Note: you are also expected to draw and solve such simple problems by hand.*

   $F(N)$ is a linear function with intercept a and slope $n - m$

[2]:
```python
def Ndot(N,n,m,a):
    return (n-m)*N+a

Ndomain = np.linspace(0,10,100)

#plot
plt.plot(Ndomain, Ndot(Ndomain,1,2,1))
plt.xlabel('$N$')
plt.ylabel('$\dot{N}$')
plt.axhline(0, color = 'black', ls = '--')
plt.axvline(0, color = 'black', ls = '--')
plt.title('n<m')
plt.show()

plt.plot(Ndomain, Ndot(Ndomain,2,1,1))
plt.axhline(0, color = 'black', ls = '--')
plt.axvline(0, color = 'black', ls = '--')
plt.xlabel('$N$')
plt.ylabel('$\dot{N}$')
plt.title('n>m')
plt.show()
```


n<m
0
−2
−4
−6
−8
$\dot{N}$
0
2
4
6
8
10
N



2) What is the main qualitative difference between the two cases and how does this affect the long time $t \to \infty$ behavior of the solution that you found above?

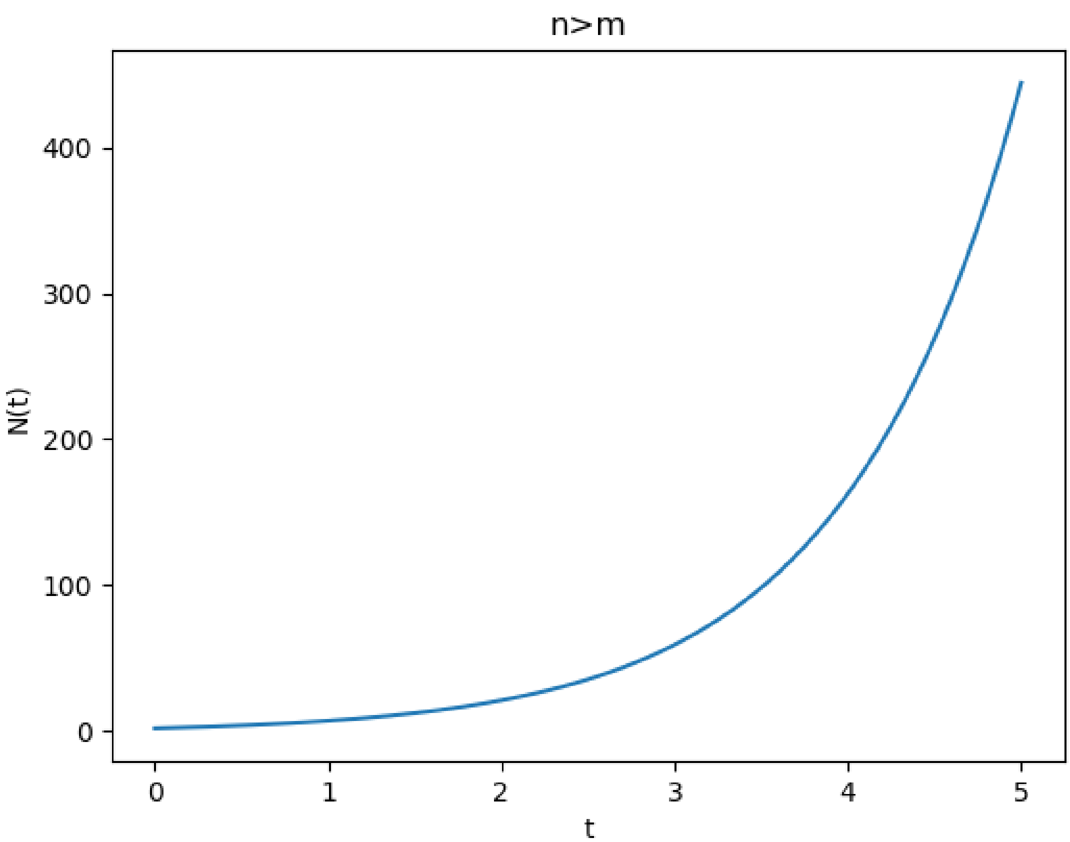
   If the death rate m is bigger than the birth rate n ($k < 0$) the number of individuals "converges" to the constant $|\frac{a}{k}|$ at late times. On the contrary, if birth rate n is bigger than death rate m ($k > 0$), then the population grows to infinity.

3) Here you can verify what you answered under 2) numerically. Generate some representative plots for $N(t)$ where you vary the parameters and initial conditions of the model.

[3]:
```
#code the analytical function for N(t)
def N(N0, a, k, t):
    return (N0+a/k)*np.exp(k*t)-a/k
```

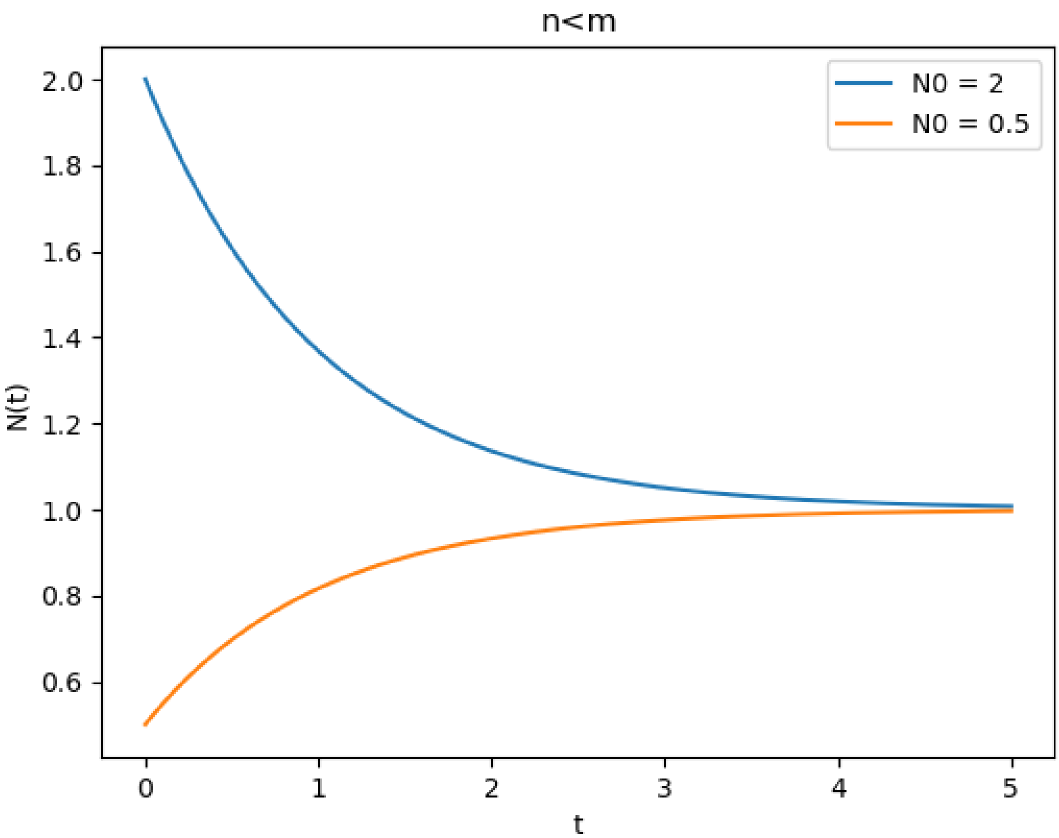
[4]:
```
#simulate it with n>m
tspan = np.linspace(0,5,1000)
a = 1.
n = 2.
m = 1.
N0 = 2.
```

```
k = n-m

#plot
plt.plot(tspan, N(N0,a,k,tspan))
plt.xlabel('t')
plt.ylabel('N(t)')
plt.title('n>m')
plt.show()
```




```
[5]: #simulate it with n<m
m = 3.
k = n-m

#plot
plt.plot(tspan, N(2,a,k,tspan), label = 'N0 = 2')
plt.plot(tspan, N(0.5,a,k,tspan), label = 'N0 = 0.5')
plt.xlabel('t')
plt.ylabel('N(t)')
plt.title('n<m')
plt.legend()
```

```
plt.show()
```



[6]:
```
# Create a widget to play with the parameters
# The widget does not work if you are using Jupyter Lab, but it works if you are␣
↪using Jupyter Notebooks.
def f(k=1.):
    plt.plot(tspan, N(N0,a,k,tspan))
    plt.xlabel('t')
    plt.ylabel('N(t)')
    plt.title('Interactive plot: n-m=' + str(n-m))
    plt.show()

a = 1.
N0 = 10.

interact(f, k = (-3.,3.,0.01))
```

```
interactive(children=(FloatSlider(value=1.0, description='k', max=3.0, min=-3.0,␣
↪step=0.01), Output()), _dom_c...
```

```
[6]: <function __main__.f(k=1.0)>
```

5) Discuss why this equation is good or bad at describing real populations.

Limitations in resources are not taken into account in this equation, thus a population can grow to infinity in this model.

1.2 Integration by separation of variables

1) Solve the following differential equations to obtain $x(t)$ by the method of separation of variables. Use the initial condition $x(t) = x_0$ when $t = 0$.

1. $\frac{dx}{dt} = xe^{-2t}$
2. $\frac{dx}{dt} = 4x^2 - 1$

Reminder: The explicit solution of a differential equation $\frac{dx}{dt} = F(x)$ can be written as a function of $t, x(t) = g(t)$, while the implicit form is written $h(x(t)) = g(t)$, where the function $h(x)$ might not be easily invertible.

1. Separating the variables gives :
   $\int_{x_0}^{x} \frac{1}{x} dx = \int_0^t e^{-2t} dt$
   After integration you obtain the implicit form:
   $\ln(x(t)) = -\frac{1}{2}e^{-2t} + C$
   With $C = \frac{1}{2} + \ln(x_0)$
   The explicit form is:
   $x(t) = e^{\frac{1}{2}} x_0 e^{-\frac{1}{2}e^{-2t}}$

2. Separating the variables gives :
   $\int_{x_0}^{x} \frac{1}{4x^2-1} dx = \int_0^t dt$
   And from partial fractions: $\frac{1}{4x^2-1} = \frac{1}{2}(\frac{1}{2x-1} - \frac{1}{2x+1})$ So after integration you get:
   $x(t) = \frac{1}{2}(\frac{2x_0+1 + (2x_0-1)e^{4t}}{2x_0+1 - (2x_0-1)e^{4t}})$

1.3 The non-autonomous Gompertz model for tumor growth

A surprisingly accurate model for the growth of a tumor of volume N is given by the following differential equation

$$\frac{dN}{dt} = r(t)N(t) \tag{2}$$

with $r(t) = r_0 e^{-at}$ and initial size $N(0) = N_0$. In other words, the population grows with a time dependent rate $r(t)$, which decreases exponentially in time with a rate a.

1) Give a plausible explanation for the proposed behavior of $r(t)$. Why should the growth rate decrease with time?

This is due to the fact that resources (i.e. nutrients) become limiting : as the population grows, the surface of the tumor grows slower than its volume, so the nutrients intake per cell decreases in time. The lack of space also limits the growth.

2) What is the meaning of r_0?

r_0 is the population *relative* growth rate at time zero ($t = 0$)

3) Show that the solution for $N(t)$ in function of the 3 parameters N_0, r_0, a can be written as $N(t) = N_0 e^{\frac{r_0}{a}(1-e^{-at})}$.
Hint: Use the method of separation of variables.

$\int_{N_0}^{N} \frac{1}{N} dN = r_0 \int_0^t e^{-at} dt$

Integration gives the solution.

4) Study the solution:

1. Show that for very short times the population grows linearly like $N(t) = N_0(1 + r_0 t)$.
2. Show that for very long times $N(t) \cong N_{max}(1 - \frac{r_0}{a} e^{-at})$.

Hint: Use the Taylor approximation $e^x \approx 1 + x$ (valid for small x) for the inner or the outer exponential when appropriate.

1. When t is close to zero, the condition for the Taylor approximation is valid for the inner exponential e^{-at}.
   Using $e^{-at} \approx 1 - at$, we find that:
   $N(t) = N_0 e^{\frac{r_0}{a}(1-1+at)} = N_0 e^{r_0 t}$
   Then, we apply the Taylor approximation again, the growth is *linear* for small times:
   $$N(t) \approx N_0 e^{r_0 t} \approx N_0(1 + r_0 t)$$
2. Rewriting the solution like:
   $N(t) = N_0 e^{\frac{r_0}{a}} e^{-\frac{r_0 e^{-at}}{a}}$
   We see that $-\frac{r_0}{a} e^{-at}$ becomes small when t is large, so we can use the Taylor expansion to the first order:
   $N(t) = N_0 e^{\frac{r_0}{a}}(1 - \frac{r_0}{a} e^{-at})$ or $N(t) = N_{max}(1 - \frac{r_0}{a} e^{-at})$ with $N_{max} = N_0 e^{\frac{r_0}{a}}$.

5) Sketch the solution. Indicate N_{max}. How does the N approaches N_{max}?

Here is the plot of the solution for arbitrary values of the constants N_0, r_0 and a. N_{max} is the asymptotic value of $N(t)$ for long times. N approaches N_{max} exponentially fast.

[13]:
```
#define analytical function for N
def N2(N0, r0, a, t):
    return N0*np.exp((r0/a)*(1-np.exp(-a*t)))

#define parameters
N0 = 2
r0 = 3
a = 0.7
Nmax = N0*np.exp(r0/a)
tspan = np.linspace(0,11,1000)

#plot
plt.plot(tspan, N2(N0,r0,a,tspan))
plt.axhline(Nmax, color = 'red', ls = '--')
plt.text(0.5, Nmax-5.5, 'Nmax', color = 'red')
plt.xlabel('t')
```

```
plt.ylabel('N(t)')
plt.show()
```