Stochasticity

February 4, 2021

We are next going to examine a model that describes the dynamics of a system in terms of **non-linear** equations in more than one variable.

With occasional exceptions, non-linear systems of equations do not yield general solutions (i.e., they are often intractable).

After examining a deterministic model, we will incorporate **demographic stochasticity** (a property of every ecological system).

Species do not exist in isolation of one another.

The simple models of exponential and logistic growth fail to capture the fact that species can

- compete for resources

- assist one another

- exclude one another

- kill one another

Here we will generalize the logistic model to take into account resource competition between two species.

Model parameters:

N_1 = number of individuals of species 1

N_2 = number of individuals of species 2

r_1 = intrinsic growth rate of species 1

r_2 = intrinsic growth rate of species 2

K_1 = carrying capacity of species 1 when species 2 is absent

K_2 = carrying capacity of species 2 when species 1 is absent

Model assumptions:

Competing species use up some of the resources available to a focal species (as if there were actually more individuals of the latter species):

# of individuals using resources of species 1 equals: $N_1 + \alpha_{12} N_2$

α_{12} is called the **competition coefficient** and measures the effect of an individual of species 2 on an individual of species 1.
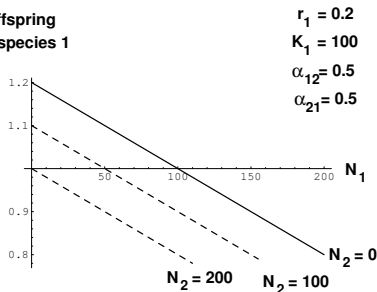
Similarly:

# of individuals using resources of species 2 equals: $N_2 + \alpha_{21} N_1$

The assumption of the logistic model is that the number of offspring per parent decreases linearly with the number of individuals (of species 1) currently in the population.

With a second competing species also present, the number of offspring per parent depends not only on N_1, but also on the N_2:

$$\text{\# of offspring per parent in species 1} = 1 + r_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1} \right)$$

**Number of offspring
per parent in species 1**

$r_1 = 0.2$
$K_1 = 100$
$\alpha_{12} = 0.5$
$\alpha_{21} = 0.5$

$N_2 = 0$

$N_2 = 200$ $N_2 = 100$

The assumption of the logistic model is that the number of offspring per parent decreases linearly with the number of individuals (of species 1) currently in the population.

With a second competing species also present, the number of offspring per parent depends not only on N_1, but also on the N_2:

$$\# \text{ of offspring per parent in species } 1 = 1 + r_1\left(1 - \frac{N_1 + \alpha_{12}N_2}{K_1}\right)$$

Therefore, the population size in the next generation will equal:

$$N_1(t+1) = N_1(t)\left(1 + r_1\left(1 - \frac{N_1(t) + \alpha_{12}N_2(t)}{K_1}\right)\right)$$

$$N_2(t+1) = N_2(t)\left(1 + r_2\left(1 - \frac{N_2(t) + \alpha_{21}N_1(t)}{K_2}\right)\right)$$

In both the discrete and continuous cases:

If $\alpha_{12} = 0$, then the dynamics of species 1 will follow the logistic equation we analysed before.

If $\alpha_{21} = 0$, then the dynamics of species 2 will follow the logistic equation we analysed before.

If $\alpha_{12} = 1$, then individuals of species 2 compete for the resources of species 1 just as strongly as do members of species 1 (interspecific competition is as strong as intraspecific competition).

If $\alpha_{12} < 0$, then the presence of species 2 increases the resources available to species 1.

If both α_{12} and α_{21} are negative, the species are said to have a **mutualistic** relationship.

If α_{12} or α_{21} is negative and the other is zero (or very nearly zero), the species are said to have a **commensal** relationship.

If one of the two is positive and one is negative, the species are said to have a **parasitic** relationship.

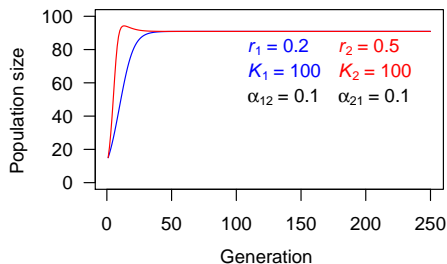If both are positive, the species are said to have a **competitive** relationship.

We will analyse the effects of competition (with $\alpha_{12} > 0$ and $\alpha_{21} > 0$) on the dynamics of two species.

The first step of an analysis might be to graph examples to see what happens to each of the species under different parameter conditions:

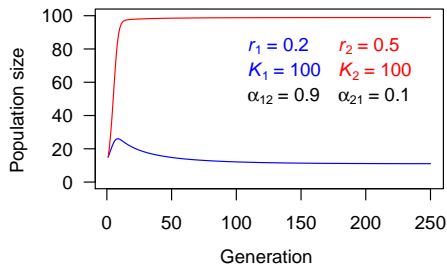$$N_1(t+1) = N_1(t)\left(1 + r_1\left(1 - \frac{N_1(t) + \alpha_{12}N_2(t)}{K_1}\right)\right)$$

$$N_2(t+1) = N_2(t)\left(1 + r_2\left(1 - \frac{N_2(t) + \alpha_{21}N_1(t)}{K_2}\right)\right)$$

<<< Code interlude >>>

What is going on here?
When α_{12} and α_{21} are small, both species approach an equilibrium level near their carrying capactities.

What is going on here?
If α_{12} is much higher than α_{21} (species 2 impacts more strongly on the resources of species 1 than vice versa), then species 1 will be kept at low numbers by the competitive superiority of species 2.

When I print the output, it looks like this:

```
         N1       N2
[1,]  15.00000 25.00000
[2,]  17.47500 34.18750
[3,]  20.23976 45.13861
[4,]  23.28570 57.06365
[5,]  26.59264 68.64979
[6,]  30.13172 78.49793
[7,]  33.86916 85.75463
[8,]  37.76787 90.41044
[9,]  41.78570 93.03812
[10,] 45.87321 94.33289
```

What's unrealistic about this?

How might we fix it?

First option is we could round.

So, replace this:

```
N1[t] <- N1[t-1] * (1+r1*(1-(N1[t-1] + a12*N2[t-1])/k1))
N2[t] <- N2[t-1] * (1+r2*(1-(N2[t-1] + a21*N1[t-1])/k2))
```

with this:

```
N1[t] <- round(N1[t-1] * (1+r1*(1-(N1[t-1] + a12*N2[t-1])/k1)))
N2[t] <- round(N2[t-1] * (1+r2*(1-(N2[t-1] + a21*N1[t-1])/k2)))
```

```
              N1        N2
 [1,] 15.00000 25.00000
 [2,] 17.47500 34.18750
 [3,] 20.23976 45.13861
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 [8,] 37.76787 90.41044
 [9,] 41.78570 93.03812
[10,] 45.87321 94.33289
```

→

```
       N1 N2
 [1,] 15 25
 [2,] 17 34
 [3,] 20 45
 [4,] 23 57
 [5,] 26 69
 [6,] 29 79
 [7,] 33 86
 [8,] 37 91
 [9,] 41 93
[10,] 45 94
```

Seems all sorted, right?

but hold on! ... for very slow growth rates ...

```
            N1       N2                              N1 N2
 [1,] 15.00000 25.00000                       [1,] 15 25
 [2,] 15.12375 25.18375                       [2,] 15 25
 [3,] 15.24831 25.36836                       [3,] 15 25
 [4,] 15.37367 25.55382      becomes          [4,] 15 25
 [5,] 15.49984 25.74013                       [5,] 15 25
 [6,] 15.62683 25.92728                       [6,] 15 25
 [7,] 15.75462 26.11528                       [7,] 15 25
 [8,] 15.88324 26.30412                       [8,] 15 25
 [9,] 16.01266 26.49379                       [9,] 15 25
[10,] 16.14291 26.68430                      [10,] 15 25
```

The take-away here is that **every** decision you make *could* have unforseen consequences, and you need to think about what these may be.

In general, when building a simulation model, you want to be wary of including steps that don't have a natural *biological* interpretation. E.g., what process does "rounding" correspond to in nature?

Back to our model - In nature, individuals have some number of offspring that could be considered a random draw from some distribution (e.g., healthier individuals might make more babies, but not necessarily every time).

Let's incorporate this stochastic process into our model and, in doing so, fix our non-integer problem.

For "number of babies," it is common to use a Poisson distribution (number of offspring are generally Poisson distributed).

$$N_1(t+1) = N_1(t)\left(1 + r_1\left(1 - \frac{N_1(t) + \alpha_{12}N_2(t)}{K_1}\right)\right)$$

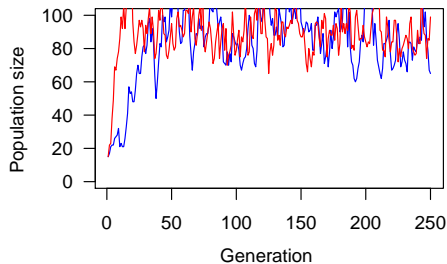$$N_2(t+1) = N_2(t)\left(1 + r_2\left(1 - \frac{N_2(t) + \alpha_{21}N_1(t)}{K_2}\right)\right)$$

Our original code:

```
N1[t] <- N1[t-1] * (1+r1*(1-(N1[t-1] + a12*N2[t-1])/k1))
N2[t] <- N2[t-1] * (1+r2*(1-(N2[t-1] + a21*N1[t-1])/k2))
```
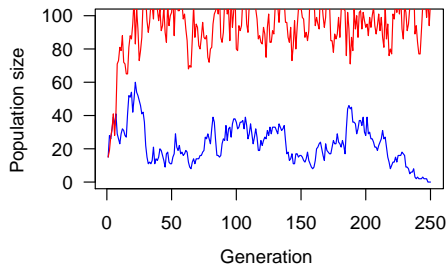
can be replaced with*:

```
N1[t] <- sum(rpois(n=N1[t-1],
            lambda=(1+r1*(1-(N1[t-1] + a12*N2[t-1])/k1))))
N2[t] <- sum(rpois(n=N2[t-1],
            lambda=(1+r2*(1-(N2[t-1] + a21*N1[t-1])/k2))))
```

*We can do this more compactly, using the fact that a sum of a Poisson draws is also a Poisson draw (we will see in workshop).

... with stochasticity

With stochasticity, dynamics are qualitatively different here! Species 1 goes extinct!

Here, we've added demographic stochasticity.

Stochastic processes are also probably appropriate in other places in the model (e.g., we could build a more complex model where individuals might interact probabilistically, so perhaps some individuals of species 1 bump into more individuals of species 2 than others, and so on). Doing this would, however, require tracking **individuals**, which we have not done yet.

When adding stochastic processes, it is important to ask yourself whether they are is essential. While biologically plausible, it only makes sense to add it if you think it will matter in important ways.