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Island Biogeography - Tutorial in EcoVirtual

In 1967 Robert MacArthur and Edward Wilson published what can be considered one of the major ecology books, "The Theory of Island Biogeography". In it, they proposed the revolutionary idea that the amount of species in a delimited place results only from the local balance between migration and extinctions. The script below will help you understand the deduction of basic model that supports this theory.
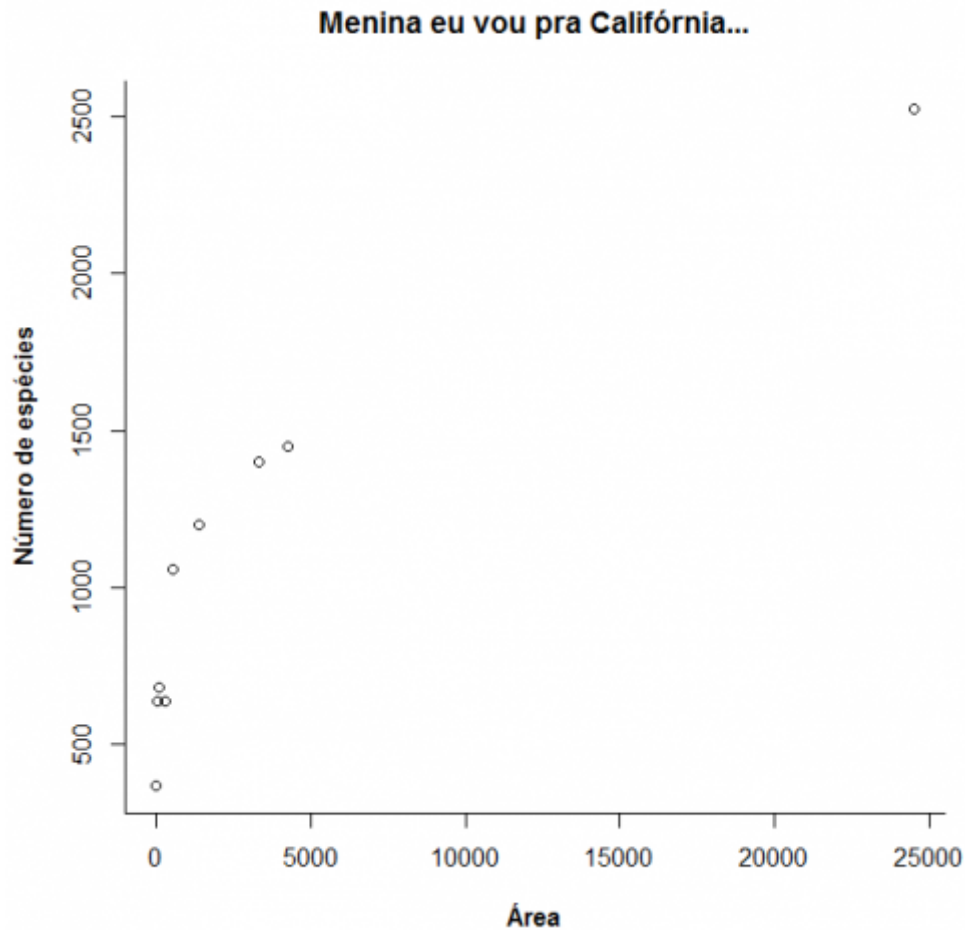
Species-area relationship

"The species-area relation is one of the few genuine **laws** in ecology" (Gotelli, 2007)

Empirical relations

The increase in species richness with the area in which they occur (islands, lakes, etc.) is the first empirical patterns identified by ecologists and biogeographers.

Let's look at how a typical species-area relationship is shaped: several species of vascular plants, which are endemic to California were collected by Johnson and colleagues and published in a paper in 1968 (see references at the bottom). They are available in this site.

Menina eu vou pra Califórnia...

This relation is empirical, and many mathematical functions have been proposed to describe it. One of the simplest, and also most used, is the power law:
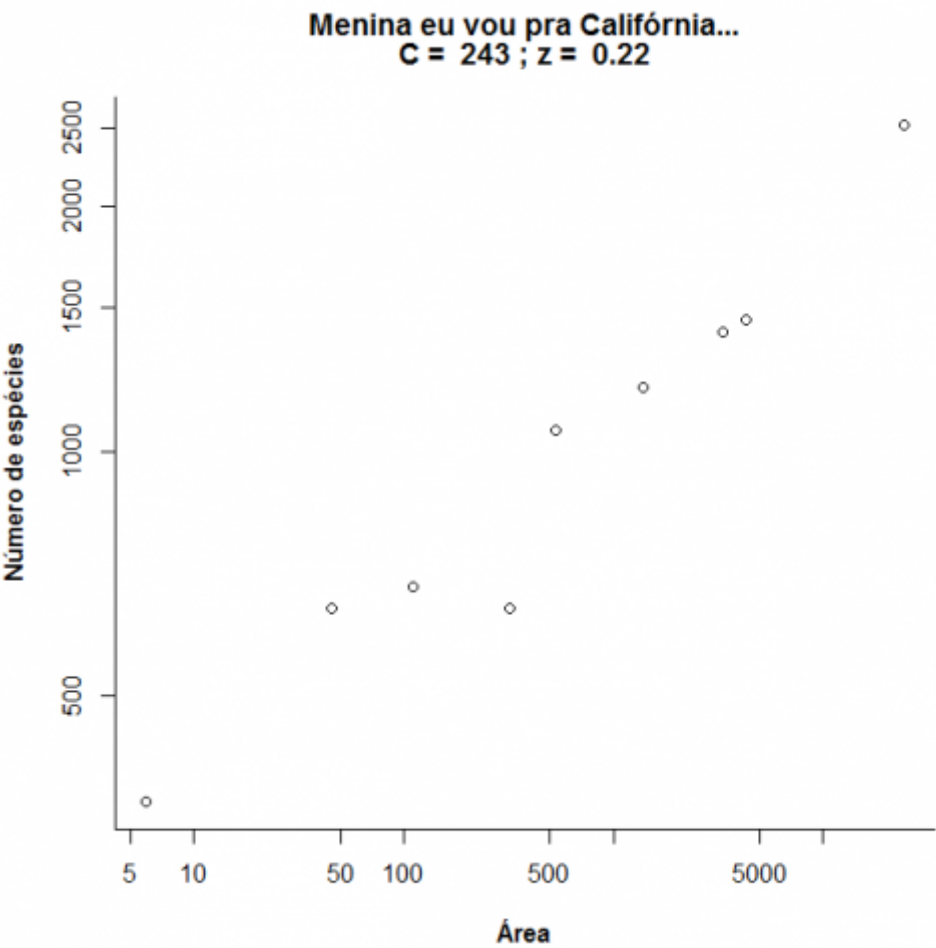
$$S\ =\ c A^z$$

here, **S** is the number of species, **A** is the area and **c** and **z** are fitted constants.

Fitting this model with a non-linear Gaussian regression, we can add this line to the graph:

Menina eu vou pra Califórnia...
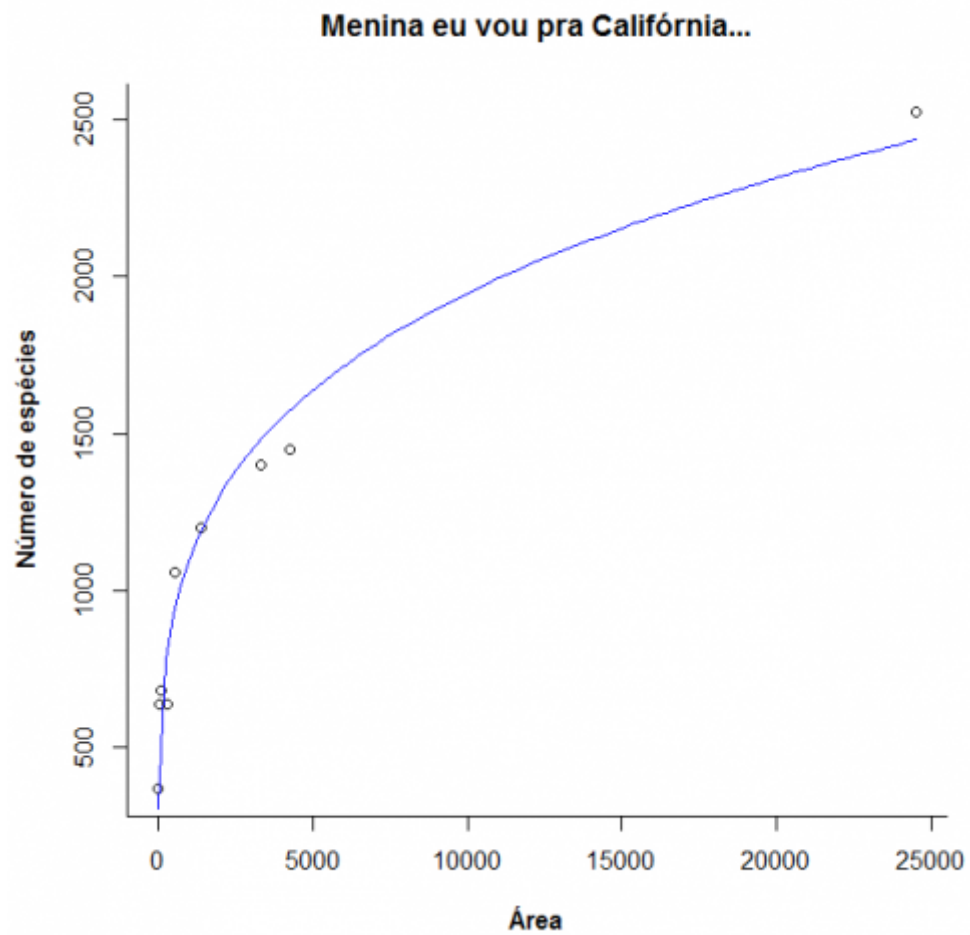
Now observe what happens if we transform the graph scale in logarithms:

Notice that what was shaped like a power-law becomes a straight line in log scale:

$$\log \ S\ = \ \log \ c + z \log \ A$$

In this regression, the inclination corresponds to the power **z** of the power function, and 10 to the intercept is the parameter **c**[1]. Compare the values obtained by the linear and non-linear regressions:

| Model	Intercept	Inclination
Linear	242.9958	0.2197585
Non-linear	195.767284	0.249416
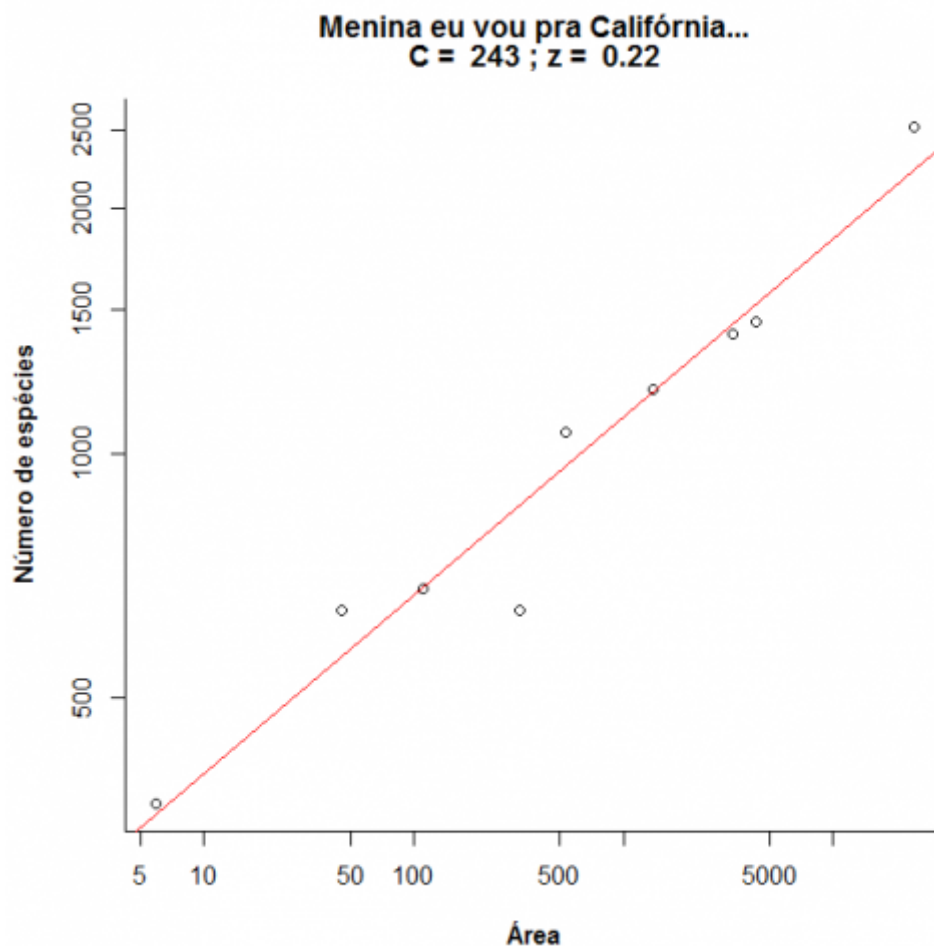
Now, let's play a bit with this species-area relationship by varying the parameters **c** and **z**. Click the button Evaluate below and use the menu to assess the effect of each parameter. Notice that both axis on the right side graph are displayed on a base-10 logarithm.

A model for colonization and extinction

In the classical metapopulation models, the processes of extinction and immigration determine the persistence of species in a system composed by several patches. Here basically we will do the same thing, only this time we will consider several species at the same time and instead of population size our interest is the number of species in each zone. We will consider the patches as being islands.

Colonization

Karen and Linda couldn't believe their luck - washed up on a **dessert island!**
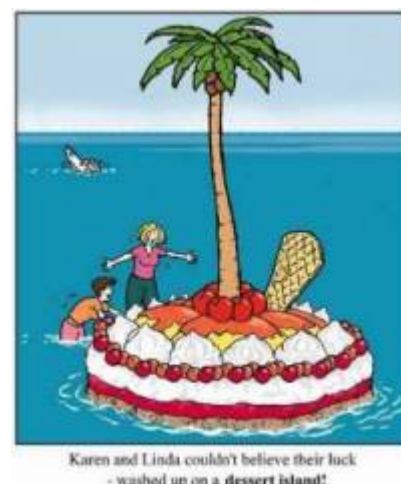
In this exercise we will use the island-continent system, which is equivalent to the classic model of metapopulation with propagules rain. In this system, there is an island (later on will be an archipelago!) that can receive seedlings from the mainland, which we assume is a reservoir containing **n** species, being an endless source of seeds.

Imagine that at every time step there comes a certain number of propagules from the mainland to our island. If so, it is to be expected that over time all species on the continent will also be present on our island, right? Want to see if this is true? Below we will simulate an island-continent system.

Sticker albums

Before we continue, let's do an exercise in imagination. Think of species such as stickers (yeah, the stickers need not be of Brazilian soccer players of the 80s), think of the desert islands as empty albums and think of the propagule rain as sticker packets coming from the sticker factory (our source of propagules). If in each package we have 5 stickers, how long does it take to complete an album with 100 stickers? Let us assume that the owner of the sticker company is honest and produces the same amount of each of the 100 different types of figurine and also that you're a bit miser and only buy one package at a time. 😕

See below the code to simulate this situation. To see the results click on the `Evaluate` button on this page or copy the code and paste it in the window *RScript* of the Rcmdr and click the `Submit`.

First we create a list of 100 figurines:

now we draw a package containing 5 stickers [2]:

Let's fast-forward in time to see what happens after 300 visits to the newsstand:
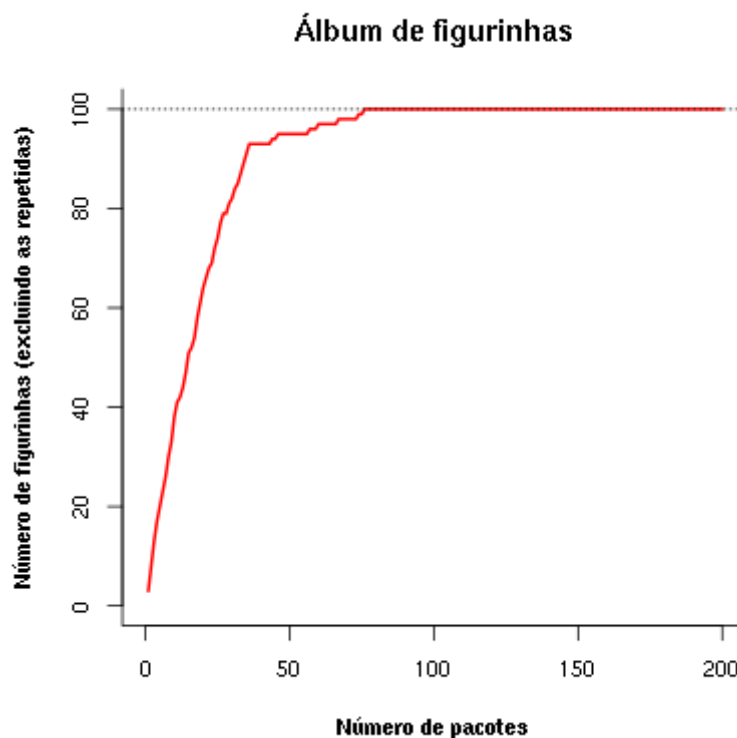
A simulation like this gives an idea of how many packages we need to buy in order to complete the album. One more public utility service! Notice that the speed in which the album is completed will slow down as the album gets more complete. But we already knew that: the more stickers we have, the more repeated stickers we get.

OK, completing this album was easy! What would happen if we had more stickers? And what if we could buy more packages at a time? And what if some stickers were more rare than others? To answer these questions, we wrote an R function that generates an interactive graph for you:

Click the button `Evaluate` to load the function. If everything went well, you should see the "Function loaded" message". If anything went wrong, try reloading the page.

Now we can graph this function!

First, in the table below, choose the **Sage** option in the Language box in the lower right corner of the code window. Then click on `Evaluate` and you get a menu with the options:

- Number of colonizing species
- Number of seedlings for colonization event
- Number of events of colonization
- Proportion of species that are abundant
- Relative abundance of abundant species, compared to other

The initial graphic simulates that on the continent there are 100 species that can colonize the island (or stickers needed to fill the album), that for each colonization event 5 propagules arrive, and that there will take place 100 years of colonization events. Try other combinations of values and suggest their the biological interpretation.

Try also to create some stickers that are more common to be drawn. Changing the `Prop abundant spp` slider to 0.1 and the `Rel Abund abundant spp` to 100, we will have 10% of species which are 100 times more abundant than the others on the continent. What is the consequence?

Extinction

In my time, we had to paste the stickers on the album with glue. We used white glue, as using stick glue was an invitation for the stickers to unstick along the way! Let's imagine now that our stickers, after being glued, have a certain probability of unsticking. How does that affect the model?

Unsticking stickers!

In our old model, which did not consider the possibility of extinction, the island always finished with the same number of species on the continent. But our function in R has an argument to exterminate some species by chance. The argument is `extinction ratio`, which is the probability of each species in the island to become extinct at every time step (measured by colonization events).

To create an interactive chart with this option first chose **Sage** option in the box Language in the lower right corner of the code window that is below. Then click the 'Evaluate' button. If you have problems reload the page, reload the R function (two code windows above) and then try again to draw the graph.

Wow! It seems that now the album is muuuuuuch more difficult to complete! Is it possible to complete it given enough time? Experiment!

What happened here? What happens if we increase the extinction rate? And if we increase the propagule rain? Maybe the owner of the sticker company has struck a deal with the owner of the glue factory! Use the function to find the answers.

MacArthur & Wilson equilibrium

To proceed, you must have the R environment with the Rcmdr and Ecovirtual packages installed and loaded. If you do not have and do not know how to have them, see the [Installation page](#).


The basic idea of this model is that the number of species in an island is determined by a balance between *immigration* of new species coming from the mainland and the *extinction* of these species. When immigration rates (λ) and extinction (μ) are equal, the number of species (**S**) reaches a dynamic equilibrium:

$$\frac{dS}{dt} \ = \ \lambda-\mu$$

The model assumes that the more species present on the island, the smaller the arrival of new species of the continent. This is illustrated by the exhaustion process with the figurines. In this case, the function that describes the migration rate is:
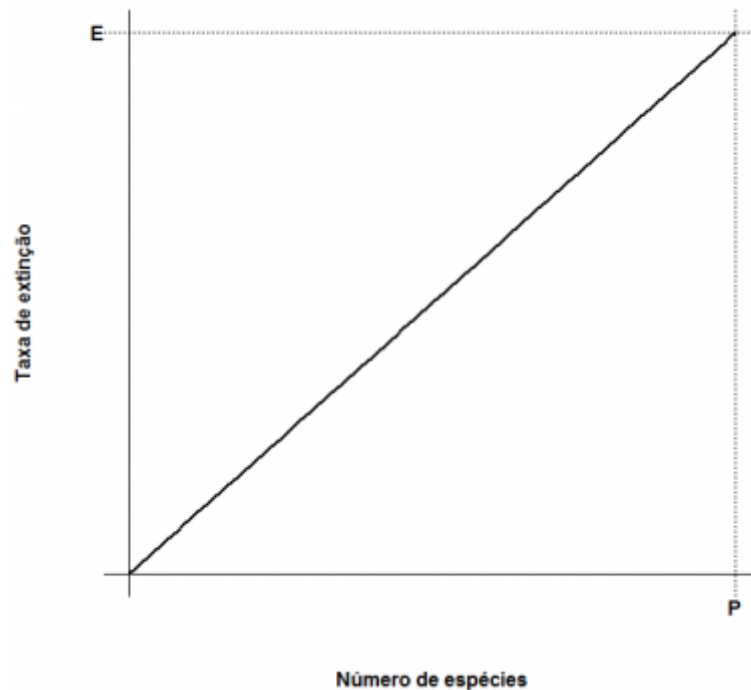
$$\lambda=I-(I/P)\ S$$

here, **I** is the highest immigration rate (when the island is deserted) and **P** is the number of species on the continent.
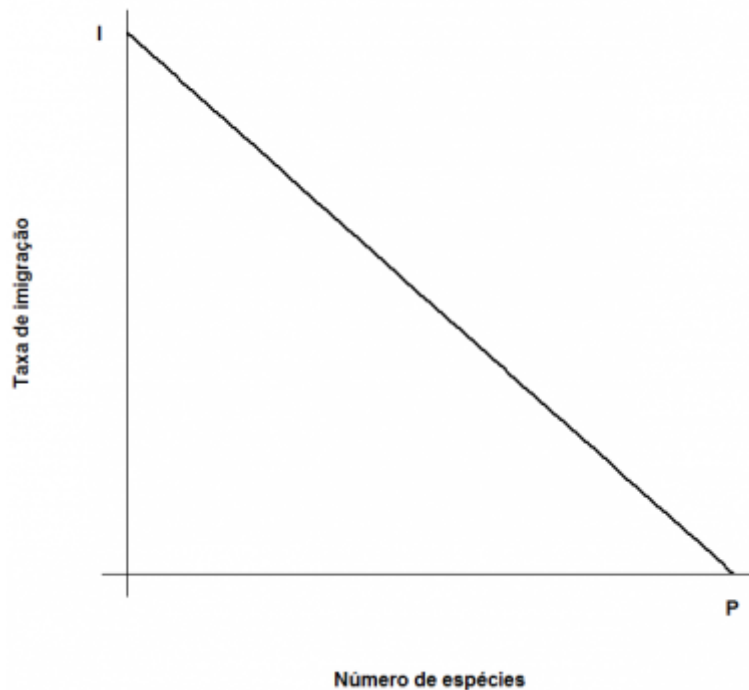
The model also assumes an extinction rate. Assuming that all species become extinct with equal probability, which is constant and independent, the average number of extinctions, or expected value, will be proportional to the number of species on the island: the more species, the greater the number that can be drawn to become extinct. When there are no species extinction is zero. Thus, the simplest model for the relationship between extinction rate and species richness on the island is:

$$\mu=(E/P)S$$

E is the maximum rate of extinction, which occurs when the number of island species is equal to the continent. See the chart:

Combining everything:

$${dS}/{dt}\ = \ I-(I/P)\ S-(E/P)\ S$$

And solving for the equilibrium condition $${dS}/{dt}\ =0$$:

$$\hat S \ = \ \frac{ I P }{I+E}$$

$$\hat T \ = \ \frac{ I E }{I+E}$$

Here, we have respectively the number of species on equilibrium ($\hat S$) and the equilibrium species substitution rate ($ \hat T$). Notice that this is not a static equilibrium, in which the composition of species is constant. Rather, the number of species remains constant because there are always new species arriving and old species becoming extinct.

In R go to the menu *Ecovirtual → Biogeographical Models → Colonization x Extinction*
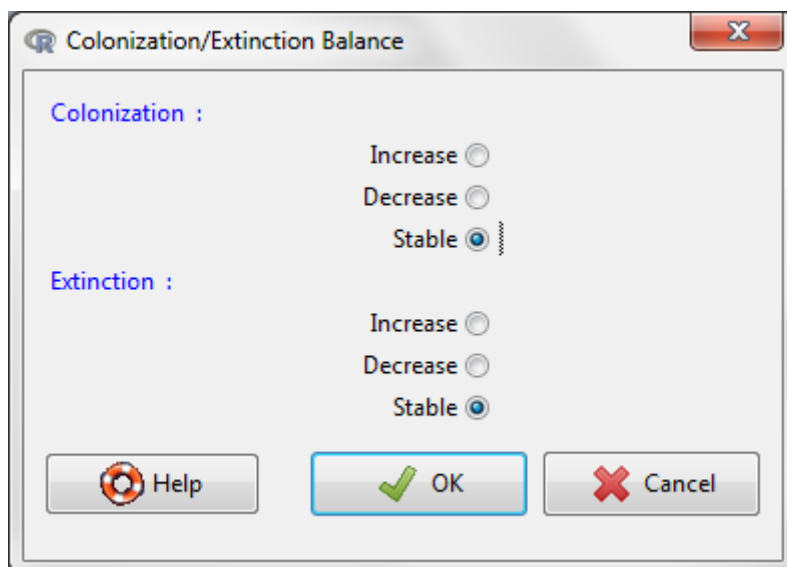
Select the options *Colonization:Stable* and *Extinction:Stable* and see what happens! Now try to thae veja o que acontece! Now try to change between states of **Ext** e **Col**.What happens with the equilibrium point in each combination? Why?
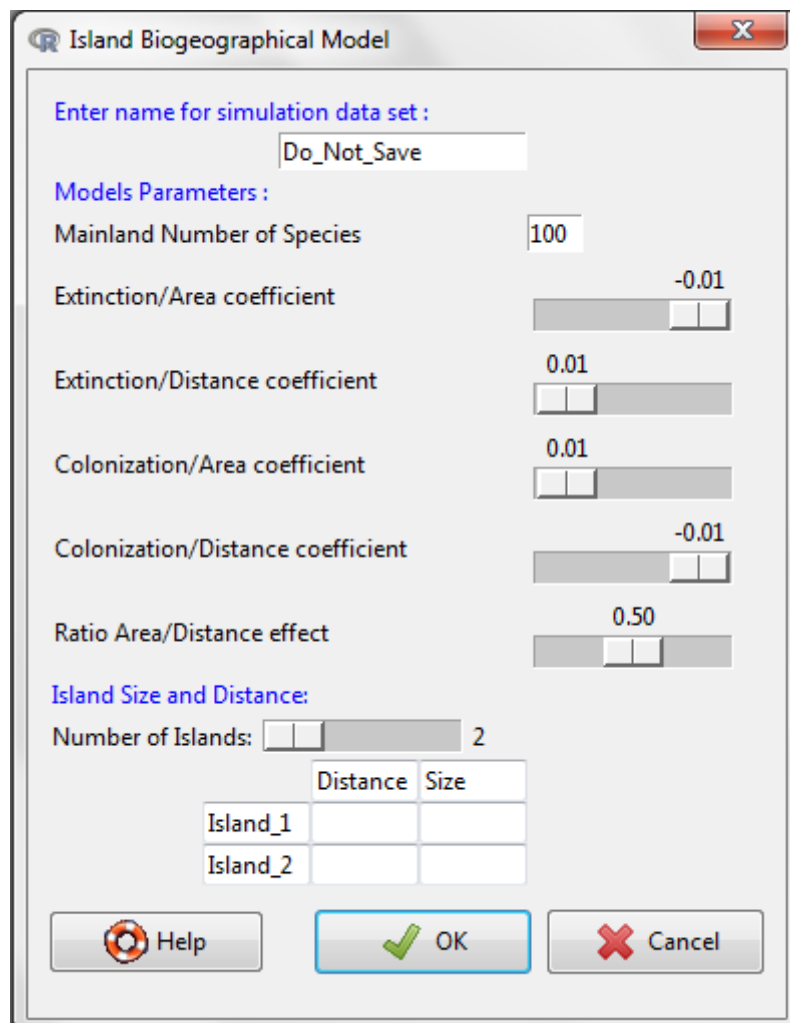
More islands
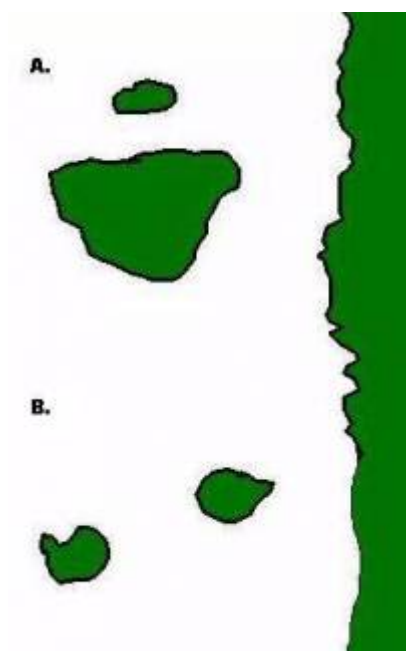
So far, so good? Then let's play a little more with our model, this time working with more than one island at a time. Our first case will be two islands equally distant from the mainland shore, but with different sizes, such as the top of the figure to the side (**A**).

In this case, let's assume that the probability of immigration does not differ between the islands, after all they are the same distance from the mainland. However, we assume that the extinction rate is higher in the smaller island: the smaller the island, the smaller the number of individuals who fit in it and thus the greater the chance of a population is extinguished. Does it seems reasonable?

Our second example is composed of two islands of the same size, but which are at different distances

from the coast, as in the bottom in the adjacent figure (**B**). In this case as they have almost the same area, the two islands have similar extinction rates. Now the problem becomes the arrival of new seedlings: it is reasonable to assume that the further an island is from the mainland, the lower the rate of immigration.

In R go to the menu *Ecovirtual → Biogeographical Models → Island Biogeographical Models* where you will be able to do any island combination and see if, in the end, you can find the species-area relationship, our first step. By the way, this theory was created to explain species-area relationship. 😊


This function plots the extinction and colonization rates for each island, given the area and distance from mainland. To do so, the function calculates the maximum extinction and colonization rates for each island, as linear functions of the area and distance. The arguments for the function are:

Option	Parameter	definition
`Mainland Number of Species`	P	number of colonizing specie in the main land
`Extinction/Area coefficient`	b.e	sploe of the linear relation between extinction rate and island area
`Extinction/Distance coefficient`	h.e	slope of the linear relation between extinction rate and distance
`Colonization/Area coefficient`	f.i	slope of the linear relation between colonization rate and island area

Option	Parameter	definition
`Colonization/Distance coefficient`	d.i	slope of the linear relation between colonization rate and distance
`Ratio Area/Distance effect`	weight.A	relative weight of the area and distance effects. Bigger values mean the area has more effect
`Number of Island`		number of islands[3]
`Distance`	dist	distance between each of the island and mainland, in arbitrary units [4]
`Size`	area	size of each of the islands, in arbitrary units[5])

Vary the areas, distances and both providing different values for these arguments. Do not worry about the other arguments, they are compatible with the distance and area scales. Explain the difference between the graphics in biological terms. Note that the islands with more species are not always those with the largest substitution rates.
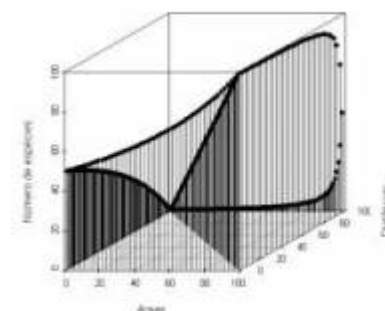
In this model we incorporated a factor that is not considered in relation species-area: distances. To do so would require a third axis containing the distances between islands and continents and then we would not have a line anymore to describe the pattern, but a surface. See next a graph in three dimensions depicting numerous imaginary islands.

To learn more

- **Gotelli, N. 2007. Ecologia.** Londrina, Ed. Planta. Capítulo 7.
- **Stevens, M. H. 2009. A primer of ecology with R.** New York. Springer. Capítulo 10.
- **MacArthur,RH. & Wilson, EO. 1967. The Theory of Island Biogeography**. Princeton University Press.

[1]
IF the logarithm used is on base 10
[2]
each time you click `Evaluate` a new package is generated
[3]
only for RMCDR tutorial
[4]
in R you must specify the distances e.g dist=c(10,20)
[5]
(in R you must specify size. e.g area=c(20,10

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