Large scale biodiversity patterns

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Short intro

Since the eighteenth century, broad-scale patterns of diversity called the attention of naturalists. Recognizing that tropical regions have higher species richness relative to temperate areas, Alexander von Humboldt was the first one to propose it to emerge from climatic differences **(Hawkins 2001)**. This ubiquitous pattern has since then been known as the Latitudinal Diversity Gradient (LDG) and, although the global distribution of biodiversity is indeed far more complex than a simple unidirectional gradient **(Hawkins and Diniz-Filho 2004)**, the difference in species richness between temperate and tropical regions tends to capture the most evident facet of the distribution of life on Earth: its geographic heterogeneity.

Early explanations for the LDG in the 1950s and 1960s followed von Humboldt's tradition and focused on the strong correlations observed between diversity (i.e., species richness) and components of current environmental variation—especially combinations of temperature and precipitation **(Simpson 1964; Pianka 1966; O'Brien 2006; Hawkins et al. 2003; Brown 2012)**. These high correlations suggested a causal explanation, and spurred the development of hypotheses that aimed to identify the mechanisms affecting species distributions and hence driving geographical patterns **(e.g., Currie et al. 2004)**. Although these diversity-environment correlations suggested "*pure ecological explanations*" that involved population-level processes tied to dispersal and aggregation of tropical organisms, it quickly became clear that deep-time evolutionary processes should also be taken into account to explain the LDG **(Rohde 1992; Ricklefs 2004)**. In fact, as early as 1937, Theodosius Dobzhansky had proposed that diversity gradients should be explained by an interaction between ecological and evolutionary mechanisms, in which evolution would drive the dimensions of the niche—the set of biotic and abiotic factors that allow a species to exist indefinitely—that would allow different patterns of niche packing throughout environmental gradients. Today, it is consensus that the LDG should be explained not only by current climatic factors, but also by the long-term dynamics of such climatic factors and by events happening throughout the evolution of the species **(Fine 2015)**.

Today we will learn basic tools in R for visualizing species distributions, build geographical ranges, testing drivers of gradients of biodiversity under different approaches.

You will need four datasets, that will be provided for you: 1. Species occurrence data points - live.oaks.txt 2. Species geograhical ranges - Furnarii_ranges_geo.shp 3. Phylogenetic tree - furnariiMCC.nex 4. Environmental predictors - bio1.bil and bio12.bil

Set up your data and your working directory

Set up a working directory and put the data files in that directory. Tell R that this is the directory you will be using, and read in your data:

You can download the data directly on your computer by clicking **Occurrences**, **Geographical Ranges**, **Phylogenetic tree** and **Environmental predictors** and store them in the folder named **Data"**.

```
setwd("path/for/your/directory")
```

Install and load the following packages

```
packages <- c("maptools", "rgdal", "raster", "rangeBuilder", "spdep", "ncf", "geiger",
              "letsR", "rworldmap", "spatialreg", "picante", "ape")
```

```
# Install packages not yet installed
installed_packages <- packages %in% rownames(installed.packages())

if (any(installed_packages == FALSE)) {
  install.packages(packages[!installed_packages], dependencies = TRUE)
}
```

```
require(maptools)
require(rgdal)
require(raster)
require(rangeBuilder)
library(spdep)
library(ncf)
require(geiger)
require(dismo)
library(rworldmap)
require(spatialreg)
require(ape)
```

From point occurrences to range maps

Load species occurrences data points. We will use occurrences from Live oaks, that were obtained from iDigBio between 20 and 24 July 2018 by Jeannine Cavender-Bares. Notice that these occurrence data points were visually examined and any localities that were outside the known range of the species, or in unrealistic locations (e.g., water bodies, crop fields) were discarded.

```
oaks <- read.table("Data/OCC/live.oaks.txt", header = TRUE)
```

let's start exploring the data.

```
head(oaks)


tail(oaks)
```

What variables we have in the object oaks? How many oak species are in the dataset?

Plot the points (x = Logitude, y = Latitude) and a world map, for reference. We need to load a data object from the {rworldmap} package

```
plot(oaks[c(2:3)], col = "blue", pch = 19)
plot(countriesCoarse, add = TRUE)
```

Let's try with a single species in this case, *Quercus virginiana*

```
unique(oaks$Species)
# Select the focal species
que_vir <- subset(oaks, oaks$Species == "Quercus_virginiana")
```

Now plot the occurrences of *Quercus virginiana*

```
plot(que_vir$Longitude, que_vir$Latitude, pch = 15)
plot(countriesCoarse, add = TRUE)
```

Cool, right?

Data checking and cleaning

Check if there are any duplicated points. We will check if exist any duplicate occurrence data point, if so, then remove all duplicates.

```
oaks_dups <- duplicated(oaks[, c(2:3)])
### NOTE: the function "duplicated" returns the results of a logical test
# (e.g. TRUE or FALSE)
# How many are duplicates?
length(which(oaks_dups == TRUE))
# How many are NOT duplicates?
length(which(oaks_dups == FALSE))
# Keep only those lines that are not duplicates
oaks_dups_row <- which(oaks_dups == TRUE)
# What's the size? That is, how many points are duplicates
length(oaks_dups_row)
# Create another object without the duplicate records
oaks_nodups <- oaks[-oaks_dups_row, ]
# What are the dimensions of the new object?
dim(oaks_nodups)
# Take a look at the first rows of data
head(oaks_nodups)
```

What was the result? Are there duplicated occurrences? if so, how many?

Let's plot the results!

```
plot(oaks$Longitude, oaks$Latitude, pch = 19, col = "red", cex = 2)
points(oaks_nodups$Longitude, oaks_nodups$Latitude, pch = 16, col = "black")
```

Range maps from point data

In this section we will learn how to create "simple" range maps based on geometry (e.g. minimum convex polygons, etc.), without considering environmental variables (e.g., ENMs or SDMs). Note that these range maps are geographical abstractions of the species ranges. **A species range is the area where a particular species can be found during its lifetime. Species range includes areas where individuals or communities can migrate or hibernate**

To create our first species geographical range let's use the **{rangeBuilder}**. This package create a polygon based on the spatial distribution of the coordinates.

Dynamic Alpha hull

```
que_vir_alphahull <- getDynamicAlphaHull(que_vir, fraction = 0.95,
                                         coordHeaders = c("Longitude", "Latitude"),
                                         clipToCoast = 'no')[[1]]
```

Now plot the output and overlap the occurrences.

```
plot(que_vir_alphahull, lwd = 2, col = "red")
points(que_vir$Longitude, que_vir$Latitude, pch = 16, col = "green")
plot(countriesCoarse, add = TRUE, lwd = 2)
```

Please explain the results. How do you feel about that?

Until here we have explored how to plot, clean and build species geographical ranges using occurrences. Now we will use species geographical ranges of the largest continental endemic radiation (**Furnariides**) to explore

the geographical gradients of species diversity.

Diversity gradients

Prepare data and mapping

The geographical ranges correspond to the Infraorder Furnariides (Aves). This data is available thorough BirdLife International (http://datazone.birdlife.org/species/requestdis) and you can use any other group available on IUCN or BIEN (for plants in the Americas). In any case, you first need to download the polygons in shapefile format.

To load the Furnariides geographical ranges we will use the function **readOGR** from the package **{rgdal}**.

```
franges <- readOGR(dsn = "Data/Franges", layer = "Furnarii_ranges_geo")
```

```
class(franges)
```

Now explore the data inside the ranges. Notice that to access to the information, we will use *@* instead of* $*.

```
head(franges@data)
```

Let's plot a couple of species.

```
fur_ruf <- subset(franges, franges$SCINAME == "Furnarius rufus")
ana_dor <- subset(franges, franges$SCINAME == "Anabazenops dorsalis")
```

```
SA <- subset(countriesCoarse, continent == "South America") # Select South America
plot(SA)
plot(fur_ruf, col = "green", add = TRUE) # Furnarius rufus
plot(ana_dor, add = TRUE, col = "red") # Anabazenops dorsalis
# Add world maps
plot(SA, add = TRUE)
```

Explain the distribution for both species (i.e., Furnarius rufus [green polygon] and Anabazenops dorsalis [red polygon])

Raster of species richness

Species richness is the number of different species represented in an ecological community, landscape or region. Species richness is simply a count of species, and it does not take into account the abundances of the species or their relative abundance distributions.

Now, let's create the a map that represent the species richness of Furnariides.

First create an empty raster for the Neotropics using the extent of the Furnariides ranges under a spatial resolution of 1º long-lat or 111 km at the equator.

```
neo_ras <- raster() # empty raster

extent(neo_ras) <- extent(franges) # Set the raster "extent"

res(neo_ras) <- 1 # Set the raster "resolution"

neo_ras # print the raster object in the console

values(neo_ras) <- 0 # assign 0 values to all pixels in the raster
```

Now using the empty raster we will **rasterize** the species identities in each cell or pixel. The resulting raster will be the species richness of Furnariides across the Neotropics.

```
f_sr_raster <- rasterize(franges, neo_ras, field = "SCINAME",
                         fun = function(x,...){length(unique(na.omit(x)))})
# this will take a while (~30 secs in Jesús's computer), please be patient.
```

Plot the raster.

```
plot(f_sr_raster)
plot(SA, add = TRUE)
```

Let's try changing the colors.

```
#change the color scale
colfuncYellows <- colorRampPalette(c("#d7191c", "#fdae61", "#ffffbf",
                                     "#abd9e9", "#2c7bb6"))
```

```
plot(f_sr_raster, col = rev(colfuncYellows(100)), axes = FALSE, box = FALSE,
     zlim = c(minValue(f_sr_raster), maxValue(f_sr_raster)),
     xlab = "Furnariides richness", legend.width = 2)
plot(SA, add = TRUE)
```

Awesome, right?. Now, please, describe the observed pattern!

Scale dependency

Now we will explore one of the oldest problems in ecology and evolution, the **scale dependency** in the data. So to explore this scale dependence, we will rasterize the Furnariides ranges, but using different spatial resolutions from 2º to 4º degrees of long-lat.

```
# 2º degrees
neo_ras_2dg <- raster()
# Set the raster "extent"
extent(neo_ras_2dg) <- extent(franges)
res(neo_ras_2dg) <- 2
neo_ras_2dg
values(neo_ras_2dg) <- 0

# 4º degrees
neo_ras_4dg <- raster()
# Set the raster "extent"
extent(neo_ras_4dg) <- extent(franges)
res(neo_ras_4dg) <- 4
neo_ras_4dg
values(neo_ras_4dg) <- 0
```

```
# Furnariides at 2º of long-lat
f_sr_2dg_raster <- rasterize(franges, neo_ras_2dg, field = "SCINAME",
                             fun = function(x,...){length(unique(na.omit(x)))})

# Furnariides at 4º of long-lat
f_sr_4dg_raster <- rasterize(franges, neo_ras_4dg, field = "SCINAME",
                             fun = function(x,...){length(unique(na.omit(x)))})
```

Plot the three maps.

```
par(mfrow = c (1, 3))
plot(f_sr_raster, main = "Furnariides richness 1dg")
plot(countriesCoarse, add = T)

plot(f_sr_2dg_raster, main = "Furnariides richness 2dg")
plot(countriesCoarse, add = T)

plot(f_sr_4dg_raster, main = "Furnariides richness 4dg")
plot(countriesCoarse, add = T)
```

So, is there an effect of scale?

Explain the differences between the three maps

How do you feel about that?

Correlative relationships

Species richness as a function of evolutionary history

Let's try to rasterize other information from the polygon data set. We will use the information in the column **RD**, this data correspond to the numbers of nodes from the tips to the root of a phylogenetic tree or just **root distance**, thus, will use the RD to calculate the MRD metric **(mean root distance)** that measures the evolutionary derivedness of species within an assemblage **(Kerr & Currie, 1999)** and can be used to determine whether a local fauna is constituted primarily by early-diverged or by recently originated species **(Hawkins et al., 2012, Pinto-Ledezma et al., 2017)**.

```
head(franges@data)
```

```
f_MRD_raster <- rasterize(franges, neo_ras, field = "RD", fun = mean)
```

```
plot(f_MRD_raster)
plot(SA, add = TRUE)
```

Let's try changing the colors.

```
plot(f_MRD_raster, col = rev(colfuncYellows(100)), axes = FALSE, box = FALSE,
     zlim = c(minValue(f_MRD_raster), maxValue(f_MRD_raster)),
     xlab = "Furnariides mean root distance", legend.width = 2)
plot(SA, add = TRUE)
```

Based on the description provided above, please describe the MRD pattern

Let's plot both raster.

```
par(mfrow = c(1, 2))
plot(f_sr_raster, col = rev(colfuncYellows(100)), axes = FALSE, box = FALSE,
     zlim = c(minValue(f_sr_raster), maxValue(f_sr_raster)),
     xlab = "Furnariides richness", legend.width = 2)

plot(f_MRD_raster, col = rev(colfuncYellows(100)), axes = FALSE, box = FALSE,
     zlim = c(minValue(f_MRD_raster), maxValue(f_MRD_raster)),
     xlab = "Furnariides mean root distance", legend.width = 2)
```

Check if there is a relationship between the species richness and the evolutionary derivedness.

```
cor.test(values(f_sr_raster), values(f_MRD_raster))
```

```
obj <- lm(values(f_sr_raster) ~ values(f_MRD_raster))
summary(obj)
```

```
plot(values(f_sr_raster) ~ values(f_MRD_raster), xlab = "MRD", ylab = "SR")
abline(obj, col = "red", lwd = 2)
```

Hmmm. What happened in here? Please answer the next questions.

From the mean root distance map, it is possible to explain the Furnariides diversity gradient? If so, please explain from an evolutionary perspective.

Species richness as a function of environment

Load the environmental variables that correspond to bio1 (**Annual Mean Temperature**) and bio12 (**Annual Precipitation**). These data correspond to two variables out of 19 from WorldClim (http://www.worldclim.org/current). We will use these two variables just for educational purposes, rather to make a complete evaluation of the species-environmental relationships.

```
bio1 <- raster("Data/Envi/bio1.bil")
bio1
bio12 <- raster("Data/Envi/bio12.bil")
bio12
```

Plot the environmental variables

```
par(mfrow = c(2, 1))
plot(bio1)
plot(bio12)
```

Ok, the bio1 and bio12 layers are at global scale, so now will need to crop them to the extent of the Neotropics.

```
bio1_neo <- crop(bio1, extent(franges))
bio12_neo <- crop(bio12, extent(franges))
```

```
par(mfrow = c(1, 2))
plot(bio1_neo, main = "Annual Mean Temperature")
plot(bio12_neo, main = "Annual Precipitation")
```

Much better!

Now we will obtain the coordinates from the Furnariides diversity raster. These coordinates then will be used to extract the information from the bio1 and bio12 climatic layers.

```
f_ras_coords <- xyFromCell(f_sr_raster, 1:length(values(f_sr_raster)))
head(f_ras_coords)
```

Obtain the values from bio1, bio12, SR and MRD for each cell or pixel using the coordinates.

```
f_ras_bios <- extract(stack(bio1_neo, bio12_neo), f_ras_coords)

fdata <- na.omit(data.frame(f_ras_coords, SR = values(f_sr_raster),
                            MRD = values(f_MRD_raster), f_ras_bios))

head(fdata)
```

Now make a simple correlation between the Furnariides richness and bio1 and bio12.

```
cor.test(fdata$SR, fdata$bio1)
```

```
cor.test(fdata$SR, fdata$bio12)
```

```
lmbio1 <- lm(SR ~ bio1, data = fdata)
summary(lmbio1)

lmbio12 <- lm(SR ~ bio12, data = fdata)
summary(lmbio12)
```

Which environmental variable is more related with Furnariides richness?

Please explain the relationship from an ecological perspective

```
par(mfrow = c(1, 2))
plot(fdata$bio1, fdata$SR, xlab = "Bio 1", ylab = "Richness")

plot(fdata$bio12, fdata$SR, xlab = "Bio 12", ylab = "Richness")
```

Considering spatial autocorrelation

This paragraph was extracted entirely from **Dormann et al. (2007)**: The analysis of spatial data is complicated by a phenomenon known as spatial autocorrelation. Spatial autocorrelation **(SAC)** occurs when the values of variables sampled at nearby locations are not independent from each other **(Tobler 1970)**. The causes of spatial autocorrelation are manifold, but three factors are particularly common: 1) biological processes such as speciation, extinction, dispersal or species interactions are distance-related; 2) non-linear relationships between environment and species are modelled erroneously as linear; 3) the statistical model fails to account for an important environmental determinant that in itself is spatially structured and thus causes spatial structuring in the response **(Besag 1974)**. Since they also lead to autocorrelated residuals, these are equally problematic. A fourth source of spatial autocorrelation relates to spatial resolution, because coarser grains lead to a spatial smoothing of data. In all of these cases, SAC may confound the analysis of species distribution data.

We know that a correlation is not a causation, so, to explore the relationship we need to build a model or fit a model. To explore this relationships we will first explore a simple Ordinary Least Square regression or OLS.

```
fols <- lm(SR ~ bio1 + bio12, data = fdata)
summary(fols)
```

Let's complicate our model a little bit... Now let's include the MRD values as a predictor.

```
fols2 <- lm(SR ~ bio1 + bio12 + MRD, data = fdata)
summary(fols2)
```

What is telling us this OLS models?

Now, explore the spatial autocorrelation of the Furnariides richness gradient. Spatial autocorrelation (it can also be temporal) is a measure of similarity (**correlation**) between nearby observations. In other words, the spatial autocorrelation describe the degree two which observations (values) at spatial locations (whether they are points, areas, or raster cells), are similar to each other.

```
autocor_SR <- ncf::correlog(fdata$x, fdata$y, z = fdata$SR, na.rm = T,
                            increment = 1, resamp = 1)
```

Let's use an correlogram to explore the spatial autocorrelation. Remember, spatial autocorrelation (it can also be temporal) is a measure of similarity (**correlation**) between nearby observations. Thus, high values means high spatial autocorrelation.

```
plot(autocor_SR$correlation[1:50], type = "b", pch = 1, cex = 1.2, lwd = 1.5,
     ylim = c(-1, 1), xlab = "Distance class", ylab = "Moran's I", cex.lab = 1.2,
     cex.axis = 1.2)
abline(h = 0)
```

Is there a spatial autocorrelation in the data?

What about the residuals? Let's explore the spatial autocorrelation in the residuals.

```
coords <- fdata[1:2]
coords <- as.matrix(coords)
```

Build a neighborhood contiguity by distance. The distance used in this example is **1.5 degrees** but you can try with a large distance if you wish to explore more models.

```
nb1.5 <- dnearneigh(coords, 0, 1.5)
```

Using the neighborhood contiguity build a spatial weights for neighbor lists.

```
nb1.5.w <- nb2listw(nb1.5, glist = NULL, style = "W", zero.policy = TRUE)
```

Extract the residuals from the OLS model

```
residuals_ols <- residuals(fols2)
plot(residuals_ols)
```

Calculate a univariate spatial correlogram.

```
autocor_ols_res <- correlog(fdata$x, fdata$y, z = residuals(fols),
                        increment = 1, resamp = 1)
```

plot the autocorrelagram for the residuals

```
plot(autocor_ols_res$correlation[1:50], type = "b", pch = 1, cex = 1.2, lwd = 1.5,
     ylim = c(-0.5, 1), xlab = "distance", ylab = "Moran's I", cex.lab = 1.5,
     cex.axis = 1.2)
abline(h = 0)
title(main = "OLS residuals", cex = 1.5)
```

Ohhh, seems that the residuals have a strong spatial autocorrelation, that is a problem because if we found autocorrelation in the residuals much of the explanation that we obtain can be biased. See explanation above.

Let's inspect two autocorrelograms.

```
par(mfrow = c(2, 1))

plot(autocor_SR$correlation[1:50], type = "b", pch = 1, cex = 1.2, lwd = 1.5,
     ylim = c(-1, 1), xlab = "Distance class", ylab = "Moran's I", cex.lab = 1.2,
     cex.axis = 1.2)
abline(h = 0)
title(main = "OLS model", cex = 1.5)

plot(autocor_ols_res$correlation[1:50], type = "b", pch = 1, cex = 1.2, lwd = 1.5,
     ylim = c(-0.5, 1), xlab = "Distance class", ylab = "Moran's I", cex.lab = 1.5,
     cex.axis = 1.2)
abline(h = 0)
title(main = "OLS residuals", cex = 1.5)
```

Hmmm, seems that there is a strong spatial autocorrelation, thus any conclusion using the OLS model can be biased.

How do you feel about that?

To try to solve this important issue, we will use **spatial simultaneous autoregressive error model estimation (Aka SAR model)**, this kind of models account for spatial autocorrelation by adding an extra term (**autoregressive**) in the form of a spatial-weight matrix that specifies the neighborhood of each cell or pixel and the relative weight of each neighbor.

Let's fit the SAR model.

```
sar_nb1.5.w <- errorsarlm(fols2, listw = nb1.5.w, data = fdata, quiet = FALSE,
                          zero.policy = TRUE, na.action = na.exclude)
# this will take a while, ~30 seconds in Jesús's computer
```

```
summary(sar_nb1.5.w)
residuals_sar_nb1.5.w <- residuals(sar_nb1.5.w) # extract the residuals from SAR model
```

Now estimate the spatial autocorrelation of the SAR model.

```
autocor_sar_nb1.5.w <- correlog(fdata$x, fdata$y, z = residuals(sar_nb1.5.w),
                                na.rm = T, increment = 1, resamp = 1)
```

Plot the autocorrelogram under the SAR model.

```
plot(autocor_sar_nb1.5.w$correlation[1:50], type = "b", pch = 4, cex = 1.2, lwd = 1.5,
     ylim = c(-0.5, 1), xlab = "distance", ylab = "Moran's I", cex.lab = 1.5,
     cex.axis = 1.2)
abline(h = 0)
title(main = "SARerr residuals", cex = 1.5)
```

Ohhh, where is the autocorrelation in the residuals? Now compare the two autocorrelograms.

```
par(mfrow = c(2, 1))
plot(autocor_ols_res$correlation[1:50], type = "b", pch = 1, cex = 1.2, lwd = 1.5,
     ylim = c(-0.5, 1), xlab = "distance", ylab = "Moran's I", cex.lab = 1.5,
     cex.axis = 1.2)
abline(h = 0)
title(main = "OLS residuals", cex = 1.5)

plot(autocor_sar_nb1.5.w$correlation[1:50], type = "b", pch = 4, cex = 1.2, lwd = 1.5,
     ylim = c(-0.5, 1), xlab = "distance", ylab = "Moran's I", cex.lab = 1.5,
     cex.axis = 1.2)
abline(h = 0)
title(main = "SARerr residuals", cex = 1.5)
```

Ok, now we know that the SAR model can solve the problem in the spatial autocorrelation in the residuals, let's try to make some inferences.

```
summary(sar_nb1.5.w)
```

```
summary(fols2)
```

By looking to the summary of the SAR and OLS models, explain the differences in the coefficients between both models.

Now let's compare the prediction of both models. To calculate a R2 to the SAR model, we will use the function **SARr2()** from Jesús's GitHub.

```
source("https://raw.githubusercontent.com/jesusNPL/BetaDivNA/master/SARr2.R")
```

```
SARr2(Lfull = sar_nb1.5.w$LL, Lnull = sar_nb1.5.w$logLik_lm.model, N = nrow(fdata))
```

Comparing the two models (OLS and SAR), please answer the following questions:

1. *Which model have the best explanation?*
2. *What can we conclude from these results?*
3. *How do you feel about that?*

The end! for now...

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