

Species distribution modeling with R

Robert J. Hijmans and Jane Elith

August 30, 2011

Chapter 1

Introduction

This document provides an introduction to species distribution modeling with R . Species distribution modeling (SDM) is also known under other names including climate envelope-modeling, habitat modeling, and (environmental or ecological) niche-modeling. The assumption of SDM is that you can predict the entire, or potential, spatial distribution of a phenomenon, by relating sites of known occurrence (and perhaps non-occurrence) with predictor variables known for these sites and for all other sites. The common application of this method is to predict species ranges with climate data as predictors.

In SDM, the following steps are usually taken: (1) locations of occurrence (and perhaps non-occurrence) of a species (or other phenomenon) are compiled. (2) values of environmental predictor variables (such as climate) at these locations are determined. (3) the environmental values are used to fit a model predicting likelihood of presence, or another measure such as abundance of the species. (4) The model is used to predict the likelihood of presence at all locations of an area of interest (and perhaps in a future climate).

In this text we assume that you are familiar with most of the concepts in SDM. If in doubt, you could consult, for example, Richard Pearson's introduction to the subject: http://biodiversityinformatics.amnh.org/index.php?section_id=111, the book by Janet Franklin (2009), and the recent review by Elith and Leathwick (2009). It is important to have a good understanding of the interplay of environmental (niche) and geographic (biotope) space – see Colwell and Rangel (2009) for a good overview. SDM is a widely used approach but there is much debate on when and how to best use this method. While we refer to some of these issues, in this document we do not provide an in-depth discussion of this scientific debate. Rather, our objective is to provide practical guidance to implementing the basic steps of SDM. We leave it to the you to use other sources to determine the appropriate methods for their research; and to use the ample opportunities provided by the R environment to improve existing approaches and to develop new ones.

We also assume that you are already familiar with the R language and environment. It would be particularly useful if you already had some experience

with statistical model fitting (e.g. the `glm` function) and with the '`raster`' package. To familiarize yourself with model fitting see, for instance, the Documentation section on the CRAN webpage (<http://cran.r-project.org/>) and any introduction to R txt. For the '`raster`' package you could consult its vignette. When we present code we will give some hints on how to understand the code, if we think it might be confusing. We will do more of this earlier on in this document, so if you are relatively inexperienced with R and would like to ease into it, read this text in the presented order.

SDM have been implemented in R in many different ways. Here we focus on the functions in the '`dismo`' and the '`raster`' packages (but we also refer to other packages). If you want to test, or build on, some of the examples presented here, make sure you have the latest versions of these packages, and their dependencies, installed. If you are using a recent version of R , you can do that with:

```
install.packages(c('raster', 'rgdal', 'dismo', 'rJava'))
```

This document consists of 4 main parts. Part I is concerned with data preparation. This is often the most time consuming part of a species distribution modeling project. You need to collect a sufficient number of occurrence records that document presence (and perhaps absence or abundance) of the species of interest. You also need to have accurate and relevant spatial predictor variables at a sufficiently high spatial resolution. We first discuss some aspects of assembling and cleaning species records, followed by a discussion of aspects of choosing and using the predictor variables. A particularly important concern in species distribution modeling is that the species occurrence data adequately represent the species' distribution. For instance, the species should be correctly identified, the coordinates of the location data need to be accurate enough to allow the general species/environment to be established, and the sample unbiased, or accompanied by information on known biases such that these can be taken into account. Part II introduces the main steps in SDM: fitting a model, making a prediction, and evaluating the result. Part III introduces different modeling methods in more detail (profile methods, regression methods, machine learning methods, and geographic methods). In Part IV we discuss a number of applications (e.g. predicting the effect of climate change), and a number of more advanced topics.

This is a work in progress. Suggestions are welcomed.

Part I

Data preparation

Chapter 2

Species occurrence data

Importing occurrence data into R is easy. But collecting, georeferencing, and cross-checking coordinate data is tedious. Discussions about species distribution modeling often focus on comparing modeling methods, but if you are dealing with species with few and uncertain records, your focus probably ought to be on improving the quality of the occurrence data (Lobo, 2008). All methods do better if your occurrence data is unbiased and free of error (Graham *et al.*, 2007) and you have a relatively large number of records (Wisz *et al.*, 2008). While we'll show you some useful data preparation steps you can do in R , it is necessary to use additional tools as well. For example, Quantum GIS, <http://www.qgis.org/>, is a very useful program for interactive editing of point data sets.

2.1 Importing occurrence data

In most cases you will have a file with point locality data representing the known distribution of a species. Below is an example of using `read.table` to read records that are stored in a text file. The R commands used are in *italics* and preceded by a '>'. Comments are preceded by a hash (#). We are using an example file that is installed with the 'dismo' package, and for that reason we use a complex way to construct the filename, but you can replace that with your own filename. (remember to use forward slashes in the path of filenames!). `system.file` inserts the file path to where dismo is installed. If you haven't used the `paste` function before, it's worth familiarizing yourself with it (type `?paste` in the command window). It's very useful.

```
> # loads the dismo library
> library(dismo)
> file <- paste(system.file(package="dismo"), '/ex/bradypus.csv', sep="")
> # this is the file we will use:
> file
```

```

[1] "C:/soft/R/R-2.13.1/library/dismo/ex/bradypus.csv"

> # let's read it
> bradypus <- read.table(file, header=TRUE, sep=',')
> # let's inspect the values of the file
> # first rows
> head(bradypus)

      species      lon      lat
1 Bradypus variegatus -65.4000 -10.3833
2 Bradypus variegatus -65.3833 -10.3833
3 Bradypus variegatus -65.1333 -16.8000
4 Bradypus variegatus -63.6667 -17.4500
5 Bradypus variegatus -63.8500 -17.4000
6 Bradypus variegatus -64.4167 -16.0000

> # we only need columns 2 and 3:
> bradypus <- bradypus[,2:3]
> head(bradypus)

      lon      lat
1 -65.4000 -10.3833
2 -65.3833 -10.3833
3 -65.1333 -16.8000
4 -63.6667 -17.4500
5 -63.8500 -17.4000
6 -64.4167 -16.0000

```

You can also read such data directly out of Excel or from a database (see e.g. the `RODBC` package). Because this is csv (comma separated values) file, we could also have used the `read.csv` function. No matter how you do it, the objective is to get a matrix (or a `data.frame`) with at least 2 columns to hold the coordinates. Coordinates are typically longitude and latitude, but they could also be Easting and Northing in UTM or another coordinate reference system (map projection). The convention used here is to organize the coordinates columns so that longitude is the first and latitude the second column (think x and y axes in a plot; longitude is x, latitude is y); they often are in the reverse order, leading to undesired results. In many cases you will have additional columns, e.g., a column to indicate the species if you are modeling multiple species; and a column to indicate whether this is a 'presence' or an 'absence' record (a much used convention is to code presence with a 1 and absence with a 0).

If you do not have any species distribution data you can get started by downloading data from the Global Biodiversity Inventory Facility (GBIF) (<http://www.gbif.org/>). In the `dismo` package there is a function '`gbif`' that you can use for this. The data used below were downloaded (and saved to a permanent data set for use in this vignette) using the `gbif` function like this:

```
acaule = gbif('solanum', 'acaule', geo=FALSE)
```

If you want to understand the order of the arguments given here to `gbif` or find out what other arguments you can use with this function, check out the help file (remember you can't access help files if the library is not loaded), by typing:

```
?gbif or help(gbif)
```

Many species occurrence records may not have geographic coordinates. Out of the 699 records that GBIF returned (March 2010), there were only 54 records with coordinates.

```
> # load the saved acaule data
> data(acaule)
> # how many rows and columns?
> dim(acaule)

[1] 699 23

> #select the records that have longitude and latitude data
> colnames(acaule)

[1] "species"           "continent"        "country"          "adm1"
[6] "locality"          "lat"              "lon"              "coordUncertain"
[11] "institution"       "collection"       "catalogNumber"    "basisOfRecord"
[16] "earliestDateCollected" "latestDateCollected" "gbifNotes"        "downloadDate"
[21] "minElevationM"     "maxDepthM"        "minDepthM"

> acgeo <- subset(acaule, !is.na(lon) & !is.na(lat))
> dim(acgeo)

[1] 54 23

> # show some values
> acgeo[1:4, c(1:5,7:10)]

  species continent country adm1 adm2      lat      lon coordUncertain
13   Solanum acaule    <NA>    BOL <NA> <NA> -18.8167 -65.90
426  Solanum acaule Bitter America Argentina Jujuy      -22.9000 -66.24
428  Solanum acaule Bitter America Bolivia La Paz Pacajes -17.4200 -68.85
429  Solanum acaule Bitter America Bolivia La Paz Pacajes -17.1200 -68.77
```

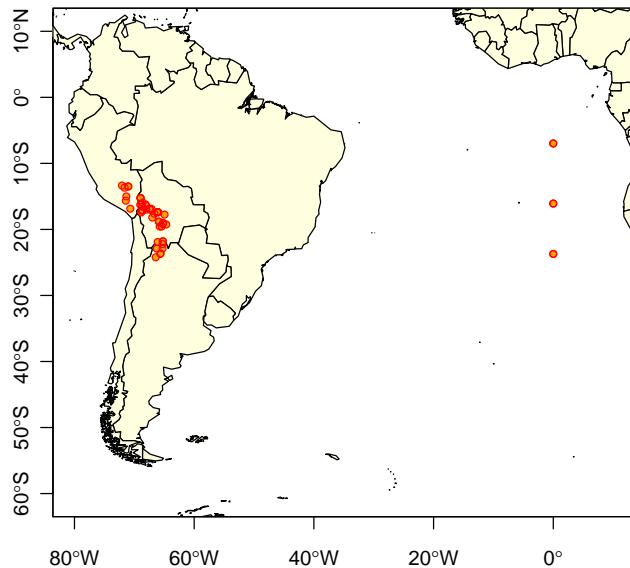
Below is a simple way to make a map of the occurrence localities of *Solanum acaule*. It is important to make such maps to assure that the points are, at least roughly, in the right location.

```
> library(maptools)
> data(wrld_simpl)
> plot(wrld_simpl, xlim=c(-80,10), ylim=c(-60,10), axes=TRUE, col='light yellow')
> # restore the box around the map
```

```

> box()
> # plot points
> points(acgeo$lon, acgeo$lat, col='orange', pch=20, cex=0.75)
> # plot points again to add a border, for better visibility
> points(acgeo$lon, acgeo$lat, col='red', cex=0.75)

```



The "wrld_simpl" dataset contains rough country outlines. You can use other datasets of polygons (or lines or points) as well. For example, you can download higher resolution data country and subnational administrative boundaries data with the `getData` function of the `raster` package. You can also read your own shapefile data into R using the `readOGR` function in the `rgdal` package or the `readShapePoly` function in the `maptools` package.

2.2 Data cleaning

Data 'cleaning' is particularly important for data sourced from species distribution data warehouses such as GBIF. Such efforts do not specifically gather data for the purpose of species distribution modeling, so you need to understand the data and clean them appropriately, for your application. Here we provide an example.

Solanum acaule is a species that occurs in the higher parts of the Andes mountains of Peru and Bolivia. Do you see any errors on the map? There

are three records that have plausible latitudes, but longitudes that are clearly wrong, as they are in the Atlantic Ocean, south of West Africa. It looks like they have a longitude that is zero. In many data-bases you will find values that are 'zero' where 'no data' was intended. The `gbif` function (when using the default arguments) sets coordinates that are (0, 0) to NA, but not if one of the coordinates is zero. Let's see if we find them by searching for records with longitudes of zero.

Let's have a look at these records:

```
> lonzero = subset(acgeo, lon==0)
> # show all records, only the first 13 columns
> lonzero[, 1:13]
```

	species	continent	country	adm1	adm2							
544	Solanum acaule Bitter subsp. acaule		<NA>	BOL	<NA>	<NA>						
551	Solanum acaule Bitter subsp. acaule		<NA>	BOL	<NA>	<NA>						
567	Solanum acaule Bitter subsp. acaule		<NA>	PER	<NA>	<NA>						km 20
638	Solanum acaule Bitter subsp. acaule		<NA>	PER	<NA>	<NA>						km 20
640	Solanum acaule Bitter subsp. acaule		<NA>	ARG	<NA>	<NA>	between Quelbrada del Ch					
641	Solanum acaule Bitter subsp. acaule		<NA>	ARG	<NA>	<NA>	between Quelbrada del Ch					
	coordUncertaintyM	alt	institution	collection	catalogNumber							
544	NA 3900		IPK	WKS 30050		304711						
551	NA 3900		IPK		GB	WKS 30050						
567	NA 4250		IPK	WKS 30048		304709						
638	NA 4250		IPK		GB	WKS 30048						
640	NA 3400		IPK	WKS 30027		304688						
641	NA 3400		IPK		GB	WKS 30027						

The records are from Bolivia (BOL), Peru (PER) and Argentina (ARG), confirming that coordinates are in error (it could have been that the coordinates were correct for a location in the Ocean, perhaps referring to a location a fish was caught rather than a place where *S. acaule* was collected).

2.2.1 Duplicate records

Interestingly, another data quality issue is revealed above: each record occurs twice. This could happen because plant samples are often split and sent to multiple herbariums. But in this case it seems that the data from IPK are duplicated in the GBIF database. Duplicates can be removed with the `duplicated` function.

```
> # which records are duplicates (only considering the first 10 columns)?
> dups <- duplicated(lonzero[, 1:10])
> # remove duplicates
> lonzero <- lonzero[dups, ]
> lonzero[, 1:13]
```

```

species continent country adm1 adm2
551 Solanum acaule Bitter subsp. acaule <NA> BOL <NA> <NA>
638 Solanum acaule Bitter subsp. acaule <NA> PER <NA> <NA>
641 Solanum acaule Bitter subsp. acaule <NA> ARG <NA> <NA> between Quelbrada del Ch
coordUncertaintyM alt institution collection catalogNumber
551 NA 3900 IPK GB WKS 30050
638 NA 4250 IPK GB WKS 30048
641 NA 3400 IPK GB WKS 30027

```

Another approach might be to detect duplicates for the same species and some coordinates in the data, even if the records were from collections by different people or in different years. (in our case, using species is redundant as we have data for only species)

```

> dups2 <- duplicated(acgeo[, c('species', 'lon', 'lat')])
> # number of duplicates
> sum(dups2)

[1] 8

> # keep the records that are _not_ duplicated
> acg <- acgeo[!dups2, ]
> # let's also remove the records with longitude=0
> acg <- acg[acg$lon != 0, ]

```

2.3 Cross-checking

It is important to cross-check coordinates by visual and other means. One approach is to compare the country (and lower level administrative subdivisions) of the site as specified by the records, with the country implied by the coordinates (Hijmans *et al.*, 1999). In the example below we use the `coordinates` function from the `'sp'` package to create a `SpatialPointsDataFrame`, and then the `overlay` function, also from `'sp'`, to do a point-in-polygon query with the countries polygons.

```

> library(sp)
> # make a SpatialPointsDataFrame
> coordinates(acgeo) <- ~lon+lat
> class(acgeo)

[1] "SpatialPointsDataFrame"
attr(,"package")
[1] "sp"

> # use the coordinates to do a spatial query of the polygons in wrld_simpl
> # which is a SpatialPolygonsDataFrame object
> class(wrld_simpl)

```

```

[1] "SpatialPolygonsDataFrame"
attr(,"package")
[1] "sp"

> ov <- overlay(acgeo, wrld_simpl)
> # ov has, for each point, the record number of wrld_simpl
> # we can use the record number to extract the country name
> # first find the variable name
> names(wrld_simpl@data)

[1] "FIPS"      "ISO2"      "ISO3"      "UN"        "NAME"      "AREA"      "POP2005"   "RE
[9] "LON"       "LAT"

> head(wrld_simpl@data)

  FIPS ISO2 ISO3 UN           NAME  AREA POP2005 REGION SUBREGION    LON    LAT
ATG   AC   AG ATG 28 Antigua and Barbuda 44  83039   19     29 -61.783 17.078
DZA   AG   DZ DZA 12          Algeria 238174 32854159   2     15  2.632 28.163
AZE   AJ   AZ AZE 31         Azerbaijan 8260 8352021 142    145 47.395 40.430
ALB   AL   AL ALB  8         Albania 2740 3153731 150    39 20.068 41.143
ARM   AM   AM ARM 51         Armenia 2820 3017661 142    145 44.563 40.534
AGO   AO   AO AGO 24         Angola 124670 16095214   2     17 17.544 -12.296

> # We clearly need the variable 'NAME' in the data.frame (stored in the 'data' slot) of wrl
>
> cntr <- as.character(wrld_simpl@data$NAME[ov])
> # which points (identified by their record numbers) do not match
> # any country (i.e. are in an ocean)
> i <- which(is.na(cntr))
> i

[1] 43 44 45 46 47 48

> # these are the same records, with longitude=0, as identified above:
> acgeo@data[i,'catalogNumber']

[1] "304711"      "WKS 30050"    "304709"      "WKS 30048"    "304688"      "WKS 30027"

> # which points has coordinates that are in a different country than
> # listed in the 'country' field of the gbif record
> j <- which(cntr != acgeo@data$country)
> j

[1] 1 49 50 51 52

> # for the mismatches, bind the country names of the polygons and points
> cbind(cntr, acgeo@data$country)[j,]

```

```

cntr
[1,] "Bolivia" "BOL"
[2,] "Bolivia" "BOL"
[3,] "Peru"      "PER"
[4,] "Peru"      "PER"
[5,] "Peru"      "PER"

> # fortunately the mismatch is simply because of the use of abbreviations
> # instead of full country names in these records.

```

See the `sp` package for more information on the `overlay` function and the related function `over`. At first it may be confusing that it returns indices (row numbers). These indices, stored in variables `i` and `j` were used to get the relevant records. Note that the polygons that we used in the example above are not very precise, and they should not be used in a real analysis. See <http://www.gadm.org/> for more detailed administrative division files, or use the `'getData'` function from the `raster` package (e.g. `getData('gadm', country='PER', level=0)`) to get the national borders of Peru.

```

> # now let's remove the records that have a longitude of 0
> acgeo <- acgeo[ coordinates(acgeo) [, 'lon'] != 0, ]

```

2.4 Georeferencing

If you have records with locality descriptions but no coordinates, you should consider georeferencing these. Not all the records can be georeferenced. Sometimes even the country is unknown (`country=="UNK"`). Here we select only records that do not have coordinates, but that do have a locality description.

```

> georef <- subset(acaule, (is.na(lon) | is.na(lat)) & ! is.na(locality) )
> dim(georef)

[1] 89 23

> georef[1:3, 1:13]

            species continent country adm1 adm2
30 Solanum acaule Bitter subsp. acaule (Juz.) Hawkes & Hjert.    <NA>    PER <NA> <NA> km
42 Solanum acaule Bitter subsp. acaule (Juz.) Hawkes & Hjert.    <NA>    BOL <NA> <NA>
81 Solanum acaule Bitter subsp. acaule (Juz.) Hawkes & Hjert.    <NA>    ARG <NA> <NA>
          coordUncertaintyM alt institution collection catalogNumber
30                  NA 4250      DEU159      DEU      WKS 30048
42                  NA 3900      DEU159      DEU      WKS 30050
81                  NA   NA      DEU159      DEU      WKS 30417

```

Among the first records is an old acquaintance. The record, with catalog number WKS 30048 was also in the set of records that had a longitude of zero degrees.

We recommend using a tool like BioGeomancer: <http://bg.berkeley.edu/latest> (Guralnick *et al.*, 2006) to georeference textual locality descriptions. An important feature of BioGeomancer is that it attempts to capture the uncertainty associated with each georeference (Wieczorek *et al.*, 2004). The dismo package has a function `biogeomancer` that you can use for this, and that we demonstrate below, but its use is generally not recommended because you really need a detailed map interface for accurate georeferencing.

Here is an example for one of the records with longitude = 0. We put the biogeomancer function into a 'try' function, to assure elegant error handling if the computer is not connected to the Internet.

```
> args(biogeomancer)

function (country = "", adm1 = "", adm2 = "", locality = "",
           singleRecord = TRUE, progress = "text")
NULL

> # the first locality:
> lonzero$locality[1]

[1] "Llave"

> b <- try( biogeomancer('Peru', locality=lonzero$locality[1], progress='')) 
> b

  id lon lat coordUncertaintyM
1   1   NA  NA                 NA
```

2.5 Sampling bias

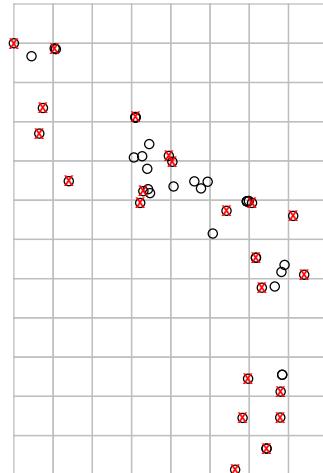
Sampling bias is frequently present in occurrence records (Hijmans *et al.*, 2001). One can attempt to remove some of the bias by subsampling records, and this is illustrated below. However, subsampling reduces the number of records, and it cannot correct the data for areas that have not been sampled at all. It also suffers from the problem that locally dense records might be a true reflection of the relative suitable of habitat. The example below illustrates how one could go about subsampling. This is not a general recommendation to subsample, or to subsample in this way. See Phillips *et al.* (2009) for an approach with MaxEnt to deal with bias in occurrence records used in SDM.

```
> # create a RasterLayer with the extent of acgeo
> r <- raster(acgeo)
> # set the resolution of the cells to 1 degrees
> res(r) <- 1
> # expand the RasterLayer a little
> r <- expand(r, extent(r)+1)
> # get the cell number for each point
```

```

> cell <- cellFromXY(r, acgeo)
> dup <- duplicated(cell)
> # select the records that are not duplicated
> # a random selection within duplicates might be better (but more elaborate)
> acsel <- acgeo[!dup, ]
> # display the results
> p <- rasterToPolygons(r)
> plot(p, border='gray')
> points(acgeo)
> # selected points in red
> points(acsel, cex=1, col='red', pch='x')

```



Chapter 3

Absence and background points

Some of the early species distribution model algorithms, such as Bioclim and Domain only use 'presence' data in the modeling process. Other methods also use 'absence' data or 'background' data. Logistic regression is the classical approach to analyzing presence and absence data (and it is still much used, often implemented in a generalized linear modeling (GLM) framework). If you have a large dataset with presence/absence from a well designed survey, you should use a method that can use these data (i.e. do not use a modeling method that only considers presence data). If you only have presence data, you can still use a method that needs absence data, by substituting absence data with background data.

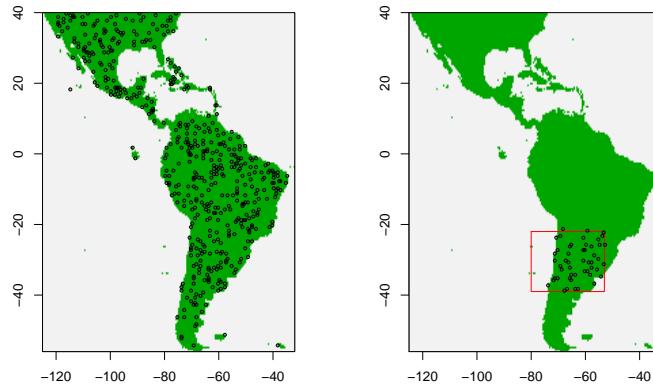
Background data (e.g. Phillips *et al.* 2009) are not attempting to guess at absence locations, but rather to characterize environments in the study region. In this sense, background is the same, irrespective of where the species has been found. Background data establishes the environmental domain of the study, whilst presence data should establish under which conditions a species is more likely to be present than on average. A closely related but different concept, that of "pseudo-absences", is also used for generating the non-presence class for logistic models. In this case, researchers sometimes try to guess where absences might occur – they may sample the whole region except at presence locations, or they might sample at places unlikely to be suitable for the species. We prefer the background concept because it requires fewer assumptions and has some coherent statistical methods for dealing with the "overlap" between presence and background points (e.g. Ward *et al.* 2009; Phillips and Elith, 2011).

Survey-absence data has value. In conjunction with presence records, it establishes where surveys have been done, and the prevalence of the species given the survey effort. That information is lacking for presence-only data, a fact that can cause substantial difficulties for modeling presence-only data well. However, absence data can also be biased and incomplete, as discussed in the

literature on detectability (e.g., Kéry et al., 2010).

`dismo` has a function to sample random points (background data) from a study area. You can use a 'mask' to exclude area with no data NA, e.g. areas not on land. You can use an 'extent' to further restrict the area from which random locations are drawn. In the example below, we first get the list of filenames with the predictor raster data (discussed in detail in the next chapter). We use a raster as a 'mask' in the `randomPoints` function such that the background points are from the same geographic area, and only for places where there are values (land, in our case). Note that if the mask has the longitude/latitude coordinate reference system, function `randomPoints` selects cells according to cell area, which varies by latitude (as in Elith et al., 2011)

```
> files <- list.files(path=paste(system.file(package="dismo"), '/ex',
+                                     sep=''), pattern='grd', full.names=TRUE )
> mask <- raster(files[[1]])
> # select 500 random points
> # set seed to assure that the examples will always have the same random sample.
> set.seed(0)
> bg <- randomPoints(mask, 500 )
> # set up the plotting area for two maps
> par(mfrow=c(1,2))
> plot(!is.na(mask), legend=FALSE)
> points(bg, cex=0.5)
> # now limiting the area of sampling by spatial extent
> e <- extent(-80, -53, -39, -22)
> bg2 <- randomPoints(mask, 50, ext=e)
> plot(!is.na(mask), legend=FALSE)
> plot(e, add=TRUE, col='red')
> points(bg2, cex=0.5)
```



There are several approaches one could use to sample 'pseudo-absence' points, i.e. points from more restricted area than 'background'. VanDerWal et al. (2009) sampled withn a radius of presence points. Here is one way to implement that, using the *Solanum acaule* data.

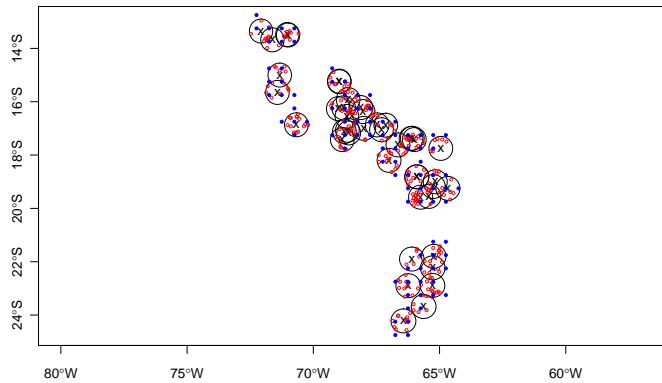
```
> pts <- acg[, c('lon', 'lat')]
> # circles with a radius of 50 km
> x <- circles(pts, d=50000, lonlat=T, col='light gray')
> plot(x@circles, axes=T)
> points(pts, pch='x')
> # sample randomly from all circles
> samp1 <- spsample(x@circles, 250, type='random', iter=25)
> points(samp1, cex=0.5, col='red')
> # get unique cells
> cells <- cellFromXY(mask, samp1)
> length(cells)

[1] 250

> cells <- unique(cells)
> length(cells)

[1] 95

> xy <- xyFromCell(mask, cells)
> points(xy, cex=0.75, pch=20, col='blue')
```



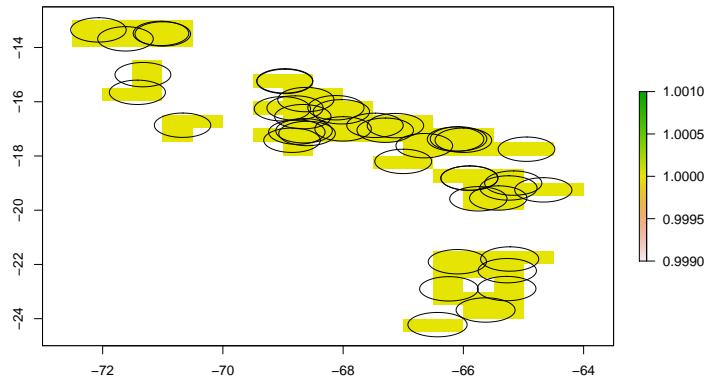
Note that the blue points are not all within the circles, as they now reprsenst the centers of the selected cells from mask. We could choose to select only those cells that have theirs centers within the circles, using the overlay function.

```
> o <- overlay(x@circles, SpatialPoints(xy))
> xyInside <- xy[!is.na(o), ]
```

Similar results could also be achieved via the raster functions `rasterize` or `extract`.

```
> # extract cell numbers for the circles
> v <- extract(mask, x@circles, cellnumbers=T)
> # use rbind to combine the elements in list v
> v <- do.call(rbind, v)
> # get unique cell numbers from which you could sample
> v <- unique(v[,1])
> v
[1] 21880 21881 23368 23554 21316 21317 21503 21131 21321 21507 21508 19822 19823 20008 209
[23] 23926 20009 20010 21510 21511 21134 21135 21320 20572 20573 20382 20568 21692 21693 213
[45] 20759 20760 20945 20944 22069 22070 21882 22068 22998 22999 19824 19825 20011 22254 233
[67] 22996 22997 23182

> # to display the results
> m <- mask
> m[] <- NA
> m[v] <- 1
> plot(m, ext=extent(x@circles)+1)
> plot(x@circles, add=T)
```



Chapter 4

Environmental data

4.1 Raster data

In species distribution modeling, predictor variables are typically organized as raster (grid) type files. Each predictor should be a 'raster' representing a variable of interest. Variables can include climatic, soil, terrain, vegetation, land use, and other variables. These data are typically stored in files in some kind of GIS format. Almost all relevant formats can be used (including ESRI grid, geoTiff, netCDF, IDRISI). Avoid ASCII files if you can, as they tend to considerably slow down processing speed. For any particular study the layers should all have the same spatial extent, resolution, origin, and projection. If necessary, use functions like `crop`, `expand`, `aggregate`, `resample`, and `projectRaster` from the '`raster`' package to prepare your predictor variable data. See the help files and the vignette of the `raster` package for more info on how to do this. The set of predictor variables (rasters) can be used to make a '`RasterStack`', which is a collection of '`RasterLayer`' objects (see the `raster` package for more info).

Here we make a list of files that are installed with the `dismo` package and then create a `rasterStack` from these, show the names of each layer, and finally plot them all.

```
> files <- list.files(path=paste(system.file(package="dismo"),
+                               '/ex', sep=''), pattern='grd', full.names=TRUE )
> # The above finds all the files with extension "grd" in the examples
> # ("ex") directory of the dismo package. You do not need such a complex
> # statement to get your own files.
> files
[1] "C:/soft/R/R-2.13.1/library/dismo/ex/bio1.grd"  "C:/soft/R/R-2.13.1/library/dismo/ex/bio16.grd"
[3] "C:/soft/R/R-2.13.1/library/dismo/ex/bio16.grd"  "C:/soft/R/R-2.13.1/library/dismo/ex/bio5.grd"
[5] "C:/soft/R/R-2.13.1/library/dismo/ex/bio5.grd"   "C:/soft/R/R-2.13.1/library/dismo/ex/bio7.grd"
[7] "C:/soft/R/R-2.13.1/library/dismo/ex/bio7.grd"   "C:/soft/R/R-2.13.1/library/dismo/ex/bio1.grd"
[9] "C:/soft/R/R-2.13.1/library/dismo/ex/bio1.grd"
```

```

> predictors <- stack(files)
> predictors

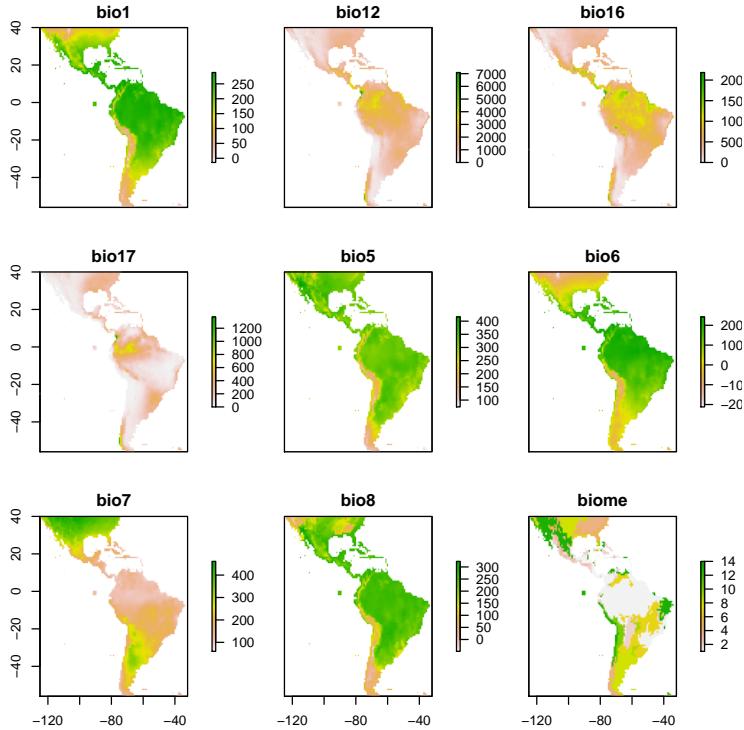
class       : RasterStack
dimensions   : 192, 186, 9  (nrow, ncol, nlayers)
resolution   : 0.5, 0.5  (x, y)
extent       : -125, -32, -56, 40  (xmin, xmax, ymin, ymax)
coord. ref.  : +proj=longlat +datum=WGS84 +ellps=WGS84 +towgs84=0,0,0
min values   : -23     0     0     0     61    -212    60    -66     1
max values   : 289    7682  2458  1496   422    242    461    323    14

> layerNames(predictors)

[1] "bio1"  "bio12" "bio16" "bio17" "bio5"  "bio6"  "bio7"  "bio8"  "biome"

> plot(predictors)

```

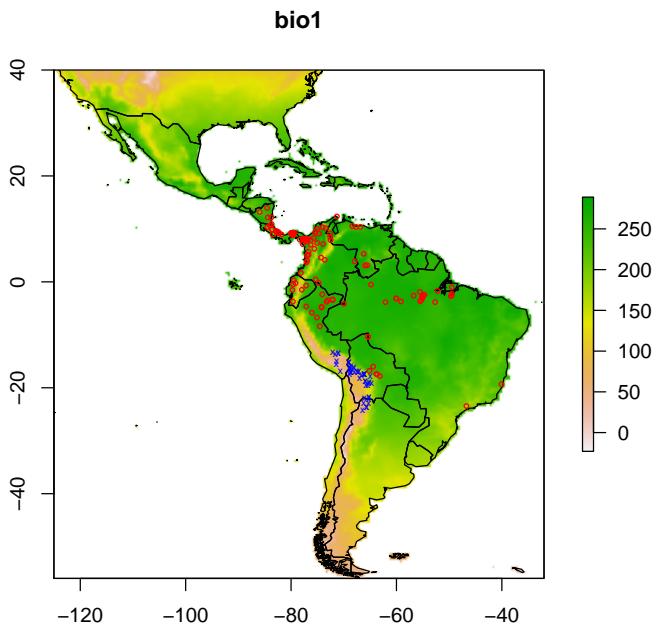


We can also make a plot of a single layer in a RasterStack, and plot some additional data on top of it:

```

> plot(predictors, 1)
> plot(wrld_simpl, add=TRUE)
> points(bradypus, col='red', cex=0.5)
> points(acegeo, col='blue', pch='x', cex=0.5)

```



The example above uses data representing 'bioclimatic variables' from the WorldClim database (<http://www.worldclim.org>, Hijmans *et al.*, 2004) and 'terrestrial biome' data from the WWF. (<http://www.worldwildlife.org/science/data/item1875.html>, Olsen *et al.*, 2001). You can go to these websites if you want higher resolution data. You can also use the `getData` function from the `raster` package to download WorldClim climate data.

Predictor variable selection can be important, particularly if the objective of a study is explanation. See, e.g., Austin and Smith (1987), Austin (2002), Mellert *et al.*, (2011). The early applications of species modeling tended to focus on explanation (Elith and Leathwick 2009). Nowadays, the objective of SDM tends to be prediction. For prediction within the same geographic area, variable selection might arguably be relatively less important, but for many prediction tasks (e.g. to new times or places, see below) variable selection is critically important. In all cases it is important to use variables that are relevant to the ecology of the species (rather than with the first data that can be found on the web!). In some cases it can be useful to develop new, more ecologically relevant, predictor variables from existing data. For example, one could use land cover data and the `focal` function in the `raster` package to create a new variable that indicates how much forest area is available within x km of a grid cell, for a species that might have a home range of x.

4.2 Extracting values from rasters

We now have a set of predictor variables (rasters) and occurrence points. The next step is to extract the values of the predictors at the locations of the points. (This step can be skipped for the modeling methods that are implemented in the dismo package). This is a very straightforward thing to do using the 'extract' function from the raster package. In the example below we use that function first for the *Bradypus* occurrence points, then for 500 random background points. We combine these into a single `data.frame` in which the first column (variable 'pb') indicates whether this is a presence or a background point. 'biome' is categorical variable (called a 'factor' in R) and it is important to explicitly define it that way, so that it won't be treated like any other numerical variable.

```
> presvals <- extract(predictors, bradypus)
> backgr <- randomPoints(predictors, 500)
> absvals <- extract(predictors, backgr)
> pb <- c(rep(1, nrow(presvals)), rep(0, nrow(absvals)))
> sdmdata <- data.frame(cbind(pb, rbind(presvals, absvals)))
> sdmdata[, 'biome'] = as.factor(sdmdata[, 'biome'])
> head(sdmdata)

  pb bio1 bio12 bio16 bio17 bio5 bio6 bio7 bio8 biome
1  1  263   1639    724     62   338   191   147   261     1
2  1  263   1639    724     62   338   191   147   261     1
3  1  253   3624   1547    373   329   150   179   271     1
4  1  243   1693    775    186   318   150   168   264     1
5  1  243   1693    775    186   318   150   168   264     1
6  1  252   2501   1081    280   326   154   172   270     1

> tail(sdmdata)

  pb bio1 bio12 bio16 bio17 bio5 bio6 bio7 bio8 biome
611 0  269   1859    840     32   351   184   168   269     1
612 0  211   246     88     18   405   28    377   306    13
613 0  126   316    207     4   233   -19   252   150     2
614 0  153   1412    418    265   323   -21   344   134     4
615 0  261   1655    733    157   335   179   156   267     1
616 0  281   1425    541     71   340   214   126   284     2

> summary(sdmdata)

      pb                  bio1                 bio12                bio16                bio17 
Min. :0.0000  Min.   : 5.0  Min.   : 9.0  Min.   : 8.0  Min.   : 0.0 
1st Qu.:0.0000  1st Qu.:179.0  1st Qu.:809.8  1st Qu.:347.0  1st Qu.: 35.0 
Median :0.0000  Median :240.0  Median :1416.0 Median :608.0  Median :106.0 
Mean   :0.1883  Mean   :214.3  Mean   :1568.7 Mean   :639.7  Mean   :160.8 
3rd Qu.:0.0000  3rd Qu.:260.0  3rd Qu.:2125.8 3rd Qu.:889.8  3rd Qu.:238.0 
                                bio5                  bio6                  bio7                  bio8 
Min.   : 0.0  Min.   : 8.0  Min.   : 0.0  Min.   : 0.0 
1st Qu.: 35.0 1st Qu.:347.0 1st Qu.:35.0 1st Qu.: 35.0 
Median :106.0 Median :608.0 Median :106.0 Median :106.0 
Mean   :160.8 Mean   :639.7 Mean   :160.8 Mean   :160.8 
3rd Qu.:238.0 3rd Qu.:889.8 3rd Qu.:238.0 3rd Qu.:238.0 
                                biome 
Min.   : 1 
1st Qu.: 1 
Median : 1 
Mean   : 1 
3rd Qu.: 1 
Max.   :13 
```

```

Max.    :1.0000   Max.    :282.0    Max.    :7682.0   Max.    :2458.0   Max.    :1496.0   Max.

          bio8      biome
Min.    :-29.0    1       :270
1st Qu.:218.0    7       : 75
Median  :251.0    13      : 70
Mean    :226.1    2       : 49
3rd Qu.:262.0    8       : 47
Max.    :315.0    4       : 40
          (Other): 65

```

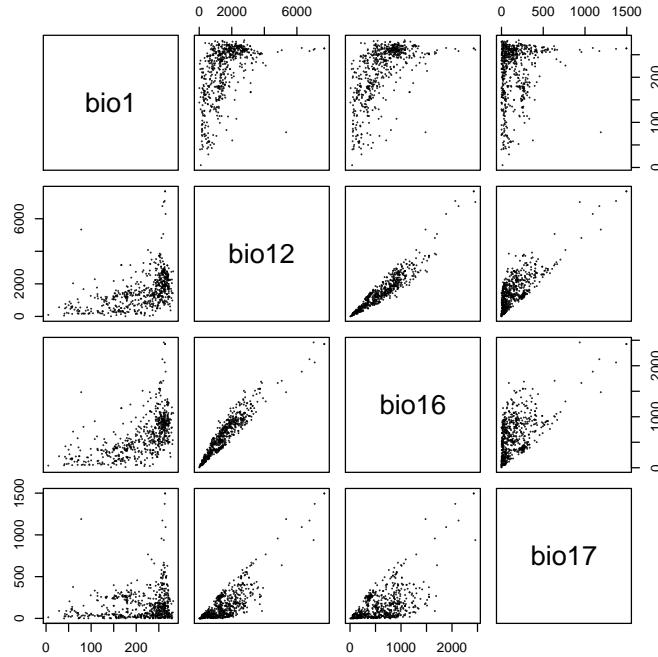
There are alternative approaches possible here. For example, one could extract multiple points in a radius as a potential means for dealing with mismatch between location accuracy and grid cell size. If one would make 10 datasets that represent 10 equally valid "samples" of the environment in that radius, that could be then used to fit 10 models and explore the effect of uncertainty in location.

To visually investigate collinearity in the environmental data (at the occurrence points) you can use a pairs plot. See Dormann *et al.* (2011) for a discussion of methods to remove collinearity.

```

> # pairs plot of the values of the climate data at the bradypus occurrence sites.
> pairs(sdmdata[,2:5], cex=0.1, fig=TRUE)

```



Part II

Model fitting, prediction, and evaluation

Chapter 5

Model fitting

Model fitting is technically quite similar across the modeling methods that exist in R . Most methods take a 'formula' identifying the dependent and independent variables, accompanied with a `data.frame` that holds these variables. Details on specific methods are provided further down on this document, in part III.

A simple formula could look like: `y ~ x1 + x2 + x3`, i.e. `y` is a function of `x1`, `x2`, and `x3`. Another example is `y ~ ..`, which means that `y` is a function of all other variables in the `data.frame` provided to the function. See `help('formula')` for more details about the formula syntax. In the example below, the function '`glm`' is used to fit generalized linear models. `glm` returns a model object.

```
> m1 = glm(pb ~ bio1 + bio5 + bio12, data=sdmdata)
> class(m1)

[1] "glm" "lm"

> summary(m1)

Call:
glm(formula = pb ~ bio1 + bio5 + bio12, data = sdmdata)

Deviance Residuals:
    Min      1Q   Median      3Q      Max 
-0.96111 -0.22477 -0.08500  0.09176  0.90424 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept) 1.336e-01  1.056e-01   1.266  0.20607  
bio1        1.589e-03  3.898e-04   4.075 5.20e-05 *** 
bio5        -1.593e-03 4.605e-04  -3.459  0.00058 *** 
bio12       1.324e-04  1.635e-05   8.102 2.93e-15 ***
```

```

---
Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.1173226)

Null deviance: 94.156 on 615 degrees of freedom
Residual deviance: 71.801 on 612 degrees of freedom
AIC: 434.14

Number of Fisher Scoring iterations: 2

> m2 = glm(pb ~ ., data=sdmdata)
> m2

Call: glm(formula = pb ~ ., data = sdmdata)

Coefficients:
(Intercept)      bio1       bio12      bio16      bio17      bio5       bio6
  0.2333407   -0.0020086    0.0004516   -0.0006237   -0.0008689   0.0366150  -0.0350067
  biome3       biome4      biome5      biome7      biome8      biome9      biome10
 -0.1736915   -0.0931831   -0.0583257   -0.2493170   -0.0445776   0.3535847  -0.0530026

Degrees of Freedom: 615 Total (i.e. Null); 596 Residual
Null Deviance: 94.16
Residual Deviance: 64.69          AIC: 401.9

Models that are implemented in dismo do not use a formula (and most
models only take presence points). For example:

> bc = bioclim(sdmdata[,c('bio1', 'bio5', 'bio12')])
> class(bc)

[1] "Bioclim"
attr(,"package")
[1] "dismo"

> bc

class      : Bioclim

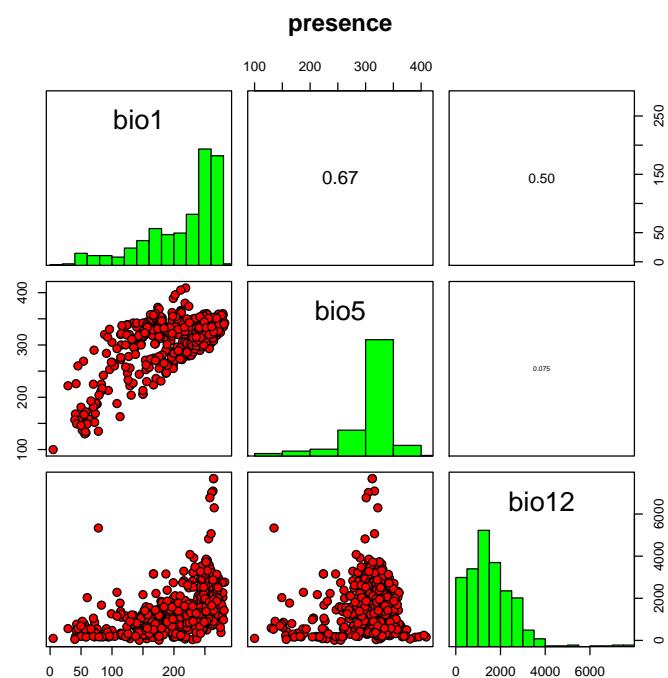
variables: bio1 bio5 bio12

presence points: 616
  bio1 bio5 bio12
  1   263   338   1639
  2   263   338   1639

```

```
3 253 329 3624  
4 243 318 1693  
5 243 318 1693  
6 252 326 2501  
7 240 317 1214  
8 275 335 2259  
9 271 327 2212  
10 274 329 2233  
(... ... ...)
```

```
> pairs(bc)
```



Chapter 6

Model prediction

Different modeling methods return different type of 'model' objects (typically they have the same name as the modeling method used). All of these 'model' objects, irrespective of their exact class, can be used to with the `predict` function to make predictions for any combination of values of the independent variables. This is illustrated in the example below where we make predictions with the `glm` model object '`m1`' and for `bioclim` model '`bc`', for three records with values for variables `bio1`, `bio5` and `bio12` (the variables used in the example above to create the model objects).

```
> bio1 = c(40, 150, 200)
> bio5 = c(60, 115, 290)
> bio12 = c(600, 1600, 1700)
> pd = data.frame(cbind(bio1, bio5, bio12))
> pd

  bio1 bio5 bio12
1    40    60    600
2   150   115   1600
3   200   290   1700

> predict(m1, pd)

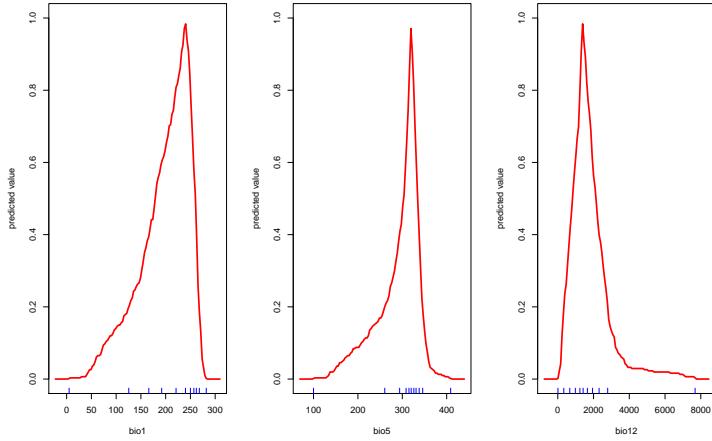
      1         2         3
0.1810886 0.4006745 0.2146168

> predict(bc, pd)

[1] 0.000000000 0.003246753 0.362012987
```

Making such predictions for a few environments can be very useful to explore and understand model predictions. For example it used in the `response` function that creates response plots for each variable, with the other variables at their median value.

```
> response(bc)
```

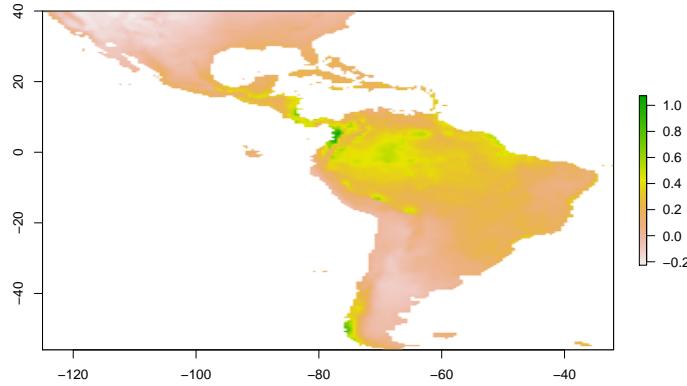


In most cases, however, the purpose of SDM is to create a map of suitability scores. We can do that by providing the predict function with a Raster* object and a model object. As long as the variable names in the model object are available as layers (layerNames) in the Raster* object.

```
> layerNames(predictors)
```

```
[1] "bio1"  "bio12" "bio16" "bio17" "bio5"   "bio6"   "bio7"   "bio8"   "biome"
```

```
> p <- predict(predictors, m1)
> plot(p)
```



Chapter 7

Model evaluation

It is much easier to create a model and make a prediction than to assess how good the model is, and whether it can be used for a specific purpose. Most model types have different measures that can help to assess how good the model fits the data. It is worth becoming familiar with these and understanding their role, because they help you to assess whether there is anything substantially wrong with your model. Most statistics or machine learning texts will provide some details. For instance, for a GLM one can look at how much deviance is explained, whether there are patterns in the residuals, whether there are points with high leverage and so on. However, since many models are to be used for prediction, much evaluation is focused on how well the model predicts to points not used in model training (see following section on data partitioning). Before we start to give some examples of statistics used for this evaluation, it is worth considering what else can be done to evaluate a model. Useful questions include:

- does the model seem sensible, ecologically?
- do the fitted functions (the shapes of the modeled relationships) make sense?
 - do the predictions seem reasonable? (map them, and think about them)
 - are there any spatial patterns in model residuals? (see Leathwick and Whitehead 2001 for an interesting example)

Most modelers rely on cross-validation. This consists of creating a model with one 'training' data set, and testing it with another data set of known occurrences. Typically, training and testing data are created through random sampling (without replacement) from a single data set. Only in a few cases, e.g. Elith *et al.*, 2006, training and test data are from different sources and pre-defined.

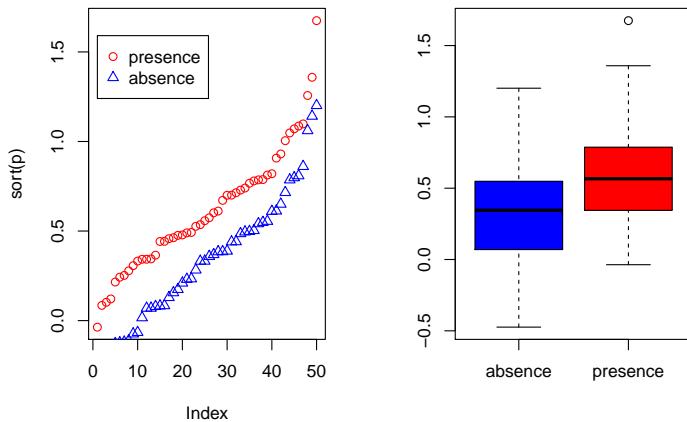
Different measures can be used to evaluate the quality of a prediction (Fielding and Bell, 1997; Liu et al., 2011; and Potts and Elith (2006) for abundance data), perhaps depending on the goal of the study. Many measures for evaluating models based on presence-absence or presence-only data are 'threshold dependent'. That means that a threshold must be set first (e.g., 0.5, though 0.5 is rarely a sensible choice – e.g. see Lui et al. 2005). Predicted values above

that threshold indicate a prediction of 'presence', and values below the threshold indicate 'absence'. Some measures emphasize the weight of false absences; others give more weight to false presences.

Much used statistics that are threshold independent are the correlation coefficient and the Area Under the Receiver Operator Curve (AUROC, generally further abbreviated to AUC). AUC is a measure of rank-correlation. In unbiased data, a high AUC indicates that sites with high predicted suitability values tend to be areas of known presence and locations with lower model prediction values tend to be areas where the species is not known to be present (absent or a random point). An AUC score of 0.5 means that the model is as good as a random guess. See Phillips *et al.* (2006) for a discussion on the use of AUC in the context of presence-only rather than presence/absence data.

Here we illustrate the computation of the correlation coefficient and AUC with two random variables. p (presence) has higher values, and represents the predicted value for 50 known cases (locations) where the species is present, and a (absence) has lower values, and represents the predicted value for 50 known cases (locations) where the species is absent.

```
> p <- rnorm(50, mean=0.7, sd=0.3)
> a <- rnorm(50, mean=0.4, sd=0.4)
> par(mfrow=c(1, 2))
> plot(sort(p), col='red', pch=21)
> points(sort(a), col='blue', pch=24)
> legend(1, 0.95 * max(a,p), c('presence', 'absence'), pch=c(21,24), col=c('red', 'blue'))
> comb = c(p,a)
> group = c(rep('presence', length(p)), rep('absence', length(a)))
> boxplot(comb~group, col=c('blue', 'red'))
```



We created two variables with random normally distributed values, but with different mean and standard deviation. The two variables clearly have different

distributions, and the values for 'presence' tend to be higher than for 'absence'. Here is how you can compute the correlation coefficient and the AUC:

```
> group = c(rep(1, length(p)), rep(0, length(a)))
> cor.test(comb, group)$estimate

      cor
0.3772834

> mv <- wilcox.test(p,a)
> auc <- as.numeric(mv$statistic) / (length(p) * length(a))
> auc

[1] 0.7124
```

Below we show how you can compute these, and other statistics more conveniently, with the **evaluate** function in the dismo package. See **?evaluate** for info on additional evaluation measures that are available. ROC/AUC can also be computed with the ROCR package.

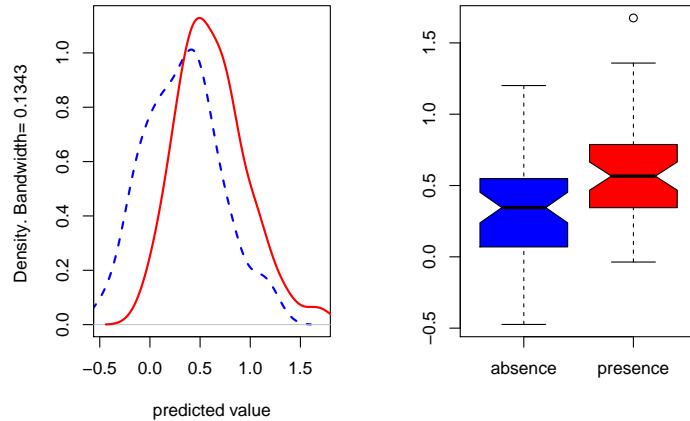
```
> e = evaluate(p=p, a=a)
> class(e)

[1] "ModelEvaluation"
attr(,"package")
[1] "dismo"

> e

  class          : ModelEvaluation
  n presences    : 50
  n absences     : 50
  AUC            : 0.7124
  cor            : 0.3772834
  TPR+TNR threshold: 0.441

> par(mfrow=c(1, 2))
> density(e)
> boxplot(e, col=c('blue', 'red'))
```



Now back to some real data, presence-only in this case. We'll divide the data in two random sets, one for training a Bioclim model, and one for evaluating the model.

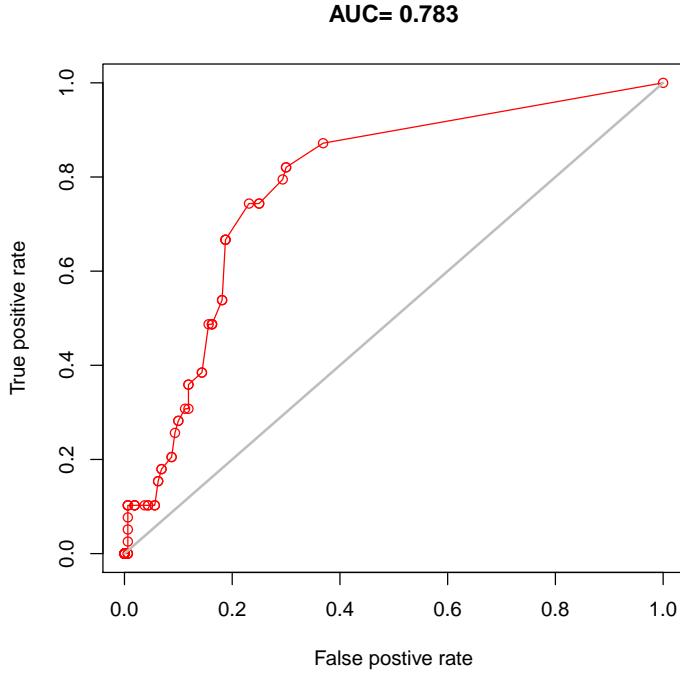
```

> rand <- round(0.75 * runif(nrow(sdldata)))
> traindata <- sdldata[rand==0,]
> traindata <- traindata[traindata[,1] == 1, 2:9]
>testdata <- sdldata[rand==1,]
> bc <- bioclim(traindata)
> e <- evaluate(testdata[testdata==1,], testdata[testdata==0,], bc)
> e

class : ModelEvaluation
n presences : 36
n absences : 168
AUC : 0.7662037
cor : 0.3269372
TPR+TNR threshold: 0.026

> plot(e, 'ROC')

```



In real projects, you would want to use *k-fold* data partitioning instead of a single random sample. The *dismo* function *kfold* facilitates that type of data partitioning. It creates a vector that assigns each row in the data matrix to a group (between 1 to k).

Let's first create presence and background data.

```
> pres <- sdmdata[sdmdata[,1] == 1, 2:9]
> back <- sdmdata[sdmdata[,1] == 0, 2:9]
```

The background data will only be used for model testing and does not need to be partitioned. We now partition the data into 5 groups.

```
> k <- 5
> group <- kfold(pres, k)
> group[1:10]
[1] 5 5 2 3 2 2 3 2 4 4
> unique(group)
[1] 5 2 3 4 1
```

Now we can fit and test our model five times. In each run, the records corresponding to one of the five groups is only used to evaluate the model, while the other four groups are only used to fit the model. The results are stored in a list called 'e'.

```

> e <- list()
> for (i in 1:k) {
+   train <- pres[group != i,]
+   test <- pres[group == i,]
+   bc <- bioclim(train)
+   e[[i]] <- evaluate(p=test, a=back, bc)
+ }

```

We can extract several things from the objects in 'e', but let's restrict ourselves to the AUC values and the "maximum of the sum of the sensitivity (true positive rate) and specificity (true negative rate)" (this is sometimes used as a threshold for setting cells to presence or absence).

```

> auc <- sapply( e, function(x){slot(x, 'auc')} )
> auc
[1] 0.7900000 0.6946522 0.8118750 0.8174783 0.8183913

> mean(auc)
[1] 0.7864793

> sapply( e, function(x){ x@t[which.max(x@TPR + x@TNR)] } )
[1] 0.040 0.006 0.040 0.040 0.040

```

The use of AUC in evaluating SDMs has been criticized (Lobo et al. 2008, Jiménez-Valverde 2011). A particularly sticky problem is that the values of AUC vary with the spatial extent used to select background points. Generally, the larger that extent, the higher the AUC value. Therefore, AUC values are generally biased and cannot be directly compared. Hijmans (2011) suggested that one could remove "spatial sorting bias" (the difference between the distance from testing-presence to training-prsence and testing-absence to training-absence points) through "point-wise distance sampling".

```

> nr <- nrow(bradypus)
> s <- sample(nr, 0.25 * nr)
> pres_train <- bradypus[-s, ]
> pres_test <- bradypus[s, ]
> nr <- nrow(backgr)
> s <- sample(nr, 0.25 * nr)
> back_train <- backgr[-s, ]
> back_test <- backgr[s, ]

> sb <- ssb(pres_test, back_test, pres_train)
> sb[,1] / sb[,2]

pd
0.08458875

```

$sb[1] / sb[2]$ is an indicator of spatial sorting bias (SSB). If there is no SSB this value should be 1, in these data it is close to zero, indicating that SSB is very strong. Let's create a subsample in which SSB is removed.

```
> i <- pwdSample(pres_test, back_test, pres_train, n=1, tr=0.1)
> pres_test_pwd <- pres_test[!is.na(i[,1]), ]
> back_test_pwd <- back_test[na.omit(as.vector(i)), ]
> sb2 <- ssb(pres_test_pwd, back_test_pwd, pres_train)
> sb2[1]/ sb2[2]

[1] 1.021588
```

Spatial sorting bias is much reduced now. The AUC drops from almost around 0.8 to 0.5!

```
> bc <- bioclim(predictors, pres_train)
> evaluate(bc, p=pres_test, a=back_test, x=predictors)

  class      : ModelEvaluation
  n presences   : 29
  n absences    : 125
  AUC          : 0.8765517
  cor          : 0.5025988
  TPR+TNR threshold: 0.023

> evaluate(bc, p=pres_test_pwd, a=back_test_pwd, x=predictors)

  class      : ModelEvaluation
  n presences   : 13
  n absences    : 13
  AUC          : 0.704142
  cor          : 0.3170807
  TPR+TNR threshold: 0.02
```

Part III

Modeling methods

Chapter 8

Types of algorithms & data used in examples

A large number of algorithms has been used in species distribution modeling. They can be classified as 'profile', 'regression', and 'machine learning' methods. Profile methods only consider 'presence' data, not absence or background data. Regression and machine learning methods use both presence and absence or background data. The distinction between regression and machine learning methods is not sharp, but it is perhaps still useful as way to classify models. Another distinction that one can make is between presence-only and presence-absence models. Profile methods are always presence-only, other methods can be either, depending if they are used with survey-absence or with pseudo-absence/background data. An entirely different class of models consists of models that only, or primarily, use the geographic location of known occurrences, and do not rely on the values of predictor variables at these locations. We refer to these models as 'spatial-only models'. Below we discuss examples of these different types of models.

We will use the same data to illustrate all models, except that some models cannot use categorical variables. So for those models we drop the categorical variables from the predictors stack.

```
> pred_nf <- dropLayer(predictors, 'biome')
```

We'll use the *Bradypus* data for presence of a species. Let's make a training and a testing set.

```
> group <- kfold(bradypus, 5)
> pres_train <- bradypus[group != 1, ]
> pres_test <- bradypus[group == 1, ]
```

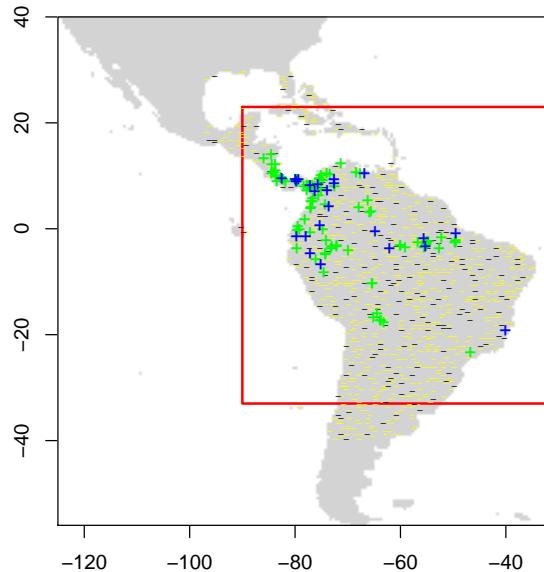
To speed up processing, let's restrict the predictions to a more restricted area (defined by a rectangular extent):

```
> ext = extent(-90, -32, -33, 23)
```

Background data for training and a testing set. The first layer in the Raster-Stack is used as a 'mask'. That ensures that random points only occur within the spatial extent of the rasters, and within cells that are not NA, and that there is only a single absence point per cell. Here we further restrict the background points to be within 12.5% of our specified extent 'ext'.

```
> backg <- randomPoints(pred_nf, n=1000, ext=ext, extf = 1.25)
> colnames(backg) = c('lon', 'lat')
> group <- kfold(backg, 5)
> backg_train <- backg[group != 1, ]
> backg_test <- backg[group == 1, ]

> r = raster(pred_nf, 1)
> plot(!is.na(r), col=c('white', 'light grey'), legend=FALSE)
> plot(ext, add=TRUE, col='red', lwd=2)
> points(backg_train, pch='-', cex=0.5, col='yellow')
> points(backg_test, pch='-', cex=0.5, col='black')
> points(pres_train, pch= '+', col='green')
> points(pres_test, pch= '+', col='blue')
```



Chapter 9

Profile methods

The three methods described here, Bioclim, Domain, and Mahal. These methods are implemented in the dismo package, and the procedures to use these models are the same for all three.

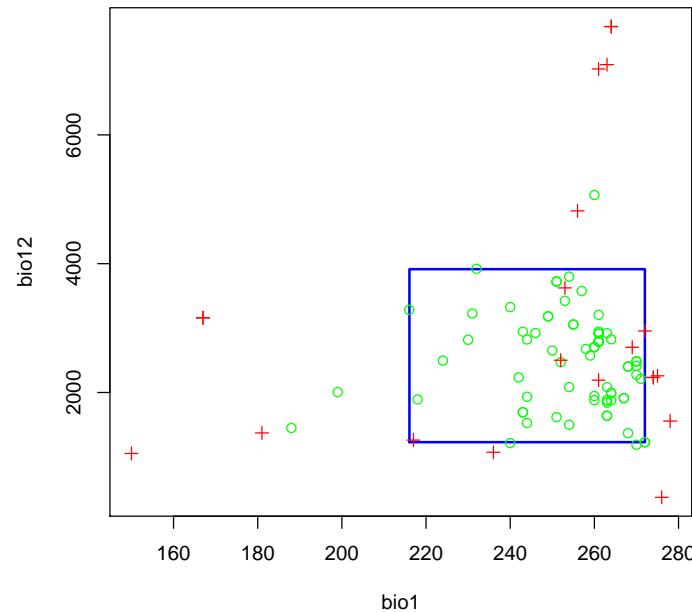
9.1 Bioclim

The BIOCLIM algorithm has been extensively used for species distribution modeling. BIOCLIM is a classic 'climate-envelope-model'. Although it generally does not perform as good as some other modeling methods (Elith *et al.* 2006), particularly in the context of climate change (Hijmans and Graham, 2006), it is still used, among other reasons because the algorithm is easy to understand and thus useful in teaching species distribution modeling. The BIOCLIM algorithm computes the similarity of a location by comparing the values of environmental variables at any location to a percentile distribution of the values at known locations of occurrence ('training sites'). The closer to the 50th percentile (the median), the more suitable the location is. The tails of the distribution are not distinguished, that is, 10 percentile is treated as equivalent to 90 percentile. In the 'dismo' implementation, the values of the upper tail values are transformed to the lower tail, and the minimum percentile score across all the environmental variables is used (i.e., BIOCLIM uses an approach like Liebig's law of the minimum). This value is subtracted from 1 and then multiplied with two so that the results are between 0 and 1. The reason for scaling this way is that the results become more like that of other distribution modeling methods and are thus easier to interpret. The value 1 will rarely be observed as it would require a location that has the median value of the training data for all the variables considered. The value 0 is very common as it is assigned to all cells with a value of an environmental variable that is outside the percentile distribution (the range of the training data) for at least one of the variables.

Earlier on, we fitted a Bioclim model using data.frame with each row representing the environmental data at known sites of presence of a species. Here we

fit a bioclim model simply using the predictors and the occurrence points (the function will do the extracting for us).

```
> bc <- bioclim(pred_nf, pres_train)
> plot(bc, a=1, b=2, p=0.85)
```



We evaluate the model in a similar way, by providing presence and background (absence) points, the model, and a RasterStack:

```
> e <- evaluate(pres_test, backg_test, bc, pred_nf)
> e

  class      : ModelEvaluation
  n presences : 23
  n absences  : 200
  AUC         : 0.708913
  cor         : 0.1716138
  TPR+TNR threshold: 0.06
```

And we use the RasterStack with predictor variables to make a prediction to a RasterLayer:

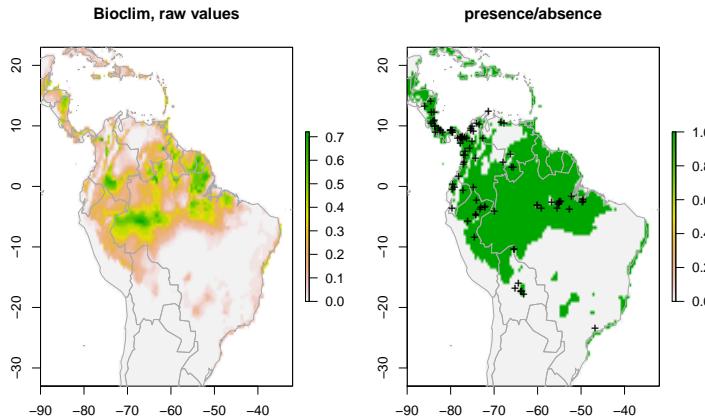
```
> pb <- predict(pred_nf, bc, ext=ext, progress='')
```

```

class      : RasterLayer
dimensions  : 112, 116, 12992 (nrow, ncol, ncell)
resolution  : 0.5, 0.5 (x, y)
extent     : -90, -32, -33, 23 (xmin, xmax, ymin, ymax)
coord. ref. : +proj=longlat +datum=WGS84 +ellps=WGS84 +towgs84=0,0,0
values     : in memory
min value   : 0
max value   : 0.7204301

> par(mfrow=c(1,2))
> plot(pb, main='Bioclim, raw values')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> threshold <- e@t[which.max(e@TPR + e@TNR)]
> plot(pb > threshold, main='presence/absence')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> points(pres_train, pch='+')

```



Please note the order of the arguments in the predict function. In the example above, we used `predict(pred_nf, bc)` (first the RasterStack, then the model object), which is little bit less efficient than `predict(bc, pred_nf)` (first the model, than the RasterStack). The reason for using the order we have used, is that this will work for all models, whereas the other option only works for the models defined in the dismo package, such as Bioclim, Domain, and Maxent, but not for models defined in other packages (random forest, boosted regression trees, glm, etc.).

9.2 Domain

The Domain algorithm (Carpenter *et al.* 1993) has been extensively used for species distribution modeling. It did not perform very well in a model

comparison (Elith *et al.* 2006) and very poorly when assessing climate change effects (Hijmans and Graham, 2006). The Domain algorithm computes the Gower distance between environmental variables at any location and those at any of the known locations of occurrence ('training sites').

The distance between the environment at point A and those of the known occurrences for a single climate variable is calculated as the absolute difference in the values of that variable divided by the range of the variable across all known occurrence points (i.e., the distance is scaled by the range of observations). For each variable the minimum distance between a site and any of the training points is taken. The Gower distance is then the mean of these distances over all environmental variables. The algorithm assigns to a place the distance to the closest known occurrence (in environmental space).

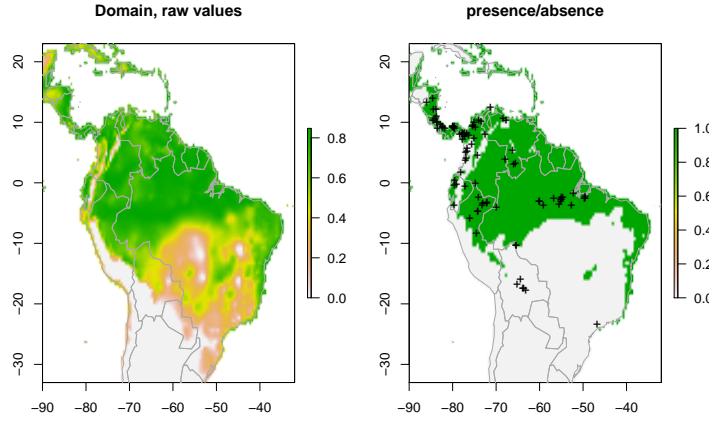
To integrate over environmental variables, the distance to any of the variables is used. This distance is subtracted from one, and (in this R implementation) values below zero are truncated so that the scores are between 0 (low) and 1 (high).

Below we fit a domain model, evaluate it, and make a prediction. We map the prediction, as well as a map subjectively classified into presence / absence.

```
> dm <- domain(pred_nf, pres_train)
> e <- evaluate(pres_test, backg_test, dm, pred_nf)
> e

  class           : ModelEvaluation
  n presences    : 23
  n absences     : 200
  AUC            : 0.765
  cor            : 0.2749732
  TPR+TNR threshold: 0.64

> pd = predict(pred_nf, dm, ext=ext, progress='')
> par(mfrow=c(1,2))
> plot(pd, main='Domain, raw values')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> threshold <- e@t[which.max(e@TPR + e@TNR)]
> plot(pd > threshold, main='presence/absence')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> points(pres_train, pch='+')
```



9.3 Mahalanobis

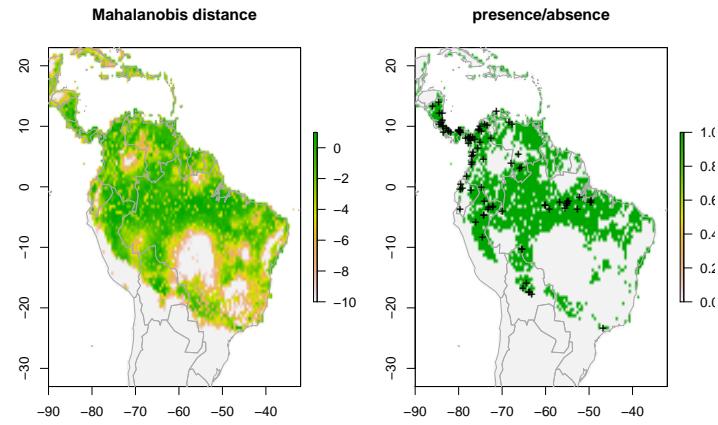
The `mahal` function implements a species distribution model based on the Mahalanobis distance (Mahalanobis, 1936). Mahalanobis distance takes into account the correlations of the variables in the data set, and it is not dependent on the scale of measurements.

```

> mm <- mahal(pred_nf, pres_train)
> e <- evaluate(pres_test, backg_test, mm, pred_nf)
> e

  class           : ModelEvaluation
  n presences     : 23
  n absences      : 200
  AUC             : 0.8306522
  cor             : 0.1280322
  TPR+TNR threshold: -2.08

> pm = predict(pred_nf, mm, ext=ext, progress='')
> par(mfrow=c(1,2))
> pm[pm < -10] <- -10
> plot(pm, main='Mahalanobis distance')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> threshold <- e@t[which.max(e@TPR + e@TNR)]
> plot(pm > threshold, main='presence/absence')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> points(pres_train, pch='+')
```



Chapter 10

Regression models

The remaining models need to be fit presence/absence (background) data. With the exception of 'maxent', we cannot fit the model with a RasterStack and points. Instead, we need to extract the environmental data values ourselves, and fit the models with these values.

```
> train <- rbind(pres_train, backg_train)
> pb_train <- c(rep(1, nrow(pres_train)), rep(0, nrow(backg_train)))
> envtrain <- extract(predictors, train)
> envtrain <- data.frame( cbind(pa=pb_train, envtrain) )
> envtrain[, 'biome'] = factor(envtrain[, 'biome'], levels=1:14)
> head(envtrain)

   pa bio1 bio12 bio16 bio17 bio5 bio6 bio7 bio8 biome
1  1  263  1639    724     62  338  191  147  261      1
2  1  263  1639    724     62  338  191  147  261      1
3  1  253  3624   1547    373  329  150  179  271      1
4  1  243  1693    775    186  318  150  168  264      1
5  1  243  1693    775    186  318  150  168  264      1
6  1  252  2501   1081    280  326  154  172  270      1

> testpres <- data.frame( extract(predictors, pres_test) )
> testbackg <- data.frame( extract(predictors, backg_test) )
> testpres[, 'biome'] = factor(testpres[, 'biome'], levels=1:14)
> testbackg[, 'biome'] = factor(testbackg[, 'biome'], levels=1:14)
```

10.1 Generalized Linear Models

A generalized linear model (GLM) is a generalization of ordinary least squares regression. Models are fit using maximum likelihood and by allowing the linear model to be related to the response variable via a link function and by allowing the magnitude of the variance of each measurement to be a function of its

predicted value. Depending on how a GLM is specified it can be equivalent to (multiple) linear regression, logistic regression or Poisson regression. See Guisan *et al* (2002) for an overview of the use of GLM in species distribution modeling.

In R , GLM is implemented in the 'glm' function, and the link function and error distribution are specified with the 'family' argument. Examples are:

```
family = binomial(link = "logit")
family = gaussian(link = "identity")
family = poisson(link = "log")
```

Here we fit two basic glm models. All variables are used, but without interaction terms.

```
> # logistic regression:
> gm1 <- glm(pa ~ bio1 + bio5 + bio6 + bio7 + bio8 + bio12 + bio16 + bio17,
+                         family = binomial(link = "logit"), data=envtrain)
> summary(gm1)

Call:
glm(formula = pa ~ bio1 + bio5 + bio6 + bio7 + bio8 + bio12 +
    bio16 + bio17, family = binomial(link = "logit"), data = envtrain)

Deviance Residuals:
    Min      1Q      Median      3Q      Max 
-2.24610 -0.45198 -0.24298 -0.05108  2.81345 

Coefficients:
            Estimate Std. Error z value Pr(>|z|)    
(Intercept) 2.3411112  1.6674732   1.404  0.16032  
bio1        0.0436849  0.0568114   0.769  0.44193  
bio5        0.2969601  0.2606709   1.139  0.25461  
bio6       -0.3645092  0.2623769  -1.389  0.16475  
bio7       -0.3731464  0.2613989  -1.427  0.15344  
bio8        0.0210382  0.0258340   0.814  0.41544  
bio12       0.0018054  0.0007101   2.542  0.01101 *  
bio16      -0.0010044  0.0014597  -0.688  0.49138  
bio17      -0.0047930  0.0016817  -2.850  0.00437 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 596.69  on 892  degrees of freedom
Residual deviance: 431.95  on 884  degrees of freedom
AIC: 449.95

Number of Fisher Scoring iterations: 8

> coef(gm1)
```

```

(IIntercept)          bio1        bio5        bio6        bio7        bio8        bio12
2.341111213  0.043684933  0.296960094 -0.364509209 -0.373146360  0.021038176  0.001805393 -0.00011111213

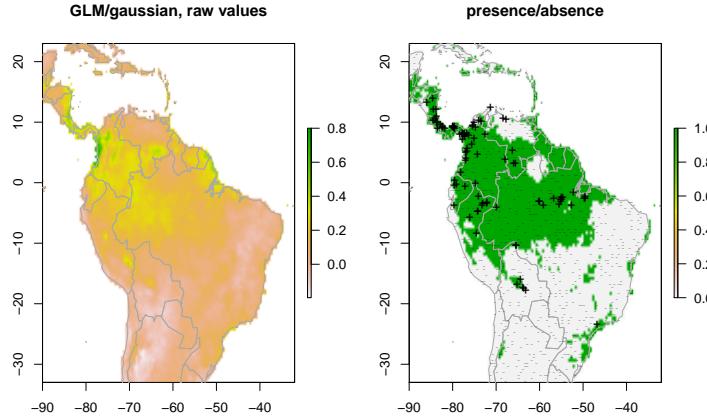
> gm2 <- glm(pa ~ bio1 + bio5 + bio6 + bio7 + bio8 + bio12 + bio16 + bio17,
+                         family = gaussian(link = "identity"), data=envtrain)
> evaluate(testpres, testbackg, gm1)

class           : ModelEvaluation
n presences    : 23
n absences     : 200
AUC            : 0.8378261
cor            : 0.2975267
TPR+TNR threshold: -2.16

> e2 <- evaluate(testpres, testbackg, gm2)

> pg <- predict(predictors, gm2, ext=ext)
> par(mfrow=c(1,2))
> plot(pg, main='GLM/gaussian, raw values')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> threshold <- e2@t[which.max(e2@TPR + e2@TNR)]
> plot(pg > threshold, main='presence/absence')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> points(pres_train, pch='+')
> points(backg_train, pch='-', cex=0.25)

```



10.2 Generalized Additive Models

Generalized additive models (GAMs; Hastie and Tibshirani, 1990; Wood, 2006) are an extension to GLMs. In GAMs, the linear predictor is the sum

of smoothing functions. This makes GAMs very flexible, and they can fit very complex functions. It also makes them very similar to machine learning methods. In R , GAMs are implemented in the 'mgcv' package. The 'grasp' package implements species distribution modeling with gam (Lehman *et al.*, 2002).

Chapter 11

Machine learning methods

There is a variety of machine learning (sometimes referred to data mining) methods in R . For a long time there have been packages to do Artificial Neural Networks (ANN) and Classification and Regression Trees (CART). More recent methods include Random Forests, Boosted Regression Trees, and Support Vector Machines. Through the dismo package you can also use the Maxent program, that implements the most widely used method (maxent) in species distribution modeling. Breiman (2001a) provides a accessible introduction to machine learning, and how it contrasts with 'classical statistics' (model based probabilistic inference). Hastie *et al.*, 2009 provide what is probably the most extensive overview of these methods.

All the model fitting methods discussed here can be tuned in several ways. We do not explore that here, and only show the general approach. If you want to use one of the methods, then you should consult the R help pages (and other sources) to find out how to best implement the model fitting procedure.

11.1 Maxent

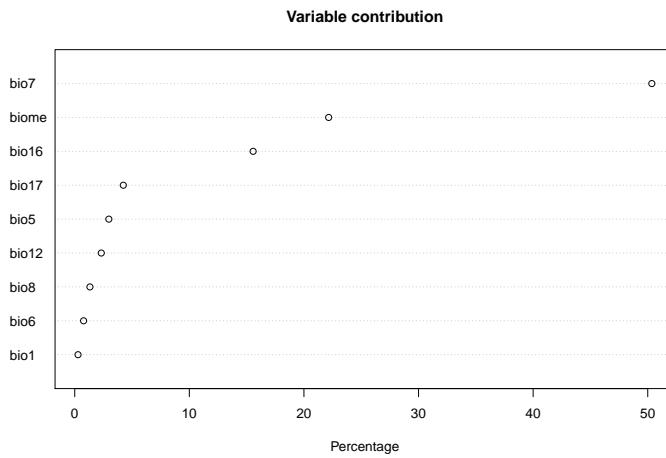
MaxEnt (Maximum Entropy; Phillips *et al.*, 2004, 2006) is the most widely used SDM algorithm. Elith *et al.*, 2010,) provide an explanation of the algorithm (and software) geared towards ecologists. MaxEnt is available as a stand-alone Java program. Dismo has a function 'maxent' that communicates with this program. To use it you must first download the program from <http://www.cs.princeton.edu/~schapire/maxent/>. Put the file 'maxent.jar' in the 'java' folder of the 'dismo' package. That is the folder returned by `system.file("java", package="dismo")`. Please note that this program (`maxent.jar`) cannot be redistributed or used for commercial purposes.

Because MaxEnt is implemented in dismo you can fit it like the profile methods (e.g. Bioclim). That is, you can provide presence points and a RasterStack. However, you can also first fit a model, like with the other methods such as `glm`. But in the case of MaxEnt you cannot use the formula notation.

```

> # checking if the jar file is present. If not, skip this bit
> jar <- paste(system.file(package="dismo"), "/java/maxent.jar", sep=' ')
> if (file.exists(jar)) {
+     xm <- maxent(predictors, pres_train, factors='biome')
+     plot(xm)
+ } else {
+     cat('cannot run this example because maxent is not available on this system')
+     plot(1)
+ }

```

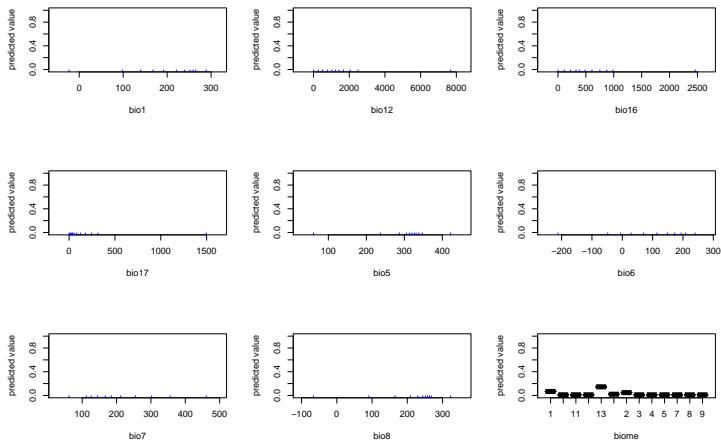


A response plot:

```

> # checking if the jar file is present. If not, skip this bit
> jar <- paste(system.file(package="dismo"), "/java/maxent.jar", sep=' ')
> if (file.exists(jar)) {
+     response(xm)
+ } else {
+     cat('cannot run this example because maxent is not available on this system')
+     plot(1)
+ }

```

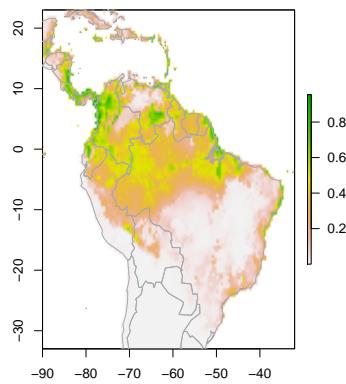


```

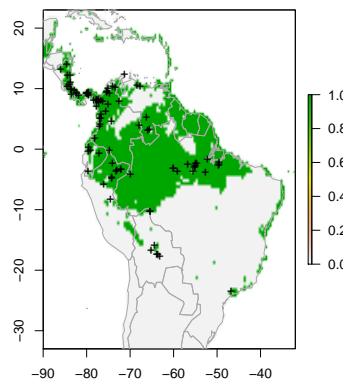
> if (file.exists(jar)) {
+   e <- evaluate(pres_test, backg_test, xm, predictors)
+   e
+   px = predict(predictors, xm, ext=ext, progress='')
+   par(mfrow=c(1,2))
+   plot(px, main='Maxent, raw values')
+   plot(wrld_simpl, add=TRUE, border='dark grey')
+   threshold <- e@t[which.max(e@TPR + e@TNR)]
+   plot(px > threshold, main='presence/absence')
+   plot(wrld_simpl, add=TRUE, border='dark grey')
+   points(pres_train, pch='+')
+ } else {
+   plot(1)
+ }

```

Maxent, raw values



presence/absence



11.2 Boosted Regression Trees

Boosted Regression Trees (BRT) is, unfortunately, known by a large number of different names. It was developed by Friedman (2001), who referred to it as a "Gradient Boosting Machine" (GBM). It is also known as "Gradient Boost", "Stochastic Gradient Boosting", "Gradient Tree Boosting". The method is implemented in the 'gbm' package in R .

The article by Elith, Leathwick and Hastie (2009) describes the use of BRT in the context of species distribution modeling. Their article is accompanied by a number of R functions and a tutorial that have been slightly adjusted and incorporated into the 'dismo' package. These functions extend the functions in the 'gbm' package, with the goal to make these easier to apply to ecological data, and to enhance interpretation. The adapted tutorial is available as a vignette to the dismo package. You can access it via the index of the help pages, or with this command: `vignette('gbm', 'dismo')`

11.3 Random Forest

The Random Forest (Breiman, 2001b) method is an extension of Classification and regression trees (CART; Breiman *et al.*, 1984). In R it is implemented in the function 'randomForest' in a package with the same name. The function randomForest can take a formula or, in two separate arguments, a data.frame with the predictor variables, and a vector with the response. If the response variable is a factor (categorical), randomForest will do classification, otherwise it will do regression. Whereas with species distribution modeling we are often interested in classification (species is present or not), it is my experience that using regression provides better results. rf1 does regression, rf2 and rf3 do classification (they are exactly the same models). See the function tuneRF for optimizing the model fitting procedure.

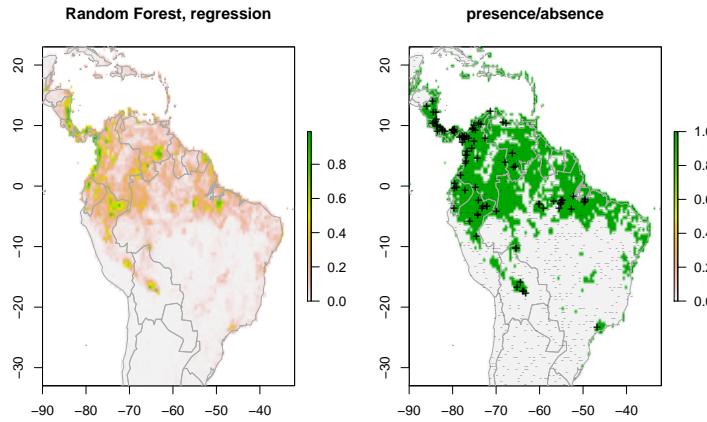
```
> library(randomForest)
> model <- pa ~ bio1 + bio5 + bio6 + bio7 + bio8 + bio12 + bio16 + bio17
> rf1 <- randomForest(model, data=envtrain)
> model <- factor(pa) ~ bio1 + bio5 + bio6 + bio7 + bio8 + bio12 + bio16 + bio17
> rf2 <- randomForest(model, data=envtrain)
> rf3 <- randomForest(envtrain[,1:8], factor(pb_train))
> e = evaluate(testpres, testbackg, rf1)
> e

  class          : ModelEvaluation
  n presences    : 23
  n absences     : 200
  AUC            : 0.8315217
  cor            : 0.3923126
  TPR+TNR threshold: 0.04
```

```

> pr <- predict(predictors, rf1, ext=ext)
> par(mfrow=c(1,2))
> plot(pr, main='Random Forest, regression')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> threshold <- e@t[which.max(e@TPR + e@TNR)]
> plot(pr > threshold, main='presence/absence')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> points(pres_train, pch='+')
> points(backg_train, pch='-', cex=0.25)

```



11.4 Support Vector Machines

Support Vector Machines (SVMs; Vapnik, 1998) apply a simple linear method to the data but in a high-dimensional feature space non-linearly related to the input space, but in practice, it does not involve any computations in that high-dimensional space. This simplicity combined with state of the art performance on many learning problems (classification, regression, and novelty detection) has contributed to the popularity of the SVM (Karatzoglou *et al.*, 2006). They were first used in species distribution modeling by Guo *et al.* (2005).

There are a number of implementations of svm in R . The most useful implementations in our context are probably function 'ksvm' in package 'kernlab' and the 'svm' function in package 'e1071'. 'ksvm' includes many different SVM formulations and kernels and provides useful options and features like a method for plotting, but it lacks a proper model selection tool. The 'svm' function in package 'e1071' includes a model selection tool: the 'tune' function (Karatzoglou *et al.*, 2006)

```

> library(kernlab)
> svm <- ksvm(pa ~ bio1 + bio5 + bio6 + bio7 + bio8 + bio12 + bio16 + bio17, data=envtrain)

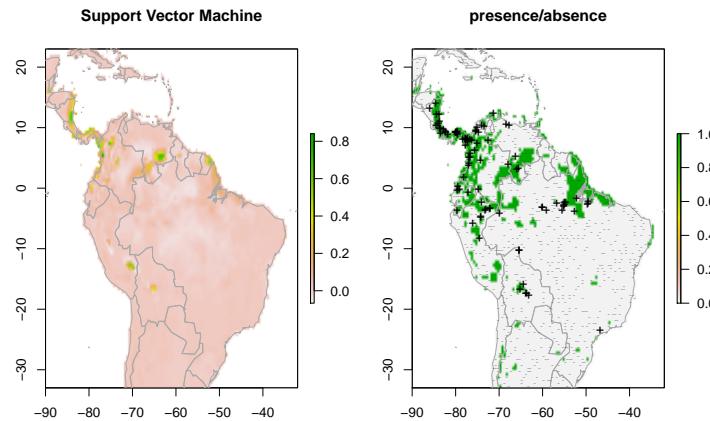
```

Using automatic sigma estimation (sigest) for RBF or laplace kernel

```
> e <- evaluate(testpres, testbackg, svm)
> e

  class          : ModelEvaluation
  n presences    : 23
  n absences     : 200
  AUC            : 0.5573913
  cor            : 0.114982
  TPR+TNR threshold: 0.038

> ps <- predict(predictors, svm, ext=ext)
> par(mfrow=c(1,2))
> plot(ps, main='Support Vector Machine')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> threshold <- e@t[which.max(e@TPR + e@TNR)]
> plot(ps > threshold, main='presence/absence')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> points(pres_train, pch='+')
> points(backg_train, pch='-', cex=0.25)
```



Chapter 12

Spatial-only models

The 'spatial-only models' described here are not commonly used in species distribution modeling. They are an attempt to formalize methods to draw 'expert range maps'. We are exploring their use in comparing and contrasting them with the other approaches (Bahn and McGill, 2007); in model evaluation as as null-models (Hijmans 2011); to sample background points; and generally to help think about the duality between geographic and environmental space (Colwel and Rangel, 2009).

12.1 Geographic Distance

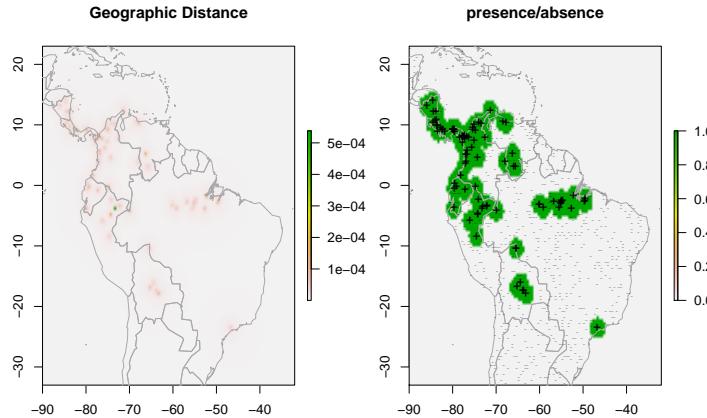
Simple model based on the assumption that the closer to a know presence point, the more likely it is to find the species.

```
> distm <- geoDist(pres_train, lonlat=TRUE)
> ds <- predict(predictors, distm, ext=ext)
> e <- evaluate(dstm, p=pres_test, a=backg_test, tr=quantile(ds, c(1:50/50)))
> e

  class           : ModelEvaluation
  n presences     : 23
  n absences      : 200
  AUC              : 0.8867391
  cor              : 0.3713449
  TPR+TNR threshold: 5.217312e-06

> par(mfrow=c(1,2))
> plot(ds, main='Geographic Distance')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> threshold <- e@t[which.max(e@TPR + e@TNR)]
> plot(ds > threshold, main='presence/absence')
> plot(wrld_simpl, add=TRUE, border='dark grey')
```

```
> points(pres_train, pch='+')
> points(backg_train, pch='-', cex=0.25)
```

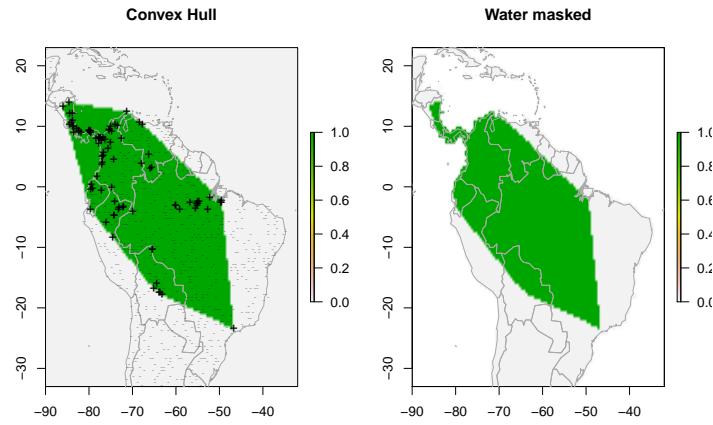


12.2 Convex hulls

```
> hull <- convHull(pres_train, lonlat=TRUE)
> e <- evaluate(hull, p=pres_test, a=backg_test)
> e

  class           : ModelEvaluation
  n presences    : 23
  n absences     : 200
  AUC            : 0.7147826
  cor            : 0.2614251
  TPR+TNR threshold: 0.02

> h <- predict(predictors, hull, ext=ext)
> par(mfrow=c(1,2))
> plot(h, main='Convex Hull')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> points(pres_train, pch='+')
> points(backg_train, pch='-', cex=0.25)
> h <- mask(h, crop(predictors[[1]], ext))
> plot(h, main='Water masked')
> plot(wrld_simpl, add=TRUE, border='dark grey')
>
```



12.3 Circles

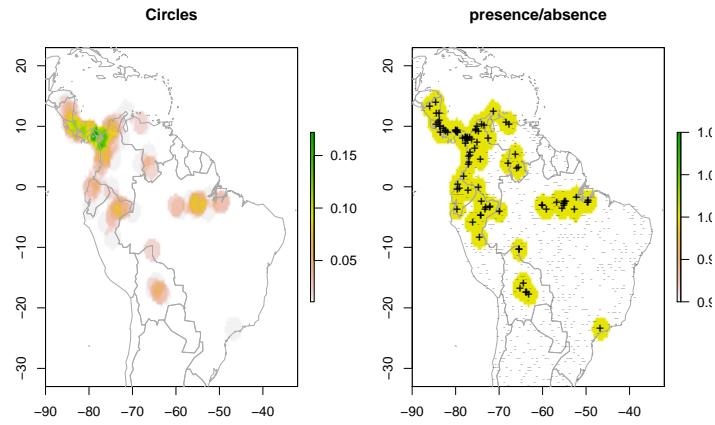
```

> circ <- circles(pres_train, lonlat=TRUE)
> pc <- predict(predictors, circ, ext=ext)
> e <- evaluate(circ, p=pres_test, a=backg_test, tr=quantile(ds, c(1:50/50)))
> e

  class          : ModelEvaluation
  n presences    : 23
  n absences     : 200
  AUC            : 0.8736957
  cor            : 0.5530658
  TPR+TNR threshold: 3.692322e-07

> par(mfrow=c(1,2))
> plot(pc, main='Circles')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> threshold <- e@t[which.max(e@TPR + e@TNR)]
> plot(pc > threshold, main='presence/absence')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> points(pres_train, pch='+')
> points(backg_train, pch='-', cex=0.25)

```



12.4 Presence/absence

Spatial-only models for presence/absence data are also available. See functions `geoIDW`, `voronoi`, and general geostatistical methods such as indicator kriging (available in the `gstat` package).

Part IV

Additional topics

Chapter 13

Model transfer in space and time

13.1 Transfer in space

13.2 Transfer in time: climate change

Chapter 14

To do list

There are many sophistications that are required by the realities that (a) there are multiple end uses of models, and (b) there are numerous issues with ecological data that mean that the assumptions of the standard methods don't hold. Could include:

- spatial autocorrelation
- imperfect detection
- mixed models (for nested data, hierarchical stuff)
- Bayesian methods
- resource selection functions
- measures of niche overlap, linked to thoughts about niche conservatism
- link to phylogeography
- advanced topics on predictors including remote sensing variables, thinking about extremes
 - species that don't "mix" with grids – freshwater systems etc..
 - quantile regression
 - model selection literature (AIC etc etc)
 - multispecies modeling: Mars, gdm
 - SDMTools
 - Model averaging
 - See the BIOMOD for on multi-model inference.
 - Dealing with uncertainty

how to target the "important" uncertainties (will vary with the application), an example of partial plots with standard errors, and predicting the upper and lower bounds; the idea of testing sensitivity to decisions made in the modeling process (including dropping out points etc etc).

Part V

References

- Austin MP, 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157:101-18.
- Austin, M.P., and T.M. Smith, 1989. A new model for the continuum concept. *Vegetatio* 83:35-47.
- Bahn, V. and B.J. McGill, 2007. Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography* 16: 733–742.
- Breiman, L., 2001a. Statistical Modeling: The Two Cultures. *Statistical Science* 16: 199-215.
- Breiman, L., 2001b. Random Forests. *Machine Learning* 45: 5-32.
- Breiman, L., J. Friedman, C.J. Stone and R.A. Olshen, 1984. *Classification and Regression Trees*. Chapman & Hall/CRC.
- Carpenter G., A.N. Gillison and J. Winter, 1993. Domain: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity Conservation* 2:667-680.
- Colwell R.K. and T.F. Rangel, 2009. Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences* 106:19651-19658.
- Dormann C.F., Elith J., Bacher S., Buchmann C., Carl G., Carré G., Diekötter T., García Marquéz J., Gruber B., Lafourcade B., Leitão P.J., Münkemüller T., McClean C., Osborne P., Reineking B., Schröder B., Skidmore A.K., Zurell D., Lautenbach S. (2011 in review) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance.
- Elith, J. and J.R. Leathwick, 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677-697. <http://dx.doi.org/10.1146/annurev.ecolsys.110308.120159>
- Elith, J., C.H. Graham, R.P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R.J. Hijmans, F. Huettmann, J. Leathwick, A. Lehmann, J. Li, L.G. Lohmann, B. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. Overton, A.T. Peterson, S. Phillips, K. Richardson, R. Scachetti-Pereira, R. Schapire, J. Soberon, S. Williams, M. Wisz and N. Zimmerman, 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129-151. <http://dx.doi.org/10.1111/j.2006.0906-7590.04596.x>
- Elith, J., S.J. Phillips, T. Hastie, M. Dudik, Y.E. Chee, C.J. Yates, 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17:43-57. <http://dx.doi.org/10.1111/j.1472-4642.2010.00725.x>
- Elith, J., J.R. Leathwick and T. Hastie, 2009. A working guide to boosted regression trees. *Journal of Animal Ecology* 77: 802-81
- Ferrier, S. and A. Guisan, 2006. Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology* 43:393-40
- Fielding, A.H. and J.F. Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38-49

- Franklin, J. 2009. Mapping Species Distributions: Spatial Inference and Prediction. Cambridge University Press, Cambridge, UK.
- Friedman, J.H., 2001. Greedy function approximation: a gradient boosting machine. *The Annals of Statistics* 29: 1189-1232. <http://www-stat.stanford.edu/~jhf/ftp/trebst.pdf>
- Graham, C.H., J. Elith, R.J. Hijmans, A. Guisan, A.T. Peterson, B.A. Loiselle and the NCEAS Predicting Species Distributions Working Group, 2007. The influence of spatial errors in species occurrence data used in distribution models. *Journal of Applied Ecology* 45: 239-247
- Guisan, A., Thomas C. Edwards, Jr, and Trevor Hastie, 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling* 157: 89-100.
- Guo, Q., M. Kelly, and C. Graham, 2005. Support vector machines for predicting distribution of Sudden Oak Death in California. *Ecological Modeling* 182:75-90
- Guralnick, R.P., J. Wieczorek, R. Beaman, R.J. Hijmans and the BioGeomancer Working Group, 2006. BioGeomancer: Automated georeferencing to map the world's biodiversity data. *PLoS Biology* 4: 1908-1909. <http://dx.doi.org/10.1371/journal.pbio.0040381>
- Hastie, T.J. and R.J. Tibshirani, 1990. Generalized Additive Models. Chapman & Hall/CRC.
- Hastie, T., R. Tibshirani and J. Friedman, 2009. The Elements of Statistical Learning: Data Mining, Inference, and Prediction (Second Edition) <http://www-stat.stanford.edu/~tibs/ElemStatLearn/>
- Hijmans, R.J., 2011 (in revision). Validating species distribution models: removing spatial sorting bias and calibration with a null-model. *Ecology*.
- Hijmans R.J., and C.H. Graham, 2006. Testing the ability of climate envelope models to predict the effect of climate change on species distributions. *Global change biology* 12: 2272-2281. <http://dx.doi.org/10.1111/j.1365-2486.2006.01256.x>
- Hijmans, R.J., M. Schreuder, J. de la Cruz and L. Guarino, 1999. Using GIS to check coordinates of germplasm accessions. *Genetic Resources and Crop Evolution* 46: 291-296.
- Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones and A. Jarvis, 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965-1978. <http://dx.doi.org/10.1002/joc.1276>
- Jiménez-Valverde, A. 2011. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography* (on-line early): DOI: 10.1111/j.1466-8238.2011.00683.
- Karatzoglou, A., D. Meyer and K. Hornik, 2006. Support Vector Machines in R . *Journal of statistical software* 15(9). <http://www.jstatsoft.org/v15/i09/>
- Kéry M., Gardner B., Monnerat C., 2010. Predicting species distributions from checklist data using site-occupancy models. *J. Biogeogr.* 37:1851–1862

- Lehmann, A., J. McC. Overton and J.R. Leathwick, 2002. GRASP: Generalized Regression Analysis and Spatial Predictions. *Ecological Modelling* 157: 189-207.
- Leathwick J., Whitehead D., 2001. Soil and atmospheric water deficits and the distribution of New Zealand's indigenous tree species. *Functional Ecology* 15:233-242.
- Liu C., Berry P.M., Dawson T.P., Pearson R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28:385-393.
- Liu C., White M., Newell G., 2011. Measuring and comparing the accuracy of species distribution models with presence-absence data. *Ecography* 34:232-243.
- Lobo, J.M. 2008. More complex distribution models or more representative data? *Biodiversity Informatics* 5: 14-19.
- Lobo, J.M., A. Jiménez-Valverde and R. Real, 2007. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17: 145-151.
- Mahalanobis, P.C., 1936. On the generalised distance in statistics. *Proceedings of the National Institute of Sciences of India* 2: 49-55.
- Mellert K.H., Fensterer V., Küchenhoff H., Reger B., Kölling C., Klemmt H.J., Ewald J. (2011 in press) Hypothesis-driven species distribution models for tree species in the Bavarian Alps. *J. Veg. Sci.*
- Nix, H.A., 1986. A biogeographic analysis of Australian elapid snakes. In: *Atlas of Elapid Snakes of Australia*. (Ed.) R. Longmore, pp. 4-15. Australian Flora and Fauna Series Number 7. Australian Government Publishing Service: Canberra.
- Olson, D.M., E. Dinerstein, E.D. Wikramanayake, N.D. Burgess, G.V.N. Powell, E.C. Underwood, J.A. D'amico, I. Itoua, H.E. Strand, J.C. Morrison, C.J. Loucks, T.F. Allnutt, T.H. Ricketts, Y. Kura, J.F. Lamoreux, W.W. Wettengel, P. Hedao, and K.R. Kassem. 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth. *BioScience* 51:933-938
- Phillips S.J., Elith J. (2011 in press) Logistic methods for resource selection functions and presence-only species distribution models, AAAI (Association for the Advancement of Artificial Intelligence), San Francisco, USA.
- Phillips, S.J., R.P. Anderson, R.E. Schapire, 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231-259.
- Phillips, S. J., M. Dudik, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick, and S. Ferrier. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19:181-197.
- Potts J., Elith J. (2006) Comparing species abundance models. *Ecol. Model.* 199:153-163.
- Vapnik, V., 1998. Statistical Learning Theory. Wiley, New York.
- VanDerWal J., Shoo L.P., Graham C., Williams S.E., 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecol. Model.* 220:589-594.

- Ward G., Hastie T., Barry S.C., Elith J., Leathwick J.R., 2009. Presence-only data and the EM algorithm. *Biometrics* 65:554-563.
- Wieczorek, J., Q. Guo and R.J. Hijmans, 2004. The point-radius method for georeferencing point localities and calculating associated uncertainty. *International Journal of Geographic Information Science* 18: 745-767.
- Wisz, M.S., R.J. Hijmans, J. Li, A.T. Peterson, C.H. Graham, A. Guisan, and the NCEAS Predicting Species Distributions Working Group, 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14: 763-773.
- Wood, S., 2006. Generalized Additive Models: An Introduction with R . Chapman & Hall/CRC.