Species distribution modeling with ${\sf R}$

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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 of a species (or other phenomenon) are compiled. (2) values of environmental predictor variables (such as climate) at these locations are extracted from spatial databases (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 across an area of interest (and perhaps for a future or past 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), or the somewhat more theoretical book by Peterson et al. (2011), or the recent review article 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) and Peterson et al. (2011) for a discussion. 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 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 en-

vironment. 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

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:/temp/RtmpwtZe30/Rinst108c31a127e6/dismo/ex/bradypus.csv"
> # let's read it
> bradypus <- read.table(file, header=TRUE,</pre>
                                                sep=',')
> # let's inspect the values of the file
> # first rows
> head(bradypus)
                            lon
                                     lat.
              species
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]</pre>
> 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 down-loading 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)

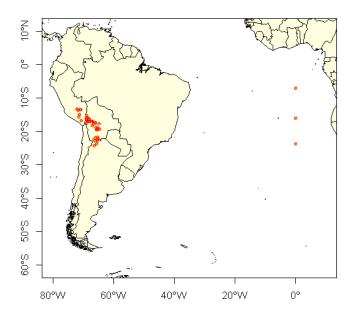
Many species occurrence records may not have geographic coordinates. Out of the 699 records that GBIF returned (March 2010), there were only 54 records with coordinates.

```
> # load the saved acaule data
> data(acaule)
> # how many rows and colums?
> dim(acaule)
[1] 699 23
> #select the records that have longitude and latitude data
> colnames(acaule)
 [1] "species"
                              "continent"
 [3] "country"
                              "adm1"
 [5] "adm2"
                              "locality"
 [7] "lat"
                              "lon"
                              "alt"
 [9] "coordUncertaintyM"
[11] "institution"
                              "collection"
[13] "catalogNumber"
                              "basisOfRecord"
[15] "collector"
                              "earliestDateCollected"
[17] "latestDateCollected"
                              "gbifNotes"
[19] "downloadDate"
                              "maxElevationM"
[21] "minElevationM"
                              "maxDepthM"
[23] "minDepthM"
> acgeo <- subset(acaule, !is.na(lon) & !is.na(lat))</pre>
> dim(acgeo)
[1] 54 23
> # show some values
> acgeo[1:4, c(1:5,7:10)]
                  species continent
                                       country
                                                  adm1
           Solanum acaule
                                                  <NA>
13
                                <NA>
                                           BOL
426 Solanum acaule Bitter
                             America Argentina Jujuy
428 Solanum acaule Bitter
                             America
                                       Bolivia La Paz
429 Solanum acaule Bitter
                             America
                                       Bolivia La Paz
       adm2
                 lat
                        lon coordUncertaintyM alt
13
       <NA> -18.8167 -65.90
                                            NA 3960
426
            -22.9000 -66.24
                                            NA 4050
428 Pacajes -17.4200 -68.85
                                            NA 3811
```

NA 3800

429 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.



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
544 Solanum acaule Bitter subsp. acaule
                                              <NA>
                                                        BOL
551 Solanum acaule Bitter subsp. acaule
                                               <NA>
                                                        BOL
567 Solanum acaule Bitter subsp. acaule
                                              <NA>
                                                        PER
638 Solanum acaule Bitter subsp. acaule
                                              <NA>
                                                        PER
640 Solanum acaule Bitter subsp. acaule
                                               <NA>
                                                        ARG
641 Solanum acaule Bitter subsp. acaule
                                               <NA>
                                                        ARG
    adm1 adm2
544 <NA> <NA>
551 <NA> <NA>
567 <NA> <NA>
638 <NA> <NA>
640 <NA> <NA>
641 <NA> <NA>
                                             locality
544
                                                Llave
551
                                                Llave
567
                       km 205 between Puno and Cuzco
638
                       km 205 between Puno and Cuzco
640 between Quelbrada del Chorro and Laguna Colorada
641 between Quelbrada del Chorro and Laguna Colorada
           lat lon coordUncertaintyM alt institution
                                   NA 3900
544 -16.083333
                                                   IPK
551 -16.083333
                 0
                                   NA 3900
                                                   IPK
567 -6.983333
                                   NA 4250
                                                   IPK
```

638	-6.983333	0	NA 4250	IPK
640	-23.716667	0	NA 3400	IPK
641	-23.716667	0	NA 3400	IPK
	collection	catalogNumber		
544	WKS 30050	304711		
551	GB	WKS 30050		
567	WKS 30048	304709		
638	GB	WKS 30048		
640	WKS 30027	304688		
641	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 send 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 for the first 10 columns)?
> dups <- duplicated(lonzero[, 1:10])</pre>
> # remove duplicates
> lonzero <- lonzero[dups, ]</pre>
> lonzero[,1:13]
                                 species continent country
551 Solanum acaule Bitter subsp. acaule
                                               <NA>
                                                        BOL
638 Solanum acaule Bitter subsp. acaule
                                               <NA>
                                                        PER
641 Solanum acaule Bitter subsp. acaule
                                               <NA>
                                                        ARG
    adm1 adm2
551 <NA> <NA>
638 <NA> <NA>
641 <NA> <NA>
                                              locality
551
                                                 Llave
638
                        km 205 between Puno and Cuzco
641 between Quelbrada del Chorro and Laguna Colorada
           lat lon coordUncertaintyM alt institution
551 -16.083333
                                   NA 3900
                                                    IPK
638 -6.983333
                 0
                                   NA 4250
                                                    IPK
641 -23.716667
                 0
                                   NA 3400
                                                    IPK
    collection catalogNumber
```

```
551 GB WKS 30050
638 GB WKS 30048
641 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, ]</pre>
```

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 wich 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"
                             "ISO3"
                                          "UN"
                 "IS02"
 [5] "NAME"
                             "POP2005"
                                          "REGION"
                 "AREA"
 [9] "SUBREGION" "LON"
                             "LAT"
> head(wrld_simpl@data)
    FIPS ISO2 ISO3 UN
                                             AREA POP2005
                                     NAME
ATG
           AG ATG 28 Antigua and Barbuda
                                               44
      AC
                                                     83039
DZA
      AG
           DZ DZA 12
                                  Algeria 238174 32854159
AZE
      AJ
           AZ AZE 31
                               Azerbaijan
                                             8260 8352021
ALB
      ΑL
           AL ALB 8
                                  Albania
                                             2740 3153731
ARM
      MA
           AM ARM 51
                                  Armenia
                                             2820 3017661
AGO
      ΑO
           AO AGO 24
                                   Angola 124670 16095214
   REGION SUBREGION
                         LON
                                 LAT
ATG
       19
                  29 -61.783 17.078
DZA
         2
                  15
                      2.632
                              28.163
AZE
       142
                 145 47.395 40.430
ALB
       150
                  39 20.068 41.143
ARM
       142
                 145 44.563 40.534
AGO
                  17 17.544 -12.296
         2
> # We clearly need the variable 'NAME' in the data.frame
> # (stored in the 'data' slot) of wrld_simpl
> cntr <- as.character(wrld_simpl@data$NAME[ov])</pre>
> # which points (identified by their record numbers) do not match
> # any country (i.e. are in an ocean)
> i <- which(is.na(cntr))</pre>
> i
[1] 43 44 45 46 47 48
> # these are the same records, with longitude=0, as identified above:
> acgeo@data[i,'catalogNumber']
                                         "WKS 30048"
[1] "304711"
                "WKS 30050" "304709"
[5] "304688"
                "WKS 30027"
> # which points has coordinates that are in a different country than
> # listed in the 'country' field of the gbif record
> j <- which(cntr != acgeo@data$country)</pre>
> 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,]

```
[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, ]</pre>
```

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.

```
42
         <NA>
                  BOL <NA> <NA>
81
         <NA>
                  ARG <NA> <NA>
                          locality lat lon coordUncertaintyM
30\ km\ 205\ between\ Puno\ and\ Cuzco
                                     NA
                                         NA
                                                             NA
42
                             Llave
                                     NA
                                         NA
                                                             NA
81
                           da Pena
                                     NA
                                         NA
                                                             NA
    alt institution collection catalogNumber
30 4250
                             DEU
                                      WKS 30048
              DEU159
42 3900
              DEU159
                             DEU
                                      WKS 30050
81
     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.

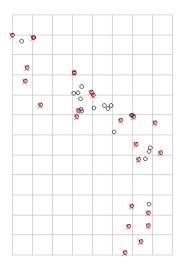
Here is an example for one of the records with longitude = 0, using Google's geocoding service. We put the function into a 'try' function, to assure elegant error handling if the computer is not connected to the Internet.

```
> args(biogeomancer)
function (country = "", adm1 = "", adm2 = "", locality = "",
    singleRecord = TRUE, progress = "text")
NULL
> # the first locality:
> loc <- paste(lonzero$locality[1], ", Peru")</pre>
> loc
[1] "Llave , Peru"
> b <- try( geocode(loc, oneRecord=T) )</pre>
> b
           lon
                    lat
                           lonmin
                                      lonmax
                                               latmin
  1 -95.88432 18.7193 -97.46226 -93.08245 16.74949
    latmax
                location
1 20.53722 Llave , Peru
```

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 (extend) the extent of the RasterLayer a little
> r <- extend(r, extent(r)+1)
> # get the cell number for each point
> cell <- cellFromXY(r, acgeo)</pre>
> dup <- duplicated(cell)</pre>
> # select the records that are not duplicated. A random selection
> # within duplicates might be better (but more elaborate).
> acsel <- acgeo[!dup, ]</pre>
> # display the results
> p <- rasterToPolygons(r)
> plot(p, border='gray')
> points(acgeo)
> # selected points in red
> points(acsel, cex=1, col='red', pch='x')
```



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/latitute coordinate reference system, function randomPoints selects cells according to cell area, which varies by latitude (as in Elith et al., 2011)

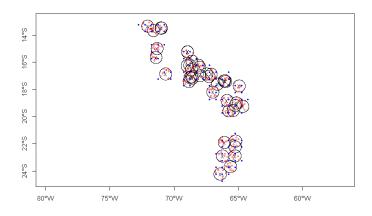
```
> files <- list.files(path=paste(system.file(package="dismo"), '/ex',
                          sep=''), pattern='grd', full.names=TRUE )
> mask <- raster(files[[1]])</pre>
> # select 500 random points
> # set seed to assure that the examples will always
> # have the same random sample.
> bg <- randomPoints(mask, 500 )</pre>
> # 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)</pre>
> 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 within 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')</pre>
> plot(x@polygons, axes=T)
> points(pts, pch='x')
> # sample randomly from all circles
> samp1 <- spsample(x@polygons, 250, type='random', iter=25)</pre>
> points(samp1, cex=0.5, col='red')
> # get unique cells
> cells <- cellFromXY(mask, samp1)</pre>
> length(cells)
[1] 250
> cells <- unique(cells)</pre>
> length(cells)
[1] 92
> xy <- xyFromCell(mask, cells)
> points(xy, cex=0.75, pch=20, col='blue')
```

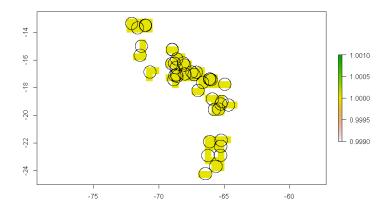


Note that the blue points are not all within the circles, as they now represent the centers of the selected cells from mask. We could choose to select only those cells that have theirs centers within the circles, using the overlay function.

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

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

```
> # extract cell numbers for the circles
> v <- extract(mask, x@polygons, 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
[10] 21507 21508 19822 19823 20008 20946 20947 22067 22253
[19] 21132 23183 23184 23925 23926 20009 20010 21510 21511
[28] 21134 21135 21320 20572 20573 20382 20568 21692 21693
[37] 21322 21323 21133 21509 23555 23741 23742 21318 20759
[46] 20760 20945 20944 22069 22070 21882 22068 22998 22999
[55] 19824 19825 20011 22254 23370 23556 21319 20753 20754
[64] 21127 21128 21313 22996 22997 23182
> # to display the results
> m <- mask
> m[] <- NA
> m[v] <- 1
> plot(m, ext=extent(x@polygons)+1)
> plot(x@polygons, add=T)
```



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, extend, 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.

[4] "c:/temp/RtmpwtZe30/Rinst108c31a127e6/dismo/ex/bio17.grd"

- [5] "c:/temp/RtmpwtZe30/Rinst108c31a127e6/dismo/ex/bio5.grd"
- [6] "c:/temp/RtmpwtZe30/Rinst108c31a127e6/dismo/ex/bio6.grd"
- [7] "c:/temp/RtmpwtZe30/Rinst108c31a127e6/dismo/ex/bio7.grd"
- [8] "c:/temp/RtmpwtZe30/Rinst108c31a127e6/dismo/ex/bio8.grd"
- [9] "c:/temp/RtmpwtZe30/Rinst108c31a127e6/dismo/ex/biome.grd"

> predictors <- stack(files)</pre>

> predictors

class : RasterStack

dimensions : 192, 186, 35712, 9 (nrow, ncol, ncell, nlayers)

resolution : 0.5, 0.5 (x, y)

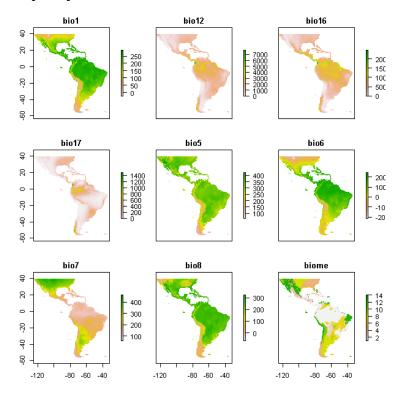
extent : -125, -32, -56, 40 (xmin, xmax, ymin, ymax)

coord. ref. : +proj=longlat +datum=WGS84 +ellps=WGS84 +towgs84=0,0,0 names : bio1, bio12, bio16, bio17, bio5, bio6, bio7, bio8, biome min values : -23, 0, 0, 0, 61, -212, 60, -66, 1 max values : 289, 7682, 2458, 1496, 422, 242, 461, 323, 14

> names(predictors)

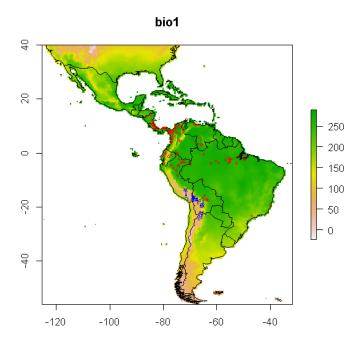
- [1] "bio1" "bio12" "bio16" "bio17" "bio5" "bio6" "bio7"
- [8] "bio8" "biome"

> 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(acgeo, 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)</pre>
> absvals <- extract(predictors, backgr)
> pb <- c(rep(1, nrow(presvals)), rep(0, nrow(absvals)))</pre>
  sdmdata <- data.frame(cbind(pb, rbind(presvals, absvals)))</pre>
> sdmdata[,'biome'] = as.factor(sdmdata[,'biome'])
> head(sdmdata)
  pb bio1 bio12 bio16 bio17 bio5 bio6 bio7 bio8 biome
      263
            1639
                    724
                            62
                                338
                                      191
                                           147
                                                 261
2
   1
      263
            1639
                    724
                                338
                                      191
                                           147
                                                 261
                                                          1
                            62
3
      253
            3624
                   1547
                           373
                                329
                                      150
                                           179
                                                 271
                                                          1
4
      243
            1693
                    775
                           186
                                318
                                                 264
   1
                                      150
                                           168
                                                          1
5
      243
            1693
                    775
                           186
                                318
                                      150
                                           168
                                                 264
                                                          1
6
      252
            2501
                   1081
                           280
                                326
                                                 270
                                      154
                                           172
                                                          1
> tail(sdmdata)
    pb bio1 bio12 bio16 bio17 bio5 bio6 bio7 bio8 biome
611
     0
        256
              1208
                      503
                             144
                                  315
                                        200
                                              115
                                                   255
     0
              2346
                                                   259
                                                            7
612
         269
                      977
                             115
                                   348
                                        217
                                              130
613
     0
         103
                29
                                  188
                                              172
                                                           12
                       17
                               1
                                         15
                                                    75
     0
         241
              1482
                     1031
                              22
                                   339
                                        130
                                              209
                                                   254
                                                            3
615
     0
         229
              2943
                     1194
                             342
                                   294
                                        169
                                              125
                                                   224
                                                            1
     0
         261
              2796
                      964
                             322
                                   319
                                        206
                                              113
                                                   258
```

> summary(sdmdata)

```
bio1
                                        bio12
      pb
       :0.0000
Min.
                          : 5.0
                                   Min.
                                           :
                                                1.0
                  Min.
1st Qu.:0.0000
                  1st Qu.:178.0
                                    1st Qu.: 739.8
Median :0.0000
                  Median :241.5
                                   Median: 1489.0
Mean
       :0.1883
                  Mean
                          :212.2
                                   Mean
                                           :1614.6
3rd Qu.:0.0000
                  3rd Qu.:260.0
                                    3rd Qu.:2259.8
Max.
       :1.0000
                  Max.
                          :286.0
                                   Max.
                                           :7682.0
    bio16
                      bio17
                                          bio5
Min.
            1.0
                              0.0
                                            : 75.0
                  Min.
                                     Min.
1st Qu.: 330.8
                  1st Qu.:
                             36.0
                                     1st Qu.:300.0
Median: 626.5
                  Median : 106.5
                                     Median :318.0
Mean
       : 654.9
                          : 166.2
                                     Mean
                                            :306.7
                  Mean
3rd Qu.: 916.2
                  3rd Qu.: 232.0
                                     3rd Qu.:332.0
Max.
       :2458.0
                  Max.
                          :1496.0
                                     Max.
                                            :405.0
     bio6
                         bio7
                                          bio8
Min.
       :-177.00
                   Min.
                           : 60.0
                                     Min.
                                            : 3.0
1st Qu.: 48.75
                   1st Qu.:117.0
                                     1st Qu.:213.0
Median: 157.00
                   Median :158.5
                                     Median :250.0
       : 118.06
                           :188.6
                                             :224.2
Mean
                   Mean
                                     Mean
3rd Qu.: 200.00
                   3rd Qu.:235.0
                                     3rd Qu.:262.0
                           :449.0
Max.
       : 242.00
                                             :319.0
                   Max.
                                     Max.
    biome
1
       :281
13
       : 77
7
       : 60
8
       : 53
2
       : 42
(Other):102
NA's
       : 1
```

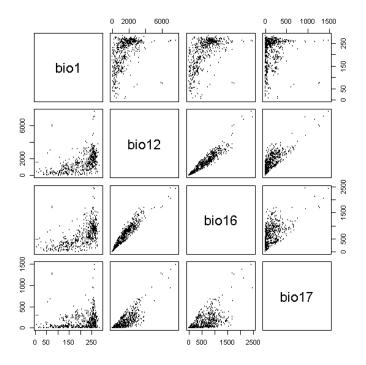
There are alternative approaches possible here. For example, one could extract multiple points in a radius as a potential means for dealing with mismatch between location accuracy and grid cell size. If one would make 10 datasets that represent 10 equally valid "samples" of the environment in that radius,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

To visually investigate colinearity 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 colinearity.

```
> # 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

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: $y \sim x1 + x2 + x3$, i.e. y is a function of x1, x2, and x3. Another example is $y \sim ...$, 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)
glm(formula = pb ~ bio1 + bio5 + bio12, data = sdmdata)
Deviance Residuals:
         10
    Min
                     Median
                                   3Q
                                           Max
-0.82681 -0.24010 -0.09947
                              0.07679
                                        0.86667
Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) 1.104e-01 1.021e-01 1.082 0.27959
            1.682e-03 3.840e-04 4.381 1.39e-05 ***
bio1
bio5
           -1.454e-03 4.538e-04 -3.205 0.00142 **
bio12
            1.034e-04 1.564e-05 6.616 8.09e-11 ***
```

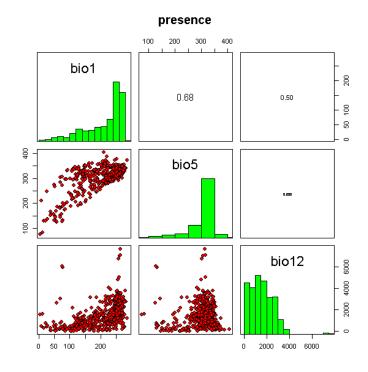
```
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Dispersion parameter for gaussian family taken to be 0.1233405)
   Null deviance: 94.156 on 615 degrees of freedom
Residual deviance: 75.484 on 612 degrees of freedom
AIC: 464.95
Number of Fisher Scoring iterations: 2
> m2 = glm(pb ~ ., data=sdmdata)
> m2
Call: glm(formula = pb ~ ., data = sdmdata)
Coefficients:
(Intercept)
                    bio1
                                bio12
                                             bio16
  3.026e-01
              -1.889e-03
                            3.147e-04
                                         -4.269e-04
      bio17
                    bio5
                                 bio6
                                               bio7
 -5.908e-04
              -2.029e-04
                            1.619e-03
                                         9.427e-05
                               biome3
                                            biome4
       bio8
                  biome2
  3.565e-04
             -1.173e-01
                           -1.908e-01
                                        -1.647e-01
     biome5
                  biome7
                               biome8
                                            biome9
 -9.556e-02
              -2.441e-01
                           -9.018e-02
                                         2.952e-02
    biome10
                 biome11
                              biome12
                                           biome13
 -1.145e-01
              -3.197e-01
                           -1.281e-01
                                        -5.218e-02
    biome14
 -2.195e-01
Degrees of Freedom: 614 Total (i.e. Null); 594 Residual
  (1 observation deleted due to missingness)
Null Deviance:
                          94.12
Residual Deviance: 70.15
                                 AIC: 454.1
  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

> pairs(bc)

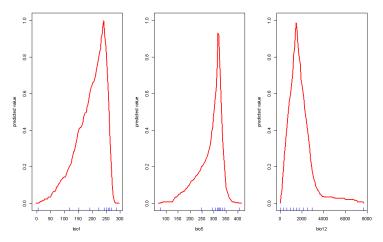


Model prediction

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).

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.

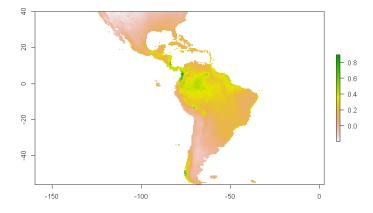
```
> response(bc)
```



In most cases, hower, the purpose is SDM is to creat 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.

> names(predictors)

- [1] "bio1" "bio12" "bio16" "bio17" "bio5" "bio6" "bio7"
- [8] "bio8" "biome"
- > p <- predict(predictors, m1)</pre>
- > plot(p)



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 is 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?
- \bullet 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)

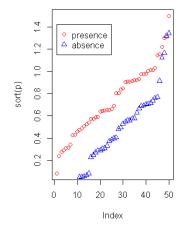
Most modelers rely on cross-validation. This consists of creating a model with one 'training' data set, and testing it with another data set of known occurrences. Typically, training and testing data are created through random sampling (without replacement) from a single data set. Only in a few cases,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

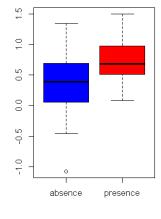
Different measures can be used to evaluate the quality of a prediction (Fielding and Bell, 1997, Liu et al., 2011; and Potts and Elith (2006) for abundance data), perhaps depending on the goal of the study. Many measures for evaluating models based on presence-absence or presence-only data are 'threshold 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.

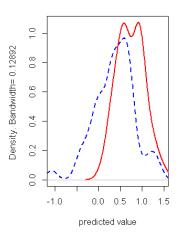


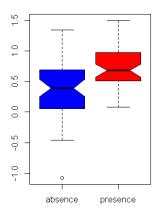


We created two variables with random normally distributed values, but with different mean and standard deviation. The two variables clearly have different distributions, and the values for 'presence' tend to be higher than for 'absence'. Here is how you can compute the correlation coefficient and the AUC:

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
              : ModelEvaluation
class
              : 50
n presences
             : 50
n absences
AUC
              : 0.7428
cor
              : 0.4259716
max TPR+TNR at : 0.4288114
> 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.

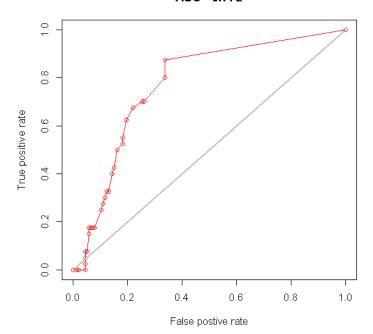
```
> rand <- round(0.75 * runif(nrow(sdmdata)))
> traindata <- sdmdata[rand==0,]
> traindata <- traindata[traindata[,1] == 1, 2:9]
> testdata <- sdmdata[rand==1,]
> bc <- bioclim(traindata)
> e <- evaluate(testdata[testdata==1,], testdata[testdata==0,], bc)
> e
```

class : ModelEvaluation
n presences : 30

n absences : 168
AUC : 0.8202381
cor : 0.3169584
max TPR+TNR at : 0.03478372

> plot(e, 'ROC')

AUC= 0.772



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 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]</pre>
```

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] 4 2 3 1 5 3 2 5 5 1
> unique(group)
[1] 4 2 3 1 5
```

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)
+ }</pre>
```

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 uses as a threshold for setting cells to presence or absence).

```
> auc <- sapply( e, function(x){slot(x, 'auc')} )
> auc

[1] 0.8070435 0.8378696 0.7332500 0.7101304 0.7925652
> mean(auc)

[1] 0.7761717
> sapply( e, function(x){ x@t[which.max(x@TPR + x@TNR)] } )

[1] 0.03215806 0.08592151 0.01076957 0.01065269 0.06441613
> # equivalent
> # sapply( e, function(x){ x@t[which.max(x@TPR + x@TNR)] } )
```

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 (2012) suggests that one could remove "spatial sorting bias" (the difference between the distance from testing-presence to training-presence and the distance from testing-absence to training-presence 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]
```

[1] 0.1040448

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] 0.9987177

Spatial sorting bias is much reduced now; notice how the AUC dropped!

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

class : ModelEvaluation

n presences : 29 n absences : 125 AUC : 0.6917241 cor : 0.2043

max TPR+TNR at : 0.03438276

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

class : ModelEvaluation

n presences : 17 n absences : 17

AUC : 0.3823529 cor : -0.1501684 max TPR+TNR at : 0.2642678

$\begin{array}{c} {\rm Part~III} \\ {\rm Modeling~methods} \end{array}$

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/backround data. An entirely different class of models consists of models that only, or primarily, use the geographic location of known occurences, and do not rely on the values of predictor variables at these locations. We refer to these models as 'geographic 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')</pre>
```

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

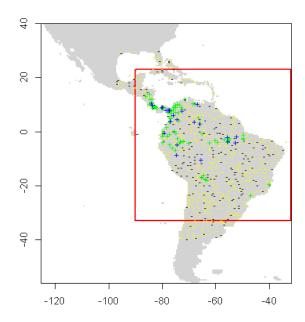
```
> group <- kfold(bradypus, 5)
> pres_train <- bradypus[group != 1, ]
> pres_test <- bradypus[group == 1, ]</pre>
```

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')
```



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.

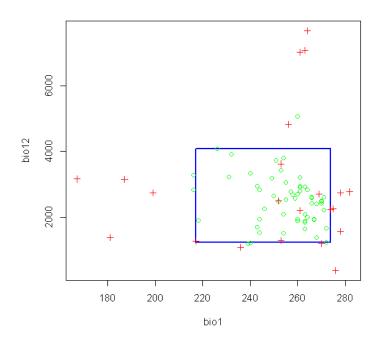
9.1 Bioclim

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

class : ModelEvaluation

n presences : 23 n absences : 200

AUC : 0.7209783 cor : 0.1589782 max TPR+TNR at : 0.04291075

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

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

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

data source : in memory
names : layer

values : 0, 0.7849462 (min, max)

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

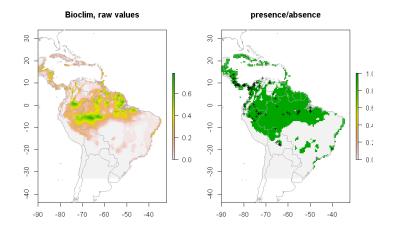
> plot(pb, main='Bioclim, raw values')

> plot(wrld_simpl, add=TRUE, border='dark grey')

> plot(pb > tr, 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').

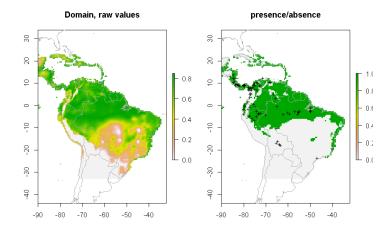
The distance between the environment at point A and those of the known occurrences for a single climate variable is calculated as the absolute difference in the values of that variable divided by the range of the variable across all known occurrence points (i.e., the distance is scaled by the range of 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)</pre>
    <- evaluate(pres_test, backg_test, dm, pred_nf)</pre>
class
                : ModelEvaluation
n presences
                : 23
n absences
                : 200
AUC
                : 0.7367391
                : 0.2445056
max TPR+TNR at : 0.6591056
> 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')
> tr <- threshold(e, 'spec_sens')</pre>
```

```
> plot(pd > tr, 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)</pre>
> e <- evaluate(pres_test, backg_test, mm, pred_nf)
> e
               : ModelEvaluation
class
n presences
               : 23
               : 200
n absences
AUC
               : 0.838587
               : 0.1310426
cor
max TPR+TNR at : -1.058378
> 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')
> tr <- threshold(e, 'spec_sens')</pre>
> plot(pm > tr, main='presence/absence')
```

- > plot(wrld_simpl, add=TRUE, border='dark grey')
 > points(pres_train, pch='+')
 - Mahalanobis distance presence/absence 30 20 T 1.0 10 - 0 9 - 0.8 - -2 0.6 -10 -10 0.4 - 0.1 -20 -20 L 0.0 -30 -30 40 -90 -80 -70 -60 -80

Regression models

The remaining models need to be fit presence textifand absence (background) data. With the exception of 'maxent', we cannot fit the model with a Raster-Stack 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)</pre>
> 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) )</pre>
> envtrain[,'biome'] = factor(envtrain[,'biome'], levels=1:14)
> head(envtrain)
  pa bio1 bio12 bio16 bio17 bio5 bio6 bio7 bio8 biome
      263
           1639
                   724
                          62
                              338
                                    191
                                         147
1
      253
   1
           3624
                  1547
                         373
                              329
                                    150
                                         179
                                              271
                                                       1
                              318
      243
           1693
                   775
                         186
                                    150
                                         168
                                              264
                                                       1
           1693
                              318
                                              264
      243
                   775
                         186
                                    150
                                         168
           2501
                         280
5
      252
                  1081
                              326
                                    154
                                         172
                                              270
                                                       1
      240 1214
                   516
                         146
                              317
                                    150
                                         168
> testpres <- data.frame( extract(predictors, pres_test) )</pre>
> 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 inter-
action 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
-1.67389 -0.47627 -0.24289 -0.04145
                                       2.73857
Coefficients:
             Estimate Std. Error z value Pr(>|z|)
(Intercept) 1.6609816 1.8232604 0.911 0.362298
bio1
            0.1007418 0.0561639 1.794 0.072859 .
            bio5
bio6
           -0.2528950
                      0.2607172 -0.970 0.332048
bio7
           -0.2418984 0.2598453 -0.931 0.351888
                      bio8
            0.0110994
            0.0020291 0.0006768
                                  2.998 0.002718 **
bio12
bio16
           -0.0018960 0.0014029 -1.351 0.176557
           -0.0052624   0.0015772   -3.336   0.000849 ***
bio17
---
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

(Dispersion parameter for binomial family taken to be 1)

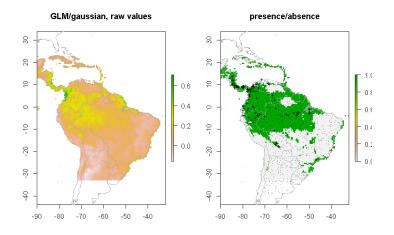
Null deviance: 596.69 on 892 degrees of freedom Residual deviance: 439.41 on 884 degrees of freedom

AIC: 457.41

Number of Fisher Scoring iterations: 8

> coef(gm1)

```
(Intercept)
                    bio1
                                 bio5
 1.660981573 \quad 0.100741766 \quad 0.143200190 \ -0.252894973
                    bio8
                                bio12
bio17
-0.005262384
> gm2 <- glm(pa ~ bio1+bio5 + bio6 + bio7 + bio8 + bio12 + bio16 + bio17,
             family = gaussian(link = "identity"), data=envtrain)
> evaluate(testpres, testbackg, gm1)
              : ModelEvaluation
class
              : 23
n presences
n absences
              : 200
AUC
              : 0.8325
              : 0.2966887
cor
max TPR+TNR at : -2.780695
> e2 <- evaluate(testpres, testbackg, gm2)
> pg <- predict(predictors, gm2, ext=ext)</pre>
> par(mfrow=c(1,2))
> plot(pg, main='GLM/gaussian, raw values')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> tr <- threshold(e2, 'spec_sens')</pre>
> plot(pg > tr, 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.

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 Artifical 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.

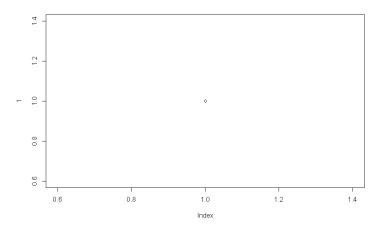
All the model fitting methods discussed here can be tuned in several ways. We do not explore that here, and only show the general approach. If you want to use one of the methods, then you should consult the R help pages (and other sources) to find out how to best implement the model fitting procedure.

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.

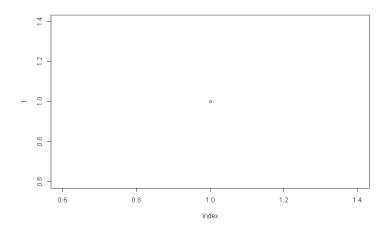
Because MaxEnt is implemented in dismo you can fit it like the profile methods (e.g. Bioclim). That is, you can provide presence points and a RasterStack. However, you can also first fit a model, like with the other methods such as glm. But in the case of MaxEnt you cannot use the formula notation.

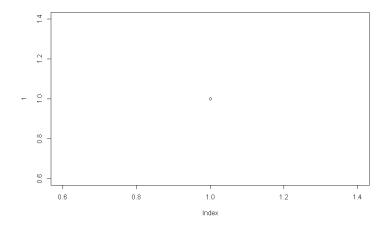
cannot run this example because maxent is not available



A response plot:

cannot run this example because maxent is not available





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 .

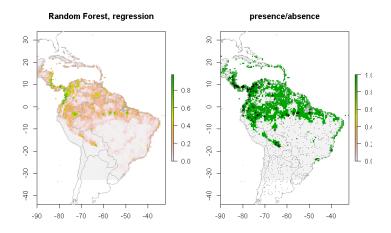
The article by Elith, Leathwick and Hastie (2009) describes the use of BRT in the context of species distribution modeling. Their article is accompanied by a number of R functions and a tutorial that have been slightly adjusted and incorporated into the 'dismo' package. These functions extend the functions 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. rfl 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)</pre>
> model <- factor(pa) ~ bio1 + bio5 + bio6 + bio7 + bio8 + bio12 + bio16 + bio17
> rf2 <- randomForest(model, data=envtrain)</pre>
> rf3 <- randomForest(envtrain[,1:8], factor(pb_train))</pre>
    = evaluate(testpres, testbackg, rf1)
> e
class
                : ModelEvaluation
                : 23
n presences
n absences
                : 200
AUC
                : 0.8722826
                : 0.4836675
max TPR+TNR at : 0.08353333
```

```
> 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')
> tr <- threshold(e, 'spec_sens')
> plot(pr > tr, 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)</pre>
```

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

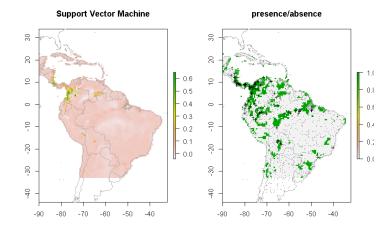
```
> e <- evaluate(testpres, testbackg, svm)
> o
```

class : ModelEvaluation

n presences : 23 n absences : 200

AUC : 0.7283696 cor : 0.3899848 max TPR+TNR at : 0.03092214

- > ps <- predict(predictors, svm, ext=ext)</pre>
- > par(mfrow=c(1,2))
- > plot(ps, main='Support Vector Machine')
- > plot(wrld_simpl, add=TRUE, border='dark grey')
- > tr <- threshold(e, 'spec_sens')
- > plot(ps > tr, main='presence/absence')
- > plot(wrld_simpl, add=TRUE, border='dark grey')
- > points(pres_train, pch='+')
- > points(backg_train, pch='-', cex=0.25)



Geographic models

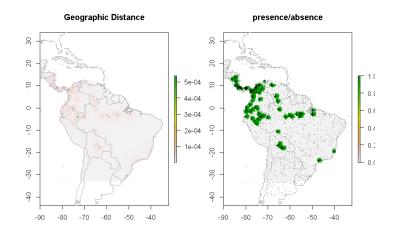
The 'geograhic models' described here are not commonly used in species distribution modeling. They use the geographic location of known occurences, and do not rely on the values of predictor variables at these locations. We are exploring their use in comparing and contrasting them with the other approaches (Bahn and McGill, 2007); in model evaluation as as null-models (Hijmans 2012); to sample background points; and generally to help think about the duality between geographic and environmental space (Colwel and Rangel, 2009). Below we show examples of these different types of models.

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.

```
> # first create a mask to predict to, and to use as a mask
> # to only predict to land areas
> seamask <- crop(predictors[[1]], ext)
> distm <- geoDist(pres_train, lonlat=TRUE)</pre>
> ds <- predict(seamask, distm, mask=TRUE)</pre>
> e <- evaluate(distm, p=pres_test, a=backg_test, tr=quantile(ds, c(1:50/50)))
> e
               : ModelEvaluation
class
               : 23
n presences
               : 200
n absences
AUC
               : 0.9286957
               : 0.429343
cor
max TPR+TNR at: 8.117192e-06
> par(mfrow=c(1,2))
> plot(ds, main='Geographic Distance')
```

```
> plot(wrld_simpl, add=TRUE, border='dark grey')
> tr <- threshold(e, 'spec_sens')
> plot(ds > tr, 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

This model draws a convex hull around all 'presence' points.

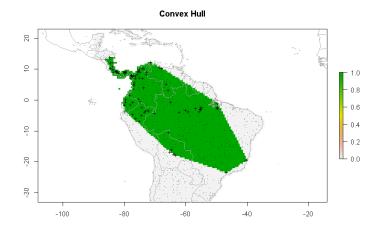
```
> hull <- convHull(pres_train, lonlat=TRUE)
> e <- evaluate(hull, p=pres_test, a=backg_test)
> e
```

class : ModelEvaluation

n presences : 23 n absences : 200 AUC : 0.7115217

cor : 0.2579133 max TPR+TNR at : 0.9999

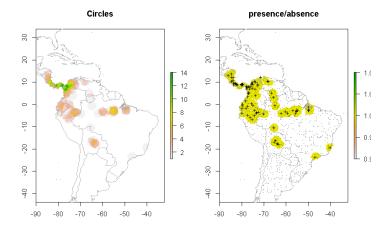
- > h <- predict(seamask, hull, mask=TRUE)</pre>
- > plot(h, main='Convex Hull')
- > plot(wrld_simpl, add=TRUE, border='dark grey')
- > points(pres_train, pch='+')
- > points(backg_train, pch='-', cex=0.25)



12.3 Circles

This model draws circles around all 'presence' points.

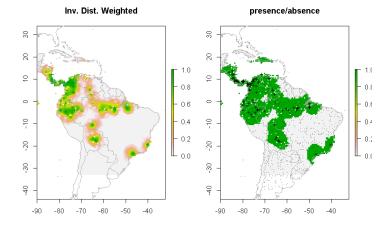
```
> circ <- circles(pres_train, lonlat=TRUE)</pre>
> pc <- predict(seamask, circ, mask=TRUE)</pre>
> e <- evaluate(circ, p=pres_test, a=backg_test, tr=quantile(ds, c(1:50/50)))
> e
               : ModelEvaluation
class
n presences
               : 23
               : 200
n absences
               : 0.8855435
AUC
               : 0.6063209
cor
max TPR+TNR at : 6.537932e-07
> par(mfrow=c(1,2))
> plot(pc, main='Circles')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> tr <- threshold(e, 'spec_sens')</pre>
> plot(pc > tr, 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/background (or absence) data are also available through functions geoIDW, voronoiHull, and general geostatistical methods such as indicator kriging (available in the gstat pacakge).

```
> idwm <- geoIDW(p=pres_train, a=data.frame(back_train))</pre>
> e <- evaluate(idwm, p=pres_test, a=backg_test, tr=quantile(ds, c(1:50/50)))
class
                : ModelEvaluation
               : 23
n presences
n absences
               : 200
AUC
               : 0.9223913
cor
               : 0.5576616
max TPR+TNR at : 6.537932e-07
> iw <- predict(seamask, idwm, mask=TRUE)</pre>
> par(mfrow=c(1,2))
> plot(iw, main='Inv. Dist. Weighted')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> tr <- threshold(e, 'spec_sens')</pre>
> pa <- mask(iw > tr, seamask)
> plot(pa, main='presence/absence')
> plot(wrld_simpl, add=TRUE, border='dark grey')
> points(pres_train, pch='+')
> points(backg_train, pch='-', cex=0.25)
```



- > # take a smallish sample of the background training data
 > va <- data.frame(back_train[sample(nrow(back_train), 100),])</pre>
- > vorm <- voronoiHull(p=pres_train, a=va)</pre>

PLEASE NOTE: The components "delsgs" and "summary" of the object returned by deldir() are now DATA FRAMES rather than matrices (as they were prior to release 0.0-18). See help("deldir").

PLEASE NOTE: The process that deldir() uses for determining duplicated points has changed from that used in version 0.0-9 of this package (and previously). See help("deldir").

> e <- evaluate(vorm, p=pres_test, a=backg_test, tr=quantile(ds, c(1:50/50))) > e

class : ModelEvaluation

n presences : 23 n absences : 200 AUC : 0.4925 cor : -0.03960028 max TPR+TNR at : 6.537932e-07

- > vo <- predict(seamask, vorm, mask=T)</pre>
- > plot(vo, main='Voronoi Hull')
- > plot(wrld_simpl, add=TRUE, border='dark grey')
- > points(pres_train, pch='+')
- > points(backg_train, pch='-', cex=0.25)



Part IV Additional topics

Model transfer in space and time

- 13.1 Transfer in space
- 13.2 Transfer in time: climate change

To do list

You can ignore this chapter, it is the authors' 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
- \bullet additional 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 using uncertainty field in georeferences. 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).

$\begin{array}{c} {\rm Part\ V} \\ {\rm References} \end{array}$

- Austin M.P., 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., T.C. Edwards Jr, and T. 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., 2012. Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null-model. Ecology 93: 679-688.
- 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., B. Gardner, and C. Monnerat, 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., and D. Whitehead, 2001. Soil and atmospheric water deficits and the distribution of New Zealand's indigenous tree species. Functional Ecology 15: 233–242.
- Liu C., P.M. Berry, T.P. Dawson, and R.G. Pearson, 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., V. Fensterer, H. Küchenhoff, B. Reger, C. Kölling, H.J. Klemmt, and J. Ewald, 2011. Hypothesis-driven species distribution models for tree species in the Bavarian Alps. Journal of Vegetation Science 22: 635–646.
- 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
- Peterson, A.T., J. Soberón, R.G. Pearson, R.P. Anderson, E. Martínez-Meyer, M. Nakamura and M.B. Araújo, 2011. Ecological Niches and Geographic Distributions. Monographs in Population Biology 49. Princeton University Press, 328p.
- Phillips S.J. and J.. Elith, 2011. 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 distri-

- bution models: implications for background and pseudo-absence data. Ecological Applications 19: 181-197.
- Potts J. and J. Elith, 2006. Comparing species abundance models. Ecological Modelling 199: 153-163.
- Vapnik, V., 1998. Statistical Learning Theory. Wiley, New York.
- VanDerWal J., L.P. Shoo, C. Graham and S.E. Williams, 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? Ecological Modelling 220: 589-594.
- Ward G., T. Hastie, S.C. Barry, J. Elith and J.R. Leathwick, 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.