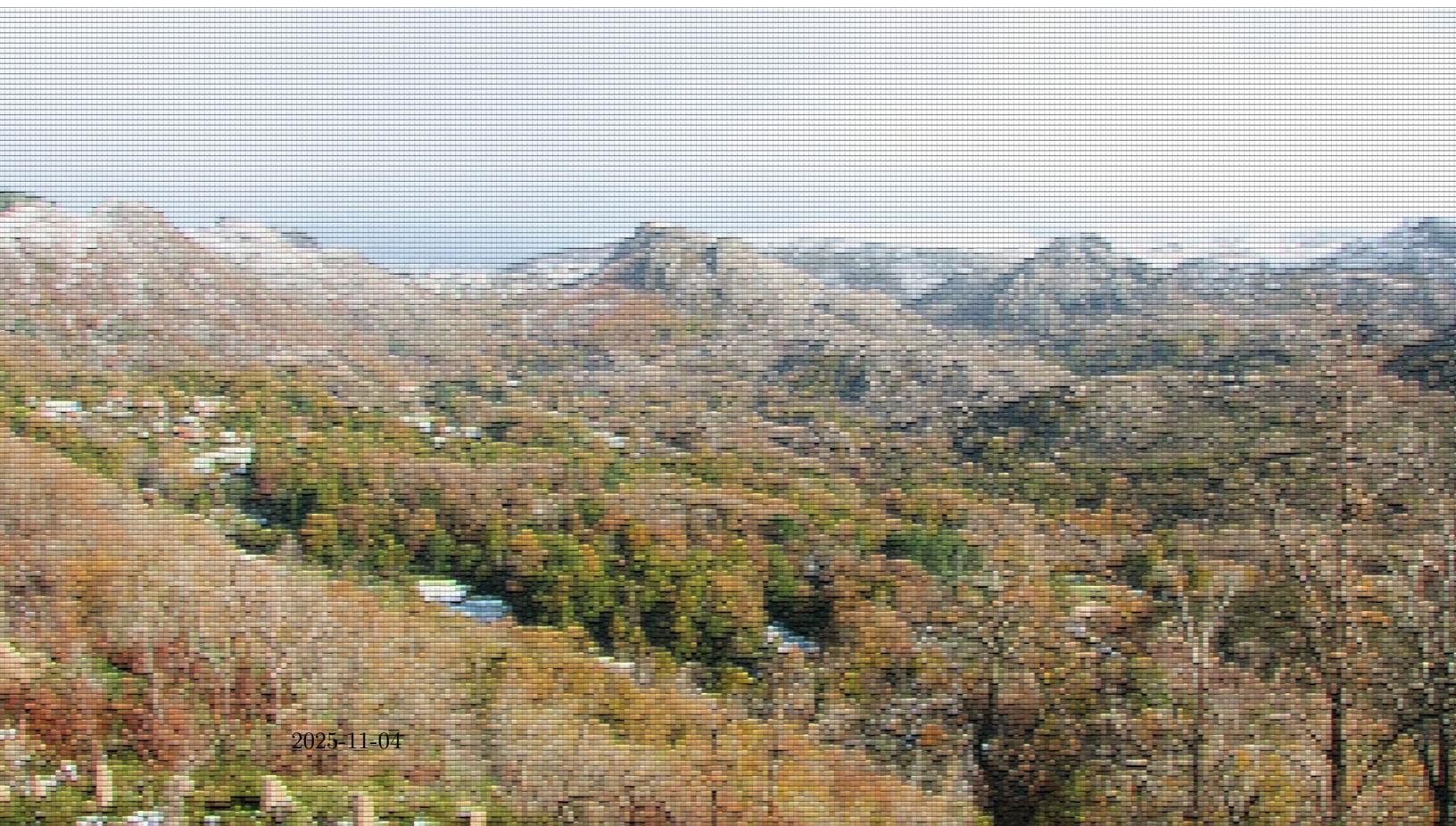


# Ecological theory for the biodiversity crisis

Henrique Miguel Pereira



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# Preface

We live in the midst of the biodiversity crisis. Biodiversity science, at first mostly a spin off from Ecology, has developed tremendously in the last two decades, becoming a truly interdisciplinary field, with contributions from Geography, Economy, Social Sciences and many other disciplines. Big data and the development of statistical ecology has also been remarkable. As I write these lines, the Global Biodiversity Information Facility or GBIF (<https://gbif.org>) is about to hit 3 billion records. The availability of large amounts of data and the availability of the open source R software (<https://www.r-project.org>) has made statistical approaches take the main stage in much of ecological research. However, at the same time, as a biodiversity researcher, practitioner, and a teacher, I find again and again the need for a good understanding of ecological theory to be able to carry out my work. This book if for all of you that have also felt a similar need.

Programming and mathematics are key tools of ecological theory. The programming language I use in this book is R (version 4, available from <https://www.r-project.org>). If you have familiarly with programming in another computer language, a fast skimming of Appendix A will be enough to get you going with the book. If you are new to programming, I recommend you spend a few hours working through the short course in Appendix A, but you may also wanna consult some web resources (e.g. <https://ourcodingclub.github.io/course>). With the advent of Large Language Models (LLM) such as ChatGPT there may be the temptation to think programming knowledge will no longer be needed. I think LLMs will accelerate our writing of computer code, but they will not replace the need for being able to read and understand the code.

You may wonder why I chose **R**. There are plenty other programming languages out there, several suitable for ecological theory and modelling (e.g. data scientists love Python). However, **R** has become the *de facto* language of ecologists with dozens of packages<sup>1</sup> for a wide range of analysis, from camera trapping to species richness estimation. **R** has also powerful packages for spatial data analysis and can work as a Geographic Information System. So R, grew from a statistics software (the origins of R are the comercial S-PLUS) to a general purpose programming language with dedicated packages for different uses.

Why was R so successful, to the point of making some commercial software companies go out of business? R was open-source and free from its beginning, part of the free and open-source movement that gained popularity in the 1990's, particularly with the development of the operating system Linux. Open-source means that the code behind R (R itself is a computer program written in C, Fortran, and other languages) is available for anyone to study. It also allows for anyone to

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<sup>1</sup>An R package is a set of functions developed by someone to extend the basic functionality of R.

contribute to improve the code in a collaborative way, including by contributing with packages. R is also free, meaning that anyone can download the software or any of its packages without any cost. Isn't that a wonderful tool for science? Scientists dedicate their life to the pursue of knowledge, and the idea that someone has to pay for accessing that knowledge has always been a bit apocryphal. So R allowed scientists to share their research and code for free in an integrated platform. Another advantage of open-source software, is that we can in theory ran programs that we wrote decades ago by downloading archived versions of the software. At least in theory, the practice of code reproducibility in science is a bit more complex and requires careful data and code management by the researcher<sup>2</sup>. Platforms such as GitHub (<https://github.com>) for sharing code and Zenodo (<https://zenodo.org>) or Dryad (<https://datadryad.org>) for sharing data are a key component of reproducible science.

In contrast a lot of the code I wrote for my PhD was based on a commercial package (Mathematica) and anyone that wants to reuse it a couple decades later has to pay a few hundred Euros for the package (well there are student discounts) and has to find a version of the Mathematica that still runs this code. This latter problem can be insurmountable, as sometimes older versions of the software are no longer commercially available. One can argue that many programming languages are also free and public, however for ecological theory and modelling a high-level language like R provides a nice integrated platform for development and is literally priceless.

But programming is not enough. In order to be able to effectively develop theory and models of biodiversity, a good grasp of mathematics, including of probability and statistics is essential. One challenge is that, and this at least the case in Europe where I have lectured the most, most biology students receive very little mathematical training. This book cannot address by itself such gap and assumes some basic familiarity with probability theory (e.g. what is a probability distribution function), some calculus training (e.g. what area a derivative and an integral), a little algebra (e.g. multiplication of a matrix by a vector). I try to take the reader forward from that level. There are excellent books out there for those that need this basic background (e.g. Otto's and Day's *A Biologist's Guide to Mathematical Modelling*). And Wikipedia (<https://www.wikipedia.org>) is often your best friend when you wanna a fast refresh of any mathematical concept or even for many of the models and ecological concepts presented in this book.

This book can be used as the support for a semester course in Ecological Theory or Ecological Modelling. I have used many of these materials over the last decade in a similar course at iDiv/University of Halle-Wittenberg. But the book can also be used as self-learning tool or even as a reference tool. This book takes a lot of inspiration from the Primer of Ecological Theory of Joan Roughgarden (the first two chapters draw heavily on her first chapters), that I was lucky to have as a mentor. As she used to say, one writes papers for the reviewers and books for the readers. This book is for you.

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<sup>2</sup>For a guide on best practices for reproducible code see <https://www.britishecologicalsociety.org/wp-content/uploads/2019/06/BES-Guide-Reproducible-Code-2019.pdf>

# Part I

## Ecology of individuals

# Chapter 1

## Ecophysiology and the climate space: when to bask in the sun?

We are now almost daily bombarded with news about climate change and its impacts on people and ecosystems. But how does climate mechanistically affects organisms? The basic foundations to address this question were laid out by ecophysiology research. Interestingly, at the time that some of seminal research on ecophysiology was carried out, back in the 1960's, climate change was not yet in the radar of most people. The research was driven by the interest in the basic understanding of how biophysical conditions affect organisms. Today the knowledge gained from this research has acquired new importance. This is an area whether the mechanistic knowledge learnt from theory and experiments is now sometimes overlooked because of the massive datasets and machine learning approaches available. But let's start with the basics.

### 1.1 A model for the body temperature of an animal

Animals can be divided in two big groups in regard to the way they regulate their temperature: ectotherms and endotherms (Figure 1.1). Endotherms such as mammals and birds are able to regulate their temperature by producing heat through metabolism. Ectotherms in contrast must regulate their temperature by obtaining heat from the environment. By obtaining energy from the environment, ectotherms have lower energy demands than endotherms, which have to be burning energy all the time to keep their bodies warm. Both do have to avoid getting too hot because indeed there can be too much from a good thing.

To build a model of the body temperature of an animal, let's consider a lizard that is perched in a rock basking in the sun (Figure 1.2). The lizard receives heat from the direct solar radiation than can be measured in for instance calories per hour. It can also receive indirect solar radiation, reflected for instance by the ground. The lizard also exchanges heat with the surrounding air through convection. If the lizard body temperature is higher than the surrounding air temperature it will lose heat, while if the lizard body temperature is lower than it will gain heat. The rate at which this exchange of heat through convection happens depends on the body of the animal



Figure 1.1: Shrews (left, *Crocidura russula*) are ectotherms and have high energy demands, eating almost their body weight every day. In contrast, vipers (right, *Vipera seonae*) can go days without eating, or even hibernate or aestivate as needed.

and the properties of its skin. These properties are captured in the heat transfer coefficient, which can be measured as calories per hour per degree Celsius. Similarly, the lizard can receive heat by conduction from being in contact with a warm rock, or lose heat to the rock if the rock is colder than the lizard's body temperature. Finally the animal can lose heat through evapotranspiration, this is by transpiring water that has a cooling effect when it evaporates. I also like to think about this model as representing our own experience on the beach. We can be laying on a towel receiving heat by conduction from the sand and solar radiation from the sun. If the air temperature is warm, we can become uncomfortable in the sun and we may seek a shade to reduce the input from solar radiation, but if there is a cool breeze we may be able to stay in the sun a bit longer. If the air temperature is really cold and it's really windy our skin hair may rise to reduce the convection coefficient.

The total flow of energy into the lizard, also known as the heat exchange equation, can be written as

$$f = q - k(b - a) \quad (1.1)$$

where

- $f$  is the energy flow (cal/h),
- $q$  is the quantity of heat in the solar radiation (cal/h),
- $k$  is the convection coefficient (cal/h/ $^{\circ}$ C),
- $b$  is the body temperature ( $^{\circ}$ C) and
- $a$  is the air temperature ( $^{\circ}$ C).

If the energy flow is positive, then the lizard is warming, while if it is negative then the lizard is



Figure 1.2: The energy flows of a lizard basking in the sun.

cooling. The equilibrium<sup>1</sup> happens when the energy flow is zero and so the lizard is neither cooling nor warming. If we solve Equation 1.1 for equilibrium by replacing  $f$  with zero and expanding the right-hand side of the equation,

$$0 = q - k b + k a$$

and rearranging for  $b$  we find the equilibrium body temperature that we denote with a hat,

$$\hat{b} = q/k + a. \quad (1.2)$$

Let's see if this equation makes sense. It says that the equilibrium body temperature is the sum of the solar radiation divided by the convection coefficient with the air temperature. So, at minimum the equilibrium body temperature is equal to the air temperature when the solar radiation is zero (e.g. during the night). But when the solar radiation is greater than zero then the equilibrium body temperature is higher than the air temperature as one would expect. How much higher? Well that depends on the convection coefficient. If the convection coefficient is very high then the body temperature is mainly determined by the air temperature. In contrast, if the convection coefficient is very low then the solar radiation can contribute significantly to the body temperature.

It's time to start using **R** to explore this model. For instance, we can use **R** to plot the relationship between the body temperature and the solar radiation. First we create variables for the heat coefficient and the air temperature and assign some values:

---

<sup>1</sup>The concept of equilibrium is very important in ecological theory. It is often introduced in the context of differential equations and corresponds to the point at which the derivative of the variable of interest is zero. The heat equation can also be seen as a differential equation where  $f$  corresponds to the derivative of the amount of heat  $Q$  in the lizard through time  $t$ , i.e.  $dQ/dt$ .

```
k = 50 #convection coefficient (cal/h/°C)
a = 18 #air temperature (°C)
```

We want to plot the equilibrium body temperature for a range of solar radiation values. So we create a vector with radiation values, for instance ranging from 0 cal/h to 1500 cal/h in steps of 500. I am going to use big letters to denote vectors in **R** code, in contrast with scalars which I will denote with small letters.

```
Q = seq(0,1500,by=500) #vector with radiation values
```

Now we can write Equation 1.2 in **R** to produce a vector of the equilibrium body temperatures for each value of radiation.

```
B_eq = Q/k+a #vector with equilibrium body temperatures
```

Let's examine the values of the vector, by binding the two vectors as a matrix,

```
rbind(Q,B_eq)
```

	[,1]	[,2]	[,3]	[,4]
Q	0	500	1000	1500
B_eq	18	28	38	48

This is nice as we can see the values of the equilibrium body temperature for each value of solar radiation. But let's visualize this as a graph, by plotting these vectors in **R**,

```
plot(Q,B_eq,type="l")
```

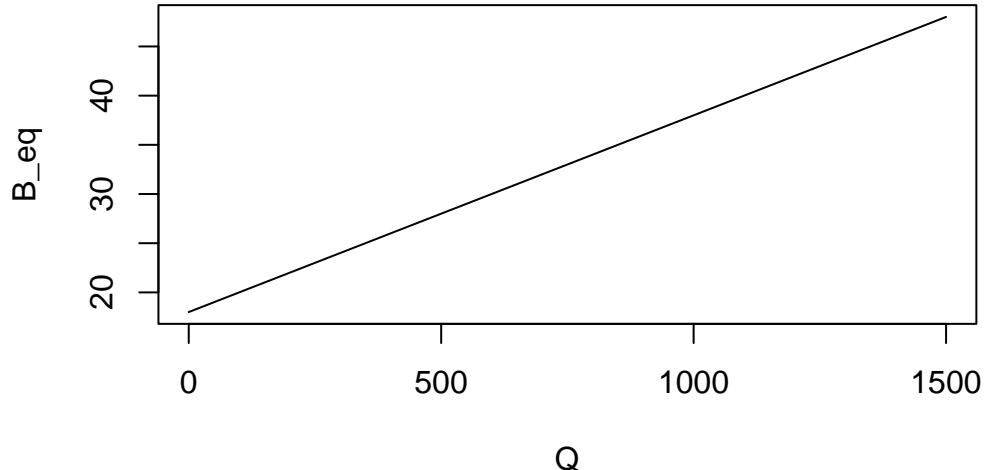


Figure 1.3: Equilibrium body temperature as a function of solar radiation.

Note that we added `type="l"` as a parameter of the plot to have a line drawn instead of a sequence of dots in the plot.

## 1.2 Understanding the climate space

Another way of looking at the heat exchange equation Equation 1.1 is to look at what combinations of air temperature and solar radiation values are livable for the lizard. This is also known as the climate space of an organism. In order to explore the climate space of the lizard we need to first assess what are the maximum and minimum body temperature that the lizard can experience. Let's assume those are respectively 36 and 24°C and store them in **R**,

```
b_max = 36 #maximum body temperature (°C)
b_min = 24 #minimum body temperature (°C)
```

We now want to solve Equation 1.1 at equilibrium for the air temperature as a function of the solar radiation and body temperature. We can do this by rearranging Equation 1.2,

$$a = b - q/k. \quad (1.3)$$

This equation can be then used in **R** to calculate vectors of the maximum and minimum survivable air temperatures for each value of the solar radiation in vector **Q**,

```
A_max = b_max - Q/k #vector with maximum air temperatures
A_min = b_min - Q/k #vector with minimum air temperatures
```

We can now visualize the climate space, this is, the combination of solar radiation and air temperatures in which the lizard can survive, by plotting these two equations (i.e. by plotting lines with x coordinates given by the vector **Q** and the y coordinates given by the vectors **A\_max** and **A\_min**),

```
plot(Q, A_max,type="l", #plots the maximum survivable air temperature
      xlab="Solar radiation (cal/h)", #adds x and y axis labels to the plot
      ylab="Air temperature (°C)")
lines(Q,A_min) #adds line for the minimum survivable air temperature
```

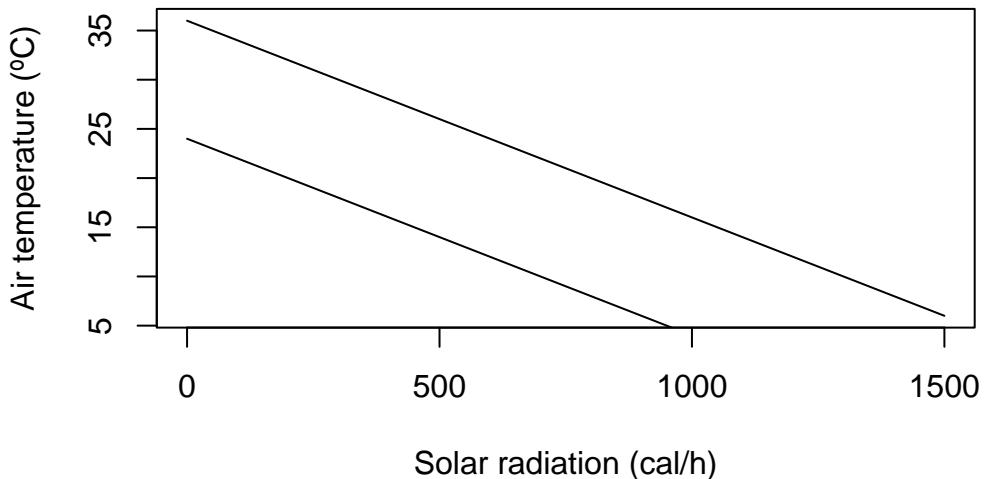


Figure 1.4: The climate space of a lizard.

Let's paint the area between the two lines which corresponds to the climate space of the lizard. We can use the **R** function `polygon`, to which we need to give the set of `x` and `y` coordinates delimiting the climate space as vectors. For instance, the upper lower corner can be the first coordinate, being 0 for the `x` vector and `b_min` for the `y` vector. The right upper corner is 1500 for `x` and `b_max-1500/k` for `y`.

```
X = c(0,0,1500,1500)
Y = c(b_min,b_max,b_max-1500/k,b_min-1500/k)
polygon(X,Y,col="green")
```

Now that we have the climate space we can plot on top of it some empirical data of how the conditions are in the field during the day. We can for instance consider two micro-habitats, a rock (in the sun) and a bush (in the shade). Suppose we obtain some data from temperature loggers that were installed in each micro-habitat , recording every three hours the values of temperature and radiation as tabled below.

Table 1.1: Hypothetical radiation values in two micro-habitats and air temperatures at different times of the day.

Time (hh:mm)	Radiation rock (cal/h)	Radiation bush (cal/h)	Temperature (°C)
00:00	150	150	18
03:00	150	150	13
06:00	800	450	10
09:00	1100	600	14
12:00	1300	650	21
15:00	1200	650	24
18:00	800	350	22
21:00	400	200	20

We can overlay these values of temperatures and radiations on the plot to understand which micro-habitat should the lizard choose at each time of the day. First we create a vector for each column of Table 1.1. Note that we must enclose the times of the day in commas as they are strings. We also append at the end of the vector the values for 0:00 in order to close the lines (otherwise there would be a gap between 21:00 and 0:00).

```
#Times of the day
T = c("00:00","03:00","06:00","09:00",
      "12:00","15:00","18:00","21:00","00:00")

#Solar radiation in the rock habitat
Rock_q = c(150,150,800,1100,1300,1200,800,400,150)

#Air temperature in the rock habitat
Rock_a = c(18,13,10,14,21,24,22,20,18)
```

```
#Solar radiation in the bush habitat
Bush_q = c(150, 150, 450, 600, 650, 650, 350, 200, 150)

# Air temperature in the bush habitat
Bush_a = c(18, 13, 10, 14, 21, 24, 22, 20, 18)
```

We overlay these vectors in the figure by invoking the function `lines(Xcoor,Ycoord)` for each micro-habitat. We add labels to each point to show the correspondence between each point and the time of the day.

```
lines(Rock_q,Rock_a,col="orange")
text(Rock_q,Rock_a,T)

lines(Bush_q,Bush_a,col="blue")
text(Bush_q,Bush_a,T)
```

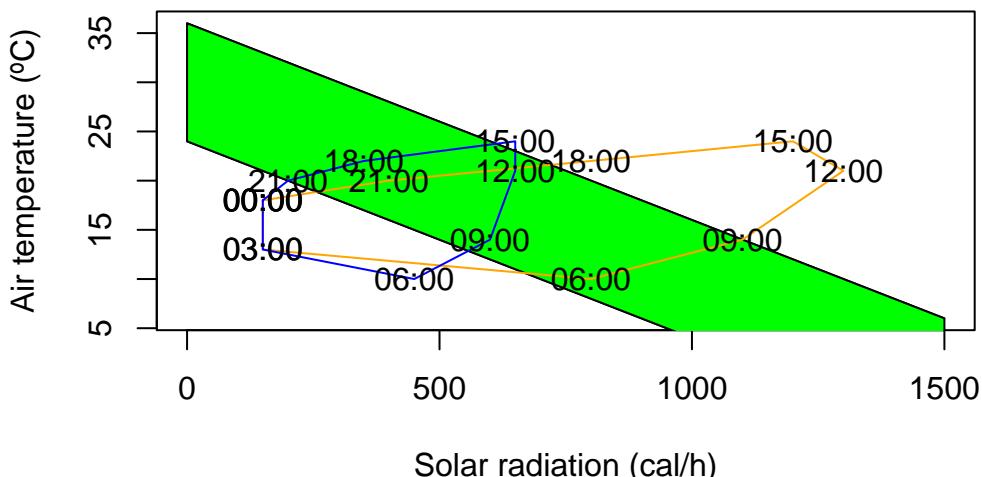


Figure 1.5: The climate space of a lizard with the conditions of two microhabitats plotted at different times of the day: rock (orange), bush (blue).

### 1.3 From ecophysiological models to species distribution models

In the previous section we developed a simple mechanistic model for the climate space of an organism. This is a micro-habitat level climate space. But one can also infer the climate space from the distribution of a species at the macro-habitat level. They are different but they are conceptually similar. The inference of such macro climate space is an area where species distribution models excel (for more on species distribution models check for example (Guisan, Thuiller, and Zimmermann 2017)). The idea is relatively simple. One starts with a bunch of locations of a species in geographical space. Then, one obtains the climate characteristics for those locations, and then plots

those locations in climate space. The convex hull in climate space delimited by those locations is the macro-habitat climate space. What species distribution models (SDMs) learn to do is to delineate that climate space, this is, SDMs try to predict the probability of a species occurring somewhere in the climate space by learning from presences and absences from species. Then the SDM can extrapolate again what happens in geographical space, by predicting the species occurrence probability for any point based on the climate data for that point. Without getting all the way into a full blown SDM, let's try to follow some of the basics.



Figure 1.6: The Iberian emerald lizard, *Lacerta schreiberi*.

I will illustrate this with one my favorite species, the Iberian emerald lizard, *Lacerta schreiberi*, a species endemic to the Iberian peninsula, often found near water streams in mountain landscapes, but also in other habitats. First we obtain the presences for a species from GBIF (Global Biodiversity Information Facility, <http://www.gbif.org>). GBIF is a repository for biodiversity observations, and has over three billions of occurrences of over a million species all over the world at the time I am writing these words. Natural history museums, citizen science platforms such as iNaturalist (<http://www.inaturalist.org>) and eBird (<http://www.ebird.org>), and scientists, publish their species records in GBIF using a data format called Darwin Core. There is a R package that allows one to download observations from GBIF and also other relevant geodata, the **geodata** package. We will be doing some geospatial processing, so let's load also the **terra** package.

```
library(geodata)
library(terra)
library(predicts)
library(ggplot2)
```

We download the observations of *Lacerta schreiberi* from GBIF with the function `sp_occurrence(genus, species)`. We also download a world map with the function `world(path)`, where path should point towards a local directory where we want to store the data.

```

occ <- sp_occurrence("Lacerta","schreiberi")
world_data <- world(path = ".") #download world countries limits
ext_eur <- c(-15,45,35,72) # coordinates of European extent

#download bioclim data
bioclim <- worldclim_global(var = 'bioc', res = 10, path = ".")

# plot the map of Europe
plot(world_data,
      xlab = "Longitude", ylab = "Latitude", axes = TRUE, ext=ext_eur)

# add the species occurrences
points(occ$lon,occ$lat,cex=.1,col="blue")

# create pseudo-absences
eumask<-crop(bioclim[[1]], ext(ext_eur))
absences<-backgroundSample(eumask,nrow(occ),vect(occ),tryf=10)
points(absences,cex=.1,col="red")

# plot the climate variables in geographic space
plot(bioclim[[19]],ext=ext_eur)
plot(bioclim[[3]],ext=ext_eur)

# plot the climate space figure
# first merge occurrences and absences into a single matrix
allpts <- rbind(cbind(occ$lon,occ$lat,rep(1,nrow(occ))),
                 cbind(absences,rep(0,nrow(absences))))
colnames(allpts)[3]<-"pres"

# extract the climate variable values for all points
bioclim_sample<-extract(bioclim,allpts[,1:2])
allpts_bioclim <- cbind(allpts,bioclim_sample)

allpts_bioclim_plot<-allpts_bioclim
allpts_bioclim_plot$pres<-as.factor(allpts_bioclim_plot$pres)
ggplot(allpts_bioclim_plot, aes(x=wc2.1_10m_bio_19,y=wc2.1_10m_bio_3,shape=pres, col=pres)) +
  geom_point(size = 3, alpha=0.5) + scale_color_manual(values = c("0" = "red", "1" = "blue"))

```

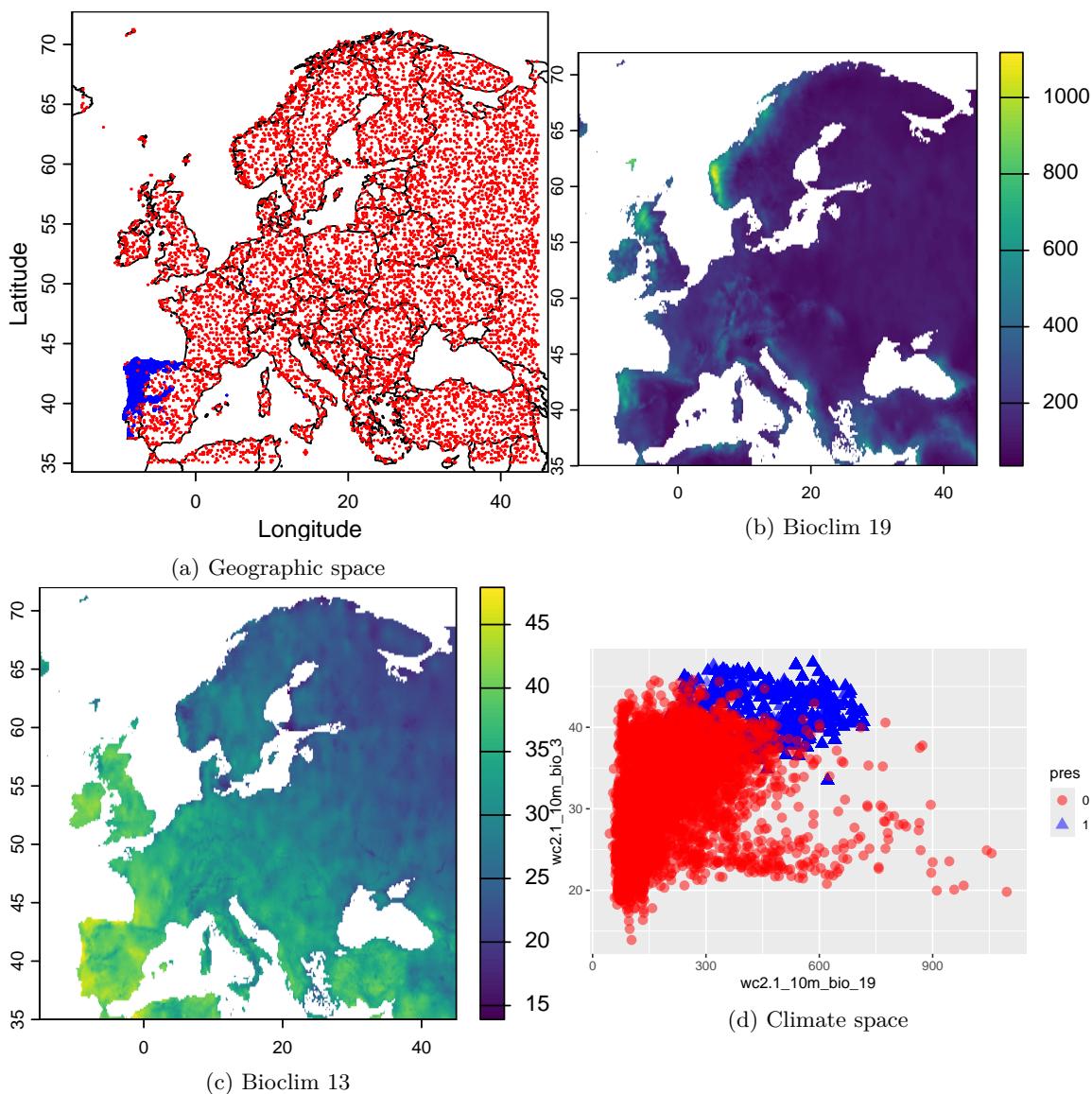


Figure 1.7: The geographic space and climate space of *Lacerta schreiberi*.

## 1.4 Statistical confrontation: regressing the climate space

## 1.5 References

Guisan, Antoine, Wilfried Thuiller, and Niklaus E. Zimmermann. 2017. *Habitat Suitability and Distribution Models: With Applications in r*. Cambridge University Press.

# Chapter 2

## Economic models of behavior: do animals optimize?

Animals have to make decisions all the time: where and when to move, when and what to eat, whom to mate, etc. How do animals make those decisions? One approach to study this question is to assume that animals take decisions that maximize their fitness. This approach is rooted in the idea that natural selection, under certain conditions, maximize the average fitness of individuals in a population. It underpins many of the studies in behavioral ecology, and lead to the development during the 1980's of a sub-field dedicated to the study of foraging decisions, known as optimal foraging. The idea of optimal foraging is to develop economic models of foraging behavior, assessing the costs and benefits of different actions, and identifying in any particular circumstance the action that maximizes benefits and minimizes costs. This is, animals are seen as optimizer of decision-making. Here we consider models for two "idealized" types of foragers: searching predator and sit-and-wait predators.

### 2.1 Searching predator

The searching predator is typified as an animal that actively searches for food. For instance, wolves roam the landscape constantly searching for their prey (Figure 2.1). The question is then, any time that a forager comes across a prey whether to spend the time catching and eating it, or continuing to search for another prey, for instance a larger or easier prey item. Joan Roughgarden also liked this type of foraging to the sushi-bar problem where dishes are coming one after the other on a moving tray, and a person needs to decide whether to pick a given dish. This decision is particularly akin to the searching predator situation when one assumes that a person can have only one dish at a time in her or his table. We consider two types of searching predators: time minimizers and energy maximizers.



Figure 2.1: A pack of wolf (*Canis lupus*) roaming around the landscape of Peneda-Gerês National Park, Portugal.

### 2.1.1 Time minimizer

Many searching predators are themselves preys to other animals. For instance shrews search for insects to eat, but can be themselves eaten by carnivores or owls. Therefore a reasonable assumption is that they are making foraging decisions that minimize the time foraging. Let's assume there are two types of prey items, type 1 and 2. These two preys occur at different abundances in the environment, let's name them  $a_1$  and  $a_2$ . These abundances can be measured as encounter rates from the predator perspective, this is the number of prey items found per unit time. The two types of prey also have different handling times, this is the amount of time required to chase and process the prey,  $h_1$  and  $h_2$ . We also convention to call the type 1 prey the prey with the lowest handling time, i.e.  $h_1 < h_2$ ,

A searching predator can adopt one of the following three strategies:

- Strategy 1: to consume only prey items of type 1
- Strategy 2: to consumer only prey items of type 2
- Strategy 1&2: to consumer both types of prey

In order to find out which strategy should be adopted by the forager, one needs to calculate the average spent per food item in each of the strategies. For Strategy 1 the average time per item,  $T_1$  is the sum of the amount of time the predator needs to encounter a prey with the amount of time that it takes to process that prey. As the abundance is measured in encounter rates, i.e. prey items

per unit time, the inverse of that is the waiting time for a prey. Therefore we have for Strategy 1,

$$T_1 = 1/a_1 + h_1 \quad (2.1)$$

Similarly, for Strategy 2, the average time per item  $T_2$  is given by

$$T_2 = 1/a_2 + h_2. \quad (2.2)$$

A more interesting case is Strategy 3. Here the waiting time is the inverse of the sum of the abundances of both times of prey, while the handling time is average of the handling times of both types of prey weighted by their relative abundance,

$$T_3 = \frac{1}{a_1 + a_2} + \frac{a_1 h_1 + a_2 h_2}{a_1 + a_2} \quad (2.3)$$

We can now define the problem that the forager has to solve as to find the strategy  $i$  that minimizes  $T_i$ :

$$\min(T_i) \quad \text{for } i = 1, 2, 3$$

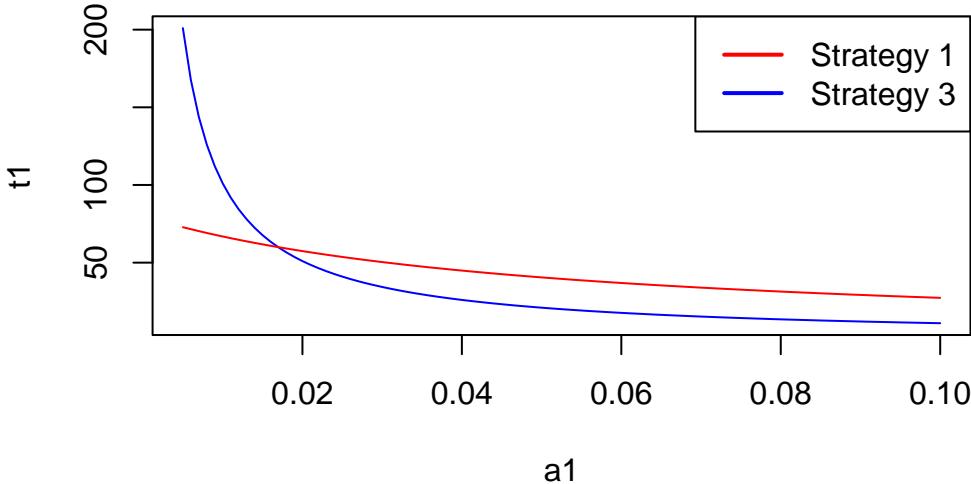
It is easy to demonstrate that Strategy 2 is always worse than Strategy 3, independently of the abundances of the two types of prey. This happens because Strategy 3 always implies a longer waiting time than the two other specialized strategies (i.e. one has to wait less time to find any item of an prey than items of a given prey time,  $1/(a_1 + a_2) < 1/a_2$ ) and the handling time of strategy 3 can never be higher than the handling time of strategy 2 (it's always a value between  $h_1$  and  $h_2$ ). So we can exclude Strategy 2 from our analysis. The choice is then between Strategy 1, just taking items of the preferred prey item, and 3, taking items of both types of prey. Let's assess this two strategies with a little bit of help from R. We start by assuming that the handling time of prey type 1 is 1 second while prey type 2 takes 60 seconds. Let's also assume that the abundance of prey type 2 is 0.05 individuals per second, i.e. one individuals needs to wait in average 20 seconds to find prey type 2.

```
h1=1          #Handling time of prey type 1 (s)
h2=60         #Handling time of prey type 2 (s)
a2=0.05       #abundance of prey type 2 (ind/s)
```

Let's now plot the time per item of each of the strategies as a function of the abundance of the preferred prey.

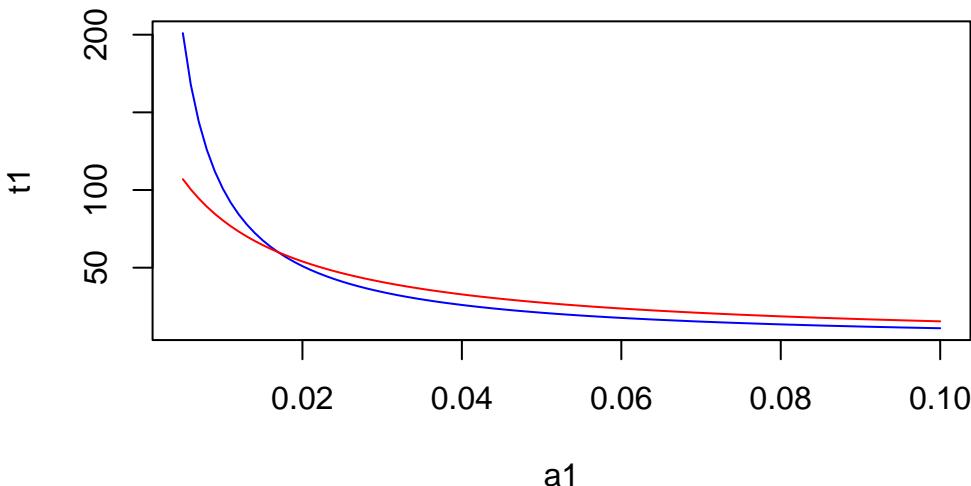
```
a1<-seq(0.005,0.1,0.001)    #abundance of prey time 1 (ind/s)
t1=1/a1+h1                  #time per item of Strategy 1 (s)
t3=1/(a1+a2)+h1*a1/(a1+a2)+h2*a2/(a1+a2) #time per item of Strategy 2 (s)
plot(a1,t1, type="l", col="blue")
lines(a1,t3, type="l", col="red")
legend("topright",
      legend = c("Strategy 1", "Strategy 3"), # Labels
```

```
col = c("red", "blue"),          # Line colors
lwd = 2,                      # Line width
lty = 1)
```



There is a critical threshold of the abundance of prey type 1 above which strategy 1 is preferable, while below that threshold strategy 3 is the best strategy. Interestingly this threshold does not depend on the abundance of the less preferable prey. For instance, if we assume a low abundance of prey time 2 at 0.01, the resulting plot is:

```
a2 = 0.01
t1=1/a1+h1           #time per item of Strategy 1 (s)
t3=1/(a1+a2)+h1*a1/(a1+a2)+h2*a2/(a1+a2) #time per item of Strategy 2 (s)
plot(a1,t1, type="l", col="blue")
lines(a1,t3, type="l", col="red")
```



To determine this critical threshold one can compare the two vectors, T1 and T3, and find the first position at which T1 becomes smaller than T3,

```
pos=which(t1<t3)[1]
a1[pos]
```

[1] 0.017

So the critical threshold for these handling times occurs when  $a_1 = 0.017$  individuals per second.

### 2.1.2 Energy per time maximizer

Perhaps more often, animals try to maximize their energy yield (benefits) while minimizing the time foraging (costs). Or in another way of looking at it, they try to maximize their energy yield per unit time. We already know the time per item associated to each of the three strategies of the searching predator. We now need to calculate the average energy yield per item. Consider now that the energy content of the prey items are  $e_1$  and  $e_2$  for prey of type 1 and 2, respectively. We define prey 1 as the preferred type of prey, so we assume that the ratio of the energetic content (measured for instance in calories) to the handling time is higher for type 1 prey, i.e.  $e_1/h_1 > e_2/h_2$ . Now we calculate the energy yield per item for each strategy. We start with the energy content of the prey, but need to subtract the energy spent while waiting the prey and the energy spent chasing and processing the prey,

$$E_1 = e_1 - ew * tw_1 - eh * h_1 \quad (2.4)$$

where  $ew$  and  $eh$  are the energy spent per unit time while waiting for the prey and the energy spent per unit time while handling, respectively. They can both be measured for instance in cal/s. We already know from the time minimizer that the waiting time for the prey is the inverse of the abundance,  $tw_1 = 1/a_1$ . Therefore substituting in Equation 2.4 we have

$$E_1 = e_1 - \frac{ew}{a_1} - eh * h_1. \quad (2.5)$$

A similar expression can be written for Strategy 2, replacing 1 with 2 in Equation 2.4.

$$E_2 = e_2 - \frac{ew}{a_2} - eh * h_2. \quad (2.6)$$

More interesting is to derive the expression for Strategy 3, where the foragers takes both types of prey. The energy content of the prey is the average of the energetic contents of each prey type, weighted by their abundances,  $(e_1 * a_1 + e_2 * a_2)/(a_1 + a_2)$ . The waiting time is the inverse of the sums of the abundances of preys of both types, as in Equation 2.3. The handling time is the average of the handling times of each prey type, weighted by their abundances. So we have,

$$E_3 = \frac{e_1 * a_1 + e_2 * a_2}{a_1 + a_2} - \frac{ew}{a_1 + a_2} - eh \frac{h_1 * a_1 + h_2 * a_2}{a_1 + a_2}. \quad (2.7)$$

Finally we can calculate the energy per unit time for each strategy by dividing Equation 2.5 by Equation 2.1 for Strategy 1, dividing Equation 2.6 by Equation 2.2 for Strategy 2, and dividing Equation 2.7 by Equation 2.3 for strategy 3,

$$ET_i = \frac{E_i}{T_i}$$

Similarly to the time minimizer, it's possible to show mathematically that strategy 2 is never an optimal strategy. So the interesting comparison is again between strategy 1 and strategy 3. Let's use R to plot the energy per time yield for both strategies. We start by setting the parameter values of our model with some realistic numbers.

```
e1<-10          #Caloric content of prey 1
e2<-100         #Caloric content of prey 2
h1<-1           #Handling time of prey 1
h2<-60          #Handling time of prey 2
ew<-1           #Energy spend per unit time while waiting (cal/s)
eh<-1           #energy spend per unit time handling the prey (cal/s)
```

We will examine the energy yields for strategy 1 and strategy 3 for a fixed abundance of prey type 2 and a sequence of abundances of prey type 1 from 0.005 individuals per second to 0.5 individuals per second

```
a1<- seq(0.005,0.5,0.001)    #Sequence of abundances of prey 1
a2<-0.05
```

With the parameter and abundance values defined, we can calculate  $E_1$ ,  $E_3$ ,  $T_1$ ,  $T_3$ , and then  $ET_1$  and  $ET_3$  based on the equations above, resulting in vectors for these variables with each entry in the vector corresponding to an abundance value in the vector of abundances `a1`.

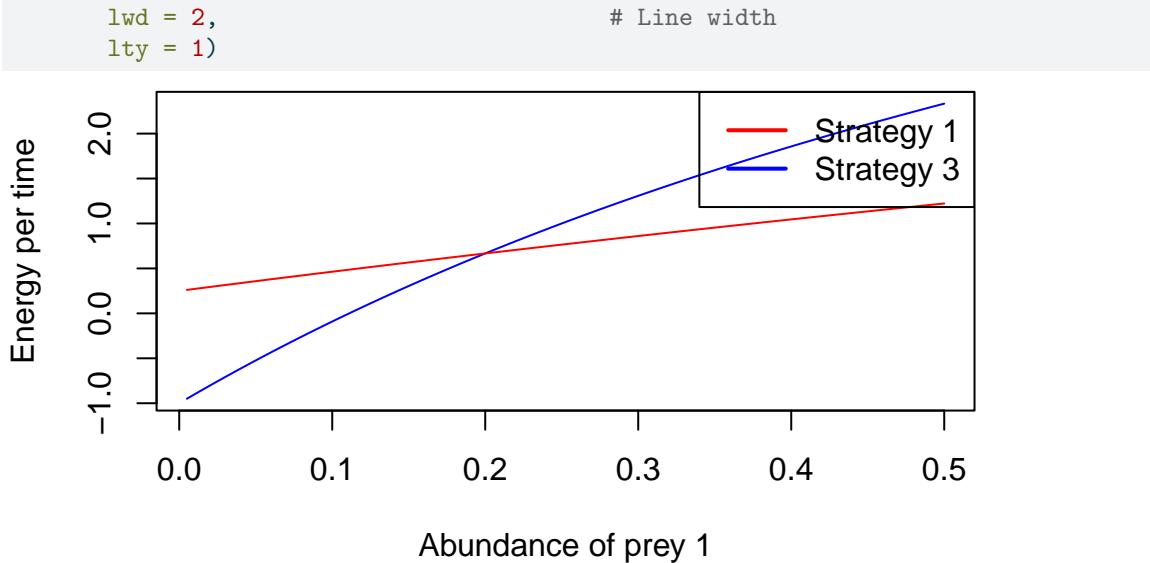
```
E1 = e1 -(eh*h1) - ew/a1    #energy per item of Strategy 1 (s)
E3 = (e1*a1+e2*a2)/(a1+a2)-
      eh*(h1*a1+h2*a2)/(a1+a2)-ew/(a1+a2) #energy per item of Strategy 3 (s)

T1=1/a1+h1                  #time per item of Strategy 1 (s)
T3=1/(a1+a2)+h1*a1/(a1+a2)+h2*a2/(a1+a2) #time per item of Strategy 3 (s)

ET1 = E1/T1 #energy per time of strategy 1
ET3 = E3/T3 #energy per time of strategy 3
```

Next we plot the energy yields against the values of abundance of prey of type 1, and add a nice legend:

```
plot(a1,ET1,type="l",xlab="Abundance of prey 1", ylab="Energy per time", col="blue")
lines(a1,ET3,type="l",col="red")
legend("topright",
       legend = c("Strategy 1", "Strategy 3"), # Labels
       col = c("red", "blue"),                 # Line colors
```



Similarly to the the time minimizer, for the energy maximizer there is also a critical threshold of the abundance of prey type 1 above which strategy 1 is preferable, while below that threshold strategy 3 is the best strategy.

## 2.2 Sit-and-wait predator

In contrast to the searching predator, the sit-and-wait predator forages by patiently ambushing its prey. For instance, the lizard *Anolis gingivinus* (Figure 2.2) waits in a perch, often a tree trunk, for a prey to come into its reach, sprinting then down the trunk or into the ground to capture its prey, returning then to its perch again.



Figure 2.2: An *Anolis gingivinus*, a sit-and-wait predator, captures a prey after running down from its perch. Photo taken in the island of Saint Martin, Leeward Islands, Caribbean.

## Part II

# Ecology of populations

## **Chapter 3**

### **Demography: boom or bust**

## Part III

# Ecology of communities

## **Chapter 4**

# **Modelling biodiversity change: winners and losers**

Every minute about 2 football fields of native forest are cleared somewhere in the world. What are the consequences of land-use change for biodiversity?

# Appendix A

## A brief R tutorial

If you are new to **R** you can have a short dive into its main features by working through this tutorial. If you had learnt programming in another computer language, you will be able to skim over this tutorial to find the main differences from what you have learnt to how things are done in **R**.

### A.1 Variables, vectors and matrices

```
# Introduction to variables
# Variables can be any sequence of letter and numbers, but
# it cannot start with a number
x = 2
x <- 4
2+2

[1] 4
y <- x^5
y

[1] 1024
# Introduction to vectors
v1 <- c(2,3,6,12)
v2 <- 1:100
length(v2)

[1] 100
v2

[1]   1   2   3   4   5   6   7   8   9   10  11  12  13  14  15  16  17  18
[19]  19  20  21  22  23  24  25  26  27  28  29  30  31  32  33  34  35  36
[37]  37  38  39  40  41  42  43  44  45  46  47  48  49  50  51  52  53  54
```

```
[55] 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72
[73] 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89 90
[91] 91 92 93 94 95 96 97 98 99 100

v3 <- seq(1,100,5) # call without naming arguments
v3
[1] 1 6 11 16 21 26 31 36 41 46 51 56 61 66 71 76 81 86 91 96

v3 <- seq(from=1,to=100,by=5) # call with names of arguments
v3
[1] 1 6 11 16 21 26 31 36 41 46 51 56 61 66 71 76 81 86 91 96

v3 <- seq(to=100,by=5) # call skipping the first argument
#and using the default value 1 - see help(seq)
v3
[1] 1 6 11 16 21 26 31 36 41 46 51 56 61 66 71 76 81 86 91 96

v3 <- seq(by=5,to=100) # call by arguments and change order or arguments

# Indexing vectors
v3[3] #uses square brackets to obtain the third element of the vector

[1] 11

v3>20 # produce a vector of boolean values that are TRUE when
[1] FALSE FALSE FALSE FALSE TRUE TRUE TRUE TRUE TRUE TRUE TRUE TRUE
[13] TRUE TRUE
#v3 is greater than 20
v3[v3>20] # select from v3 all the values that are greater than 20
[1] 21 26 31 36 41 46 51 56 61 66 71 76 81 86 91 96

v4<-c(1,2,3,4,5)
v4[c(FALSE,TRUE,FALSE,TRUE,FALSE)] #select from v4 the second and fourth element

[1] 2 4

v3[1:10] # first ten elements
[1] 1 6 11 16 21 26 31 36 41 46
v3[-1] # dropping first element
[1] 6 11 16 21 26 31 36 41 46 51 56 61 66 71 76 81 86 91 96
head(v2) # prints the first few elements of v2
[1] 1 2 3 4 5 6
```

```

tail(v2) # prints the last few elements of v2

[1] 95 96 97 98 99 100

which(v3 == 26) # returns the position of v3 that equals 26

[1] 6

#Numerical operations with vectors
2^v2

[1] 2.000000e+00 4.000000e+00 8.000000e+00 1.600000e+01 3.200000e+01
[6] 6.400000e+01 1.280000e+02 2.560000e+02 5.120000e+02 1.024000e+03
[11] 2.048000e+03 4.096000e+03 8.192000e+03 1.638400e+04 3.276800e+04
[16] 6.553600e+04 1.310720e+05 2.621440e+05 5.242880e+05 1.048576e+06
[21] 2.097152e+06 4.194304e+06 8.388608e+06 1.677722e+07 3.355443e+07
[26] 6.710886e+07 1.342177e+08 2.684355e+08 5.368709e+08 1.073742e+09
[31] 2.147484e+09 4.294967e+09 8.589935e+09 1.717987e+10 3.435974e+10
[36] 6.871948e+10 1.374390e+11 2.748779e+11 5.497558e+11 1.099512e+12
[41] 2.199023e+12 4.398047e+12 8.796093e+12 1.759219e+13 3.518437e+13
[46] 7.036874e+13 1.407375e+14 2.814750e+14 5.629500e+14 1.125900e+15
[51] 2.251800e+15 4.503600e+15 9.007199e+15 1.801440e+16 3.602880e+16
[56] 7.205759e+16 1.441152e+17 2.882304e+17 5.764608e+17 1.152922e+18
[61] 2.305843e+18 4.611686e+18 9.223372e+18 1.844674e+19 3.689349e+19
[66] 7.378698e+19 1.475740e+20 2.951479e+20 5.902958e+20 1.180592e+21
[71] 2.361183e+21 4.722366e+21 9.444733e+21 1.888947e+22 3.777893e+22
[76] 7.555786e+22 1.511157e+23 3.022315e+23 6.044629e+23 1.208926e+24
[81] 2.417852e+24 4.835703e+24 9.671407e+24 1.934281e+25 3.868563e+25
[86] 7.737125e+25 1.547425e+26 3.094850e+26 6.189700e+26 1.237940e+27
[91] 2.475880e+27 4.951760e+27 9.903520e+27 1.980704e+28 3.961408e+28
[96] 7.922816e+28 1.584563e+29 3.169127e+29 6.338253e+29 1.267651e+30

log(v2)

[1] 0.0000000 0.6931472 1.0986123 1.3862944 1.6094379 1.7917595 1.9459101
[8] 2.0794415 2.1972246 2.3025851 2.3978953 2.4849066 2.5649494 2.6390573
[15] 2.7080502 2.7725887 2.8332133 2.8903718 2.9444390 2.9957323 3.0445224
[22] 3.0910425 3.1354942 3.1780538 3.2188758 3.2580965 3.2958369 3.3322045
[29] 3.3672958 3.4011974 3.4339872 3.4657359 3.4965076 3.5263605 3.5553481
[36] 3.5835189 3.6109179 3.6375862 3.6635616 3.6888795 3.7135721 3.7376696
[43] 3.7612001 3.7841896 3.8066625 3.8286414 3.8501476 3.8712010 3.8918203
[50] 3.9120230 3.9318256 3.9512437 3.9702919 3.9889840 4.0073332 4.0253517
[57] 4.0430513 4.0604430 4.0775374 4.0943446 4.1108739 4.1271344 4.1431347
[64] 4.1588831 4.1743873 4.1896547 4.2046926 4.2195077 4.2341065 4.2484952
[71] 4.2626799 4.2766661 4.2904594 4.3040651 4.3174881 4.3307333 4.3438054
[78] 4.3567088 4.3694479 4.3820266 4.3944492 4.4067192 4.4188406 4.4308168
[85] 4.4426513 4.4543473 4.4659081 4.4773368 4.4886364 4.4998097 4.5108595
[92] 4.5217886 4.5325995 4.5432948 4.5538769 4.5643482 4.5747110 4.5849675

```

```
[99] 4.5951199 4.6051702
```

```
v5 <- 101:200
```

```
v5-v2
```

```
[1] 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100  

[19] 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100  

[37] 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100  

[55] 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100  

[73] 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100  

[91] 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100
```

```
v5/v2
```

```
[1] 101.000000 51.000000 34.333333 26.000000 21.000000 17.666667  

[7] 15.285714 13.500000 12.111111 11.000000 10.090909 9.333333  

[13] 8.692308 8.142857 7.666667 7.250000 6.882353 6.555556  

[19] 6.263158 6.000000 5.761905 5.545455 5.347826 5.166667  

[25] 5.000000 4.846154 4.703704 4.571429 4.448276 4.333333  

[31] 4.225806 4.125000 4.030303 3.941176 3.857143 3.777778  

[37] 3.702703 3.631579 3.564103 3.500000 3.439024 3.380952  

[43] 3.325581 3.272727 3.222222 3.173913 3.127660 3.083333  

[49] 3.040816 3.000000 2.960784 2.923077 2.886792 2.851852  

[55] 2.818182 2.785714 2.754386 2.724138 2.694915 2.666667  

[61] 2.639344 2.612903 2.587302 2.562500 2.538462 2.515152  

[67] 2.492537 2.470588 2.449275 2.428571 2.408451 2.388889  

[73] 2.369863 2.351351 2.333333 2.315789 2.298701 2.282051  

[79] 2.265823 2.250000 2.234568 2.219512 2.204819 2.190476  

[85] 2.176471 2.162791 2.149425 2.136364 2.123596 2.111111  

[91] 2.098901 2.086957 2.075269 2.063830 2.052632 2.041667  

[97] 2.030928 2.020408 2.010101 2.000000
```

```
v1/v2
```

```
[1] 2.00000000 1.50000000 2.00000000 3.00000000 0.40000000 0.50000000  

[7] 0.85714286 1.50000000 0.22222222 0.30000000 0.54545455 1.00000000  

[13] 0.15384615 0.21428571 0.40000000 0.75000000 0.11764706 0.16666667  

[19] 0.31578947 0.60000000 0.09523810 0.13636364 0.26086957 0.50000000  

[25] 0.08000000 0.11538462 0.22222222 0.42857143 0.06896552 0.10000000  

[31] 0.19354839 0.37500000 0.06060606 0.08823529 0.17142857 0.33333333  

[37] 0.05405405 0.07894737 0.15384615 0.30000000 0.04878049 0.07142857  

[43] 0.13953488 0.27272727 0.04444444 0.06521739 0.12765957 0.25000000  

[49] 0.04081633 0.06000000 0.11764706 0.23076923 0.03773585 0.05555556  

[55] 0.10909091 0.21428571 0.03508772 0.05172414 0.10169492 0.20000000  

[61] 0.03278689 0.04838710 0.09523810 0.18750000 0.03076923 0.04545455  

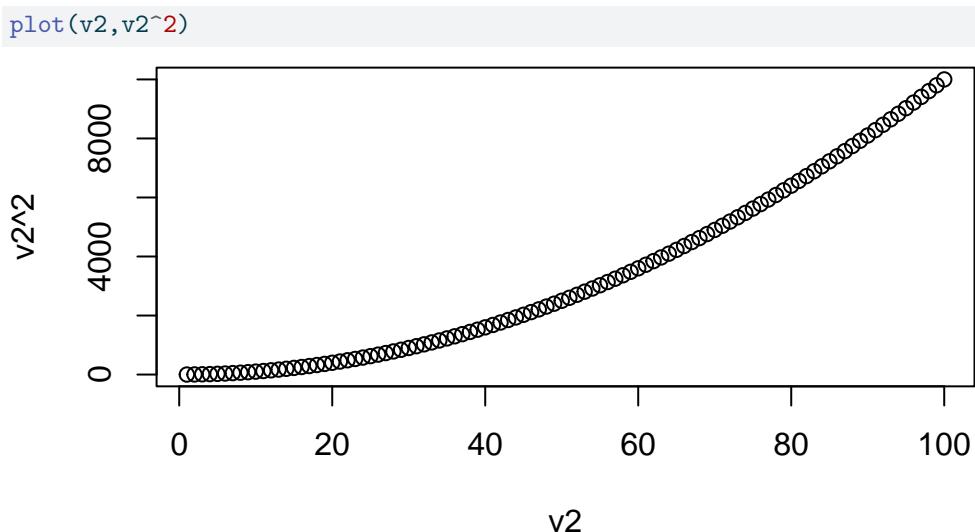
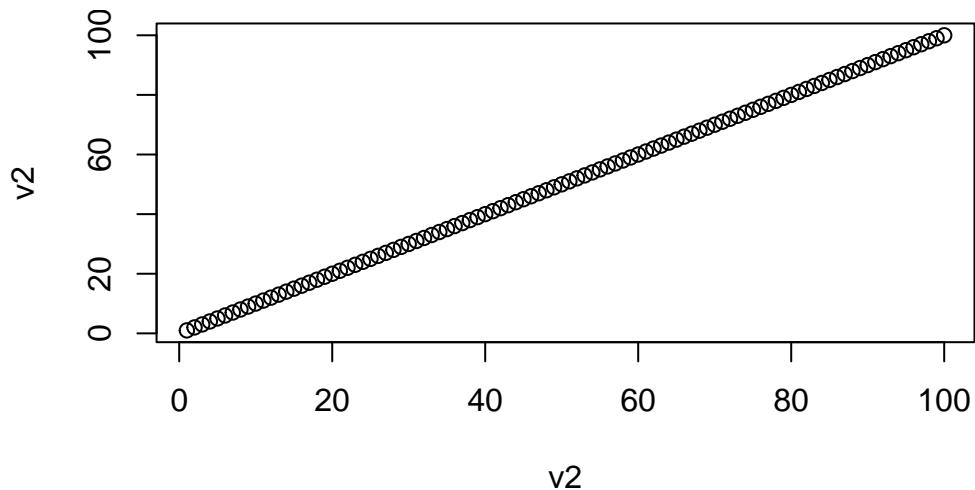
[67] 0.08955224 0.17647059 0.02898551 0.04285714 0.08450704 0.16666667  

[73] 0.02739726 0.04054054 0.08000000 0.15789474 0.02597403 0.03846154  

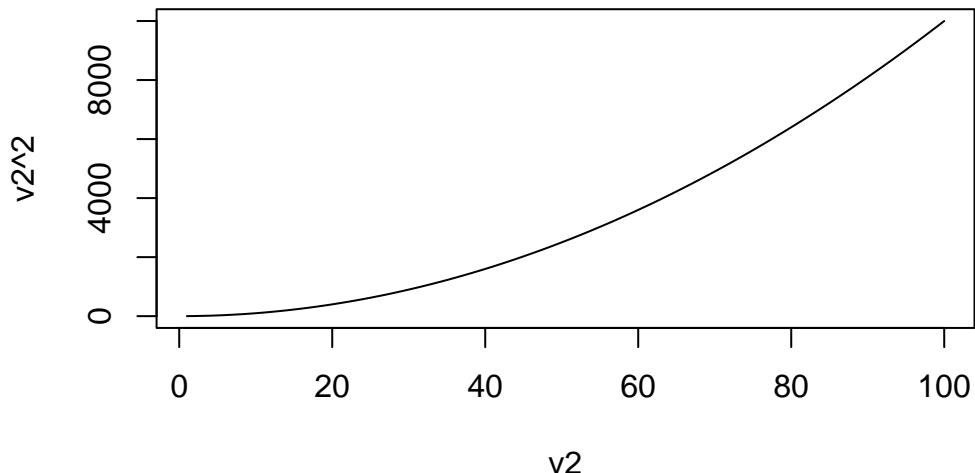
[79] 0.07594937 0.15000000 0.02469136 0.03658537 0.07228916 0.14285714  

[85] 0.02352941 0.03488372 0.06896552 0.13636364 0.02247191 0.03333333
```

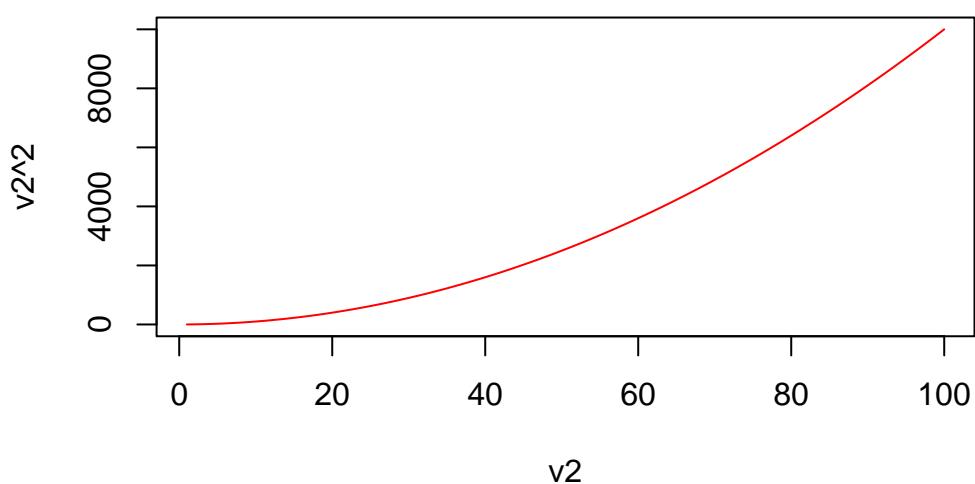
```
[91] 0.06593407 0.13043478 0.02150538 0.03191489 0.06315789 0.12500000  
[97] 0.02061856 0.03061224 0.06060606 0.12000000  
#Using strings in R  
mystring <- "Ecology"  
vstrg <- c("Anna", "Peter", "Xavier")  
vstrg[2]  
  
[1] "Peter"  
#making plots in R  
plot(v2,v2)
```



```
plot(v2,v2^2,type="l")
```

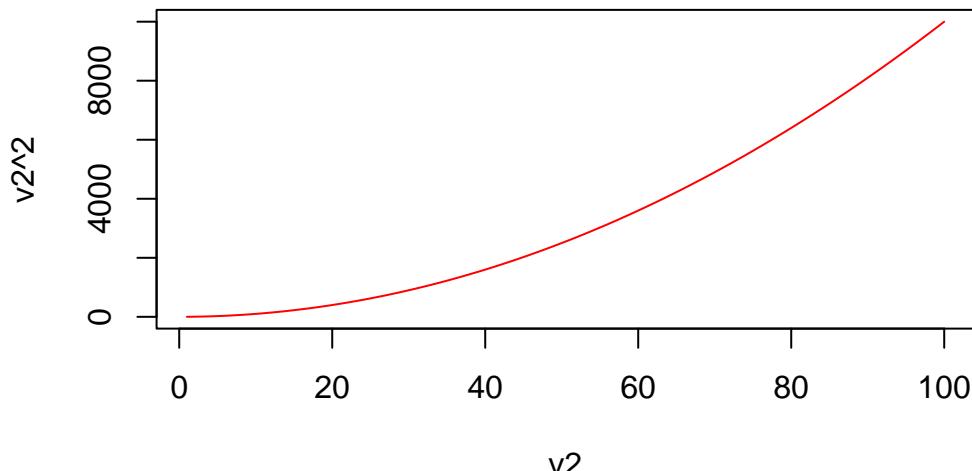


```
plot(v2,v2^2,type="l",col="red")
```



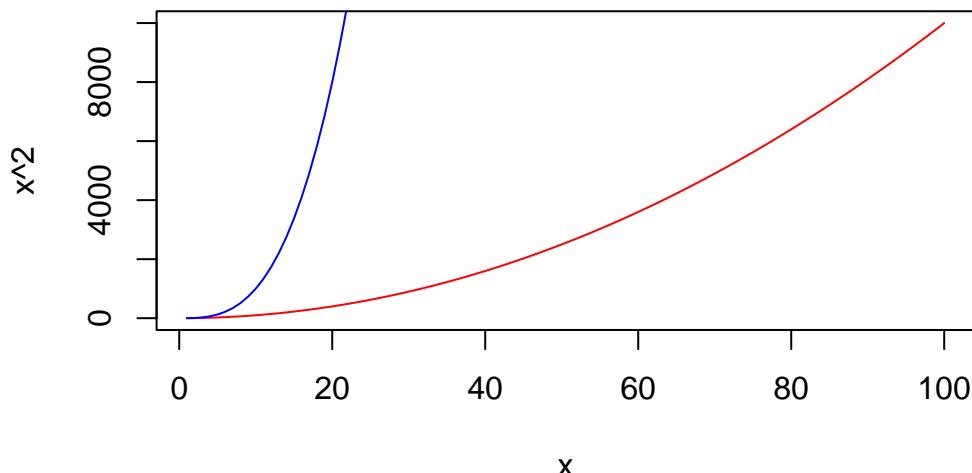
```
plot(v2,v2^2,type="l",col="red",main="My beautiful plot")
```

## My beautiful plot



```
plot(v2,v2^2,type="l",col="red",main="My beautiful plot",xlab="x",
      ylab="x^2")
lines(v2,v2^3,col="blue")
```

## My beautiful plot



```
# Matrices in R
m <- matrix(5,3,2)
m
```

```
[,1] [,2]
[1,]    5     5
```

```
[2,]    5    5
[3,]    5    5
m2 <- matrix(1:6,3,2)
m2
 [,1] [,2]
[1,]    1    4
[2,]    2    5
[3,]    3    6
t(m2) # transposes matrix

 [,1] [,2] [,3]
[1,]    1    2    3
[2,]    4    5    6

x <- 1:4
y <- 5:8

m3<-cbind(x,y)
m3

      x  y
[1,] 1 5
[2,] 2 6
[3,] 3 7
[4,] 4 8
m4<-rbind(x,y)
m4

 [,1] [,2] [,3] [,4]
x     1     2     3     4
y     5     6     7     8
# Indexing matrices
m3[3,2] #element in row 3 and column 2

y
7
m3[1,] #entire first row

x  y
1 5
m3[,1] #entire first column

[1] 1 2 3 4
```

```

colnames(m3)<-c("col1","col2")
m3

  col1 col2
[1,]    1    5
[2,]    2    6
[3,]    3    7
[4,]    4    8

m3[, "col2"]

[1] 5 6 7 8

# Lists in R
mylist <- list(elem1=m, elem2=v2, elem3="my list")
mylist$elem2

[1]   1   2   3   4   5   6   7   8   9   10  11  12  13  14  15  16  17  18
[19]  19  20  21  22  23  24  25  26  27  28  29  30  31  32  33  34  35  36
[37]  37  38  39  40  41  42  43  44  45  46  47  48  49  50  51  52  53  54
[55]  55  56  57  58  59  60  61  62  63  64  65  66  67  68  69  70  71  72
[73]  73  74  75  76  77  78  79  80  81  82  83  84  85  86  87  88  89  90
[91]  91  92  93  94  95  96  97  98  99 100

# Dataframes
df <- as.data.frame(m3)
df$col1

[1] 1 2 3 4

```

## A.2 Iterations and conditional expressions

```

# FOR loops

for (k in 1:10) # for k =1, 2, 3, 4, 5,...10
  print (k^2)  #do this

[1] 1
[1] 4
[1] 9
[1] 16
[1] 25
[1] 36
[1] 49
[1] 64
[1] 81
[1] 100

```

```
R <- 1.2
n <- 1
print(n[1])

[1] 1
for (t in 1:100)
{
  n[t+1] <- R*n[t]
  print(n[t+1])
}

[1] 1.2
[1] 1.44
[1] 1.728
[1] 2.0736
[1] 2.48832
[1] 2.985984
[1] 3.583181
[1] 4.299817
[1] 5.15978
[1] 6.191736
[1] 7.430084
[1] 8.9161
[1] 10.69932
[1] 12.83918
[1] 15.40702
[1] 18.48843
[1] 22.18611
[1] 26.62333
[1] 31.948
[1] 38.3376
[1] 46.00512
[1] 55.20614
[1] 66.24737
[1] 79.49685
[1] 95.39622
[1] 114.4755
[1] 137.3706
[1] 164.8447
[1] 197.8136
[1] 237.3763
[1] 284.8516
[1] 341.8219
[1] 410.1863
[1] 492.2235
[1] 590.6682
```

```
[1] 708.8019
[1] 850.5622
[1] 1020.675
[1] 1224.81
[1] 1469.772
[1] 1763.726
[1] 2116.471
[1] 2539.765
[1] 3047.718
[1] 3657.262
[1] 4388.714
[1] 5266.457
[1] 6319.749
[1] 7583.698
[1] 9100.438
[1] 10920.53
[1] 13104.63
[1] 15725.56
[1] 18870.67
[1] 22644.8
[1] 27173.76
[1] 32608.52
[1] 39130.22
[1] 46956.26
[1] 56347.51
[1] 67617.02
[1] 81140.42
[1] 97368.5
[1] 116842.2
[1] 140210.6
[1] 168252.8
[1] 201903.3
[1] 242284
[1] 290740.8
[1] 348889
[1] 418666.7
[1] 502400.1
[1] 602880.1
[1] 723456.1
[1] 868147.4
[1] 1041777
[1] 1250132
[1] 1500159
[1] 1800190
[1] 2160228
[1] 2592274
```

```
[1] 3110729
[1] 3732875
[1] 4479450
[1] 5375340
[1] 6450408
[1] 7740489
[1] 9288587
[1] 11146304
[1] 13375565
[1] 16050678
[1] 19260814
[1] 23112977
[1] 27735572
[1] 33282687
[1] 39939224
[1] 47927069
[1] 57512482
[1] 69014979
[1] 82817975

R <- 1.2
n <- 1
for (t in 1:100)
  n[t+1] <- R*n[t]

# IF conditional statement

# logical operators
# == equal to
# > greater than
# < smaller than
# >= greater or equal
# <= smaller or equal
# != different from
# && and
# || or

if (3>2) print ("yes")

[1] "yes"
if (3==2) print ("yes") else print("no")

[1] "no"
if ((3>2)&&(4>5)) print ("yes")

for (k in 1:10) # for k =1, 2, 3, 4, 5,...10
```

```
if (k^2>20) print (k^2)

[1] 25
[1] 36
[1] 49
[1] 64
[1] 81
[1] 100
```

### A.3 Writing functions

```
# creating FUNCTIONS in r

pythagoras <- function (c1,c2)
{
  h <- sqrt (c1^2 + c2^2)
  return (h)
}
```

```
pythagoras(1,1)
```

```
[1] 1.414214
```

```
pythagoras(5,5)
```

```
[1] 7.071068
```

```
pythagoras(10,1)
```

```
[1] 10.04988
```

```
# regression in R
```

```
help(lm)
x <- c(1,2,3,4)
y <- c(1.1,2.3,2.9,4.1)
plot(x,y)
myreg<-lm(y ~ x)
summary(myreg)
```

Call:

```
lm(formula = y ~ x)
```

Residuals:

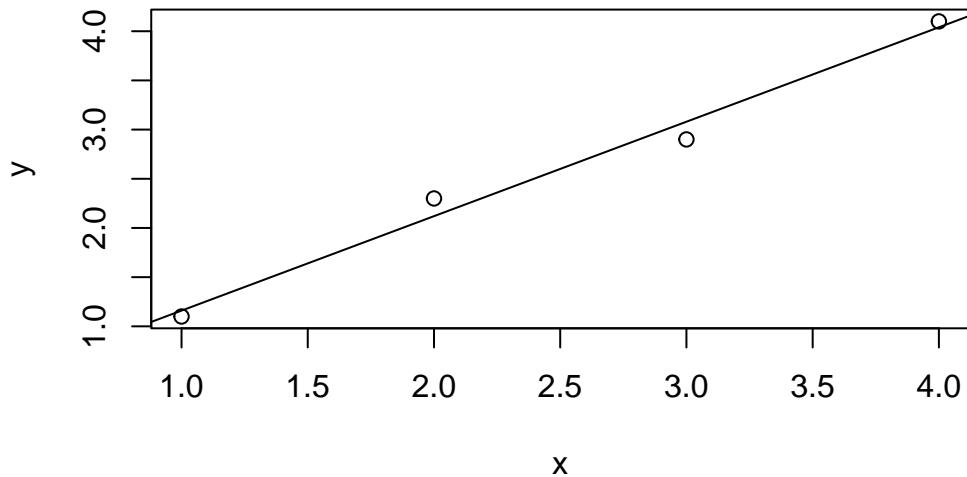
1	2	3	4
-0.06	0.18	-0.18	0.06

```
Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) 0.20000   0.23238   0.861  0.48012
x           0.96000   0.08485  11.314  0.00772 **

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Residual standard error: 0.1897 on 2 degrees of freedom  
 Multiple R-squared: 0.9846, Adjusted R-squared: 0.9769  
 F-statistic: 128 on 1 and 2 DF, p-value: 0.007722

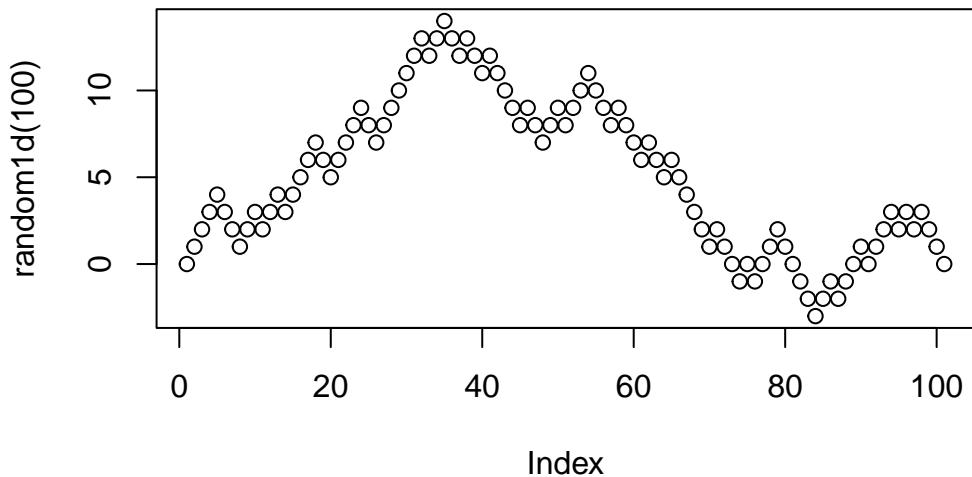
```
abline(myreg)
```



## A.4 Random numbers and statistical distributions

```
random1d<-function(tmax)
{
x<-0
for (t in 1:tmax)
{
  r<-runif(1)
  if (r<1/2)
    x[t+1]<-x[t]+1 else
    x[t+1]<-x[t]-1
}
return(x)
}

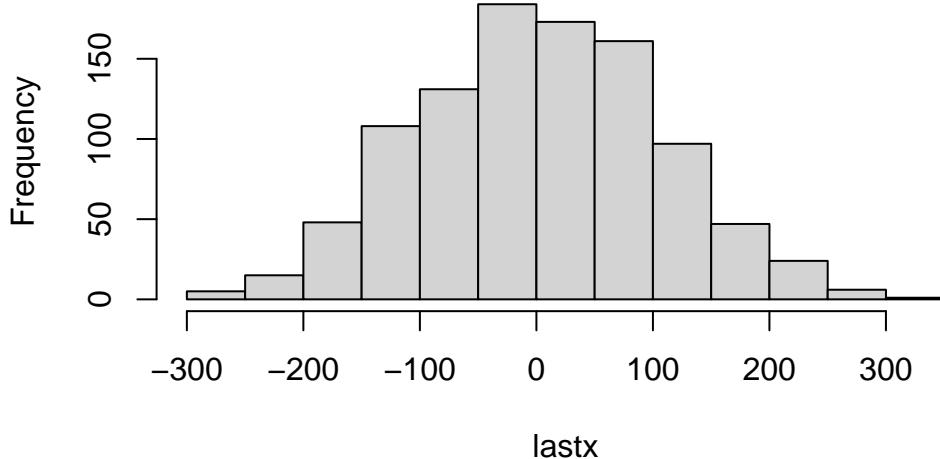
plot(random1d(100))
```



```
tmax<-10000
lastx<-0
for (i in 1:1000)
{
  x<-random1d(tmax)
  lastx[i]<-x[tmax]
}

hist(lastx)
```

Histogram of lastx

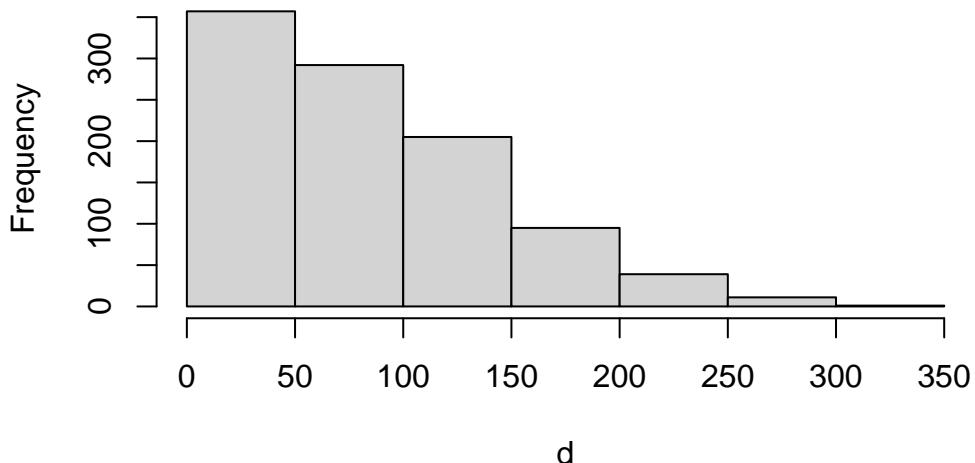


```
mean(lastx)
```

```
[1] 2.556
```

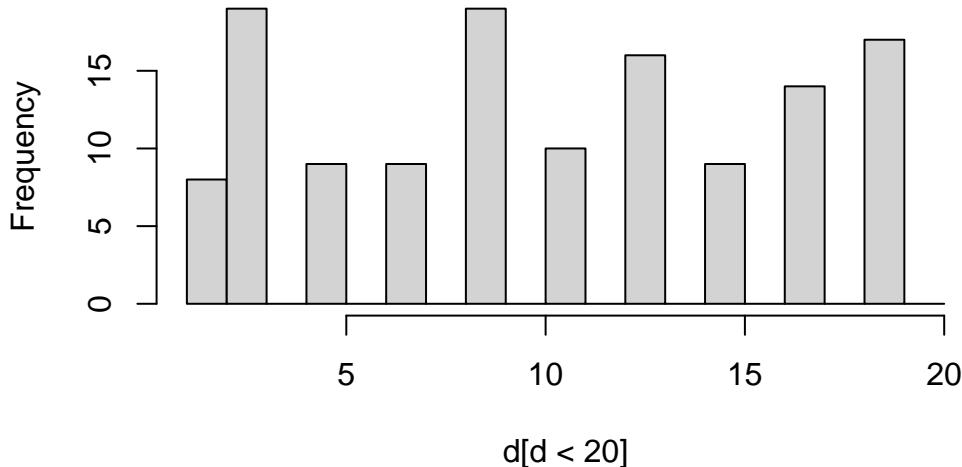
```
d<-sqrt(lastx^2)  
hist(d)
```

Histogram of d



```
mean(d)  
[1] 84.246  
median(d)  
[1] 73  
max(d)  
[1] 313  
hist(d[d<20],breaks=c(1:20))
```

## Histogram of $d[d < 20]$



## A.5 Spatial analysis

### A.5.1 Shapefiles and Raster (Isabel Rosa)

When you work with spatial data, essentially you use two types of data:

- 1) vector data (i.e., shapefiles): stores the geometric location and attribute information of geographic features. These can be represented by points, lines, or polygons (areas).
- 2) matricial data (i.e., raster): consists of a matrix of cells (or pixels) organized into rows and columns (or a grid) where each cell contains a value representing information. They can be categorical or continuous and have multiple bands.

For more information on the tree cover datasets, please see: [https://earthenginepartners.appspot.com/science-2013-global-forest/download\\_v1.2.html](https://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.2.html)

```
# read in shapefile using rgdal
sc <- readOGR(".", "SantaCatarina")

# import municipalities and settlements shapefiles
sc_mun <- readOGR(".", "SantaCatarina_mun")
br_sett <- readOGR(".", "Brazil_settlements")

# always good to check the contents of your dat
#str(br_sett)

# visualize one of the variables
spplot(sc_mun, z="Shape_Area", main = "Municipality Area (km2)")
```

```
# read in raster
tc<-raster("tree_cover.tif")

# import loss and gain rasters here
tl<-raster("loss.tif")
tg<-raster("gain.tif")

# for multiple band rasters, you can choose to import just one or all bands
#r2 <- raster("tree_cover_multi.tif", band=2)

# note that the value 255, which is Hansen's nodata value was not recognized as such
NAvalue(tg) # check first
NAvalue(tc)<-255 #fix it by forcing 255 to be the nodata
NAvalue(tl)<-255 #fix it by forcing 255 to be the nodata
NAvalue(tg)<-255 #fix it by forcing 255 to be the nodata

# visualize one of the rasters
par(mfrow=c(1,3))
plot(tc, main = "Tree Cover (%)")
plot(tl, main = "Tree Cover Loss (binary)")
plot(tg, main = "Tree Cover Gain (binary)")
```

### A.5.2 Reference systems

Coordinate systems are essential to understand when working with spatial data. Some reading material on this can be found here: Essentially, if one wants to know which position of the Earth we refer to, coordinates of geospatial data require a reference system:

- 1) geodesic/geographic coordinates need an order (lat/long), a unit (e.g., degrees) and a datum (a reference ellipsoid: e.g. WGS84)
- 2) cartesian/projected coordinates (e.g. UTM, web Mercator) need also measurement units (e.g., meters), and some way of encoding how they relate to geodesic coordinates, in which datum (this is handled by the GIS system)

### A.5.3 Operations with Shapefiles

Clip: in R you can clip using the command “intersect”, so that intersect(feature to be clipped, clip feature) Select: you can use a boolean selection to subset the features of your shapefile, for instance if you just want to look at settlements with a minimum number of habitants, so that Population > median(Population) There are several options, have a look at this great tutorial: <http://www.rspatial.org/spatial/rst/7-vectmanip.html>

```
# Clip the settlement features using the Santa Catarina shapefile
sc_sett<-intersect(br_sett, sc)

#sc_sett$med <- sc_sett$population > median(sc_sett$population) # oops! annoyingly our population va
```

```
# convert to original numerical values
sc_sett$population<-as.numeric(as.vector(sc_sett$population))
# careful! applying as.numeric alone it will not work!!

# visualize results
plot(sc_sett, main = "Settlements in Santa Catarina")
spplot(sc_sett, z="population", main = "Population per Settlement (people)")

# select settlements larger than the median value
sc_sett$med <- sc_sett$population > median(sc_sett$population)
sc_largesett <- sc_sett[sc_sett$med == 1, ]

# visualize results
par(mfrow=c(1,2))
plot(sc_sett, main = "All Settlements")
plot(sc_largesett, main = "Largest Settlements")
```

#### A.5.4 Operations with Rasters

There are many operations you can do with rasters, and these are more frequently used in spatial analyses than shapefiles. Here I will just illustrate a couple of simple operations: - Global/Raster statistics - obtain a value that summarizes the whole raster layer - Cell statistics (pixel-by-pixel operation): obtains a value per pixel - Focal statistics (operation that takes into account neighborhood of central cell) - results in raster of same of different size - Zonal statistics - calculates summary statistics of a give raster (e.g., elevation) based on pre-defined zones (e.g., administrative boundaries, biomes). Outputs a table with the values per zone. For more great examples, have a look here: <http://www.rspatial.org/spatial/rst/8-rastermanip.html>

```
# sum the loss and gain rasters to know where there was simultaneous loss and gain in Santa Catarina
tclg<-tl+tg
par(mfrow=c(1,3))
plot(tl, main = "Forest Loss")
plot(tg, main = "Forest Gain")
plot(tclg, main = "Forest Loss and Gain")

# you can also try to create three new rasters and work with them
# create a new raster
r <- raster(ncol=10, nrow=10, xmx=-80, xmn=-150, ymn=20, ymx=60)
values(r) <- runif(ncell(r)) # assign random values
#plot(r)

# create two more rasters based on the first one
r2 <- r * r
r3 <- sqrt(r)

# either stack or brick them
```

```

s <- stack(r, r2, r3)
#b <- brick(s)

# Raster statistics - calculate several statistics per raster layer (i.e., sum, mean, median)
cellStats(s, "sum") # outputs a value per raster

# Cell statistics - calculate several statistics per pixel (i.e., sum, mean, median)
par(mfrow=c(2,2))
plot(r, main ="Random 1")
plot(r2, main ="Random 2")
plot(r3, main ="Random 3")
plot(overlay(s, fun="mean"), main="Average Values") # outputs a new raster

# Focal statistics - calculate mean accounting for the neighborhood values, compare with previous ou
f1 <- focal(tc, w=matrix(1,nrow=5,ncol=5) , fun=mean)
plot(f1, main = "Average forest cover 5x5")
# sum the loss, vary window size
f2 <- focal(tl, w=matrix(1,nrow=5,ncol=5) , fun=sum)
plot(f2, main = "Total forest loss 5x5")
# sum the gain, vary window size
f3 <- focal(tg, w=matrix(1,nrow=5,ncol=5) , fun=sum)
plot(f3, main = "Total forest gain 5x5")

# plot 4 maps with different window sizes
par(mfrow=c(2,2))
for(i in c(5,15,25,55)){
  f_w <- focal(tc, w=matrix(1,nrow=i,ncol=i) , fun=sum)
  plot(f_w, main = paste0("Window size: ", i))
}

# Zonal Statistics - using two rasters
sc_tc_mean_loss <- zonal(tc, tl, fun=mean) #average tree cover in loss areas
sc_tc_mean_gain <- zonal(tc, tg, fun=mean) #average tree cover in gain areas

# average tree cover loss
sc_tc_mean_loss

# average tree cover gain
sc_tc_mean_gain

```

### A.5.5 Operations with both Rasters and Shapefiles

Here I'll show a couple of examples of operation that use feature data as inputs and output rasters: Distance to features - calculates the euclidean distance from each cell/pixel to the closest feature (e.g., roads, settlements). Outputs a raster file with these distances. Interpolation: a world in itself!

Very vey short example provided here (based on a single method, IDW), please see more here: <http://www.rspatial.org/analysis/rst/4-interpolation.html> To better understand interpolation I advise you to read first about spatial autocorrelation: <http://www.rspatial.org/analysis/rst/3-spauto.html>

To use interpolation metrics you need to load another packaged called gstat Inverse distance weighted (IDW) - See more also here: <http://desktop.arcgis.com/en/arcmap/10.3/tools/3d-analyst-toolbox/how-idw-works.htm>

```
# create an empty raster (little trick using existing raster)
dist_sett<-tc*0
# or you can create an empty one like before
# dist_sett <- raster(ncol=ncol(tc), nrow=nrow(tc), xmx=extent(tc)$xmax, xmn=extent(tc)$xmin, ymn=exten

# Distance to points
dist_sett <- distanceFromPoints(dist_sett, sc_sett)

# you can then mask the outside area of Santa Catarina
dist_sett <- mask(dist_sett, tc)

# plot results
plot(dist_sett, main = "Distance to settlements (m)")

# load gstat
library(gstat)
idw_sett<-tc*0

# compute the model, see reference for more detail
gs <- gstat(formula=population~1, locations=sc_sett, nmax=5, set=list(idp = 2))
idw_out <- interpolate(idw_sett, gs)

## [inverse distance weighted interpolation]
sc_pop <- mask(idw_out, tc)
plot(sc_pop, main = "Santa Catarina Population")
```

### A.5.6 Export Shapefiles and Rasters

It's very easy to export both shapefiles and rasters from R to be visualized in QGIS or ArcMap.

```
# Save feature layers (point, polygon, polyline) to shapefile
writeOGR(sc_largesett, dsn=".\"", layer="SC_largeSett", driver="ESRI Shapefile" )

# or
#shapefile(sc_largesett, "SC_largeSett.shp", overwrite=TRUE)

#Exporting raster
writeRaster(sc_pop, filename="SC_popmap", format="GTiff" )
```

## A.6 Working with biodiversity data: GBIF, EBV Portal (Corey Callaghan, Luise Quoss)

First we load the library `rgbif`.

```
library(rgbif)
library(tidyverse)
```

Now we will download observations of a species. Let's download observations of the common toad "Bufo bufo".

```
matbufobufo<-occ_search(scientificName="Bufo bufo", limit=500, hasCoordinate = TRUE, hasGeospatialIssue = FALSE)
```

Let's examine the object `matbufobufo`

```
class(matbufobufo)
matbufobufo
```

Let's download data about octupusses. They are in the order "Octopoda". First we need to find the GBIF search key for Octopoda.

```
a<-name_suggest(q="Octopoda",rank="Order")
key<-a$data$key
```

```
octopusses<-occ_search(orderKey=key,limit=2000, hasCoordinate = TRUE, hasGeospatialIssue = FALSE)
```

Show the result

```
octmat<-octopusses$data
head(octmat)
```

Count the number of observations per species using tidyverse and pipes

```
#class(octmat)
octmat %>%
  group_by(scientificName) %>%
  summarise(sample_size=n()) %>%
  arrange(desc(sample_size)) %>%
  mutate(sample_size_log=log(sample_size,2)) %>%
  ggplot(aes(x = sample_size_log)) + geom_histogram()
```

Plot the records on an interactive map. First load the leaflet package.

```
library(leaflet)
leaflet(data=octmat) %>% addTiles() %>%
  addCircleMarkers(lat= ~decimalLatitude, lng = ~decimalLongitude, popup=~scientificName)
```

### A.6.1 Version 2 (Isabel Rosa)

Here are the packages we'll need.

```
library(rgbif)
library(tidyverse)
library(raster)
library(maps)
library(leaflet)
library(sdm predictors)
```

First let's pick an example species to download data for. We will only download 500 observations to keep it simple for now. If you were doing this for real, you would download all data for that species (see notes at the end). I will choose the European Robin: [https://en.wikipedia.org/wiki/European\\_robin](https://en.wikipedia.org/wiki/European_robin).

```
species <- occ_search(scientificName="Erithacus rubecula", limit=500, hasCoordinate = TRUE, hasGeosp
```

What does this object look like?

```
class(species)

species
```

It is a special object of class `gbif` which allows for the metadata and the actual data to all be included, as well as taxonomic hierarchy data, and media metadata. We won't worry too much about the details of this object now. But we do want to get a dataframe we can work with! To do this, we have one extra step.

```
sp_dat <- species$data

class(sp_dat)

head(sp_dat)
```

So this was just for one species. Lets broaden this out a little bit. What if we were interested in many species of a given order/class? Here, we will choose an entire order to download. I will choose owls! <https://en.wikipedia.org/wiki/Owl>. First, we need to find the 'key' that `gbif` uses for that order and then pass it to our GBIF download function. Again, we are only getting a small number of records for illustration purposes.

```
a <- name_suggest(q='Strigiformes')

key <- a$data$key

order <- occ_search(orderKey=key, limit=1000, hasCoordinate = TRUE, hasGeospatialIssue=FALSE)
```

What kind of object is 'order'? As with `species`, we need to turn it into a dataframe to work with.

```
order_dat <- order$data

class(order_dat)
```

```
head(order_dat)
```

Count the number of observations by species

```
order_dat %>%
  group_by(scientificName) %>%
  summarize(sample_size=n()) %>%
  arrange(desc(sample_size))
```

Plot the records on an interactive map. First for our chosen species.

```
leaflet(data = sp_dat) %>%
  addTiles() %>%
  addCircleMarkers(lat = ~decimalLatitude, lng = ~decimalLongitude, popup = ~scientificName)
```

Then for the order we chose.

```
leaflet(data = order_dat) %>%
  addTiles() %>%
  addCircleMarkers(lat = ~decimalLatitude, lng = ~decimalLongitude, popup = ~scientificName)
```

## A.7 Climate data

Let's play with some global climate data and overlay that with our GBIF observations.

```
mean_temp_map <- getData(name="worldclim", res=10, var="tmean")
plot(mean_temp_map)
```

Each month has separate values for each cell. To combine to a yearly value, we just take the mean.

```
annual_mean_temp <- mean(mean_temp_map)/10 #data comes as degrees * 10
```

Now plot this.

```
plot(annual_mean_temp)
```

To get out the values for the organism of interest, we use `extract`.

```
org_temp <- extract(annual_mean_temp, cbind(x=sp_dat$decimalLongitude, y=sp_dat$decimalLatitude))
```

Now we will visualize how the global distribution of temperature values compares with the species' distribution of temperature values. This shows the distribution of temps where robins are found versus the global distribution of temps.

```
temp <- tibble(mean_temp=getValues(annual_mean_temp)) %>%
  filter(!is.na(mean_temp))

temp_org <- tibble(organism_temp=org_temp) %>%
  filter(!is.na(organism_temp))
```

```
ggplot(temp, aes(x=mean_temp))+  
  geom_density(fill="blue") +  
  geom_density(data=temp_org, aes(x=organism_temp), fill="red") +  
  theme_bw()
```

## A.8 Intro to apply, pipes, ggplot2, tidyverse.

### A.8.1 Introduction to ggplot

```
cars  
library(ggplot2)  
  
ggplot(data=cars, mapping=aes(x=speed,y=dist)) + geom_point(colour="red")  
  
plot(cars$speed,cars$dist)  
  
#Introduction to R - 9  
  
  
# a recursive function that calculates a factorial  
myfun <- function(x)  
{  
  if (x==1)  
    return (1)  
  else return(x*myfun(x-1))  
}  
  
myfun(1:10) # does not work  
  
#option1 - with a for loop  
start_time <- Sys.time()  
y<-0  
for (i in 1:100)  
  y[i]<-myfun(i)  
end_time <- Sys.time()  
end_time-start_time  
y  
plot(y,type="l")  
  
#option 2 - with apply  
start_time <- Sys.time()  
y<-sapply(1:100,myfun)  
end_time <- Sys.time()  
end_time-start_time  
y
```

```
# selecting a subset from a matrix and applying a function to a column of that subset

setwd("~/iDiv Dropbox/Henrique Pereira/Teaching/Spatial Ecology/Spatial Ecology 2022/2_Lab_assignment")
Florida <- read.csv("Florida.csv")

# number of species for year 1970 and route 20
tapply(Florida$Abundance, Florida$Route==20 & Florida$Year==1970, length)

# matrix with number of species per route and per year
out<-tapply(Florida$Abundance, list(Florida$Route, Florida$Year), length)

names(out[,1])
plot(out[10,])
plot(out[20,])

shannon<-function(x)
{
  p<-x/sum(x)
  - sum(p*log(p))
}

out<-tapply(Florida$Abundance, list(Florida$Route, Florida$Year), shannon)
plot(out[10,])

library(tidyverse)

#our first pipe
x<-rnorm(1000)
hist(x)

rnorm(1000) %>% hist

t<-1:ncol(out)
myreg<-lm(out[10,]~t)
summary(myreg)
plot(out[10,])
abline(myreg)

lm(out[10,]~t) %>% summary
plot(out[10,])
lm(out[10,]~t) %>% abline

#ggplot
mat=cbind(t,out[10,])
```

```
data(cars)
colnames(mat)<-c("time","shannon")
mat<-as.data.frame(mat)

myplot <- ggplot(mat, aes(time,shannon))+  
  geom_point()  
myplot

myplot <- ggplot(mat, aes(time,shannon))+  
  geom_line()  
myplot

data(cars)
myplot <- ggplot(cars, aes(speed,dist))+  
  geom_point()+geom_line()
myplot

data(cars)
myplot <- ggplot(cars, aes(speed,dist))+  
  geom_point()+geom_smooth(method="lm")
myplot

data(cars)
myplot <- ggplot(cars, aes(speed,dist))+  
  geom_point()+geom_smooth(method="lm")+scale_x_log10()+scale_y_log10()
myplot
```

## Appendix B

# Computational labs

### B.1 Climate space of an ectotherm

Solar radiation and convection are the two main pathways for animals such as small lizards. In this case, the total heat flux ( $f$ ) into the animal is given by the **heat flux equation**:

$$f = q - h * (b - a)$$

- $q$  = solar radiation (cal/h)
- $h * (b - a)$  = heat loss through convection
- $b$  = body temperature of the animal ( $^{\circ}$ C)
- $a$  = air temperature ( $^{\circ}$ C)
- $h$  = convection heat transfer coefficient (cal/h/  $^{\circ}$ C)

#### 1. *Equilibrium body temperature*

- a. Assuming that air temperature is  $18^{\circ}$ C, and  $h = 50$  cal/h, plot the lizard's equilibrium body temperature as a function of solar radiation. Assume that solar radiation varies between 0 and 1500 cal/h

#### 2. *Climate space of a Lizard*

- a. Draw the climate space of the lizard by drawing the polygon that is limited by the minimum and maximum temperatures that the lizard can support, as a function of solar radiation. Consider that the upper lethal limit for the body temperature ( $b_{max}$ ) is  $36^{\circ}$ C and the lower lethal limit for the body temperature ( $b_{min}$ ) is  $24^{\circ}$ C.

**Hint:** `Polygon` - draws the polygons whose vertices are given in x and y.

#### 3. *Air Temperature and solar radiation throughout the day in two locations*

- a. Plot the following values of air temperature and solar radiation that are available throughout a day in two locations. For:
  - Times of the day

```
t = c("00:00", "03:00", "06:00", "09:00", "12:00",
    "15:00", "18:00", "21:00", "00:00")
```

- Solar radiation in the rock habitat

```
rock_q = c(150, 150, 800, 1100, 1300, 1200, 800, 400, 150)
```

- Air temperature in the rock habitat

```
rock_a = c(18, 13, 10, 14, 21, 24, 22, 20, 18)
```

- Solar radiation in the bush habitat

```
bush_q = c(150, 150, 450, 600, 650, 650, 350, 200, 150)
```

- Air temperature in the bush habitat

```
bush_a = c(18, 13, 10, 14, 21, 24, 22, 20, 18)
```

- b. At which time of the day is the lizard on the rock, and at which time is it at the bush?  
Is there any time when the lizard cannot be at any of the locations?

#### 4. *Body temperature of A. cristatellus in two different habitats*

Start by reading the Section C.1. The tutorial has a data frame containing data on individuals *A. cristatellus* living in urban and forested areas in three cities in Puerto Rico, giving us the perfect opportunity to assess the potential thermal effects of habitat upon this species. To do this:

- Make a linear model for individuals of *A. cristatellus* living only in natural habitats (`context = natural`) and another for individuals living in urban habitats (`context = urban`).

**Hint:** to filter the data you can use the `subset` function in R

```
# example filtering data from anoles only from San Jose sites
df_sanjose <- subset(df, Site == "San Jose")
```

- Is there a habitat where lizards are consistently warmer? If so, provide an ecological explanation (quantitatively) for this observation (assume an ambient temperature of 30 °C).
- Is your model appropriate for explaining your data?

## B.2 Optimal foraging theory

### 1. Predator with a strategy for maximizing energy.

Let  $ai$  be the point abundance per unit of time of prey type  $i$ ,  $ei$  be the caloric content of prey type  $i$ ,  $hi$  be the time it takes to consume prey type  $i$ ,  $ew$  is the energy expended per unit of time by the predator while searching for prey, and  $eh$  is the energy expended per unit of time by the predator to ingest prey. Consider that there are only two types of prey and that:

Strategy 1: Chosing prey of type 1

Strategy 2: Chosing prey of type 2

Strategy 3: Chosing both preys

- a. Show that if  $e1 > e2$  and  $h1 < h2$  then the second strategy is never a optimal strategy
- b. Plot and comment the graph of the energy gain per unit of time for the strategy of consuming both preys and for the strategy of consuming only the best prey. Make the abundances vary between 0.005 and 0.5 ind/s for the best prey. Consider the abundance of the worse prey to be 0.05 ind/s and 0.01 ind/s. Consider an active predator with the following physiological parameters:

$$e1 = 10J; e2 = 100J; h1 = 1s; h2 = 60s; ew = 1 J/s; eh = 1 J/S$$

### 2. Predator with a strategy of sit-and-wait.

$Ew$  is the energy expended per unit of time by the predator while waiting for its prey,  $ep$  is the energy expended per unit of time by the predator while chasing the prey,  $v$  is the velocity of the predator in chase and  $a$  is the point abundance of preys per unit of time.

- a. Produce a graph of energy gain per unit of time in function of the size of the feeding territory. Consider the following values for the parameters of the predator and prey:  $ew = 0,1 J/s$ ;  $ep = 1 J/S$ ;  $v = 0,5 m/s$ ;  $a = 0,005 \text{ ind/s/m}^2$ ; and  $e = 10$ ;

### B.3 Evolutionary games

1. **The Prisoners Dilemma Competition.** In this class we will have a competition of algorithms for playing the prisoner's dilemma.

a) Write a function that takes as parameters two vectors that account with the history of the previous plays and returns one play (i.e., Cooperate – “C” or defect – “D”). This play should try to be the best response to the history of past moves. One example of such a function is:

```
strat<-function(own,opponent)
{
  n <- length(opponent)
  if(n==0) "D"
  else
    if(own[n]=="D") opponent[n]
    else "C"
}
```

- b) Use the function pd\_sim (see below) to play your strategy with the strategy of the other groups (ask for each group their function(s)) and with itself, in an iterative game with x moves. Compare the results of the cumulative rewards as well as the sequence of moves. Report to the rest of groups the values of the rewards for each of the tournaments. What was the best strategy? What strategies are best responses to themselves?

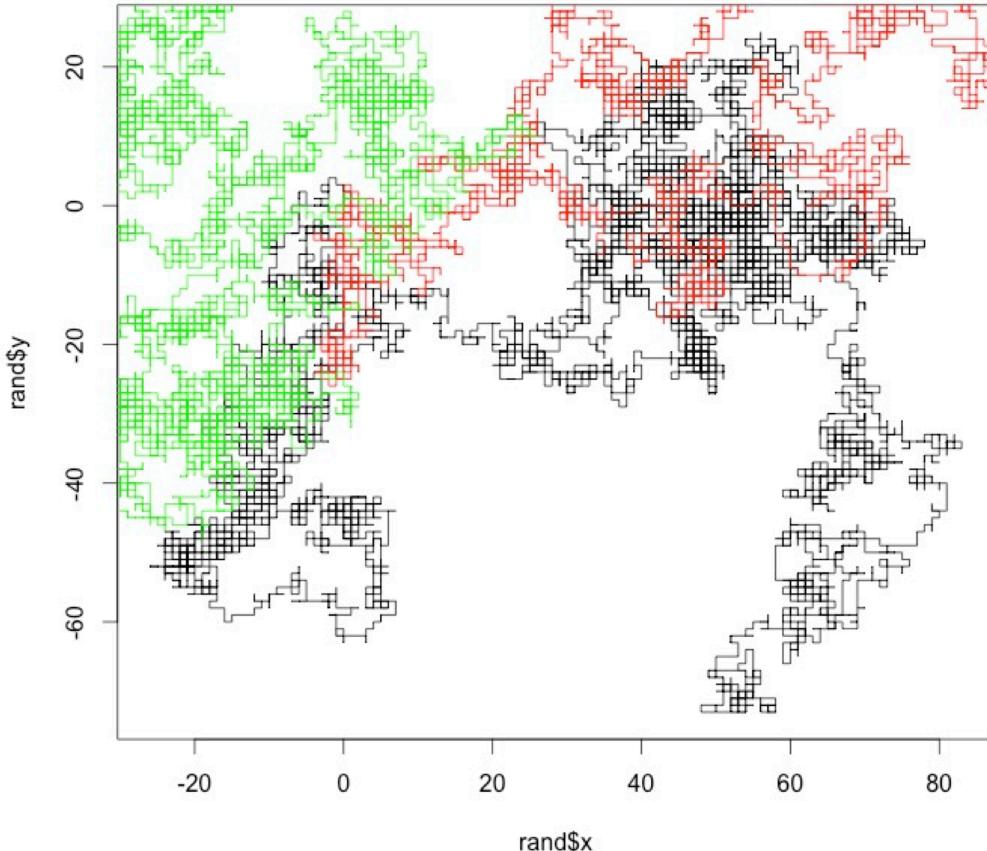
```
pd_sim<-function(p1_strat,p2_strat,n)
{
  w1<-0          #accumulated pay-off (fitness) of player 1
  w2<-0          #accumulated pay-offs of player 2
  h1<-NULL        #history of plays of player 1
  h2<-NULL        #history of plays of player 2

  for (t in 1:n)
  {
    a1<-p1_strat(h1,h2)
    a2<-p2_strat(h2,h1)
    p1<-mat[a1,a2]
    p2<-mat[a2,a1]
    w1<-w1+p1
    w2<-w2+p2
    h1[t]<-a1
    h2[t]<-a2
  }
  list(w1=w1,w2=w2,h1=h1,h2=h2)
}
```

## B.4 Dispersal and the random-walk

### 1. Random walk for 1 individual

- a) Create your own code to simulate an individual random walk. Assume that the starting point is always  $x,y = (0,0)$  and the probability of an individual to choose any direction (i.e. left, right, up or down) is the same. It should be a function taking as argument the number of steps and returning a list of two vectors, one with the x positions over time and another with the y positions overtime.
- b) Plot together the random walks (at least 5000 steps) of a few individuals.



### 2. Random walk for several ( $n$ ) individuals

- a) Create your own code to simulate random walks by several ( $n$ ) individuals and returns the last position of each individual. It should be a function that takes as arguments the number of individuals and the numbers of time steps, and returns a list of two vectors, the last x position of each individual, and the last y position of each individual.
- b) Create a histogram showing the distribution of the x and y last positions of 10 000 individuals after 10 time steps, 100 time steps and 1 000 time steps.
- c) Create a function that receives as parameters a vector of values  $xlast$ , a mean value ( $meanx$ ) and a standard deviation ( $stdx$ ) and returns the log-likelihood of observing those values for those parameters.

- d) Find the value meanx and stdx that maximize the likelihood of the observations. Are they the same as mean(xlast) and std(xlast)? Why?
- e) **Extra credit:** Create a histogram showing the distribution of the distance to the origin ( $\sqrt{x^2 + y^2}$ ) of the last positions of 10 000 individuals for 10 time steps, 100 time steps, 1000 time steps and 10000 time steps. What is the relationship between the length of the randomwalk and the mean distance? Fit the Rayleigh distribution  $(2 r / \sigma^2) * \exp(-r^2/2 \sigma^2)$  using non-linear fitting to each of the histograms and overlay it on the graph.

## B.5 Pandemic growth

1. **The exponential dynamics of the pandemic.** In early 2020, the first wave of the global pandemic of COVID-19 hit several European countries. Here we will plot the data for those countries and fit an exponential growth model.

- a. Load the cumulative infected individuals time series from the COVID-19 pandemic in five countries. Each time series starts after the first fifteen infections are detected.<sup>1</sup>

```
it <- c(17, 79, 132, 229, 322, 400, 650, 888, 1128, 1689, 2036, 2502,
3089, 3858, 4636, 5883, 7375, 9172, 10149, 12462, 15113, 17660, 21157,
23980, 27980, 31506, 35713, 41035, 47021, 53578) #Feb22–March22

es <- c(17, 35, 54, 82, 136, 192, 267, 348, 531, 764, 1094, 1527, 2299,
3274, 4427, 5958, 7641, 9785, 11491, 13994, 17688, 21735, 26304, 31750,
36616, 41262, 48953, 57506, 66460, 75641) #Feb27–March27

fr <- c(17, 38, 57, 100, 130, 178, 212, 285, 423, 613, 716, 1126, 1412,
1784, 2281, 2876, 3661, 4499, 5423, 6633, 7730, 9134, 10995, 12612, 14459,
16018, 19856, 22302, 25233, 29155) #Feb27–March27

uk <- c(18, 22, 30, 42, 47, 69, 109, 164, 220, 271, 352, 412, 469, 617,
876, 1282, 1766, 2244, 2605, 3047, 3658, 4427, 5426, 6481, 7736, 8934,
10312, 12650, 15025, 17717) #Feb27–March27

de <- c(17, 21, 47, 57, 111, 129, 157, 196, 262, 400, 684, 847, 902, 1139,
1296, 1567, 2369, 3062, 3795, 4838, 6012, 7156, 8198, 14138, 18187, 21463,
24774, 29212, 31554, 36508) #Feb26–March26
```

- c. Plot the data in a linear plot, coloring each country with a different colour. What do you observe?  
d. Plot the data in a semi-log plot (using the plot option `log="y"`), coloring each country with a different color. What do you observe?  
e. Carry out a linear regression with the data of each country (using the log of the n values) and estimate the growth rate R. Are the values the same for all countries? Do they vary over time?  
f. Knowing that

$$R_0 = R^\tau$$

and that the infectious period ( $\tau$ ) duration is 10 days, what are the  $R_0$ 's in different countries?

- g. Write a for loop to simulate geometric (exponential) growth, going from time t in 1:100, and storing the population size values at each time step t+1 in variable n based on the population values at time t, i.e. `n[t+1] <- R*n[t]`. Don't forget to initialize the population size before the for loop with `n<-1`. Plot a couple of runs of the for loop with different R values (for instance `R=1.01` and `R=1.1`) in linear scale.

---

<sup>1</sup>Data source: <https://github.com/owid/covid-19-data/tree/master/public/data>, accessed 8 Nov 2020

- h. Given that you know the solution of the geometric growth equation to be  $n(t) = n_0 R^t$ , create a vector of values with this formula using the same R as you used above, but starting with  $n_0 < -2$  and overlay them on the plot.

## B.6 Population Viability Analysis



1. Consider a population with exponential growth but that exhibits environmental stochasticity, with the logarithm of the population growth rate following a normal distribution with mean  $\bar{r} = \log(\bar{R})$  and variance  $v$ . Assume that the population has an on-off density dependence and cannot grow above the carrying capacity  $K$ . According to Foley (1994)<sup>2</sup> the expect time to extinction is

$$T = \frac{1}{sr} [e^{s \log(k)} (1 - e^{-s \log(N_0)}) - s \log(N_0)]$$

where  $s = 2r/v$ .

- a. Plot the mean extinction times,  $T$ , as a function of  $r$ ,  $v$ ,  $n_0$ , and  $K$ . Please comment each plot.  $r$  can carry from 0.01 to 0.2,  $v$  can vary from 0.05 to 1.0,  $n_0$  can vary from 0 to 10, and  $K$  can vary from 10 to 500. Use as base parameters  $n0=10$ ,  $K=100$ ,  $v=0.3$  and  $r=0.01$ .
- b. Write a function that simulates a population with these dynamics numerically. Start by using the for loop that you developed in Lab 2 and modify it to include a carrying capacity and growth rate that is taken every year from a normal distribution. The function should take parameter  $n0$ ,  $r$ ,  $v$ , and  $K$ . It should return the vector of the population sizes over time.
- c. Simulate the dynamics with the following parameters:
  1.  $n0=3$ ;  $r=0.01$ ;  $v=0.2$ ;  $K=500$
  2.  $n0=100$ ;  $r=0.01$ ;  $v=0.2$ ;  $K=500$ ;

---

<sup>2</sup>Foley, P. (1994) Predicting Extinction Times from Environmental Stochasticity and Carrying-Capacity. *Conservation Biology* 8: 124–137.

- d. **Extended credit:** Compare the model predictions with the results from the analytical approximation of Foley. You need to do many simulations to reach the predicted extinction times from Foley. For instance, you can create a function that call the function developed in (b) and executes it 100 times, returning the median time to extinction across the simulations.

## B.7 The camera trapper

A researcher place camera traps at a grid of sites during 19 days to observe roe-deer.

1. Load the data on the file roe\_deer\_2016\_r.csv into R. Briefly describe the structure of the dataset.
2. Case 1: Ignoring detection probability.
  - a) Build a vector that for each site takes value 1 when roe-deer is present and 0 when is absent.
  - b) Using maximum-likelihood estimate the occupancy probability ( $\psi$ ). First create a function that takes as parameters psi and a vector of presence/absences and returns the likelihood. Then plot that function for a range of  $\Psi$  values and find the  $\psi$  value that maximizes the function.
  - c) Assume that based on previous work we know that occupancy is somewhat between 0.2 and 0.5. Using a Bayesian approach, calculate the posterior probability distribution for the occupancy  $P(\psi)$ .

Help: A function returning the  $P(\psi|data)$ . It takes as parameters a vector y of presences/absences, a value for `psi`, and a function for the prior distribution of  $\psi$  named `priorpsi`:

```
occupancybayesian <- function(y,psi,priorpsi)
{
  integrand <- function(x)
    occupancylikelihood(y,x)*priorpsi(x)
  occupancylikelihood(y,psi)*priorpsi(psi)/
    integrate(integrand, lower = 0.01, upper = 0.99)$value
}
```

A function returning  $P(\psi)$ , the prior distribution of  $\psi$  values. It takes as parameters a value for `psi`.

```
prior <- function(psi)
{
  dunif(psi,0.2,0.5)
}
```

3. Case 2: Using a hierarchical model with detection probability
  - a. Using maximum-likelihood estimate the occupancy probability ( $\Psi$ ) and detection probability ( $p$ ).



## B.8 Managing a fishery

1. Consider that you are managing a fishery with the following dynamics:

$$dn/dt = 0.2n(1 - n/10000)$$

- Plot the production function of the fishery, indicating the stock size for the maximum sustainable yield and the corresponding production level.
- Suppose you establish an annual quota (harvest) that is equivalent to 50% of the maximum sustainable yield. What are the two stock size levels that sustainably allow that exploitation level?
- Explore what happens when you manage this fishery for 100 years. Start by writing a function that simulates the logistic growth above with a constant harvest. The function should take as parameters the initial population size  $n_0$  (the stock of the fishery), the annual harvest  $h$ , and the number of years for which you simulate the population dynamics and return a vector with the population sizes over time. Discuss the results of the following experiments.
  - Experiment 1:** Set the harvest equal to the production at MSY and initial population size at carrying capacity.
  - Experiment 2.** Set the harvest equal to the production at MSY and initial population size at the stock size of MSY
  - Experiment 3.** Set the harvest equal to 50% of the maximum sustainable yield and initial population size at carrying capacity.
  - Experiment 4.** Set the harvest equal to the production at MSY and initial population size at the stock size of MSY - 1000 individuals.
  - Experiment 5.** Set the harvest equal to the production at MSY and initial population size at the stock size of MSY - 1000 individuals.
- Explain why in a system with constant quotas, MSY is not stable and should not be the management goal.
- Extra credit:** Modify the logistic growth function to have stochastic dynamics so that there is a variance of 10% in the annual productivity. Simulate again experiment 2 a few times. What happens?
- Discuss how these results relate with the paper of Worm et al (2009) about the need to rebuild fisheries.



Figure B.1: Atlantic cod (*Gadus morhua*). Source: Hans-Petter Fjeld, CC-BY-SA, Wikipedia.

## B.9 Road Kill

### Populations in space and the impacts of roads

#### *The Red fox*

*...So, while they may be most active at night. Red foxes are especially active during the daytime in spring and summer (April-Sept) as they are foraging for food to feed their young.*

Source photo: Wikipedia, CC0.



#### Goals of the exercise:

- Identify road segments with hotspots of red fox-car-collisions.
  - What impact do activity patterns have on the rate of animal-car-collision hotspots?
  - Use the False Discovery Rate (FDR) method to identify such hotspots.
1. Please install the following R packages
 

```
library(readxl)
library(dplyr)
library(sf)
library(ggplot2)
library(fuzzySim)
library(grid)
```

    - a. Load the *roadkill* dataset.
    - b. Explain the structure of the dataset.
    - c. Show that differences in seasonal activity patterns impact the FDR hotspot results in red fox-car-collisions.
    - d. How many hotspots were detected for the active season?
    - e. Plot, based on the FDR method, true and “false” hotspots. Explain the general geographic locations of the hotspots and those vary between the two different seasons.
    - f. Think about conservation management implications.

## B.10 Simulating a neutral community

The neutral theory in ecology provides a mechanistic explanation for species abundance distributions. It seeks to understand the impact of speciation, extinction, dispersal and ecological drift on the species abundance distribution (SAD), assuming that all species have equal opportunities (Hubbell, 2001).

It is important to note that the neutral theory is a model created to explain a pattern of relative abundance within communities, but it does not necessarily reflect reality (communities' mechanisms). The neutral theory utilizes a model based on the dynamics of a species' population, which is governed by generalized birth and death events, including speciation, immigration, and emigration (Rosindell et al (2011)).

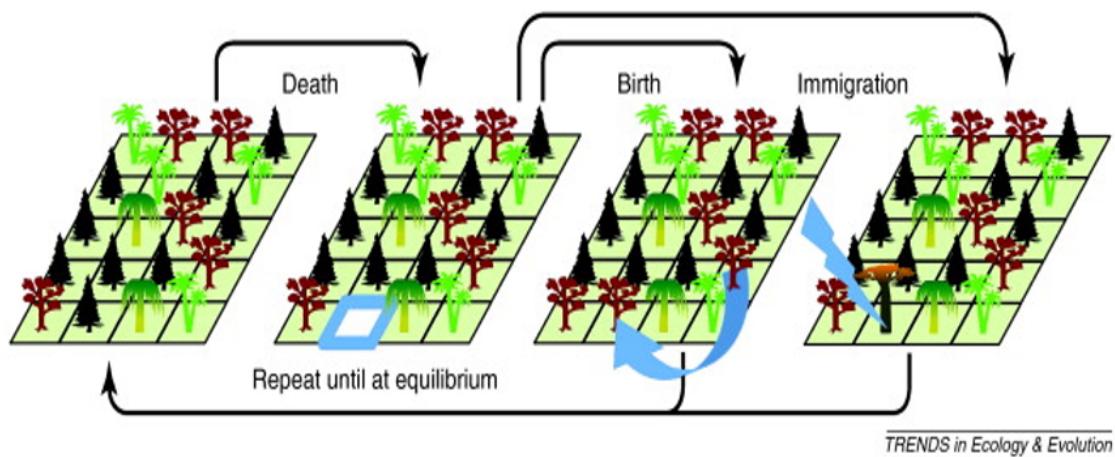


Figure B.2: Diagram of the dynamics of communities in the neutral theory of biodiversity (from Rosindell et al 2011).

The neutral theory paradox is that in absence of migration or mutation diversity gradually declines to zero or monodominance. Let's see what happens to species richness and the species abundance distribution over time for different parameters of the model. Start by installing the package `untb`.

1. **Without mutation or dispersal (pure ecological drift):** We start with a local community with 20 species, each with 25 individuals. The simulation then runs for 2500 generations where 10 individuals die per generation. Mutation rate is zero and immigration rate is zero
  - a. Plot the number of species over time.
  - b. Plot the species abundance distribution at time 1, 100 and 2500
  - c. Plot the map of individuals at those time steps.
2. **With point mutation:** Same parameters as (1) but with speciation rate of 0.1.
  - a. Plot the number of species over time.

- b. Plot the species abundance distribution at time 1, 100 and 2500
  - c. Plot the map of individuals at those time steps.
3. [Extra Credit] **With immigration:** Same parameters as (1) but immigration rate greater than zero. Play with different abundance distributions for the metacommunity.

## B.11 Monitoring biodiversity

1. Exploring the BBS dataset
  - a. Load the file Florida.csv into R. Briefly describe the structure of the dataset.
  - b. Map the monitored transects/routes in Florida's map. Use the maps library to plot the counties of florida as a base map.
  - c. For transect 4 and transect 109 in year 2018 plot calculate the species richness, Shannon diversity index H and evenness J of both transects, with H being

$$H = - \sum_i (p_i \ln p_i)$$

where  $p_i$  is defined as the proportion of individuals found in species  $i$ . Compare the two transects.

- d. Plot the species abundance distribution and abundance-rank for both transects. What do you observe?
- e. Choose one transect and plot the species richness, Shannon diversity, and geometric mean abundance over time
- f. *Extra credit 1:* Produce a map of the trends of one these metrics across Florida (for instance coloring different points according to the trend)
- g. *Extra credit 2:* Estimate the number of species in Florida by combining the different transects and using one of the estimators. Use bootstrap and/or jackknife to calculate confidence intervals.

# Appendix C

## Tutorials to support computational labs

### C.1 Plotting real life ecophysiological from *Anolis* lizards

By Andres Marmol

Why anoles? Anoles are among the most studied reptile organisms. They are vastly diverse with more than 488 species described until today — circa 11% of all the squamates without considering snakes — due to their outstanding adaptive radiation, which has inspired many to dive-in-depth into understanding how evolution has operated within this group (Lizards in an Evolutionary Tree by J. B. Losos is a highly recommended instructive reading for more info). As a result, very detailed data sets on many species of anoles, including information on micro habitat, field body temperature, activity patterns and morphological traits, performance, etc., can be found online in relatively few time.

In the following steps we will be downloading from Dryad and using a data set created by Winchell et al. (2016) (<https://doi.org/10.5061/dryad.h234n>) on *Anolis cristatellus* making a pair-comparison of several morphological and thermal traits of individuals living in urban and forested areas at Puerto Rico. *A. cristatellus* is widely distributed across Puerto Rico and can be found in natural and human-intervened spaces easily. It can be seen over ground and laying on the trunks of trees in natural settings, and on walls and metal fences in more urban areas.

#### C.1.1 Calling the dataset from Dryad

To download the dataset, it is necessary to install the R package `rdryad`.

```
install.packages("rdryad")
```

Then we open the newly installed package and download the dataset by specifying the DOI associated to this dataset.

```
#calling rdryad
library(rdryad)

# Specify the DOI
doi <- "10.5061/dryad.h234n"

# Download the dataset using the dryad_download function
downloaded_file <- dryad_download(dois = doi)
```

The data sets are now downloaded on the paths indicated in the box below, although for this exercise only table [2] `winchell_evol_phenshifts.csv` is needed.

```
# The downloaded_file will contain the file path where the dataset is saved
print(downloaded_file)

$`10.5061/dryad.h234n`
[1] "/Users/henrique/Library/Caches/R/rdryad/10_5061_dryad_h234n/winchell_evol_CG.csv"
[2] "/Users/henrique/Library/Caches/R/rdryad/10_5061_dryad_h234n/winchell_evol_phenshifts.csv"
```

Once this is done, it is always good practice to check if the recently open data frame works by checking the columns within the data frame.

```
#calling the dataset of interest as df
df <- read.csv(downloaded_file[[1]][2])

# checking the columns (variables) available in the data frame df using the str function
names(df)

[1] "ID"                  "date"                 "Site"
[4] "context"              "perch"                "bodytemp.C"
[7] "perch.temp.C"         "ambient.temp.C"    "humidity.percent"
[10] "perch.height.cm"     "perch.diam.cm"     "weight.g"
[13] "head.height.mm"      "svl.mm"               "local.time.decimal"
[16] "flags"                "JL"                   "JW"
[19] "METC"                 "RAD"                  "ULN"
[22] "HUM"                  "FEM"                  "TIB"
[25] "FIB"                  "METT1"                "METT2"
[28] "FL"                   "HL"
```

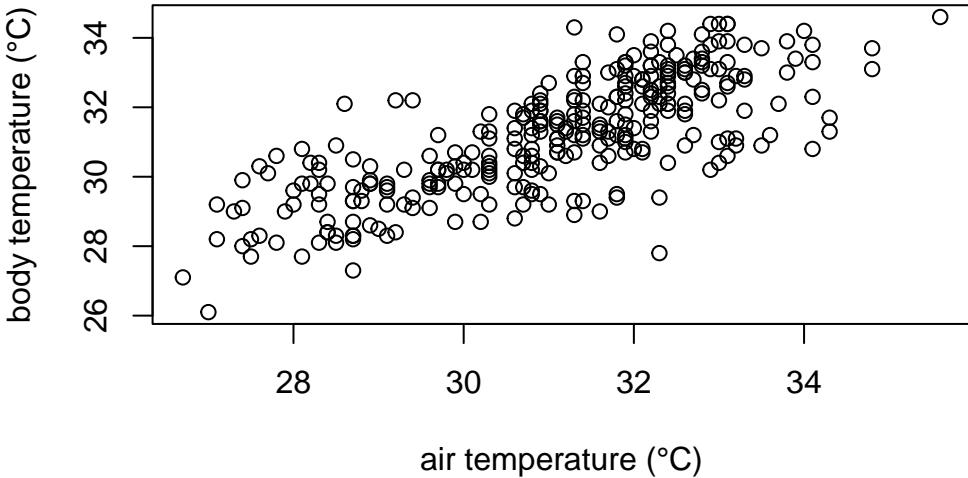
There are 29 different variables within `df`, but this exercise will focus only in a few of them including `context`, `perch`, `bodytemp.C`, `perch.temp.C`, `ambient.temp.C`, and `local.time.decimal` where `context` indicates if the lizard was captured in natural or urban spaces; `perch` refers to the micro-habitat where the lizard was found; `bodytemp.C` is body temperature  $b$ ; `perch.temp.C` is substrate temperature  $T_s$ ; `ambient.temp.C` is air temperature  $a$ ; and `local.time.decimal` is the time of the day in hours when the lizards was captured and measured.

### C.1.2 Exploring the thermophysiological data of *A. cristatellus*.

As covered in the first chapter,  $b$  increases proportionally to  $a$  as indicated in equation (1.2). Let's check if the data confirms this equation.

```
# to call a variable directly from a data frame one must use $, indicating the name of the data frame

plot(df$ambient.temp.C, df$bodytemp.C,
      xlab="air temperature (°C)",
      ylab="body temperature (°C)")
```



In the plot we can observe that indeed body temperature increases with increasing temperature. However, we cannot quantitatively know how much is this increase. For that, we can model how air temperature affects body temperature modelling them a a line with the equation:

$$\hat{y} = \alpha + \beta * x + e \quad (\text{C.1})$$

where  $\hat{y}$  is the predicted value of  $y$  for any given  $x$ ;  $\alpha$  is point of intersection of the line when  $x = 0$ ,  $\beta$  is the slope of the regression line (i.e. how much increases  $\hat{y}$  with a unit increase in  $x$ ) and  $e$  is the random error.

Placing our variables in formula, it would look like this:

$$b = b_0 + \beta * a + e \quad (\text{C.2})$$

where  $b$  is body temperature,  $a$  is ambient temperature, and  $b_0$  is the body temperature when  $a$  is zero.

Now lets model it using a least-squares linear regression using the `lm` function in R.

```
#define the linear model
#the variable at the left of the tilde (~) is the dependent variable
#data calls the specific data frame to be used.
```

```
model1 <- lm(bodytemp.C ~ ambient.temp.C, data=df)

# print model outputs
print(model1)
```

Call:  
`lm(formula = bodytemp.C ~ ambient.temp.C, data = df)`

Coefficients:

(Intercept)	ambient.temp.C
8.7004	0.7237

### C.1.3 Interpreting the results of our model.

The results of our model indicates that if the air temperature ( $a$ ) is zero, *A. cristatellus* would show a body temperature ( $b$ ) of 8.7 °C, which increases in approximately 0.7 °C for each 1 °C increase in air temperature.

Now it is also possible to draw a few predictions

```
# a number of possible ambient temperatures that can be found in Puerto Rico during the day

amb_temps = data.frame(ambient.temp.C = seq(27,38, 1))# defines a vector with values from 27 to 38, step 1

predict(model1, newdata=amb_temps)
```

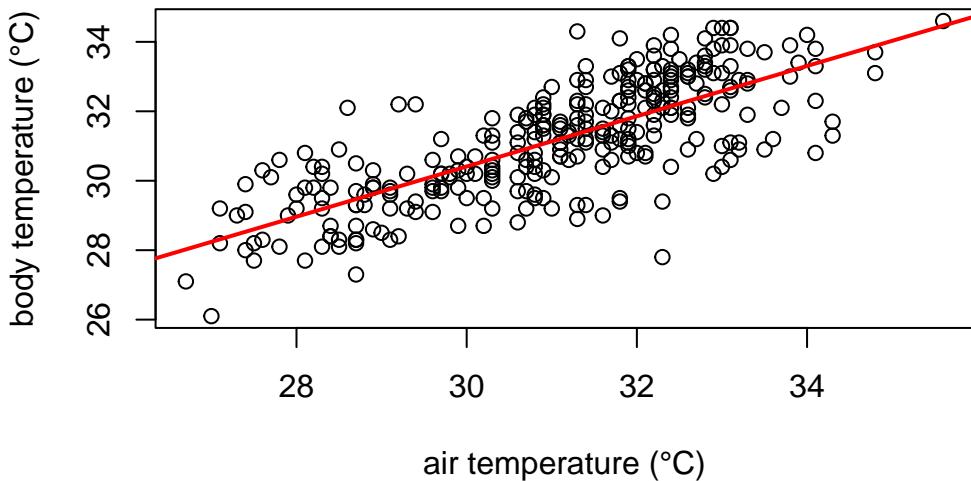
1	2	3	4	5	6	7	8
28.23967	28.96335	29.68702	30.41070	31.13437	31.85805	32.58172	33.30540
9	10	11	12				
34.02907	34.75275	35.47642	36.20010				

## C.2 How good our model is performing?

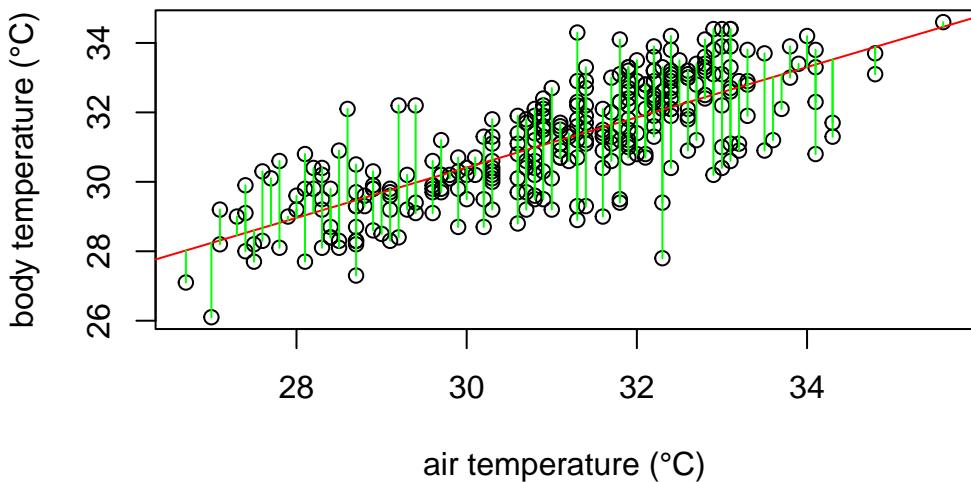
Graphically the linear model fits the data as follows:

```
# Create the scatter plot
plot(df$ambient.temp.C, df$bodytemp.C,
      xlab="air temperature (°C)",
      ylab="body temperature (°C)")

# add the line of fit from our recently created linear model "model1"
abline(model1, col = "red", lwd= 2)
```



The red line in the plot follows very well the pattern of increase shown by our data. It is noticeable, however, that some points fall farther from the line of best fit than others. In other words, many  $\hat{y}$  values (body temperature) are predicted with larger errors than others, for a given  $x$  value (ambient temperature). These errors are also known as residuals, and are the vertical distance between the observed values and the line of best fit. They are graphically represented in green in our plot:



What a least square linear regression does is to find the lowest sum of squares of the residuals (every green line in the plot) so that the least amount of error is kept in the linear model.

Finally, how well the model fits the data? In our example, the body temperatures do not perfectly fall on the line of best fit, and many of them are scattered around it. A common metric to assess this question in a simple regression model is the  $r^2$ .  $r^2$  values indicate how much of the variance of body temperature (our dependent variable) is explained by ambient temperature (our independent variable). A perfect fit is indicated by an  $r^2$  of 1, while no fit would be zero. To check the  $r^2$  in our model we can simply use the `summary` function in R.

```
# obtaining the r-squared of our model  
summary(model1)$r.squared
```

```
[1] 0.5736088
```

$r^2$  equals 0.574 indicating that almost 60% of the variance in body temperature is explained by ambient temperature.

In summary, our expectation that lizards body temperature increases depending on how the temperature in their environment changes has been confirmed. Specifically for *A. cristatellus* in this study, body temperature increases  $\sim 0.7$  °C every 1 degree increase in air temperature. A few questions remain. For example, does habitat has an effect in the body temperature in *A. cristatellus*, and if it does, how different could the body temperatures of the lizards in habitat A are from those in habitat B?