

Simulation Models of Cultural Evolution in R

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Introduction

This tutorial shows how to create very simple simulation or agent-based models of cultural evolution in R (R Core Team 2021). It uses the RStudio notebook or RMarkdown (.Rmd) format, allowing you to execute code as you read the explanatory text. Each model is contained in a separate RMarkdown file which you should open in RStudio. Currently these are:

- Model 1: Unbiased transmission
- Model 2: Unbiased and biased mutation
- Model 3: Biased transmission (direct/content bias)
- Model 4: Biased transmission (indirect bias)
- Model 5: Biased transmission (conformist bias)
- Model 6: Vertical and horizontal transmission
- Model 7: Migration
- Model 8: Blending inheritance
- Model 9: Demography and cultural gain/loss
- Model 10: Polarization
- Model 11: Cultural group selection

I assume you have basic knowledge of R as a programming language, e.g. the use of variables, dataframes, functions, subsetting and loops. If not, *Hands On Programming With R* by Garrett Grolemund is a good introduction.

I'm putting all model parameters in italicised *equation* text. This allows useful features such as superscripts (e.g. x^y) and subscripts (e.g. $x_{t=1}$). Hover the cursor over the equation text to see this in RStudio. All code variables are in regular *italics*, and all commands and functions in **bold**.

Use the green triangles above each code chunk to run that piece of code. Be sure to do this in the order they appear, as some chunks depend on previous chunks to work. You can also output the entire document including your executed code and formatting to html or pdf using the Knit button in the toolbar. Check the RMarkdown Cheat Sheet accessible via the Help menu for more details.

All the concepts covered here are introduced, discussed and mathematically modelled at an advanced level in Cavalli-Sforza & Feldman (1981) and Boyd & Richerson (1985). I explain them informally in Mesoudi (2011). A recent article (Mesoudi 2017) gives a current overview of cultural evolution research, with references to recent studies.

Each chapter has some exercises with suggestions for how to fully explore the models and extend the models in interesting ways. Each chapter also has an ‘Analytic Appendix’, where I show how to derive the same results analytically.

What is cultural evolution?

The theory of evolution is typically applied to genetic change. Darwin pointed out that the diversity and complexity of living things can be explained in terms of a deceptively simple process. Organisms vary in

their characteristics. These characteristics are inherited from parent to offspring. Those characteristics that make an organism more likely to survive and reproduce will tend to increase in frequency. That's pretty much it. Since Darwin, biologists have filled in many of the details of this abstract idea. Geneticists have shown that 'characteristics' are determined by genes, and worked out where genetic variation comes from (e.g. mutation, recombination) and how genetic inheritance works (e.g. via Mendel's laws, and DNA). The details of selection have been explored, revealing the many reasons why some genes spread and others don't. Others realised that not all biological change results from selection, it can also result from random processes like population bottlenecks (genetic drift).

The theory of cultural evolution rests on the observation that culture constitutes a similar evolutionary process to that outlined above. By 'culture' we mean information that passes from one individual to another socially, rather than genetically. This could include things we colloquially call knowledge, beliefs, ideas, attitudes, customs, words, or values. These are all learned from others via various 'social learning' mechanisms such as imitation or spoken/written language. The key point is that social learning is an inheritance system. Cultural characteristics (or cultural traits) vary across individuals, they are passed from individual to individual, and in many cases some traits are more likely to spread than others. This is Darwin's insight, applied to culture. Cultural evolution researchers think that we can use similar evolutionary concepts, tools and methods to explain the diversity and complexity of culture, just as biologists have done for the diversity and complexity of living forms.

Importantly, we do not need to assume that cultural evolution is identical to genetic evolution. Many of the details will be different. To take an obvious example, we get DNA only from our two parents, but we can get ideas from many sources: teachers, strangers on the internet, long-dead authors' books, or even our parents. Cultural evolution researchers seek to build models and do empirical research to fill in these details.

Why model?

A formal model is a simplified version of reality, written in mathematical equations or computer code. Formal models are useful because reality is complex. We can observe changes in species or cultures over time, or particular patterns of biological or cultural diversity, but there are always a vast array of possible causes for any particular pattern or trend, and huge numbers of variables interacting in many different ways. A formal model is a highly simplified recreation of a small part of this complex reality, containing a few elements or processes that the modeller suspects are important. A model, unlike reality, can be manipulated and probed in order to better understand how each part works. No model is ever a complete recreation of reality. That would be pointless: we would have replaced a complex, incomprehensible reality with a complex, incomprehensible model. Instead, models are useful *because* of their simplicity.

Formal modelling is rare in the social sciences (with some exceptions, such as economics). Social scientists tend to be sceptical that very simple models can tell us anything useful about something as immensely complex as human culture. But the clear lesson from biology is that models are extremely useful in precisely this situation. Biologists face similarly immense complexity in the natural world. Despite this, models are useful. Population genetics models of the early 20th century helped to reconcile new findings in genetics with Darwin's theory of evolution. Ecological models helped understand interactions between species, such as predator-prey cycles. These models are hugely simplified: population genetics models typically make ridiculous assumptions like infinitely large populations and random mating. But they are useful because they precisely specify each part of a complex system, improving understanding of reality.

Another way to look at it is that all social scientists use models, but only some use *formal* models. Most models are verbal models, written in words. The problem is that words can be imprecise, and verbal models contain all kinds of hidden or unstated assumptions. The advantage of formal modelling is that we are forced to precisely specify every element and process that we propose, and make all of our assumptions explicit. Maths and code do not accept any ambiguity: they must be told absolutely everything. For more on the virtues of formal models for social scientists, see Paul Smaldino's 'Models are stupid, and we need more of them' (2017).

With these ideas in mind, let's turn to our first extremely simplified model of cultural evolution.

References

- Boyd, R., & Richerson, P. J. (1985). Culture and the evolutionary process. University of Chicago Press.
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- Grolemund, G. (2014). Hands-on programming with R: Write your own functions and simulations. O'Reilly Media.
- Mesoudi, A. (2011). Cultural evolution: How Darwinian theory can explain human culture and synthesize the social sciences. University of Chicago Press.
- Mesoudi, A. (2017). Pursuing Darwin's curious parallel: Prospects for a science of cultural evolution. *Proceedings of the National Academy of Sciences*, 114(30), 7853-7860.
- R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
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Simulation Models of Cultural Evolution in R

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Model 1: Unbiased transmission

Here we will simulate perhaps the simplest possible case of cultural evolution. We assume N individuals each of whom possesses one of two cultural traits, denoted A and B . Each generation, the N agents are replaced with N new agents. Each new agent picks a member of the previous generation at random and copies their cultural trait. This is known as unbiased oblique cultural transmission: unbiased because traits are copied entirely at random, and oblique because one generation learns from the previous non-overlapping generation (as opposed to horizontal cultural transmission where individuals copy members of the same generation, and vertical cultural transmission where offspring copy their parents - our model is way too simple to have actual parents and offspring though).

We are interested in tracking the proportion of individuals who possess trait A over successive generations. We will call this proportion p . We could also track the proportion who possess trait B , but this will always be $1 - p$ given that everyone who does not possess A must possess B , so there is really no need. For example, if 70% of the population have trait A , then $p = 0.7$. The remaining 30% must have trait B , which is a proportion $1 - p = 1 - 0.7 = 0.3$.

The output of the model will be a plot showing p over all generations up to the last generation, which we will call t_{max} . Generations (aka timesteps) are denoted by t , where generation one is $t = 1$, generation two is $t = 2$, up to the last generation $t = t_{max}$. These could correspond to biological generations, but could equally be ‘cultural generations’ (or learning episodes) within the same fixed population, which would be much shorter.

First we need to specify the fixed parameters of the model. These are N (the number of individuals) and t_{max} (the number of generations). Let’s start with $N = 100$ and $t_{max} = 200$.

```
N <- 100  
t_max <- 200
```

Run this code snippet in RStudio using the green ‘play’ triangle in the top right of the snippet. If you have the Environment pane visible on the right, you should be able to see N and t_{max} appear, with their assigned values. The Environment pane is useful for keeping track of active variables and their current values.

Now we need to create our agents. These will be stored in a data frame, a commonly-used data format in R. The only information we need to keep about our agents is their cultural trait (A or B). Hence we need a data frame that is N rows long, with a single column for the trait. We’ll call this data frame $agent$. Initially, we will give each agent either an A or B at random, using the **sample** command.

```
agent <- data.frame(trait = sample(c("A", "B"), N, replace = TRUE))
```

Here, *trait* specifies the name of the sole variable/column in the *agent* data frame. This is filled using **sample**. The first part of the **sample** command lists the elements to pick at random, in our case, the traits A and B . The second part gives the number of times to pick, in our case N times, once for each agent. The final part says to replace or reuse the elements after they’ve been picked (otherwise there would only be one copy of A and one copy of B , so we could only give two agents traits before running out).

We can see the first few lines of *agent* using the **head** command, to check it worked:

```
head(agent)
```

```
## trait
## 1    A
## 2    B
## 3    A
## 4    B
## 5    B
## 6    A
```

As expected, there is a single column called *trait* containing *As* and *Bs*. Note that **head** only shows the first 6 rows for brevity; the other 94 are not shown. The numbers on the left are automatically generated in a dataframe as row labels, but in our case we can think of them as the agents' id numbers (agent 1, agent 2, ..., agent 100).

A specific agent's trait can be retrieved using standard dataframe indexing. For example, agent 4's trait can be retrieved using:

```
agent$trait[4]
```

```
## [1] "B"
```

This should match the fourth row in the **head** output above.

We also need a dataframe to track the trait frequency p in each generation. This will have a single column with t_{max} rows, one for each generation. We'll call this dataframe *output*, because it is the output of the model. At this stage we don't know what p will be in each generation, so for now let's fill the *output* dataframe with lots of NAs, which is R's symbol for Not Available, or missing value. We can use the **rep** (repeat) command to repeat NA t_{max} times.

```
output <- data.frame(p = rep(NA, t_max))
```

Here, p is the name of the sole variable/column in the *output* dataframe, and it's filled entirely with NAs. We're using NA rather than, say, zero, because zero could be misinterpreted as $p = 0$, which would mean that all agents have trait *B*. This would be misleading, because at the moment we haven't yet calculated p , so it's non-existent, rather than zero.

We can, however, fill in the first value of p for our already-created first generation of agents, held in *agent*. The command below sums the number of *As* in *agent* and divides by N to get a proportion out of 1 rather than an absolute number. It then puts this proportion in the first slot of p in *output*, the one for the first generation, $t = 1$. We can again use **head** to check it worked.

```
output$p[1] <- sum(agent$trait == "A") / N
head(output)
```

```
##      p
## 1 0.49
## 2 NA
## 3 NA
## 4 NA
## 5 NA
## 6 NA
```

This first p value should be approximately 0.5: maybe not exactly, because we have a finite and relatively small population size. Analogously, flipping a coin 100 times will not always give exactly 50 heads and 50 tails. Sometimes we would get 51 heads, sometimes 52 heads, sometimes 48. Similarly, sometimes we will have 51 As, sometimes 48, etc.

Now we need to iterate our population over t_{max} generations. In each generation, we need to:

- copy the current agents to a separate dataframe called *previous_agent* to use as demonstrators for the new agents; this allows us to implement oblique transmission with its non-overlapping generations, rather than mixing up the generations and getting in a muddle
- create a new generation of agents, each of whose trait is picked at random from the *previous_agent* dataframe
- calculate p for this new generation and store it in the appropriate slot in *output*

To iterate, we'll use a for-loop, using t to track the generation. We've already done generation 1 so we'll start at generation 2. The random picking of models is done with **sample** again, but this time picking from the traits held in *previous_agent*. Note that I've added comments briefly explaining what each line does. This is perhaps superfluous in a tutorial like this, but it's always good practice. Code often gets cut-and-pasted into other places and loses its context. Explaining what each line does lets other people - and a future, forgetful you - know what's going on.

```
for (t in 2:t_max) {

  # copy agent dataframe to previous_agent dataframe
  previous_agent <- agent

  # randomly copy from previous generation's agents
  agent <- data.frame(trait = sample(previous_agent$trait, N, replace = TRUE))

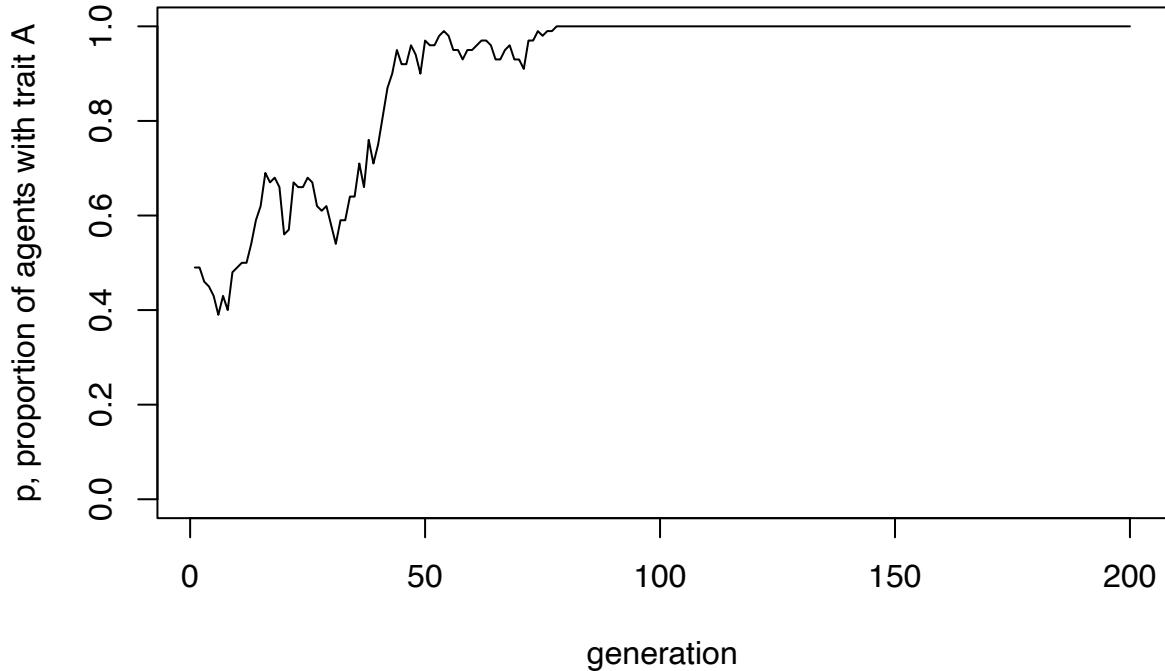
  # get p and put it into the output slot for this generation t
  output$p[t] <- sum(agent$trait == "A") / N

}
```

Now we should have 200 values of p stored in *output*, one for each generation. Let's plot them.

```
plot(output$p,
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      main = paste("N =", N))
```

N = 100



Note the title of the graph, which gives the value of N for this simulation. It's easy to create plots and forget what the parameters were. It's therefore a good idea to include it somewhere on the graph. There's no need to include our other parameter, t_{max} , because that can be seen from the x-axis scale.

Unbiased transmission, or random copying, is by definition random, so different runs of this simulation will generate different plots. If you rerun all the code you'll get something different again. It probably starts off hovering around 0.5, the approximate starting value of p , and might go to 0 or 1 at some point. At $p = 0$ there are no A s and every agent possesses B . At $p = 1$ there are no B s and every agent possesses A . This is a typical feature of cultural drift, analogous to genetic drift: in small populations, with no selection or other directional processes operating, traits can be lost purely by chance.

Ideally we would like to repeat the simulation to explore this idea in more detail, perhaps changing some of the parameters. For example, if we increase N , are we more or less likely to lose one of the traits? With our code scattered about in chunks, it is hard to quickly repeat the simulation. Instead we can wrap it all up in a function, like so:

```
UnbiasedTransmission <- function (N, t_max) {
  agent <- data.frame(trait = sample(c("A", "B"), N, replace = TRUE))
  output <- data.frame(p = rep(NA, t_max))
  output$p[1] <- sum(agent$trait == "A") / N
  for (t in 2:t_max) {
    # copy agent to previous_agent dataframe
```

```

previous_agent <- agent

# randomly copy from previous generation
agent <- data.frame(trait = sample(previous_agent$trait, N, replace = TRUE))

# get p and put it into output slot for this generation t
output$p[t] <- sum(agent$trait == "A") / N

}

plot(output$p,
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      main = paste("N =", N))

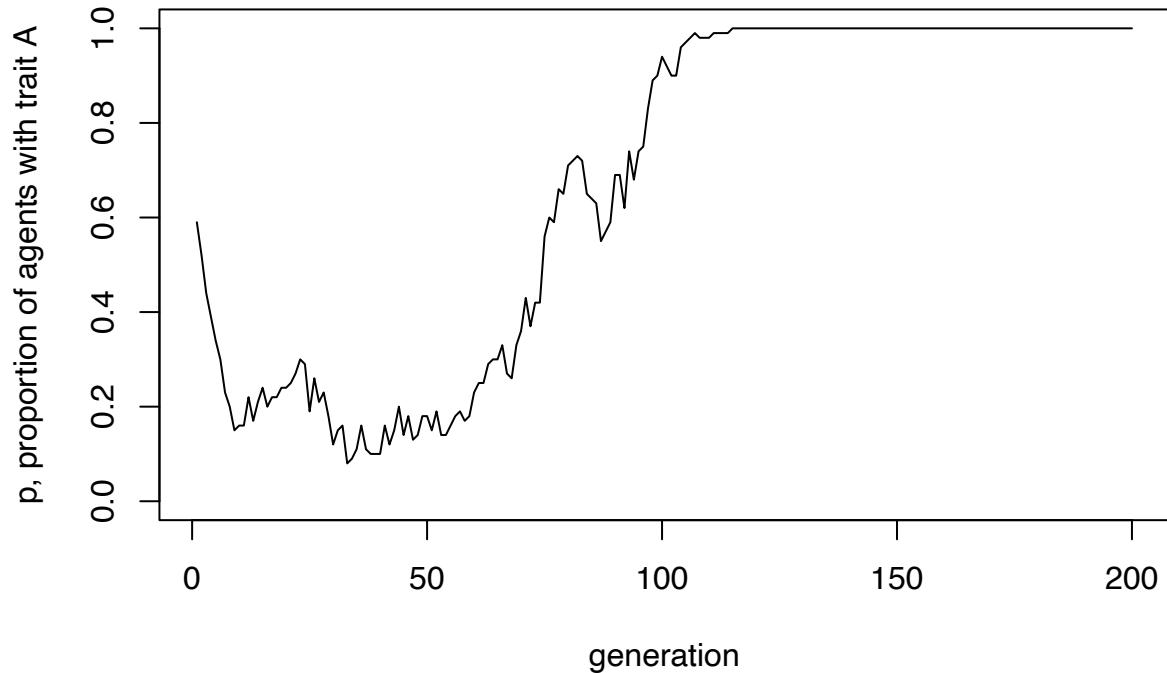
}

```

This is just all of the code snippets that we already ran above, but all within a function with parameters N and t_{max} as arguments to the function. Nothing will happen when you run the above code, because all you've done is define the function, not actually run it. The point is that we can now call the function in one go, easily changing the values of N and t_{max} . Let's try first with the same values of N and t_{max} as before, to check it works. You can re-run the code below several times, to see different dynamics. It should be different every time.

```
UnbiasedTransmission(N = 100,
                     t_max = 200)
```

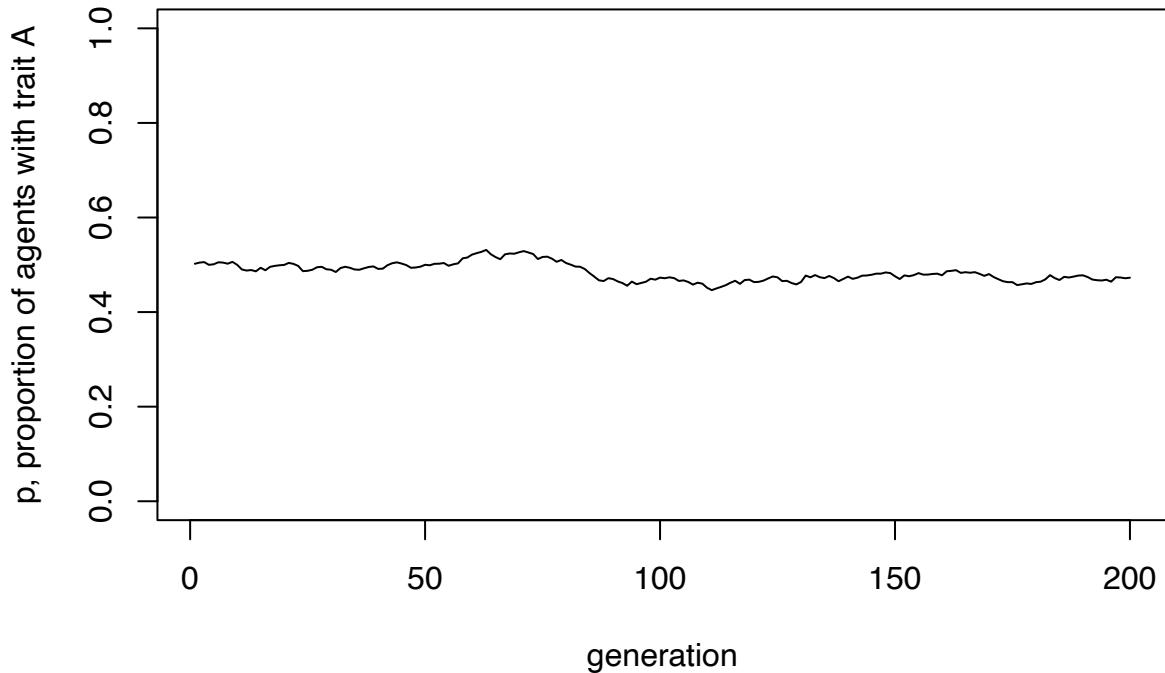
N = 100



Now let's try changing the parameters. The following code re-runs the simulation with a much larger N .

```
UnbiasedTransmission(N = 10000,  
                     t_max = 200)
```

N = 10000



You should see much less fluctuation. Rarely in a population of $N = 10000$ will either trait go to fixation.

Wrapping a simulation in a function like this is good because we can easily re-run it with just a single command. However, it's a bit laborious to manually re-run it. Say we wanted to re-run the simulation 10 times with the same parameter values to see how many times A goes to fixation, and how many times B goes to fixation. Currently, we'd have to manually run the **UnbiasedTransmission** function 10 times and record somewhere else what happened in each run. It would be better to automatically re-run the simulation several times and plot each run as a separate line on the same plot. We could also add a line showing the mean value of p across all runs.

Let's use a new parameter r_{max} to specify the number of independent runs, and use another for-loop to cycle over the r_{max} runs. We also need to expand the number of columns in the *output* data frame, because we need one column of p values for each of the runs. Let's rewrite the **UnbiasedTransmission** function to handle multiple runs.

```
UnbiasedTransmission <- function (N, t_max, r_max) {

  # create a matrix with t_max rows and r_max columns, fill with NAs, convert to data frame
  output <- as.data.frame(matrix(NA, t_max, r_max))

  # purely cosmetic: rename the columns with run1, run2 etc.
  names(output) <- paste("run", 1:r_max, sep="")

  for (r in 1:r_max) {

    # create first generation
    agent <- data.frame(trait = sample(c("A", "B"), N, replace = TRUE))
  }
}
```

```

# add first generation's p to first row of column r
output[1,r] <- sum(agent$trait == "A") / N

for (t in 2:t_max) {

  # copy agent to previous_agent dataframe
  previous_agent <- agent

  # randomly copy from previous generation
  agent <- data.frame(trait = sample(previous_agent$trait, N, replace = TRUE))

  # get p and put it into output slot for this generation t and run r
  output[t,r] <- sum(agent$trait == "A") / N

}

# first plot a thick line for the mean p
plot(rowMeans(output),
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("N =", N))

for (r in 1:r_max) {

  # add lines for each run, up to r_max
  lines(output[,r], type = 'l')

}

output # export data from function
}

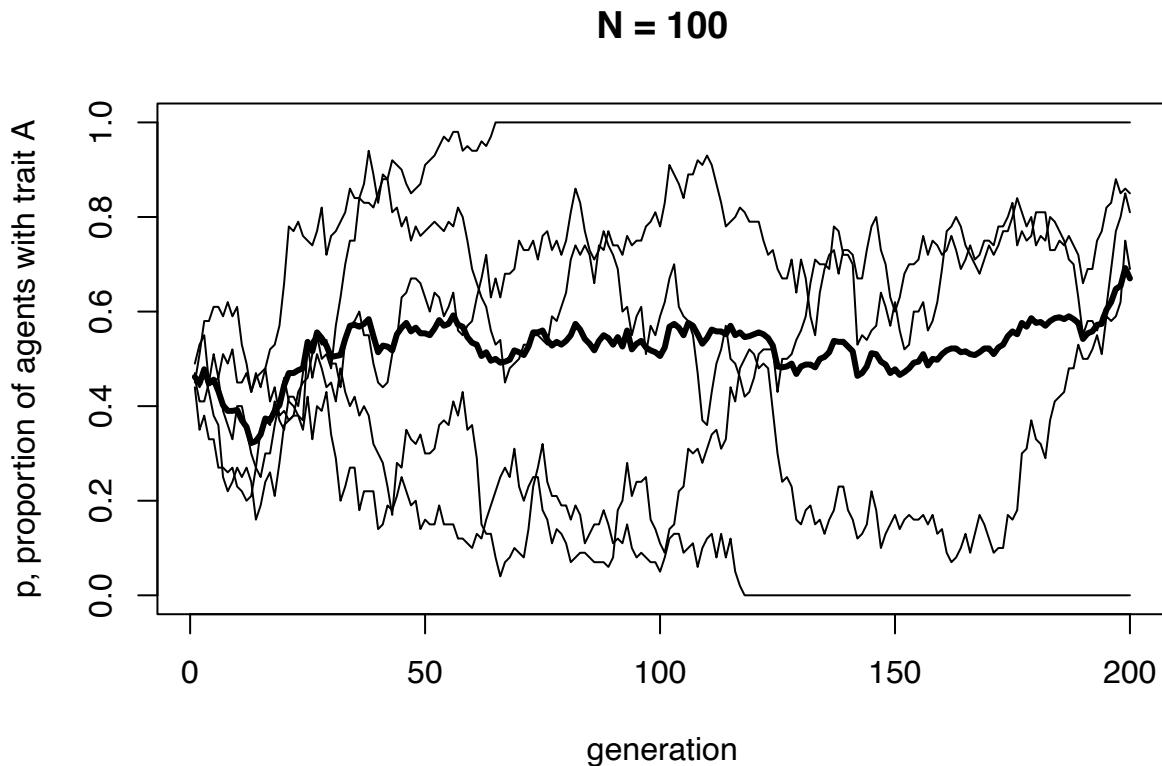
```

There are a few changes here. First, we created *output* initially as a matrix, and then immediately converted it into a dataframe. This seems weird, but is just because it is easier to create a multi-row data structure using the **matrix** command than the **dataframe** command. The next command is purely cosmetic, and re-names the columns of *outcome* as run1, run2 etc.

Then we set up our *r* loop, which executes once for each run. The code is mostly the same as before, except that we now use the “[row,column]” notation to put *p* into the right place in *output*. The row is *t* as before, and now the column is *r*. The **plot** command is also changed to handle multiple runs: first we plot the mean as a thick line, then we add one plotted line for each run.

Finally, the **UnbiasedTransmission** function now ends with the *output* dataframe. This means that this dataframe will be exported from the function when it is run. This can be useful for storing data from simulations wrapped in functions, otherwise that data is lost after the function is executed. In the function call below, the raw data from the simulation is put into a dataframe called *data_model1*, as a record of what happened. Run it now to display the new plot.

```
data_model1 <- UnbiasedTransmission(N = 100,
                                     t_max = 200,
                                     r_max = 5)
```



You should be able to see five independent runs of our simulation shown as regular thin lines, along with a thicker line showing the mean of these lines. Some runs have probably gone to 0 or 1, and the mean should be somewhere in between. The data is stored in `data_model1`, which we can inspect with `head`:

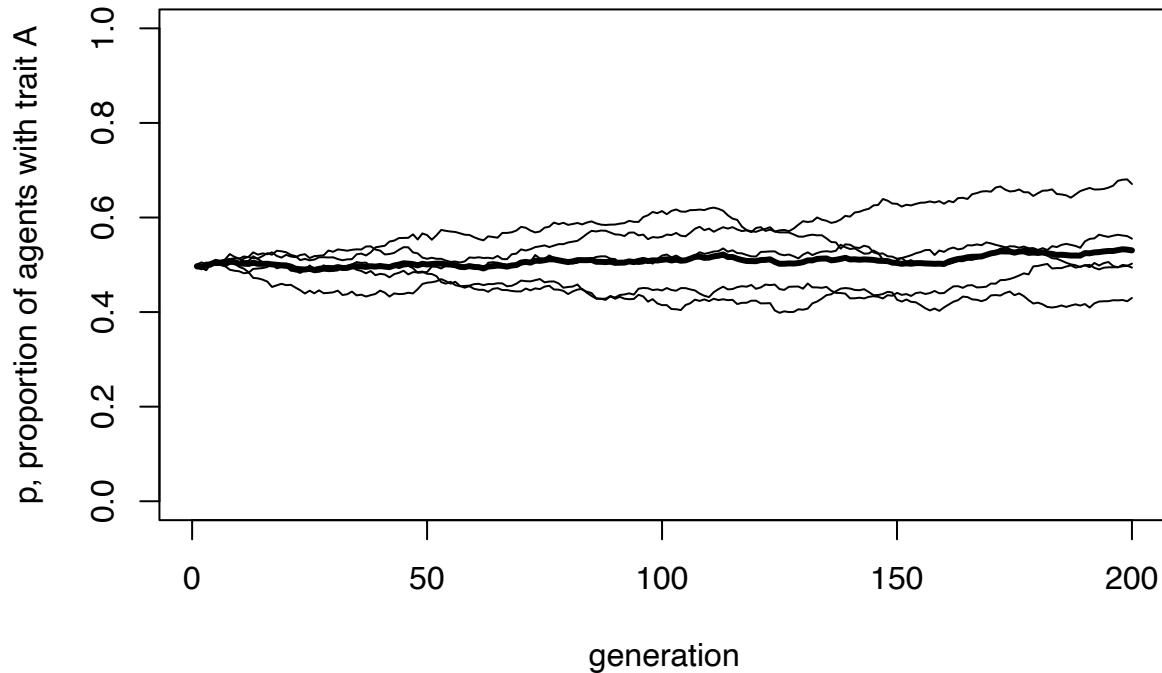
```
head(data_model1)
```

```
##   run1 run2 run3 run4 run5
## 1 0.49 0.46 0.44 0.45 0.47
## 2 0.53 0.41 0.35 0.51 0.44
## 3 0.55 0.41 0.38 0.58 0.47
## 4 0.45 0.45 0.33 0.58 0.43
## 5 0.45 0.51 0.33 0.61 0.38
## 6 0.46 0.46 0.27 0.61 0.36
```

Now let's run the updated **UnbiasedTransmission** model with $N = 10000$, to compare with $N = 100$.

```
data_model1 <- UnbiasedTransmission(N = 10000,
                                     t_max = 200,
                                     r_max = 5)
```

N = 10000



The mean line should be almost exactly at $p = 0.5$ now, with the five independent runs fairly close to it.

Let's add one final modification. So far the starting frequencies of A and B have been the same, roughly 0.5 each. But what if we were to start at different initial frequencies of A and B ? Say, $p = 0.2$ or $p = 0.9$? Would unbiased transmission keep p at these initial values, or would it go to $p = 0.5$ as we have found so far?

To find out, we can add another parameter, p_0 , which specifies the initial probability of drawing an A rather than a B in the first generation. Previously this was always $p_0 = 0.5$, but in the new function below we add it to the `sample` function to weight the initial allocation of traits in $t = 1$.

```
UnbiasedTransmission <- function (N, p_0, t_max, r_max) {

  # create a matrix with t_max rows and r_max columns, fill with NAs, convert to dataframe
  output <- as.data.frame(matrix(NA,t_max,r_max))

  # purely cosmetic: rename the columns with run1, run2 etc.
  names(output) <- paste("run", 1:r_max, sep="")

  for (r in 1:r_max) {

    # create first generation
    agent <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                         prob = c(p_0,1-p_0)))

    # add first generation's p to first row of column r
    output[1,r] <- sum(agent$trait == "A") / N
  }
}
```

```

for (t in 2:t_max) {

  # copy agent to previous_agent dataframe
  previous_agent <- agent

  # randomly copy from previous generation
  agent <- data.frame(trait = sample(previous_agent$trait, N, replace = TRUE))

  # get p and put it into output slot for this generation t and run r
  output[t,r] <- sum(agent$trait == "A") / N

}

}

# first plot a thick line for the mean p
plot(rowMeans(output),
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("N =", N))

for (r in 1:r_max) {

  # add lines for each run, up to r_max
  lines(output[,r], type = 'l')

}

output # export data from function
}

```

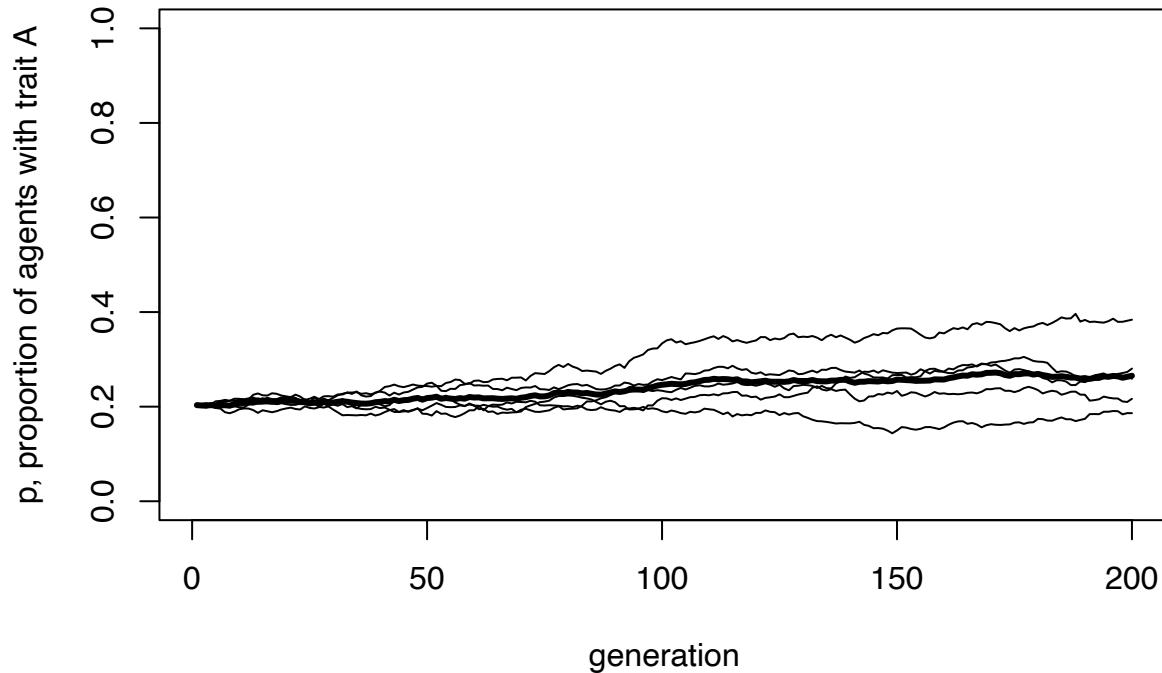
The only change here is the addition of p_0 as a definable parameter for the function, and the **prob** argument in the **sample** command. The **prob** argument gives the probability of picking each option, in our case A and B , in the first generation. The probability of A is now p_0 , and the probability of B is now $1 - p_0$. Let's see what happens with a different value of p_0 .

```

data_model1 <- UnbiasedTransmission(N = 10000,
                                      p_0 = 0.2,
                                      t_max = 200,
                                      r_max = 5)

```

N = 10000



With $p_0 = 0.2$, trait frequencies stay at $p = 0.2$. Unbiased transmission is truly non-directional: it maintains trait frequencies at whatever they were in the previous generation, barring random fluctuations caused by small population sizes.

A final useful skill is to be able to export the plot we created to an external image file. This file can then be inserted into other documents, e.g. as a figure in a manuscript. This is done in the code below by wrapping the **UnbiasedTransmission** function (or any function that outputs a plot) within two commands. First, the **png** command specifies the file format (you can also use **bmp**, **jpeg** or **tiff**), and takes arguments that set the file name, height and width, units of the height and width ("cm", "mm", "in" or "px"), and resolution (in ppi, pixels per inch). Then after the plot is created using **UnbiasedTransmission**, the **dev.off()** command tells R that we are done plotting and can export the file. It's wrapped in **invisible** just to hide the text output in this Rmd file.

Note that this code puts the plot file into the current working directory. To set the working directory to the same place as this Rmd file, use the menu command Session->Set Working Directory->To Source File Location before running the code below. Otherwise, use the command **setwd** to set the working directory to somewhere else, or add a full path to the **file** argument below, within the quote marks where the file name is given.

```
png(file = "unbiased_transmission.png",
  height = 10,
  width = 12,
  units = "cm" ,
  res = 300)

data_model1 <- UnbiasedTransmission(N = 10000,
                                     p_0 = 0.2,
```

```

    t_max = 200,
    r_max = 5)

invisible(dev.off())

```

Summary of Model 1

Even this extremely simple model provides some valuable insights. First, unbiased transmission does not in itself change trait frequencies. As long as populations are large, trait frequencies remain the same.

Second, the smaller the population size, the more likely traits are to be lost by chance. This is a basic insight from population genetics, known there as genetic drift, but it can also be applied to cultural evolution. More advanced models of cultural drift (sometimes called ‘random copying’) can be found in Cavalli-Sforza & Feldman (1981) and Bentley et al. (2004), with the latter showing that various real-world cultural traits exhibit dynamics consistent with this kind of process, including baby names, dog breeds and archaeological pottery types.

Furthermore, generating expectations about cultural change under simple assumptions like random cultural drift can be useful for detecting non-random patterns like selection. If we don’t have a baseline, we won’t know selection or other directional processes when we see them.

In Model 1 we have introduced several programming techniques that will be useful in later models. We’ve seen how to use dataframes to hold characteristics of agents, how to use loops to cycle through generations and simulation runs, how to use `sample` to pick randomly from sets of elements, how to wrap simulations in functions to easily re-run them with different parameter values, how to plot the results of simulations, how to store the output of the simulation in a dataframe that persists after the simulation function is run, and how to export a plot to an external image file.

Exercises

1. Try different values of p_0 with large N to confirm that unbiased transmission does not change the frequency of p , irrespective of the starting value p_0 .
 2. Re-run the **UnbiasedTransmission** model to find the approximate value of N at which one of the traits rarely, if ever, goes to fixation after a reasonably large number of timesteps (‘fixation’ means that p goes to either zero or one and stays there).
 3. Modify the **UnbiasedTransmission** function to record and output the number of timesteps it takes for a run to go to fixation, i.e. p goes to zero or one. If a run does not go to fixation after a sufficiently large number of timesteps, record this as NA. Make a plot of time to fixation against population size N . Before creating the plot, what do you think the plot will look like?
-

Analytical Appendix

If p is the frequency of A in one generation, we are interested in calculating p' , the frequency of A in the next generation under the assumption of unbiased transmission. Each new individual in the next generation picks a demonstrator at random from amongst the previous generation. The demonstrator will have A with probability p . The frequency of A in the next generation, then, is simply the frequency of A in the previous generation:

$$p' = p \quad (1.1)$$

Equation 1.1 simply says that under unbiased transmission there is no change in p over time. If, as we assumed above, the initial value of p in a particular population is p_0 , then the equilibrium value of p , p^* , at which there is no change in p over time, is just p_0 .

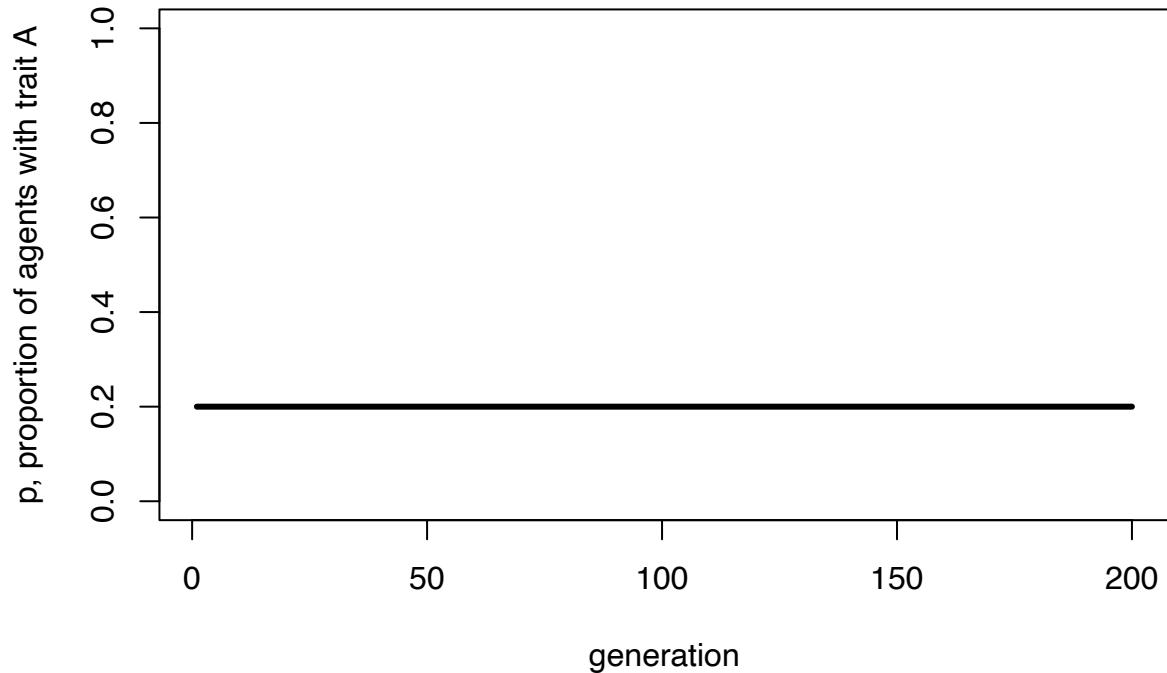
We can plot this recursion, to recreate the final simulation plot above:

```
p_0 <- 0.2
t_max <- 200

p <- rep(NA, t_max)
p[1] <- p_0

for (i in 2:t_max) {
  p[i] <- p[i-1]
}

plot(p,
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3)
```



Don't worry, it gets more complicated than this in later chapters. The key point here is that analytical or deterministic models like these assume infinite populations - note there is no N in the above recursion - and no stochasticity. Simulations with very large populations should give the same results as analytical models. Basically, the closer we can get in stochastic models to the assumption of infinite populations, the closer the match to infinite-population deterministic models. Deterministic models give the ideal case; stochastic models permit more realistic dynamics based on finite populations.

More generally, creating deterministic recursion-based models can be a good way of verifying simulation models, and vice versa. If the same dynamics occur in both agent-based and recursion-based models, then we can be more confident that those dynamics are genuine and not the result of a programming error or mathematical mistake.

References

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Simulation Models of Cultural Evolution in R

Alex Mesoudi

Model 2: Unbiased and biased mutation

Evolution doesn't work without a source of variation that introduces new variation upon which selection, drift and other processes can act. In genetic evolution, mutation is almost always blind with respect to function. Beneficial genetic mutations are no more likely to arise when they are needed than when they are not needed - in fact most genetic mutations are neutral or detrimental to an organism. Cultural evolution is more interesting, in that novel variation may sometimes be directed to solve specific problems, or systematically biased due to features of our cognition. In the models below we'll simulate both unbiased and biased mutation.

Model 2a: Unbiased mutation

First we will simulate unbiased mutation in the same basic model as used in Model 1. We'll remove unbiased transmission to see the effect of unbiased mutation alone.

As in Model 1, we assume N individuals each of whom possesses one of two cultural traits, denoted A and B . In each generation from $t = 1$ to $t = t_{max}$, the N agents are replaced with N new agents. Instead of random copying, each agent now gives rise to a new agent with exactly the same cultural trait as them. (Another way of looking at this is in terms of timesteps, such as years: the same N agents live for t_{max} years, and keep their cultural trait from one year to the next.)

Each generation, there is a probability μ that each agent mutates from their current trait to the other trait. This probability applies to each agent independently; whether an agent mutates has no bearing on whether or how many other agents have mutated. On average, that means that μN agents mutate each generation. Like in Model 1, we are interested in tracking the proportion p of agents with trait A over time.

We'll wrap this in a function called **UnbiasedMutation**, using much of the same code as **UnbiasedTransmission**. Now though we have an extra parameter, μ , to specify.

```
UnbiasedMutation <- function (N, mu, p_0, t_max, r_max) {  
  
  # create a matrix with t_max rows and r_max columns, fill with NAs, convert to data frame  
  output <- as.data.frame(matrix(NA, t_max, r_max))  
  
  # purely cosmetic: rename the columns with run1, run2 etc.  
  names(output) <- paste("run", 1:r_max, sep="")  
  
  for (r in 1:r_max) {  
  
    # create first generation  
    agent <- data.frame(trait = sample(c("A", "B"), N, replace = TRUE,  
                                         prob = c(p_0, 1-p_0)))  
  
    # add first generation's p to first row of column r  
    output[r, 1] <- agent$trait  
  }  
}  
  
# test the function  
output <- UnbiasedMutation(N = 10, mu = 0.01, p_0 = 0.5, t_max = 10, r_max = 10)  
head(output)
```

```

output[1,r] <- sum(agent$trait == "A") / N

for (t in 2:t_max) {

  # copy agent to previous_agent dataframe
  previous_agent <- agent

  # get N random numbers each between 0 and 1
  mutate <- runif(N)

  # if agent was A, with probability mu, flip to B
  agent$trait[previous_agent$trait == "A" & mutate < mu] <- "B"

  # if agent was B, with probability mu, flip to A
  agent$trait[previous_agent$trait == "B" & mutate < mu] <- "A"

  # get p and put it into output slot for this generation t and run r
  output[t,r] <- sum(agent$trait == "A") / N

}

}

# first plot a thick line for the mean p
plot(rowMeans(output),
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("N = ", N, ", mu = ", mu, sep = ""))
}

for (r in 1:r_max) {

  # add lines for each run, up to r_max
  lines(output[,r], type = 'l')

}

output # export data from function
}

```

The only changes from Model 1 are the addition of μ in the function definition and the plot title, and three new lines of code within the t **for** loop which replace the random copying command with unbiased mutation. Let's examine these three lines to see how they work.

The most obvious way of implementing unbiased mutation - which is NOT done above - would have been to set up another **for** loop. We would cycle through each agent one by one, each time calculating whether it should mutate or not based on μ . This would certainly work, but R is notoriously slow at loops. It's always preferable in R, where possible, to use 'vectorised' code. That's what is done above in our three added lines.

First we pre-specify the probability of mutating for each agent. This is done with the **runif** (random draws from a **uniform distribution**) command which generates N random numbers each between 0 and 1, and puts them into a variable called *mutate*. If the i th value in *mutate* is less than or equal to μ , then the i th agent

in our *agent* dataframe will mutate. This is done on the subsequent two lines, first for agents that were previously *A*, and then for agents that were previously *B*.

We can think about this by imagining what happens at extreme values of μ . If $\mu = 1$, then that agent's *mutate* value will always be less than μ , because the maximum value of *mutate* is 1 (we can ignore the case when *mutate* happens to be exactly 1.000, as it will very rarely happen). The inequality is therefore always true, and the agent always mutates. That's what we want to happen, if $\mu = 1$. The following code illustrates this:

```
N <- 100
mu <- 1 # maximum mutation rate of 1

# get N random numbers each between 0 and 1
mutate <- runif(N)

# always mutate
mutate < mu

## [1] TRUE TRUE
## [16] TRUE TRUE
## [31] TRUE TRUE
## [46] TRUE TRUE
## [61] TRUE TRUE
## [76] TRUE TRUE
## [91] TRUE TRUE
```

If $\mu = 0$, then that agent's *mutate* value will never be less than μ , because the minimum value of *mutate* is 0. The inequality is therefore never true, and the agent never mutates. Again, that's what we want, if $\mu = 0$. In code:

```
N <- 100
mu <- 0 # minimum mutation rate of 0

# get N random numbers each between 0 and 1
mutate <- runif(N)

# never mutate
mutate < mu

## [1] FALSE FALSE FALSE FALSE FALSE FALSE FALSE FALSE FALSE FALSE
## [13] FALSE FALSE
## [25] FALSE FALSE
## [37] FALSE FALSE
## [49] FALSE FALSE
## [61] FALSE FALSE
## [73] FALSE FALSE
## [85] FALSE FALSE
## [97] FALSE FALSE FALSE FALSE
```

At intermediate values, say $\mu = 0.1$, then the inequality is true for 10% of the *mutate* values, or in other words for 10% of the agents. Again, in code:

```

N <- 100
mu <- 0.1 # mutation rate of 10%

# get N random numbers each between 0 and 1
mutate <- runif(N)

# 10% of agents mutate
mutate < mu

## [1] FALSE FALSE FALSE TRUE FALSE FALSE FALSE TRUE FALSE FALSE FALSE FALSE
## [13] FALSE FALSE FALSE FALSE FALSE TRUE FALSE TRUE FALSE FALSE FALSE FALSE
## [25] FALSE FALSE
## [37] FALSE TRUE
## [49] FALSE FALSE FALSE FALSE FALSE FALSE FALSE FALSE FALSE TRUE FALSE FALSE
## [61] FALSE FALSE TRUE FALSE FALSE FALSE FALSE FALSE FALSE FALSE FALSE FALSE FALSE
## [73] FALSE FALSE FALSE TRUE FALSE FALSE TRUE FALSE FALSE FALSE FALSE FALSE FALSE
## [85] FALSE FALSE FALSE FALSE FALSE FALSE TRUE FALSE FALSE TRUE FALSE FALSE
## [97] FALSE FALSE TRUE FALSE

sum(mutate < mu) / N

## [1] 0.12

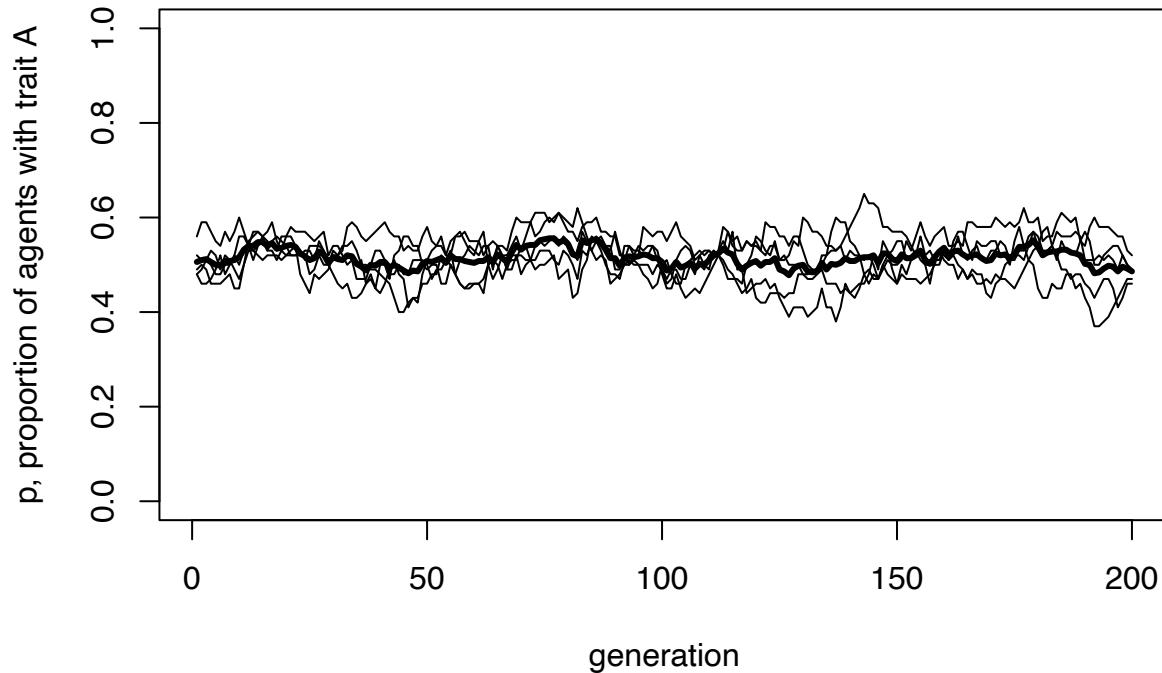
```

The value gives the proportion of mutating agents, and should be approximately (not necessarily exactly) 0.1.

Let's run this unbiased mutation model.

```
data_model2a <- UnbiasedMutation(N = 100, mu = 0.05, p_0 = 0.5, t_max = 200, r_max = 5)
```

N = 100, mu = 0.05



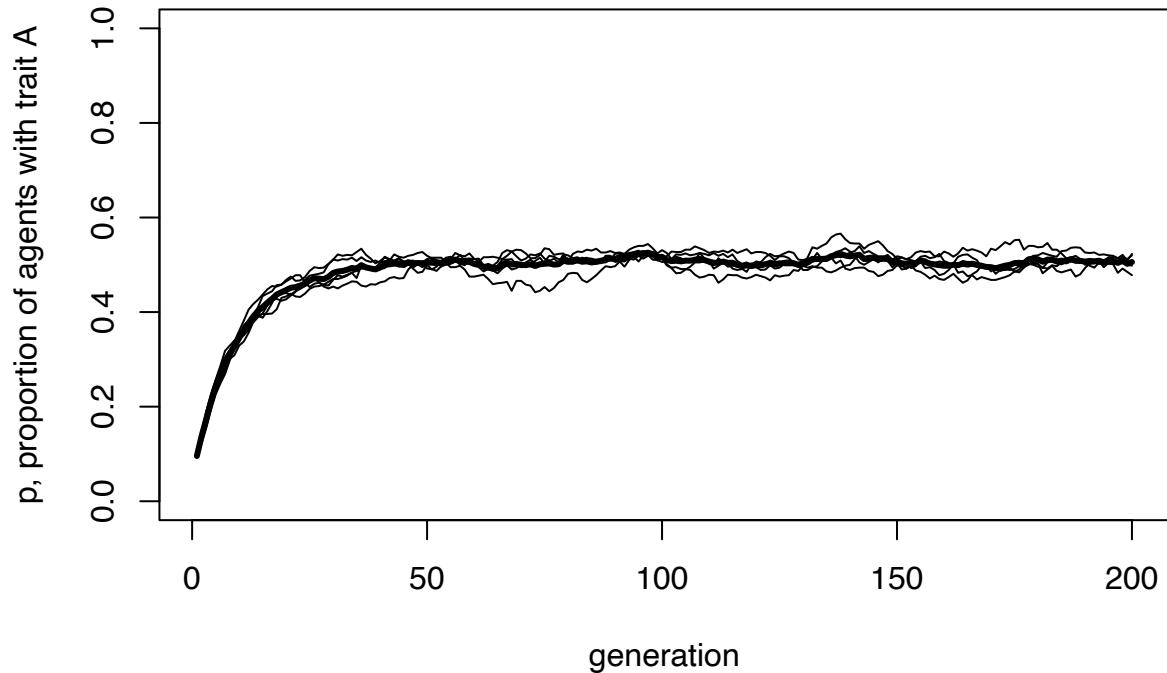
As one might expect, unbiased mutation produces random fluctuations over time, and does not alter the overall frequency of A which stays around $p = 0.5$. Because mutations from A to B are as equally likely as B to A , there is no overall directional trend.

But what if we were to start at different initial frequencies of A and B ? Say, $p = 0.2$ or $p = 0.9$? Would unbiased mutation keep p at these initial values, like we saw unbiased transmission does in Model 1?

To find out, let's change p_0 , which, as you may recall from Model 1, specifies the initial probability of drawing an A rather than a B in the first generation.

```
data_model2a <- UnbiasedMutation(N = 1000, mu = 0.05, p_0 = 0.1, t_max = 200, r_max = 5)
```

N = 1000, mu = 0.05



You should see p go from 0.1 up to 0.5. In fact, whatever the initial starting frequencies of A and B , unbiased mutation always leads to $p = 0.5$. Unlike the unbiased transmission simulated in Model 1, with unbiased mutation it is impossible for one trait to be lost and the other go to fixation. Unbiased mutation introduces and maintains cultural variation in the population.

Model 2b: Biased mutation

A more interesting case is biased mutation. Let's assume now that there is a probability μ_b that an agent with trait B mutates into A , but there is no possibility of trait A mutating into trait B . Perhaps trait A is a particularly catchy or memorable version of a story, or an intuitive explanation of a phenomenon, and B is difficult to remember or unintuitive.

The function **BiasedMutation** captures this unidirectional mutation.

```
BiasedMutation <- function (N, mu_b, p_0, t_max, r_max) {

  # create a matrix with t_max rows and r_max columns, fill with NAs, convert to dataframe
  output <- as.data.frame(matrix(NA, t_max, r_max))

  # purely cosmetic: rename the columns with run1, run2 etc.
  names(output) <- paste("run", 1:r_max, sep="")

  for (r in 1:r_max) {

    # create first generation
    agent <- data.frame(trait = sample(c("A", "B"), N, replace = TRUE,
```

```

prob = c(p_0, 1-p_0))

# add first generation's p to first row of column r
output[1,r] <- sum(agent$trait == "A") / N

for (t in 2:t_max) {

  # copy agent to previous_agent dataframe
  previous_agent <- agent

  # get N random numbers each between 0 and 1
  mutate <- runif(N)

  # if agent was B, with prob mu_b, flip to A
  agent$trait[previous_agent$trait == "B" & mutate < mu_b] <- "A"

  # get p and put it into output slot for this generation t and run r
  output[t,r] <- sum(agent$trait == "A") / N

}

# first plot a thick line for the mean p
plot(rowMeans(output),
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("N = ", N, ", mu = ", mu_b, sep = ""))

for (r in 1:r_max) {

  # add lines for each run, up to r_max
  lines(output[,r], type = 'l')

}

output # export data from function
}

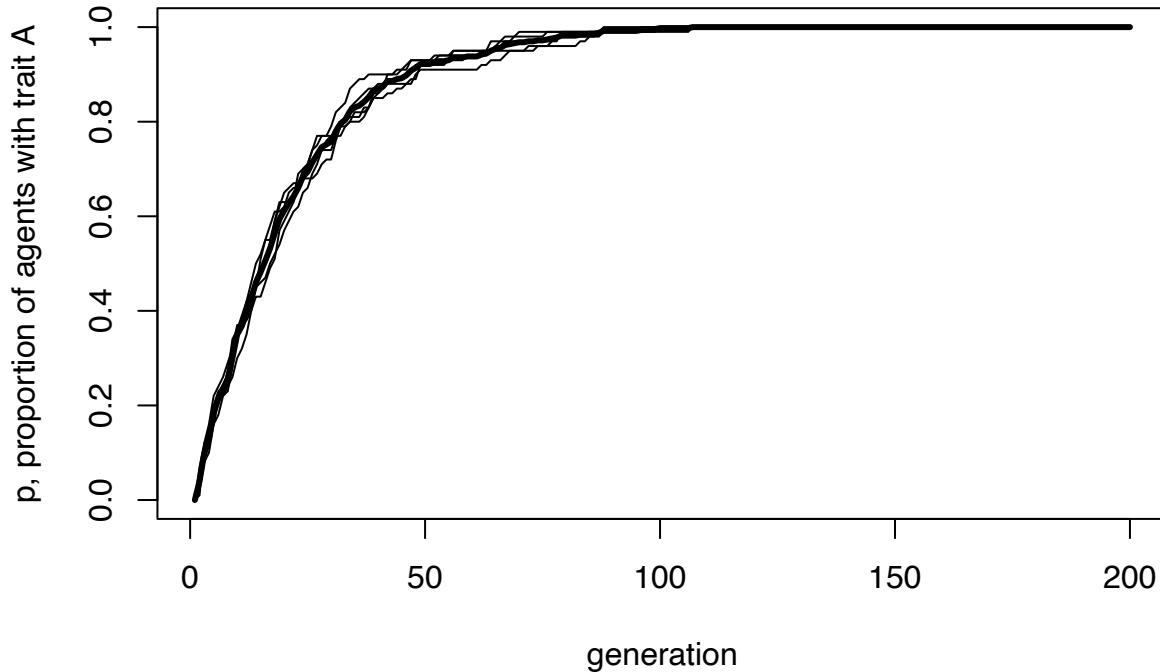
```

There are just two changes in this code compared to **UnbiasedMutation**. First, we've replaced μ with μ_b to keep the two parameters distinct and avoid confusion. Second, the line in **UnbiasedMutation** which caused agents with A to mutate to B has been deleted.

Let's see what effect this has by running **BiasedMutation**. We'll start with the population entirely composed of agents with B , i.e. $p_0 = 0$, to see how quickly and in what manner A spreads via biased mutation.

```
data_model2b <- BiasedMutation(N = 100, mu_b = 0.05, p_0 = 0, t_max = 200, r_max = 5)
```

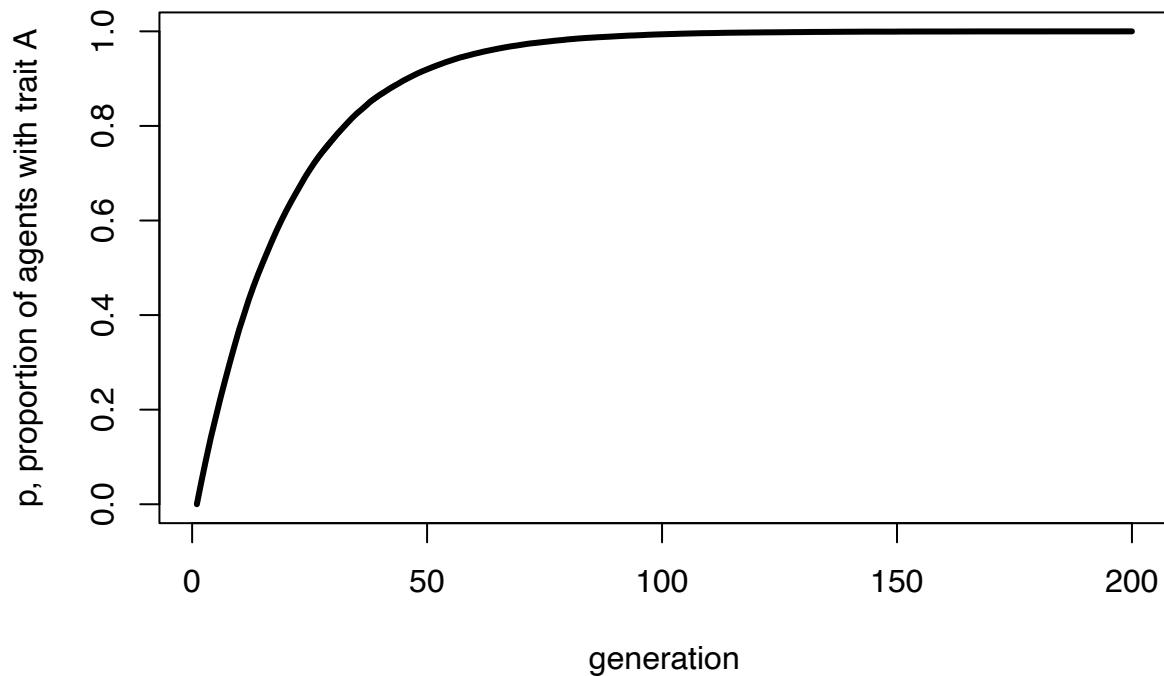
N = 100, mu = 0.05



The plot should show a steep increase that slows and plateaus at $p = 1$ by around generation $t = 100$. There should be a bit of fluctuation in the different runs, but not much. Now let's try a larger sample size.

```
data_model2b <- BiasedMutation(N = 10000, mu_b = 0.05, p_0 = 0, t_max = 200, r_max = 5)
```

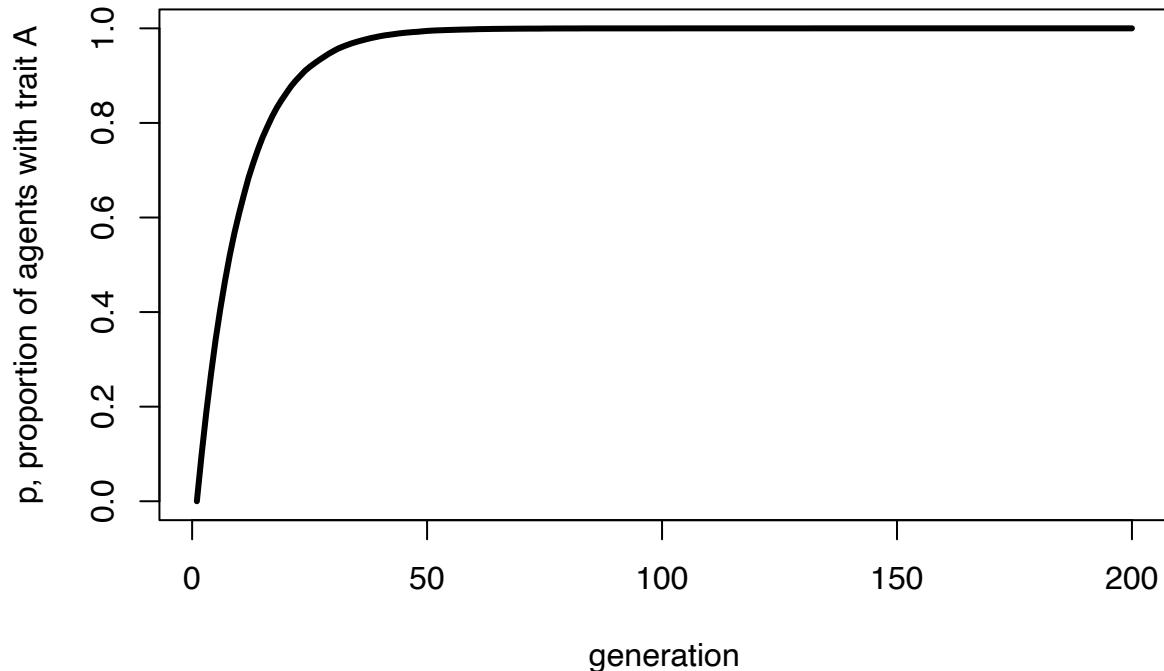
N = 10000, mu = 0.05



With $N = 10000$ the line should be smooth with little fluctuation across the runs. But notice that it plateaus at about the same generation, around $t = 100$. Population size has little effect on the rate at which a novel trait spreads via biased mutation. μ_b , on the other hand, does affect this speed. Let's double the biased mutation rate to 0.1.

```
data_model2b <- BiasedMutation(N = 10000, mu_b = 0.1, p_0 = 0, t_max = 200, r_max = 5)
```

N = 10000, mu = 0.1



Now trait A reaches fixation around generation $t = 50$. Play around with N and μ_b to confirm that the latter determines the rate of diffusion of trait A , and that it takes the same form each time - roughly an ‘r’ shape with an initial steep increase followed by a plateauing at $p = 1$.

Summary of Model 2

With this simple model we can draw the following insights. Unbiased mutation, which resembles genetic mutation in being non-directional, always leads to an equal mix of the two traits. It introduces and maintains cultural variation in the population. It is interesting to compare unbiased mutation to unbiased transmission from Model 1. While unbiased transmission did not change p over time, unbiased mutation always converges on $p^* = 0.5$, irrespective of the starting frequency. (NB $p^* = 0.5$ assuming there are two traits; more generally, $p^* = 1/v$, where v is the number of traits.)

Biased mutation, which is far more common - perhaps even typical - in cultural evolution, shows different dynamics. Novel traits favoured by biased mutation spread in a characteristic fashion - an r-shaped diffusion curve - with a speed characterised by the mutation rate μ_b . Population size has little effect, whether $N = 100$ or $N = 10000$. This is because mutation is an individual-level process, and does not depend on the traits of any other agent(s) in the population. Whenever biased mutation is present ($\mu_b > 0$), the favoured trait goes to fixation, even if it is not initially present.

A form of unbiased cultural mutation can be observed when people try to copy artifact sizes or shapes, and the limits of our perceptual systems introduces random noise into the copied form. This has been studied in the context of the transmission of archaeological artifacts such as handaxes and arrowheads (Eerkens & Lipo 2005) and confirmed experimentally (Kempe et al. 2012). Another form of biased cultural mutation has

been argued to result from universal features of human cognition, as different people or groups independently transform cultural traits towards certain ‘attractive’ forms. For example, studies have shown how portraits of subjects averting their gaze systematically mutated into portraits of subjects with direct eye gaze (Morin 2013), and how blood-letting as a medical practice independently emerged in different societies around the world (Miton et al. 2015).

In terms of programming techniques, the major novelty in Model 2 is the use of `runif` to generate a series of N random numbers from 0 to 1 and compare these to a fixed probability (in our case, μ or μ_b) to determine which agents should undergo whatever the fixed probability specifies (in our case, mutation). This could be done with a loop, but vectorising code in the way we did here is much faster in R than loops.

Exercises

1. Try different values of p_0 in **UnbiasedMutation** to confirm that any starting value converges on approximately $p = 0.5$.
 2. Try different values of p_0 in **BiasedMutation** to confirm that any starting value converges on $p = 1$.
 3. Try different values of N and μ_b in **BiasedMutation** to confirm that μ_b does, and N does not, affect the speed with which p reaches fixation.
 4. Create an alternative **UnbiasedMutation** function which uses a for-loop to cycle through each agent and, for each one, mutate its cultural trait with probability μ . Use the function `system.time()` to compare the time that this looping function takes with the time the original vectorised **UnbiasedMutation** function takes, for the same parameter values. Is the vectorised version faster? If so, how many times faster?
 5. Add a parameter μ_a to **BiasedMutation** which determines the probability that an agent with A mutates to B . Run the simulation to show that the equilibrium value of p , and the speed at which this equilibrium is reached, depends on the difference between μ_a and μ_b .
 6. Add a third trait, C , to the **UnbiasedMutation** function. The first generation should have traits set using `sample` with `c("A", "B", "C")` rather than `c("A", "B")`. You will need to define a new parameter, q_0 , which gives the probability of drawing a B , equivalent to how p_0 gives the probability of drawing an A . The probability of drawing a C is then $1 - p_0 - q_0$, given that all the probabilities have to add up to one. These probabilities can be entered into the `prob` argument of `sample`. Then modify the unbiased mutation lines such that, if an agent has trait A , with probability μ they have an equal chance of mutating into either B or C ; agents with trait B similarly have a probability μ of mutating into either A or C ; and agents with C mutate with probability μ into either A or B . Record and plot p , the frequency of A , as before. Does p still converge on 0.5, as it does with only two traits?
-

Analytical Appendix

If p is the frequency of A in one generation, we are interested in calculating p' , the frequency of A in the next generation under the assumption of unbiased mutation. The next generation retains the cultural traits of the previous generation, except that μ of them switch to the other trait. There are therefore two sources of A in the next generation: members of the previous generation who had A and didn’t mutate, therefore staying A , and members of the previous generation who had B and did mutate, therefore switching to A . The frequency of A in the next generation is therefore:

$$p' = p(1 - \mu) + (1 - p)\mu \quad (2.1)$$

The first term on the right-hand side of Equation 2.1 represents the first group, the $(1 - \mu)$ proportion of the p A -carriers who didn't mutate. The second term represents the second group, the μ proportion of the $1 - p$ B -carriers who did mutate.

To calculate the equilibrium value of p , p^* , we want to know when $p' = p$, or when the frequency of A in one generation is identical to the frequency of A in the next generation. This can be found by setting $p' = p$ in Equation 2.1, which gives:

$$p = p(1 - \mu) + (1 - p)\mu \quad (2.2)$$

Rearranging Equation 2.2 gives:

$$\mu(1 - 2p) = 0 \quad (2.3)$$

The left-hand side of Equation 2.3 equals zero when either $\mu = 0$, which given our assumption that $\mu > 0$ cannot be the case, or when $1 - 2p = 0$, which after rearranging gives the single equilibrium $p^* = 0.5$. This matches our simulation results above. As we found in the simulations, this does not depend on μ or the starting frequency of p .

We can also plot the recursion in Equation 2.1 like so:

```

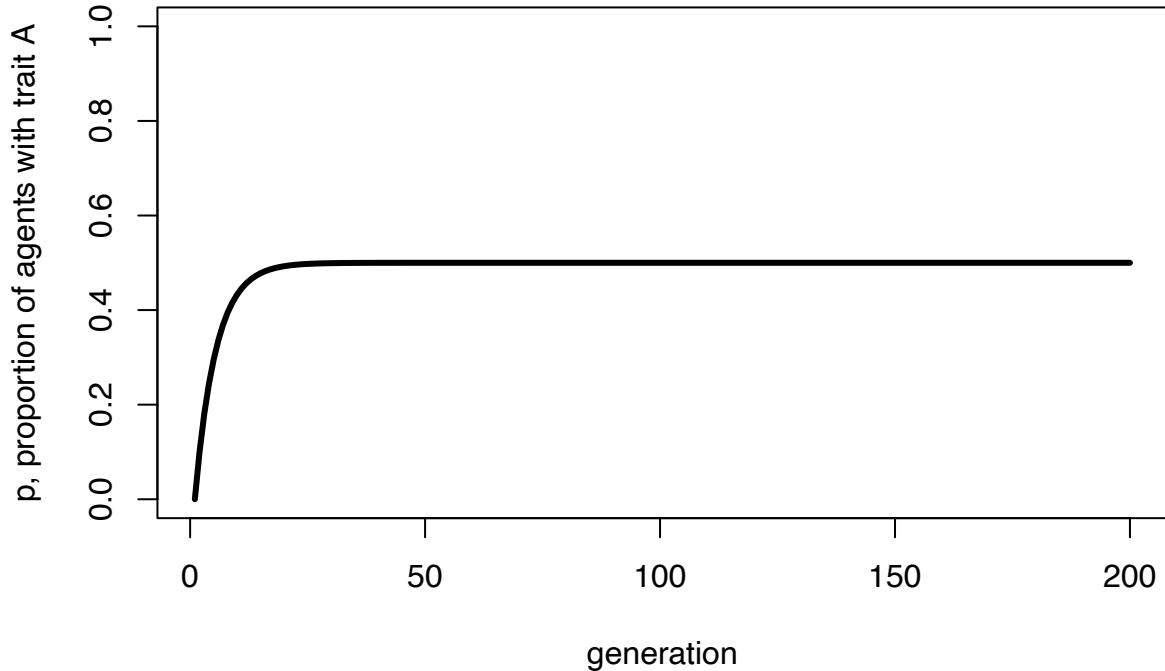
p_0 <- 0
t_max <- 200
mu <- 0.1

p <- rep(NA, t_max)
p[1] <- p_0

for (i in 2:t_max) {
  p[i] <- p[i-1]*(1 - mu) + (1-p[i-1])*mu
}

plot(p,
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3)

```



Again, this should resemble the figure generated by the simulations above, and confirm that $p^* = 0.5$.

For biased mutation, assume that only Bs are switching to A , and with probability μ_b instead of μ . The first term on the right hand side becomes simply p , because As do not switch. The second term remains the same, but with μ_b . Thus,

$$p' = p + (1 - p)\mu_b \quad (2.4)$$

The equilibrium value p^* can be found by again setting $p' = p$ and solving for p . Assuming $\mu_b > 0$, this gives the single equilibrium $p^* = 1$, which again matches the simulation results.

We can plot the above recursion like so:

```

p_0 <- 0
t_max <- 200
mu_b <- 0.1

p <- rep(NA, t_max)
p[1] <- p_0

for (i in 2:t_max) {
  p[i] <- p[i-1] + (1 - p[i-1])*mu_b
}

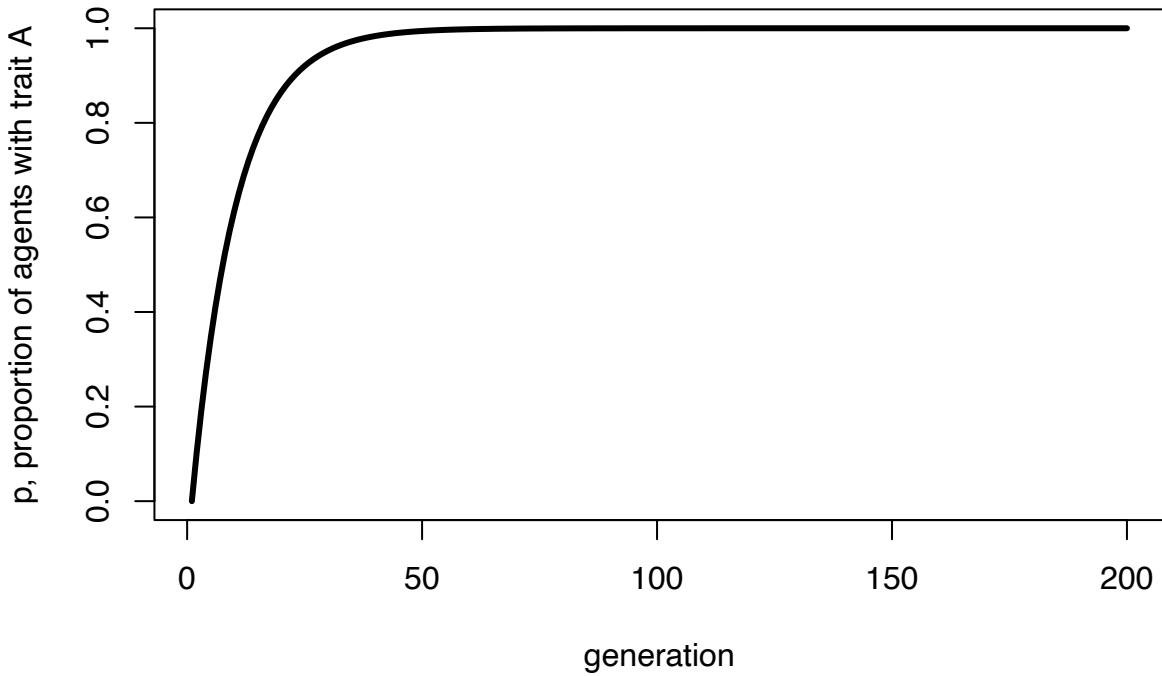
plot(p,
      type = 'l',
      ylab = "p, proportion of agents with trait A",

```

```

xlab = "generation",
ylim = c(0,1),
lwd = 3)

```



Hopefully, this looks identical to the final simulation plot with the same value of μ_b .

Furthermore, we can specify an equation for the change in p from one generation to the next, or Δp . We do this by subtracting p from both sides of Equation 2.4, giving:

$$\Delta p = p' - p = (1 - p)\mu_b \quad (2.5)$$

Seeing this helps explain two things. First, the $1 - p$ part explains the r-shape of the curve. It says that the smaller is p , the larger Δp will be. This explains why p increases in frequency very quickly at first, when p is near zero, and the increase slows when p gets larger. We have already determined that the increase stops altogether (i.e. $\Delta p = 0$) when $p = p^* = 1$.

Second, it says that the rate of increase is proportional to μ_b . This explains our observation in the simulations that larger values of μ_b cause p to reach its maximum value faster.

References

Eerkens, J. W., & Lipo, C. P. (2005). Cultural transmission, copying errors, and the generation of variation in material culture and the archaeological record. *Journal of Anthropological Archaeology*, 24(4), 316-334.

Kempe, M., Lycett, S., & Mesoudi, A. (2012). An experimental test of the accumulated copying error model of cultural mutation for Acheulean handaxe size. *PLoS One*, 7(11), e48333.

Miton, H., Claidière, N., & Mercier, H. (2015). Universal cognitive mechanisms explain the cultural success of bloodletting. *Evolution and Human Behavior*, 36(4), 303-312.

Morin, O. (2013). How portraits turned their eyes upon us: visual preferences and demographic change in cultural evolution. *Evolution and Human Behavior*, 34(3), 222-229.

Simulation Models of Cultural Evolution in R

Alex Mesoudi

Model 3: Biased transmission (direct/content bias)

So far we have looked at unbiased transmission (Model 1) and unbiased/biased mutation (Model 2). Let's complete the set by looking at biased transmission. This occurs when one trait or one demonstrator is more likely to be copied than another trait or demonstrator. Trait-based copying is often called 'direct' or 'content' bias, while demonstrator-based copying is often called 'indirect' or 'context' bias. Both are sometimes also called 'cultural selection' because one thing (trait or demonstrator) is selected to be copied over another. In Model 3 we'll look at trait-based (direct, content) bias.

(As an aside, there is a confusing array of terminology in the field of cultural evolution, as illustrated by the preceding paragraph. That's why models are so useful. Words and verbal descriptions can be ambiguous. Often the writer doesn't realise that there are hidden assumptions or unrecognised ambiguities in their descriptions. They may not realise that what they mean by 'cultural selection' is entirely different to how someone else uses it. Models are great because they force us to specify exactly what we mean by a particular term or process. I can use the words in the paragraph above to describe biased transmission, but it's only really clear when I model it, making all my assumptions explicit.)

As in Models 1 and 2, we assume there are two traits A and B . Let's assume that biased transmission favours trait A . Perhaps A is a more effective tool, more memorable story, or more easily pronounced word. We're not including any mutation in the model, so we need to include some A s at the beginning of the simulation otherwise it would never appear. However, let's make it initially rare. Then we can see how selection favours this initially-rare trait.

To simulate biased transmission, following Model 1, we assume that each agent chooses another agent from the previous generation at random. But this time, if that chosen agent possesses trait A , then the focal agent copies trait A with probability s . This parameter s gives the strength of biased transmission, or the probability that an agent encountering another agent with a more favourable trait than their current trait abandons their current trait and adopts the new trait. If $s = 0$, there is no selection and agents never switch as a result of biased transmission. If $s = 1$, then agents always switch when encountering a favoured alternative.

Below is a function **BiasedTransmission** that implements all of these processes.

```
BiasedTransmission <- function (N, s, p_0, t_max, r_max) {  
  
  # create a matrix with t_max rows and r_max columns, fill with NAs, convert to dataframe  
  output <- as.data.frame(matrix(NA, t_max, r_max))  
  
  # purely cosmetic: rename the columns with run1, run2 etc.  
  names(output) <- paste("run", 1:r_max, sep="")  
  
  for (r in 1:r_max) {  
  
    # create first generation  
    agent <- data.frame(trait = sample(c("A", "B"), N, replace = TRUE,  
                                         prob = c(p_0, 1 - p_0)))  
  
    for (i in 1:N) {  
  
      # randomly choose another agent to copy from  
      j <- sample(1:N, 1)  
  
      if (agent$trait[i] == "A" & agent$trait[j] == "B") {  
        if (runif(1) < s) {  
          agent$trait[i] <- "B"  
        }  
      } else if (agent$trait[i] == "B" & agent$trait[j] == "A") {  
        if (runif(1) < 1 - s) {  
          agent$trait[i] <- "A"  
        }  
      }  
    }  
  }  
}
```

```

prob = c(p_0, 1-p_0))

# add first generation's p to first row of column r
output[1,r] <- sum(agent$trait == "A") / N

for (t in 2:t_max) {

  # biased transmission

  # copy agent to previous_agent dataframe
  previous_agent <- agent

  # for each agent, pick a random agent from the previous generation
  # as demonstrator and store their trait
  demonstrator_trait <- sample(previous_agent$trait, N, replace = TRUE)

  # get N random numbers each between 0 and 1
  copy <- runif(N)

  # if demonstrator has A and with probability s, copy A from demonstrator
  agent$trait[demonstrator_trait == "A" & copy < s] <- "A"

  # get p and put it into output slot for this generation t and run r
  output[t,r] <- sum(agent$trait == "A") / N

}

}

# first plot a thick line for the mean p
plot(rowMeans(output),
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("N = ", N, ", s = ", s, sep = ""))
}

for (r in 1:r_max) {

  # add lines for each run, up to r_max
  lines(output[,r], type = 'l')

}

output # export data from function
}

```

Most of **BiasedTransmission** is recycled from Models 1 and 2. As before, we set up a dataframe to hold the *output* from multiple runs, and in generation $t = 1$ create a dataframe to hold the trait of each *agent*. The plot function is also similar, but now we add s to the plot title so we don't forget it.

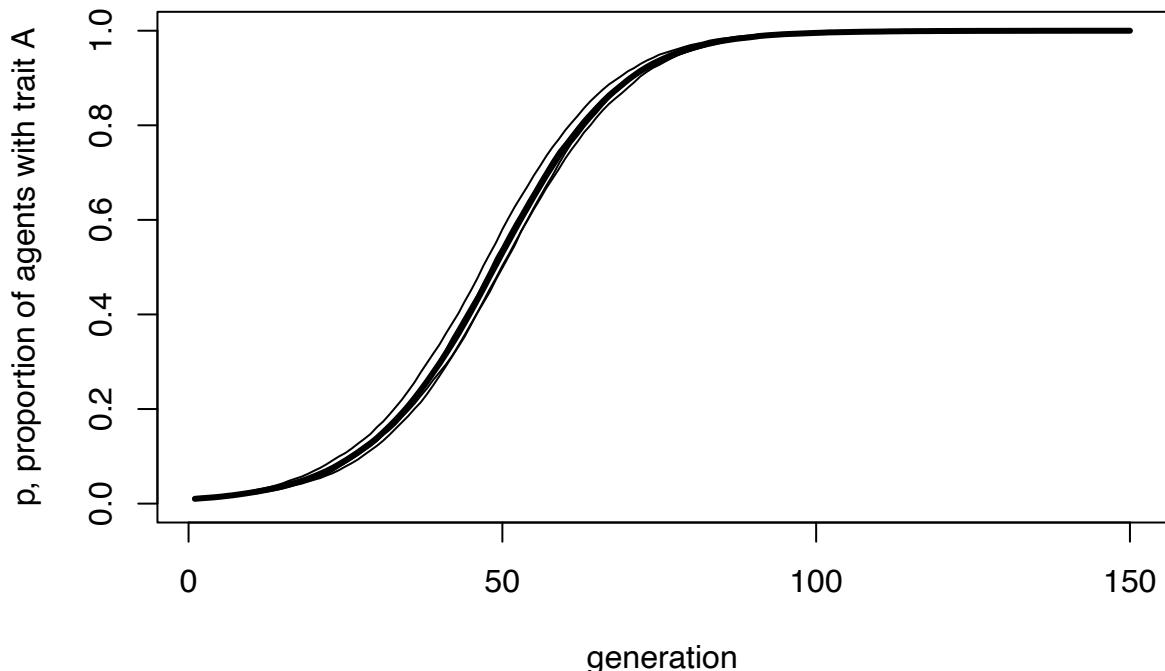
The major change is that we now include biased transmission from the second generation onwards. Using vectorised code, we pick for each of N agents one of the previous generation's agents at random and store

their trait in `demonstrator_trait`. Then we get random numbers between 0 and 1 for each agent and store these in `copy`. If the demonstrator has trait A (`demonstrator_trait == "A"`), and with probability s (`copy < s`), then the agent adopts trait A .

Let's run our **BiasedTransmission** model. Remember we are starting with a population with a small number of A s, so $p_0 = 0.01$.

```
data_model3 <- BiasedTransmission(N = 10000, s = 0.1, p_0 = 0.01, t_max = 150, r_max = 5)
```

N = 10000, s = 0.1



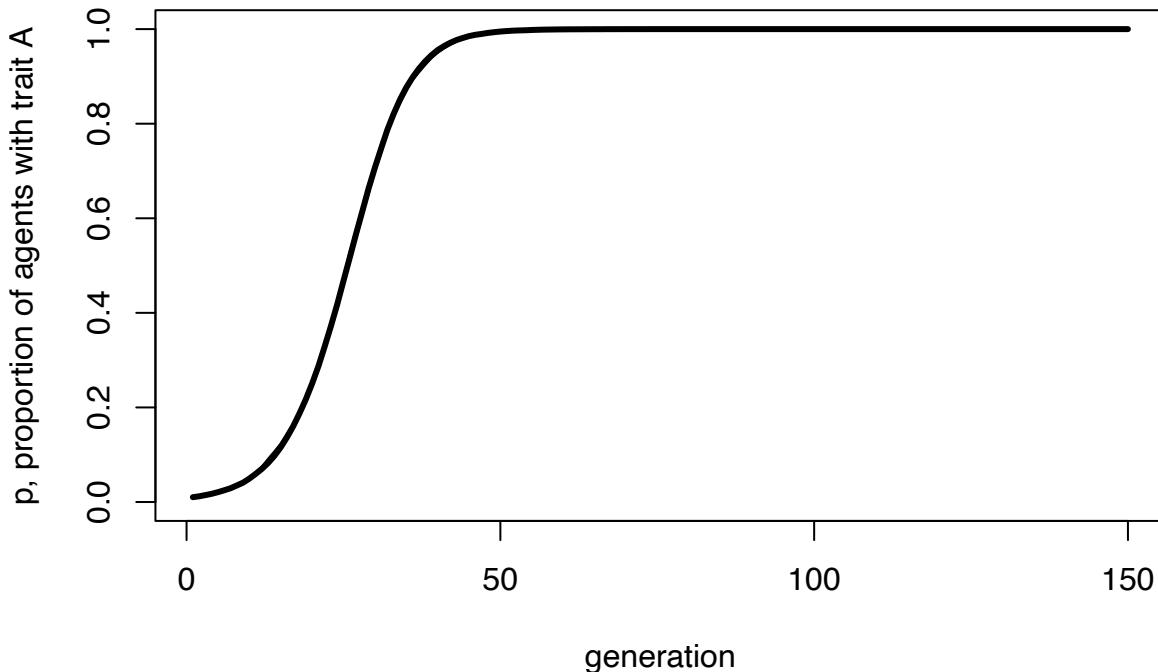
With a moderate selection strength of $s = 0.1$, we can see that A gradually replaces B and goes to fixation. It does this in a characteristic manner: the increase is slow at first, then picks up speed, then plateaus.

Note the difference to biased mutation. Where biased mutation was r-shaped, with a steep initial increase, biased transmission is s-shaped, with an initial slow uptake. This is because the strength of biased transmission, like selection in general, is proportional to the variation in the population. When A is rare initially, there is only a small chance of picking another agent with A . As A spreads, the chances of picking an A agent increases. As A becomes very common, there are few B agents left to switch.

Let's double the selection strength to $s = 0.2$, below.

```
data_model3 <- BiasedTransmission(N = 10000, s = 0.2, p_0 = 0.01, t_max = 150, r_max = 5)
```

N = 10000, s = 0.2

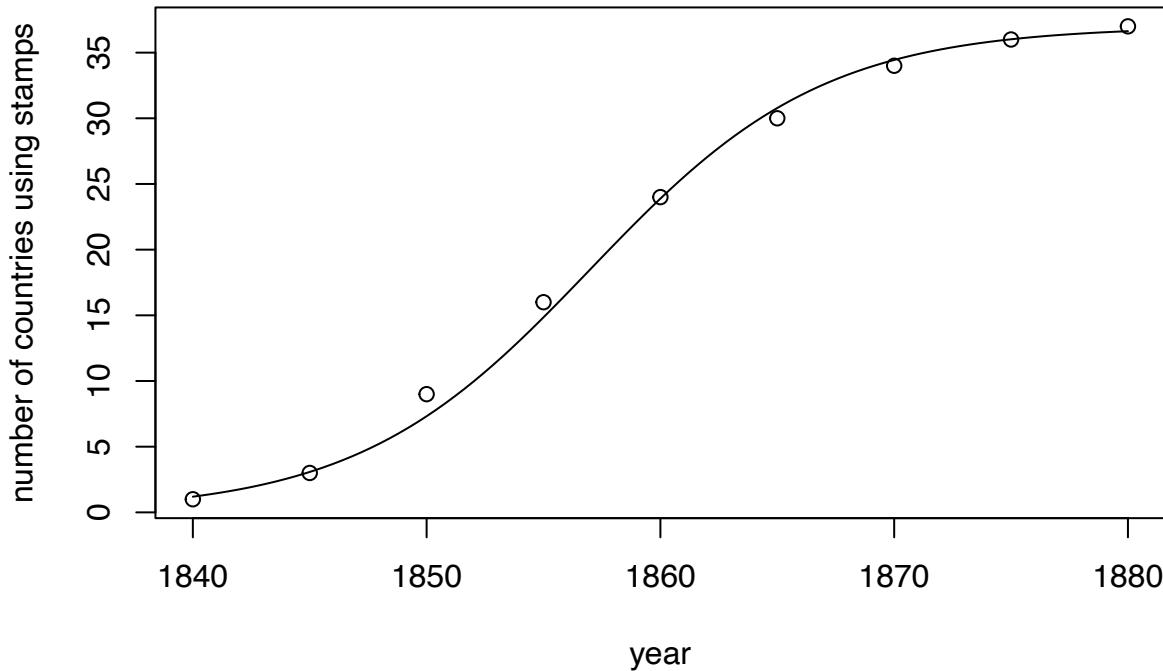


As we might expect, increasing the strength of selection increases the speed with which *A* goes to fixation. Note, though, that it retains the s-shape.

Summary of Model 3

In Model 3 we saw how biased transmission causes a trait favoured by the selection bias to spread and go to fixation in a population, even when it is initially very rare. Biased transmission differs in its dynamics from biased mutation. Its action is proportional to the variation in the population at the time at which it acts. It is strongest when there is lots of variation (in our model, when there are equal numbers of *A* and *B* at $p = 0.5$), and weakest when there is little variation (when p is close to 0 or 1). This generates an s-shaped pattern of diffusion over time.

S-shaped diffusion curves like the ones we generated using Model 3 are ubiquitous in the real world. Rogers (2010) catalogued numerous examples of the s-shaped diffusion of novel technological and social innovations, from the spread of hybrid seed corn to the spread of new methods for teaching mathematics. Here is one example at the country level, concerning the spread of postage stamps in different European countries (data from Pemberton 1936):



Given that it is unlikely that 37 countries independently invented postage stamps over such a brief period, we can probably attribute the diffusion of postage stamps to a form of biased cultural transmission, as national postal services observed and copied the effective use of stamps in neighbouring countries. Henrich (2001) explicitly linked s-shaped diffusion curves to directly biased cultural transmission, rather than biased mutation, which as we saw in Model 2 generates r-shaped diffusion curves. Similarly, Newberry et al. (2017) provided evidence of s-shaped diffusion curves in the spread of novel grammatical forms, using them to distinguish biased transmission / cultural selection from unbiased transmission (see Model 1). However, we should also be cautious not to jump to conclusions. Many processes generate s-shaped diffusion curves, not just biased transmission, including sometimes purely individual-level biased mutation (Reader 2004; Hoppitt et al. 2010).

Exercises

1. Try different values of s to confirm that larger s increases the speed with which A goes to fixation.
2. Change s in **BiasedTransmission** to s_a , and add a new parameter s_b which specifies the probability of an agent copying trait B from a demonstrator who possesses that trait. Run the simulation to show that the equilibrium value of p , and the speed at which this equilibrium is reached, depends on the difference between s_a and s_b . How do these dynamics differ from the μ_a and μ_b you implemented in Model 2 Q5?

Analytical Appendix

As before, we have p agents with trait A and $1 - p$ agents with trait B . The p agents with trait A keep their A s, because A is favoured by biased transmission. The $1 - p$ agents with trait B pick another agent at random. If the random agent has B then nothing happens. However if the random agent has A , which they will with probability p , then with probability s they switch to that trait A . We can therefore write the recursion for p under biased transmission as:

$$p' = p + p(1 - p)s \quad (3.1)$$

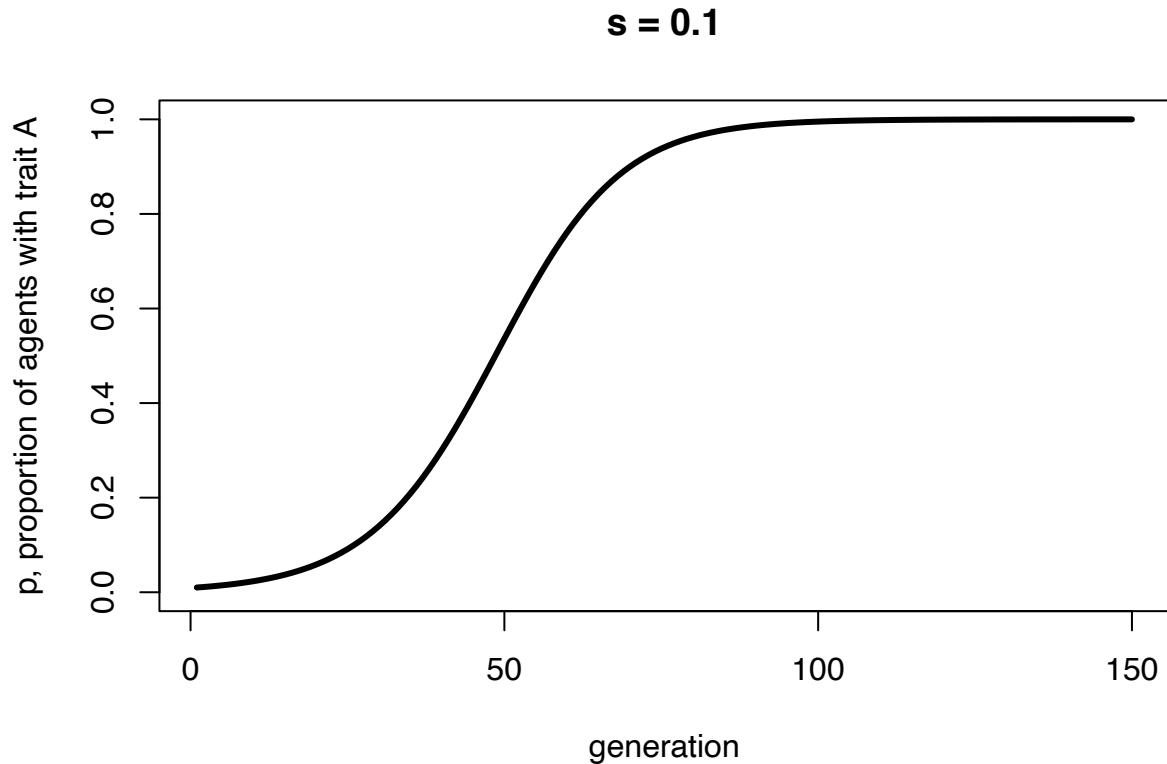
The first term on the right-hand side is the unchanged A bearers, and the second term is the $1 - p$ B -bearers who find one of the p A -bearers and switch with probability s .

Here is some code to plot this biased transmission recursion:

```
p <- rep(0, 150)
p[1] <- 0.01
s <- 0.1

for (i in 2:150) {
  p[i] <- p[i-1] + p[i-1]*(1-p[i-1])*s
}

plot(p,
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("s = ", s, sep = ""))
```



The curve above should be identical to the simulation curve, given that the simulation had the same biased transmission strength s and a large enough N to minimise stochasticity.

From Equation 3.1 above, we can see how the strength of biased transmission depends on variation in the population, given that $p(1 - p)$ is the formula for variance. This determines the shape of the curve, while s determines the speed with which the equilibrium p^* is reached.

But what is the equilibrium p^* here? In fact there are two. As before, the equilibrium can be found by setting the change in p to zero, or when:

$$p(1 - p)s = 0 \quad (3.2)$$

There are three ways in which the left-hand side can equal zero: when $p = 0$, when $p = 1$ and when $s = 0$. The last case is uninteresting: it would mean that biased transmission is not occurring. The first two cases simply say that if either trait reaches fixation, then it will stay at fixation. This is to be expected, given that we have no mutation in our model. It contrasts with unbiased and biased mutation, where there is only one equilibrium value of p .

We can also say that $p = 0$ is an unstable equilibrium, meaning that any slight perturbation away from $p = 0$ moves p away from that value. This is essentially what we simulated above: a slight perturbation starting at $p = 0.01$ went all the way up to $p = 1$. In contrast, $p = 1$ is a stable equilibrium: any slight perturbation from $p = 1$ immediately goes back to $p = 1$.

References

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Simulation Models of Cultural Evolution in R

Alex Mesoudi

Model 4: Biased transmission (indirect bias)

In Model 3 we examined direct bias, where certain cultural traits are preferentially copied from a randomly chosen demonstrator. Here we will simulate *indirect bias* (Boyd & Richerson 1985). This is another form of biased transmission, or cultural selection, but where certain demonstrators are more likely to be copied than other demonstrators. For this reason, indirect bias is sometimes called ‘demonstrator-based’ or ‘context’ bias.

Indirect bias comes in several forms. Learners might preferentially copy demonstrators who have high success or payoffs (which may or may not derive from their cultural traits), demonstrators who are old (and perhaps have accrued valuable knowledge, or at least good enough to keep them alive to old age), demonstrators who are the same gender as the learner (if cultural traits are gender-specific), or demonstrators who possess high social status or prestige.

Model 4 presents a simple model of indirect bias, first showing how payoff-based indirect bias can look very similar to payoff-based direct bias (Model 4a), then exploring a more interesting case when payoff-based indirect bias allows a neutral trait to ‘hitch-hike’ along with a high-payoff functional trait when both are exhibited by high payoff demonstrators (Model 4b).

Model 4a: Payoff bias

In Model 4a we will simulate a case where new agents preferentially copy the cultural traits of agents from the previous generation who have higher relative payoffs. This is sometimes called ‘payoff’ or ‘success’ bias.

We will start with the skeleton of Model 3. As in Model 3, there are N agents, each of whom possess a single cultural trait, either A or B . The frequency of trait A is denoted p , and the initial frequency in the first generation is p_0 . There are t_{max} timesteps and r_{max} independent runs.

In Model 3, agents were picked at random from the previous generation, and if that randomly-chosen agent possessed trait A then trait A was copied with probability s . For indirect bias, we need to change this. Demonstrator choice is no longer random: demonstrators are chosen non-randomly based on their payoffs. To implement this, we need to specify payoffs for each agent.

We will assume that an agent’s payoff is determined solely by the agent’s cultural trait. Agents with trait B have payoff of 1 (a ‘baseline’ payoff), while agents with trait A have payoff of $1 + s$. This means that trait A gives a payoff advantage to its bearers, relative to agents possessing trait B . The larger is s , the bigger this relative advantage.

Payoff-based indirect bias is then implemented by making the probability that an agent is chosen as a demonstrator proportional to that agents’ relative payoff, i.e. its payoff relative to all other agents in the population. Once an agent is chosen, its trait is copied with no error and with probability 1.

Rather than going straight to a simulation function, let’s explore this notion of relative payoff a bit further. First let’s create a population of N agents, with traits determined by p_0 , as usual.

```

N <- 1000
p_0 <- 0.5
s <- 0.1

agent <- data.frame(trait = sample(c("A", "B"), N, replace = TRUE,
                                    prob = c(p_0, 1-p_0)))

head(agent)

## trait
## 1     A
## 2     A
## 3     B
## 4     A
## 5     B
## 6     A

```

Given that $p_0 = 0.5$, you should see that the first few agents have a mix of trait A and trait B . Now let's add a payoff variable to the *agent* dataframe:

```

agent$payoff[agent$trait == "A"] <- 1 + s
agent$payoff[agent$trait == "B"] <- 1

head(agent)

## trait payoff
## 1     A    1.1
## 2     A    1.1
## 3     B    1.0
## 4     A    1.1
## 5     B    1.0
## 6     A    1.1

```

Agents with trait A are given fitness $1 + s$, which in this case is 1.1, while agents with trait B are given fitness of 1.

The relative payoff of an agent can be calculated by dividing its payoff by the sum of all payoffs of all agents:

```

relative_payoffs <- agent$payoff / sum(agent$payoff)

head(relative_payoffs)

## [1] 0.001048518 0.001048518 0.000953198 0.001048518 0.000953198 0.001048518

sum(relative_payoffs)

## [1] 1

```

These relative payoffs are obviously much smaller than the absolute payoffs because they have all been divided by N , which is a large number. They also all add up to 1. This is useful because in our simulation

we can set the probability of picking an agent from whom to copy as equal to its relative fitness. Probabilities, like our relative payoffs, must sum to 1.

In previous models we implemented random copying by using the `sample` command to pick N previous-generation agents at random to copy. This worked because by default the `sample` command picks each item - in our case, each previous-generation agent - with equal probability. However, we can override this default by adding a `prob` argument. If we set `prob` to be our *relative_payoffs*, then each agent will be chosen in proportion to its relative payoff. The following code does this for one new generation, after putting *agent* into *previous_agent*.

```
previous_agent <- agent

agent$trait <- sample(previous_agent$trait, N, replace = TRUE, prob = relative_payoffs)

sum(previous_agent$trait == "A") / N

## [1] 0.491

sum(agent$trait == "A") / N

## [1] 0.528
```

You should see that the frequency of trait *A* has increased from *previous_agent* to our new *agent* generation. This is what we would expect, given that there is a greater chance of selecting agents with the higher payoff trait *A*.

The following function incorporates the preceding code into our standard simulation model:

```
IndirectBias <- function (N, s, p_0, t_max, r_max) {

  # create a matrix with t_max rows and r_max columns, fill with NAs, convert to dataframe
  output <- as.data.frame(matrix(NA, t_max, r_max))

  # purely cosmetic: rename the columns with run1, run2 etc.
  names(output) <- paste("run", 1:r_max, sep="")

  for (r in 1:r_max) {

    # create first generation
    agent <- data.frame(trait = sample(c("A", "B"), N, replace = TRUE,
                                         prob = c(p_0, 1-p_0)))

    # add payoffs
    agent$payoff[agent$trait == "A"] <- 1 + s
    agent$payoff[agent$trait == "B"] <- 1

    # add first generation's p to first row of column r
    output[1,r] <- sum(agent$trait == "A") / N

    for (t in 2:t_max) {

      # copy agent to previous_agent dataframe
      previous_agent <- agent
```

```

# get relative payoffs of previous agents
relative_payoffs <- previous_agent$payoff / sum(previous_agent$payoff)

# new traits copied from previous generation, biased by payoffs
agent$trait <- sample(previous_agent$trait,
                       N, replace = TRUE,
                       prob = relative_payoffs)

# add payoffs
agent$payoff[agent$trait == "A"] <- 1 + s
agent$payoff[agent$trait == "B"] <- 1

# get p and put it into output slot for this generation t and run r
output[t,r] <- sum(agent$trait == "A") / N

}

}

# first plot a thick line for the mean p
plot(rowMeans(output),
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("N = ", N, ", s = ", s, sep = ""))
for (r in 1:r_max) {

  # add lines for each run, up to r_max
  lines(output[,r], type = 'l')

}

output # export data from function
}

```

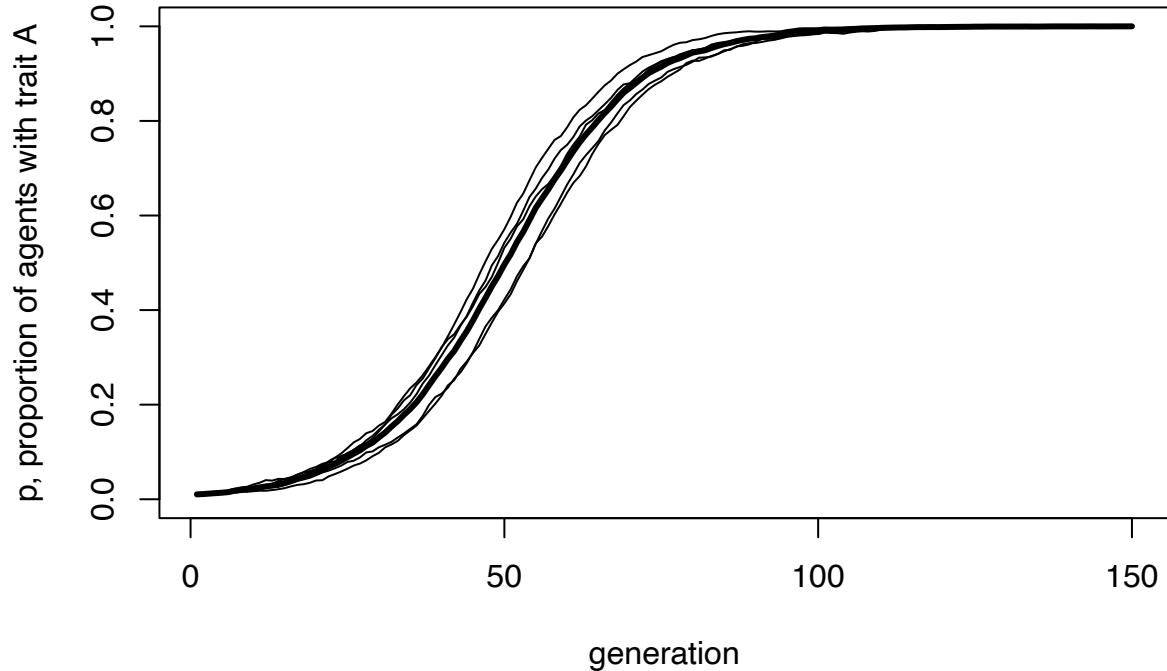
Now we can run **IndirectBias** with a small payoff advantage to agents with trait *A*:

```

data_model4a <- IndirectBias(N = 10000,
                             s = 0.1,
                             p_0 = 0.01,
                             t_max = 150,
                             r_max = 5)

```

N = 10000, s = 0.1



This S-shaped curve is very similar to the one we generated in Model 3 for direct bias, with the same value of $s = 0.1$. This is not too surprising, given that in Model 4a an agent's payoff is entirely determined by their cultural trait. Under these assumptions, preferentially copying high payoff agents is functionally equivalent to preferentially copying high payoff traits. This is not always the case, however, as we will see in Model 4b.

Model 4b: Cultural hitch-hiking

A more interesting case of indirect bias occurs when individuals possess two cultural traits, one functional and the other neutral. Under certain circumstances, payoff based indirect bias can cause the neutral trait to 'hitch-hike' alongside the functional trait. Neutral traits can spread in the population simply because they are associated with high payoff traits in high payoff demonstrators, even though they have no effect on payoffs themselves.

The trait already incorporated into **IndirectBias** above is functional, in that one of its variants, A , has higher payoff than the alternative variant, B , when $s > 0$ (or vice versa when $s < 0$). A neutral trait has no effect on payoffs, and all variants are equally effective, much like the trait subject to unbiased transmission in Model 1.

In Model 4b we will add a neutral trait to **IndirectBias**. We keep the functional trait 1 that can be either A or B , with payoff advantage s to trait A . We add a second trait, trait 2, which can be either X or Y . We define q as the proportion of X in trait 2, with $1 - q$ the proportion of Y . Whether an individual has trait X or Y has no effect on their payoff.

We will model a situation where the two traits may be initially linked. We are not going to be concerned here with why the two traits are initially linked. The link could, for example, have arisen by chance due to drift in historically small populations. We will leave this as an assumption of our model, which is fine as long as we are explicit about this. We define a parameter L that specifies the probability in the initial generation

(at $t = 1$) that, if an individual has an A for trait 1, they also have an X for trait 2. With probability $1 - L$, they pick X with probability q_0 , analogously to how p_0 specifies the probability of picking an A for trait 1 in the first generation). In this model, q_0 will be fixed at 0.5, i.e. an equal chance of having X or Y .

The following code defines a new *agent* dataframe. What was previously *trait* now becomes *trait1*. A new *trait2* is initially set to *NA* for all agents. We then, with probability L , link *trait2* to *trait1*, otherwise set *trait2* at random.

```
N <- 1000
p_0 <- 0.5
q_0 <- 0.5
L <- 1

agent <- data.frame(trait1 = sample(c("A","B"), N, replace = TRUE,
                                      prob = c(p_0,1-p_0)),
                     trait2 = rep(NA, N))

# with prob L, trait 2 is tied to trait 1, otherwise trait X with prob q_0
prob <- runif(N)
agent$trait2[agent$trait1 == "A" & prob < L] <- "X"
agent$trait2[agent$trait1 == "B" & prob < L] <- "Y"

agent$trait2[prob >= L] <- sample(c("X","Y"), sum(prob >= L), replace = TRUE,
                                      prob = c(q_0,1-q_0))

head(agent)

##   trait1 trait2
## 1     A     X
## 2     A     X
## 3     A     X
## 4     B     Y
## 5     A     X
## 6     B     Y
```

When $L = 1$, there is maximum linkage between the two traits. All individuals with A also have X , and all individuals with B have Y . As L gets smaller, this linkage breaks down.

Now we can insert this code into the **IndirectBias** function from above, with a few other additions. Note that payoffs are calculated exactly as before, based solely on whether *trait1* is A or B . The *demonstrators* are picked as before, based on *relative_payoffs*, except now *trait2* is copied from the same demonstrator alongside *trait1*. Finally, we create an additional output dataframe for *trait2*, use this second output dataframe to record q , the frequency of X in trait 2, in each timestep, and use it to plot both p and q in different colours. Note the new **legend** command, which allows us to label the two lines in the plot, and the use of **list** to export two output dataframes, rather than one.

```
IndirectBias2 <- function (N, s, L, p_0, q_0, t_max, r_max) {

  # create matrices with t_max rows and r_max columns, fill with NAs, convert to dataframe
  output_trait1 <- as.data.frame(matrix(NA, t_max, r_max))
  output_trait2 <- as.data.frame(matrix(NA, t_max, r_max))

  # purely cosmetic: rename the columns with run1, run2 etc.
  names(output_trait1) <- paste("run", 1:r_max, sep="")
```

```

names(output_trait2) <- paste("run", 1:r_max, sep="")

for (r in 1:r_max) {

  # create first generation
  agent <- data.frame(trait1 = sample(c("A","B"), N, replace = TRUE,
                                         prob = c(p_0,1-p_0)),
                        trait2 = rep(NA, N))

  # with prob L, trait 2 is tied to trait 1, otherwise trait X with prob q_0
  prob <- runif(N)
  agent$trait2[agent$trait1 == "A" & prob < L] <- "X"
  agent$trait2[agent$trait1 == "B" & prob < L] <- "Y"

  agent$trait2[prob >= L] <- sample(c("X","Y"), sum(prob >= L), replace = TRUE,
                                         prob = c(q_0,1-q_0))

  # add payoffs
  agent$payoff[agent$trait1 == "A"] <- 1 + s
  agent$payoff[agent$trait1 == "B"] <- 1

  # add first generation's p and q to first row of column r
  output_trait1[1,r] <- sum(agent$trait1 == "A") / N
  output_trait2[1,r] <- sum(agent$trait2 == "X") / N

  for (t in 2:t_max) {

    # copy agent to previous_agent dataframe
    previous_agent <- agent

    # get relative payoffs of previous agents
    relative_payoffs <- previous_agent$payoff / sum(previous_agent$payoff)

    # new traits copied from previous generation, biased by payoffs
    demonstrators <- sample(1:N,
                             N, replace = TRUE,
                             prob = relative_payoffs)

    agent$trait1 <- previous_agent$trait1[demonstrators]
    agent$trait2 <- previous_agent$trait2[demonstrators]

    # add payoffs
    agent$payoff[agent$trait1 == "A"] <- 1 + s
    agent$payoff[agent$trait1 == "B"] <- 1

    # put p and q into output slot for this generation t and run r
    output_trait1[t,r] <- sum(agent$trait1 == "A") / N
    output_trait2[t,r] <- sum(agent$trait2 == "X") / N
  }
}

```

```

# first plot a thick grey line for the mean p
plot(rowMeans(output_trait1),
      type = 'l',
      ylab = "proportion of agents with trait A (orange) or X (blue)",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("N = ", N, ", s = ", s, ", L = ", L, sep = ""),
      col = "orange")

# now thick orange line for mean q
lines(rowMeans(output_trait2), col = "royalblue", lwd = 3)

for (r in 1:r_max) {

  # add lines for each run, up to r_max
  lines(output_trait1[,r], type = 'l', col = "orange")
  lines(output_trait2[,r], type = 'l', col = "royalblue")

}

legend("bottomright",
       legend = c("p (trait 1)", "q (trait 2)",
       lty = 1,
       lwd = 3,
       col = c("orange", "royalblue"),
       bty = "n")

list(output_trait1, output_trait2) # export data from function
}

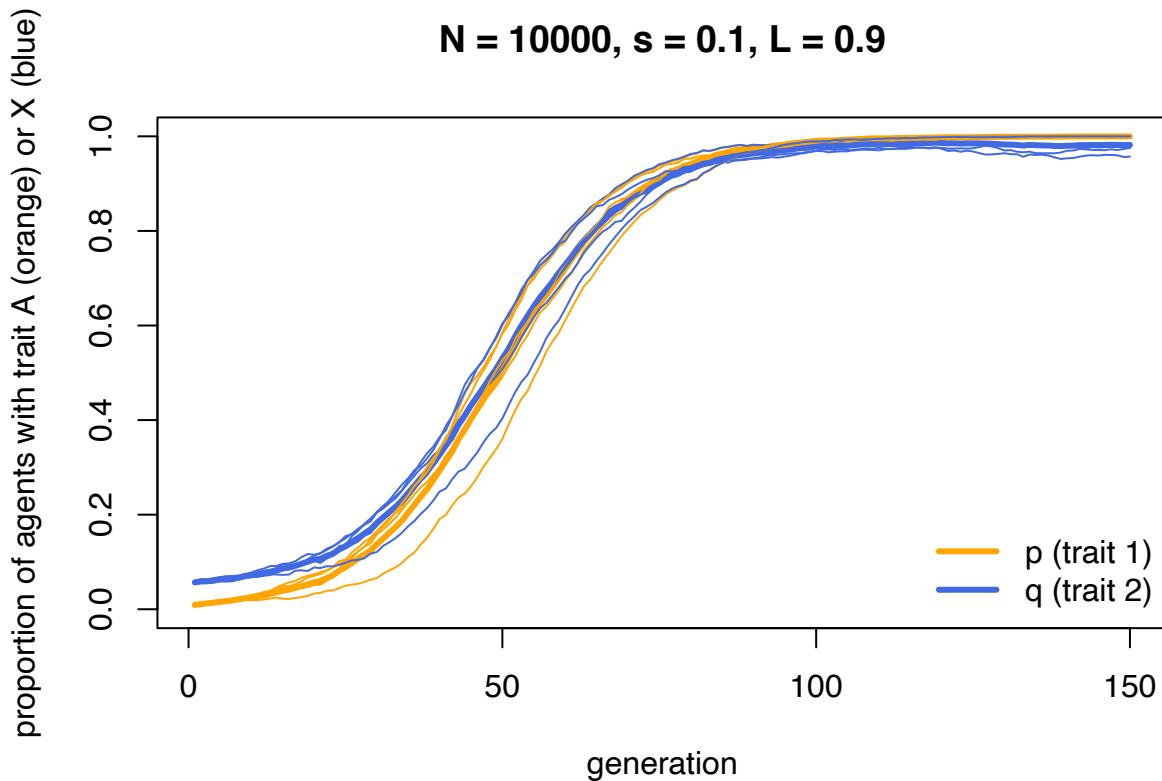
```

Now we can run **IndirectBias2** with a high linkage between trait 1 and trait 2, $L = 0.9$

```

data_model4b <- IndirectBias2(N = 10000,
                               s = 0.1,
                               L = 0.9,
                               p_0 = 0.01,
                               q_0 = 0.5,
                               t_max = 150,
                               r_max = 5)

```



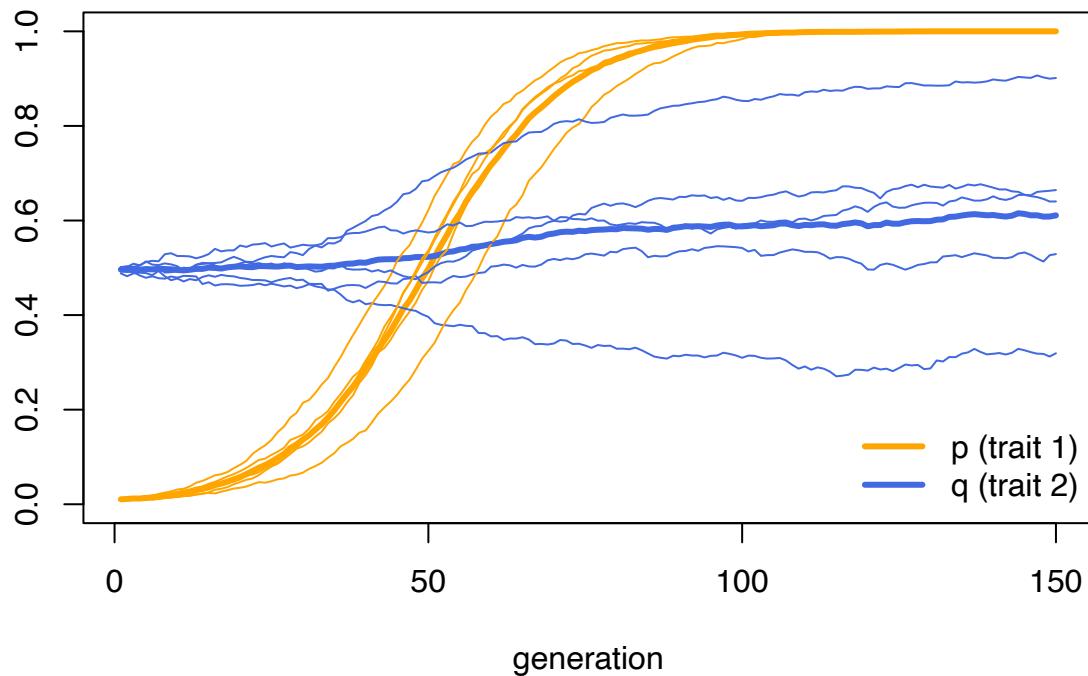
As you might expect, trait A (the orange line) goes to fixation exactly as for **IndirectBias** above. However, trait X (the blue line) shows a similar increase - not quite all the way to fixation, because $L < 1$, but very nearly. Hence the neutral trait X is hitch-hiking along with the functional trait A due to payoff based indirect bias. Trait X has no effect on payoffs, but because it happens to be associated with trait A at the start, it spreads through the population.

If we remove the linkage by setting $L = 0$, we see that this hitch-hiking no longer occurs. Instead trait X drifts randomly as we would expect for a neutral trait:

```
data_model4b <- IndirectBias2(N = 10000,
                               s = 0.1,
                               L = 0.0,
                               p_0 = 0.01,
                               q_0 = 0.5,
                               t_max = 150,
                               r_max = 5)
```

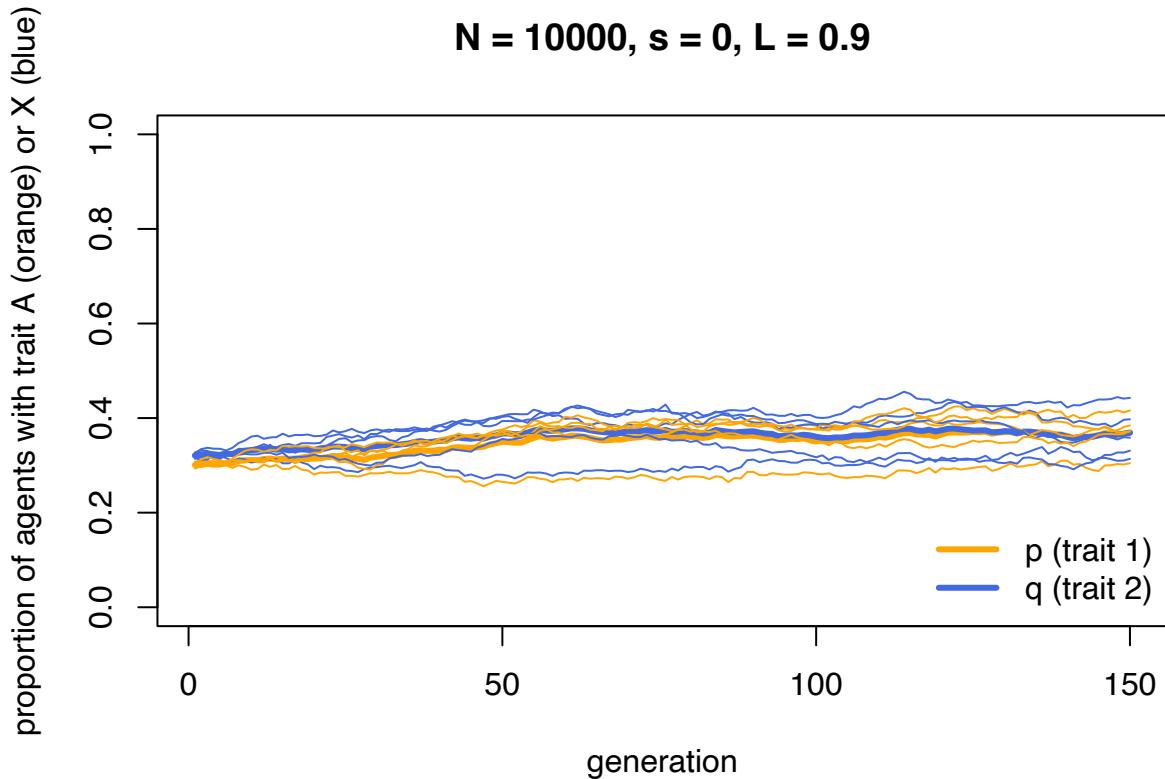
proportion of agents with trait A (orange) or X (blue)

N = 10000, s = 0.1, L = 0



And when we remove the payoff biased indirect bias by setting $s = 0$, and reintroduce the linkage ($L = 0.9$), neither trait increases in frequency. Both are now effectively neutral.

```
data_model4b <- IndirectBias2(N = 10000,
                               s = 0.0,
                               L = 0.9,
                               p_0 = 0.3,
                               q_0 = 0.5,
                               t_max = 150,
                               r_max = 5)
```



Summary of Model 4

Indirect bias occurs when individuals preferentially learn from demonstrators who have particular characteristics, such as being wealthy or socially successful (having high ‘payoffs’ in the language of modelling), being old, having a particular gender, or being prestigious. There is extensive evidence for these indirect transmission biases from the broad social and behavioural sciences (e.g. Rogers 2010; Labov 1972; Bandura, Ross & Ross 1963) and cultural evolution research specifically (e.g. Mesoudi 2011; Henrich & Gil-White 2001; Brand et al. 2020; Wood et al. 2012; McElreath et al. 2008; Henrich & Henrich 2010). Consequently, it is worth modelling indirect bias to understand its dynamics, and how it is similar or different to other forms of biased transmission.

Our first simple model of indirect bias, Model 4a, showed that when individuals preferentially learn from high payoff demonstrators, and demonstrator payoff is determined directly by the demonstrator’s cultural trait, then the trait that gives demonstrators higher relative payoff spreads through the population. This is entirely expected and intuitive. The resulting S-shaped diffusion curve for Model 4a looks extremely similar to that generated in Model 3 for direct bias with the same selection parameter s . This is to be expected, given our assumptions that demonstrator payoff is determined solely by trait payoff. So in this case direct bias and indirect bias are functionally equivalent.

This should strike a note of caution. If we see the same cultural dynamics generated from different underlying models, then we cannot be certain which of these underlying processes generated similar real-world cultural dynamics. Nevertheless, it’s better to know this, than to incorrectly attribute a dynamic to the wrong process.

Model 4b examined the more interesting case where there are two cultural traits, one functional and one neutral. If these traits are initially linked, via our parameter L , then the neutral trait can hitch-hike along with the functional trait. Everyday examples of cultural hitch-hiking might be where people copy fashion styles from wealthy and talented sportstars: a footballer's tattoos or hairstyle is unlikely to have anything to do with their sporting success, but these neutral traits may nevertheless be copied if people generally copy all traits associated with successful demonstrators. There is experimental evidence for cultural hitch-hiking (Mesoudi & O'Brien 2008), while Yeh et al. (2019) have created more elaborate models of cultural hitch-hiking with more than two traits and copyable links between those traits.

While we did not model the evolution of indirect bias itself, we might imagine that this global copying of successful demonstrators might be less costly to the learner when demonstrators exhibit multiple traits than direct bias, where learners would have to identify which of the multiple traits actually contribute to the demonstrator's success. The cost of indirect bias is potentially copying neutral traits, as we saw in Model 4b, or even maladaptive traits, alongside the functional traits. But in some circumstances this cost may be less than the aforementioned cost of direct bias. If it is, then this may be an explanation for the presence of neutral or maladaptive traits in human culture.

Boyd & Richerson (1985) modelled another interesting case of indirect bias, where the criterion of demonstrator success is copied alongside the actual cultural trait. For example, one might copy not only the specific tattoo of a successful footballer, but also copy their preference for tattoos. Under certain conditions this can lead to the runaway selection of both traits and preferences, with both getting more and more extreme over time. In our example this would lead to more and more extensive tattoos (which perhaps has happened in Micronesia, but for yam-growing rather than football: Boyd & Richerson 1985). This is roughly analogous to runaway sexual selection in genetic evolution that can lead to elaborate traits such as peacock's tails, which may occur because both elaborate tails and preferences for elaborate tails are genetically inherited together. Both cultural hitch-hiking and runaway selection are interesting dynamics of indirectly bias which are not observed for direct bias.

In terms of programming innovations, we saw in Model 4a how to assign payoffs to different agents on the basis of their cultural trait, and then use the *relative_payoffs* in the **sample** command to implement payoff-based selection of demonstrators from whom to learn. In Model 4b we introduced a second trait, keeping track of both the frequency of A in trait 1 (p) and the frequency of X in trait 2 (q). We also saw how to link these traits together using the L parameter. Finally, we saw how to draw two results lines on the same plot in different colours, include a legend for those lines, and export multiple dataframes from the simulation function as a list.

Exercises

1. Try different values of s in **IndirectBias** to confirm that larger s increases the speed with which A goes to fixation.
 2. Try different values of L in **IndirectBias2** to confirm that as L gets smaller, the hitch-hiking effect gets weaker.
 3. In **IndirectBias2** the hitch-hiking trait is neutral. But can a detrimental trait also hitch-hike? Modify the function to make the second trait functional, with a payoff disadvantage to X over Y (e.g. by introducing an equivalent selection parameter to s which affects X relative to Y , and making this new parameter negative). Set the initial linkage conditions such that the high payoff *trait1* variant A is associated with the low payoff *trait2* variant X . Are there any conditions under which the detrimental, low-payoff trait X hitch-hikes on the beneficial, high-payoff trait A ?
-

Analytical Appendix

In Model 4a, the frequency of trait A in the next generation, p' , is simply the relative payoff of all agents with trait A in the previous generation. This is given by:

$$p' = \frac{p(1+s)}{p(1+s) + (1-p)} = \frac{p(1+s)}{1+sp} \quad (4.1)$$

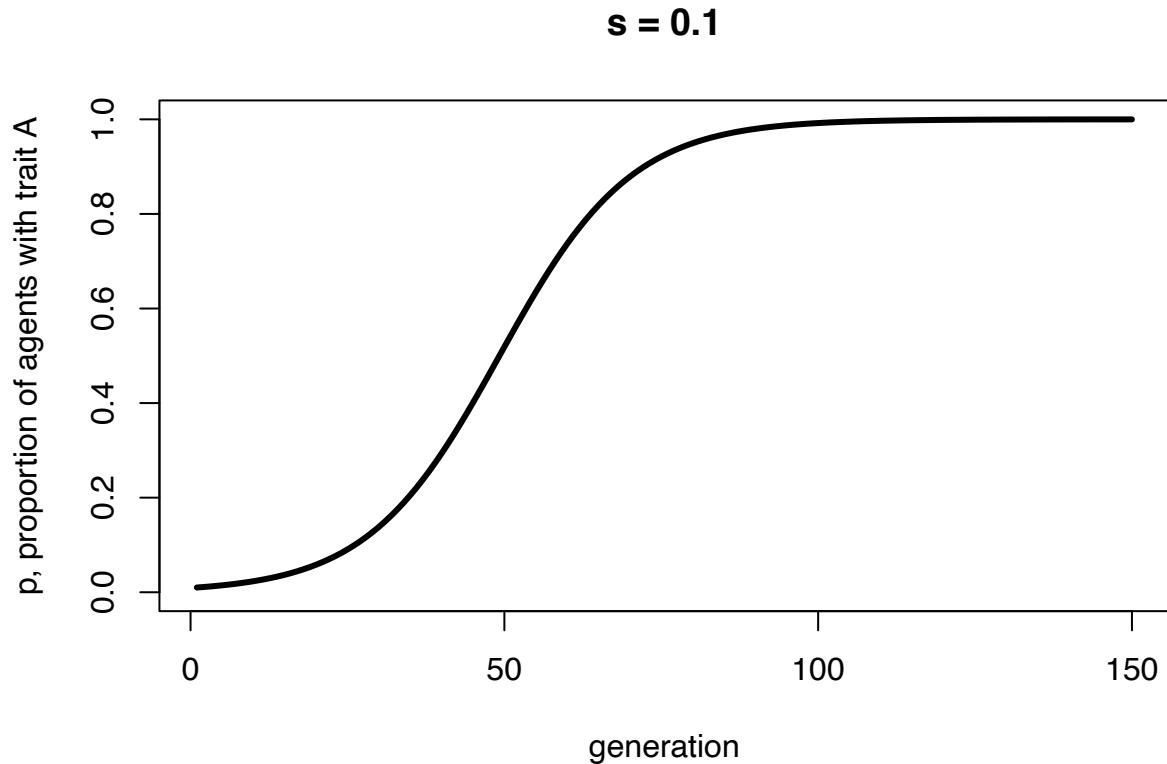
where $p(1+s)$ is the payoff of all agents with trait A , and $(1-p)$ is the payoff of all agents with trait B .

Plotting this recursion gives a curve that matches the one generated above by the simulation model:

```
p <- rep(0, 150)
p[1] <- 0.01
s <- 0.1

for (i in 2:150) {
  p[i] <- (p[i-1])*(1+s) / (1 + (p[i-1])*s)
}

plot(p,
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("s = ", s, sep = ""))
```



To find the equilibria, we can set $p' = p$ in Equation 4.1, and rearrange to give:

$$p(1 - p)s = 0 \quad (4.2)$$

This is identical to Equation 3.2, the equivalent for direct bias. Again, there are three equilibria, one when $p = 0$, one when $s = 0$, and one when $1 - p = 0$, or when $p = 1$. While Equation 4.1 is not the same as Equation 3.1, the resulting equilibria are identical.

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Simulation Models of Cultural Evolution in R

Alex Mesoudi

Model 5: Biased transmission (conformist bias)

Model 3 looked at the case where one cultural trait is intrinsically more likely to be copied than another trait, and in Model 4 the case where one type of demonstrator is more likely to be copied than another. Here we will look at a third kind of biased transmission: conformity (or ‘positive frequency dependent bias’). Here, individuals are disproportionately more likely to adopt the most common trait in the population, irrespective of its intrinsic characteristics or who bears it.

For example, imagine trait A has a frequency of 0.7 in the population, with the rest possessing trait B . An unbiased learner would adopt trait A with a probability exactly equal to 0.7. This is unbiased transmission, and is what happens in Model 1: by picking a member of the previous generation at random, the probability of adoption in Model 1 is equal to the frequency of that trait amongst the previous generation.

A conformist learner, on the other hand, would adopt trait A with a probability greater than 0.7. In other words, common traits get an ‘adoption boost’ relative to unbiased transmission. Uncommon traits get an equivalent ‘adoption penalty’. The magnitude of this boost or penalty can be controlled by a parameter, which we will call D .

Let’s keep things simple in our model. Rather than assuming that individuals sample across the entire population, which in any case might be implausible in large populations, let’s assume they pick only three demonstrators at random. Why three? This is the minimum number of demonstrators that can yield a majority (i.e. 2 vs 1), which we need in order to implement conformity. When two demonstrators have one trait and the other demonstrator has a different trait, we want to boost the probability of adoption for the majority trait, and reduce it for the minority trait.

Following Boyd and Richerson (1985), we can specify the probability of adoption as in the following table:

Demonstrator 1	Demonstrator 2	Demonstrator 3	Probability of adopting trait A
A	A	A	1
A	A	B	
A	B	A	$2/3 + D/3$
B	A	A	
A	B	B	
B	A	B	$1/3 - D/3$
B	B	A	
B	B	B	0

The first row says that when all demonstrators have trait A , then trait A is definitely adopted. Similarly, the bottom row says that when all demonstrators have trait B , then trait A is never adopted, and by implication trait B is always adopted.

For the three combinations where there are two A s and one B , the probability of adopting trait A is $2/3$, which it would be under unbiased transmission (because two out of three demonstrators have A), plus the conformist adoption boost specified by D . D is divided by three so that it varies from 0 to 1.

Similarly, for the three combinations where there are two B s and one A , the probability of adopting A is $1/3$ minus the conformist adoption penalty specified by D .

Let's implement these assumptions in the kind of agent-based model we've been building so far. As before, assume N agents each of whom possess one of two traits A or B . The frequency of A is denoted by p . The initial frequency of A in generation $t = 1$ is p_0 . Rather than going straight to a function, let's go step by step.

First we'll specify our parameters, N and p_0 as before, plus the new conformity parameter D . We can also create an *agent* dataframe and fill it with A s and B s in the proportion specified by p_0 , again exactly as before. To remind ourselves what *agent* looks like, we use the **head** command.

```
N <- 100
p_0 <- 0.5
D <- 1

# create first generation
agent <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                      prob = c(p_0,1-p_0)))

head(agent)

##   trait
## 1     A
## 2     A
## 3     A
## 4     A
## 5     A
## 6     A
```

Now we'll create a dataframe called *demonstrators* that picks, for each new agent in the next generation, three demonstrators at random from the current population of agents. It therefore needs three columns/variables, one for each of the demonstrators, and N rows, one for each new agent. We fill each column with randomly chosen traits from the *agent* dataframe. We can view this with **head**.

```
# create dataframe with a set of 3 randomly-picked demonstrators for each agent
demonstrators <- data.frame(dem1 = sample(agent$trait, N, replace = TRUE),
                             dem2 = sample(agent$trait, N, replace = TRUE),
                             dem3 = sample(agent$trait, N, replace = TRUE))

head(demonstrators)

##   dem1 dem2 dem3
## 1     A     B     A
## 2     B     B     B
## 3     A     B     B
## 4     B     A     A
## 5     A     A     A
## 6     B     B     A
```

Think of each row here as containing the traits of three randomly-chosen demonstrators chosen by each new next-generation agent. Now we want to calculate the probability of adoption of A for each of these three-trait demonstrator combinations.

First we need to get the number of A s in each combination. Then we can replace the traits in $agent$ based on the probabilities in the table above. When all demonstrators have A , we set to A . When no demonstrators have A , we set to B . When two out of three demonstrators have A , we set to A with probability $2/3 + D/3$ and B otherwise. When one out of three demonstrators have A , we set to A with probability $1/3 - D/3$ and B otherwise.

To check it works, we can add the new $agent$ dataframe as a column to $demonstrators$ and view the latter with `head`. This will let us see the three demonstrators and the resulting new trait side by side.

```
# get the number of As in each 3-dem combo
numAs <- rowSums(demonstrators == "A")

agent$trait[numAs == 3] <- "A" # for dem combos with all As, set to A
agent$trait[numAs == 0] <- "B" # for dem combos with no As, set to B

prob <- runif(N)

# when A is a majority, 2/3
agent$trait[numAs == 2 & prob < (2/3 + D/3)] <- "A"
agent$trait[numAs == 2 & prob >= (2/3 + D/3)] <- "B"

# when A is a minority, 1/3
agent$trait[numAs == 1 & prob < (1/3 - D/3)] <- "A"
agent$trait[numAs == 1 & prob >= (1/3 - D/3)] <- "B"

# for testing only, add the new traits to the demonstrator dataframe and show it
demonstrators$newtrait <- agent$trait
head(demonstrators, 20)
```

```
##   dem1 dem2 dem3 newtrait
## 1     A     B     A      A
## 2     B     B     B      B
## 3     A     B     B      B
## 4     B     A     A      A
## 5     A     A     A      A
## 6     B     B     A      B
## 7     A     A     B      A
## 8     B     B     B      B
## 9     A     B     A      A
## 10    B    B     A      B
## 11    A     A     A      A
## 12    B     B     A      B
## 13    A     B     A      A
## 14    B     B     B      B
## 15    B     B     A      B
## 16    A     B     B      B
## 17    A     B     A      A
## 18    A     A     A      A
## 19    A     A     B      A
## 20    B     B     B      B
```

Because we set $D = 1$ above, we should see above that the new trait is always the majority trait amongst the three demonstrators. This is perfect conformity. We can weaken conformity by reducing D , in the code below.

```

N <- 100
p_0 <- 0.5
D <- 0.1

# create first generation
agent <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                      prob = c(p_0,1-p_0)))

# create dataframe with a set of 3 randomly-picked demonstrators for each agent
demonstrators <- data.frame(dem1 = sample(agent$trait, N, replace = TRUE),
                             dem2 = sample(agent$trait, N, replace = TRUE),
                             dem3 = sample(agent$trait, N, replace = TRUE))

# get the number of As in each 3-dem combo
numAs <- rowSums(demonstrators == "A")

agent$trait[numAs == 3] <- "A" # for dem combos with all As, set to A
agent$trait[numAs == 0] <- "B" # for dem combos with no As, set to B

prob <- runif(N)

# when A is a majority, 2/3
agent$trait[numAs == 2 & prob < (2/3 + D/3)] <- "A"
agent$trait[numAs == 2 & prob >= (2/3 + D/3)] <- "B"

# when A is a minority, 1/3
agent$trait[numAs == 1 & prob < (1/3 - D/3)] <- "A"
agent$trait[numAs == 1 & prob >= (1/3 - D/3)] <- "B"

# for testing only, add the new traits to the demonstrator dataframe and show it
demonstrators$newtrait <- agent$trait
head(demonstrators, 20)

```

```

##      dem1 dem2 dem3 newtrait
## 1      B     B     A      B
## 2      A     A     A      A
## 3      B     B     A      B
## 4      B     B     A      B
## 5      B     B     A      B
## 6      B     A     B      B
## 7      A     A     B      B
## 8      B     B     B      B
## 9      B     B     B      B
## 10     B     B     B      B
## 11     A     B     B      B
## 12     B     B     B      B
## 13     B     B     A      B
## 14     A     A     B      A
## 15     B     B     A      B
## 16     B     B     B      B

```

```

## 17    B    B    B
## 18    A    A    B
## 19    B    B    B
## 20    A    A    A

```

Now that conformity is weaker, sometimes the new trait is not the majority amongst the three demonstrators. With the small sample shown above, it's perhaps not possible to notice it. Hopefully when we put it all together now into a function and run it over multiple generations, we will notice an effect. The code below is a combination of Model 1 (unbiased transmission) and the code above for conformity.

```

ConformistTransmission <- function (N, p_0, D, t_max, r_max) {

  # create a matrix with t_max rows and r_max columns, fill with NAs, convert to dataframe
  output <- as.data.frame(matrix(NA,t_max,r_max))

  # purely cosmetic: rename the columns with run1, run2 etc.
  names(output) <- paste("run", 1:r_max, sep="")

  for (r in 1:r_max) {

    # create first generation
    agent <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                         prob = c(p_0,1-p_0)))

    # add first generation's p to first row of column r
    output[1,r] <- sum(agent$trait == "A") / N

    for (t in 2:t_max) {

      # create dataframe with a set of 3 randomly-picked demonstrators for each agent
      demonstrators <- data.frame(dem1 = sample(agent$trait, N, replace = TRUE),
                                   dem2 = sample(agent$trait, N, replace = TRUE),
                                   dem3 = sample(agent$trait, N, replace = TRUE))

      # get the number of As in each 3-dem combo
      numAs <- rowSums(demonstrators == "A")

      agent$trait[numAs == 3] <- "A"  # for dem combos with all As, set to A
      agent$trait[numAs == 0] <- "B"  # for dem combos with no As, set to B

      prob <- runif(N)

      # when A is a majority, 2/3
      agent$trait[numAs == 2 & prob < (2/3 + D/3)] <- "A"
      agent$trait[numAs == 2 & prob >= (2/3 + D/3)] <- "B"

      # when A is a minority, 1/3
      agent$trait[numAs == 1 & prob < (1/3 - D/3)] <- "A"
      agent$trait[numAs == 1 & prob >= (1/3 - D/3)] <- "B"

      # get p and put it into output slot for this generation t and run r
      output[t,r] <- sum(agent$trait == "A") / N
    }
  }
}

```

```

}

# first plot a thick line for the mean p
plot(rowMeans(output),
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("N = ", N, ", D = ", D, ", p_0 = ", p_0, sep = ""))
      
for (r in 1:r_max) {

  # add lines for each run, up to r_max
  lines(output[,r], type = 'l')

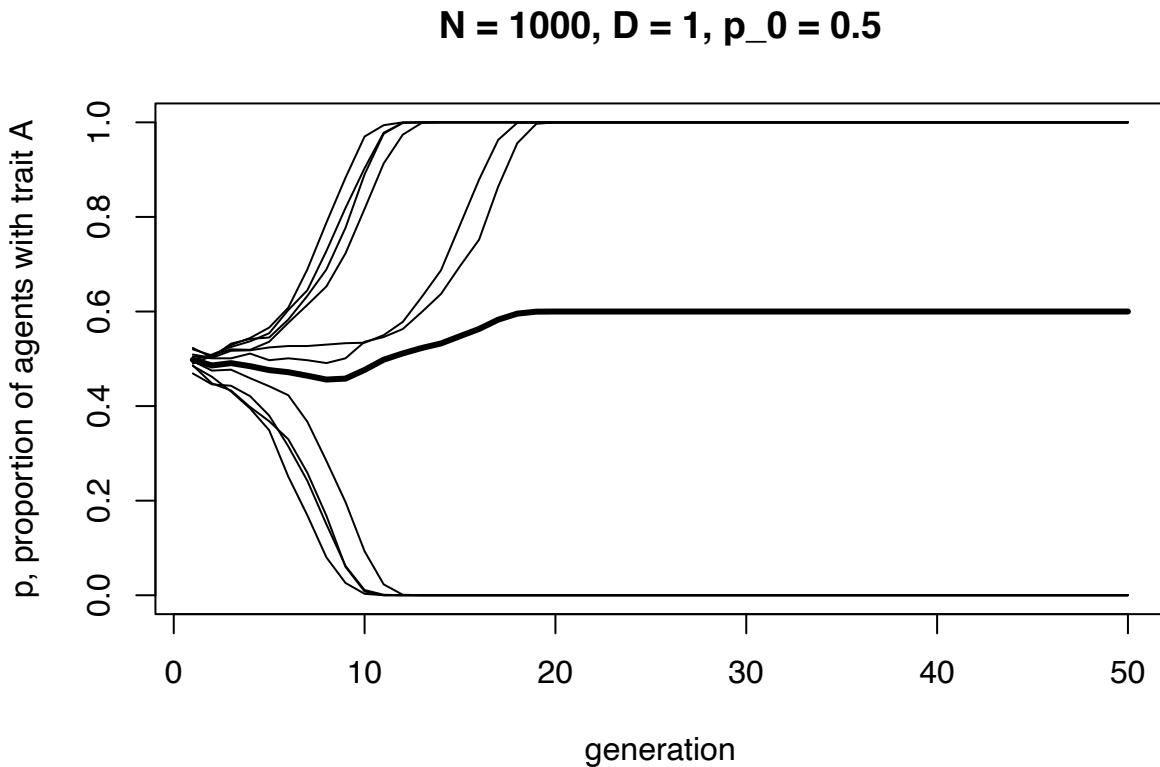
}

output # export data from function
}

```

Note that we omit the testing code above (we've tested it and it works!), and there's no need to put *agent* into *previous_agent* because we have the *demonstrator* dataframe doing that job. Let's run the function.

```
data_model5 <- ConformistTransmission(N = 1000, p_0 = 0.5, D = 1, t_max = 50, r_max = 10)
```

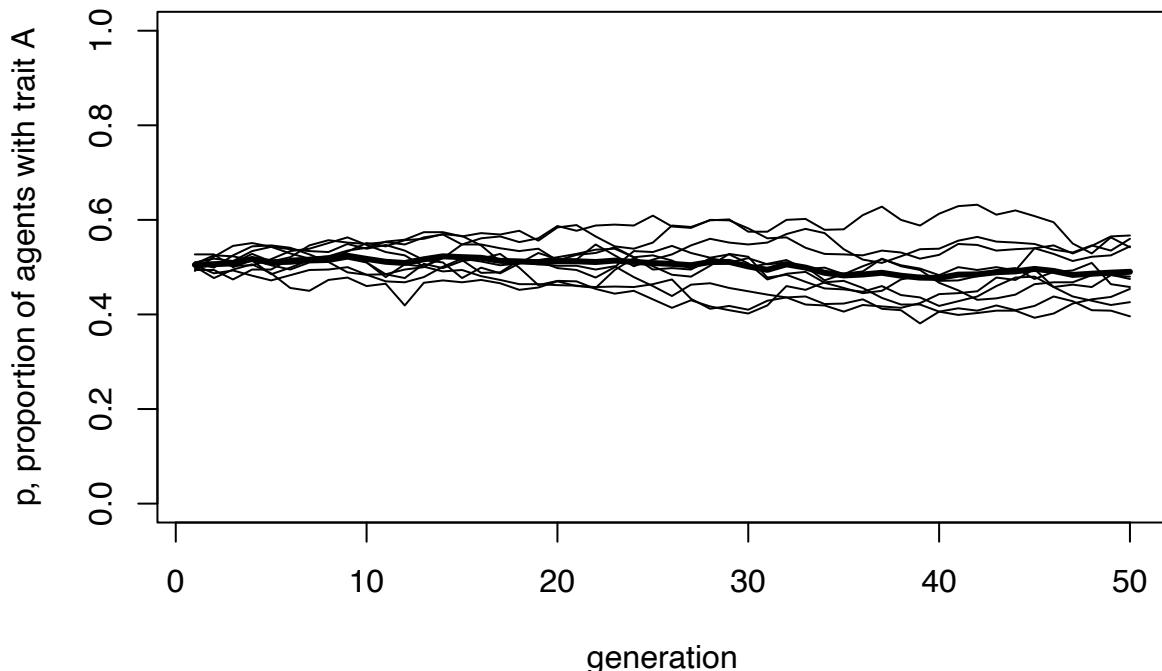


Here we should see some lines going to $p = 1$, and some lines going to $p = 0$. Conformity acts to favour the majority trait. This will depend on the initial frequency of A in the population. In different runs with $p_0 = 0.5$, sometimes there will be slightly more A s, sometimes slightly more B s (remember, in our model this is probabilistic, like flipping coins, so initial frequencies will rarely be precisely 0.5).

Let's compare conformity to unbiased transmission, by setting $D = 0$.

```
data_model5 <- ConformistTransmission(N = 1000, p_0 = 0.5, D = 0, t_max = 50, r_max = 10)
```

N = 1000, D = 0, p_0 = 0.5



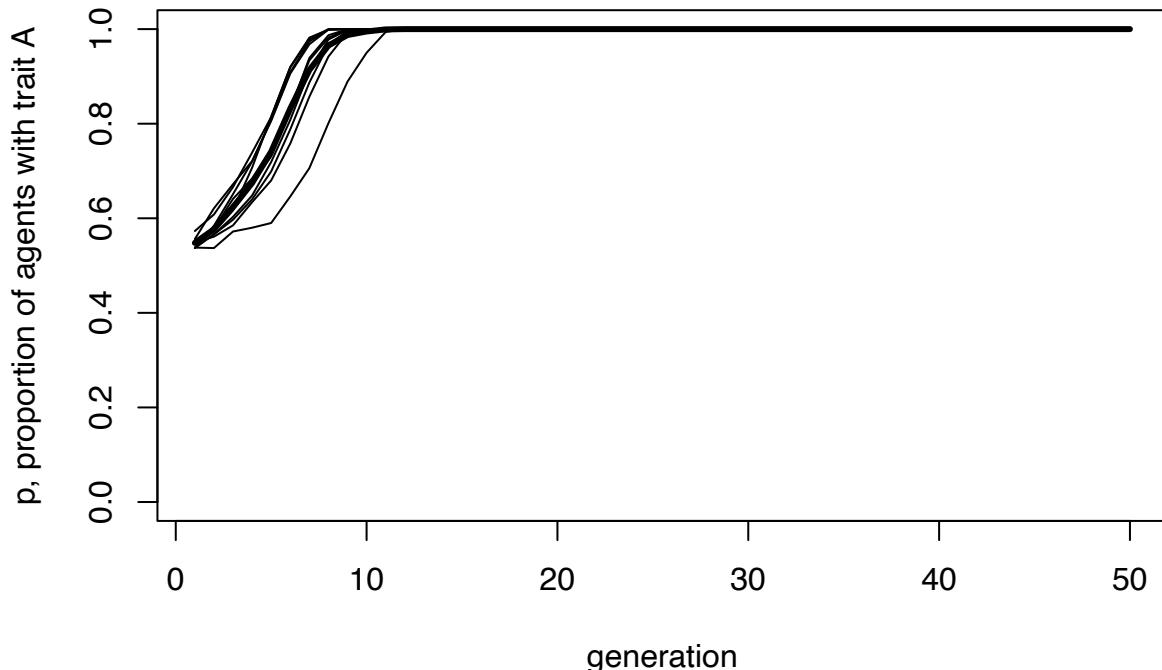
As in Model 1 with a sufficiently large N , we should see frequencies fluctuating around $p = 0.5$. This underlines the effect of conformity: it drives traits to fixation as they become more and more common.

As an aside, note that the last two graphs have roughly the same thick black mean frequency line, which hovers around $p = 0.5$. This highlights the dangers of looking at means alone. If we hadn't plotted the individual runs and relied solely on mean frequencies, we might think that $D = 0$ and $D = 1$ gave identical results. But in fact, they are very different. Always look at the underlying distribution that generates means.

Now let's explore the effect of changing the initial frequencies by changing p_0 , and adding conformity back in.

```
data_model5 <- ConformistTransmission(N = 1000, p_0 = 0.55, D = 1, t_max = 50, r_max = 10)
```

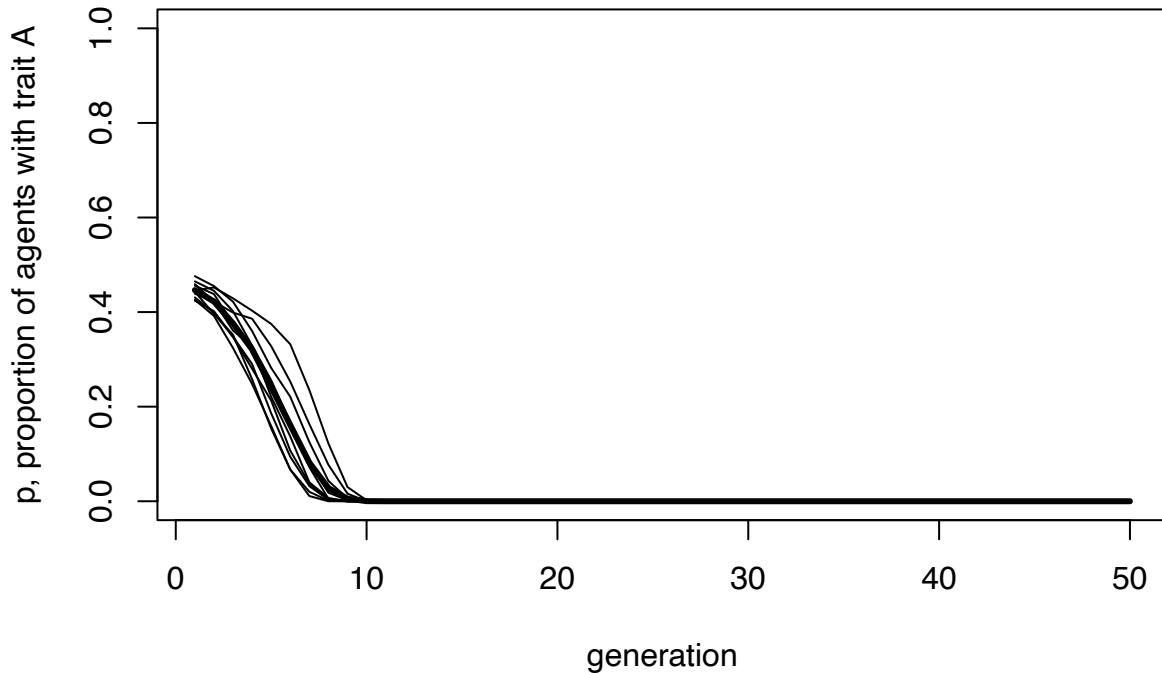
$$N = 1000, D = 1, p_0 = 0.55$$



When A starts off in a slight majority ($p_0 = 0.55$), most if not all of the runs should result in A going to fixation. Now let's try the reverse.

```
data_model5 <- ConformistTransmission(N = 1000, p_0 = 0.45, D = 1, t_max = 50, r_max = 10)
```

$$N = 1000, D = 1, p_0 = 0.45$$



When A starts off in a minority ($p_0 = 0.45$), most if not all runs should result in A disappearing. These last two graphs show how initial conditions affect conformity. Whichever trait is more common is favoured by conformist transmission.

Summary of Model 5

Model 5 explored conformist biased cultural transmission, or ‘conformity’ for short. This is where individuals are disproportionately more likely to adopt the most common trait among a set of demonstrators. We can contrast this with the direct or content biased transmission from Model 3, where one trait is intrinsically more likely to be copied. With conformity, the traits have no intrinsic attractiveness and are preferentially copied simply because they are common.

We saw how conformity increases the frequency of whichever trait is more common. Initial trait frequencies are important here: traits that are initially more common typically go to fixation. This in turn makes stochasticity important, which in small populations can affect initial frequencies.

Experimental studies have shown that people exhibit conformity as defined and modelled here (Efferson et al. 2008; Muthukrishna et al. 2016; Deffner et al. 2020), and models have extended Boyd & Richerson’s (1985) initial treatment to consider more than two traits, more than three demonstrators, and the effects of spatial and temporal environmental variation (Henrich & Boyd 1998; Nakahashi et al. 2012; Mesoudi 2018). Conformity is thought to have important implications for real-world patterns of cultural evolution by affecting the spread of novel innovations through societies (Henrich 2001), and by acting to maintain between-group cultural variation in the face of migration, as we will explore further in a later model.

The major programming innovation in Model 5 was the use of an intermediate dataframe to hold the demonstrators. We then created the next generation using a table of probabilities, which specified for each combination of demonstrators the probability of adopting each trait.

Exercises

1. Try different values of D and p_0 to confirm that conformity acts to always favour the majority trait. Also try smaller values of N . How does the stochasticity at small values of N affect conformity?
 2. The conformity parameter D can also be negative, which reduces the probability of adopting majority traits and increases the probability of adopting minority traits. This is *anti-conformity*, or *negative frequency-dependent cultural transmission*. Explore the effect on cultural dynamics of varying D between -1 and 0, for different values of p_0 .
 3. Create a new function **ConformityPlusBiasedTransmission**, using code from Model 3. First, agents should engage in directly biased transmission from the previous generation, according to parameter s . Then they should engage in conformity, with the demonstrators for conformity being the set of traits after biased transmission. Vary s (which favours trait A) and D (which favours the majority) starting at small values of p_0 to explore when selection can overpower conformity, and vice versa. See Henrich (2001) for a similar model of conformity plus directly biased transmission.
-

Analytic Appendix

An alternative way of doing all the above is with deterministic recursions, as Boyd & Richerson (1985) originally did.

Let's revise our table above to add the probabilities of each combination of three demonstrators coming together, assuming they are picked at random. These probabilities can be expressed in terms of p , the frequency of A , and $(1 - p)$, the frequency of B .

Dem 1	Dem 2	Dem 3	Prob of adopting A	Prob of combination forming
A	A	A	1	p^3
A	A	B		
A	B	A	$2/3 + D/3$	$p^2(1 - p)$
B	A	A		
A	B	B		
B	A	B	$1/3 - D/3$	$p(1 - p)^2$
B	B	A		
B	B	B	0	$(1 - p)^3$

To get the frequency of A in the next generation, p' , we multiply, for each of the eight rows in the table, the probability of adopting A by the probability of that combination forming (i.e. the final two columns in the table), and add up all of these eight products. After rearranging, this gives the following recursion:

$$p' = p + Dp(1 - p)(2p - 1) \quad (5.1)$$

Now we can create a function for this recursion:

```
ConformityRecursion <- function(D, t_max, p_0) {

  p <- rep(0,t_max)
  p[1] <- p_0

  for (i in 2:t_max) {
    p[i] <- p[i-1] + D*p[i-1]*(1-p[i-1])*(2*p[i-1] - 1)
  }

  plot(p,
    type = "l",
    ylim = c(0,1),
    ylab = "frequency of p",
    xlab = "generation",
    main = paste("D = ", D, ", p_0 = ", p_0, sep = ""))
}

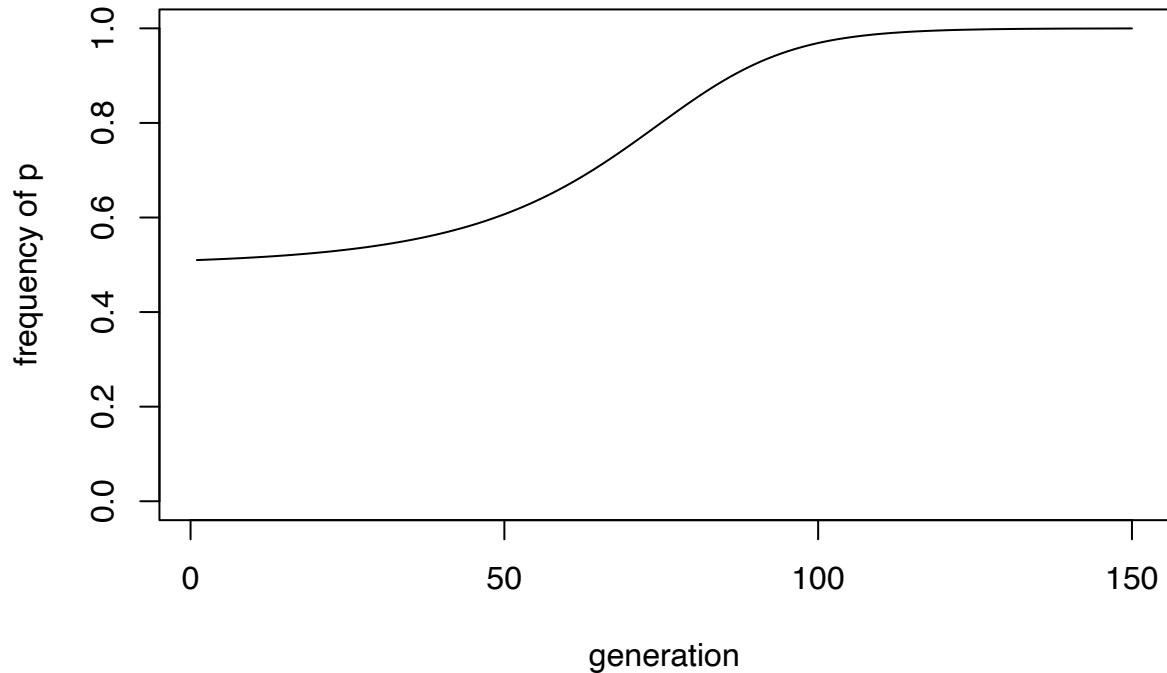
}
```

Here, we use a **for** loop to cycle through each generation, each time updating p according to the recursion equation above. Remember, there is no N here because the recursion is deterministic and assumes an infinite population size; hence there is no stochasticity due to finite population sizes. There is also no need to have multiple runs as each run is identical, hence no r_{max} .

The following code runs the **ConformityRecursion** function with weak conformity ($D = 0.1$) and slightly more A in the initial generation ($p_0 = 0.51$).

```
ConformityRecursion(D = 0.1, t_max = 150, p_0 = 0.51)
```

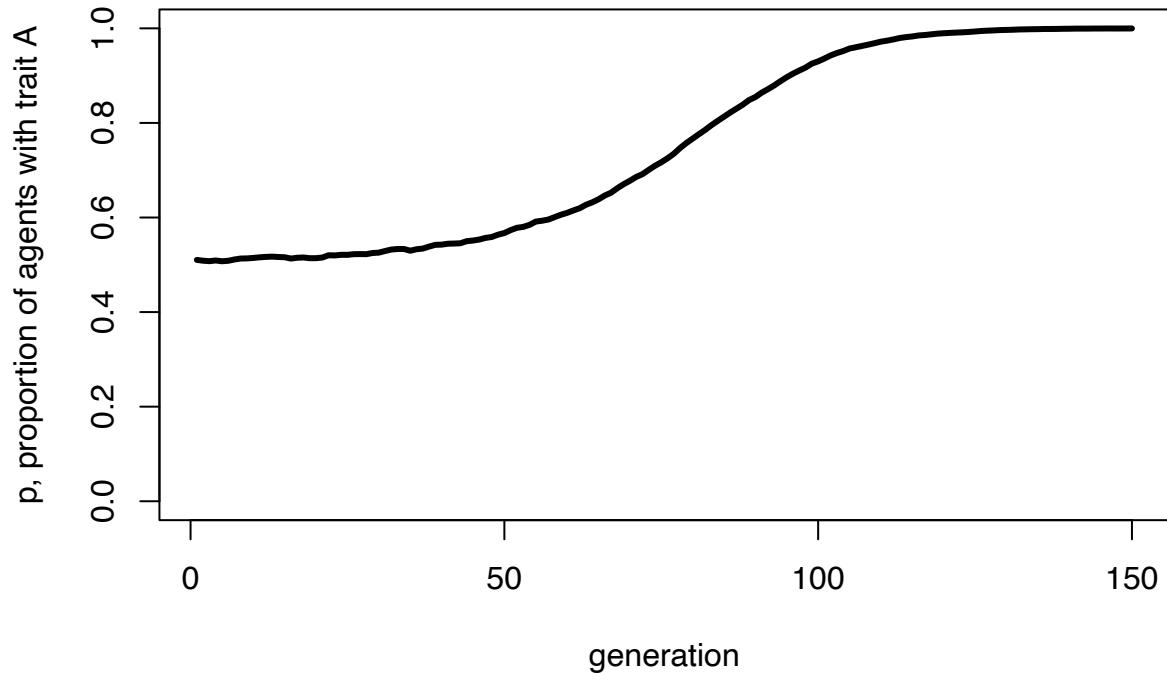
D = 0.1, p_0 = 0.51



As in the agent-based model, the initially most-frequent trait, here A , goes to fixation. Let's compare to the agent-based model with the same parameters, and a large enough N to make stochasticity unimportant.

```
data_model5 <- ConformistTransmission(N = 100000, p_0 = 0.51, D = 0.1, t_max = 150, r_max = 1)
```

$$N = 1e+05, D = 0.1, p_0 = 0.51$$



It should be a pretty good match. Try playing around with smaller N to show that stochastic agent-based models are most likely to match deterministic recursion models when N is large.

Let's modify the **ConformityRecursion** function to accept multiple values of p_0 , so we can plot different starting frequencies on the same graph.

```
ConformityRecursion <- function(D, t_max, p_0) {
  numSims <- length(p_0)

  p <- as.data.frame(matrix(NA, nrow = t_max, ncol = numSims))
  p[,1] <- p_0

  for (i in 2:t_max) {
    p[i,] <- p[i-1,] + D*p[i-1,]*(1-p[i-1,])*(2*p[i-1,] - 1)
  }

  plot(p[,1],
    type = "l",
    ylim = c(0,1),
    ylab = "frequency of A (p)",
    xlab = "generation",
    main = paste("D =", D))

  if (numSims > 1) {
    for (i in 2:numSims) {
      lines(p[,i], type = 'l')
    }
  }
}
```

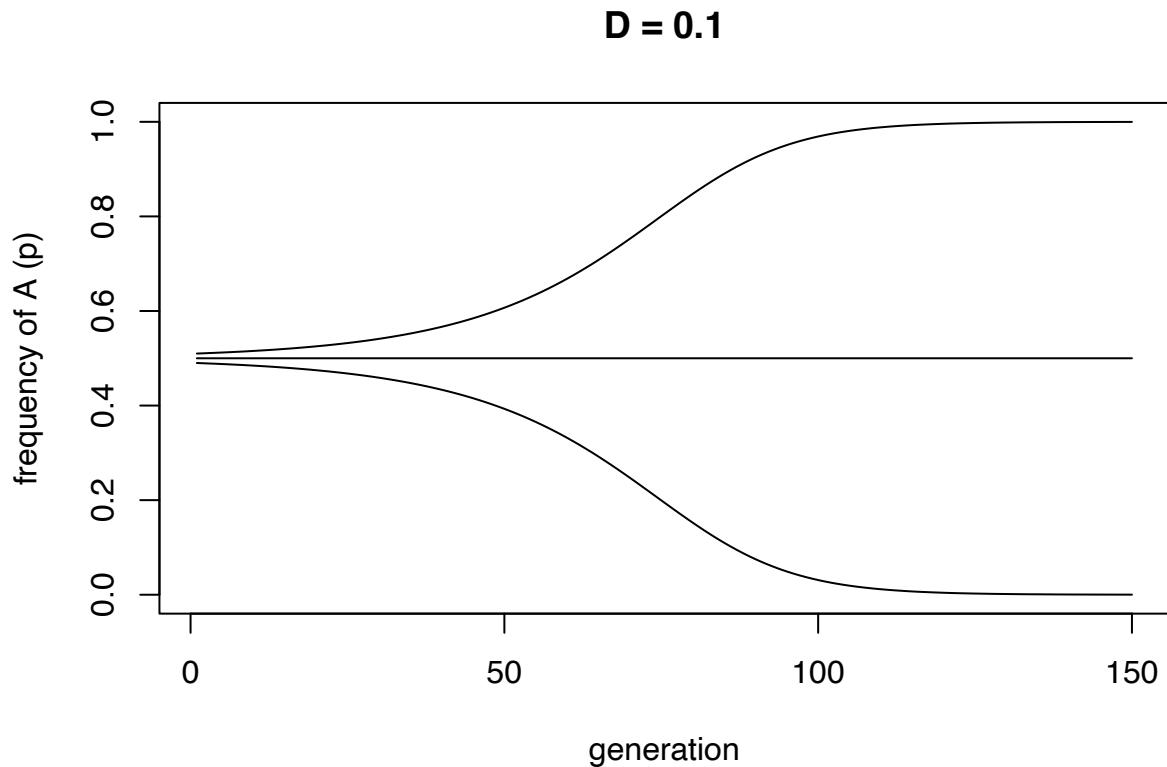
```

    }
}

}
}
```

The following command plots three different values of p_0 , one less than 0.5, one equal to 0.5, and one greater than 0.5. This should confirm that conformity favours whichever trait is initially most frequent.

```
ConformityRecursion(D = 0.1, t_max = 150, p_0 = c(0.49, 0.5, 0.51))
```



Again, this matches the simulations above where some runs are randomly initially above 0.5 and others below 0.5.

Finally, we can use the recursion equation to generate a plot that has become a signature for conformity in the cultural evolution literature. The following code plots, for all possible values of p , the probability of adopting p in the next generation.

```
p <- seq(0,1,length.out = 101)

D <- 1
p_next <- p + D*p*(1-p)*(2*p-1)

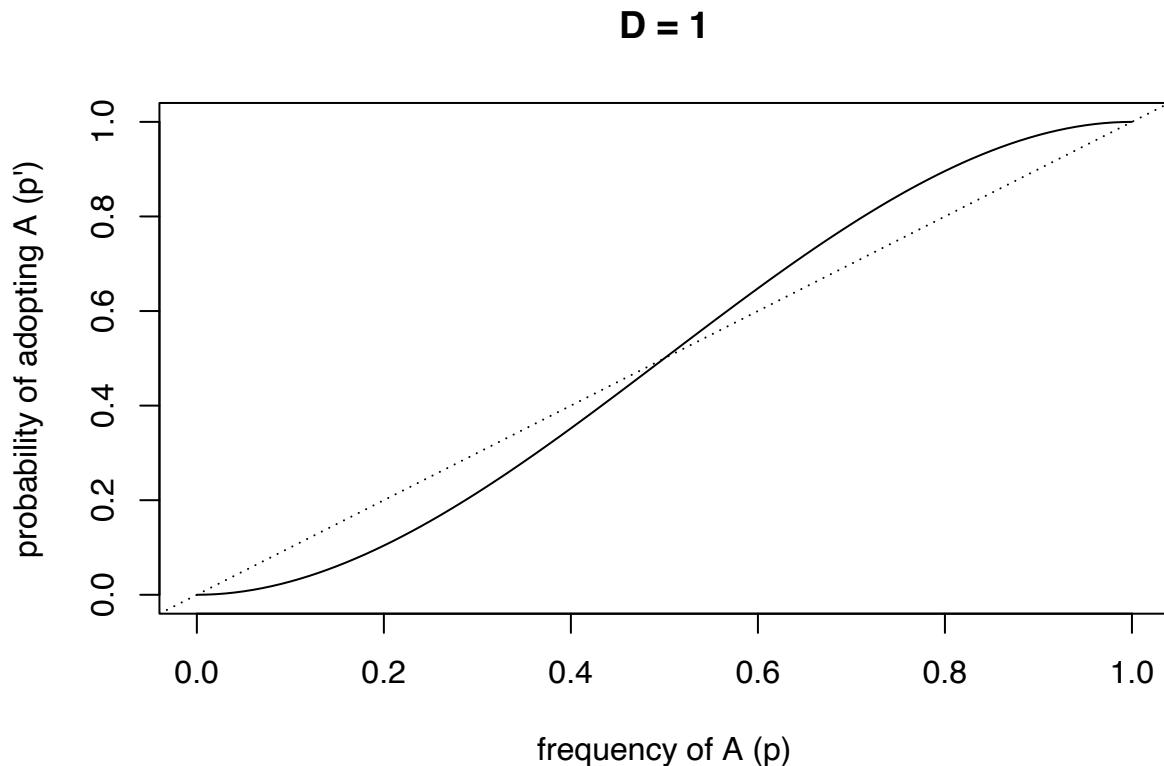
plot(p, p_next,
      type = 'l',
      ylab = "probability of adopting A (p')",
      xlab = "frequency of A (p)",
```

```

main = paste("D =", D))

abline(a = 0, b = 1, lty = 3)

```



This encapsulates the process of conformity. The dotted line shows unbiased transmission: the probability of adopting A is exactly equal to the frequency of A in the population. The s-shaped solid curve shows conformist transmission. When A is common ($p > 0.5$), then the curve is higher than the dotted line: there is a disproportionately higher probability of adopting A . When A is uncommon ($p < 0.5$), then the curve is lower than the dotted line: there is a disproportionately lower probability of adopting A .

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Simulation Models of Cultural Evolution in R

Alex Mesoudi

Model 6: Vertical and horizontal cultural transmission

One obvious difference between cultural and genetic evolution is in their pathways of transmission. In genetic evolution - in humans at least - we get our genes exclusively from our two biological parents. In cultural evolution, we get cultural traits (ideas, attitudes, skills, languages etc.) from a wide array of sources, not just our biological parents but also other relatives, biologically unrelated teachers and peers, or complete strangers via books or the internet.

All of the models we have made so far assume *oblique cultural transmission*, such that agents learn from one or more members of the previous generation. In Model 6 we will consider *vertical cultural transmission*, in which agents learn from two parents, and *horizontal cultural transmission*, where agents learn from members of the same generation.

The models are still extremely simple, with no actual biological reproduction or proper family lineages. We are also maintaining the *non-overlapping generations* of prior models, which neatly separates each generation. Real life is more messy, with overlapping generations that blur distinctions between, say, oblique and horizontal transmission. But as we have seen, models are useful because of, not despite, their simplicity. In this case, we consider three interesting features of vertical and horizontal transmission. First, the case of assortative cultural mating, where one's parents are more similar in cultural traits than two randomly chosen members of the population. Second, the case where biases in vertical and horizontal transmission act in opposite directions. Third, we examine the claim that cultural evolution is faster than genetic evolution because it features horizontal transmission.

All of these pathways of transmission were modelled in depth by Cavalli-Sforza & Feldman (1981), and the simulation models here follow their general form.

Model 6a: Vertical cultural transmission

Following the same approach as we did for conformity in Model 4, we can make a table specifying the outcome of vertical cultural transmission for an offspring's cultural traits given its two parents' cultural traits. As before, we will use two discrete traits A and B , with the frequency of A being p and of B being $1 - p$.

Mother's trait	Father's trait	Probability of child adopting A
A	A	1
A	B	$1/2 + s_v/2$
B	A	$1/2 + s_v/2$
B	B	0

This table assumes that if both parents have the same trait, then the child inherits that trait with 100% certainty. If parents have different traits, then the child has a 50% chance of inheriting either one, plus an

additional chance $s_v/2$. This is similar to the conformity parameter D in giving an adoption boost to a trait, except that now trait A is always getting a boost, irrespective of which parent has A .

Consequently, s_v can be seen as a form of directly biased transmission or cultural selection, similar to that explored in Model 3: it gives the probability of preferentially adopting trait A above that expected under unbiased cultural transmission. It ranges from zero (unbiased transmission) to one (fully biased transmission, where A is always adopted if either parent has it). It can also be negative (up to -1), in which case trait B is favoured over A .

The following function takes the structure of **ConformistTransmission** from Model 5, replacing the three randomly-chosen demonstrators with two randomly-chosen parents, and setting the offspring traits as per the table above.

```
VerticalTransmission <- function (N, p_0, s_v, t_max, r_max) {

  # create matrix with t_max rows and r_max columns, fill with NAs, convert to dataframe
  output <- as.data.frame(matrix(NA,t_max,r_max))

  # purely cosmetic: rename the columns with run1, run2 etc.
  names(output) <- paste("run", 1:r_max, sep="")

  for (r in 1:r_max) {

    # create first generation
    agent <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                         prob = c(p_0,1-p_0)))

    # add first generation's p to first row of column r
    output[1,r] <- sum(agent$trait == "A") / N

    for (t in 2:t_max) {

      # create dataframe with a set of 2 randomly-picked parents for each agent
      parents <- data.frame(mother = sample(agent$trait, N, replace = TRUE),
                            father = sample(agent$trait, N, replace = TRUE))

      prob <- runif(N)

      # if both parents have A, child has A
      agent$trait[parents$mother == "A" & parents$father == "A"] <- "A"

      # if both parents have B, child has B
      agent$trait[parents$mother == "B" & parents$father == "B"] <- "B"

      # if mother has A and father has B, child has A with prob (1/2 + s_v/2), otherwise B
      agent$trait[parents$mother == "A" & parents$father == "B" &
                  prob < (1/2 + s_v/2)] <- "A"
      agent$trait[parents$mother == "A" & parents$father == "B" &
                  prob >= (1/2 + s_v/2)] <- "B"

      # if mother has B and father has A, child has A with prob (1/2 + s_v/2), otherwise B
      agent$trait[parents$mother == "B" & parents$father == "A" &
                  prob < (1/2 + s_v/2)] <- "A"
      agent$trait[parents$mother == "B" & parents$father == "A" &
                  prob >= (1/2 + s_v/2)] <- "B"
    }
  }
}
```

```

# get p and put it into output slot for this generation t and run r
output[t,r] <- sum(agent$trait == "A") / N

}

}

# first plot a thick line for the mean p
plot(rowMeans(output),
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("N = ", N, ", s_v = ", s_v, sep = ""))
for (r in 1:r_max) {

  # add lines for each run, up to r_max
  lines(output[,r], type = 'l')
}

output # export data from function
}

```

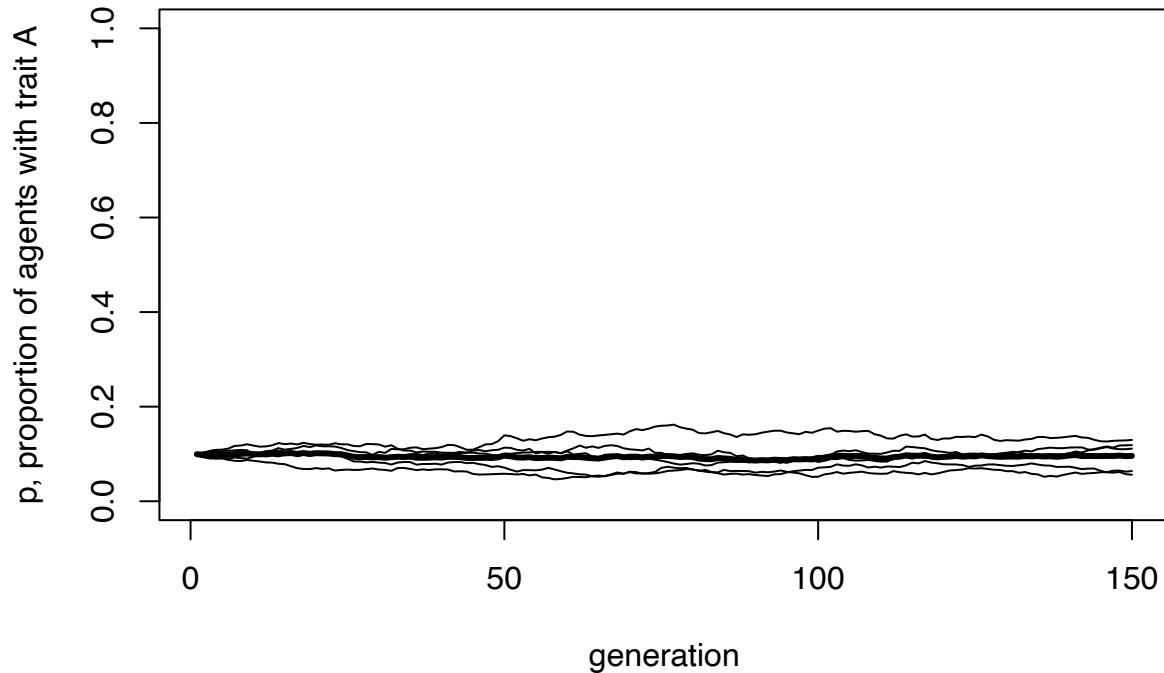
First we can check that when $s_v = 0$, we do indeed see unbiased transmission:

```

data_model6a <- VerticalTransmission(N = 10000,
                                      p_0 = 0.1,
                                      s_v = 0.0,
                                      t_max = 150,
                                      r_max = 5)

```

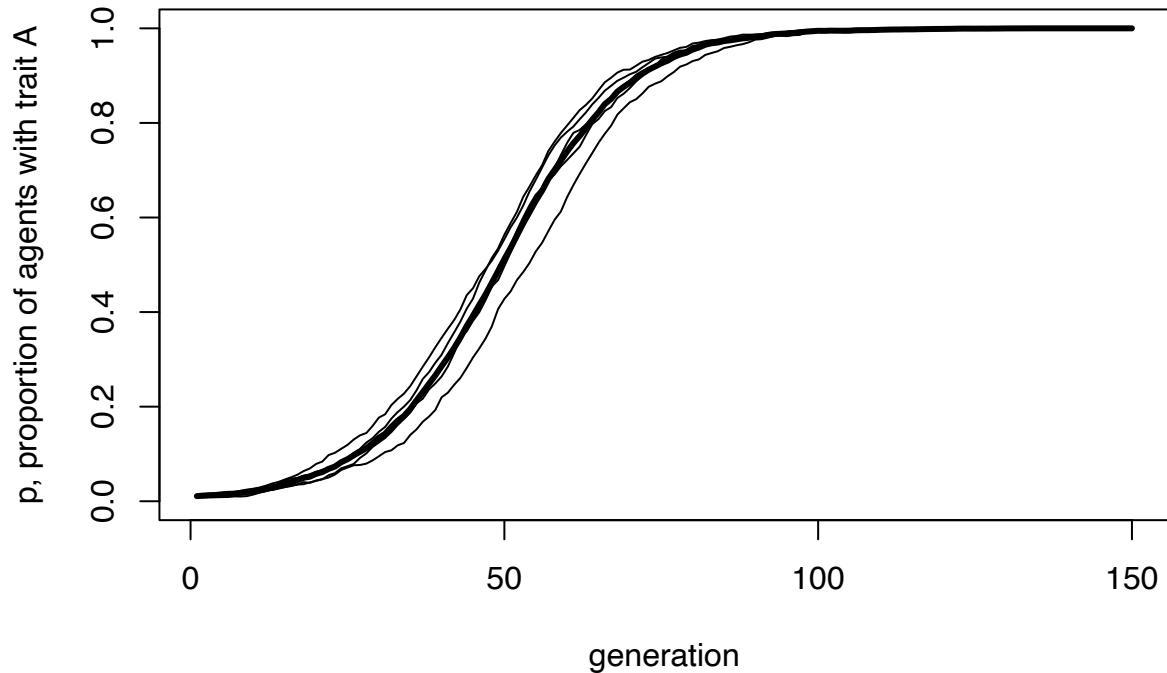
N = 10000, s_v = 0



As in previous models, unbiased transmission results in no change in trait frequencies except random fluctuation due to chance. Now we can add selection:

```
data_model6a <- VerticalTransmission(N = 10000,  
                                     p_0 = 0.01,  
                                     s_v = 0.1,  
                                     t_max = 150,  
                                     r_max = 5)
```

N = 10000, s_v = 0.1



This looks a lot like the s-shaped curve we found in Model 3 for $s = 0.1$. We have recapitulated unbiased transmission from Model 2 combined with biased transmission from Model 3, but assuming vertical cultural transmission from two parents, rather than randomly picking one demonstrator from the previous generation.

Model 6b: Assortative mating

We can use this vertical transmission model to explore what happens when we relax our assumption that parents form entirely at random. In reality, parents may be more culturally similar than average: two conservatives (or two liberals) may be more likely to get together than a conservative and a liberal; two vegans more likely than one vegan and one meat-eater. In evolutionary biology, this is known as *assortative mating*. For genetic evolution, it is assumed that the mates assort on genetically inherited characteristics. In cultural evolution, the mates assort on culturally inherited characteristics.

We now assume that a fraction a of matings are assortative, such that they must involve two parents with identical cultural traits, either both A or both B . A fraction $1 - a$ of matings are random as before, and can be any combination of traits. The following function implements this.

```
VerticalAssortative <- function (N, p_0, s_v, a, t_max, r_max) {
  # create matrix with t_max rows and r_max columns, fill with NAs, convert to dataframe
  output <- as.data.frame(matrix(NA,t_max,r_max))

  # purely cosmetic: rename the columns with run1, run2 etc.
  names(output) <- paste("run", 1:r_max, sep="")

  for (r in 1:r_max) {
```

```

# create first generation
agent <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                     prob = c(p_0,1-p_0)))

# add first generation's p to first row of column r
output[1,r] <- sum(agent$trait == "A") / N

for (t in 2:t_max) {

  # 1. assortative mating:

  # create dataframe with a set of 2 parents for each agent
  # mother is picked randomly, father is blank for now
  parents <- data.frame(mother = sample(agent$trait, N, replace = TRUE),
                        father = rep(NA, N))

  # probabilities for a
  prob <- runif(N)

  # with prob a, make father identical
  parents$father[prob < a] <- parents$mother[prob < a]

  # with prob 1-a, pick random trait for father
  parents$father[prob >= a] <- sample(agent$trait,
                                         sum(prob >= a),
                                         replace = TRUE)

  # 2. vertical transmission:

  # new probabilities for s_v
  prob <- runif(N)

  # if both parents have A, child has A
  agent$trait[parents$mother == "A" & parents$father == "A"] <- "A"

  # if both parents have B, child has B
  agent$trait[parents$mother == "B" & parents$father == "B"] <- "B"

  # if mother has A and father has B, child has A with prob (1/2 + s_v/2), otherwise B
  agent$trait[parents$mother == "A" & parents$father == "B" &
              prob < (1/2 + s_v/2)] <- "A"
  agent$trait[parents$mother == "A" & parents$father == "B" &
              prob >= (1/2 + s_v/2)] <- "B"

  # if mother has B and father has A, child has A with prob (1/2 + s_v/2), otherwise B
  agent$trait[parents$mother == "B" & parents$father == "A" &
              prob < (1/2 + s_v/2)] <- "A"
  agent$trait[parents$mother == "B" & parents$father == "A" &
              prob >= (1/2 + s_v/2)] <- "B"

  # 3. store results:

  # get p and put it into output slot for this generation t and run r
}

```

```

    output[t,r] <- sum(agent$trait == "A") / N
}

}

# first plot a thick line for the mean p
plot(rowMeans(output),
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("N = ", N, " , s_v = ", s_v, " , a = ", a, sep = ""))
for (r in 1:r_max) {

  # add lines for each run, up to r_max
  lines(output[,r], type = 'l')

}
output # export data from function
}

```

Most of **VerticalAssortative** is the same as **VerticalTransmission**, except for changes in the way parents are created. Rather than picking all mothers and fathers randomly, we first pick mothers randomly, then with probability a give the fathers the same cultural trait as the mother. With probability $1 - a$ we pick traits randomly for fathers, as in **VerticalTransmission**. The rest is the same, except that we add a to the figure title.

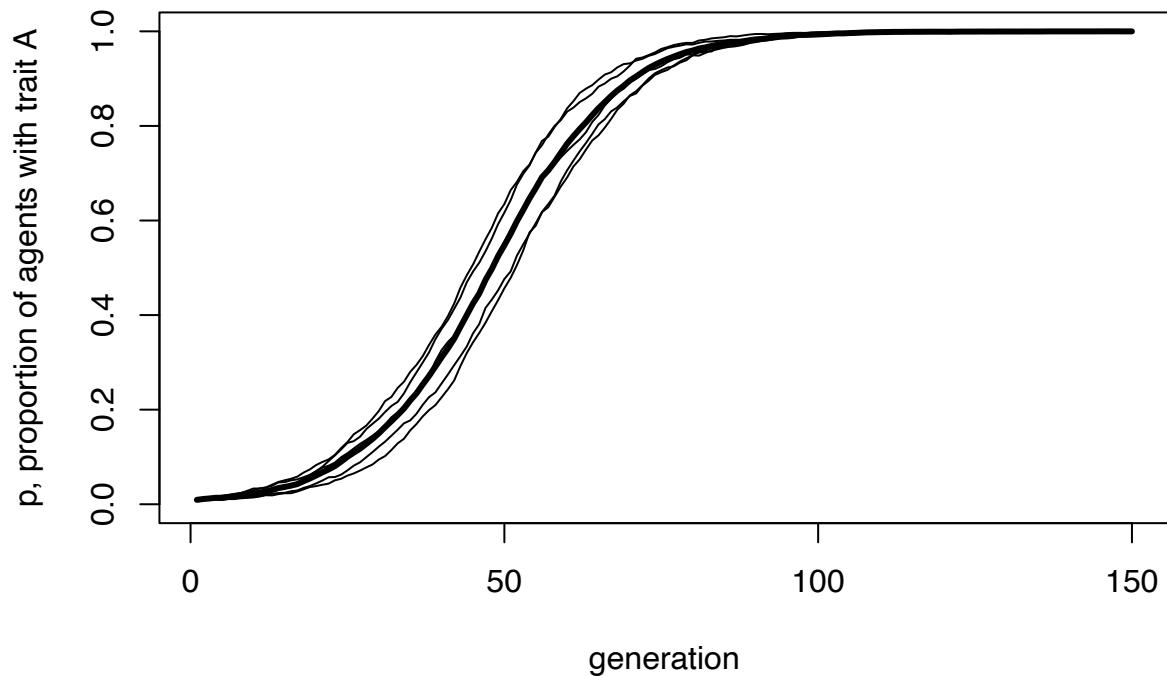
Let's first check that when $a = 0$, i.e. no assortative mating, the output is identical to that with **VerticalTransmission** above:

```

data_model6b <- VerticalAssortative(N = 10000,
                                      p_0 = 0.01,
                                      s_v = 0.1,
                                      a = 0,
                                      t_max = 150,
                                      r_max = 5)

```

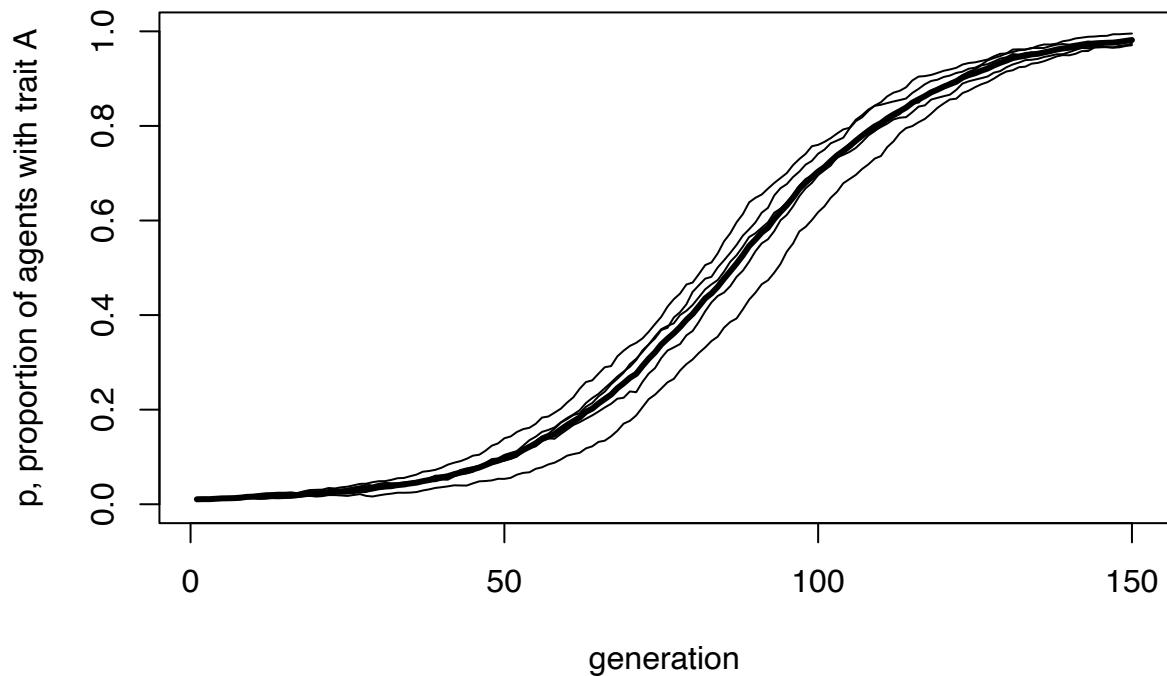
N = 10000, s_v = 0.1, a = 0



It's identical to before, with an s-shaped curve indicative of directly biased transmission. Now let's add some assortative mating, with $a = 0.4$:

```
data_model6b <- VerticalAssortative(N = 10000,
                                     p_0 = 0.01,
                                     s_v = 0.1,
                                     a = 0.4,
                                     t_max = 150,
                                     r_max = 5)
```

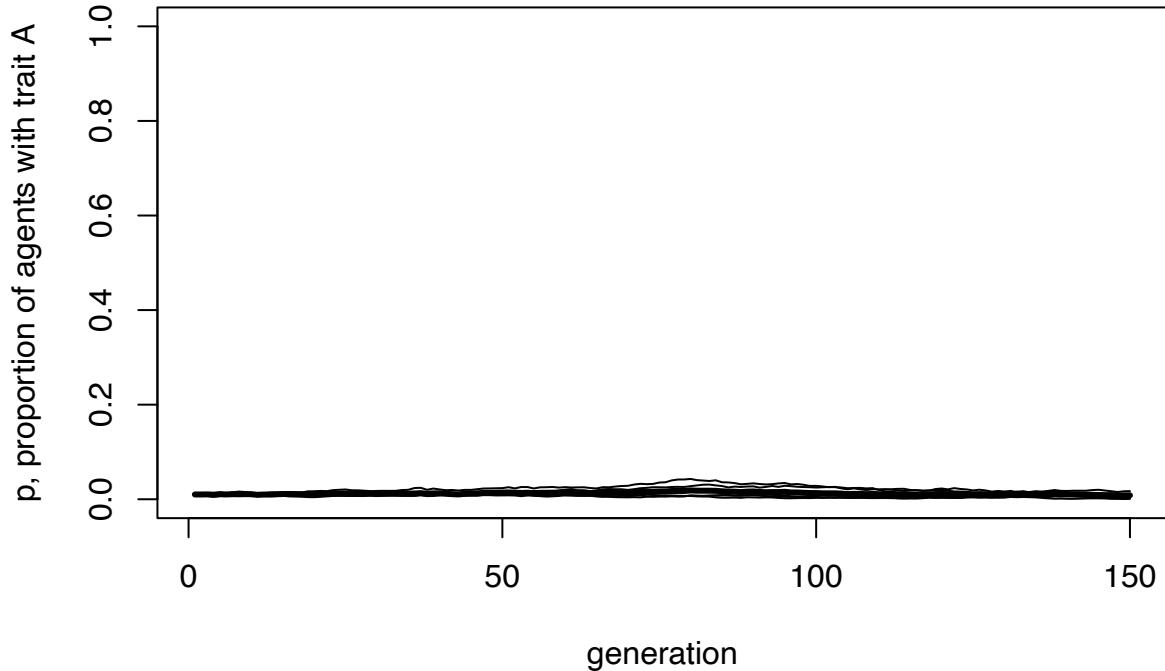
N = 10000, s_v = 0.1, a = 0.4



The curve is still s-shaped, but takes longer to reach $p = 1$. What happens when all mating is assortative, i.e. $a = 1$?

```
data_model6b <- VerticalAssortative(N = 10000,
                                      p_0 = 0.01,
                                      s_v = 0.1,
                                      a = 1,
                                      t_max = 150,
                                      r_max = 5)
```

$$N = 10000, s_v = 0.1, a = 1$$



Complete assortative mating results in no cultural change, beyond random fluctuations, even when selection is acting. In general, the more assortative mating there is, the weaker cultural selection will be.

In hindsight this is perhaps obvious. If assortative mating results in parents who have identical cultural traits, and as per the table above identical parents always give rise to identical children, then there will be no change resulting from these matings even when $s_v > 0$. However, under different assumptions about mating and transmission this may not always be the case. And hindsight does not always match foresight. It's always good to check and verify even simple predictions and intuitions.

Model 6c: Horizontal cultural transmission

Now we can add horizontal cultural transmission, which involves learning from members of the same generation. We will build this into the **VerticalAssortative** function above, such that vertical transmission (with assortative mating if $a > 0$) occurs first, and then horizontal cultural transmission occurs within the new generation of agents that form after vertical transmission.

There are many ways of implementing horizontal cultural transmission, just like there are many ways of implementing oblique transmission, as covered in other models (e.g. directly biased transmission, conformist biased transmission, blending inheritance). To allow a comparison with vertical transmission, here we will assume directly biased horizontal transmission. We will use a slightly different version of directly biased transmission from Model 3, modified to capture the key advantage of horizontal transmission over vertical transmission: the larger number of potential demonstrators.

Recall that Model 3 involved each agent randomly choosing one member of the previous generation and, if that demonstrator has trait A , then trait A is adopted with probability s . This reflects a situation where A is favoured by selection: perhaps A is a more effective tool, more memorable story, or more easily pronounced word. We are interested in when and how A spreads when initially rare in the population.

In Model 6c we assume that agents now choose n members of the *same* generation, i.e. the set of agents who have already undergone vertical transmission. If at least one of those n demonstrators has trait A , then the learner adopts trait A with probability s_h .

This is directly biased transmission, as in Model 3, because s_h allows agents with B to switch to A . There is no possibility of agents with A switching to B . The difference from Model 3 is that now there are n demonstrators rather than one, and we use the symbol s_h to distinguish this selection parameter from the one incorporated into vertical transmission, s_v , and the one originally used in Model 3, s .

The following function adds horizontal transmission to **VerticalAssortative**. We add n and s_h to the parameter list, and add some code to implement the horizontal transmission rule.

```
VerticalHorizontal <- function (N, p_0, s_v, s_h, a, n, t_max, r_max, make_plot = TRUE) {

  # create matrix with t_max rows and r_max columns, fill with NAs, convert to dataframe
  output <- as.data.frame(matrix(NA,t_max,r_max))

  # purely cosmetic: rename the columns with run1, run2 etc.
  names(output) <- paste("run", 1:r_max, sep="")

  for (r in 1:r_max) {

    # create first generation
    agent <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                         prob = c(p_0,1-p_0)))

    # add first generation's p to first row of column r
    output[1,r] <- sum(agent$trait == "A") / N

    for (t in 2:t_max) {

      # 1. assortative mating:

      # create dataframe with a set of 2 parents for each agent
      # mother is picked randomly, father is blank for now
      parents <- data.frame(mother = sample(agent$trait, N, replace = TRUE),
                            father = rep(NA, N))

      # probabilities for a
      prob <- runif(N)

      # with prob a, make father identical
      parents$father[prob < a] <- parents$mother[prob < a]

      # with prob 1-a, pick random trait for father
      parents$father[prob >= a] <- sample(agent$trait,
                                            sum(prob >= a),
                                            replace = TRUE)

      # 2. vertical transmission:

      # new probabilities for s_v
      prob <- runif(N)

      # if both parents have A, child has A
    }
  }
}
```

```

agent$trait[parents$mother == "A" & parents$father == "A"] <- "A"

# if both parents have B, child has B
agent$trait[parents$mother == "B" & parents$father == "B"] <- "B"

# if mother has A and father has B, child has A with prob (1/2 + s_v/2), otherwise B
agent$trait[parents$mother == "A" & parents$father == "B" &
            prob < (1/2 + s_v/2)] <- "A"
agent$trait[parents$mother == "A" & parents$father == "B" &
            prob >= (1/2 + s_v/2)] <- "B"

# if mother has B and father has A, child has A with prob (1/2 + s_v/2), otherwise B
agent$trait[parents$mother == "B" & parents$father == "A" &
            prob < (1/2 + s_v/2)] <- "A"
agent$trait[parents$mother == "B" & parents$father == "A" &
            prob >= (1/2 + s_v/2)] <- "B"

# 3. horizontal transmission:

# create matrix for holding n demonstrators for N agents
# fill with randomly selected agents from current gen
demonstrators <- matrix(data = sample(agent$trait, N*n, replace = TRUE),
                           nrow = N, ncol = n)

# record whether there is at least one A in each row
oneA <- rowSums(demonstrators == "A") > 0

# new probabilities for s_h
prob <- runif(N)

# adopt trait A if oneA is true and with prob s_h
agent$trait[oneA & prob < s_h] <- "A"

# 4. store results:

# get p and put it into output slot for this generation t and run r
output[t,r] <- sum(agent$trait == "A") / N

}

}

if (make_plot == TRUE) {

# first plot a thick line for the mean p
plot(rowMeans(output),
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      main = paste("N = ", N, ", s_v = ", s_v, ", s_h = ", s_h,
                  ", a = ", a, ", n = ", n, sep = ""))
}

```

```

for (r in 1:r_max) {

  # add lines for each run, up to r_max
  lines(output[,r], type = 'l')

}

output # export data from function
}

```

In the horizontal transmission section of **VerticalHorizontal** we first create a table of demonstrators using the **matrix** command. We use **matrix** rather than **data.frame** because in R the number of rows of a matrix can be generated on-the-fly, unlike dataframes. Here we create a matrix with n rows, representing the number of demonstrators, and N columns, representing the number of agents. We fill this with randomly-chosen members of the current generation using **sample**, as normal.

We then use the **rowSums** command to count the number of times in each row an A appears, and create a vector $oneA$ which is *TRUE* whenever there is at least one A , and *FALSE* if there are no A s. Then, if an agent has a *TRUE* in its corresponding $oneA$ vector, and with probability s_h , it adopts A . Otherwise, it keeps the same trait that it received during vertical transmission.

There is one final modification. We add a variable *make_plot* to the function definition, and wrap all the plotting code within an **if** statement such that plots are only drawn when *make_plot == TRUE*. This is a useful way of turning off the plot generation, and will come in handy later. In the function call, the default value of *make_plot* is given as *TRUE*, so if we omit this in the function call, the plot is generated by default.

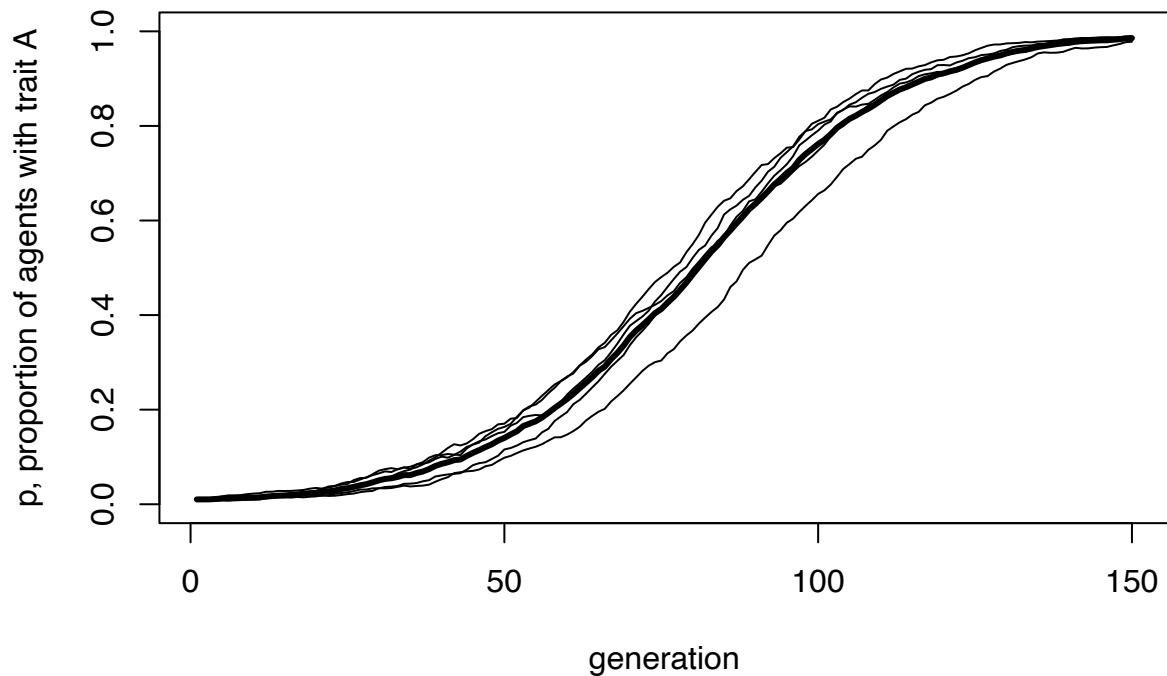
First let's check that vertical cultural transmission and assortative mating work as before, to make sure we didn't break anything.

```

data_model6c <- VerticalHorizontal(N = 10000,
                                    p_0 = 0.01,
                                    s_v = 0.1,
                                    s_h = 0,
                                    a = 0.4,
                                    n = 0,
                                    t_max = 150,
                                    r_max = 5)

```

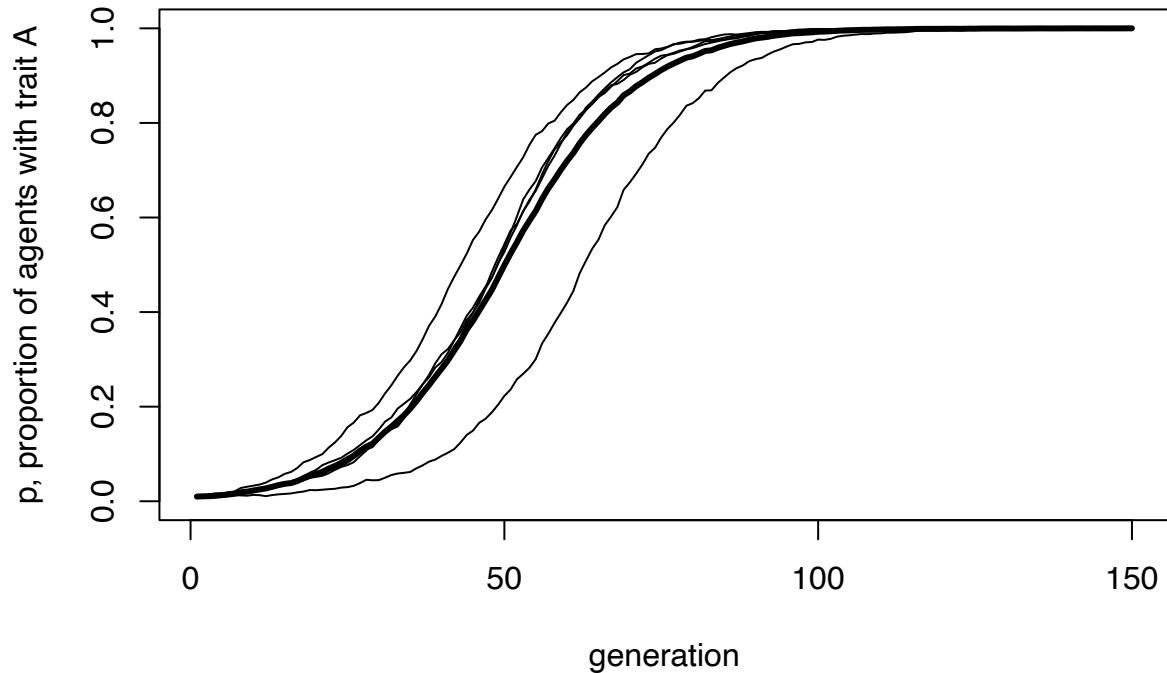
N = 10000, s_v = 0.1, s_h = 0, a = 0.4, n = 0



This should be roughly the same shape as the corresponding figure above with $s_v = 0.1$ and $a = 0.4$. Now let's turn off vertical transmission and try just horizontal transmission:

```
data_model6c <- VerticalHorizontal(N = 10000,
                                    p_0 = 0.01,
                                    s_v = 0,
                                    s_h = 0.1,
                                    a = 0,
                                    n = 1,
                                    t_max = 150,
                                    r_max = 5)
```

N = 10000, s_v = 0, s_h = 0.1, a = 0, n = 1



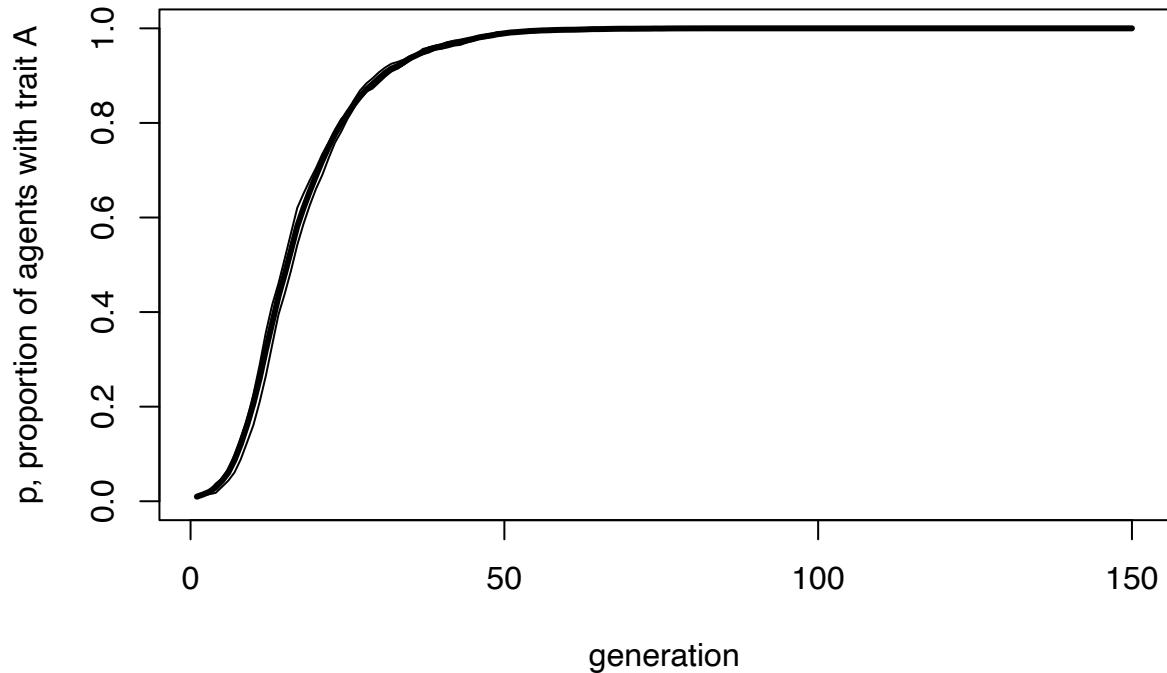
Horizontal transmission with $s_h = 0.1$ and $n = 1$ looks almost identical to the plot generated from **BiasedTransmission** in Model 3 with $s = 0.1$. This makes sense because **BiasedTransmission** used the same rule, but with n fixed at one.

The curve above also looks almost identical to the first vertical transmission curve generated above in Model 6a using **VerticalTransmission** with $s_v = 0.1$ and $a = 0$. Under these assumptions, vertical cultural transmission from two randomly chosen parents is equivalent to horizontal cultural transmission from one randomly chosen demonstrator.

Now let's increase n , the number of demonstrators in horizontal transmission:

```
data_model6c <- VerticalHorizontal(N = 10000,
                                    p_0 = 0.01,
                                    s_v = 0,
                                    s_h = 0.1,
                                    a = 0,
                                    n = 5,
                                    t_max = 150,
                                    r_max = 5)
```

N = 10000, s_v = 0, s_h = 0.1, a = 0, n = 5

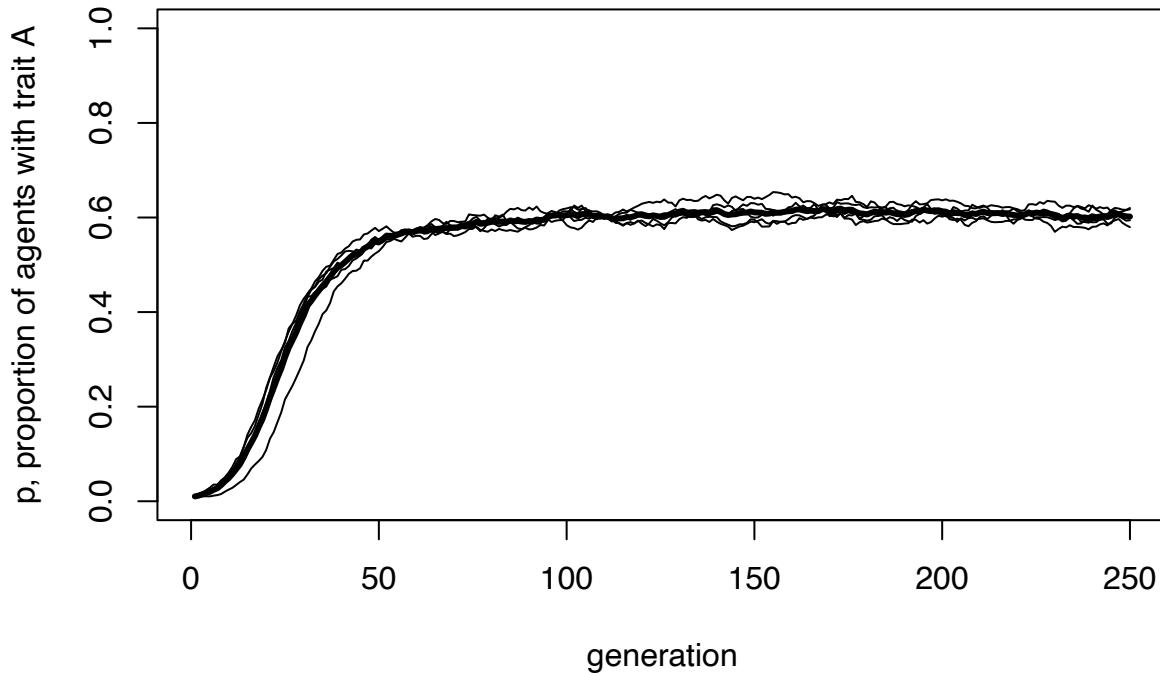


Increasing n greatly increases the strength of selection due to horizontal cultural transmission. If you only need one out of five demonstrators to have A for selection to operate, then selection for A will be more frequent than if you need one out of one demonstrator to have A .

If we set $-1 < s_v < 0$ then biased vertical transmission favours B , rather than A . Combining this with $s_h > 0$ gives the case where vertical and horizontal transmission act in opposite directions. This might represent a ‘clash of the generations’ over traits such as smoking: parents exert pressure on children not to smoke, while peer pressure encourages smoking. The following illustrates such a case:

```
data_model16c <- VerticalHorizontal(N = 10000,
                                     p_0 = 0.01,
                                     s_v = -0.2,
                                     s_h = 0.1,
                                     a = 0.1,
                                     n = 5,
                                     t_max = 250,
                                     r_max = 5)
```

$$N = 10000, s_v = -0.2, s_h = 0.1, a = 0.1, n = 5$$



Whereas before there was always a single equilibrium at $p = 1$, here there is a stable mix of A and B agents co-existing at equilibrium at a point where the vertical and horizontal transmission biases balance out. In the plot above, this equilibrium value is approximately $p^* = 0.6$, but this varies with different combinations of s_v , a , s_h and n .

We started this discussion by comparing vertical-only genetic inheritance with cultural inheritance, which can be horizontal as well as (or instead of) vertical. Let's create a plot to compare three cases: vertical-only, horizontal-only and vertical-plus-horizontal. In each, vertical and horizontal transmission are now acting in the same direction, to favour trait A . We are interested in how quickly this favoured trait A spreads and goes to fixation.

The following code runs these three scenarios with `make_plot = FALSE` to avoid automatically plotting the results. Instead we store the output from each case, and plot all three on the same graph using different colours and a legend.

```
data_model6c_v <- VerticalHorizontal(N = 10000,
                                      p_0 = 0.01,
                                      s_v = 0.1,
                                      s_h = 0,
                                      a = 0.1,
                                      n = 0,
                                      t_max = 150,
                                      r_max = 5,
                                      make_plot = FALSE)

data_model6c_h <- VerticalHorizontal(N = 10000,
                                      p_0 = 0.01,
```

```

            s_v = 0,
            s_h = 0.1,
            a = 0,
            n = 5,
            t_max = 150,
            r_max = 5,
            make_plot = FALSE)

data_model6c_vh <- VerticalHorizontal(N = 10000,
                                         p_0 = 0.01,
                                         s_v = 0.1,
                                         s_h = 0.1,
                                         a = 0.1,
                                         n = 5,
                                         t_max = 150,
                                         r_max = 5,
                                         make_plot = FALSE)

# plot vertical-only in blue
plot(rowMeans(data_model6c_v),
      type = 'l',
      ylab = "p, proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      lwd = 3,
      col = "royalblue")

for (r in 1:ncol(data_model6c_v)) {
  lines(data_model6c_v[,r], type = 'l', col = "royalblue")
}

# plot horizontal-only in orange
lines(rowMeans(data_model6c_h), type = 'l', lwd = 3, col = "orange")

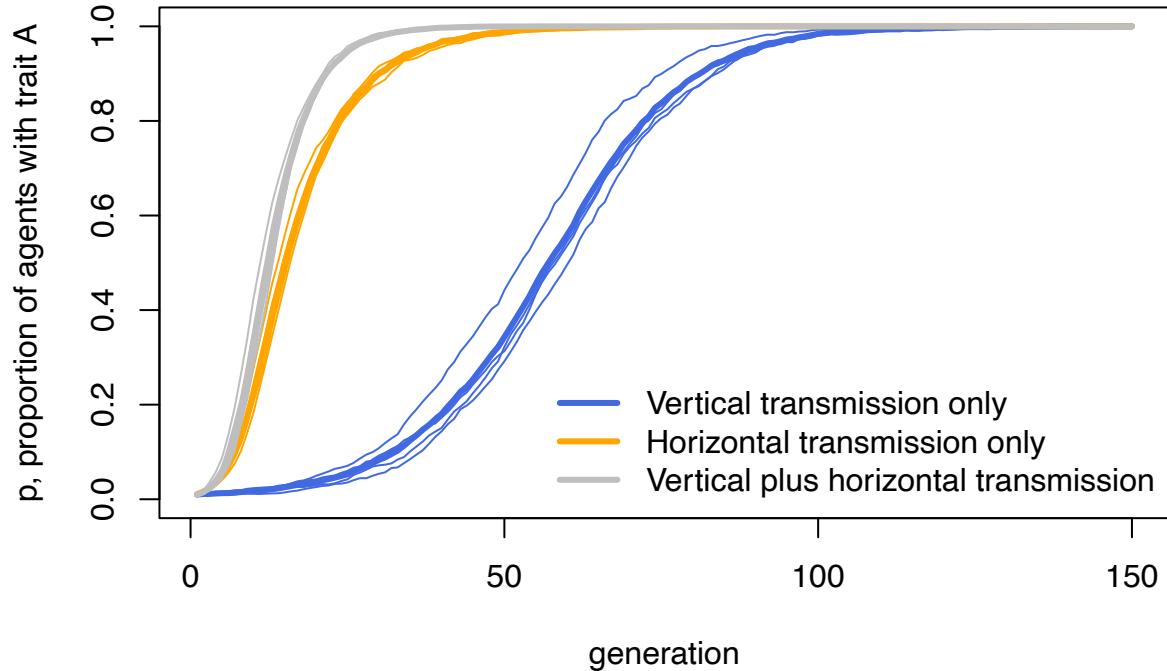
for (r in 1:ncol(data_model6c_h)) {
  lines(data_model6c_h[,r], type = 'l', col = "orange")
}

# plot vertical-horizontal in grey
lines(rowMeans(data_model6c_vh), type = 'l', lwd = 3, col = "grey")

for (r in 1:ncol(data_model6c_vh)) {
  lines(data_model6c_vh[,r], type = 'l', col = "grey")
}

legend("bottomright",
       legend = c("Vertical transmission only",
                 "Horizontal transmission only",
                 "Vertical plus horizontal transmission"),
       lty = 1,
       lwd = 3,
       col = c("royalblue", "orange", "grey"),
       bty = "n")

```



As we might expect, vertical plus horizontal transmission is fastest, with both forms of biased transmission combining together to favour A . This is closely followed by horizontal transmission alone, which has the advantage of a large pool of demonstrators. The genetic-inheritance-like vertical transmission alone is slowest.

Summary of Model 6

Our previous models all assumed oblique cultural transmission, where new agents learn from members of the previous generation. Here we modelled vertical cultural transmission, where agents learn from two parents (akin to genetic evolution), and horizontal cultural transmission, where agents learn from members of the same generation.

In Model 6a vertical cultural transmission was modelled in a simple way by picking two random members of the previous generation to be the parents for each new agent, then unbiased or biased transmission of traits occurs from those parents. This effectively recapitulated our previous unbiased and directly biased oblique transmission models but with slightly different assumptions. This consistency gives us confidence in the findings. It is always good to implement the same concept in different ways, to check that its effects are consistent or whether they depend on particular assumptions.

In Model 6b we extended vertical transmission by adding assortative mating, where the two parents are more culturally similar than expected under random mating. Assortative cultural mating acts in Model 6b to reduce the strength of cultural selection. This is because we assume that culturally identical parents always produce culturally identical offspring, and the selection bias only acts when parents have different traits. We can change these assumptions to explore other scenarios, and get different results (see Cavalli-Sforza & Feldman 1981). In general, assortative mating can potentially have positive effects, such as improving

communication or cooperation between the parents thus making transmission more likely, or negative effects, such as generating cultural segregation or inequality in the population.

Finally, in Model 6c we implemented horizontal transmission, which we assume occurs after vertical transmission, is also directly biased, and occurs from n demonstrators in the same generation as the learner. Model 6c showed that the strength of directly biased horizontal transmission increases not only with the selection strength parameter s_h , but also with n . This reflects an often-cited advantage of horizontal over vertical transmission: one can potentially learn from many more sources than just your two parents.

When vertical and horizontal transmission act in different directions, i.e. to favour different traits, then we see a stable mixed equilibrium where A and B co-exist in the population. This might reflect a case where parents favour one cultural trait (e.g. not smoking), and peer-pressure favours a different trait (e.g. smoking). Whereas previously biased vertical and horizontal transmission both eliminate variation from the population, in this case cultural variation is maintained.

Model 6c showed that horizontal transmission can be faster at spreading favoured traits than vertical transmission, especially when there are many demonstrators from whom agents learn. Vertical plus horizontal transmission is faster still, assuming both act in the same direction. Empirically, vertical plus horizontal (or vertical plus oblique) transmission is thought to be typical of real life human cultural inheritance, with children initially learning from their parents then updating from peers and elders later in life (Aunger 2000; Henrich & Broesch 2011).

The empirical record also shows that, over long timescales, cultural evolution is faster than genetic evolution (Perreault 2012). It is likely that horizontal cultural transmission is responsible for this speed, and has allowed human populations to adapt culturally to novel environments faster than they would have been able to via vertical-only genetic evolution alone. When a novel trait emerges in a population via mutation or migration, whether it is the bow-and-arrow or the smart phone, horizontal transmission allows it to spread far faster than if transmission were purely vertical. On the other hand, horizontal transmission might also allow harmful traits to rapidly spread before their negative effects become known, or before natural selection has had a chance to act on them.

The models here can be extended to look at uniparental vertical transmission, where either the mother or father is more culturally influential, rather than the biparental transmission we implemented above. Some traits are known to be transmitted uniparentally, or more strongly by one parent than the other. For example, one survey of Stanford students in the early 1980s found that religious denomination was more strongly maternally transmitted, and political orientation more strongly paternally transmitted (Cavalli-Sforza et al. 1982). Uniparental transmission will exhibit different long-term dynamics than biparental transmission (see Cavalli-Sforza & Feldman 1981).

Note that there is a subtle difference between vertical and horizontal transmission in this model. For vertical transmission, we assume (quite reasonably) that children come into the world lacking any cultural traits. Consequently, the vertical transmission table above gives the probabilities of adopting either A or B given the parents' values and the selection strength parameter s_v . For horizontal transmission, on the other hand, children already have a cultural trait, the one they obtained as a result of vertical transmission. We assume that if they already have A , there is no possibility of switching to B . If they already have B , then there is a chance of switching to A , depending on s_h and whether any of the n demonstrators have A . We can imagine here that individuals who have direct experience of A can be sure that it is better than B , so never switch. Individuals with B need one exposure to A in order to learn it, and do so with probability s_h . You might think that this unfairly weights the influence of horizontal transmission greater than that of vertical transmission. And that's fine! You are welcome to modify the model to better match how you think the transmission pathways should work, or better match empirical data. That's the beauty of models: because they are formally specified, it's easy to see where you might disagree with assumptions (which are often hidden or implicit in verbal models) and change them.

In terms of programming techniques, there is not much new here. We have recycled code from several previous models, especially the directly biased transmission from Model 3 and the ‘mating table’ approach of Model 5. Don’t be afraid to re-use code, if it’s been tried and tested elsewhere (with appropriate attribution, if it’s not your own code). The one minor innovation was wrapping the plotting in a `for` statement and using a

parameter `make_plot` to turn the automatic plotting on or off. This is useful if you want to combine plots from multiple runs, as we did in the final graph comparing the different pathways of inheritance.

Exercises

1. Try different values of s_v in **VerticalTransmission** to confirm that increasing s_v increases the speed with which A goes to fixation, and confirm that these dynamics are identical to how s acts in **Biased-Transmission** from Model 3.
 2. Try running **VerticalTransmission** with $s_v = -0.1$ and $p_0 = 0.9$. What happens? What does a negative value of s_v mean?
 3. Modify **VerticalTransmission** to allow the mother and the father to have different levels of influence. Replace the single s_v parameter with two selection parameters, one for the mother and one for the father. Explore the dynamics of uniparental biased transmission, compared to the biparental biased transmission implemented in the original model.
 4. Try different values of a in **VerticalAssortative** to confirm that as a increases, selection slows. Write a function to record the number of timesteps it takes for a run to go to fixation ($p = 1$) for different values of a , and constant s_v . Plot a against this measure.
 5. Try different values of s_h and n in **VerticalHorizontal** to confirm that as both parameters increase, the speed with which A goes to fixation increases. Again, create plots to show how fixation time varies with s_h and with n , with all other variables constant.
 6. Try different negative values of s_v , along with different values of a , s_h and n , to confirm that there are different mixed equilibria depending on the balance of vertical and horizontal transmission bias.
 7. Rewrite **VerticalHorizontal**, replacing the horizontal cultural transmission rule with conformity, using code from Model 5. Does this change the conclusions regarding the speed of vertical vs horizontal transmission?
-

Analytic Appendix

Following Cavalli-Sforza & Feldman (1981, Table 2.2.1), we can write out the full mating table for two parents as follows. For simplicity, we assume that their $b_3 = 1$, $b_0 = 0$, and $b_1 = b_2 = 1/2 + s/2$. In other words, there is no mutation and so two parents with the same trait always give rise to children with that trait, and when parental traits conflict then s_v represents the strength of selection for A under vertical transmission, irrespective of which parent the trait comes from.

Mother's trait	Father's trait	Probability of child adopting A	Probability of pair forming under random mating	Probability of pair forming under assortative mating
A	A	1	p^2	$p^2 + ap(1 - p)$
A	B	$1/2 + s_v/2$	$p(1 - p)$	$p(1 - p)(1 - a)$
B	A	$1/2 + s_v/2$	$p(1 - p)$	$p(1 - p)(1 - a)$
B	B	0	$(1 - p)^2$	$(1 - p)^2 + ap(1 - p)$

Considering random mating first, the frequency of p in the next generation, p' , is given by multiplying the probability of a child adopting A (column 3) by the probability of a pair forming under random mating (column 4) for each parental trait combination, then summing these products. This gives

$$p' = p^2 + (1 + s_v)p(1 - p)$$

which simplifies to

$$p' = p + p(1 - p)s_v \quad (6.1)$$

This is identical to Equation 3.1 from Model 3 where there was a single randomly-selected demonstrator (i.e. one ‘parent’), rather than two. As in Equation 3.1, the change in p from one generation to the next is proportional to the strength of selection, s_v , and the variance in p , $p(1 - p)$. In the Analytic Appendix to Model 3 we plotted this recursion to show that it takes the form of an s-shaped curve.

Following Cavalli-Sforza & Feldman (1981, Table 2.5.1) we can alternatively use the probability of a pair forming under assortative mating (column 5). (Note that I’ve used a rather than Cavalli-Sforza & Feldman’s m to avoid confusion with the migration parameter m used elsewhere.) As in the simulation model, a proportion a of matings are assortative, i.e. between two agents with the same cultural trait (either A and A or B and B), and $1 - a$ matings are random as before. For example, for the first $A \times A$ row, there are $(1 - a)$ matings that are random and so have probability p^2 as previously, and a matings that are assortative and will have probability p (because of the a matings that are assortative, the $A \times A$ pairings will occur with probability p and the $B \times B$ pairings will occur with probability $1 - p$). This gives:

$$\text{prob}(A \times A) = (1 - a)p^2 + ap = p^2 - ap^2 + ap = p^2 + ap(1 - p) \quad (6.2)$$

and so on for the other rows.

As for random mating, we then multiply and sum the third and fifth columns to get p' under assortative mating:

$$p' = p^2 + ap(1 - p) + (1 + s_v)p(1 - p)(1 - a)$$

which simplifies to:

$$p' = p + p(1 - p)s_v(1 - a) \quad (6.3)$$

This is the same as Equation 6.1 but with the difference between p in successive generations also proportional to $(1 - a)$. That is, the larger is a , the less change there is (at the extreme, $a = 1$, then $\Delta p = 0$). Assortative mating acts against selection.

Finally we can introduce a recursion for horizontal transmission. As in the simulation model, we assume that individuals observe n individuals and adopt A with probability s_h if at least one of those n individuals possesses trait A .

If p'' denotes the frequency of A after horizontal transmission, and p' the frequency before horizontal transmission but after vertical transmission as per Equation 6.1 or 6.3, then:

$$p'' = p' + (1 - p')s_h(1 - (1 - p')^n) \quad (6.4)$$

Here, there are p' individuals who already have A and so can’t change, and $(1 - p')$ individuals who have B and change to A with probability equal to the strength of selection in horizontal transmission, s_h , multiplied by the probability that at least one of the n demonstrators has an A . This latter probability will be one minus the probability of none of the n individuals possessing A , i.e. $1 - (1 - p')^n$.

The potency of horizontal transmission lies in this last term. When $n = 1$, then $1 - (1 - p)^n$ reduces to p , and we retrieve the same directly biased transmission form as Equations 3.1 and 6.1. As n increases, then $1 - (1 - p)^n$ tends to 1. Because p must be less than or equal to 1, when $n > 1$ then horizontal transmission must be stronger than vertical transmission, for identical selection strength parameters, until an equilibrium is reached at $p = 1$ at which there is no change.

We can simulate the two recursions specified in Equations 6.3 and 6.4:

```
VerticalHorizontalRecursion <- function(s_v, a, s_h, n, t_max, p_0) {

  p <- rep(0,t_max)
  p[1] <- p_0

  for (i in 2:t_max) {

    p[i] <- p[i-1] + p[i-1]*(1-p[i-1])*s_v*(1-a) # Eq 6.3

    p[i] <- p[i] + (1-p[i])*s_h*(1-(1-p[i])^n) # Eq 6.4

  }

  plot(x = 1:t_max, y = p,
        type = "l",
        ylim = c(0,1),
        ylab = "p, frequency of A trait",
        xlab = "generation",
        main = paste("s_v = ", s_v, ", a = ", a, ", s_h = ", s_h, ", n = ", n, sep = ""))
}

p # output p
}
```

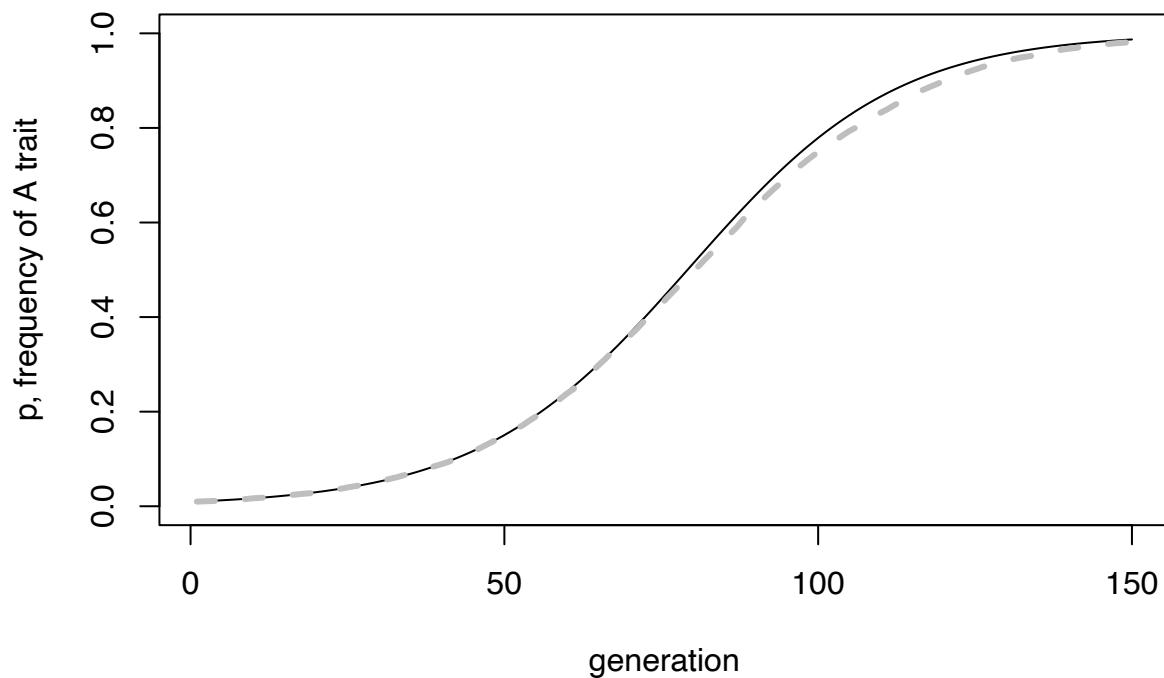
The following code plots the recursion line in black and the simulation data with a grey dashed line, for the same parameter values specifying vertical transmission only. We increase r_{max} to 20 to make the simulation mean as accurate as possible. They should match pretty well, confirming that both our simulation code and our maths is correct.

```
recursion_data <- VerticalHorizontalRecursion(p_0 = 0.01,
                                               s_v = 0.1,
                                               s_h = 0,
                                               a = 0.4,
                                               n = 0,
                                               t_max = 150)

simulation_data <- VerticalHorizontal(N = 10000,
                                       p_0 = 0.01,
                                       s_v = 0.1,
                                       s_h = 0,
                                       a = 0.4,
                                       n = 0,
                                       t_max = 150,
                                       r_max = 20,
                                       make_plot = FALSE)

lines(rowMeans(simulation_data), col = "grey", lwd = 3, lty = 2)
```

$$s_v = 0.1, a = 0.4, s_h = 0, n = 0$$



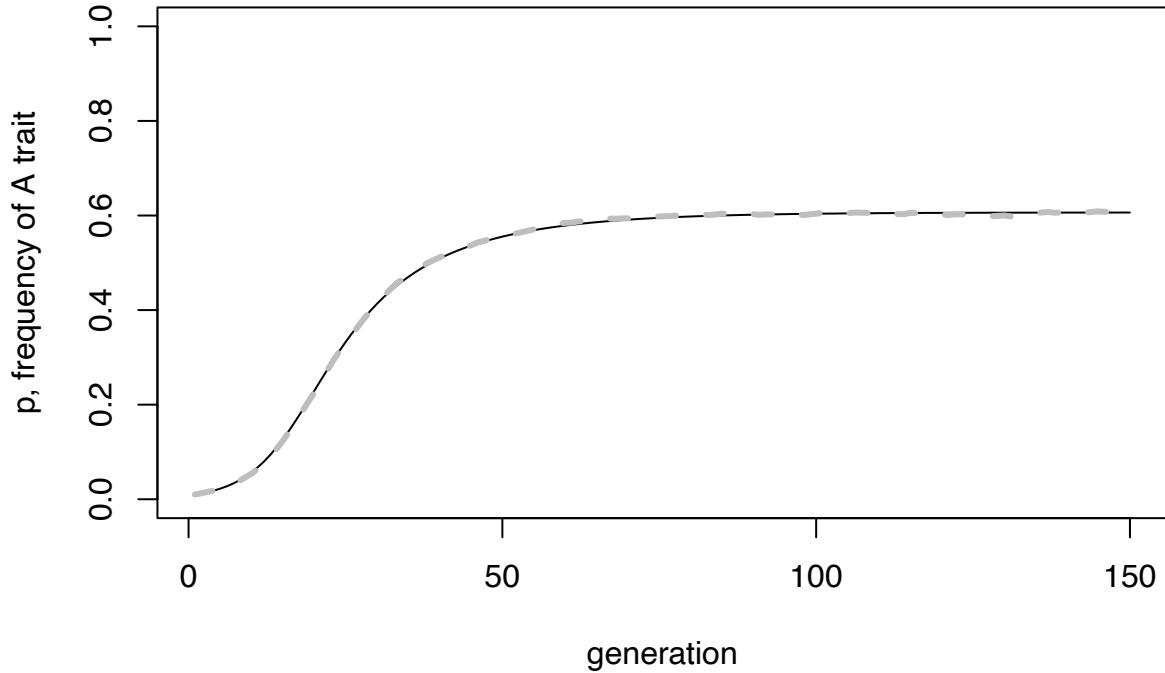
Here is the same for the case where vertical and horizontal transmission act in opposite directions:

```
recursion_data <- VerticalHorizontalRecursion(p_0 = 0.01,
                                              s_v = -0.2,
                                              s_h = 0.1,
                                              a = 0.1,
                                              n = 5,
                                              t_max = 150)

simulation_data <- VerticalHorizontal(N = 10000,
                                       p_0 = 0.01,
                                       s_v = -0.2,
                                       s_h = 0.1,
                                       a = 0.1,
                                       n = 5,
                                       t_max = 150,
                                       r_max = 20,
                                       make_plot = FALSE)

lines(rowMeans(simulation_data), col = "grey", lwd = 3, lty = 2)
```

$$s_v = -0.2, a = 0.1, s_h = 0.1, n = 5$$



Again, a good match.

The equilibrium value p^* can be found when $p = p''$. To make things easier, we can assume that $(1 - p')^n$ in Equation 6.4 is approximately zero when n is large, and so $(1 - (1 - p)^n)$ is approximately 1. Removing this term, substituting Equation 6.3 into 6.4, and setting $p = p''$ gives:

$$p = p + p(1 - p)s_v(1 - a) + s_h(1 - (p + p(1 - p)s_v(1 - a)))$$

This can be rearranged to give:

$$(1 - p)(p(s_v(1 - a) - s_h s_v(1 - a)) + s_h) = 0 \quad (6.5)$$

Hence there is one equilibrium when the first term $1 - p = 0$, such that $p^* = 1$. There is another where

$$p(s_v(1 - a) - s_h s_v(1 - a)) + s_h = 0$$

which rearranges to give

$$p^* = -\frac{s_h}{(1 - a)(s_v - s_h s_v)} \quad (6.6)$$

With the values used in the previous graph, we can use Equation 6.6 to find the value of the internal equilibrium that we observed:

```

s_v <- -0.2
s_h <- 0.1
a <- 0.1

-s_h / ((1-a)*(s_v - s_h*s_v))

## [1] 0.617284

```

This should approximately match the final values of both the simulation and recursion data:

```

mean(as.numeric(simulation_data[nrow(simulation_data),]))

## [1] 0.610355

recursion_data[length(recursion_data)]

## [1] 0.606279

```

It's not an exact match due to the removal of the term with n . The match should get better as n increases.

Given that p^* must be less than one, an internal equilibrium can only exist when the right hand side of Equation 6.6 is less than one. After rearranging, this gives the inequality:

$$s_v(1 - a) < -\frac{s_h}{(1 - s_h)} \quad (6.7)$$

Because s_h must be positive by assumption, the right hand side of Equation 6.7 must be negative. Consequently the inequality in Equation 6.7 can only be true when s_v is negative, and moreover negative enough (after being reduced in strength by assortative cultural mating) to outweigh s_h acting in the opposite direction.

References

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Simulation Models of Cultural Evolution in R

Alex Mesoudi

Model 7: Migration

Along with selection, mutation and drift, another fundamental driver of genetic evolution is migration. The same is true of cultural evolution. Migration has been a permanent fixture of our species since we first dispersed out of Africa. The movement of people from group to group can shape between-group cultural diversity, and spread beneficial technologies or ideas from group to group.

In Model 7 we will examine the effect of migration on between-group diversity. Previous models all featured a single group of agents. Now that we are interested in migration, we need to simulate multiple groups. Let's keep things simple and add one other group, making two in total: group 1 and group 2. As before, each group has N individuals in it.

As before, let's assume that there are two traits, A and B . We'll assume for now that they are neutral, i.e. not subject to selection / biased transmission. We assume that, initially, every member of group 1 has A , and every member of group 2 has B . Hence, in generation 1, $p = 1$, and $q = 0$, where p denotes the frequency of trait A in group 1 and q denotes the frequency of trait A in group 2. Such a case of maximum group difference might seem extreme, but is not too far from a situation where everyone in one society speaks one language and everyone in another society speaks another language, or everyone in one group practices one religion and everyone in another practices a different religion. In any case, remember that models are simplified, extreme cases designed to check the logic of verbal arguments, not exact recreations of reality.

The following code creates two agent dataframes, one for each group, and populates them with agents according to starting frequencies $p_0 = 1$ and $q_0 = 0$. Unlike before, we create another column recording which group this is, 1 or 2. We then combine the two dataframes into a single one using the **rbind** command, which combines dataframes by rows. Finally, we check it worked by calling the first five agents in group 1, i.e. agents one to five, who should all have trait A , and the first five agents in group 2, i.e. agents $N + 1$ to $N + 5$, who should all have trait B .

```
N <- 100
p_0 <- 1
q_0 <- 0

# create first generation of group 1
agent1 <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                      prob = c(p_0,1-p_0)),
                      group = 1)

# create first generation of group 2
agent2 <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                      prob = c(q_0,1-q_0)),
                      group = 2)

# combine agent1 and agent2 into a single agent dataframe
agent <- rbind(agent1,agent2)
```

```
agent[1:5,]
```

```
## trait group
## 1     A     1
## 2     A     1
## 3     A     1
## 4     A     1
## 5     A     1
```

```
agent[(N+1):(N+5),]
```

```
## trait group
## 101    B     2
## 102    B     2
## 103    B     2
## 104    B     2
## 105    B     2
```

We can also calculate the frequency of *A* in groups 1 and 2, i.e. p and q , and check that $p = 1$ and $q = 0$, with this code:

```
p <- sum(agent$trait[agent$group == 1] == "A") / N
q <- sum(agent$trait[agent$group == 2] == "A") / N
```

```
paste("p =", p)
```

```
## [1] "p = 1"
```

```
paste("q =", q)
```

```
## [1] "q = 0"
```

This code uses subsetting to get the number of *A*s in group 1, and then in group 2, and divides both by N to get a proportion.

Now for migration. In each timestep, we assume that each agent has a probability m of migrating. There is a problem, though. Because this is stochastic, this might result in the groups changing size. Maybe in one generation five agents move from group 1 to group 2, while only two move from group 2 to group 1. Then, group 1 would be smaller than group 2, and neither would be N . This gets complicated to model, as the size of the dataframes holding agents would need to change during the simulations.

To avoid N from changing during the simulation, we can do the following, drawing inspiration from what's known as Wright's Island Model from population genetics. First, each agent migrates with probability m , ignoring group membership. On average, this gives $2Nm$ migrants across the entire population, given that there are two groups of N agents. We take the migrants out of their groups, leaving empty slots where they used to be. Then we put these migrants back into the empty slots at random, ignoring which group the slot is in. This keeps N constant: for every empty slot, there is a migrating agent. Some might go back into their original group, but this won't change anything so it doesn't really matter.

Finally, we are assuming that agents take their traits with them, for now. We will change this later.

The following code simulates one bout of migration, i.e. one generation in the model.

```

m <- 0.1

# 2N probabilities, one for each agent, to compare against m
probs <- runif(1:(2*N))

# with prob m, add an agent's trait to list of migrants
migrants <- agent$trait[probs < m]

# put migrants randomly into empty slots
agent$trait[probs < m] <- sample(migrants, length(migrants))

p <- sum(agent$trait[agent$group == 1] == "A") / N
q <- sum(agent$trait[agent$group == 2] == "A") / N

paste("p =", p)

## [1] "p = 0.95"

paste("q =", q)

## [1] "q = 0.05"

```

You should see here that p has decreased slightly to be less than 1, and q has increased slightly to be greater than 0. Migration seems to be bringing the frequencies closer together.

The following function simply repeats the above over t_{max} generations and plots p and q , all within a single function, similar to previous models. We omit multiple runs and r_{max} , for brevity.

```

Migration <- function (N, p_0, q_0, m, t_max) {

  # create output dataframe to hold t_max values of p and q
  output <- data.frame(p = rep(NA, t_max), q = rep(NA, t_max))

  # create first generation of group 1
  agent1 <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                         prob = c(p_0,1-p_0)),
                        group = 1)

  # create first generation of group 2
  agent2 <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                         prob = c(q_0,1-q_0)),
                        group = 2)

  # combine agent1 and agent2 into a single agent dataframe
  agent <- rbind(agent1,agent2)

  # store first generation frequencies
  output$p[1] <- sum(agent$trait[agent$group == 1] == "A") / N
  output$q[1] <- sum(agent$trait[agent$group == 2] == "A") / N

  for (t in 2:t_max) {

```

```

# migration

# 2N probabilities, one for each agent, to compare against m
probs <- runif(1:(2*N))

# with prob m, add an agent's trait to list of migrants
migrants <- agent$trait[probs < m]

# put migrants randomly into empty slots
agent$trait[probs < m] <- sample(migrants, length(migrants))

# store frequencies in output slot t
output$p[t] <- sum(agent$trait[agent$group == 1] == "A") / N
output$q[t] <- sum(agent$trait[agent$group == 2] == "A") / N

}

plot(x = 1:nrow(output), y = output$p,
      type = 'l',
      col = "orange",
      ylab = "proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      main = paste("N = ", N, ", m = ", m, sep = ""))

lines(x = 1:nrow(output), y = output$q, col = "royalblue")

legend("topright",
       legend = c("p (group 1)", "q (group 2)"),
       lty = 1,
       col = c("orange", "royalblue"),
       bty = "n")

output # export data from function
}

```

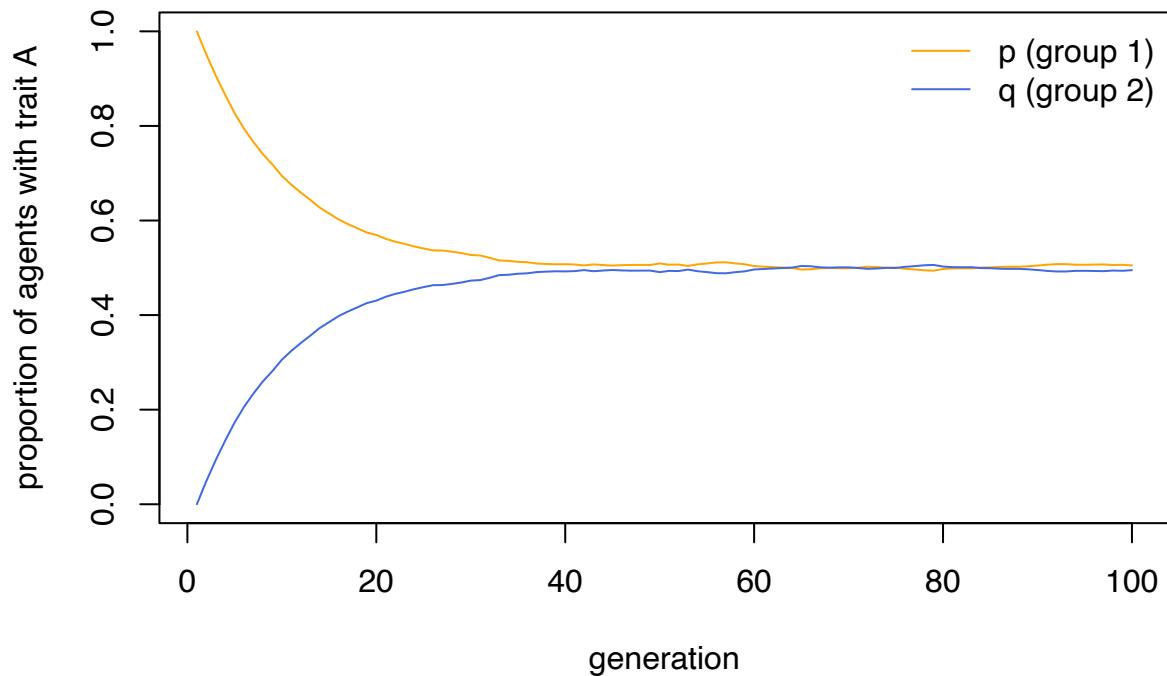
Now we can run the function with a reasonably strong migration rate of $m = 0.1$:

```

data_model7 <- Migration(N = 10000,
                         p_0 = 1,
                         q_0 = 0,
                         m = 0.1,
                         t_max = 100)

```

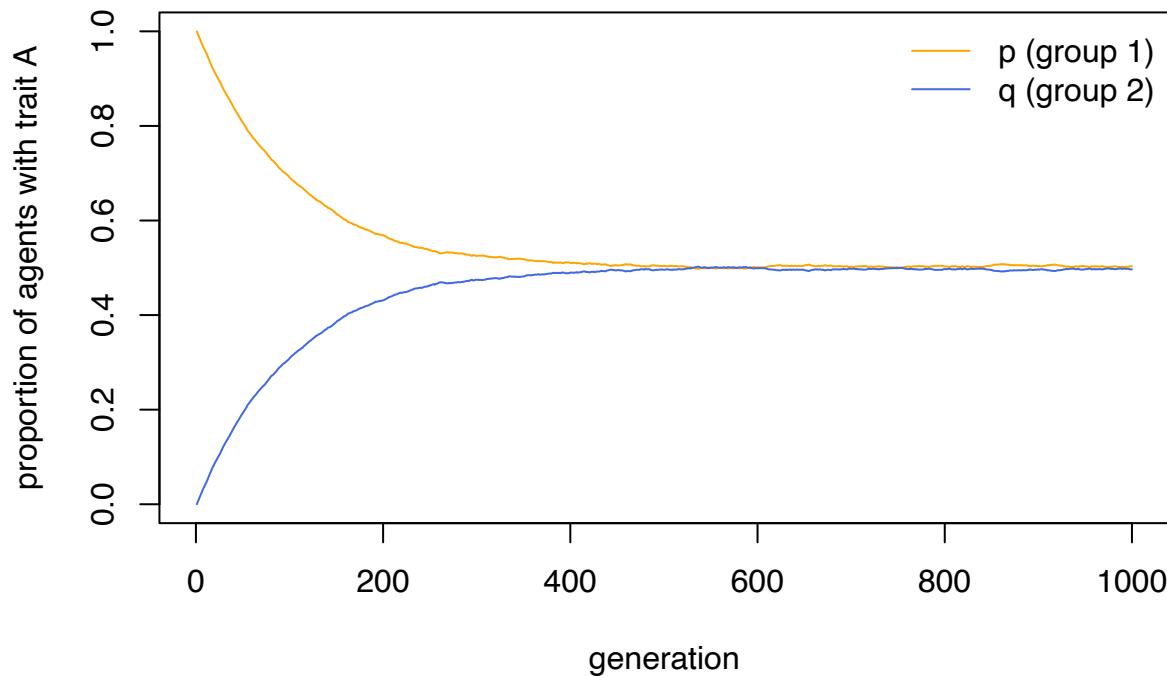
N = 10000, m = 0.1



Migration causes both groups to converge on a 50:50 split of A and B , i.e. $p = q = 0.5$. Two groups that are initially entirely different in their cultural traits become identical, barring small random fluctuations. Even very small amounts of migration eventually yield between-group homogeneity:

```
data_model7 <- Migration(N = 10000,
                         p_0 = 1,
                         q_0 = 0,
                         m = 0.01,
                         t_max = 1000)
```

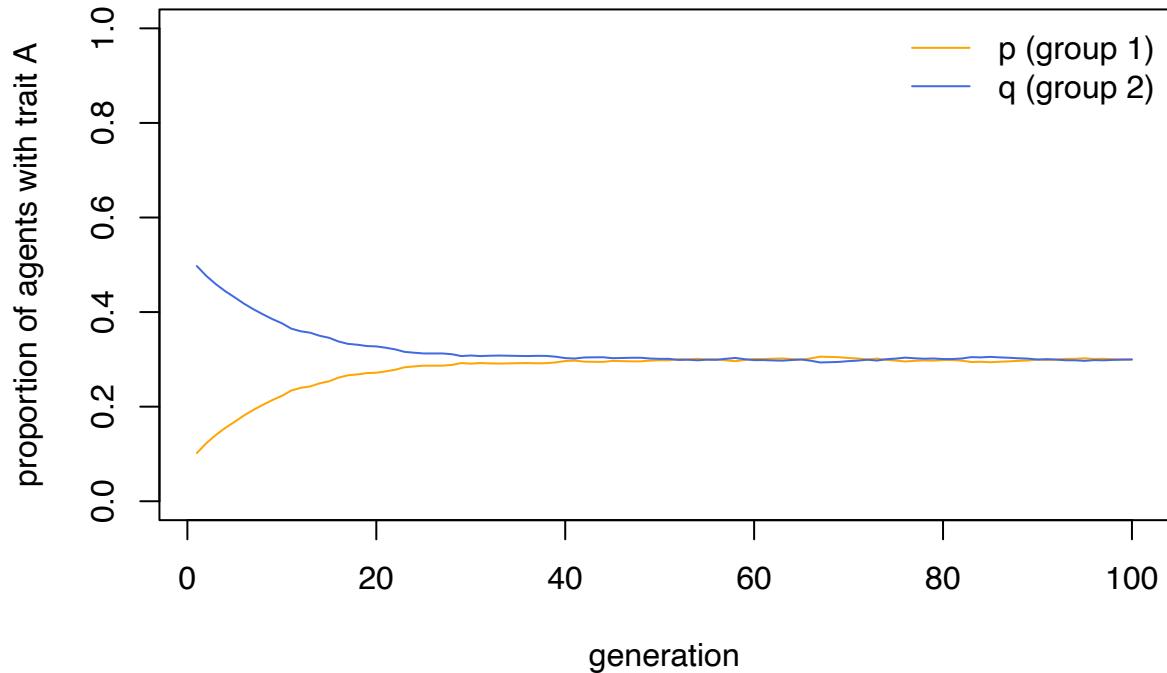
N = 10000, m = 0.01



Changing the starting frequencies reveals that p and q do not always converge on 0.5. Rather, they converge on the average initial frequency of A across both groups (i.e. $(p_0 + q_0)/2$, which in the case below is 0.3):

```
data_model7 <- Migration(N = 10000,
                         p_0 = 0.1,
                         q_0 = 0.5,
                         m = 0.1,
                         t_max = 100)
```

$$N = 10000, m = 0.1$$



This consequence of migration, to break down between-group differences and make each group identical, is well known from population genetics. In order to maintain between-group variation in the face of even small amounts of migration, we therefore need some additional process.

In genetic evolution one such process is natural selection, if selection favours different alleles in different groups. This might happen, for example, if the groups inhabit different environments in which different traits are optimal. In Models 3 and 5 we saw how directly biased transmission and conformist transmission can act as forms of cultural selection. Perhaps, then, these processes can maintain between-group variation in cultural evolution.

The following function adds directly biased transmission using code from the **BiasedTransmission** function of Model 3. We assume that trait *A* is favoured in group 1, and trait *B* is favoured in group 2. The parameter *s* determines the strength of this biased transmission / cultural selection, which we assume is equal in strength (but opposite in direction) in each group. For simplicity again we'll omit the multiple runs, hence no *r_{max}*.

```
MigrationPlusBiasedTransmission <- function (N, p_0, q_0, m, s, t_max) {

  # create output dataframe to hold t_max values of p and q
  output <- data.frame(p = rep(NA, t_max), q = rep(NA, t_max))

  # create first generation of group 1
  agent1 <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                         prob = c(p_0,1-p_0)),
                        group = 1)

  # create first generation of group 2
  agent2 <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
```

```

    prob = c(q_0, 1-q_0)),
    group = 2)

# combine agent1 and agent2 into a single agent dataframe
agent <- rbind(agent1, agent2)

# store first generation frequencies
output$p[1] <- sum(agent$trait[agent$group == 1] == "A") / N
output$q[1] <- sum(agent$trait[agent$group == 2] == "A") / N

for (t in 2:t_max) {

  # migration:

  # 2N probabilities, one for each agent, to compare against m
  probs <- runif(1:(2*N))

  # with prob m, add an agent's trait to list of migrants
  migrants <- agent$trait[probs < m]

  # put migrants randomly into empty slots
  agent$trait[probs < m] <- sample(migrants, length(migrants))

  # biased transmission:

  # get 2N random numbers, one per agent, each between 0 and 1
  copy <- runif(2*N)

  # group 1 favours A:
  # for each group 1 agent, pick a random agent as demonstrator and store their trait
  demonstrator_trait <- sample(agent$trait[agent$group == 1], N, replace = TRUE)
  # if demonstrator has A and with probability s, copy A from demonstrator
  agent$trait[agent$group == 1 & demonstrator_trait == "A" & copy < s] <- "A"

  # group 2 favours B:
  # for each group 1 agent, pick a random agent as demonstrator and store their trait
  demonstrator_trait <- sample(agent$trait[agent$group == 2], N, replace = TRUE)
  # if demonstrator has B and with probability s, copy B from demonstrator
  agent$trait[agent$group == 2 & demonstrator_trait == "B" & copy < s] <- "B"

  # store frequencies in output slot t
  output$p[t] <- sum(agent$trait[agent$group == 1] == "A") / N
  output$q[t] <- sum(agent$trait[agent$group == 2] == "A") / N

}

plot(x = 1:nrow(output), y = output$p,
      type = 'l',
      col = "orange",
      ylab = "proportion of agents with trait A",
      xlab = "generation",
      ylim = c(0,1),
      main = paste("N = ", N, ", m = ", m, ", s = ", s, sep = ""))

```

```

lines(x = 1:nrow(output), y = output$q, col = "royalblue")

legend("topright",
       legend = c("p (group 1)", "q (group 2)",
       lty = 1,
       col = c("orange", "royalblue"),
       bty = "n")

output # export data from function
}

```

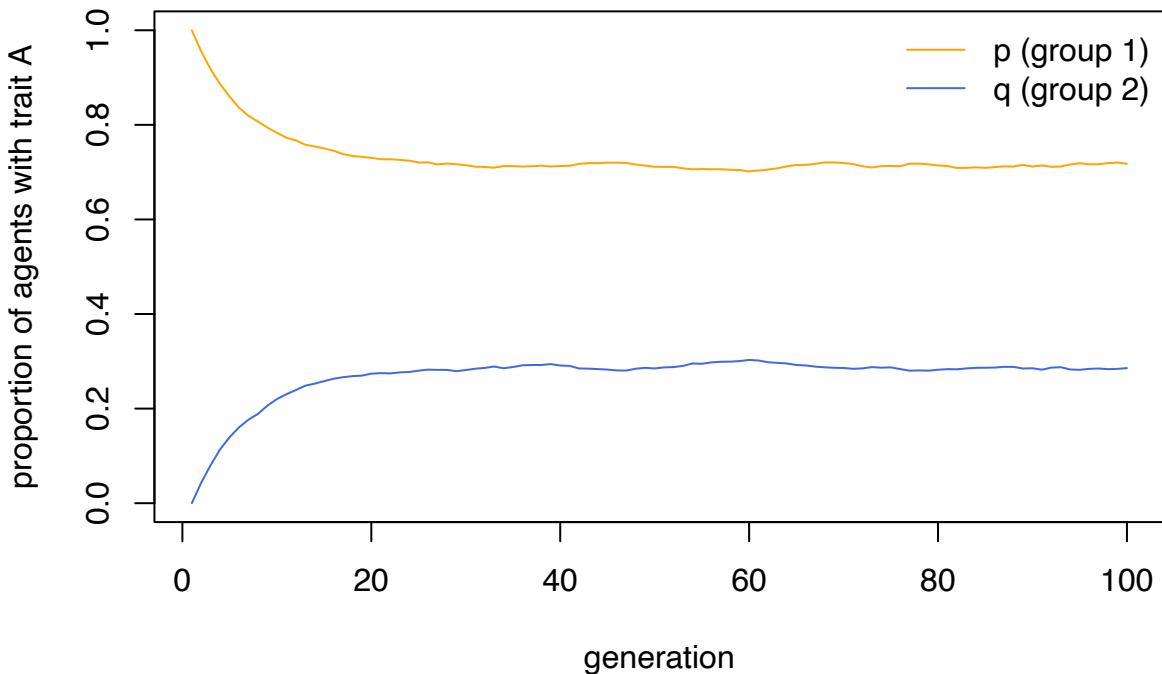
And we run the function with $s = 0.1$:

```

data_model7 <- MigrationPlusBiasedTransmission(N = 10000,
                                               p_0 = 1,
                                               q_0 = 0,
                                               m = 0.1,
                                               s = 0.1,
                                               t_max = 100)

```

N = 10000, m = 0.1, s = 0.1



Here we can see how adding cultural selection in the form of directly biased transmission maintains some degree of between-group cultural variation. Group 1 has around 70% A and 30% B, while group 2 has around 30% A and 70% B. You can play around with different values of s and m to see how the frequencies change in response. When s is large relative to m , then the groups maintain more distinctive cultural profiles.

Finally, we can see how conformist cultural transmission can also act to maintain between-group cultural variation in the face of migration. The following function integrates the original **Migration** function above with the **ConformistTransmission** function from Model 5. Note that conformity operates *within* each group, on the assumption that individuals are interacting only with other members of their own group, and never with members of the other group.

```
MigrationPlusConformity <- function (N, p_0, q_0, m, D, t_max) {

  # create output dataframe to hold t_max values of p and q
  output <- data.frame(p = rep(NA, t_max), q = rep(NA, t_max))

  # create first generation of group 1
  agent1 <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                         prob = c(p_0,1-p_0)),
                        group = 1)

  # create first generation of group 2
  agent2 <- data.frame(trait = sample(c("A","B"), N, replace = TRUE,
                                         prob = c(q_0,1-q_0)),
                        group = 2)

  # combine agent1 and agent2 into a single agent dataframe
  agent <- rbind(agent1,agent2)

  # store first generation frequencies
  output$p[1] <- sum(agent$trait[agent$group == 1] == "A") / N
  output$q[1] <- sum(agent$trait[agent$group == 2] == "A") / N

  for (t in 2:t_max) {

    # migration:

    # 2N probabilities, one for each agent, to compare against m
    probs <- runif(1:(2*N))

    # with prob m, add an agent's trait to list of migrants
    migrants <- agent$trait[probs < m]

    # put migrants randomly into empty slots
    agent$trait[probs < m] <- sample(migrants, length(migrants))

    # conformity in group 1:

    # create dataframe with a set of 3 randomly-picked group 1 demonstrators for each agent
    demonstrators <- data.frame(dem1 = sample(agent$trait[agent$group == 1], N, replace = TRUE),
                                 dem2 = sample(agent$trait[agent$group == 1], N, replace = TRUE),
                                 dem3 = sample(agent$trait[agent$group == 1], N, replace = TRUE))

    # get the number of As in each 3-dem combo
    numAs <- rowSums(demonstrators == "A")

    agent$trait[agent$group == 1 & numAs == 3] <- "A" # for dem combos with all As, set to A
    agent$trait[agent$group == 1 & numAs == 0] <- "B" # for dem combos with no As, set to B
  }
}
```

```

prob <- runif(N)

# when A is a majority, 2/3
agent$trait[agent$group == 1 & numAs == 2 & prob < (2/3 + D/3)] <- "A"
agent$trait[agent$group == 1 & numAs == 2 & prob >= (2/3 + D/3)] <- "B"

# when A is a minority, 1/3
agent$trait[agent$group == 1 & numAs == 1 & prob < (1/3 - D/3)] <- "A"
agent$trait[agent$group == 1 & numAs == 1 & prob >= (1/3 - D/3)] <- "B"

# conformity in group 2:

# create dataframe with a set of 3 randomly-picked group 2 demonstrators for each agent
demonstrators <- data.frame(dem1 = sample(agent$trait[agent$group == 2], N, replace = TRUE),
                             dem2 = sample(agent$trait[agent$group == 2], N, replace = TRUE),
                             dem3 = sample(agent$trait[agent$group == 2], N, replace = TRUE))

# get the number of As in each 3-dem combo
numAs <- rowSums(demonstrators == "A")

agent$trait[agent$group == 2 & numAs == 3] <- "A" # for dem combos with all As, set to A
agent$trait[agent$group == 2 & numAs == 0] <- "B" # for dem combos with no As, set to B

prob <- runif(N)

# when A is a majority, 2/3
agent$trait[agent$group == 2 & numAs == 2 & prob < (2/3 + D/3)] <- "A"
agent$trait[agent$group == 2 & numAs == 2 & prob >= (2/3 + D/3)] <- "B"

# when A is a minority, 1/3
agent$trait[agent$group == 2 & numAs == 1 & prob < (1/3 - D/3)] <- "A"
agent$trait[agent$group == 2 & numAs == 1 & prob >= (1/3 - D/3)] <- "B"

# store frequencies in output slot t
output$p[t] <- sum(agent$trait[agent$group == 1] == "A") / N
output$q[t] <- sum(agent$trait[agent$group == 2] == "A") / N

}

plot(x = 1:nrow(output), y = output$p,
      type = 'l',
      col = "orange",
      ylab = "proportion of agents with trait A",
      xlab = "generation", ylim = c(0,1),
      main = paste("N = ", N, ", m = ", m, ", D = ", D, sep = ""))

lines(x = 1:nrow(output), y = output$q, col = "royalblue")

legend("topright",
       legend = c("p (group 1)", "q (group 2)"),
       lty = 1,
       col = c("orange", "royalblue"),
       bty = "n")

```

```

    output # export data from function
}

```

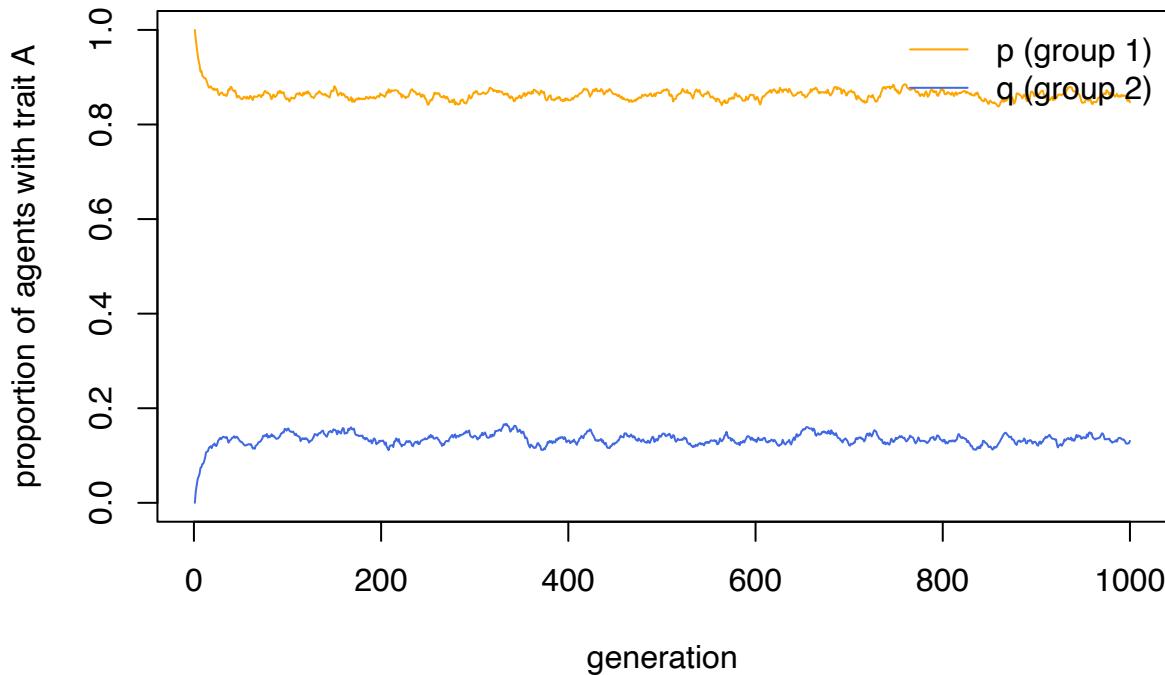
With a moderate amount of conformity, $D = 0.2$, i.e. a 20% chance of adopting the majority trait:

```

data_model7 <- MigrationPlusConformity(N = 10000,
                                         p_0 = 1,
                                         q_0 = 0,
                                         m = 0.05,
                                         D = 0.2,
                                         t_max = 1000)

```

N = 10000, m = 0.05, D = 0.2



Here again, conformist transmission - a form of cultural selection - maintains between-group cultural variation even in the face of migration. The difference to directly biased transmission is that we do not need to assume different environments or selection pressures in the two groups. Conformity works simply on the basis of the different frequencies of the traits in the different groups.

Summary of Model 7

Model 7 looked at how migration across group boundaries can break down between-group cultural variation to create a homogenous, undifferentiated mass culture where every group is culturally identical. While

globalisation via the mass media or global markets has perhaps been making real-life human societies more similar to one another in recent years, we can still discern culturally distinct societies across the world, marked by traits such as dress, language, religion, psychological characteristics, cuisine and so on. Prior to the invention of mass transit and mass communication, societies would have been even more distinct. Yet migration has been a constant fixture of our species since we dispersed across the world. How then can we reconcile the extensive between-group cultural variation of our species with this frequent migration?

We modelled two potential answers to this question, both forms of cultural selection. Where different traits are favoured in different groups, then directly biased transmission (see Model 3) can maintain between-group cultural variation even in the face of migration. Similarly, conformity (see Model 5) can maintain between-group cultural variation by causing migrants to adopt the majority trait in their new society. The latter works even for neutral, arbitrary traits, which may describe well many real-life group markers. Directly and conformist biased transmission can be seen as mechanisms of *acculturation*, which describes the cultural change that may occur as a result of migration. Given that psychological processes such as conformity are unique to cultural evolution, this may also be an explanation for why there is a lot more between-group cultural variation in our species than there is between-group genetic variation (for further details and data on migration, conformity and between-group cultural variation, see Henrich & Boyd 1998; Bell et al. 2009; Mesoudi 2018; Deffner et al. 2020).

The major programming innovation in Model 7 was the introduction of two groups of agents. This allows us to simulate migration between groups, as well as processes that are likely to occur predominantly within groups such as conformity. There are many ways of extending Model 7, including adding more groups, adding non-random migration, using measures like FST to quantify the amount of between-group cultural variation, making the cultural traits cooperative / non-cooperative rather than neutral, and modelling other processes that might maintain variation such as punishment (see Mesoudi 2018).

Exercises

1. Try different values of m , p_0 and q_0 in the **Migration** function to confirm that migration causes groups to converge on the initial mean frequency of trait A across all groups, i.e. $(p_0 + q_0)/2$.
 2. Try different values of m and s in **MigrationPlusBiasedTransmission**, and m and D in **MigrationPlusConformity**, to explore how strong s and D need to be relative to m to prevent population homogenisation.
 3. Add a third group of N agents. As before, m is the probability that each agent moves to a random group. Where before there were two groups to randomly select, now there are three. Show that migration still causes convergence on the initial mean frequency of trait A across all three groups.
 4. Change the function to allow a user-defined number of groups. The function should take the number of groups as a parameter, and create this number of groups on-the-fly. Either allow the user to specify the starting frequencies of A across all groups (e.g. by having a parameter that can take sets of values such as $c(0.3, 0.5, 0.8, 0.9)$), or make the starting values random. Show that migration still causes convergence on the initial mean frequency of trait A across all groups.
 5. Make migration non-random, such that agents are more likely to migrate to groups that have a higher frequency of trait A . How do the dynamics of non-random migration compare to those of the random migration simulated in the original **Migration** function?
-

Analytic Appendix

Let's derive the recursions and equilibrium frequency for the basic migration model, to understand analytically why the frequency of A in each group converges on the initial average frequency of A across the two groups.

Recall that the frequency of A in generation t in the first group is p_t and in the second group is q_t . The frequency of A in the previous generation is denoted p_{t-1} and q_{t-1} respectively, and in the first generation it is p_0 and q_0 respectively. Let's consider group 1 first. We want to write an expression for p_t , in terms of p_{t-1} , the migration rate m , and any other parameter that is necessary.

In generation t , $1 - m$ individuals in group 1 do not migrate. The frequency of A amongst these $1 - m$ individuals will therefore be the same as in the previous generation in group 1, i.e. p_{t-1} . This gives an overall frequency for these group 1 non-migrants of $p_{t-1}(1 - m)$.

The other m individuals in group 1 are migrants. These migrants are drawn from the entire population, which in this case is groups 1 and 2 combined. The frequency of A in the entire population is the average frequency of A across the two groups, which we will denote \bar{x} . The frequency of A amongst the m migrants in generation t in group 1 will therefore be $\bar{x}m$. What is the value of $\bar{x}m$? Because there is no mutation or drift in this model, new A s never appear, and existing A s never disappear, when considering the entire population. Hence the total frequency of A in the entire population will always remain the same, from the first generation to the last. This will be $\bar{x} = (p_0 + q_0)/2$, i.e. the average frequency of A across the two groups in the first generation. This means that \bar{x} is a constant, i.e. it never changes from one generation to the next.

Putting these together, the frequency of A in generation t in group 1, p_t , will be

$$p_t = p_{t-1}(1 - m) + \bar{x}m \quad (7.1)$$

Equivalently, the frequency of A in generation t in group 2, q_t , will be

$$q_t = q_{t-1}(1 - m) + \bar{x}m \quad (7.2)$$

Now we have two recursions, and we can plot them.

```
MigrationRecursion <- function(m, t_max, p_0, q_0) {
  p <- rep(0,t_max)
  p[1] <- p_0

  q <- rep(0,t_max)
  q[1] <- q_0

  for (i in 2:t_max) {
    x_bar <- (p[i-1] + q[i-1]) / 2

    p[i] <- p[i-1]*(1-m) + x_bar*m
    q[i] <- q[i-1]*(1-m) + x_bar*m
  }

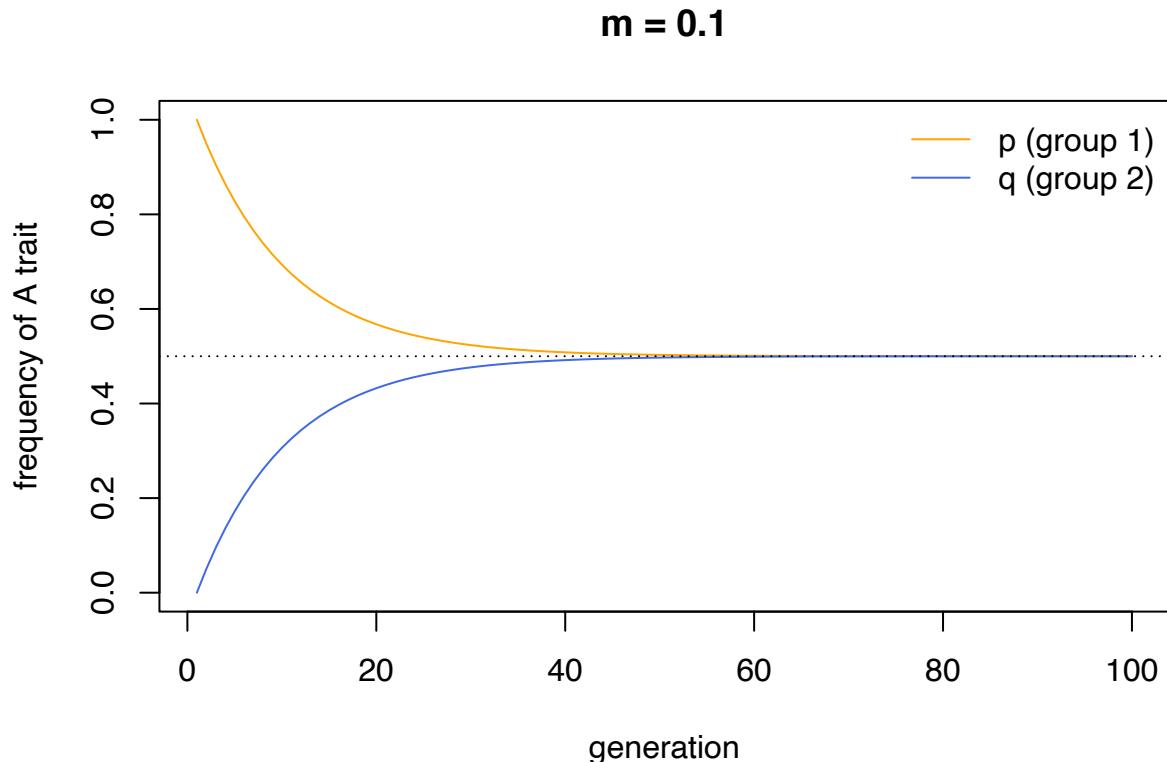
  plot(x = 1:t_max, y = p,
        type = "l",
        ylim = c(0,1),
        ylab = "frequency of A trait",
        xlab = "generation",
```

```

    col = "orange",
    main = paste("m = ", m, sep = ""))
lines(x = 1:t_max, y = q, col = "royalblue")
abline(h = (p_0 + q_0) / 2, lty = 3)
legend("topright",
       legend = c("p (group 1)", "q (group 2)" ),
       lty = 1,
       col = c("orange", "royalblue"),
       bty = "n")
}

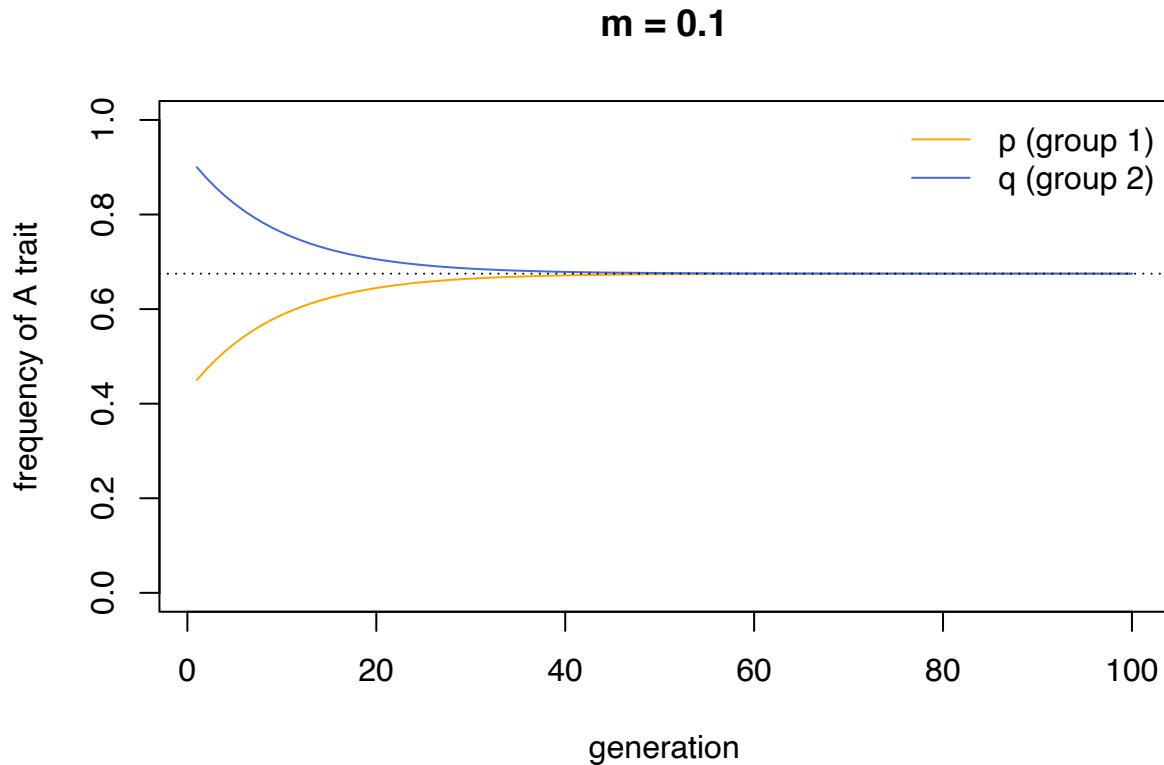
MigrationRecursion(m = 0.1, t_max = 100, p_0 = 1, q_0 = 0)

```



This looks almost identical to the first plot we created above from the simulations. I added a dotted line denoting the initial mean frequency of A in the entire population, \bar{x} , to verify that the two groups converge on this mean. We can change the starting values to provide a further check:

```
MigrationRecursion(m = 0.1, t_max = 100, p_0 = 0.45, q_0 = 0.9)
```



To understand better why this convergence occurs, we need to solve these recursions. Hartl & Clark (1997, p.168) provide a trick for solving such equations, where the recursion can be expressed in the form $p_t - X = (p_{t-1} - X)Y$, where X and Y are constants. Rearranging this expression gives $p_t = p_{t-1}Y - XY + X = p_{t-1}Y - X(Y + 1)$. This fits equation 7.1 if we say that $Y = 1 - m$ and $X = \bar{x}$. Hence we can rewrite equation 7.1 as:

$$p_t - \bar{x} = (p_{t-1} - \bar{x})(1 - m) \quad (7.3)$$

Because the relation between p_{t-1} and p_{t-2} is the same as that between p_t and p_{t-1} , all the way back to p_0 , the solution to equation 7.3 is

$$p_t - \bar{x} = (p_0 - \bar{x})(1 - m)^t \quad (7.4)$$

After many generations, when t becomes very large, then the last term on the right which is raised to the power of t will be approximately zero. Even if m is very small, and $(1 - m)$ is very close to 1, any number less than 1 raised to a large power (i.e. multiplied by itself many times) will be approximately zero. Consequently the whole right hand side of equation 7.4 becomes zero, and p_t remains the same generation after generation. So we can set the right-hand side of equation 7.4 to zero and rearrange to find this equilibrium value, p^* :

$$p^* = \bar{x} \quad (7.5)$$

And as we noted at the beginning, $\bar{x} = (p_0 + q_0)/2$, i.e. the average of the two starting frequencies of A in the two groups. This is what we found in the agent-based simulations as well as the recursion simulations in this section.

References

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Simulation Models of Cultural Evolution in R

Alex Mesoudi

Model 8: Blending inheritance

When Darwin wrote *The Origin of Species*, it was typically thought that biological inheritance involved the blending of parental traits. For example, the offspring of a tall and a short individual would have intermediate height, the average (or blend) of its two parents. This presented a problem for Darwin's theory, one which Darwin himself acknowledged. If traits blend together, then they are unlikely to persist for long enough for selection to act on them. All traits will quickly converge on a blended average, destroying the variation that is necessary for evolution.

This puzzle was resolved when Mendel's famous pea plant experiments were rediscovered around the turn of the 20th century. These showed that genetic inheritance is actually particulate, not blending. This means that inheritance involves the passing of discrete particles of information - what became known as 'genes' - in an all-or-nothing fashion from parent to offspring. Some simple phenotypic traits, like Mendel's pea plant varieties, show this directly. A white plant crossed with a purple plant gives rise to either a white or purple offspring, not a blend. Complex phenotypic traits like human height, which appear to 'blend' in offspring, are actually determined by many discrete genes.

A common objection to cultural evolution follows similar lines. Cultural traits, it is argued, are often continuous, and appear to blend in learners. Someone who grew up in Britain before moving to the States might have a blended 'transatlantic' accent. Someone with a liberal father and conservative mother might end up with moderate political views. If cultural inheritance is blending, then the same objection as that levied at Darwin above should also apply: variation will be rapidly lost, and evolution can't operate. This is a common specific criticism of memetics, which assumes that there are discrete particles of inheritance analogous to genes.

One problem with this objection is that it is not at all clear that cultural inheritance *is* blending. We don't know enough about how brains store and receive information to say with certainty that there is not a discrete, particulate inheritance system underlying what appears to be blending at the 'phenotypic' level, just like biological traits such as height appear to blend but are actually determined by an underlying particulate inheritance system. Another problem is that the objection cannot be true: there is huge cultural variation in the world that patently does exist, and upon which selection can and does act. So even if cultural inheritance is blending, perhaps some other feature of cultural evolution means that blending does not have the problematic consequences described above. Either way, it is worth exploring the case of blending inheritance with formal models to go beyond verbal arguments. Indeed, it was not until the formal population genetic models of R.A. Fisher and others in the early 20th century that Mendelian genetic inheritance and Darwinian evolution were definitively shown to be consistent with one another.

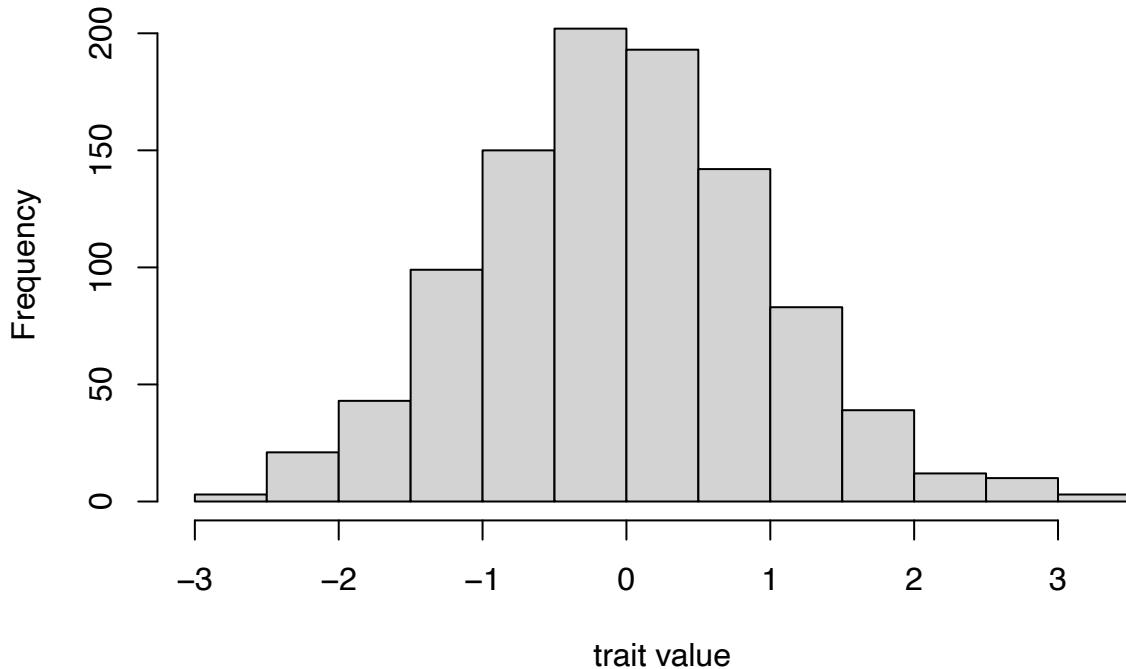
Model 8a

In Model 8a we will simulate blending cultural inheritance, inspired by a formal mathematical model presented by Boyd & Richerson (1985). We assume a population of N individuals. Each of these individuals possesses a value of a continuously varying cultural trait. While previous models have assumed discrete traits that can take on one of two forms (A or B), in this case we are modelling a trait that can take any value on a continuous scale. Many cultural traits are continuous, from handaxe length to political orientation.

In the first generation / timestep, we assume that trait values are drawn randomly from a standard normal distribution. This is a symmetrical, bell-shaped distribution with mean 0 and standard deviation 1. It does not really matter what distribution or parameter values we use here. However, lots of naturally-occurring cultural traits are normally distributed. We might think of political orientation, where some people are on the extreme left or extreme right, and most are somewhere in the middle.

The **rnorm** command generates random numbers from this standard normal distribution, like this:

```
N <- 1000
values <- rnorm(N)
hist(values, main = "", xlab = "trait value")
```



Hence this will be our initial distribution of trait values in the first generation. Then, in each new generation the N individuals are replaced with N new individuals. Each of these new agents picks n agents from the previous timestep at random and adopts the mean trait value of these n demonstrators. We assume that $n > 1$ because we cannot really take a blended mean of a single trait value, and we assume that $n \leq N$ because learners can only learn from a previous generation agent once.

In each timestep we track the mean trait value to see whether blending inheritance generates directional cultural change. We also track the variance of the trait across the entire population, in order to see whether and when blending inheritance destroys variation as per the objection above.

Below I have taken the skeleton of Model 1's **UnbiasedTransmission** function, which has multiple independent runs and keeps track of and plots mean trait frequency, and adapted it to create a **BlendingInheritance** function. Examine the code before reading the explanation of the changes afterwards.

```

BlendingInheritance <- function (N, n, t_max, r_max) {

  # create a matrix for trait means with t_max rows and r_max columns,
  # fill with NAs, convert to dataframe
  trait_mean <- as.data.frame(matrix(NA, t_max, r_max))

  # purely cosmetic: rename the columns with run1, run2 etc.
  names(trait_mean) <- paste("run", 1:r_max, sep="")

  # same for holding trait variance
  trait_var <- as.data.frame(matrix(NA, t_max, r_max))
  names(trait_var) <- paste("run", 1:r_max, sep="")

  for (r in 1:r_max) {

    # create first generation, N random numbers from a standard normal distribution
    agent <- rnorm(N)

    # add first generation's mean to first row of column r
    trait_mean[1,r] <- mean(agent)

    # add first generation's variance to first row of column r
    trait_var[1,r] <- var(agent)

    for (t in 2:t_max) {

      # create matrix with N rows and n columns,
      # fill with traits from random members of agent
      m <- matrix(sample(agent, N*n, replace = TRUE), N, n)

      # create new generation by taking rowMeans, i.e. mean of n demonstrators,
      # to implement blending inheritance
      agent <- rowMeans(m)

      # get mean trait value and put it into output slot for this generation t and run r
      trait_mean[t,r] <- mean(agent)

      # get trait variance and put it into output slot for this generation t and run r
      trait_var[t,r] <- var(agent)

    }

  }

  # create two plots, one for means and one for variances
  par(mfrow=c(1,2)) # 1 row, 2 columns

  # plot a thick line for the mean mean of all runs
  plot(rowMeans(trait_mean),
        type = 'l',
        ylab = "trait mean",
        xlab = "generation",
        ylim = c(min(trait_mean,-1), max(trait_mean,1)),

```

```

lwd = 3,
main = paste("N = ", N, " , n = ", n, sep = ""))
# add lines for each run, up to r_max
for (r in 1:r_max) {
  lines(trait_mean[,r], type = 'l')
}

# plot a thick line for the mean variance across all runs
plot(rowMeans(trait_var),
      type = 'l',
      ylab = "trait variance",
      xlab = "generation",
      ylim = c(0, max(trait_var)),
      lwd = 3,
      main = paste("N = ", N, " , n = ", n, sep = ""))
# add lines for each run, up to r_max
for (r in 1:r_max) {
  lines(trait_var[,r], type = 'l')
}

# export data from function
list(final_agent = agent, mean = trait_mean, variance = trait_var)
}

```

First, rather than a single *output* dataframe, we create two, one called *trait_mean* to hold the mean trait value over all timesteps for all runs, and one called *trait_variance* to hold the variance of the trait over all timesteps and all runs. Then, in each run, we create an initial population which has N agents each with a trait value drawn randomly from a standard normal distribution using the **rnorm** command, as shown above. We then record the initial mean and variance in the appropriate slots of *trait_mean* and *trait_variance* respectively.

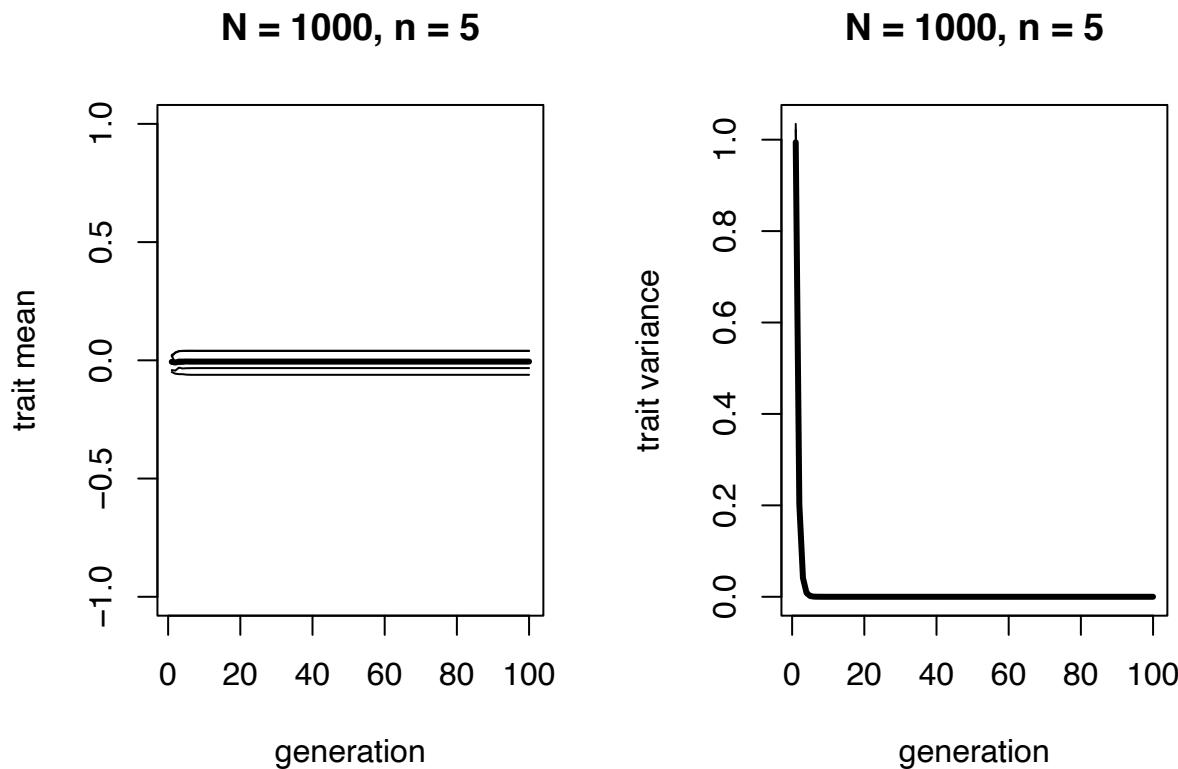
Within the timestep loop, we then create a matrix with N rows and n columns, and fill it with trait values from agents randomly selected using the **sample** command. Each row here represents a new agent, and each column of that row contains the trait values of n randomly chosen demonstrators, just like for horizontal transmission in Model 6c. We then use the **rowMeans** command to get the means of each row of this matrix. This is the blending inheritance rule. This mean (or blend) of the n demonstrators is put into the *agent* dataframe, over-writing the previous generation's traits, and the new mean and variance are added to the output dataframes.

The subsequent plotting code now makes two plots side-by-side, one for the means and one for the variances. This is done with the **par(mfrow([rows],[cols]))** command, where [rows] is the number of rows and [cols] the number of columns. Here I've set one row and two columns. The actual plots use the same code as in previous models, with means across all runs plotted with thick lines and separate lines for each run. We do this twice, once for means, and once for variances.

Finally, rather than outputting a single dataframe, we now output three dataframes after the function is run: the *final_agent* dataframe, which allows us to explore the distribution of trait values at the very end of the simulation, and the *trait_mean* and *trait_variance* dataframes which contain the means and variances. We do this by exporting a list, which contains three dataframes.

Let's run this function with a reasonably large N and small n :

```
data_model8 <- BlendingInheritance(N = 1000,
                                    n = 5,
                                    t_max = 100,
                                    r_max = 5)
```



The left-hand plot shows that the mean across all runs remains at roughly 0, which is the mean of the initial standard normal distribution. Blending inheritance does not change mean trait value over time. It is non-directional, just like unbiased mutation or unbiased transmission. This is to be expected, as all we are doing is taking the mean of random draws from the previous generation's trait distribution, which will be the same as the mean in the previous generation.

The right-hand plot shows that the variance quickly drops to zero. Again as we expected, blending inheritance acts to reduce variation to zero. We can confirm this by displaying some of the values of the final agent dataframe, to confirm that every agent has exactly the same trait:

```
head(data_model8$final_agent)

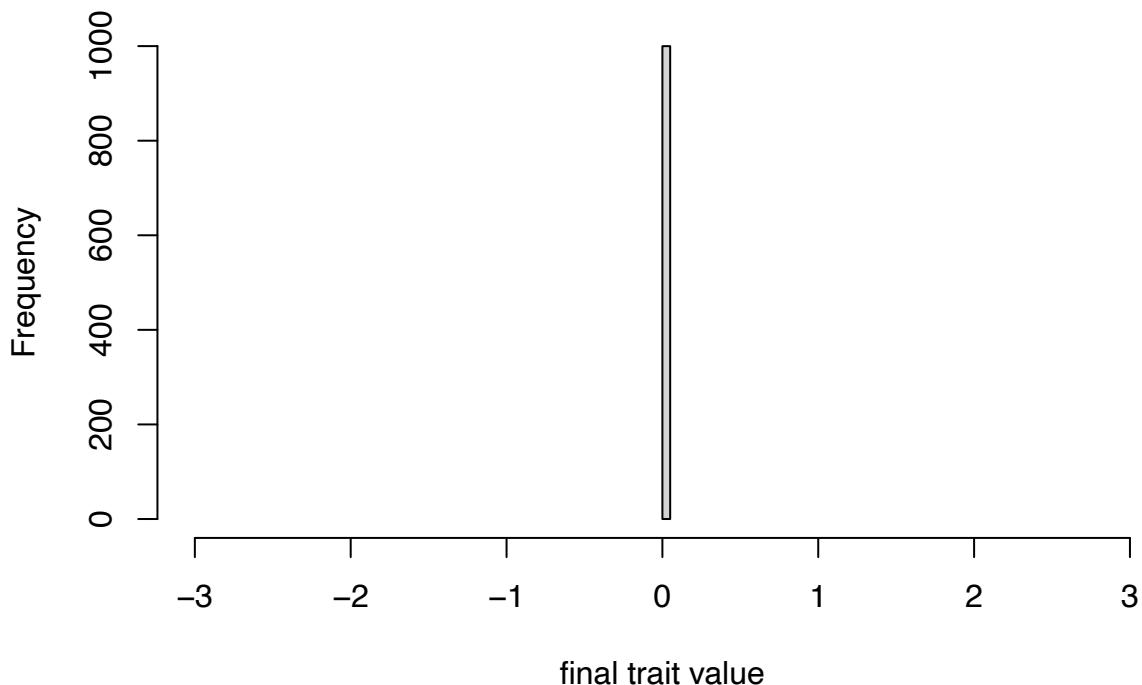
## [1] 0.04055885 0.04055885 0.04055885 0.04055885 0.04055885 0.04055885

tail(data_model8$final_agent)

## [1] 0.04055885 0.04055885 0.04055885 0.04055885 0.04055885 0.04055885
```

We can also plot the final trait distribution on the same scale as the graph above showing the initial standard normal distribution, confirming that all of the initial variation has been lost.

```
hist(data_model8$final_agent, xlim = c(-3,3), main = "", xlab = "final trait value")
```



Model 8b

All we have done so far is confirm the intuition that blending inheritance destroys variation, just as Darwin's critics originally argued. If we assume that cultural traits in real life blend (which, as noted above, is far from certain), then it is hard to reconcile this conclusion with the observation of extensive cultural variation in real life.

However, we must remember that other aspects of cultural evolution may also differ from genetic evolution. Boyd & Richerson (1985) pointed out that blending inheritance is potentially problematic in biological evolution because rates of genetic mutation are low, and so cannot replenish the variation that blending inheritance destroys. Yet rates of cultural mutation may be much higher. In Model 8b we will follow their example and add unbiased cultural mutation, or copying error, to the blending inheritance model.

Previously we assumed that new agents could copy the traits of n agents from the previous timestep with no error, and then take the mean of these 100% accurate trait values. Now we assume that each of the n cultural traits are copied with some error, similar to unbiased cultural mutation in Model 2. So before the blended mean is taken, random error is added to each copied trait value.

We do this by again using the **rnorm** command to draw randomly from a normal distribution. This time, the normal distribution has a mean of the copied trait values, which are stored in the m matrix, and the random error or deviation is introduced to each one using a new parameter e . This is the variance of this normal distribution. The larger is e , the more error or mutation there is in the estimates of each of the n traits. Note that each of the n copied traits are subject to independent error. Some might be copied quite

faithfully, others less faithfully. Blending inheritance then proceeds as before, but now it is the mean of the modified trait values.

The following code modifies the **BlendingInheritance** function above by adding a parameter e , and adding a line after the trait copying in which the m matrix is modified according to e . Note that because e is the variance of the error distribution (following Boyd & Richerson 1985), and the **rnorm** function takes a standard deviation, we need to give the function the square root of e . We also add e to the plot title.

```
BlendingInheritance <- function (N, n, e, t_max, r_max) {

  # create a matrix for trait means with t_max rows and r_max columns,
  # fill with NAs, convert to dataframe
  trait_mean <- as.data.frame(matrix(NA, t_max, r_max))

  # purely cosmetic: rename the columns with run1, run2 etc.
  names(trait_mean) <- paste("run", 1:r_max, sep="")

  # same for holding trait variance
  trait_var <- as.data.frame(matrix(NA, t_max, r_max))
  names(trait_var) <- paste("run", 1:r_max, sep="")

  for (r in 1:r_max) {

    # create first generation, N random numbers from a standard normal distribution
    agent <- rnorm(N)

    # add first generation's mean to first row of column r
    trait_mean[1,r] <- mean(agent)

    # add first generation's variance to first row of column r
    trait_var[1,r] <- var(agent)

    for (t in 2:t_max) {

      # create matrix with N rows and n columns,
      # fill with traits from random members of agent
      m <- matrix(sample(agent, N*n, replace = TRUE), N, n)

      # add random error to each demonstrator value, with variance e
      m <- matrix(rnorm(N*n, mean = m, sd = sqrt(e)), N, n)

      # create new generation by taking rowMeans, i.e. mean of n demonstrators,
      # to implement blending inheritance
      agent <- rowMeans(m)

      # get mean trait value and put it into output slot for this generation t and run r
      trait_mean[t,r] <- mean(agent)

      # get trait variance and put it into output slot for this generation t and run r
      trait_var[t,r] <- var(agent)

    }

  }

}
```

```

# create two plots, one for means one for variances
par(mfrow=c(1,2)) # 1 row, 2 columns

# plot a thick line for the mean mean of all runs
plot(rowMeans(trait_mean),
      type = 'l',
      ylab = "trait mean",
      xlab = "generation",
      ylim = c(min(trait_mean,-1), max(trait_mean,1)),
      lwd = 3,
      main = paste("N = ", N, ", n = ", n, ", e = ", e, sep = ""))

# add lines for each run, up to r_max
for (r in 1:r_max) {
  lines(trait_mean[,r], type = 'l')
}

# plot a thick line for the mean variance across all runs
plot(rowMeans(trait_var),
      type = 'l',
      ylab = "trait variance",
      xlab = "generation",
      ylim = c(0, max(trait_var)),
      lwd = 3,
      main = paste("N = ", N, ", n = ", n, ", e = ", e, sep = ""))

# add lines for each run, up to r_max
for (r in 1:r_max) {
  lines(trait_var[,r], type = 'l')
}

# export data from function
list(final_agent = agent, mean = trait_mean, variance = trait_var)
}

```

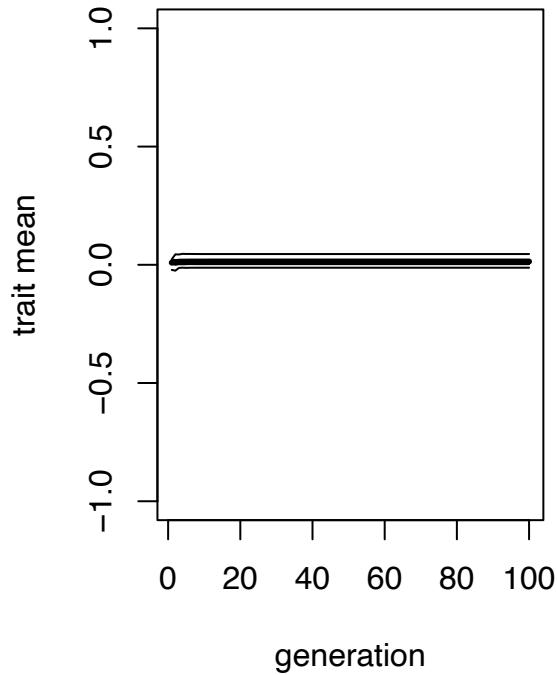
First we can run this code with $e = 0$, to confirm that this matches the original function which had no error.

```

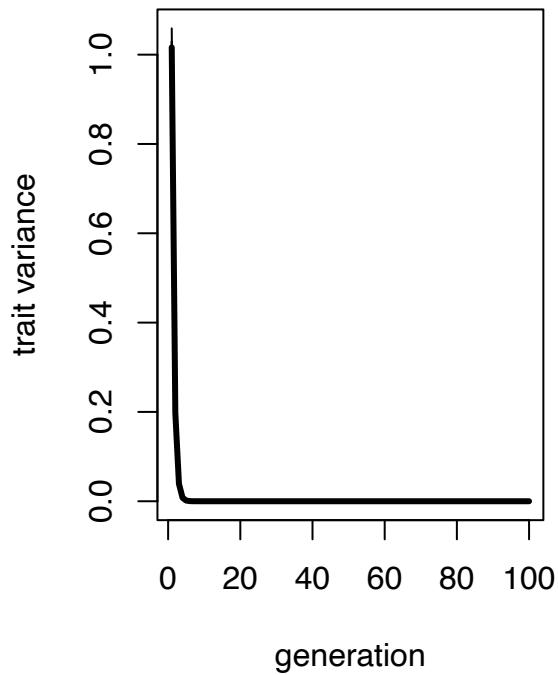
data_model8 <- BlendingInheritance(N = 1000,
                                    n = 5,
                                    e = 0,
                                    t_max = 100,
                                    r_max = 5)

```

N = 1000, n = 5, e = 0



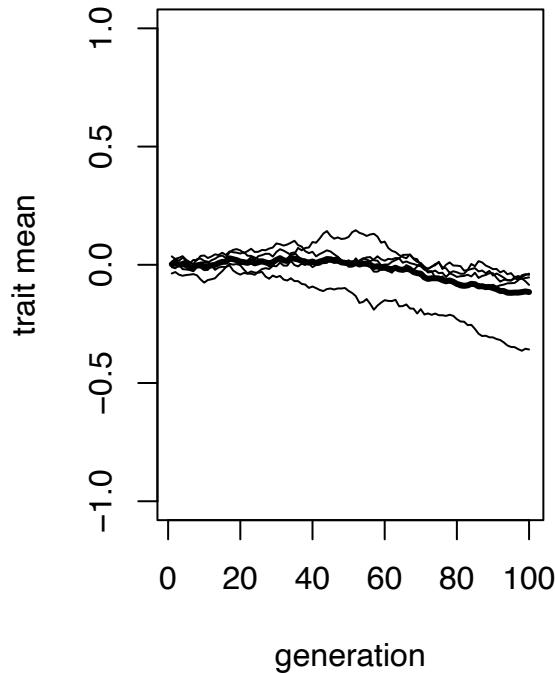
N = 1000, n = 5, e = 0



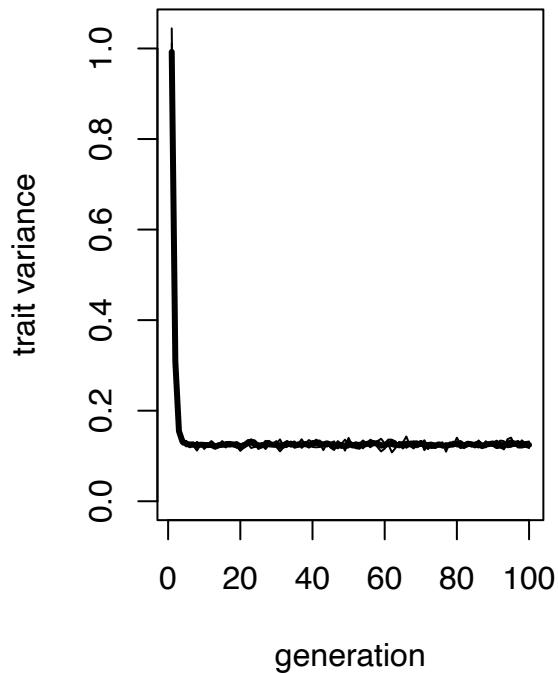
As before, the mean does not change, and variation decreases to zero. Now let's increase e :

```
data_model8 <- BlendingInheritance(N = 1000,  
                                    n = 5,  
                                    e = 0.5,  
                                    t_max = 100,  
                                    r_max = 5)
```

N = 1000, n = 5, e = 0.5



N = 1000, n = 5, e = 0.5



There are two changes here. First, in the left hand plot we can see that while the mean of the mean trait value still does not change and remains around zero, there is more variation around this line in the different runs. Consistent with this, the right hand plot shows that while the variance still drops, it does not drop to zero. For $n = 5$ and $e = 0.5$, the variance converges on around 0.125. We can see this more exactly by displaying the mean variances for each run over the last 50 timesteps (to avoid the initial value from skewing the estimate):

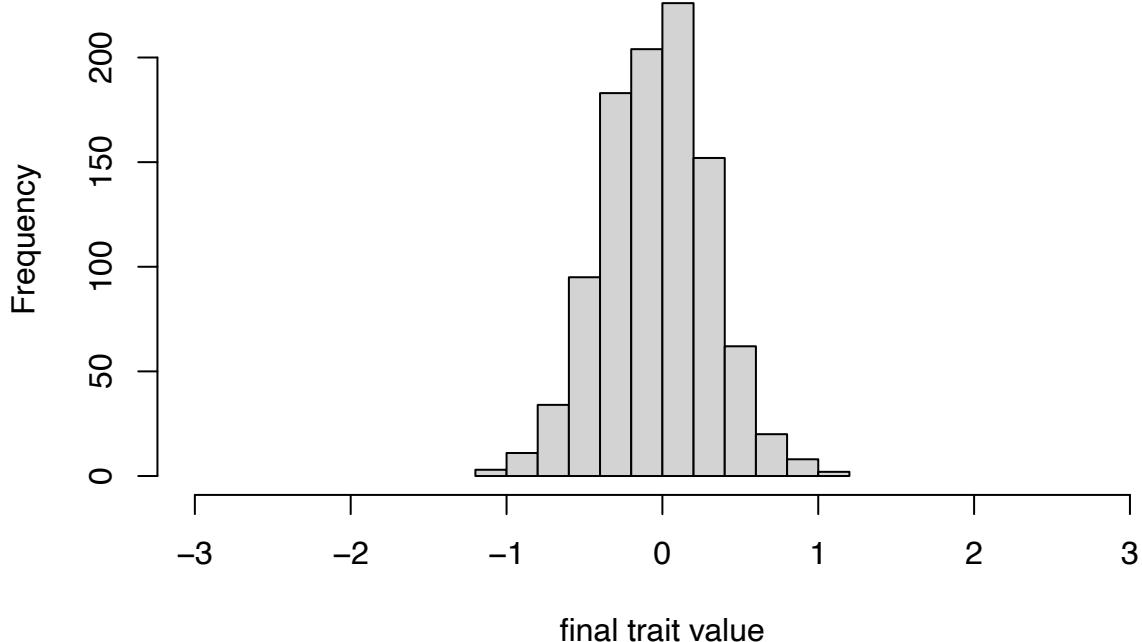
```
colMeans(data_model18$variance[50:100,])
```

```
##      run1      run2      run3      run4      run5
## 0.1266282 0.1250990 0.1255381 0.1254876 0.1238542
```

Try playing around with n and e to show that the equilibrium amount of variance increases as e increases and as n decreases. In the analytical appendix we will see how to calculate this equilibrium value from n and e .

Finally, we can plot the trait distribution in the final generation.

```
hist(data_model8$final_agent, xlim = c(-3,3), main = "", xlab = "final trait value")
```



While the first plot above showed that the initial distribution ranged from around -3 to 3, this final distribution ranges from around -1 to 1. So while there is less variation than in the first generation, there is still variation, and it still resembles a normal distribution.

Summary of Model 8

A common objection to cultural evolution is that cultural inheritance blends different traits together, destroying the variation that is necessary for evolution to operate. While the claim that cultural inheritance is blending can be contested, and obviously it is not the case that there is no cultural variation in the real world, we can still use formal models to explore these claims.

Model 8a confirmed that blending inheritance destroys variation, as expected. However, Model 8b showed that this can be countered by cultural mutation. While genetic mutation is very infrequent, cultural mutation is probably much more common. People typically misremember facts, distort stories, and modify tools as they attempt to copy others. So even if cultural inheritance does take the form of blending, it is quite plausible that cultural mutation is potent enough to re-introduce variation that blending destroys. While we did not model this here, a similar argument can be made for cultural selection. While natural selection tends to be weak, cultural selection may be much stronger. So even if blending inheritance reduces variation, strong cultural selection can still act before the variation is depleted.

There are also a few programming innovations introduced in Model 8. We modelled a continuously varying cultural trait, rather than a discrete trait that could take one of two values as in previous models. This means we had to specify the distribution of the continuous trait, and track the mean and variance of that distribution, rather than a trait frequency. We used the command **rnorm** to draw random trait values from a normal distribution in order to create the initial generation's trait values. We also used **rnorm** to simulate random error or mutation in the transmission of the continuous trait. The copied trait value is set as the mean of the normal distribution, with the error around this value set by the standard deviation (or variance) of the normal distribution. Finally, we saw how to create two plots side-by-side using the **par(mfrow=c([rows],[cols]))** command.

Exercises

1. Try different values of N and n in **BlendingInheritance** to see how blending inheritance reduces variation to zero whenever $n > 1$.
 2. Try different values of n and e to show that the former increases the blending effect, and the latter reduces it.
 3. Forgetting about blending for now, combine Models 3 and 8 to create a function that models selection (i.e. directly biased transmission, from Model 3) on a continuous cultural trait (as implemented in Model 8). Instead of s being the probability of switching to trait A upon encountering a demonstrator with that trait as in Model 3, instead assume that there is a particular value of the continuous trait that is particularly attractive, memorable or intuitive. Allow the user to set this value when calling the function. For example, it might be zero (the mean of the starting normal distribution), or a different value (say +3, or -2). Then, each agent picks a random member of the previous generation, and if the demonstrator's value is closer to the favoured value, and with probability s (as in Model 3), then the copying agent adopts the demonstrator's value. Otherwise they do not copy and retain their previous value. Run the simulation to see what happens to the mean and variance over time.
 4. Modify the function you just created to allow selection for two different trait values, rather than just one. Now, with probability s , each agent picks a random demonstrator from the previous generation, and if the demonstrator's value is closer to either of the two favoured values, then the agent adopts that closest value. Run the simulation to see what happens to the mean and variance over time.
 5. Add blending inheritance to the function you just created, using the code from Model 8. Use a parameter to switch blending on (e.g. $blend = \text{TRUE}$) or off (e.g. $blend = \text{FALSE}$). With $e = 0$, explore under what conditions selection (via s) prevents blending from destroying variation.
-

Analytic Appendix

The simulation model presented above recreates an analytical model presented in Chapter 3 of Boyd & Richerson (1985), and we replicate their conclusions. They also include assortative transmission, which has a similar effect to mutation: if the n demonstrators have similar cultural traits, then blending inheritance is less effective at reducing variation. Box 3.22 in Boyd & Richerson (1985) provides a proof that the mean trait value after blending inheritance, \bar{X}' , equals the mean trait value before blending inheritance, \bar{X} . Their equation 3.28 does the same for variance under the assumption of transmission error, where variance after blending inheritance, V' , is given by:

$$V' = (1/n)(V + \bar{E}) \quad (8.1)$$

where \bar{E} is the mean value of e across all demonstrators, and e is defined as in the simulation model. Because e is a constant across all demonstrators, and the errors are independent, \bar{E} will equal e . To get the equilibrium variance, \hat{V} , we can set $V' = V$ in the above equation and rearrange to find:

$$\hat{V} = \frac{e}{n - 1} \quad (8.2)$$

For the $e = 0.5$ and $n = 5$ simulated above, this gives $\hat{V} = 0.5/4 = 0.125$, as was found in the simulation. This equation confirms that the variation remaining after blending inheritance increases with e and decreases with n .

References

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Simulation Models of Cultural Evolution in R

Alex Mesoudi

Model 9: Demography and cultural gain/loss

Demography refers to the study of populations: their size, structure, and movements in and out. We have already examined demography in previous models. This was most explicit in Model 7 where we looked at migration between two separate sub-populations. However, in all of the models so far, we have seen how small populations are more likely to lose traits purely by chance, while large populations have more stable dynamics that more closely match analytical models with infinite population sizes.

Here we will pursue this further by examining an influential model created by Henrich (2004) that links demography - specifically, population size, N - to cultural losses and cultural gains. Henrich (2004) did this in the context of an archaeological example. Around 12,000 years ago, Tasmania became cut off from the mainland of Australia due to rising sea levels. Upon first contact with European explorers, the Aboriginal Tasmanians had strikingly simple technology compared to the Aborigines of the mainland: they lacked bone tools, fishhooks, traps and nets, spearthrowers and boomerangs, all of which were used on the mainland. Henrich argued that this technological loss or stagnation was not because the Tasmanians were less smart or skilful than their mainland counterparts. Rather, it was because when they were cut off from the mainland their population size dropped dramatically. Tools such as fishhooks are hard to make, and subject to error. When there are few skilled fishhook-makers, fishhook technology is easily lost and unlikely to be reinvented. In large populations, however, there will be lots of skilled fishhook makers. Even if some forget or fail to pass on their fishhook-making skill, there will be others to carry on the tradition. This is an example of cumulative cultural evolution, where individuals acquire skills and knowledge from others that they could not invent on their own. While Henrich framed his model in the context of prehistoric Tasmania, we can generalise this principle to any case where hard-to-learn traits are dependent on population size.

Henrich (2004) used a simple model to explore this scenario of cultural loss due to small population size. We assume N individuals who each possess a value of a continuously varying, culturally transmitted skill (e.g. fishhook making). This skill is denoted z_i for individual i , where i ranges from 1 to N . Note that, technically, N is the ‘effective’ population size. This is the number of individuals who would be able to possess the trait in question. It may be less than the actual (‘census’) population size if, for example, infants or some other class of individual do not or cannot make fishhooks.

In each new generation, every individual copies the z value of the most highly skilled individual from the previous generation, denoted z_h . This is a form of biased transmission or cultural selection, similar to the payoff-based indirectly-biased transmission explored in Model 4. Here, demonstrators are preferentially selected based on their superior culturally-transmitted skill or knowledge.

If individuals perfectly copied the highest trait value from the previous generation, then the model would not be very interesting. It would also not be very realistic. Instead, we assume that this indirectly biased transmission is imperfect. It is imperfect in two ways. First, there is skill loss due to mistakes in the copying process. This always reduces the copier’s z value relative to the target z_h . Second, there are experiments, guesses and inferences. These sometimes result in worse skill, but sometimes better skill than the target z_h .

To formalise these two kinds of variation, Henrich (2004) assumed that naive learners’ skill z_i is drawn from a gumbel distribution. This is similar to the blending inheritance of Model 8 where we drew copied values from a normal distribution. A gumbel distribution is generated when extreme values are repeatedly picked.

This is what we are doing when we pick the highest-skilled demonstrator to learn from in each generation, so it is more appropriate than a normal distribution.

Unfortunately R does not provide built-in functions to work with gumbel distributions. However, we can write our own, using the formula for the probability density of the distribution. The following functions, `dgumbel` and `rgumbel`, generate the probability density and random draws for a gumbel distribution. I won't go into details on the formulae, but you can look them up if you want.

```
# probability density of the gumbel, for values x
# a is the mode, beta is the dispersion
# defaults to standard gumbel with a=0 and beta=1
dgumbel <- function(x, a = 0, beta = 1) {
  b <- (x - a)/beta
  (1/beta)*exp(-(b+exp(-b)))
}

# n random draws from a gumbel distribution with mode a and dispersion beta
# defaults to standard gumbel with a=0 and beta=1
rgumbel <- function(n, a = 0, beta = 1) {
  a + beta * (-log(-log(runif(n))))
}
```

Gumbel distributions take two parameters, a mode a and a dispersion β . Here is an example gumbel distribution, with additional labels showing Henrich's model parameters (recreating Fig 1 in Henrich 2004).

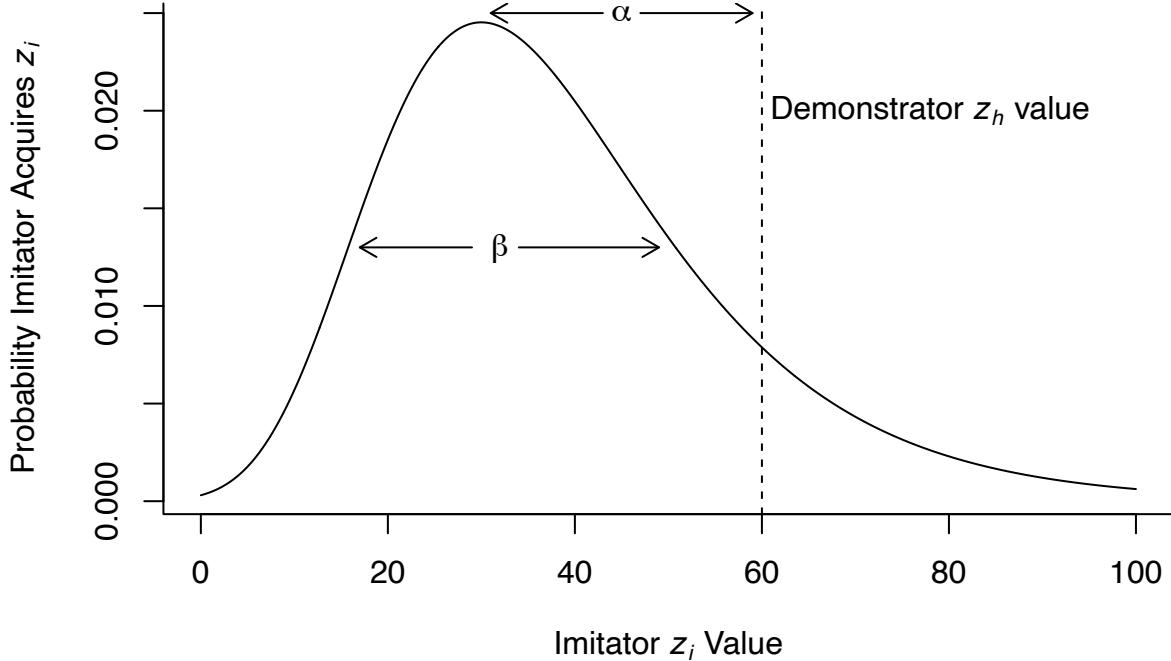
```
x <- seq(0,100,0.1) # x-axis values
a <- 30 # mode
beta <- 15 # dispersion

# plot gumbel distribution for the parameters defined above
plot(x, dgumbel(x, a, beta),
      type = 'l',
      ylab = expression("Probability Imitator Acquires " * italic("z"[i])),
      xlab = expression("Imitator " * italic("z"[i]) * " Value"),
      bty='1')

# add a vertical dotted line for the demonstrator with z_h
alpha <- 30
abline(v = a + alpha, lty=2)
text(a + alpha + 18, 0.02,
     labels = expression("Demonstrator " * italic("z"[h]) * " value"))

# add beta label and arrows
text(a+2, 0.013,
     labels = expression(beta))
arrows(a+4, 0.013, a+19, 0.013, length=0.1)
arrows(a-1, 0.013, a-13, 0.013, length=0.1)

# add alpha label and arrows
text(a+alpha/2, 0.025,
     labels = expression(alpha))
arrows(a+2+alpha/2, 0.025, a+14+alpha/2, 0.025, length=0.1)
arrows(a-2+alpha/2, 0.025, a-14+alpha/2, 0.025, length=0.1)
```



Notice how the gumbel distribution looks like an asymmetric normal distribution which is elongated at the upper end. This reflects the fact that we are sampling extreme high values. A demonstrator z_h value is shown on the plot with a dotted vertical line. This is the highest-skill value that the imitator is trying to copy. Their actual copied z_i value is drawn randomly from this gumbel distribution.

The α parameter determines the first kind of deviation described above, the transmission error. This is the difference between the demonstrator z_h value and the mode of the gumbel distribution (which is a - try not to confuse the mode a with the transmission error parameter α . It's not ideal notation, but I'll stick with it because that's what Henrich used. z_h is therefore $a + \alpha$). The larger is α , the further the mode will be below the z_h value, and the more likely the copied z_i value will be less than z_h .

The β parameter is the dispersion of the gumbel distribution, controlling the width. This represents the second kind of deviation described above, the inferential guesses or experiments. The larger is β , the more likely the copied z_i value will be different to the copied z_h value. Occasionally, the copied z_i value will be higher than the demonstrator z_h value. This occurs with probability equal to the area under the curve to the right of the dotted vertical line, in the extreme right-hand tail of the distribution. The larger is β , the larger this area will be. So while α always makes copied values worse than z_h , β increases the chances that copied values will occasionally exceed z_h .

Let's simulate this model to confirm this, and find out when the mean skill in the population \bar{z} increases, representing cultural gain, and when it decreases, representing cultural loss.

The following function follows the structure of previous models. After repeating the `rgumbel` function definition from above (just to make sure that this function is defined, and make **DemographyModel** self-contained), first we set up an output dataframe. In this case the output dataframe needs to store the mean trait value \bar{z} in each generation from 1 to t_{max} . Then we set up the agent dataframe: each of N agents' initial trait value is randomly drawn from a gumbel distribution with mode 0 and dispersion β . After storing the first generation mean trait value, we start cycling through generations. Each generation, we find the

maximum skill value for the current generation z_h , then draw N new agents from a gumbel distribution with mode $z_h - \alpha$ and dispersion β as per the figure above and using `rgumbel`. Each generation we store the new mean trait value, before plotting them all at the end and outputting the data from the function. Note the use of `expression()` in the plot axis labels; this allows us to use italics, subscripts and bars in the plot text.

```
DemographyModel <- function(N, alpha, beta, t_max) {

  rgumbel <- function(n, a = 0, beta = 1) {
    a + beta * (-log(-log(runif(n))))
  }

  # create output dataframe to hold mean trait value for each generation
  output <- data.frame(z_bar = rep(NA, t_max))

  # create 1st generation, N random draws from a gumbel with mode a=0 and dispersion beta
  agent <- data.frame(trait = rgumbel(N, beta = beta))

  # store first generation trait mean
  output$z_bar[1] <- sum(agent$trait) / N

  for (t in 2:t_max) {

    # get highest skill from current generation
    z_h <- max(agent$trait)

    # draw new values
    agent$trait <- rgumbel(N, a = z_h - alpha, beta = beta)

    # store new mean trait value
    output$z_bar[t] <- sum(agent$trait) / N
  }

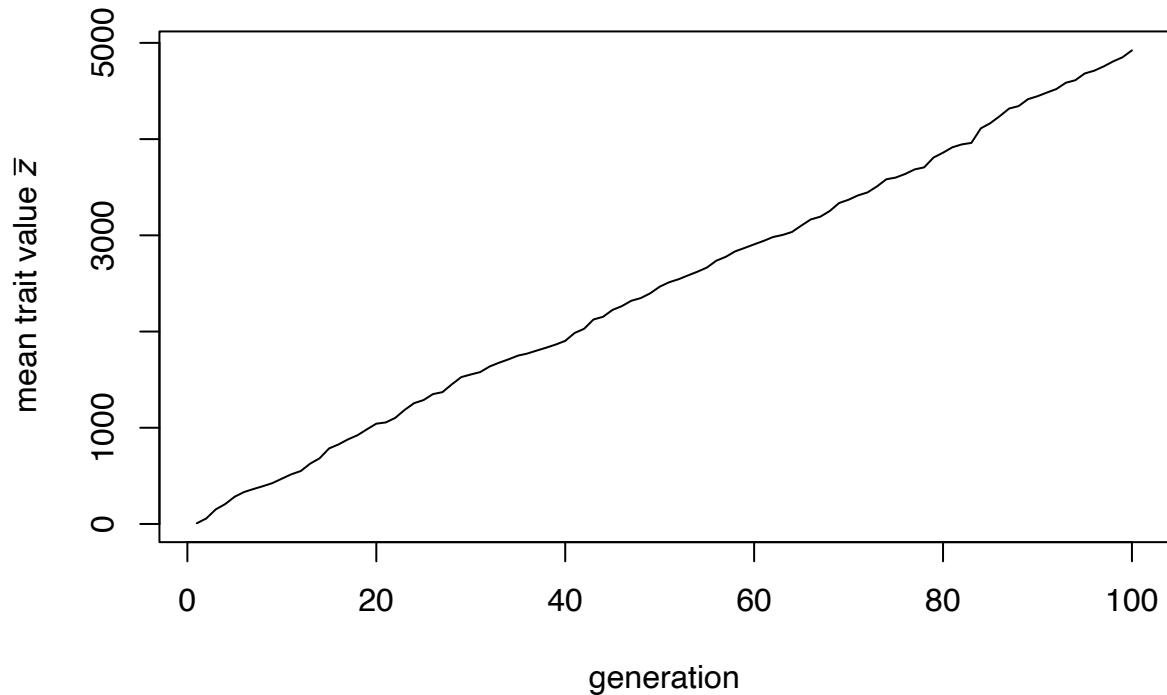
  plot(x = 1:nrow(output), y = output$z_bar,
        type = 'l',
        ylab = expression("mean trait value " * italic(bar("z"))),
        xlab = "generation",
        main = paste("N = ", N, ", alpha = ", alpha, ", beta = ", beta, sep = ""))
}

output
}
```

Let's run the demography model with the values of α and β used in the first figure above, and $N = 100$:

```
data_model9 <- DemographyModel(N = 100,
                                alpha = 30,
                                beta = 15,
                                t_max = 100)
```

N = 100, alpha = 30, beta = 15

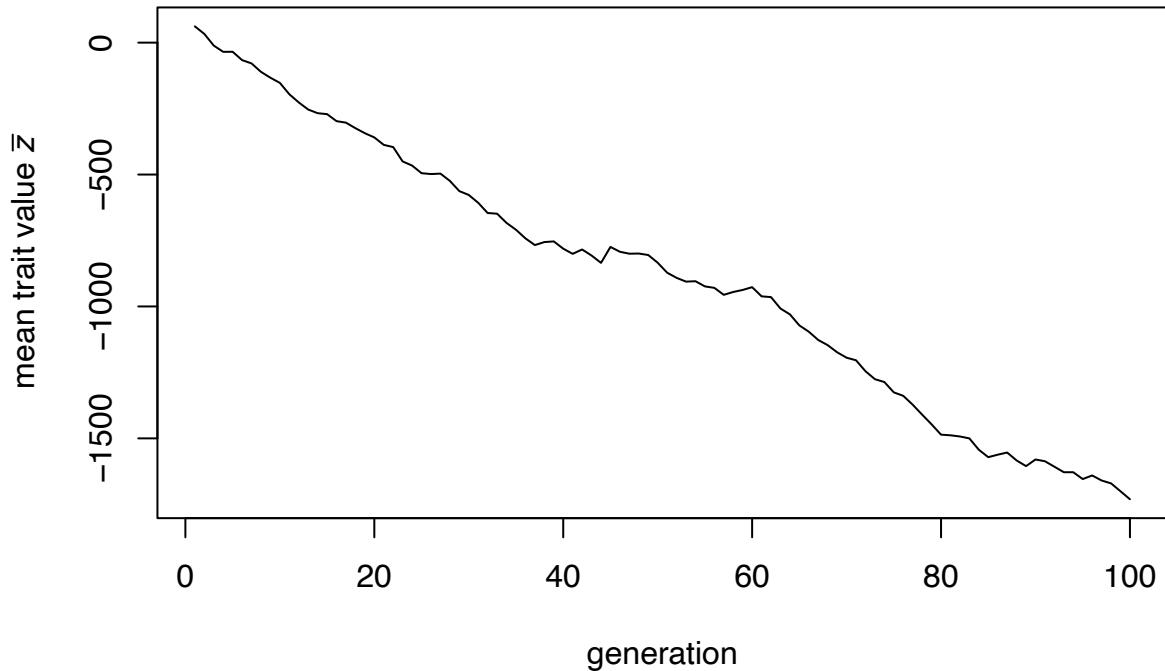


Here we can see that, for these parameter values, there is cultural gain: the mean trait value \bar{z} increases linearly over time.

Now let's try the smallest population size possible, $N = 1$:

```
data_model9 <- DemographyModel(N = 1,  
                                alpha = 30,  
                                beta = 15,  
                                t_max = 100)
```

N = 1, alpha = 30, beta = 15



Now there is cultural loss: the mean trait value \bar{z} decreases linearly over time.

Note that in both of these cases, trait values either increase indefinitely, or decrease indefinitely. Obviously this is unrealistic: at the least, there will be a minimum value ('zero skill') below which skills cannot fall. These upper and lower bounds are outside the scope of this model (although see Mesoudi 2011 for how to implement an upper bound, derived from the increasing costs of acquiring increasingly-complex traits). But the key aim of this model is not to realistically simulate actual cumulative cultural change, it is to identify qualitatively the parameter values - particularly population size - which lead to cultural gains and cultural losses.

Now that we know that there are usually only two outcomes of the model, linear cultural gain and linear cultural loss, we can switch our focus to a different outcome measure, $\Delta\bar{z}$. This is the change in mean trait value from one generation to the next. Because the change in \bar{z} is linear, $\Delta\bar{z}$ should be the same on average for all generations.

The following function runs the basic demography model for t_{max} generations across a range of values of N , from 1 to N_{max} . For each N , we record $\Delta\bar{z}$ in the output dataframe. This allows us to explore what values of N lead to cultural gain, i.e. $\Delta\bar{z} > 0$ and what values lead to cultural loss, i.e. $\Delta\bar{z} < 0$. Note that this function can take a long time to run when N_{max} is large. Consequently, there are a few tweaks to make it run as fast as possible. First, we ditch the dataframes and use simple vectors instead, for both *output* and *agent*. Vectors are faster than dataframes, and the latter are really not necessary with only a single measure and trait respectively. Second, rather than storing each $\Delta\bar{z}$ for each generation, we keep a running total and divide by t_{max} at the end of the loop. Finally, we remove the plot for now, and instead create plots from the output later on.

```
DemographyModel2 <- function(N_max, alpha, beta, t_max) {
  rgumbel <- function(n, a = 0, beta = 1) {
```

```

    a + beta * (-log(-log(runif(n))))
}

# create output dataframe to hold change in mean trait value for each N
output <- rep(0, N_max)

for (N in 1:N_max) {

  # create 1st generation, n random draws from a gumbel with mode a=0 and dispersion beta
  agent <- rgumbel(N, beta = beta)

  for (t in 1:t_max) {

    # current mean z
    z_bar <- sum(agent) / N

    # get highest skill from current generation
    z_h <- max(agent)

    # draw new values
    agent <- rgumbel(N, a = z_h - alpha, beta = beta)

    # add new delta_z_bar to total delta_z_bar for this n
    output[N] <- output[N] + sum(agent) / N - z_bar

  }

  # divide total delta_z_bar by t_max to get mean
  output[N] <- output[N] / t_max

}

output
}

```

Let's run this for $t_{max} = 50$ and $N_{max} = 5000$, and $\alpha = 7$ and $\beta = 1$. It might take a little while.

```

data_model9_1 <- DemographyModel2(N_max = 5000,
                                    alpha = 7,
                                    beta = 1,
                                    t_max = 100)

```

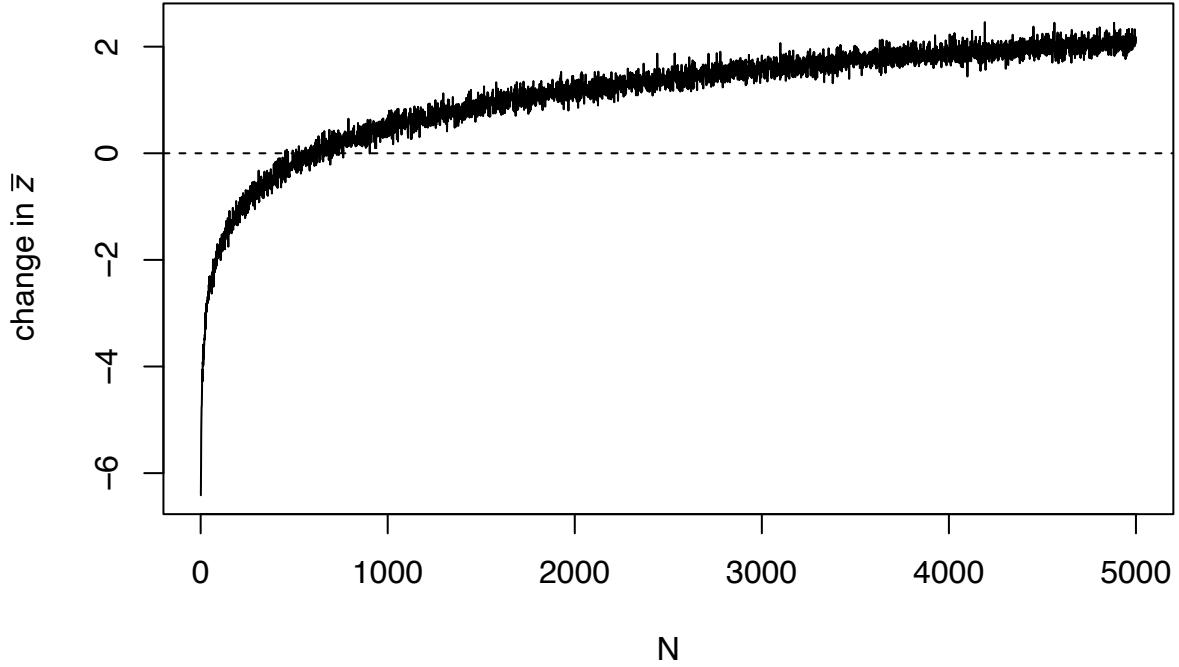
Now we can plot the results:

```

plot(1:length(data_model9_1), data_model9_1,
      type = 'l',
      ylab = expression("change in " * italic(bar("z"))),
      xlab = "N")

abline(h = 0, lty = 2)

```



This plot shows that as N increases, $\Delta\bar{z}$ flips from negative to positive. At low N there is cultural loss, at high N there is cultural gain. Note that there is some noise increasing the thickness of the line. This comes from the stochasticity of the simulation. The more generations we run, the less noise there is, but also the longer the simulation will take to run.

We can also run another pair of α and β and compare the two lines on the same plot:

```
data_model9_2 <- DemographyModel2(N_max = 5000,
                                    alpha = 9,
                                    beta = 1,
                                    t_max = 100)

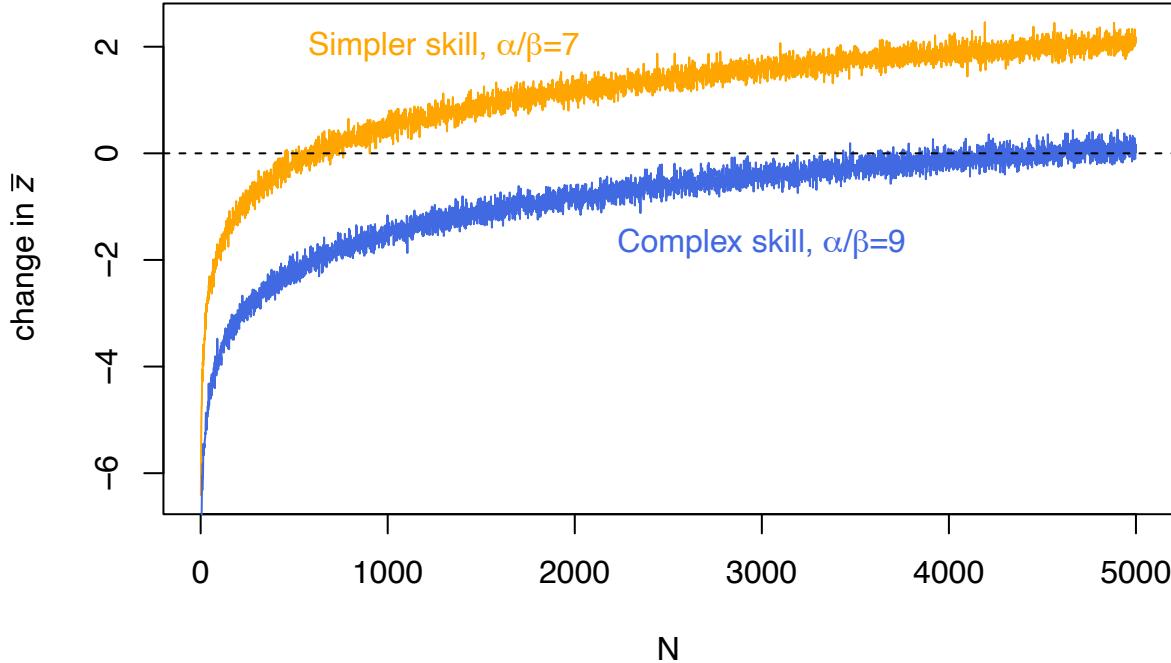
plot(1:length(data_model9_1), data_model9_1,
     type = 'l',
     ylab = expression("change in " * italic(bar("z"))),
     xlab = "N",
     col = "orange")

lines(data_model9_2, col = "royalblue")

abline(h = 0, lty = 2)

text(1300, 2,
     labels = expression("Simpler skill, " * alpha * "/" * beta * "=7"),
     col = "orange")
text(3000, -1.7,
     labels = expression("Complex skill, " * alpha * "/" * beta * "=9"),
```

```
col = "royalblue")
```



Here we have recreated Henrich's (2004) Figure 3, comparing a 'simple' skill and a 'complex' skill. A simple skill is easier to learn than a complex skill, such that it has a smaller α relative to β (remember, α is copying error that always reduces skill, while β is inferences and guesses that sometimes leads to higher skill). The plot above shows that simpler skills require a smaller population size to be maintained ($\Delta\bar{z} = 0$) or improve ($\Delta\bar{z} > 0$) than more complex skills. This reflects the postulated Tasmanian case that we started with: when population sizes dropped when Tasmania became cut off from the mainland, complex skills like fishhooks were lost and never reinvented, while simpler skills remained. In the figure above, this would be like going from $N = 5000$ to $N = 1000$.

Summary of Model 9

Cultural evolution occurs within populations of certain sizes and structures, and this population size and structure affects evolutionary dynamics. In previous models we have seen how population size can lead to the accidental loss of traits, which is a basic principle of genetic and cultural drift. Model 9 extended this basic finding to show how population size can determine whether there is cultural gain or cultural loss of a continuous cultural trait such as the skill required to make a hard-to-learn tool. Assuming that copying is imperfect, small populations are less able to maintain and accumulate cultural skill than large populations, even when every learner can identify and is attempting to learn from the highest skilled individual from the previous generation. Fewer learners means less chance that one of those learners will match or exceed that highest skilled individual from the previous generation. This effect of population size interacts with

the ‘learnability’ and ‘improvability’ of the trait: more easily learned (lower α) and more easily improved (higher β) traits require smaller populations to maintain and improve.

This model by Henrich (2004) has inspired a large body of subsequent models (e.g. Powell, Shennan & Thomas, 2009; Mesoudi 2011) and empirical research (e.g. Derex et al. 2013; Kline & Boyd 2010). These have extended the predictions of the model, and tested those predictions both in the laboratory and in real world datasets (see Derex & Mesoudi 2020). To be sure, population size is not the only determinant of cultural gains and losses. Even Henrich’s original model demonstrates this, given that learnability and improvability are also crucial. And more recent work has focused on population structure (e.g. social networks) rather than simply the number of individuals that are present. But there is no doubt that demography cannot be ignored when studying cultural evolution. Simulation models are often useful for studying demography, as complex population structures are difficult to implement in analytical models.

A few new programming techniques were used in Model 9. First, we introduced another continuous distribution, the gumbel distribution. Unlike the normal distribution used in Model 8, there are no built-in R functions for using the gumbel. We therefore had to write our own, and incorporate the **rgumbel** function into the simulation function. It is common practice to write user-defined functions for small routines and then call them within other functions. Indeed, it is often good practice, especially when the same set of lines of code are repeated in multiple places. Second, we used commands like **expression**, **text** and **arrows** to annotate plots. It is preferable to create plots entirely in R and then export the finished version (see Model 1 for how to do this), rather than export basic plots and annotate them in separate visual editing software or Powerpoint. Creating plots entirely in R is more reproducible because others can re-run your code and re-create your figures exactly. It also avoids loss of image resolution. Finally, we saw a few tricks to speed up code that takes a long time to run. Dataframes can be replaced with one-dimensional vectors when they are made up of just one variable. Means can be calculated by keeping a running total within a loop then dividing by the total number of data points once the loop has finished. Simplifying code as much as possible can often lead to significantly faster simulation runs, although try not to sacrifice code understandability in doing so.

Exercises

1. Try different values of α , β and N in **DemographyModel** to determine that, for given values of α and β , there is a threshold value of N above which there is cultural gain, and below which there is cultural loss.
 2. Change **DemographyModel** so that there are two different population sizes, N_1 and N_2 , both user-defined in the function call. For the first half of the generations, i.e. from $t = 1$ to $t = t_{max}/2$, the population size is N_1 . For the second half, i.e. from $t = (t_{max}/2) + 1$ to $t = t_{max}$, the population size is N_2 . For a given pair of α and β values, pick an N_1 that leads to cultural gain, and an N_2 that leads to cultural loss. Run the simulation to see what happens. Is this a reasonable simulation of the purported ‘Tasmanian’ case described above and in Henrich (2004), where isolation due to rising sea levels caused a reduction in population size?
 3. In Mesoudi (2011) I suggested that a simple way of making the Henrich (2004) model more realistic is to tie the copying error parameter α to the mean skill level, \bar{z} , in each generation. As skills become ever more complex, they should become harder to learn. If they are harder to learn, there will be more error in their transmission. Thus as \bar{z} increases over the generations, so should α . Modify the **DemographyModel** function to implement this additional assumption. As before, there should be a user-defined starting value of α . However, in each new timestep from $t = 2$ onwards, α should be multiplied by the mean skill level in the previous timestep (the latter is already being stored in the output dataframe). Run the simulation to see how this changes the dynamics of the model.
-

Analytic Appendix

Henrich's (2004) model was analytical rather than simulation-based. We can use the analytical model to check our simulation results above, as well as additional things like calculate the exact N at which losses switch to gains for a given α and β .

As in the model above, we assume N individuals indexed by i , with the i th individual possessing trait value z_i . Each individual of each new generation draws a value from the gumbel distribution shown above, with mode $z_h - \alpha$ and dispersion β . As in the simulation model, we want to calculate $\Delta\bar{z}$, the change in the mean trait value from one generation to the next.

The next generation mean trait value, \bar{z}' , is given by:

$$\bar{z}' = z_h + \Delta z_h \quad (9.1)$$

Equation 9.1 says that the new mean trait value is the highest trait value in the previous generation, z_h , plus any change in z_h as a result of imperfect copying. Henrich shows that the former can be approximated by:

$$z_h = a + \beta(\epsilon + \ln(N)) \quad (9.2)$$

where ϵ is Euler's constant, which is approximately 0.577.

The other term Δz_h is given by $z'_h - z_h$. The new maximum value, z'_h , is given by the mean of the gumbel distribution, $a + \beta\epsilon$. The old maximum, z_h , is given by $a + \alpha$, as per the gumbel distribution figure above. Consequently:

$$\Delta z_h = a + \beta\epsilon - a - \alpha = -\alpha + \beta\epsilon \quad (9.3)$$

Substituting Equation 9.2 and 9.3 into Equation 9.1 gives:

$$\bar{z}' = a + \beta(\epsilon + \ln(N)) - \alpha + \beta\epsilon$$

As $\bar{z}' = \bar{z} + \Delta\bar{z}$ and $a = \bar{z} - \beta\epsilon$,

$$\Delta\bar{z} = \bar{z} - \beta\epsilon + \beta(\epsilon + \ln(N)) - \alpha + \beta\epsilon - \bar{z}$$

Simplifying, this gives:

$$\Delta\bar{z} = -\alpha + \beta(\epsilon + \ln(N)) \quad (9.4)$$

which is Henrich's Equation 2. This says that, as we found in the simulation model, whether we see cultural gain or cultural loss depends on α , β and N , but it also provides an exact relation between them.

By setting $\Delta\bar{z} = 0$ and rearranging, we find that the equilibrium value of N at which there is neither gain nor loss, N^* , is:

$$N^* = e^{(\frac{\alpha}{\beta} - \epsilon)} \quad (9.5)$$

and this is Henrich's Equation 3. For the values $\alpha = 30$ and $\beta = 15$ used in the simulation model above, equation 9.5 gives $N^* = 4.15$. When N is 4 or less we would expect cultural loss, and when N is 5 or more we would expect cultural gain. Try using the simulation model to confirm this.

Finally, we can use Equation 9.4 to recreate the figure above with the 'simpler' and 'complex' skills:

```

N_max <- 5000
delta_z <- rep(NA,N_max)

alpha <- 7
beta <- 1

for (N in 1:N_max) {

  delta_z[N] <- -alpha + beta * (-digamma(1) + log(N))

}

plot(1:length(delta_z), delta_z,
      type = 'l',
      ylab = expression("change in " * italic(bar("z"))),
      xlab = "N",
      col = "orange")

abline(h = 0, lty = 2)

alpha <- 9
beta <- 1

for (N in 1:N_max) {

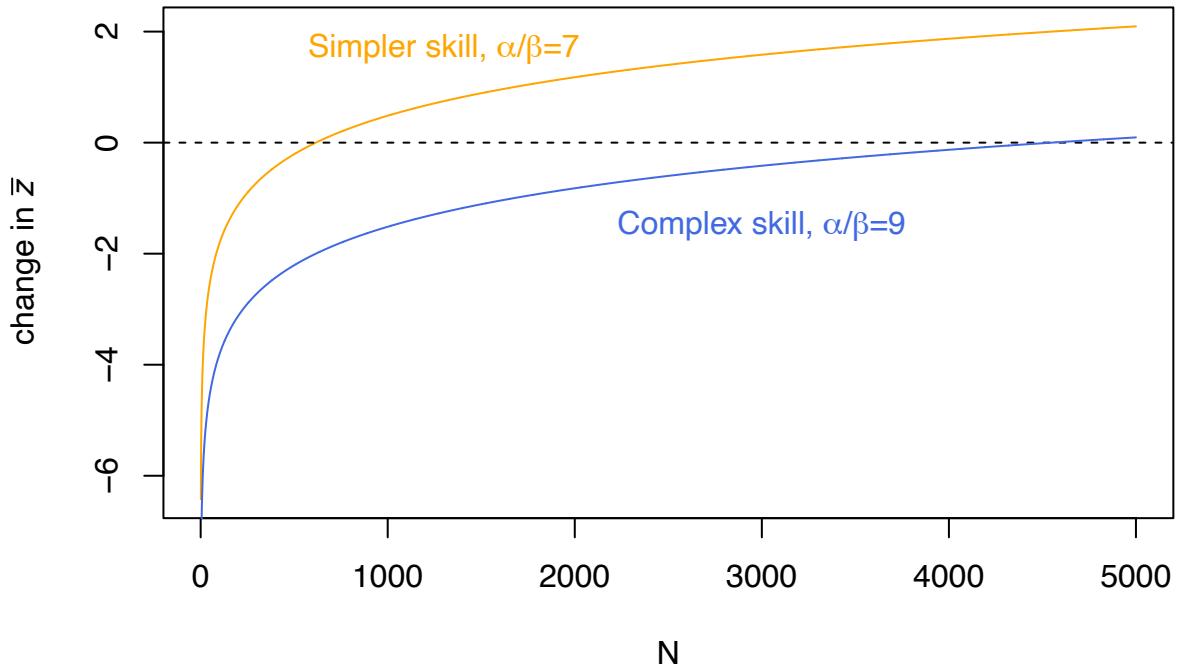
  delta_z[N] <- -alpha + beta * (-digamma(1) + log(N))

}

lines(delta_z, col = "royalblue")

text(1300, 1.7,
     labels = expression("Simpler skill, " * alpha * "/" * beta * "=7"),
     col = "orange")
text(3000, -1.5,
     labels = expression("Complex skill, " * alpha * "/" * beta * "=9"),
     col = "royalblue")

```



Note that Euler's constant is provided in R as `-digamma(1)`. Here we have reproduced the simulation figure above but in a fraction of the time, and with less noise.

References

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Simulation Models of Cultural Evolution in R

Alex Mesoudi

Model 10: Polarization

A central question in cultural evolution research is how cultural diversity is generated and maintained. One counter-intuitive answer to this question was offered by Axelrod (1997) using what has become an influential agent-based model. Axelrod showed that regional differences in cultural traits - or ‘polarization’ when neighbouring regions are maximally culturally different to one another - can be generated and maintained even though individual agents are trying to become as similar as possible to other agents. In Axelrod’s terminology, global cultural divergence at the population level can emerge despite local cultural convergence at the individual level. This conclusion has implications for a variety of social phenomena, from political polarization in social media to racial segregation in cities.

Axelrod demonstrated this using a spatially explicit agent-based model. ‘Spatially explicit’ means that rather than a homogenous mass of agents existing all with an equal probability of interacting with any other agent, instead each agent exists in a specific location in space, with a set of neighbouring agents with whom they may be more likely to interact than agents further away in space. Agent-based models are particularly suited for this kind of spatially explicit simulation compared to analytical models. Our previous models have already incorporated non-random interaction between agents and minimal population structure, such as the assortative cultural mating of Model 6 (vertical/horizontal transmission) and the movement across groups of Model 7 (migration). In Model 10 we will go further and recreate Axelrod’s classic model, learning how to create and analyse spatially explicit agent-based models where each agent inhabits a specific position in a spatial grid.

Another distinct feature of Axelrod’s model is his assumption that agents possess multiple cultural traits, and these can serve as markers of identity and influence interaction. Specifically, he assumed that each agent possesses a number of cultural ‘features’. Each feature can take on one of several trait values. In his basic model, there are five cultural features, each of which can take one of ten possible trait values. When modelling cultural diversity, it makes sense to model multiple cultural traits. Each member of a real society possesses multiple culturally-transmitted traits - language(s) spoken, dialects of those languages, dress customs, whether cars are driven on the left or the right, using knives and forks or chopsticks, bowing vs handshakes, etc. These traits in combination - rather than any single trait - define a society’s culture. While we modelled two cultural traits in Model 4 (indirect bias), in Model 10 we will model more than two.

Axelrod’s model, like all good agent-based models, is simple. Each agent is placed in a fixed position on a square grid. There are N_{side} agents along each side of the grid, giving N_{side}^2 agents in total. Each agent has $g = 5$ cultural features. Each feature takes one of ten values, denoted with the integers 0-9. For example, an agent might have traits 58290. Here, the first feature is 5, the second 8, and so on.

In the first timestep each agent’s trait values are picked at random. Then in each timestep, the following three rules are applied:

1. Pick an agent at random (the focal agent)
2. Pick one of the focal agent’s neighbours at random. A neighbour is an agent to the immediate north, south, east or west of the focal agent’s grid position. Focal agents at the corner or edge of the grid may have no neighbour in one of those positions, and so have only two or three neighbours respectively.

- With probability equal to the proportion of shared cultural traits between the focal agent and its chosen neighbour, pick one feature at random that differs between focal agent and its neighbour, and set the focal agent's value of that feature to the neighbour's value.

These rules plausibly assume that agents are more likely to interact with, and be influenced by, other agents to the extent that they are culturally similar, as indexed by the proportion of cultural traits that they share. When two agents are completely dissimilar, then the proportion of shared features will be zero, and no interaction / influence will occur. The more traits they share, the more likely they are to interact and potentially become even more similar.

The outcome that we are interested in is the cultural diversity or homogeneity that emerges after a certain number of timesteps, or iterations of the above three rules. The only cultural change that can occur according to the three rules above is that agents become more similar to one another. There is no mutation, and no rules that make agents more dissimilar. We would expect, therefore, that all agents will gradually become more and more similar, perhaps identical, and eventually every agent will be culturally identical.

Let's build the model step by step before putting it together in a function. First we need to create agents and their traits. Rather than a dataframe, we will use a matrix. A matrix is perfect because it has a fixed number of rows and columns, and these rows and columns will serve as the coordinates for our spatial grid. In our case the matrix will be square, with N_{side} rows and N_{side} columns. Each agent inhabits a fixed position in the matrix. Indexing starts at the top left and has the notation [row,column]. The agent in the top left position is therefore at position [1,1]; its neighbour to the east is in position [1,2]; and its neighbour to the south is at [2,1].

First we create a 10x10 matrix (i.e. $N_{side} = 10$) filled for now with NAs:

```
N_side <- 10

# make agent matrix of size N_size x N_size
agent <- matrix(NA,
                 nrow = N_side,
                 ncol = N_side)

agent

##      [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10]
## [1,]    NA    NA    NA    NA    NA    NA    NA    NA    NA    NA
## [2,]    NA    NA    NA    NA    NA    NA    NA    NA    NA    NA
## [3,]    NA    NA    NA    NA    NA    NA    NA    NA    NA    NA
## [4,]    NA    NA    NA    NA    NA    NA    NA    NA    NA    NA
## [5,]    NA    NA    NA    NA    NA    NA    NA    NA    NA    NA
## [6,]    NA    NA    NA    NA    NA    NA    NA    NA    NA    NA
## [7,]    NA    NA    NA    NA    NA    NA    NA    NA    NA    NA
## [8,]    NA    NA    NA    NA    NA    NA    NA    NA    NA    NA
## [9,]    NA    NA    NA    NA    NA    NA    NA    NA    NA    NA
## [10,]   NA    NA    NA    NA    NA    NA    NA    NA    NA    NA
```

The rows are labelled along the left hand side, and the columns along the top.

Now we need g features each of which initially takes one integer from 0 to 9. The following code sets $g = 5$, and then uses **sample.int** to pick g integers from 0 to 9, with replacement (so integers can repeat). Note that the **sample.int** command returns random integers from one up to the first argument. Because we want to include 0 as a trait, we pick random integers from 1 to 10, then subtract 1 to get the range 0 to 9.

```

g <- 5

sample.int(10, g, replace = TRUE) - 1

## [1] 1 5 9 9 5

```

Because we want each one to fit into a single cell of the matrix, we need to condense them into a single value. We could turn them into a g -digit number. However, this would lose the leading zeroes (e.g. 0 0 4 8 5 would become 485, not 00485). Instead we will convert to a character (chr) variable, using the **paste** command with collapse = "" to remove the spaces:

```

paste(sample.int(10, g, replace = TRUE) - 1,
      collapse = "")

## [1] "68575"

```

Now we can fill the *agent* matrix with random traits and display them (the **options** command simply widens the print area on the pdf output to see the matrix properly).

```

# fill agent with g numbers each a random integer 0-9, stored as chr
for (n_width in 1:N_side) {

  for (n_height in 1:N_side) {

    agent[n_width,n_height] <- paste(sample.int(10, g, replace = TRUE) - 1,
                                      collapse = "")

  }

}

options(width = 300)
agent

```

```

##      [,1]     [,2]     [,3]     [,4]     [,5]     [,6]     [,7]     [,8]     [,9]     [,10]
## [1,] "69039" "77991" "55688" "13712" "12275" "22937" "61604" "20244" "54719" "32648"
## [2,] "14800" "90953" "81322" "47116" "22904" "11324" "92324" "22235" "50988" "35005"
## [3,] "09402" "75124" "41492" "40455" "74078" "67278" "40662" "55176" "16019" "84039"
## [4,] "08508" "04170" "51373" "43708" "71973" "59211" "26376" "88613" "14008" "65639"
## [5,] "37080" "30682" "57443" "11281" "29591" "10292" "74540" "63189" "73182" "21575"
## [6,] "69934" "90088" "51941" "60791" "35706" "05060" "13728" "37313" "26260" "75625"
## [7,] "84489" "79385" "97354" "65659" "89201" "16142" "93520" "87508" "61651" "29276"
## [8,] "43641" "27415" "66886" "30035" "65407" "21159" "49826" "56050" "95585" "94131"
## [9,] "23888" "05331" "09969" "44807" "37568" "84212" "99637" "24309" "61992" "01663"
## [10,] "03686" "74674" "21688" "86417" "91690" "96151" "98478" "50070" "01027" "52067"

```

Here we have reproduced Table 1 from Axelrod (1997): a 10 x 10 grid containing g -length cultural traits for 100 agents.

Now to convert the three rules above into code. First we pick a random agent to be the focal agent. We do this by picking a random row value and a random column value, and setting *focal* to the agent in that position.

```

# pick a focal agent at random
focal_row <- sample(1:N_side, 1)
focal_col <- sample(1:N_side, 1)
focal <- agent[focal_row, focal_col]

focal

## [1] "55176"

```

Now we pick one of the focal's neighbours at random, as per rule 2. This is complicated by the fact that some focal agents will have four neighbours (those in the middle of the grid), some will have three (those at the edges) and some will have only two (those in the corners). We don't want to pick a non-existent neighbour to compare with the focal. The following code creates a vector of *all_neighbours*, adds ('appends') to this vector only those neighbours that exist given the focal's position, and picks one of the existing neighbours at random to be the *neighbour*.

```

# pick one of its neighbours at random
# ignoring non-existent agents outside boundaries

all_neighbours <- NULL

if (focal_row-1 >= 1)
  all_neighbours <- append(all_neighbours,
                            agent[focal_row-1, focal_col])
if (focal_row+1 <= N_side)
  all_neighbours <- append(all_neighbours,
                            agent[focal_row+1, focal_col])
if (focal_col-1 >= 1)
  all_neighbours <- append(all_neighbours,
                            agent[focal_row, focal_col-1])
if (focal_col+1 <= N_side)
  all_neighbours <- append(all_neighbours,
                            agent[focal_row, focal_col+1])

neighbour <- sample(all_neighbours, 1)

neighbour

## [1] "88613"

```

We can now simulate rule 3, the cultural change. First we convert the *focal* and *neighbour*'s traits from a single character into numbers using the **unlist** and **strsplit** commands. This is essentially the reverse of the **paste** command above. We can then get the cultural *similarity* between *focal* and *neighbour* by adding the number of features that are identical and dividing by the total number of features. Then, if this *similarity* is greater than zero and less than one, i.e. the two agents are not completely dissimilar nor identical, then with probability equal to *similarity* we pick a random feature that differs between the *focal* and *neighbour* and store it as *feature*. These are identified using the **which** command (i.e. `which(focal != neighbour)`). If there is a single dissimilar feature (i.e. `sum(focal != neighbour) == 1`) then this single dissimilar feature is stored in *feature*. If there is more than one, then we pick one at random using **sample**. Note that we do this because, if there is a single dissimilar feature, **sample** will not work properly. Always make sure **sample** is picking from more than one element, never a single element (try running `sample(2, 10, replace = TRUE)` to see this). Finally, we set the *focal* agent's chosen dissimilar trait value to that of its *neighbour*, and insert the modified *focal* traits back into the agent matrix.

```

# separate out traits and make them numeric, for comparing
focal <- as.numeric(unlist(strsplit(focal, split = NULL)))
neighbour <- as.numeric(unlist(strsplit(neighbour, split = NULL)))

# get similarity
similarity <- sum(focal == neighbour) / length(focal)

if (similarity > 0 & similarity < 1) {

  if (runif(1) < similarity) {

    if (sum(focal != neighbour) == 1) {
      feature <- which(focal != neighbour)
    } else {
      feature <- sample(which(focal != neighbour), 1)
    }

    focal[feature] <- neighbour[feature]

    agent[focal_row, focal_col] <- paste(focal, collapse = "")

  }

}

paste(focal, collapse = "")

## [1] "55176"

paste(neighbour, collapse = "")

## [1] "88613"

similarity

## [1] 0

agent[focal_row, focal_col]

## [1] "55176"

```

The output shows the original focal agent, its neighbour, their similarity, and the modified focal agent. The latter may well be identical to the original focal traits, given that our randomised agents are currently highly dissimilar to one another (probably $similarity = 0$, in which case there is definitely no change). Try repeating the above code but with the *focal* and *neighbour* set to be maximally similar without being identical, e.g. “12345” and “12340” respectively. In this case $similarity = 0.8$ and the final feature in *focal* is likely to flip from 5 to 0.

We now have all the code to write a function. **Polarization** below combines all the previous code, wrapping the three rules in a loop to repeat them t_{max} times. The output of the simulation is the final *agent* matrix at $t = t_{max}$ and the number of timesteps at which this was produced (this will be used later when plotting the results).

```

Polarization <- function(N_side, g, t_max) {

  # make agent matrix of size N_size x N_size
  agent <- matrix(NA,
                  nrow = N_side,
                  ncol = N_side)

  # fill agent with g numbers each a random integer 0-9, stored as chr
  for (n_width in 1:N_side) {

    for (n_height in 1:N_side) {

      agent[n_width,n_height] <- paste(sample.int(10, g, replace = TRUE) - 1,
                                         collapse = "")

    }

  }

  for (t in 1:t_max) {

    # pick a focal agent at random
    focal_row <- sample(1:N_side, 1)
    focal_col <- sample(1:N_side, 1)
    focal <- agent[focal_row, focal_col]

    # pick one of its neighbours at random
    # ignoring non-existent agents outside boundaries

    all_neighbours <- NULL

    if (focal_row-1 >= 1)
      all_neighbours <- append(all_neighbours,
                                agent[focal_row-1, focal_col])
    if (focal_row+1 <= N_side)
      all_neighbours <- append(all_neighbours,
                                agent[focal_row+1, focal_col])
    if (focal_col-1 >= 1)
      all_neighbours <- append(all_neighbours,
                                agent[focal_row, focal_col-1])
    if (focal_col+1 <= N_side)
      all_neighbours <- append(all_neighbours,
                                agent[focal_row, focal_col+1])

    neighbour <- sample(all_neighbours, 1)

    # compare focal and neighbour agents:
    # if there's at least one dissimilar trait,
    # and with prob equal to the similarity between focal and neighbour,
    # set a random dissimilar focal trait to that of the neighbour's

    # separate out traits and make them numeric, for comparing
    focal <- as.numeric(unlist(strsplit(focal, split = NULL)))
  }
}

```

```

neighbour <- as.numeric(unlist(strsplit(neighbour, split = NULL)))

# get similarity
similarity <- sum(focal == neighbour) / length(focal)

if (similarity > 0 & similarity < 1) {

  if (runif(1) < similarity) {

    if (sum(focal != neighbour) == 1) {
      feature <- which(focal != neighbour)
    } else {
      feature <- sample(which(focal != neighbour), 1)
    }

    focal[feature] <- neighbour[feature]

    agent[focal_row, focal_col] <- paste(focal, collapse = "")

  }
}

}

# output agent matrix and t_max
list(agent = agent, t = t)

}

```

Here is one run of the *Polarization* function, with $N_{side} = 10$, $g = 5$ and $t_{max} = 100000$. We display the final *agent* matrix that has been stored in *data_model10*.

```

data_model10 <- Polarization(N_side = 10,
                             g = 5,
                             t_max = 100000)

data_model10$agent

##      [,1]     [,2]     [,3]     [,4]     [,5]     [,6]     [,7]     [,8]     [,9]     [,10]
## [1,] "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837"
## [2,] "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837"
## [3,] "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837"
## [4,] "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837"
## [5,] "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837"
## [6,] "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837"
## [7,] "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837"
## [8,] "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837"
## [9,] "04837" "69270" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837"
## [10,] "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "04837" "82602"

```

After 100,000 timesteps, there should be noticeable similarity in the agent traits above. Probably not complete similarity, however. While most agents should have the same traits, there should be some areas of the matrix where some agents have a different trait.

Axelrod plotted the output of the model using lines of different thickness to denote the cultural similarity between neighbouring agents. The function **PolarizationPlot** below does this, using the *data_model10* output from **Polarization**. First we retrieve the *agent* matrix and *t_{max}* from *data_model10*, as well as *N_{side}* from *agent*. We then make an empty *N_{side}* x *N_{side}* plot, add a title recording the number of timesteps, and add lines around the sides using **segments**. Then we cycle through each agent along the rows (the *Row* loop) and columns (the *Col* loop) to draw vertical lines. We pick each agent and its neighbour to the east, calculate their *similarity* in the same way as we did above, set the *lwd* (line width) in proportion to the *similarity*, and draw a line using **segments**. Once all the vertical lines are drawn we cycle through again, this time comparing each agent to its neighbour to the south and drawing horizontal lines at the boundaries between them.

```
PolarizationPlot <- function(data_model10) {

  agent <- data_model10$agent
  t_max <- data_model10$t

  # retrieve N_side from matrix
  N_side <- dim(agent)[1]

  # make an empty N_side x N_side plot
  plot(NULL,
    ylim = c(0, N_side),
    xlim = c(0, N_side),
    ylab = "",
    xlab = "",
    axes = FALSE,
    main = paste("After ", format(t_max, scientific = F), " timesteps",
                sep = ""))

  # add a frame around the edges
  segments(x0 = 0, y0 = 0,
            x1 = 0, y1 = N_side)
  segments(x0 = 0, y0 = 0,
            x1 = N_side, y1 = 0)
  segments(x0 = 0, y0 = N_side,
            x1 = N_side, y1 = N_side)
  segments(x0 = N_side, y0 = 0,
            x1 = N_side, y1 = N_side)

  # vertical lines

  for (Row in 1:N_side) {
    for (Col in 1:(N_side-1)) {

      # agent2 is to the right of agent1
      agent1 <- agent[Row, Col]
      agent2 <- agent[Row, Col+1]

      # make numeric
      agent1 <- as.numeric(unlist(strsplit(agent1, split = NULL)))
      agent2 <- as.numeric(unlist(strsplit(agent2, split = NULL)))

      # get similarity
    }
  }
}
```

```

similarity <- sum(agent1 == agent2) / length(agent1)

# set line thickness
if (similarity < 1)    lwd <- 0.5
if (similarity <= 0.8) lwd <- 1
if (similarity <= 0.6) lwd <- 3
if (similarity <= 0.4) lwd <- 5
if (similarity <= 0.2) lwd <- 7

if (similarity < 1) {

  segments(x0 = Col, x1 = Col,
           y0 = N_side-Row, y1 = N_side-Row+1,
           lwd = lwd)

}

}

# horizontal lines

for (Row in 1:(N_side-1)) {

  for (Col in 1:N_side) {

    # agent2 is directly below agent1
    agent1 <- agent[Row,Col]
    agent2 <- agent[Row+1,Col]

    # make numeric
    agent1 <- as.numeric(unlist(strsplit(agent1, split = NULL)))
    agent2 <- as.numeric(unlist(strsplit(agent2, split = NULL)))

    # get similarity
    similarity <- sum(agent1 == agent2) / length(agent1)

    # set line thickness
    if (similarity < 1)    lwd <- 0.5
    if (similarity <= 0.8) lwd <- 1
    if (similarity <= 0.6) lwd <- 3
    if (similarity <= 0.4) lwd <- 5
    if (similarity <= 0.2) lwd <- 7

    if (similarity < 1) {

      segments(y0 = N_side-Row, y1 = N_side-Row,
               x0 = Col-1, x1 = Col,
               lwd = lwd)

    }

  }

}

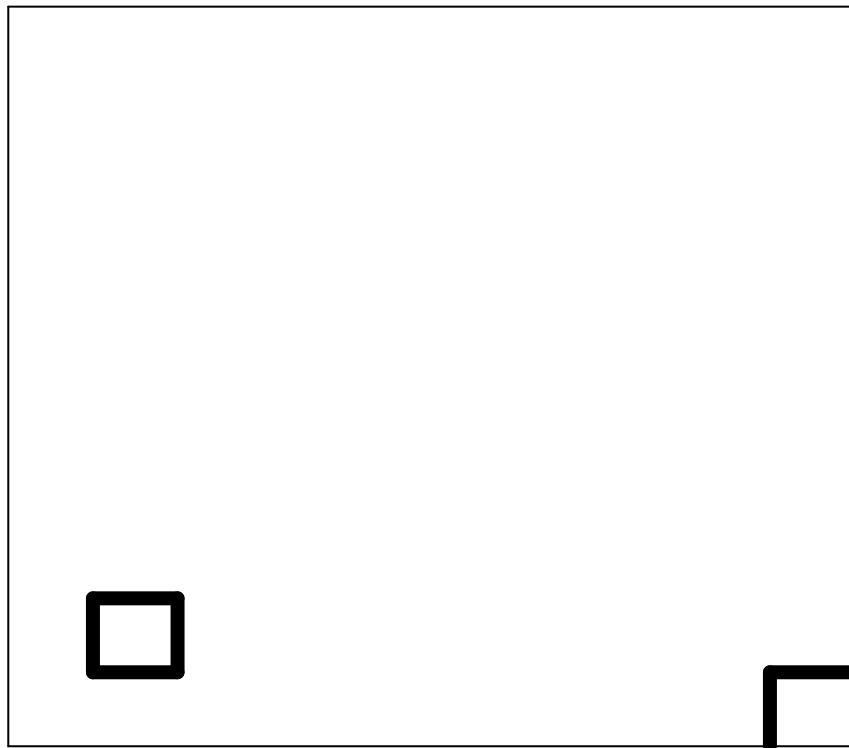

```

```
    }  
}  
}
```

Below is the plot for the run created above. It should match the *agent* matrix, with lines separating agents that are dissimilar. The thicker the lines, the more dissimilar the agents are.

```
PolarizationPlot(data_model10)
```

After 100000 timesteps



The plot should show a small number of regions that are dissimilar to the neighbouring regions. Despite individual agents' preferences to interact with and copy similar others, different regions of the grid have polarized into groups with different cultural traits.

How many distinct regions are there in the plot above? We could count them visually, but better would be to use the code below. We convert the *agent* matrix to a vector, and count the number of unique traits using the **unique** command.

```
length(unique(as.vector(data_model10$agent)))
```

```
## [1] 3
```

Note that this is the number of unique traits in the entire population. It may not be the same as the number of regions shown in the plot, if there are two non-contiguous regions that have the same trait. Axelrod doesn't specify whether he recorded the number of unique traits or the number of non-contiguous regions. These are unlikely to differ too much though, as the chances of two non-contiguous regions having identical traits is slim.

How did these regions form over time? The function **PolarizationMultiplot** below creates a multi-panel 2 x 2 plot which plots the *agent* matrix at four different points of the same run, as in Axelrod's Figure 1. The parameter *t_{plot}* replaces *t_{max}*. *t_{plot}* is a list of four timesteps at which the output is plotted; the final value in *t_{plot}* will effectively therefore be *t_{max}*. Most of the code in **PolarizationMultiplot** is the same as **Polarization**, except that we set up a 2 x 2 plot using `par(mfrow = c(2,2))`, store each of the four *agent* matrices in *agent_list* whenever the timestep *t* matches one of the *t_{plot}* values (using `if (t %in% t_plot)`), and plot each *agent* matrix using **PolarizationPlot** at the end.

```
PolarizationMultiplot <- function(N_side, g, t_plot) {

  # make agent matrix of size N_size x N_size
  agent <- matrix(NA,
                  nrow = N_side,
                  ncol = N_side)

  # fill agent with g-digit codes, stored as chr
  for (n_width in 1:N_side) {

    for (n_height in 1:N_side) {

      agent[n_width,n_height] <- paste(sample.int(10, g, replace = TRUE) - 1,
                                         collapse = "")

    }

  }

  # set up 2x2 plot panels
  par(mfrow = c(2,2))

  # set up agent list to store data
  agent_list <- list(NULL)

  for (t in 1:max(t_plot)) {

    # pick a focal agent at random
    focal_row <- sample(1:N_side, 1)
    focal_col <- sample(1:N_side, 1)
    focal <- agent[focal_row, focal_col]

    # pick one of its neighbours at random
    # ignoring non-existent agents outside boundaries
```

```

all_neighbours <- NULL

if (focal_row-1 >= 1)
  all_neighbours <- append(all_neighbours,
                            agent[focal_row-1, focal_col])
if (focal_row+1 <= N_side)
  all_neighbours <- append(all_neighbours,
                            agent[focal_row+1, focal_col])
if (focal_col-1 >= 1)
  all_neighbours <- append(all_neighbours,
                            agent[focal_row, focal_col-1])
if (focal_col+1 <= N_side)
  all_neighbours <- append(all_neighbours,
                            agent[focal_row, focal_col+1])

neighbour <- sample(all_neighbours, 1)

# compare focal and neighbour agents:
# if there's at least one dissimilar trait,
# and with prob equal to the similarity between focal and neighbour,
# set a random dissimilar focal trait to that of the neighbour's

# separate out traits and make them numeric, for comparing
focal <- as.numeric(unlist(strsplit(focal, split = NULL)))
neighbour <- as.numeric(unlist(strsplit(neighbour, split = NULL)))

# get similarity
similarity <- sum(focal == neighbour) / length(focal)

if (similarity > 0 & similarity < 1) {

  if (runif(1) < similarity) {

    if (sum(focal != neighbour) == 1) {
      feature <- which(focal != neighbour)
    } else {
      feature <- sample(which(focal != neighbour), 1)
    }

    focal[feature] <- neighbour[feature]

    agent[focal_row, focal_col] <- paste(focal, collapse = "")
  }
}

# add agent to agent_list if t is in t_plot
if (t %in% t_plot) {

  agent_list[[match(t, t_plot)]] <- agent
}

```

```

}

# create plots using PolarizationPlot
for (t in 1:length(t_plot)) {

  PolarizationPlot(list(agent = agent_list[[t]],
                       t = t_plot[t]))

}

# output agent matrix list and t from function
list(agent = agent_list, t = t_plot)
}

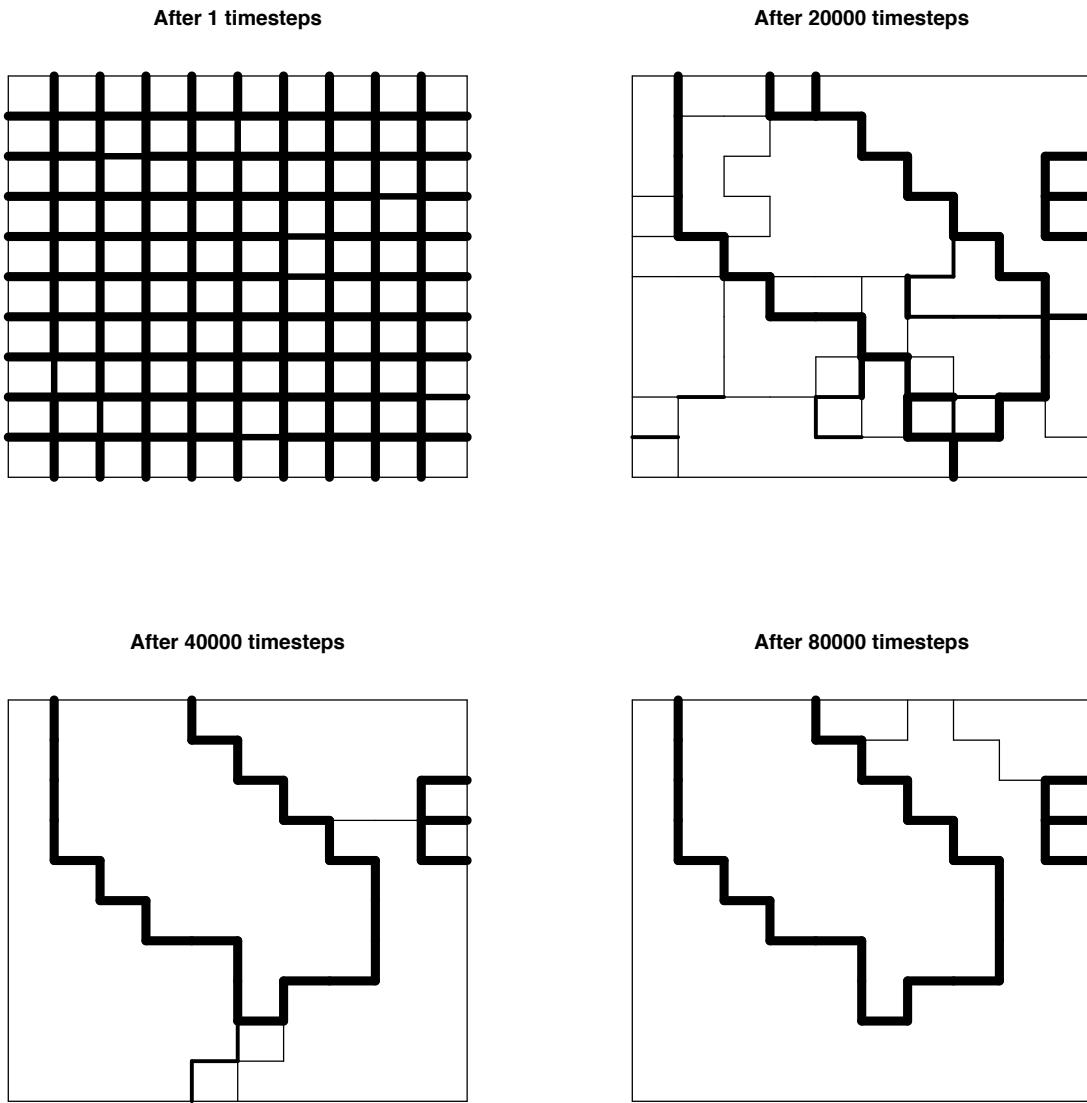
```

Now we can recreate Axelrod's Figure 1, with plots for $t = 1, 20000, 40000, 80000$. You should be able to see the thick lines that indicate dissimilarity gradually disappear, leaving a small number of distinct regions by $t = 80000$.

```

data_model10 <- PolarizationMultiplot(N_side = 10,
                                       g = 5,
                                       t_plot = c(1,20000,40000,80000))

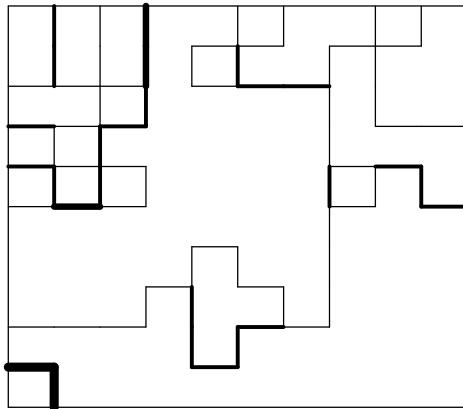
```



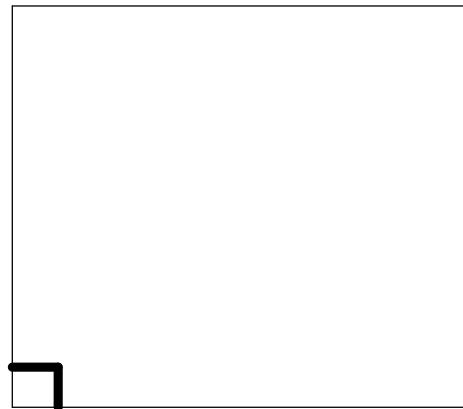
It is likely that by $t = 80000$ the population has reached stability. This means that all neighbours of every agent are either culturally identical (indicated in the plot by no lines) or maximally culturally dissimilar (indicated by the thickest lines). In both of these cases, no further change can occur. Let's run the simulation for more timesteps. It should be guaranteed to reach stability by $t = 200000$.

```
data_model10 <- PolarizationMultiplot(N_side = 10,
                                         g = 5,
                                         t_plot = c(50000, 100000, 150000, 200000))
```

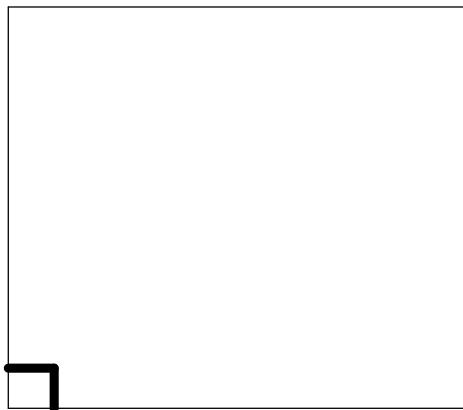
After 50000 timesteps



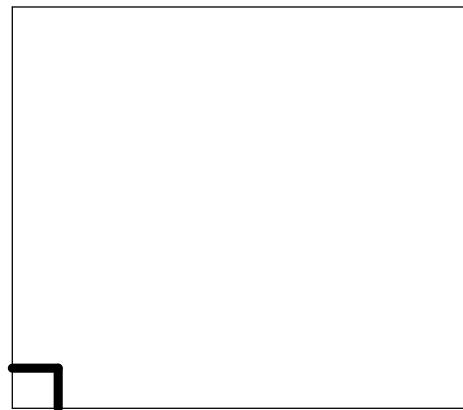
After 100000 timesteps



After 150000 timesteps

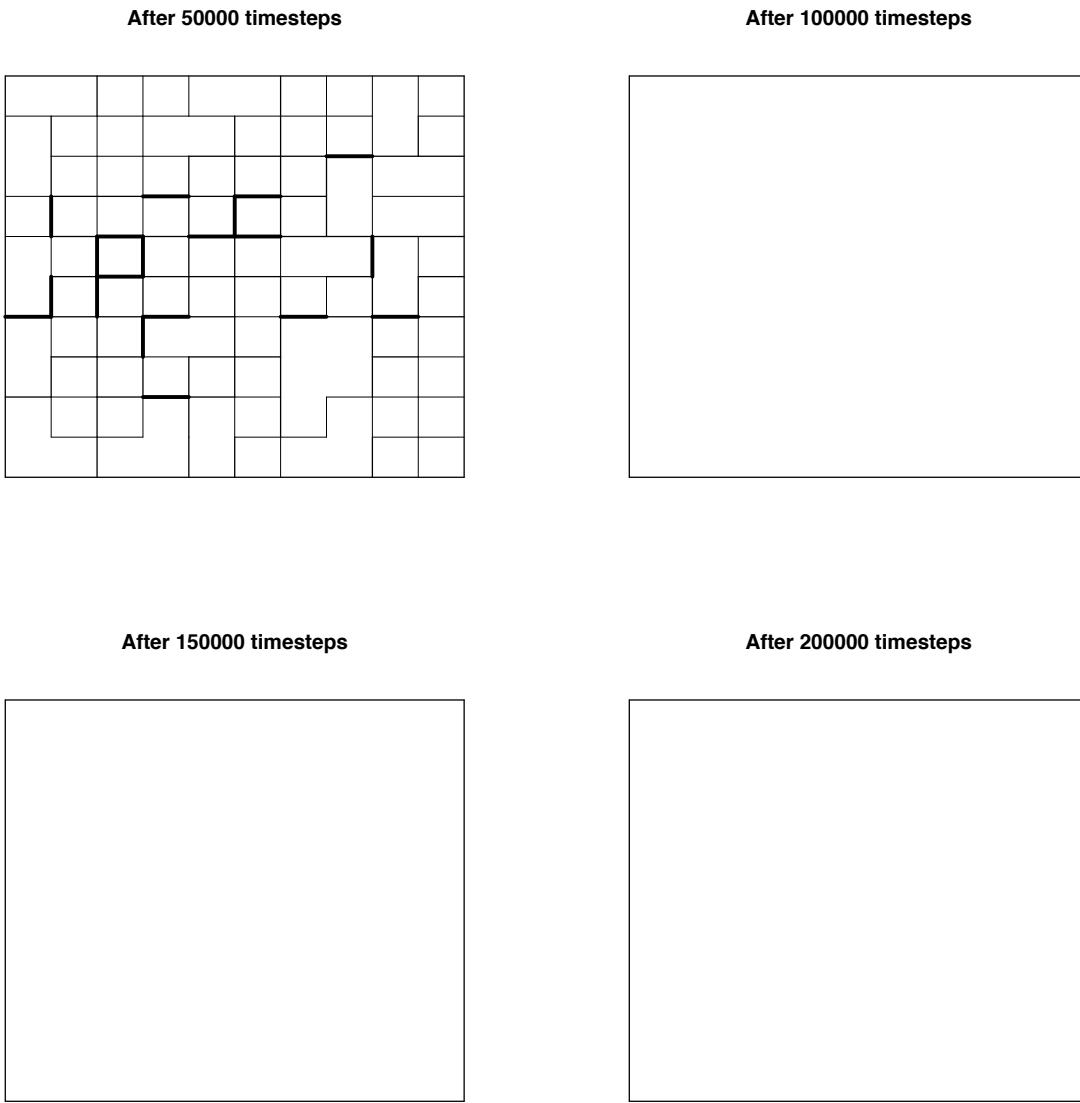


After 200000 timesteps



Now let's vary g , the number of cultural features, to see how this affects the number of stable regions. With $g = 15$:

```
data_model10 <- PolarizationMultiplot(N_side = 10,  
                                      g = 15,  
                                      t_plot = c(50000,100000,150000,200000))
```



Interestingly, with a larger g we are almost certain to converge on a single stable region that encompasses the entire grid. What's more, at $t = 100000$ there are no highly dissimilar boundaries, only weakly similar ones. This was also observed by Axelrod. Counter-intuitively, having more cultural features increases the likelihood of global homogeneity rather than polarization. This is because with more features, there is a higher chance that two agents will have the same trait value on at least one of those features, and therefore be able to interact and switch traits.

It would be useful to know exactly when a simulation run reaches stability. If a run reaches stability before t_{max} , there is little point continuing the run. We can save time by stopping the simulation at the point at which stability is reached and recording the final *agent* configuration. We also don't have to try to guess beforehand when stability might be reached, and risk ending the simulation at t_{max} before that point.

The following function **stability** takes an *agent* matrix as its input and tests whether stability has been reached. The function cycles through each agent (much like in **PolarizationPlot**, first along rows then along columns), and calculates the similarity of each pair of neighbouring agents. If any of these similarities

are greater than zero and less than one, then a variable *stable* is set to FALSE and the loops are broken using **break**. Because *stable* starts out initially TRUE, if the function gets to the end of the cycles without finding a non-stable pair of neighbours, then *stable* remains TRUE. *stable* is then outputted from the function at the end.

```

stability <- function(agent) {

  # cycle thru each agent, compare with neighbours,
  # if similarity >0 and <1 then set stable=false and break the loop(s)

  # retrieve N_side from agent matrix
  N_side <- dim(agent)[1]

  # start with the assumption of stability
  stable <- TRUE

  # cycle thru agents horizontally
  for (Row in 1:N_side) {

    for (Col in 1:(N_side-1)) {

      # agent2 is to the right of agent1
      agent1 <- agent[Row, Col]
      agent2 <- agent[Row, Col+1]

      # make numeric
      agent1 <- as.numeric(unlist(strsplit(agent1, split = NULL)))
      agent2 <- as.numeric(unlist(strsplit(agent2, split = NULL)))

      # get similarity
      similarity <- sum(agent1 == agent2) / length(agent1)

      if (similarity > 0 & similarity < 1) {

        stable <- FALSE
        break
      }
    }

    if (stable == FALSE) break
  }

  # if still possibly stable, cycle vertically
  if (stable == TRUE) {

    for (Row in 1:(N_side-1)) {

      for (Col in 1:N_side) {

        # agent2 is directly below agent1
        agent1 <- agent[Row, Col]
        agent2 <- agent[Row+1, Col]
      }
    }
  }
}

```

```

# make numeric
agent1 <- as.numeric(unlist(strsplit(agent1, split = NULL)))
agent2 <- as.numeric(unlist(strsplit(agent2, split = NULL)))

# get similarity
similarity <- sum(agent1 == agent2) / length(agent1)

if (similarity > 0 & similarity < 1) {

  stable <- FALSE
  break

}

if (stable == FALSE) break

}

# return stable
stable
}

```

Now we can rewrite the **Polarization** function to add this stability test. We add a new parameter *stable_stop* to the function definition. When *stable_stop* is FALSE (the default), **Polarization** functions as before and continues until t_{max} . When *stable_stop* is TRUE, then the stability test is activated. At the end of every timestep, the **stability** function is called. If the returned *stable* variable is TRUE, then the *t* loop is broken. As before, *t* is part of the output of the function. While previously this was always t_{max} , now it is the *t* at which the simulation reached stability, if *stable_stop* is TRUE and stability was reached before t_{max} .

```

Polarization <- function(N_side, g, t_max, stable_stop = FALSE) {

  # make agent matrix of size N_size x N_size
  agent <- matrix(NA,
                  nrow = N_side,
                  ncol = N_side)

  # fill agent with g numbers each a random integer 0-9, stored as chr
  for (n_width in 1:N_side) {

    for (n_height in 1:N_side) {

      agent[n_width,n_height] <- paste(sample.int(10, g, replace = TRUE) - 1,
                                         collapse = "")

    }

  }

  for (t in 1:t_max) {

```

```

# pick a focal agent at random
focal_row <- sample(1:N_side, 1)
focal_col <- sample(1:N_side, 1)
focal <- agent[focal_row, focal_col]

# pick one of its neighbours at random
# ignoring non-existent agents outside boundaries

all_neighbours <- NULL

if (focal_row-1 >= 1)
  all_neighbours <- append(all_neighbours,
                            agent[focal_row-1, focal_col])
if (focal_row+1 <= N_side)
  all_neighbours <- append(all_neighbours,
                            agent[focal_row+1, focal_col])
if (focal_col-1 >= 1)
  all_neighbours <- append(all_neighbours,
                            agent[focal_row, focal_col-1])
if (focal_col+1 <= N_side)
  all_neighbours <- append(all_neighbours,
                            agent[focal_row, focal_col+1])

neighbour <- sample(all_neighbours, 1)

# compare focal and neighbour agents:
# if there's at least one dissimilar trait,
# and with prob equal to the similarity between focal and neighbour,
# set a random dissimilar focal trait to that of the neighbour's

# separate out traits and make them numeric, for comparing
focal <- as.numeric(unlist(strsplit(focal, split = NULL)))
neighbour <- as.numeric(unlist(strsplit(neighbour, split = NULL)))

# get similarity
similarity <- sum(focal == neighbour) / length(focal)

if (similarity > 0 & similarity < 1) {

  if (runif(1) < similarity) {

    if (sum(focal != neighbour) == 1) {
      feature <- which(focal != neighbour)
    } else {
      feature <- sample(which(focal != neighbour), 1)
    }

    focal[feature] <- neighbour[feature]

    agent[focal_row, focal_col] <- paste(focal, collapse = "")
  }
}

```

```

}

# if stable_stop is TRUE, break the t-loop if stability is reached
if (stable_stop) {
  stable <- stability(agent)
  if (stable) break
}

}

# output agent matrix and t
list(agent = agent, t = t)

}

```

Running **Polarization** with $stable_stop = TRUE$ and a very large $t_{max} = 1000000$ reveals that stability is reached long before this point, most likely less than 100000 timesteps.

```

data_model <- Polarization(N_side = 10,
                           g = 5,
                           t_max = 1000000,
                           stable_stop = TRUE)

data_model$agent

##      [,1]     [,2]     [,3]     [,4]     [,5]     [,6]     [,7]     [,8]     [,9]     [,10]
## [1,] "53867" "53867" "53867" "53867" "53867" "53867" "79504" "87635" "87635" "87635"
## [2,] "79504" "79504" "79504" "53867" "53867" "79504" "79504" "01813" "01813" "01813"
## [3,] "79504" "79504" "79504" "79504" "79504" "79504" "01813" "01813" "01813" "01813"
## [4,] "79504" "79504" "79504" "61420" "79504" "79504" "01813" "01813" "01813" "79900"
## [5,] "79504" "79504" "79504" "79504" "79504" "79504" "79504" "01813" "01813" "01813"
## [6,] "01813" "79504" "79504" "79504" "65676" "79504" "79504" "01813" "01813" "01813"
## [7,] "01813" "01813" "01813" "79504" "79504" "79504" "01813" "01813" "01813" "01813"
## [8,] "01813" "01813" "01813" "01813" "01813" "01813" "01813" "01813" "01813" "01813"
## [9,] "01813" "01813" "01813" "01813" "01813" "01813" "01813" "01813" "01813" "01813"
## [10,] "01813" "01813" "01813" "01813" "01813" "01813" "01813" "01813" "01813" "43357" "01813" "01813"

data_model$t

## [1] 91238

```

Now we have a more nimble simulation, we can systematically vary parameters and measure the effect on the average number of stable regions across multiple runs. The code below runs **Polarization** for $g = 5$, $g = 10$ and $g = 15$, each for $r_{max} = 10$ independent runs. The output, both the number of stable regions at stability and the number of timesteps at which this was reached, is recorded in a dataframe called $g_analysis$. As in previous models, we add the values of each run to a running total then divide by r_{max} at the end. Finally, because it can take a while to run, we add progress messages using the **cat** function. This tells us which g value and which run the simulation is currently at. While this is largely cosmetic, it can be useful to know that a simulation is still running and hasn't hung up, and how long it might take to finish so you know whether you have time to go get a cup of tea.

```

g_values <- c(5, 10, 15)

r_max <- 10

g_analysis <- data.frame(cultural_features = g_values,
                           stable_regions = 0,
                           timesteps = 0)

for (g in 1:length(g_values)) {

  cat("Running g =", g_values[g], fill=T)

  for (r in 1:r_max) {

    cat("...Run", r, "of", r_max, fill=T)

    data_model10 <- Polarization(N_side = 10,
                                  g = g_values[g],
                                  t_max = 1000000,
                                  stable_stop = TRUE)

    g_analysis$stable_regions[g] <- g_analysis$stable_regions[g] +
      length(unique(as.vector(data_model10$agent)))

    g_analysis$timesteps[g] <- g_analysis$timesteps[g] +
      data_model10$t

  }

}

## Running g = 5
## ...Run 1 of 10
## ...Run 2 of 10
## ...Run 3 of 10
## ...Run 4 of 10
## ...Run 5 of 10
## ...Run 6 of 10
## ...Run 7 of 10
## ...Run 8 of 10
## ...Run 9 of 10
## ...Run 10 of 10
## Running g = 10
## ...Run 1 of 10
## ...Run 2 of 10
## ...Run 3 of 10
## ...Run 4 of 10
## ...Run 5 of 10
## ...Run 6 of 10
## ...Run 7 of 10
## ...Run 8 of 10
## ...Run 9 of 10
## ...Run 10 of 10

```

```

## Running g = 15
## ...Run 1 of 10
## ...Run 2 of 10
## ...Run 3 of 10
## ...Run 4 of 10
## ...Run 5 of 10
## ...Run 6 of 10
## ...Run 7 of 10
## ...Run 8 of 10
## ...Run 9 of 10
## ...Run 10 of 10

g_analysis$stable_regions <- g_analysis$stable_regions / r_max
g_analysis$timesteps <- g_analysis$timesteps / r_max

g_analysis

##   cultural_features stable_regions timesteps
## 1                  5            2.6    75978.4
## 2                  10           1.0   103602.0
## 3                  15           1.0   124562.3

```

The *stable_regions* column in the *g_values* dataframe should show that when there are five cultural features ($g = 5$), there is more than one stable region, i.e. polarization. When there are ten or fifteen features, there is a single stable region, i.e. homogeneity. This matches the middle column of Axelrod's Table 2, for 10 traits per feature (Axelrod found a mean of 3.2 stable regions for $g = 5$, and 1.0 for $g = 10$ and $g = 15$). The *timesteps* column in *g_values* reassures us that stability was reached, because they are all much less than the t_{max} value that was defined.

Summary of Model 10

The notable feature of Model 10, a replication of Axelrod (1997), is the apparent contradiction between the local interactions of agents and the global dynamics of the model. At the local level, individual agents preferentially interact with neighbours who are more culturally similar to themselves. Their only possible action is to become even more similar by adopting their neighbour's traits with a probability proportional to their similarity. Yet at the global level, we often see the emergence of stark cultural divisions between regional clusters of agents who are maximally different to other clusters.

Global polarization can therefore emerge despite local preferences for cultural convergence. This perhaps gives some insight into real-world polarization, from racial and socio-economic segregation in cities, to the balkanization of regions within states, to political polarization on social media. These socially undesirable patterns may not necessarily be the result of people's tendencies to denigrate outgroups or make themselves as dissimilar as possible to others. They may instead be a by-product of the benign desire to preferentially assort with culturally similar others, and become even more similar to those similar others. If the latter is true (and such a claim needs to be empirically tested), this may change how we try to tackle such real world social problems.

Interestingly and counter-intuitively, polarization is more likely to be observed when there are fewer cultural features (a smaller g in the model). One way of avoiding polarization may therefore be to emphasise the many ways in which people differ. There are not just conservatives and liberals, there are conservatives

who are also football fans and enjoy hiking and like romantic comedies and listen to country music. The more features people may assort on, the more likely interactions are to occur. Axelrod (1997) also found that polarization is reduced when (i) agents interact with more agents, i.e. have more neighbours than just the four we simulated in Model 10, and (ii) when territories are larger, i.e. there are more agents overall. Increasing the range of interactions and number of interactants may therefore be another way to reduce polarization.

On the other hand, the alternative outcome of the model is complete cultural homogeneity. This is also often undesirable. Cultural evolution requires variation on which selection for better alternatives can act. No variation means no adaptation. The loss of minority knowledge, customs and traditions leaves societies less culturally rich and less resilient to environmental change. The cause of homogeneity in Model 10 is similar to the assortation from Model 6, but on multiple traits not just one. The outcome is also similar to conformity (Model 5), which similarly causes the cultural majority to subsume the minority. To preserve minority traditions, some way is needed to counter the benign desire to assort with and copy similar others.

Of course, there are many processes missing from this simple model. Cultural mutation would constantly introduce new variation, acting against both homogeneity and polarization (although see Klemm et al. 2005). Inter-regional competition may shift or dissolve the boundaries between stable regions. The cultural features in Model 10 are simply markers of identity; if instead they affected payoffs, then individuals might happily adopt high-payoff traits from otherwise dissimilar others. Agents are fixed in position and stuck with the same neighbours forever, rather than being able to form new links to other agents (see Centola et al. 2007). Real-world cultural evolution is complex, but the value of simple models like Axelrod's is to better understand the many simple processes that contribute to a messy, complex reality. What's more, the dynamics of even simple models like this are often counter-intuitive, as we have seen with the emergence of global polarization despite local convergence, and the effect of g .

One programming innovation of Model 10 was using a matrix to simulate agents within a spatially explicit grid. Each agent's traits were placed in a fixed position in a square matrix. The [row,column] matrix notation was used to retrieve an agent's position as well as their neighbours with whom they interact. Matrices can be rectangular as well as square, and also one-dimensional (essentially a line of agents). We also modelled multiple cultural traits per agent, specifically g cultural features each of which could take one of ten values. This goes beyond the one or two traits and trait values of previous models. We encoded these as character variables to preserve the leading zeroes, which would disappear if we used numeric variables. We converted the character to numeric to compare agents and their neighbours. You should use whatever variable type is most appropriate for the task. Some other minor coding tips: first, use **break** to break out of loops once you know there will be no further change, or once some condition has been fulfilled, to avoid wasting time; second, always make sure that **sample** is picking from more than one element, never a single element, otherwise things can go wrong; and second, add messages using **cat** to keep track of the progress of the simulation.

Exercises

1. Create some code to track the number of unique regions in every timestep, averaged across r_{max} independent runs. Plot this average value over time. Does the number of unique regions decline steadily over time or show a different pattern?
2. In the Model 10 simulations, the number of traits per feature is fixed at 10 (the integers 0-9). Axelrod varied this, comparing 10 with 5 and 15. Modify **Polarization** to make the number of traits per feature a user-defined variable. Run a similar analysis to the *g_analysis* above, but varying both g and the number of traits per feature. Use this to replicate all of Axelrod's Table 2, showing the mean number of stable regions for every combination of five, ten and fifteen features and traits per feature.

3. Analyse the effect of varying N_{side} , the size of the grid within which agents are placed, and hence the number of agents in the population. Run a similar analysis to the *g_analysis* above, but varying N_{side} , and keeping $g = 5$ and fifteen traits per feature. Plot the average number of stable regions against N_{side} to replicate Axelrod's Figure 2.
 4. In **Polarization** we assumed that each agent had at most four neighbours, to the north, south, east and west (agents at edges and corners had fewer). This is known as a von Neumann neighbourhood, after the mathematician and computer scientist John von Neumann. An alternative is to also include the four agents to the north-west, north-east, south-west and south-east. This gives a maximum of eight neighbours (again, agents at edges and corners will have fewer). This is known as a Moore neighbourhood, after the mathematician and computer scientist Edward F Moore. Modify **Polarization** such that agents have a Moore neighbourhood rather than a von Neumann neighbourhood. Does this increase or decrease the number of stable regions?
 5. Modify **Polarization** (with either von Neumann or Moore neighbourhoods) such that neighbourhoods wrap around to the other side of the grid. In other words, an agent at the extreme west edge of the grid will have neighbours to the north, east and south as previously, but also a neighbour to the west, which will be the agent in the same row at the extreme east of the grid. Agents in the corners wrap around in both the north-south and east-west axes. Every agent therefore has exactly four neighbours assuming von Neumann neighbourhoods, or exactly eight assuming Moore neighbourhoods. Do overlapping edges increase or decrease the number of stable regions?
 6. Add mutation to **Polarization**. In each timestep, pick an agent at random, pick one of their features at random, and with a certain probability determined by a user-defined parameter, switch this feature to a different, random trait value. Complete stability will never be reached with mutation, but explore the effect of mutation on the number of approximately stable regions, and the speed with which this approximate stability is reached, compared to the case of no mutation.
-

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Simulation Models of Cultural Evolution in R

Alex Mesoudi

Model 11: Cultural group selection

The evolution of human cooperation

The evolution of cooperation is a major topic across the biological and social sciences. Cooperation is defined as helping another individual, often at some cost to the helper (costly cooperation is sometimes called ‘altruism’ or ‘altruistic cooperation’). Cooperation is rife in nature, from parents looking after their offspring to sterile worker bees feeding their queen. It also underpins all human societies, from sharing food to paying taxes. Yet altruistic cooperation is a puzzle. All else being equal, a defector (or ‘free-rider’) who never cooperates yet receives help from others will do better than an altruistic cooperator who bears the cost of helping. Consequently, the emergence and maintenance of cooperation requires explanation (West et al. 2007).

This basic free-rider problem applies to the genetic evolution of cooperative behaviour in nature, where costs and benefits are incurred and accrued in the currency of lifetime biological fitness (West et al. 2007). It also applies to human societies where costs and benefits take the form of monetary or other kinds of more immediate payoffs (Apicella & Silk 2019). Examples include taxation systems where free-riding is not paying tax yet benefiting from publicly-funded roads, schools and hospitals, or communal living, where defectors who never wash dishes free-ride on the washing up effort of others. Such systems are characterised by a conflict between the individual and group level: within groups, free-riding individuals do better than cooperating individuals, yet groups of cooperators collectively do better than groups of free-riders. Non-dish-washing free-riders expend less effort than diligent dish-washers yet benefit from using clean dishes washed by others. Yet if everyone free-rides, the dishes quickly pile up.

Solutions to the free-rider problem include kin selection, where cooperators direct help to genetic relatives; reciprocity, where cooperators direct help to others who are likely to return the favour; and punishment, where cooperators punish defectors for not cooperating (West et al. 2007; Apicella & Silk 2019). Yet each of these has limitations with respect to human cooperation: kin selection cannot explain cooperation towards non-kin, which humans do frequently; reciprocity cannot explain cooperation between strangers and breaks down in large groups, which are again common features of human societies; and punishment is itself costly, leading to a second-order free-rider problem where non-punishing cooperators outcompete punishing cooperators.

Consequently, some cultural evolution researchers have suggested that human cooperation can arise via *cultural group selection* (Richerson et al. 2016). This occurs when more-cooperative groups outcompete less-cooperative groups in between-group competition. Genetic group selection does not seem to work: between-group genetic variation is easily broken down by migration, and individual-level natural selection is too strong. Cultural evolution, however, provides better conditions: rapid cultural selection (Model 3) can generate differences between groups, and processes such as conformity (Model 5) or polarisation (Model 10) can maintain between-group cultural variation despite frequent migration (see Model 7). Between-group competition can occur via direct conquest, e.g. warfare, where more-cooperative societies full of self-sacrificial fighters out-compete less-cooperative societies full of deserting back-stabbers. Or it can occur indirectly, such as where more-cooperative societies, e.g. ones with better social welfare systems, attract more migrants than less-cooperative societies. Success in between-group competition does not necessarily require the death of the defeated group’s members. Instead, defeated group members can disband and join the winning group.

The evolution of cooperation is a highly contentious topic. Verbal arguments often go round in circles because different scholars have different understandings of terms like cooperation, punishment and group selection. This makes formal models crucial for clarifying assumptions and arguments.

Here we will recreate an influential agent-based model of cultural group selection from Boyd, Gintis, Bowles & Richerson (2003). This model features costly (i.e. altruistic) punishment within groups, mixing / migration between groups, payoff-biased social learning and between-group selection. While it is not the only model of cultural group selection, it provides a good example to help understand and evaluate the hypothesis.

The model

Let's introduce the model step by step, with code, before putting it all inside a function. There are N groups each containing a fixed number of n individuals. Individuals come in three types, characterised by three different behaviours: cooperators (C), defectors (D) and punishers (P).

As the model is quite complex, we will use matrices instead of dataframes as they are faster. The code below creates a matrix with N columns, one per group, and n rows, one per agent, to hold the type (C, D or P). As before, we use [row,column] notation to access a specific agent. For example, `agent[3,2]` returns the behaviour of the second agent in the third group. For now we assume $N = 4$ groups with $n = 4$ agents per group. One group has Cs and Ds, one Ps and Ds, one a mix of all three types, and one all Ds.

```
N <- 4 # 4 groups
n <- 4 # 4 agents per group

# create agent matrix, each column is a group
# can be C (cooperator), D (defector) or P (punisher)
agent <- matrix(nrow = n, ncol = N)

agent[,1] <- c("C", "C", "D", "D")
agent[,2] <- c("D", "D", "P", "P")
agent[,3] <- c("P", "P", "C", "D")
agent[,4] <- c("D", "D", "D", "D")

agent
```

```
##      [,1] [,2] [,3] [,4]
## [1,] "C"  "D"  "P"  "D"
## [2,] "C"  "D"  "P"  "D"
## [3,] "D"  "P"  "C"  "D"
## [4,] "D"  "P"  "D"  "D"
```

Now we create a payoff matrix. This has the same structure as `agent`. Each position in `payoff` holds the payoff for the individual in the equivalent position in `agent`. For example, `payoff[3,2]` holds the payoff of the second agent in group 3. All individuals start with a baseline payoff of 1, from which various costs are subtracted. (NB While this baseline payoff of 1 is not explicitly specified in Boyd et al. 2003, it is needed to avoid negative payoffs. Negative payoffs would mess up subsequent calculations of relative payoffs.)

```
# create payoff matrix, with baseline payoff 1
payoff <- matrix(1, nrow = n, ncol = N)

payoff
```

```
##      [,1] [,2] [,3] [,4]
```

```

## [1,] 1 1 1 1
## [2,] 1 1 1 1
## [3,] 1 1 1 1
## [4,] 1 1 1 1

```

Now we simulate five stages that occur in each timestep.

Stage 1 is cooperation. Cooperators and punishers cooperate with probability $1 - e$ and defect with probability e . The parameter e represents errors, where Cs or Ps defect by mistake when they meant to cooperate. For now we will set $e = 0$ to keep the output the same when you run it, but you can increase it to explore its effect here. We will increase it in the simulations below to $e = 0.01$.

Cooperation reduces the cooperating agent's payoff by c . This makes cooperation costly, i.e. altruistic. Defectors always defect and pay no cost. We set $c = 0.2$, representing a fairly substantial cost.

The following vectorised code implements this. To identify contributors we create a matrix of probabilities, *contribute*, to compare against $1 - e$ for each P and C agent. This gives a matrix *contributors* that is TRUE if the agent contributes and FALSE if they don't. Contributing agents' payoffs are then reduced by c . Because $e = 0$, the matrices will show that all the Ps and Cs pay the cost, and the Ds do not. At this stage, defection pays.

```

e <- 0 # cooperation error rate
c <- 0.2 # cost of cooperation

# probs for contribution (1-e)
contribute <- matrix(runif(n*N), nrow = n, ncol = N)

# contributors are Ps or Cs with prob 1-e
contributors <- (agent == "P" | agent == "C") & contribute > e

# reduce payoffs of contributing Ps and Cs by c
payoff[contributors] <- payoff[contributors] - c

contributors

##      [,1]  [,2]  [,3]  [,4]
## [1,] TRUE FALSE TRUE FALSE
## [2,] TRUE FALSE TRUE FALSE
## [3,] FALSE TRUE  TRUE FALSE
## [4,] FALSE TRUE FALSE FALSE

payoff

##      [,1]  [,2]  [,3]  [,4]
## [1,] 0.8  1.0  0.8   1
## [2,] 0.8  1.0  0.8   1
## [3,] 1.0  0.8  0.8   1
## [4,] 1.0  0.8  1.0   1

```

Stage 2 is punishment. Punishers (Ps) punish every agent in their group who defected in the first stage. Punishment reduces each punished agent's payoff by p/n at a cost of k/n to the punisher. The parameter k makes punishment costly, i.e. altruistic.

Note that punishment scales with the number of defectors: the more punishers there are in a group, the more punishment defectors receive. The more defectors there are, the more costly punishment is to the punisher.

We set $p = 0.8$ and $k = 0.2$ such that punishment is more costly for the punished than the punisher. For example, the cost of burning down someone's house is less than the cost of having your house burned down.

In the following code, we first identify groups that have at least one P using *Pgroups*. We only need to apply our punishment routine to these groups. This saves a bit of time. Then we get a matrix of *defections*, those agents who are D or who are P or C with probability e . Then we cycle through each agent i of each punishment group j using two **for** loops. For each punishing agent, we reduce the punisher's payoff by k/n per defector in their group, and each defector's payoff by p/n . Note that to get all group members except the focal individual, we use the negative sign. For example, *payoff*[-i, j] returns all payoffs of agents in group j who are not i .

```

p <- 0.8 # cost to punished
k <- 0.2 # cost to punisher

# columns/groups with at least one P
Pgroups <- unique(which(agent=="P", arr.ind=TRUE)[, "col"])

# defections (Ds and Ps/Cs with probability e)
defections <- agent == "D" | ((agent == "P" | agent == "C") & contribute <= e)

# cycle thru Pgroups (j) and agents (i)
for (j in Pgroups) {

  for (i in 1:n) {

    # if the agent is P
    if (agent[i,j] == "P") {

      # reduce punisher's payoff by k/n per defection
      payoff[i,j] <- payoff[i,j] - sum(defections[-i,j]) * k / n

      # reduce each defector's payoff by p/n
      payoff[-i,j][defections[-i,j]] <- payoff[-i,j][defections[-i,j]] - p / n
    }
  }
}

payoff

##      [,1] [,2] [,3] [,4]
## [1,]  0.8  0.6  0.75   1
## [2,]  0.8  0.6  0.75   1
## [3,]  1.0  0.7  0.80   1
## [4,]  1.0  0.7  0.60   1

```

In the resulting *payoff* matrix above, the first and last groups are unchanged because they contain no punishers and so there is no punishment. The Ds of the second group have each been punished by two Ps, reducing their payoffs by $2p/n = 0.4$. The Ps in group 2 pay the cost of punishing two individuals, which is $2k/n = 0.1$. This is subtracted from the 0.8 they already had after paying the costs of cooperation. In the third group, the two Ps each punish the single D via similar calculations. The C is unchanged, as it neither punishes nor is punished.

Note the effect of punishment. Ds now do worst in the second and third groups because they receive punishment. However, in the third group, the C does better than the Ps because punishment is costly. This illustrates the second-order free rider problem that characterises punishment: it's better to let others punish than to do the punishment yourself. But if no one punishes, defectors do best.

Stage 3 is payoff-biased social learning combined with inter-group mixing. With probability $1 - m$, agents interact with a random member of their own group. With probability m , agents interact with a random member of another group. Hence m controls the rate of between-group mixing. We will set $m = 0.01$, giving a 1/100 chance of interacting with members of other groups. Technically this is not quite 'migration', because the original agent remains in its group. But it has the same effect of transmitting behavioural types between groups.

Once a demonstrator is chosen, the focal individual then copies the behaviour (C, D or P) of the demonstrator with probability

$$\frac{W_{dem}}{(W_{dem} + W_{focal})}$$

where W_{dem} is the payoff of the demonstrator and W_{focal} is the payoff of the focal agent, after the cooperation and punishment costs have been subtracted. High-payoff behaviours are therefore more likely to be copied.

The following code implements this by cycling through each agent. We store *agent* as *previous_agent* to make sure that all social leaning occurs from the same population of agents. Otherwise, as we cycle through the agents, the later agents might copy agents who have already copied. Then we cycle through groups (j) and agents (i). Each agent picks a random demonstrator from the same group with probability $1 - m$ and a different group with probability m . *dem* takes two integers that denote the [row,col] coordinates of the demonstrator. This is done with **sample** on a set of numbers excluding self (i) for within-group copying (assuming you cannot copy yourself), and excluding one's own group (j) for other-group copying. Relative fitness W is calculated as per the equation above, and with this probability, the agent adopts the demonstrator's behaviour.

```
m <- 0.01 # rate of between-group mixing

# store agent in previous agent to avoid overlap
previous_agent <- agent

# cycle thru groups (j) and agents (i)
for (j in 1:N) {

  for (i in 1:n) {

    # with prob 1-m, choose demonstrator from same group (excluding self)
    if (runif(1) > m) {

      dem <- c(sample((1:n)[(1:n)!=i], 1), j)

      # with prob m, choose demonstrator from different group
    } else {

      dem <- c(sample(1:n, 1),
              sample((1:N)[(1:N)!=j], 1))

    }

    # get W, relative payoff of demonstrator
    W <- payoff[dem[1],dem[2]] / (payoff[dem[1],dem[2]] + payoff[i,j])
  }
}
```

```

# copy dem's behaviour with prob W
# use previous_agent to avoid copying an agent who has already copied
if (runif(1) < W) {

  agent[i,j] <- previous_agent[dem[1],dem[2]]

}

}

agent

##      [,1] [,2] [,3] [,4]
## [1,] "C"  "D"  "C"  "D"
## [2,] "C"  "P"  "P"  "D"
## [3,] "C"  "P"  "D"  "D"
## [4,] "D"  "P"  "D"  "D"

```

Each output will be different, but you should see that some agents in each group have switched to a different behaviour. It will be hard to see here, but over multiple generations higher-payoff behaviours will spread at the expense of lower-payoff behaviours.

Stage 4 is group selection. Groups are paired at random and with probability ε enter into a contest. We set $\varepsilon = 0.5$, an unrealistically high rate of inter-group conflict for demonstration purposes. (Boyd et al. set $\varepsilon = 0.015$ to reflect the estimated rate of inter-group conflict in small-scale societies.)

Groups with more cooperators (i.e. cooperating Cs and Ps) are more likely to win contests. This reflects the assumption that cooperation contributes to group success. More cooperation means greater effort in battle, greater willingness to pay taxes that fund armies, lower likelihood of selling secrets to the enemy, etc., all of which improves a group's chances of winning a contest relative to less-cooperative groups full of back-stabbing, deserting, tax-evasive free-riders.

Formally, the probability that group 1 defeats group 2 in a pair is

$$\frac{1}{2} + \frac{(d_2 - d_1)}{2}$$

where d_1 is the proportion of defectors in group 1 of a pair and d_2 is the proportion of defectors in group 2 of the pair. When both groups have the same proportion of defectors, then $d_2 - d_1 = 0$ and there is a 50% chance of either group winning. When group 1 has fewer defectors than group 2, then $d_2 - d_1 > 0$ and group 1 has a greater chance ($>50\%$) of winning. When group 2 has fewer defectors than group 1, then $d_2 - d_1 < 0$ and group 1 has a smaller chance ($<50\%$) of winning.

The following code implements this. First we pair up each group at random in a dataframe *contests*, with a proportion ε kept and the rest discarded. (We use a dataframe here because sometimes we have only one contest left; a single-row matrix becomes a vector, which becomes a problem later on.) After re-calculating *defections* given the new post-social-learning behaviours, we cycle through each contest and calculate the probability d of the first group winning based on the equation above. With this probability, group 1 wins and group 2 takes on group 1's behaviours. Otherwise group 2 wins and group 1 takes on group 2's behaviours.

```
epsilon <- 0.5 # frequency of conflict
```

```

# dataframe of randomly selected pairs of groups
contests <- as.data.frame(matrix(sample(N), nrow = N/2, ncol = 2))

# keep contests with prob epsilon
contests <- contests[runif(N/2) < epsilon,]

# recalculate defections (Ds and Ps/Cs with probability e)
defections <- agent == "D" | ((agent == "P" | agent == "C") & contribute <= e)

# if there are any contests left
if (nrow(contests) > 0) {

  # cycle thru pairs
  for (i in 1:nrow(contests)) {

    # prob group 1 beats group 2 in pair i
    d1 <- sum(defections[,contests[i,1]]) / n
    d2 <- sum(defections[,contests[i,2]]) / n
    d <- 0.5 + (d2 - d1)/2

    # group 1 wins
    if (runif(1) < d) {

      agent[,contests[i,2]] <- agent[,contests[i,1]]

      # group 2 wins
    } else {

      agent[,contests[i,1]] <- agent[,contests[i,2]]
    }
  }
}

agent

##      [,1] [,2] [,3] [,4]
## [1,] "C"  "D"  "D"  "D"
## [2,] "C"  "P"  "P"  "D"
## [3,] "C"  "P"  "P"  "D"
## [4,] "D"  "P"  "P"  "D"

```

With $\varepsilon = 0.5$ there is a good chance that one of the groups has been replaced with another (re-run the code above if not). The winning group has effectively replicated themselves, at the expense of the losing group. This is cultural group selection.

Stage 5 is mutation. There is a probability μ that each agent will mutate into one of the other two types (i.e. C into D or P; P into C or D; and D into C or P). This keeps a small, constant supply of new variation coming into the population so that we are not entirely reliant on the starting combination of behaviours.

The following code does this, with an unrealistically high $\mu = 0.5$ for demonstration purposes. Much like in Model 2, we create $N * n$ probabilities for each agent, and if the probability for an agent is less than μ

then we mutate into one of the other two types at random. In the resulting *agent* matrix, roughly half of the agents should have switched behaviours.

```

mu <- 0.5 # mutation rate

# probs for mutation
mutate <- runif(N*n)

# store agent in previous agent to avoid overlap
previous_agent <- agent

# mutating D agents
agent[mutate < mu & previous_agent == "D"] <-
  sample(c("P", "C"),
         sum(mutate < mu & previous_agent == "D"),
         replace = TRUE)

# mutating C agents
agent[mutate < mu & previous_agent == "C"] <-
  sample(c("P", "D"),
         sum(mutate < mu & previous_agent == "C"),
         replace = TRUE)

# mutating D agents
agent[mutate < mu & previous_agent == "P"] <-
  sample(c("D", "C"),
         sum(mutate < mu & previous_agent == "P"),
         replace = TRUE)

agent

##      [,1] [,2] [,3] [,4]
## [1,] "C"  "D"  "D"  "P"
## [2,] "C"  "P"  "P"  "D"
## [3,] "D"  "D"  "P"  "P"
## [4,] "C"  "D"  "C"  "D"

```

These five stages comprise the events that happen in each timestep of the model, from $t = 1$ to $t = t_{max}$. As is often the case, it's not clear what will happen in the long run. Defectors have higher payoffs within groups, unless they are punished in which case punishers can do better, unless there are cooperators who get the benefit of punishment without its cost. Which type will payoff-biased social learning favour? Group selection favours groups of cooperators over defectors, but will there be enough Cs or Ps in a group to allow this to happen? To find out, we need to simulate over many generations.

The code below puts all five stages together into a single function called **Cooperation**. As in previous models, we add a t-loop iterating all of the five stages, create a dataframe called *output* which records in each timestep the frequency of cooperating agents (Cs and Ps combined) and just the Ps, and end by plotting the results. The plot contains a solid line for overall cooperation (all Cs and Ps), and a dotted line for just the Ps, over all timesteps. The output of the model comprises the final generation *agent* matrix, the *output* dataframe, and the mean cooperation in the last 50% of generations as reported by Boyd et al. (2003).

Following Boyd et al., the initial generation consists of one group containing all Ps, and the rest containing all Ds. This reflects a situation where drift or individual learning has created a single punishing group amongst a larger population of defectors. Also following Boyd et al., we assume $N = 128$ groups, so the odds are stacked in the D's favour.

Given that there are lots of parameters, we specify default parameter values from Boyd et al. (2003) so there is no need to remember them.

```
Cooperation <- function(N = 128,
                        n = 4,
                        t_max = 2000,
                        e = 0.02,
                        c = 0.2,
                        m = 0.01,
                        p = 0.8,
                        k = 0.2,
                        mu = 0.01,
                        epsilon = 0.015,
                        show_plot = TRUE) {

  # create agent matrix, each column is a group
  # can be C (cooperator), D (defector) or P (punisher)
  agent <- matrix(nrow = n, ncol = N)

  # initial conditions: group 1 all punishers, others are all defectors
  agent[,1] <- "P"
  agent[,-1] <- "D"

  # create output for freq of cooperation in each timestep
  # and freq of punishment
  output <- data.frame(PandC = rep(NA, t_max),
                        P = rep(NA, t_max))

  # store for t = 1
  output$PandC[1] <- sum(agent == "C" | agent == "P") / (N*n)
  output$P[1] <- sum(agent == "P") / (N*n)

  for (t in 2:t_max) {

    # create/initialise payoff matrix, with baseline payoff 1
    payoff <- matrix(1, nrow = n, ncol = N)

    # 1. Cooperation

    # probs for contribution (1-e)
    contribute <- matrix(runif(n*N), nrow = n, ncol = N)

    # contributors are Ps or Cs with prob 1-e
    contributors <- (agent == "P" | agent == "C") & contribute > e

    # reduce payoffs of contributing Ps and Cs by c
    payoff[contributors] <- payoff[contributors] - c

    # 2. Punishment

    # columns/groups with at least one P
    Pgroups <- unique(which(agent=="P", arr.ind=TRUE)[,"col"])

    # defections (Ds and Ps/Cs with probability e)
```

```

defections <- agent == "D" | ((agent == "P" | agent == "C") & contribute <= e)

# cycle thru Pgroups (j) and agents (i)
for (j in Pgroups) {

  for (i in 1:n) {

    # if the agent is P
    if (agent[i,j] == "P") {

      # reduce punisher's payoff by k/n per defection
      payoff[i,j] <- payoff[i,j] - sum(defections[-i,j]) * k / n

      # reduce each defector's payoff by p/n
      payoff[-i,j][defections[-i,j]] <- payoff[-i,j][defections[-i,j]] - p / n

    }

  }

}

# 3. Social learning

# store agent in previous agent to avoid overlap
previous_agent <- agent

# cycle thru groups (j) and agents (i)
for (j in 1:N) {

  for (i in 1:n) {

    # with prob 1-m, choose demonstrator from same group (excluding self)
    if (runif(1) > m) {

      dem <- c(sample((1:n)[(1:n)!=i], 1), j)

      # with prob m, choose demonstrator from different group
    } else {

      dem <- c(sample(1:n, 1),
              sample((1:N)[(1:N)!=j], 1))

    }

    # get W, relative payoff
    W <- payoff[dem[1],dem[2]] / (payoff[dem[1],dem[2]] + payoff[i,j])

    # copy dem's behaviour with prob W
    # use previous_agent to avoid copying an agent who has already copied
    if (runif(1) < W) {

      agent[i,j] <- previous_agent[dem[1],dem[2]]

    }

  }

}

}

```

```

    }

}

}

# 4. Group selection

# dataframe of randomly selected pairs of groups
contests <- as.data.frame(matrix(sample(N), nrow = N/2, ncol = 2))

# keep contests with prob epsilon
contests <- contests[runif(N/2) < epsilon,]

# recalculate defections (Ds and Ps/Cs with probability e)
defections <- agent == "D" | ((agent == "P" | agent == "C") & contribute <= e)

# if there are any contests left
if (nrow(contests) > 0) {

  # cycle thru pairs
  for (i in 1:nrow(contests)) {

    # prob group 1 beats group 2 in pair i
    d1 <- sum(defections[,contests[i,1]]) / n
    d2 <- sum(defections[,contests[i,2]]) / n
    d <- 0.5 + (d2 - d1)/2

    # group 1 wins
    if (runif(1) < d) {

      agent[,contests[i,2]] <- agent[,contests[i,1]]

      # group 2 wins
    } else {

      agent[,contests[i,1]] <- agent[,contests[i,2]]
    }
  }
}

# 5. Mutation

# probs for mutation
mutate <- runif(N*n)

# store agent in previous agent to avoid overlap
previous_agent <- agent

# mutating D agents

```

```

agent[mutate < mu & previous_agent == "D"] <-
  sample(c("P", "C"),
         sum(mutate < mu & previous_agent == "D"),
         replace = TRUE)

# mutating C agents
agent[mutate < mu & previous_agent == "C"] <-
  sample(c("P", "D"),
         sum(mutate < mu & previous_agent == "C"),
         replace = TRUE)

# mutating D agents
agent[mutate < mu & previous_agent == "P"] <-
  sample(c("D", "C"),
         sum(mutate < mu & previous_agent == "P"),
         replace = TRUE)

# 6. Record freq of cooperation

output$PandC[t] <- sum(agent == "C" | agent == "P") / (N*n)
output$P[t] <- sum(agent == "P") / (N*n)

}

if (show_plot == TRUE) {

  plot(x = 1:nrow(output),
        y = output$PandC,
        type = 'l',
        ylab = "frequency of cooperation",
        xlab = "generation",
        ylim = c(0,1))

  # dotted line for freq of Ps
  lines(x = 1:nrow(output),
        y = output$P,
        type = 'l',
        lty = 3)

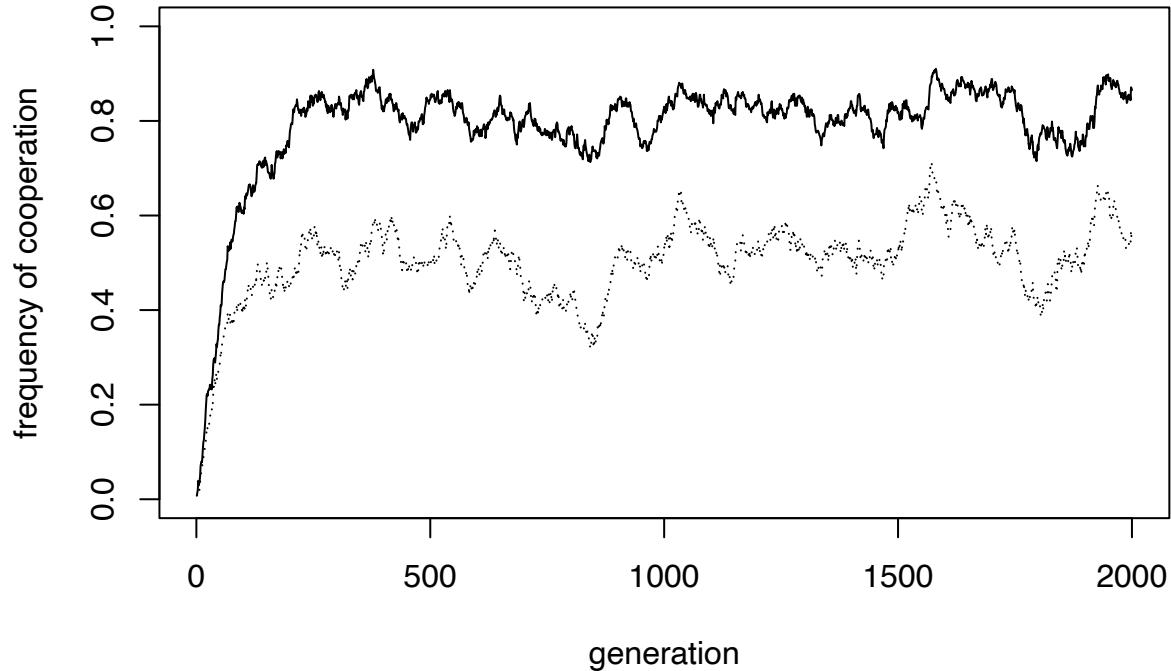
}

# output final agent, full output, and mean cooperation of last 50% of timesteps
list(agent = agent,
     output = output,
     mean_coop = mean(output$PandC[(t_max/2):t_max]))
```

}

One run of the model with default values gives the following plot:

```
data_model11 <- Cooperation()
```



In small groups of $n = 4$, cooperation increases to around 0.8. For the above output, the mean cooperation in the final 50% of timesteps is 0.83. A slight majority are Ps, with the rest Cs.

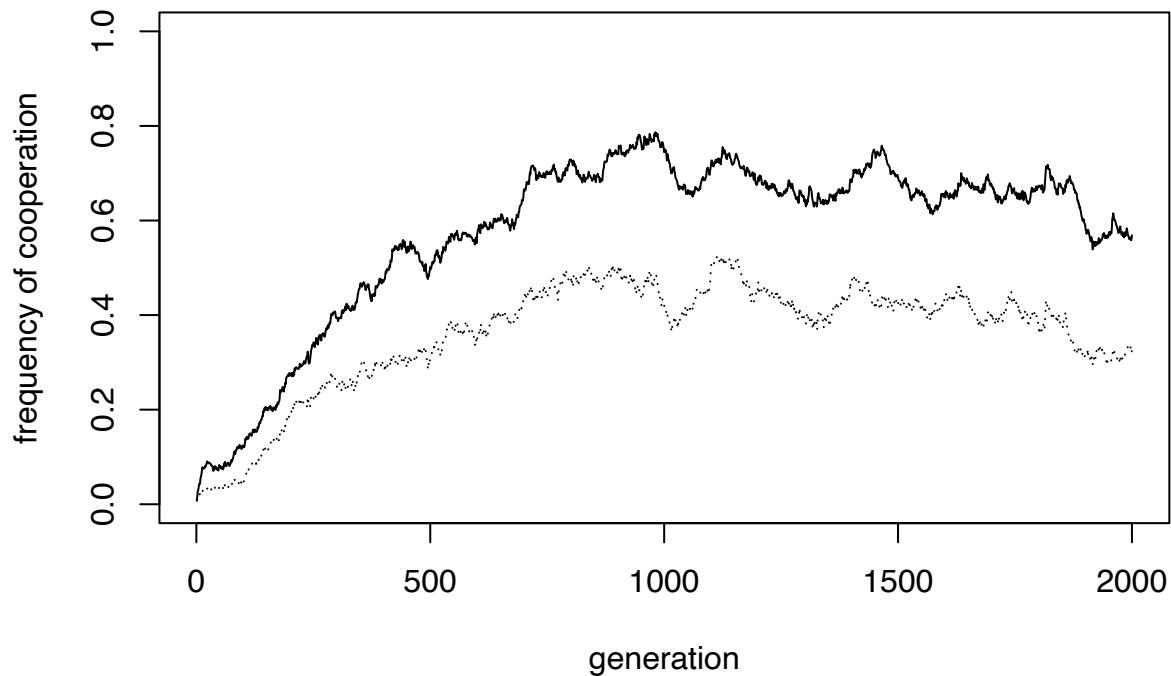
A look at a sample of the final generation population shows that groups are quite homogenous, comprising either all Ps, all Cs or all Ds. There are some dissimilar agents, most likely due to mutation or between-group social learning. This within-group homogeneity and between-group heterogeneity is a hallmark of cultural group selection.

```
data_model11$agent[,1:25]
```

```
##      [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10] [,11] [,12] [,13] [,14]
## [1,] "P"  "C"  "C"  "P"  "D"  "P"  "C"  "P"  "P"  "P"  "P"  "P"  "P"  "C"  "P"
## [2,] "P"  "C"  "D"  "P"  "C"  "P"  "C"  "P"  "P"  "P"  "P"  "P"  "P"  "C"  "P"
## [3,] "P"  "C"  "C"  "P"  "C"  "P"  "C"  "P"  "P"  "P"  "P"  "P"  "P"  "C"  "P"
## [4,] "P"  "C"  "D"  "P"  "C"  "P"  "C"  "P"  "P"  "P"  "P"  "P"  "P"  "C"  "P"
##      [,15] [,16] [,17] [,18] [,19] [,20] [,21] [,22] [,23] [,24] [,25]
## [1,] "P"  "P"  "C"  "C"  "C"  "P"  "P"  "D"  "C"  "P"  "P"
## [2,] "P"  "C"  "C"  "C"  "C"  "P"  "P"  "D"  "C"  "P"  "P"
## [3,] "P"  "C"  "C"  "C"  "C"  "P"  "P"  "D"  "C"  "P"  "P"
## [4,] "P"  "C"  "C"  "C"  "C"  "P"  "P"  "D"  "C"  "P"  "P"
```

Increasing the group size to $n = 32$ reduces the frequency of cooperation slightly, to around 0.7.

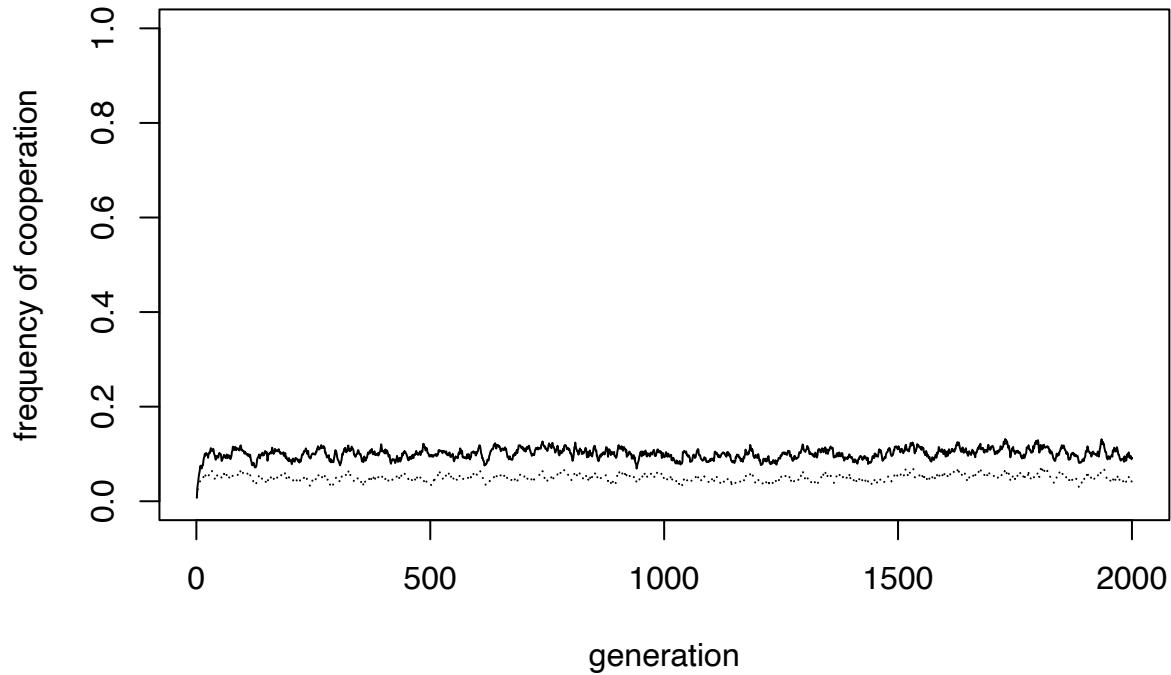
```
data_model11 <- Cooperation(n = 32)
```



In the plot above, the mean cooperation in the last 50% of timesteps is 0.67. It is a well-established finding that cooperation is harder to maintain in larger groups, but here cooperation only slightly declines.

By setting $p = k = 0$ we can remove punishment from the model:

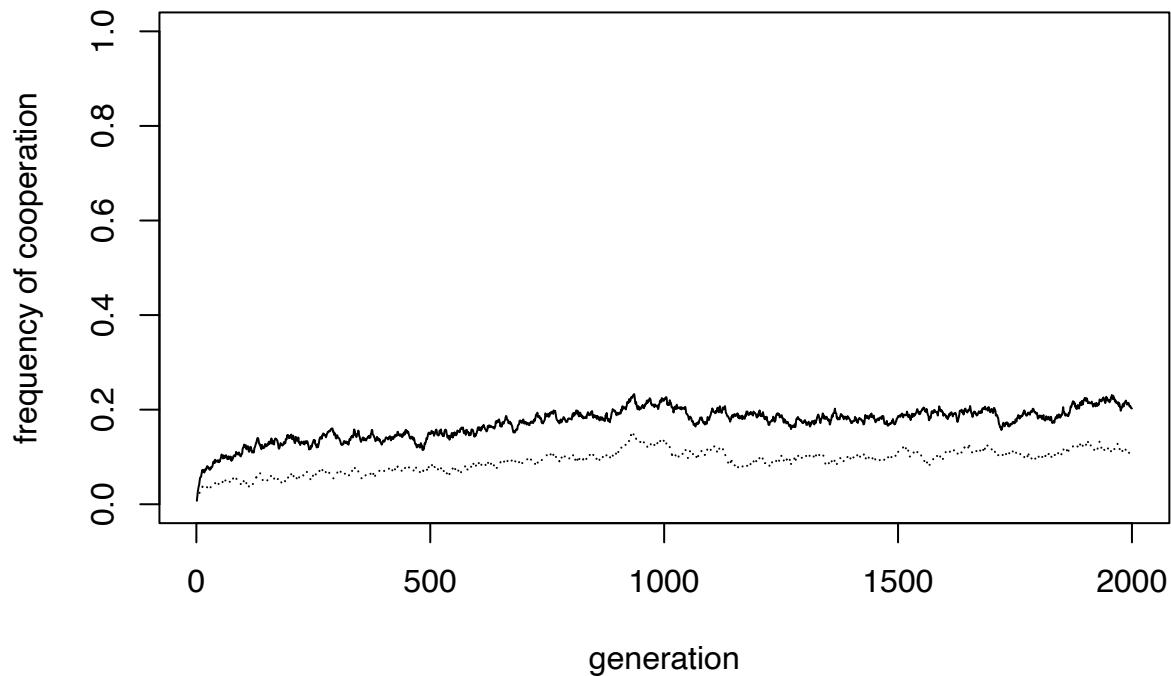
```
data_model11 <- Cooperation(n = 32, p = 0, k = 0)
```



Without punishment, cooperation almost disappears (in the plot above, the frequency of cooperation is 0.1). This shows that, even with group selection, some mechanism is needed to maintain cooperation within groups. These cooperative groups are then favoured by group selection. But if there is no such mechanism, group selection has nothing to select.

Conversely, we can remove group selection by setting the probability of inter-group competition $\varepsilon = 0$, and restoring punishment.

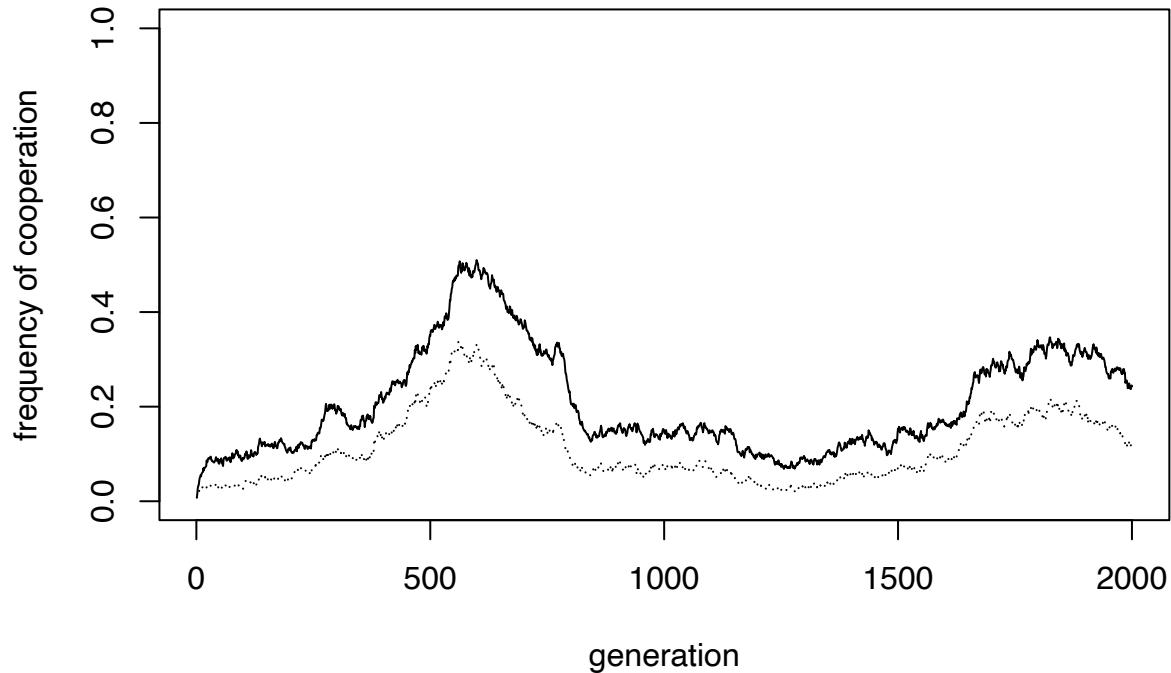
```
data_model11 <- Cooperation(n = 32, epsilon = 0)
```



Again, cooperation has all but disappeared (to 0.19 in the above plot). Without group selection, cooperation has no benefit, and is selected against.

Now let's increase the inter-group mixing rate from $m = 0.01$ to $m = 0.05$:

```
data_model11 <- Cooperation(n = 32, m = 0.05)
```



Inter-group mixing reduces cooperation (in the plot above to 0.18). Mixing, like migration, breaks down between-group variation and prevents group selection from acting. Because mixing operates alongside payoff-biased social learning, and defectors typically have higher fitness than cooperators, this results in the spread of defectors.

Finally, let's recreate one of the figures from Boyd et al. (2003). Their Figure 1b shows the frequency of cooperation across a range of group sizes (n), for three different rates of intergroup conflict (ε). The following code recreates this figure. Warning: it can take a while to run so many simulations. (NB Boyd et al. took an average of 10 independent runs for each parameter combination and went up to $n = 256$; the code below only has one run per parameter combination and goes up to $n = 64$. However, the results are qualitatively the same.)

```

n <- c(4,8,16,32,64)
epsilon <- c(0.0075,0.015,0.03)

output <- data.frame(matrix(NA, ncol = length(epsilon), nrow = length(n)))
rownames(output) <- n
colnames(output) <- epsilon

for (j in 1:length(epsilon)) {
  for (i in 1:length(n)) {
    output[i,j] <- Cooperation(n = n[i],
                                 epsilon = epsilon[j],
                                 show_plot = FALSE)$mean_coop
  }
}
  
```

```

}

}

plot(x = 1:length(n), y = output[,1],
      type = 'o',
      ylab = "frequency of cooperation",
      xlab = "group size",
      col = "darkblue",
      pch = 15,
      ylim = c(0,1),
      xlim = c(1,length(n)),
      xaxt = "n")

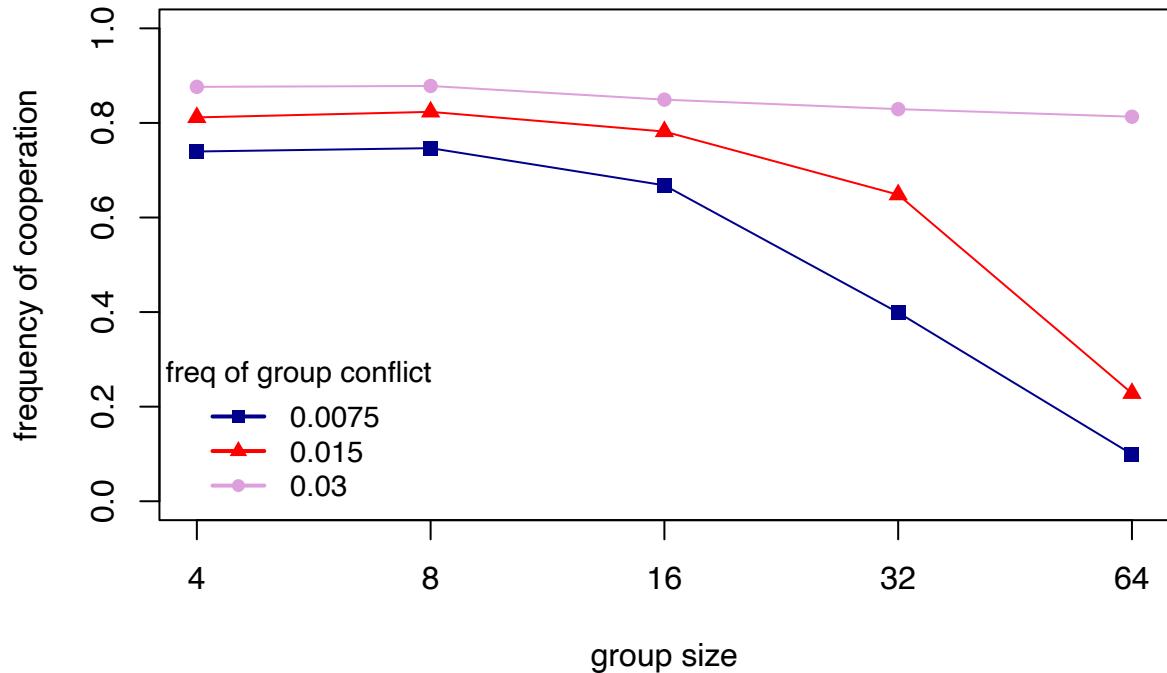
axis(1, at=1:length(n), labels=n)

lines(x = 1:length(n), output[,2],
      type = 'o',
      col = "red",
      pch = 17)

lines(x = 1:length(n), output[,3],
      type = 'o',
      col = "plum",
      pch = 16)

legend("bottomleft",
       legend = epsilon,
       title = "freq of group conflict",
       lty = 1,
       lwd = 2,
       pch = c(15,17,16),
       col = c("darkblue", "red","plum"),
       bty = "n",
       cex = 0.9)

```



The above figure shows that (i) cooperation declines with group size; (ii) higher rates of inter-group conflict maintain higher frequencies of cooperation; and (iii) at the highest rates of inter-group conflict, cooperation is maintained even in large groups.

Summary of Model 11

Cooperation underpins the social lives of countless species, including (and perhaps especially) human societies. Given the advantage that free-riders have over cooperators, cooperation requires special explanation. Many such explanations have been offered. Model 11, recreating a model by Boyd et al. (2003), provides one such explanation, combining altruistic punishment, payoff-biased social learning and cultural group selection.

We found, as did Boyd et al. (2003), that cooperation can be maintained in relatively large groups when these processes are acting together. Within groups, payoff-biased social learning is the selection mechanism. Because defectors have higher payoffs than cooperators, defection is selected and spreads within groups. Adding punishers turns the tables, with defectors' payoffs reduced by punishment. Yet without group selection, altruistic punishers will be out-competed by non-punishing cooperators, who benefit from others' punishment but do not pay the costs of punishing. But then we are back where we started, and defectors will out-compete the non-punishing cooperators. With group selection, however, groups of cooperating punishers spread at the expense of groups of defectors due to the benefit of cooperation in inter-group competition. Hence, cooperation spreads. Neither punishment nor group selection alone maintain cooperation; both are needed.

The model presented here is one version of a broad class of models of cultural group selection (Smith 2020). This one involves punishment. Others assume that rapid cultural adaptation or conformity maintain between-

group cultural variation, and inter-group competition favours more-cooperative groups. Some models assume preferential migration plus acculturation (see Model 7) rather than group extinction/replacement as we simulated here. There is no single ‘cultural group selection’ hypothesis, there are several. It is important to recognise that within-group mechanisms like punishment are not alternatives to cultural group selection, but rather are complementary. In Model 11, punishment favours cooperation within groups, while group selection solves the second-order free-rider problem that comes with punishment.

Cultural group selection is a controversial explanation for human cooperation (see Richerson et al. 2016 and associated commentaries; and also Smith 2020). This may be a legacy of the rejection of naive genetic group selection in biology in the 1960s. However, cultural group selection is different: it involves cultural rather than genetic variation, it applies only to humans, and it incorporates special assumptions about biased social learning, inter-group interactions etc. Nevertheless, models like Model 11 are just that: models. Evidence is needed to demonstrate that cultural group selection has been an important driver of cooperation in real human societies. Some such evidence exists, such as findings of substantial between-group cultural variation in cooperation-related behaviours (Richerson et al. 2016). Other evidence opposes cultural group selection, such as findings that people do not reliably socially learn cooperative behaviour (Lamba 2014). The value of models like Model 11 lies in clarifying theoretical assumptions and predictions, allowing those assumptions and predictions to be tested empirically.

In terms of programming, Model 11 is probably the most complex in this series so far. There are several stages within each timestep, and more parameters than any previous model. As a result, run times can be slow, particularly for large groups. Where possible we used matrices rather than dataframes and vectorised the code to improve speed. Unfortunately there is no straightforward way of vectorising the punishment and social learning stages (if you can think of one let me know!). We must accept that sometimes complex models take a while to run. Grab a cup of tea and watch TV, smug in the knowledge that your code is working for you in the background. More seriously, the important thing with complex models is to make and test each stage in turn under manageable assumptions (e.g. $N = 4$ rather than $N = 128$) before putting them all together, as we did above. This makes it much easier to catch bugs and to make sure that your code does what you think it does.

Exercises

1. Use the **Cooperation** function to explore the effect of the remaining parameters on the frequency of cooperation: (a) the error rate e ; (b) the cost of cooperation c ; (c) the mutation rate μ ; and (d) the number of groups N .
 2. Recreate Boyd et al.’s (2003) other figures, adapting the code above used to recreate their Figure 1b. Do you get the same results?
 3. Change the starting conditions, to (a) one group of all Cs and the rest all Ds; (b) all Ds (with Ps and Cs only appearing via mutation); and (c) random behaviours. Does cooperation still emerge with these different starting conditions?
 4. Add a new parameter b to the **Cooperation** function. Each cooperator (Cs and Ps with probability $1 - e$) generates a payoff benefit b which is shared equally amongst all group members (including defectors). This simulates the standard ‘Public Goods Game’ from economics. Now cooperation generates within-group benefits, as well as between-group benefits via group selection. Explore the effect of different values of b on overall cooperation levels.
-

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Simulation Models of Cultural Evolution in R

Alex Mesoudi

Table of parameters

Parameter	Definition	Model first introduced
N	Number of agents in the population.	1
t_{max}	Maximum number of timesteps or generations.	1
r_{max}	Maximum number of independent simulation runs.	1
p	Frequency of trait A .	1
p_0	Starting value of p .	1
μ	Probability of unbiased cultural mutation. Specifically, the probability of trait A mutating into trait B , or trait B mutating into trait A .	2
μ_b	Probability of biased cultural mutation. Specifically, the probability of trait B mutating into trait A .	2
s	Strength of biased transmission / cultural selection. Specifically, in Model 3 (direct bias) the probability of switching to a more favourable trait upon encountering another agent with that trait, or in Model 4 (indirect bias) the payoff advantage to trait A relative to trait B .	3
q	Frequency of a second trait in a two-trait model (trait X in Model 4), or the frequency of trait A in a second sub-population or group (Model 7).	4
q_0	Starting value of q .	4
L	Probability in two-trait models that the two traits are linked. Specifically, the probability that, if trait 1 is A , then trait 2 is X .	4
D	Strength of conformity. Specifically, the increased probability of adopting a majority trait, relative to unbiased transmission.	5
s_v	Strength of biased transmission / cultural selection under vertical cultural transmission. Specifically, the increased probability of adopting a favoured trait, relative to unbiased transmission, when only one parent holds that favoured trait.	6

Parameter	Definition	Model first introduced
s_h	Strength of biased transmission / cultural selection under horizontal cultural transmission. Specifically, the probability of switching to a more favourable trait upon encountering at least one of n demonstrators with that trait.	6
a	Probability of assortative mating under vertical cultural transmission, such that both parents have identical cultural traits.	6
n	Number of demonstrators from whom an agent learns under horizontal transmission (Model 6) or blending inheritance (Model 8).	6
m	Strength of migration. Specifically, the probability that each agent migrates to a randomly chosen sub-population.	7
e	Error in copying the traits of n demonstrators under blending inheritance. Specifically, the variance of the normal distribution with mean of the demonstrator trait value, from which the copied trait value is drawn.	8
α	Copying error in the ‘Tasmanian’ model of cultural gain/loss. Specifically, the amount by which the mode of a gumbel distribution is reduced relative to the highest skill level in the previous generation.	9
β	Inferential guesses or experimentation in the ‘Tasmanian’ model of cultural gain/loss. Specifically, the dispersion of the gumbel distribution from which the new skill level is drawn.	9
z_i	Culturally transmitted skill level of the i th agent in the ‘Tasmanian’ model of cultural gain/loss.	9
\bar{z}	Mean culturally transmitted skill level across all agents of one generation in the ‘Tasmanian’ model of cultural gain/loss.	9
g	The number of cultural features in Axelrod’s model of polarization, with each feature taking one of ten possible trait values.	10
N_{side}	The number of agents along one side of a square grid in Axelrod’s model of polarization, giving N_{side}^2 agents in total.	10