

Fisher-Wright: Children Choosing Parents
Dem260 Math Demog
Spring 2020
Lecture 10

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April 2, 2020

Agenda for today

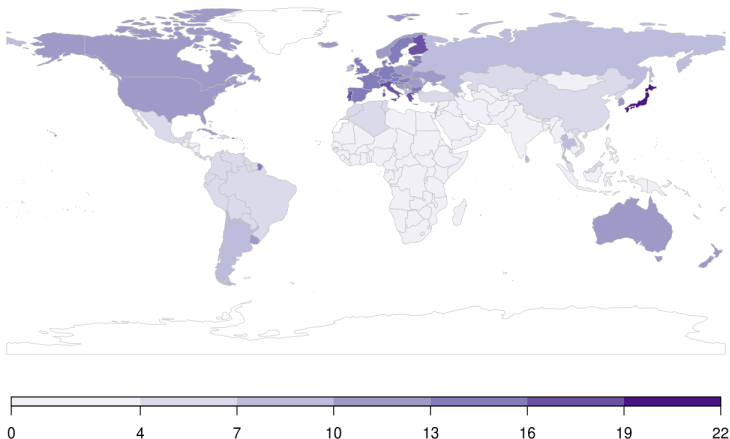
1. Formal demography of epidemic mortality (about an hour)
2. Fisher-Wright introduction
3. Baby naming as an example of neutral evolution

My questions

1. How does age-structure of population affect epidemic mortality?
2. How does mortality change affect life expectancy in normal times?
3. How much remaining life is lost from an epidemic?

(1) Population aging

Older people % (age > 70) in 2020



Source: Tuljapurkar and Zuo

<https://u.demog.berkeley.edu/~josh/demogblog/>

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The crude death rate is deaths / population

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A homework problem? Do indirect standardization of state CDR using observed age structure and national mortality. How much of observed CDR variation does it explain?

(2) Keyfitz's entropy

- ▶ Let $\mu^*(x) = (1 + \Delta)\mu_0(x)$
- ▶ So, $H^*(x) = (1 + \Delta)H(x)$.
- ▶ And, $\ell^*(x) = \ell(x)^{1+\Delta}$.
- ▶ What is $\frac{de(0)}{d\Delta}$?

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$$\mathcal{H} = \frac{d \log e(0)}{d\Delta} = \frac{- \int \ell(x) \log \ell(x) dx}{e(0)}$$

A demographic translation

Reverse order of integration to get

$$\mathcal{H} = \frac{\int d(x)e(x) dx}{e(0)}$$

(3) Loss of person years remaining

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Before epidemic:

$$PYR = \int N(x)e(x) dx$$

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Loss of person years remaining

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After (“instant”) epidemic

$$PYR = \int [N(x) - D^*(x)] e(x) dx$$

Proportion of person years lost

$$\frac{\int D^*(x)e(x) dx}{\int N(x)e(x) dx}$$

Stationary theory

If

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A doubling of mortality in epidemic year ($\Delta = 1$) causes “only” a 0.38% loss of remaining life expectancy.

Workspace

These numbers seem small

- ▶ Even an epidemic *doubling* mortality has small effect on remaining life expectancy (\approx 2 months per person)
- ▶ But all-cause mortality also small (\approx 2 months per person)
- ▶ Covid-19: 1 million deaths = 30% more mortality, but older (\approx 2 weeks per person)

Cookie Break

Fisher-Wright: Big picture

Galton-Watson-Bienaymé Branching Process

- ▶ Branching process models independent parents randomly producing offspring. “Generative”
- ▶ Total population size can vary, and has a random component and deterministic one m
- ▶ Qualitative result when $m = 1$ is that there is one longest surviving line. This is “fixation”, when one *type* becomes universal.

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Fisher-Wright

- ▶ Children picking their parents (not “generative”)
- ▶ Total population size is constant
- ▶ Qualitatively similar to BP. Extinction and fixation.
- ▶ Flexible: mutation, selection, even changes in pop size.
- ▶ With apologies, biologists take FW “seriously” even if they don’t take it “literally.”

Another cell phone example

Let's simulate and draw lines

Gen 1	0	1	2	3	4	5	6	7	8	9
Gen 2										
Gen 3										

- ▶ What will happen?

Simulation code

```
fwm <- function(N, n_gen, mu = 0) ## mu != 4/N
{
  ## simulate fisher-wright (with mutations)
  x <- paste(1:N) ## starting types
  A <- matrix(NA, nrow = n_gen, ncol = N)
  for (i in 1:n_gen)
  {
    A[i,] <- x
    x <- sample(x, size = N, replace = T)
    x <- mut(x, mu)
    x
  }
  return(A) ## matrix of types, each line a generation.
}
```

Simulation code

```
mut <- function(x, mu)
{
  ## m, the individuals that mutate
  m <- which(rbinom(length(x), 1, mu) == 1)
  if (length(m) == 0) ## if no-one mutates
    return(x)
  ## add a suffix to their ID, so it will be unique (inf
  suffix <- 10000*round(runif(length(m)),4)
  x[m] <- paste0(x[m], ".", suffix)
  x
}
```

Trying it out

```
set.seed(1)
fwm(N = 10, n_gen = 2, mu = 0)

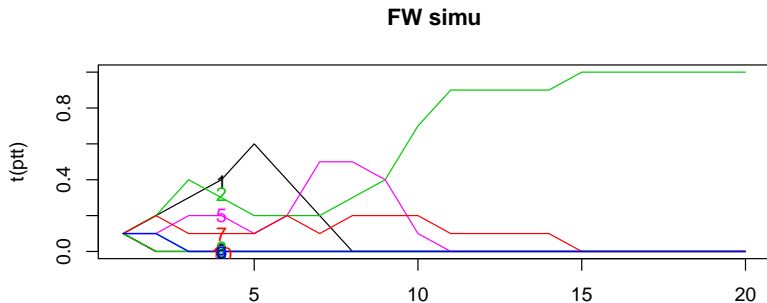
##      [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10]
## [1,] "1"  "2"  "3"  "4"  "5"  "6"  "7"  "8"  "9"  "10"
## [2,] "9"  "4"  "7"  "1"  "2"  "7"  "2"  "3"  "1"  "5"

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##      [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10]
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## [2,] "5"  "5"  "2"  "10" "9"  "1"  "4"  "3"  "6"  "10"
```

Trying it out some more

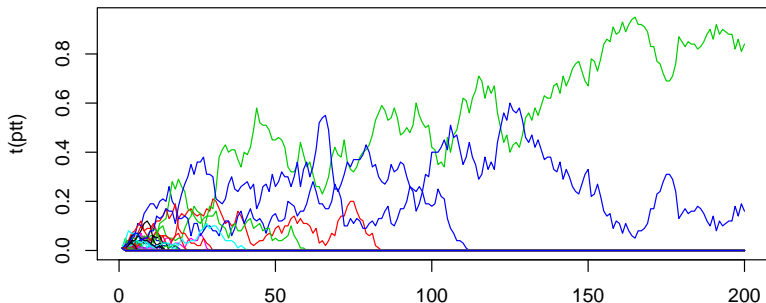
```
set.seed(1)
A <- fwm(N = 10, n_gen = 20, mu = 0)
tt <- table(A, row(A)) ## count types by row
ptt <- prop.table(tt, 2) ## proportions
matplot(t(ptt), type = 'l', lty = 1, main = "FW simu")
text(x = 4, y = jitter(ptt[,4]), rownames(ptt), col = 1:6)
```



Qs: What happens at time 15? Why does line 5 rise and fall?
What happens at time 2? What is $E(p_i(t)|p_i(t-1))$?

Bigger pop and more time

```
set.seed(1)
A <- fwm(N = 100, n_gen = 200, mu = 0)
tt <- table(A, row(A)) ## count types by row
ptt <- prop.table(tt, 2) ## proportions
matplot(t(ptt), type = 'l', lty = 1)
```

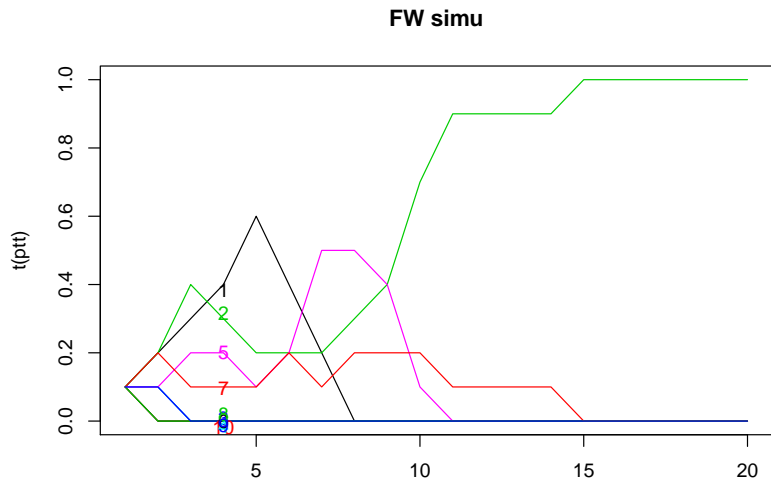


- ▶ What does this remind you of? What will happen in long run?
- ▶ What other questions could we ask?

Questions we can ask

- ▶ What is probability that line i will “fix”? (Hint: easy)
- ▶ What is expected time until some line fixes? (We’ll demo the result)
- ▶ How can we describe the path to fixation? (We’ll derive the result)

Probability that a particular line will “fix”



Expected time until fixation?

Answer for us is

$$\bar{T}_{fixed} = 2 \cdot N$$

Note: Biologists say $4N_e$
See Wikipedia "Genetic drift"

Simulation of time to fixation

```
T.vec <- NULL
all.the.same <- function(x){length(unique(x)) == 1}
set.seed(10)
for (i in 1:100)
{
  A <- fwm(N = 100, n_gen = 1000, mu = 0)
  extinction_time = min(row(A)[apply(A, 1, all.the.same)])
  T.vec[i] <- extinction_time
}
mean(T.vec)
## [1] 202.89
```

Path to fixation: a measure of homogeneity/heterogeneity

Chance that two randomly drawn individuals are of same type.

$$G = \sum_i p_i^2$$

If we have two types, $p_1 = \pi$, $p_2 = 1 - \pi$? What is G if $\pi = 0, .5, 1$?

Let's derive time path of G

Let's assume just two types, $\pi(t)$
Chance two indiv are of same type

$$G_{t+1} = P(\text{same parent}) \cdot 1 + P(\text{different parent}) \cdot G_t$$

Notation: I'm going use K for pop size. Bio uses $2N$.

$$G_{t+1} = \frac{1}{K} \cdot 1 + \left(1 - \frac{1}{K}\right) \cdot G_t$$

Let's derive time path of G , continued

$$G_{t+1} = \frac{1}{K} \cdot 1 + \left(1 - \frac{1}{K}\right) \cdot G_t$$

Easier to solve letting $H = 1 - G$. Some algebra gives

$$H_{t+1} = H_t(1 - 1/K)$$

Or,

$$H_t = H_0(1 - 1/K)^t$$

So, H goes to 0 exponentially, just as G goes to 1.

Cookie Break number 2

Coming up, Baby Names.

Baby Names

“Drift as a mechanism for cultural change: an example from baby names” by Matthew W. Hahn and R. Alexander Bentley *Proc. R. Soc. Lond. B* 2003 270, S120-S123

What's the basic idea?

- ▶ How is naming a baby like Fisher-Wright?
- ▶ How is it not?

Basic idea

- ▶ Like Fisher-Wright
 - ▶ people choose from existing set (?)
 - ▶ names are “neutral” (?)
 - ▶ draw proportionally (?)
- ▶ They test to see if they can reject FW
 - ▶ compare observed histograms to FW simulation
- ▶ They include mutation to get a stationary disn

Note: failing to reject FW doesn't mean it's correct

Their picture

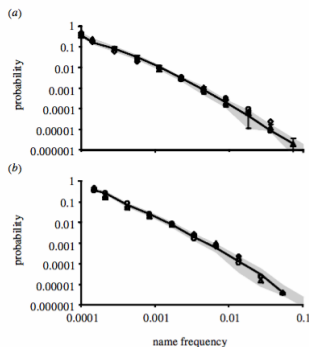


Figure 1. Power law distributions of baby names. Frequencies of the top 1000 (a) male and (b) female baby names in the United States, for three representative decades

Figure 1. Power law distributions of baby names. Frequencies of the top 1000 (a) male and (b) female baby names in the United States, for three representative decades during the twentieth century. The x-axis represents the frequency of a name in the total sample of individuals, and the y-axis represents the probability that a certain name would fall within the bin at that frequency (proportional to the fraction of names in the top 1000). As common for such log-log plots (e.g. Jensen 1998; Zanette & Manrubia 2001; Albert & Barabasi 2002), the bin sizes increase in powers of 2 (0.0001–0.0002, 0.0002–0.0004, 0.0004–0.0008,...), data are plotted at the middle of each bin and probabilities are normalized for the increasing bin sizes. Also shown are the mean (solid line) and 95% confidence intervals (grey ribbon) resulting from 20 runs of the neutral-trait model with $\theta = 4N\mu = 4$. A regression between $\log(\text{average model value})$ and $\log(\text{average data value})$ yields $r^2 = 0.993$ for male names and $r^2 = 0.994$ for female names. Key: triangles, 1900–1909; diamonds in (a), 1950–1959; diamonds in (b), 1940–1949; circles, 1980–1989; solid line, $\theta = 4$ model.

Drawing their picture with the data

babynames.R

Drawing their picture with simulation

Doesn't quite work

Some potential criticism

- ▶ While we can't reject that there's some parameterization of FW that gives us similar disn, this doesn't mean that we've found the right mechanism. (Just that we can't reject it).

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- ▶ While we can't reject that there's some parameterization of FW that gives us similar disn, this doesn't mean that we've found the right mechanism. (Just that we can't reject it).
- ▶ What are some other tests of this mechanism?
- ▶ Markov assumption. We could see if each frequency really followed random walk.
- ▶ Perhaps we could see if variances were scaled to frequencies correctly.

Conclusions

1. Fisher-Wright an alternative to branching processes
2. It reverses logic of reproduction, but gives similar quantitative and qualitative results
3. A neutral model for other processes?
4. Starting point for coalescent

Future path

1. Coalescent
2. Population History
3. Mini-project presentations