Review from last time:

$n(t)$ = # cells in generation t

$n(t+1) = 4p\, n(t)$

$\rightarrow n(t) = (4p)^{(t-1)}\, n(1)$; Let $\lambda = 4p$

$= \lambda^{t-1}\, n(1)$

$\leftrightarrow$ let $r = \log \lambda$

$= \exp(r(t-1))\, n(1)$

EXPONENTIAL GROWTH IN TIME...

See, is typical of much more-complex population models.
[Anderson + May, '92: A "law" of population biology]

OK, but don't get caught up in idea of testing laws...

Euler-Lot shows always can have exp-growth/decay – is one solution...

Matrix theory tells us when that's only solution will see... or something like that...

Think abt. Bernadelli pop waves + Euler-Lotka formula...

Structured Population Models in Discrete Time

- Motivation: conservation biology + ecology
- Population with different subpopulations...

  DIFFERENCES in...

  - growth rate
  - Survival rate
  - reproduction rate

- Goal: Evolution of numbers $n_a(t)$ in these subpopulations over time.
- Time: discrete. Typically t in units of years, consider t integer values. Do this below.
- Rich history: Back to Euler, 1700's.

Note: "Fractional numbers in population" occur.

2 Alternative interpretations:

1) [redacted]... let the relative values $\{n_a(t)\}$ represent proportions in various subpopulations.

2) or average numbers, over many realiz. of pop. dynamics

NOTE: A) If start w/ much larger initial population numbers $\{n_a(0)\}$ in same proportion, will have better approx. to integer population counts.

B) Warning: if $n_a(t)$ become small, the present approach can (not always) make erroneous predictions — see agent-based simulations later in course.

AGE-STRUCTURED MODELS : Assign subpops based on AGE.

- $n_a(t)$ = # individuals of age a at timestep t
- A = max. possible age
- p_a = probability of age-a individuals surviving to age a+1

  OR "fraction" " " " " " " "

E.g.] $p_{20} \approx$ ~~0.8~~ 0.995 → ~80% survive age 20→40, OK

$p_{100} \approx 0.5$ (guesses for human population).

RULE 1: $\boxed{\begin{array}{l} \text{for } a > 0 \text{ (not newborn)} \\ n_a(t+1) = p_{a-1}\, n_{a-1}(t) \end{array}}$

Now, INTRODUCE CONVENTION ... only keep track of females

$n_a(t)$ = # females of age a at timestep t.

- f_a = # newborns per year, per age-a female

RULE 2: $$\boxed{\begin{aligned} n_0(t+1) &= f_0\, n_0(t) + f_1\, n_1(t) + \cdots \\ &= \sum_{a=0}^{A} f_A\, n_a(t) \end{aligned}} \quad (*)$$

USE RULE 1, and

- Compute: $n_a(t) = p_{a-1}\, n_{a-1}(t-1)$

$n_{a-1}(t-1) = p_{a-2}\, n_{a-2}(t-2)$

$\rightarrow n_a(t) = p_{a-1}\, p_{a-2}\, n_{a-2}(t-2)$

$\vdots$

$\rightarrow n_a(t) = p_{a-1}\, p_{a-2}\, p_{a-3} \cdots p_0\, n_0(t-a) \quad (**)$.

Therefore: $n_0(t+1) = \sum_{a=0}^{A} f_a I_a n_0(t-a)$ (*) $\uparrow$ L2

[plug (++) into (+)]

where, $I_a = p_{a-1} p_{a-2} \cdots p_0$, Age-a survival fraction

Note: I_0=1

Test our "laws" of pop. biology.

Claim: For $t \gg 1$ (large times),

$n_0(t) \approx c\lambda^t$. "Asymptotic" large-t growth rate λ.

GET FORMULA FOR λ:

Plug into (*), get

$$c\lambda^{t+1} = \sum_{a=0}^{A} f_a I_a c\lambda^{t-a}$$

$$\boxed{1 = \sum_{a=0}^{A} f_a I_a \lambda^{-(a+1)}}$$

Euler-Lotka Formula for λ.

• How many positive values of λ occur as solutions to Euler-Lotka Formula?

[Breakout for students to brainstorm on how to prove]

A: ONE.

Proof: Ex. 2.4 of E+G

Let $G(\lambda) = \sum_{a=0}^{A} f_a I_a \lambda^{-(a+1)} - 1$ } $G(\lambda)=0$ for pop. growth rate λ.

1. $\frac{dG}{d\lambda} < 0$, for all $\lambda > 0$

2. $\lim_{\lambda \to 0} G(\lambda) = \infty$ (Note: $f_a I_a \geq 0$)

3. $\lim_{\lambda \to \infty} G(\lambda) = -1$

$\longrightarrow$ $G(\lambda) = 0$ at exactly one value.

What have we actually shown with Euler-Lotka formula?

* There does exist a solution of form n0(t)=c*lambda^t ... where lambda real and positive, and there is a unique such real, positive lambda. We've found formula for it.

(We accomplished that by plugging our solution, not just for n0(t) but for all the na(t), into dynamical equations.)

IS THAT ENOUGH TO ACTUALLY CHARACTERIZE WHAT HAPPENS AS EXP GROWTH/DECAY?

No. Haven't really tested the "law."

Could simultaneously be other lambdas that have same absolute value, but neg or complex, so produces osc. Moreover, c could be negative -- so have to wheel in other eigenvectors to explain actual dynamics with a reasonable IC. So is not a complete characterization of solutions ...

UNLESS know additionally that matrix is power-positive. (more later ...)

Then have unique real positive dominant evl. We have found the only real positive evl so it's the (unique) dominant one. Moreover know it has positive evr, so can actually describe the pop. dynamics.

OTHERWISE --
If have non-power-positive Leslie Matrix (I think this is possible -- if have localized fecundity?) ... see something other than exp growth+decay -- Euler-Lot actually fails to capture everything. Indeed this is possible -- Ex 2.11 of Book, and a HW problem!

Continued aside on...

What we are really showing: with Euler-Lot...

→ yes... $n_0(t)$ evolves exponentially.
get corresp. time-delayed exponentials for $n_a(t)$ via rule 1.

So satisfy rule 1.

Euler Lotkerra is, then, rule 2 being satisfied for n_0 (given such $n_a(t)$).

Thus... have found sol^{n} that satisfies all rules.

Try with: $A = 2$ [max. age]

$p_0 = .5$ ← proba. survive to age 1

$p_1 = .25$ 2

$$\Rightarrow \left.\begin{array}{l} I_0 = 1 \\ I_1 = p_0 = .5 \\ I_2 = p_0 p_1 = .125 \end{array}\right\} \rightarrow I_a\text{list} = [1, .5, .25]$$

$$\left.\begin{array}{l} f_0 = 0 \\ f_1 = 1 \\ f_2 = 5 \end{array}\right\} \rightarrow f_a\text{list} = [0, 1, 5]$$

Code: pop1_eulot_and_Leslie_iterate.ipynb

[Breakouts for playing with root finding]

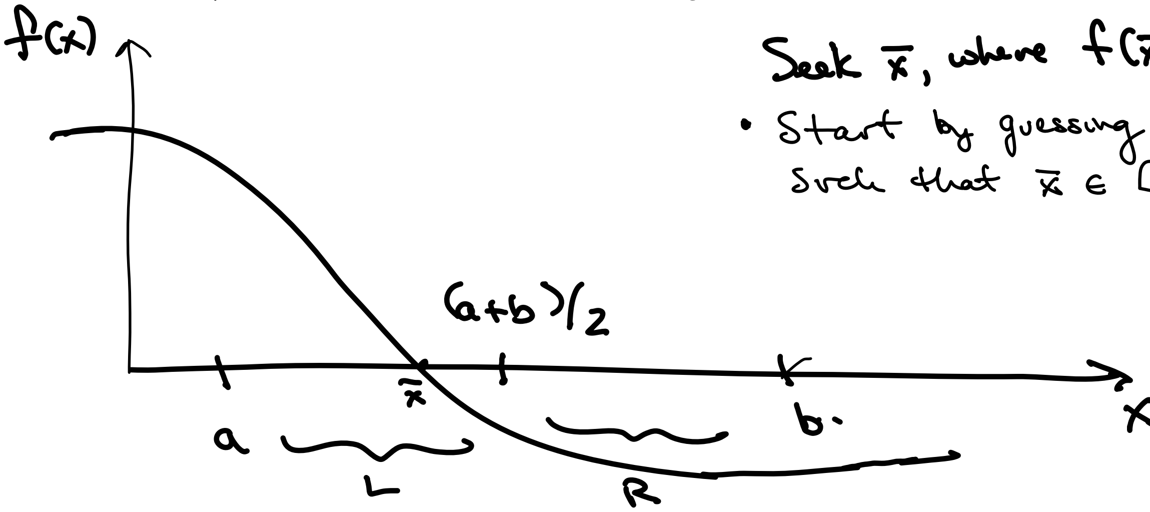
Note:

BISECTION METHOD: find zeros of G(λ)

Implemented by MATLAB fzero command... R uniroot command.

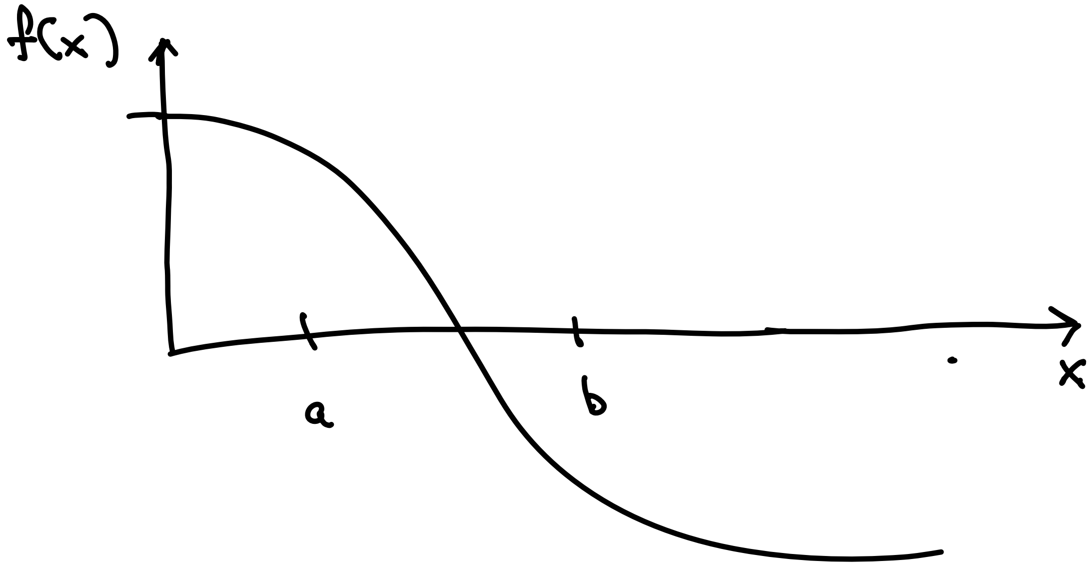
Seek $\bar{x}$, where $f(\bar{x}) = 0$

- Start by guessing endpoints a, b such that $\bar{x} \in [a, b]$



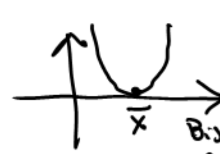
Concept: if $f(a) \cdot f\left(\frac{a+b}{2}\right) < 0$ (diff signs), then L contains $\bar{x}$: discard R
else R contains $\bar{x}$. : discard L.

Repeat on the remaining intervals!



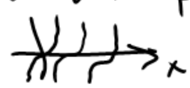
...

LIMITATIONS: - Need $f'(\bar{x}) \neq 0$: real zero crossing



Bisection / fzero will fail

- fzero will find discontinuities: be careful in interpreting results! Eg



$f(x) = \tan(x)$