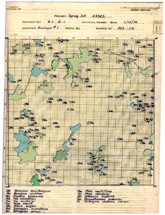
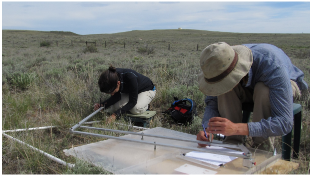
IDEs as models for individuals: who gets into the 1%, and why?

Stephen Ellner
Ecology and Evolutionary Biology, Cornell





Collaborators

Peter Adler, Utah State

Robin Snyder, Case Western

Giles Hooker, Cornell

Brittany Teller, Utah State

Mark Rees, Sheffield

Dylan Childs, Sheffield

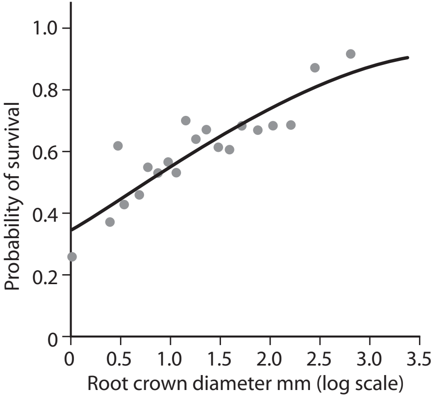
NSF National Science Foundation
WHERE DISCOVERIES BEGIN

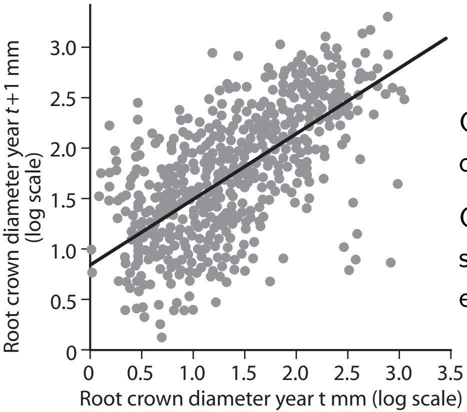
IDEs for movement in “trait space”

Plants & other organisms with indeterminate growth: size is most important trait.

Size varies continuously: effects of size described by regression models.

Platte thistle, *Cirsium canescens* (Rose et al. 2005)





Growth $\sim$ size: dynamic model for changes in individual state.

Can be: nonlinear, non-Gaussian, size-dependent variance, random year effects, etc.

Integral Projection Model (IPM)

$n(z, t) =$ distribution of individual state, z

Transitions z (now) to z' (next census) described by

$$K(z', z) = \underbrace{P(z', z)}_{Survival/growth} + \underbrace{F(z', z)}_{Reproduction}$$

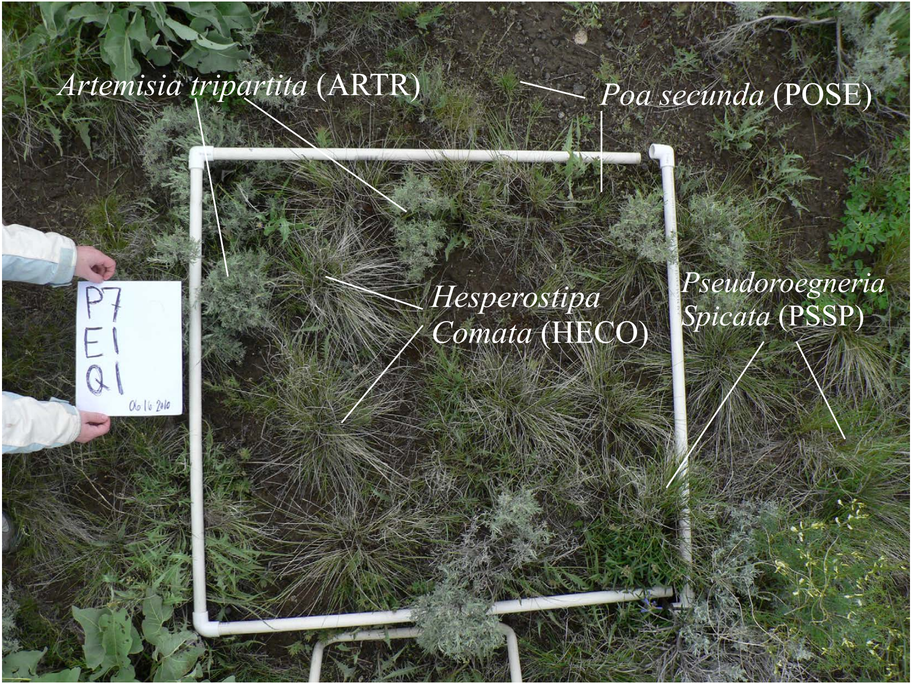
$$n(z', t+1) = \int_{\mathbf{Z}} K(z', z) n(z, t)\, dz$$

NOTE: $'$ always means "value at next census"

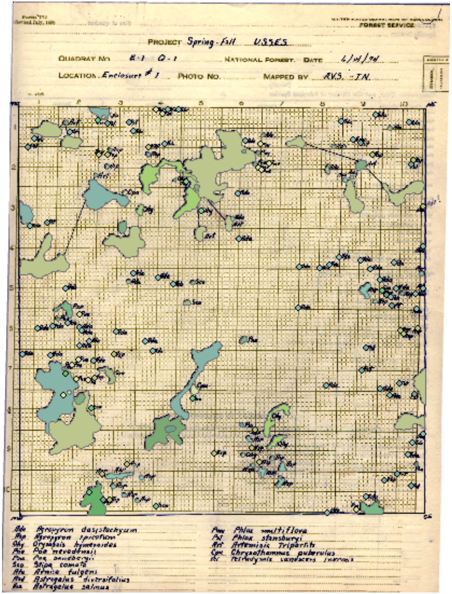
NOTE: trait space $\mathbf{Z}$ compact.

Idaho sagebrush steppe

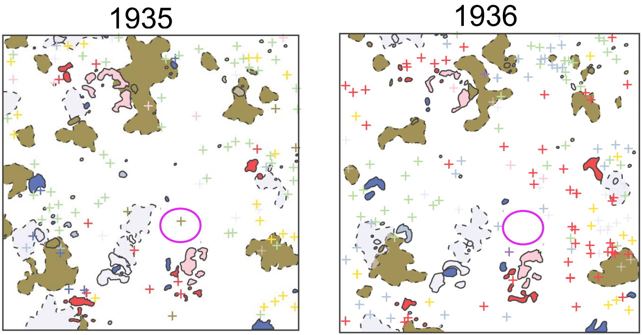
That's where the data are: 26 quadrats established 1926-1932 at US Sheep Expt. Station, mapped most years until 1957 (22 annual transitions)


Artemisia tripartita (ARTR)
Poa secunda (POSE)
P7
E1
Q1
06 16 2010
Hesperostipa Comata (HECO)
Pseudoroegneria Spicata (PSSP)

Hand-drawn maps...



...digitized by Peter Adler to GIS shapefiles



For each plant, we know:

- size
- survival
- growth
- location, size, species of competitors
- daily temperature, rainfall, snowfall

Survival and growth fitted as regression models of individual area, site covariates (grazed/ungrazed, etc.), and competitive pressure W.

Competitive pressure $W =$ the sum over all neighboring plants of

Size of neighbor

$\times$ "competition coeffient" α_{ij}

(effect of species-j neighbor on species-i focal plant)

$\times$ "competition kernel" (near vs. far neighbors)

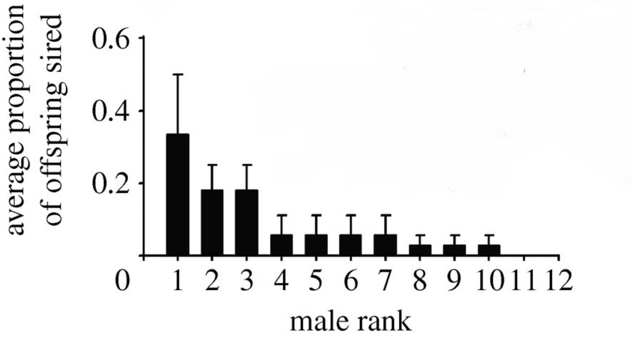
(B. Teller et al. 2016, *Methods in Ecology and Evolution*)

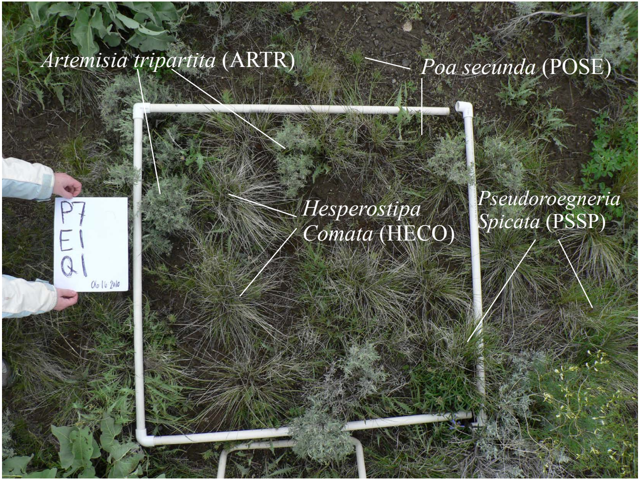
Demographic variability among individuals

Reproductive skew:

A few parents have many offspring
most parents have few offspring.

Wire-tailed manakin *Pipra filicauda* (Ryder et al. 2009, *Proc. RSL B*)





"Canopy" plants are the lucky few.

MANY seedlings/yr, FEW become full-size adult.

R. Snyder and SPE (Am. Nat. 2016): who becomes one of lucky few plants, and why?

Survival/growth kernel P is Markov chain for individual paths through life (add death as absorbing state)
$\Rightarrow$ Many life-cycle properties can be computed!

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where $N = (I - P)^{-1}, \mathbf{e} \equiv 1.$

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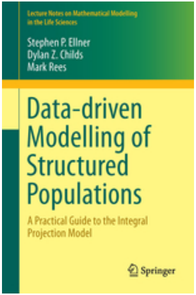
MANY more: download (free?)
and see chapter 3.



Who becomes one of the lucky few, and why?

1. Compute the *conditional* transition kernels for the Lucky and Unlucky.
2. Compare these to ask: when and how do paths diverge?

Possible absorbing sets $A_1, A_2, \cdots A_M$:
- Process conditional on absorbing into A_j is Markov chain
- Easy to compute Prob(absorb into A_j), $P(z', z|$ absorb into $A_j)$

Define the “Lucky” absorbing set:

- Size at death is $\geq z^*$
- Maximum size (at any age) is $\geq z^*$
- Lifetime total # offspring[1] $\geq T^*$
- Lifetime total # breeding times $\geq T^*$
- and so on...

[1]state $z =$(size, #kids so far)

Examples

Dacryidium elatum, tropical tree

Deterministic growth.

Eelke Jongejans et al. (2010), Journal of Ecology

Examples

Artemisia ordosica on Mongolian sand dunes

Variable growth.

S-L Li et al. (2011), Journal of Ecology

Examples

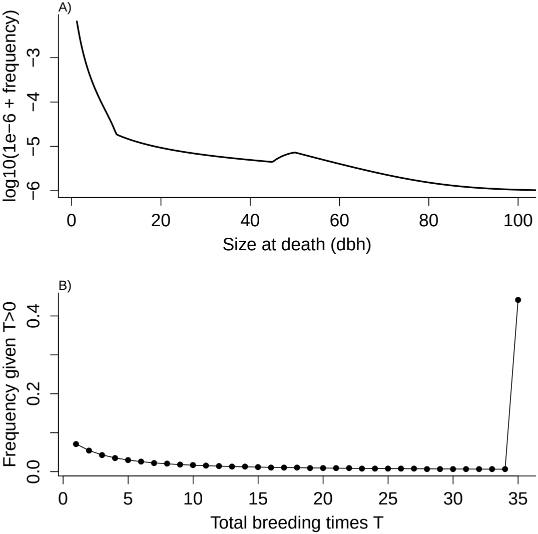
Cedrela odorata (Spanish cedar), tropical tree

Variable growth; differences among individuals are persistent.

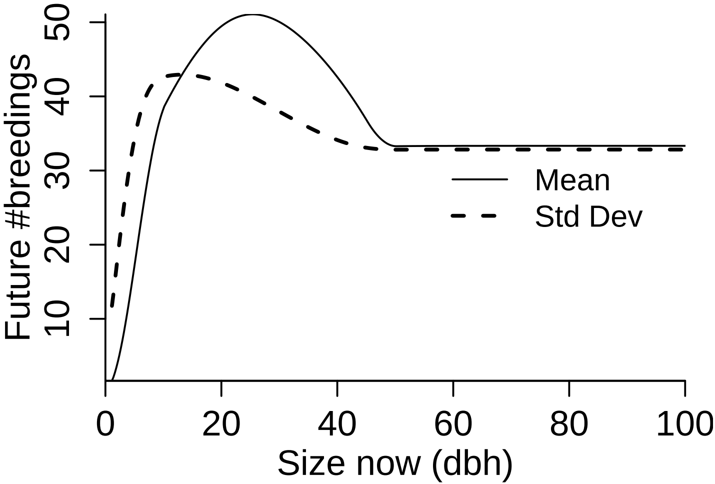
Zuidema et al. (2009): the "lucky few" are consistently fast-growing trees.

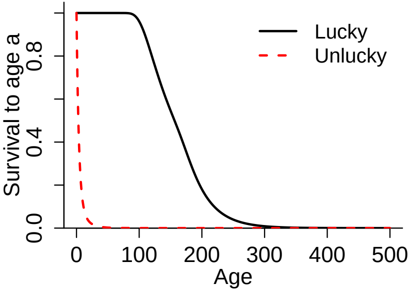
Dacrydium elatum: the 1%

Size at death and LRS are bimodal

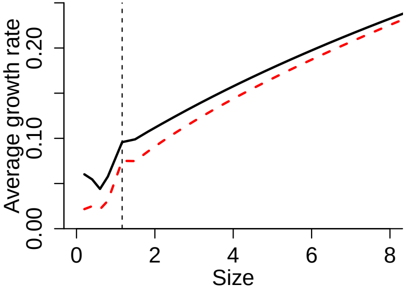


Dacrydium elatum: Lucky=20cm dbh

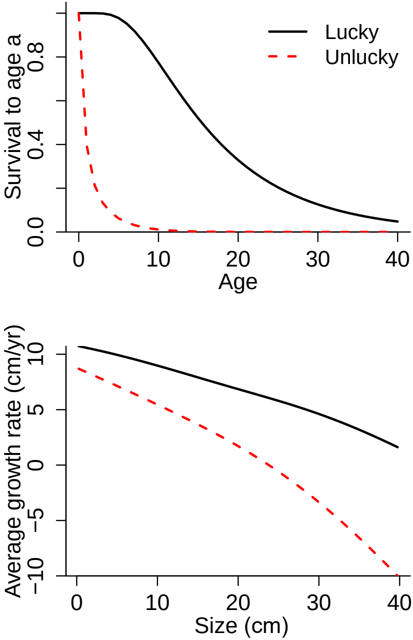




Dacrydium: Enormous survival differences.

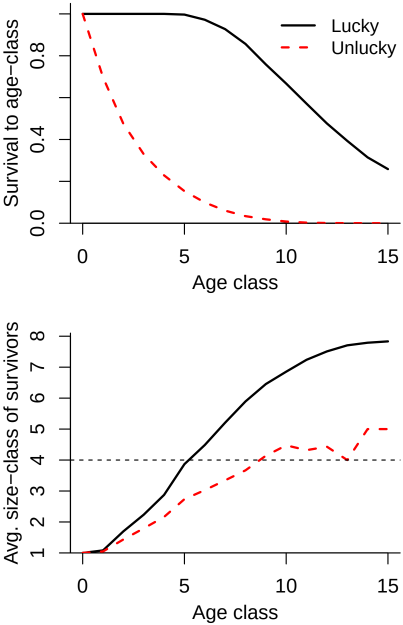


Tiny growth differences except in seedlings – where it aids survival.



Artemisia (Lucky = 40cm)

Same story.



Cedrela (Lucky = size class 6)

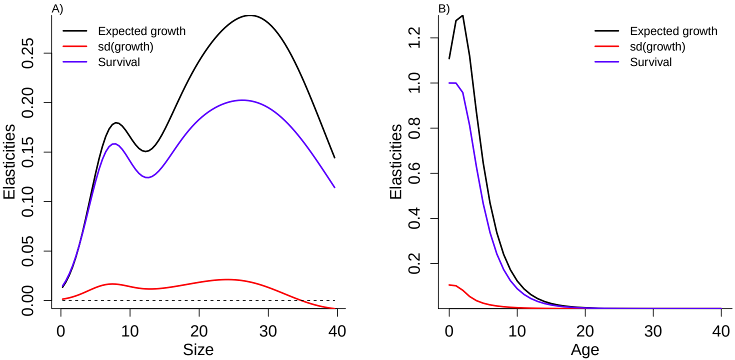
Big growth divergence: big enough to get Lucky in one time-step.

To a large extent, the Lucky are just those who do not die early.

What kind of lucky break is most helpful?

Sensitivity of $q_{\mathbb{L}} = P(\text{die Lucky})$ to perturbation at age a:

$$\frac{\partial q_{\mathbb{L}}}{\partial \phi} = \frac{\partial a_{\mathbb{L}}}{\partial \phi} P^a + a_{\mathbb{L}} N \frac{\partial P}{\partial \phi} P^a, \quad N = (I - P)^{-1}.$$



Traits vs. luck (R. Snyder & SPE, in prep)

Ecologists want to believe that there is a <u>reason</u> for large differences in reproductive success.

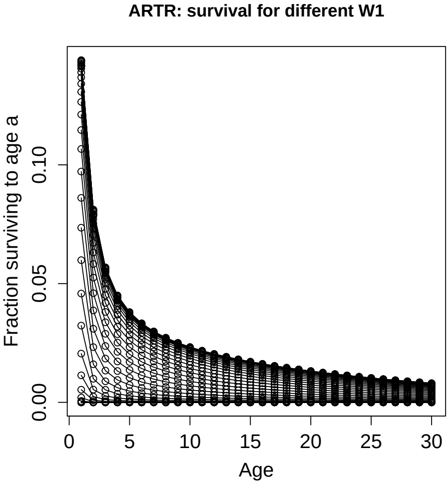
- To what extent can trait differences override luck?
- Do these determine who joins the Lucky few, or is it still mostly luck?

Motivating example (Idaho): how much does it matter if a seedling germinates in a good spot or a bad spot?

Good = no close conspecifics!

Artemisia: site quality matters

Site quality: W_1, competition at first census



Good site: some chance of surviving to age 10, large and fecund.

Poor site: no.

Partitioning variance in LRS: Trait vs. Luck

$R =$ Lifetime Reproductive Success (LRS)

W_1=site quality at birth, Z=size at age 2.

Partitioning variance in LRS: Trait vs. Luck

R = Lifetime Reproductive Success (LRS)

W_1=site quality at birth, Z=size at age 2.

$Var(LRS) =$

$$\underbrace{\mathbb{E}[s(W_1)\, Var(R^*|W_1, Z)]}_{①} + \underbrace{\mathbb{E}[s(W_1)(1 - s(W_1))(\mathbb{E}(R^*|W_1, Z))^2]}_{②}$$

$$+ \underbrace{\mathbb{E}_{W_1}[s(W_1)^2\, Var_Z\, E(R^*|W_1, Z)]}_{③} + \underbrace{Var_{W_1}[\mathbb{E}(R|W_1)]}_{④}$$

where R^* = LRS conditional on surviving to age 2.

Partitioning variance in LRS: Trait vs. Luck

$Var(\text{LRS}) =$

1. Effect of trait variation (site quality)
2. Components of luck
   a. Do you survive to age 2?
   b. How big are you, if you survive?
   c. Variation independent of state at age 2.

Results: Luck dominates!

	Artemisia	*Pseudoroegneria*
Trait: W_1	0.2%	0.5%
Luck: survive to 2?	11%	12%
Luck(?): size at 2	0.8%	1.4%
Luck: later variation	88%	86%

Not just shrubs in Idaho!

Kittiwake *Rissa tridactyla*

Not just shrubs in Idaho!

Emmanuele Cam, University of Toulouse III

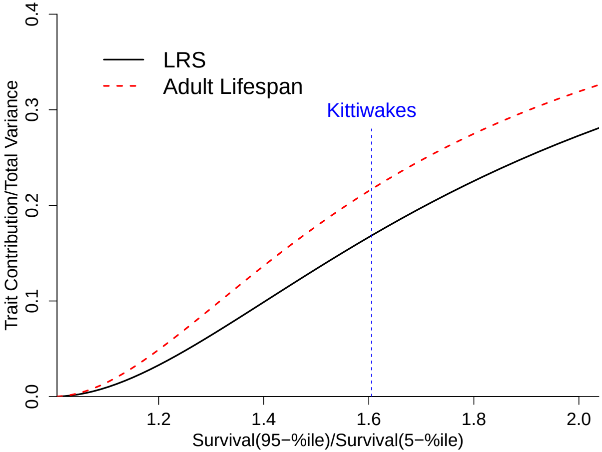
The idea of differences in individual quality has been put forward ...to explain differences in lifetime production among individuals. (Cam et al. 2004, *Oikos*)

In kittiwake adults (Cam et al. 2002, *American Naturalist*)

Survival probability, $CV \approx 0.2 \quad (CV = \frac{\sigma}{\mu})$

Breeding probability, $CV \approx 0.1$

But variation in LRS is still mostly luck!



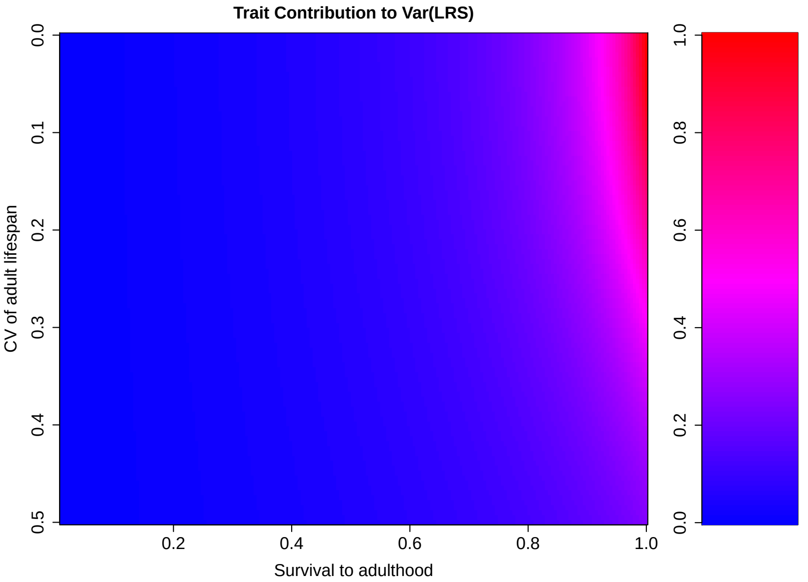
Trait variation + kittiwake model from Steiner & Tuljapurkar (2012)

Bonnet & Postma (2016), snow voles

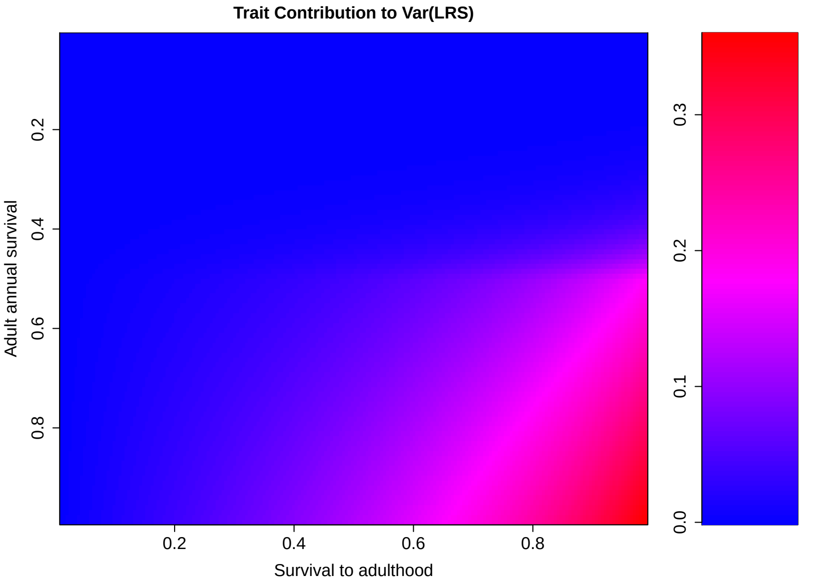
Is LRS always dominated by luck? (R.Snyder & SPE)

- Two life stages, Juvenile and Adult
- Juvenile survival s_J, adult lifetime τ (random), F offspring/yr on average.
- Stable population at trait mean: $R_0 = 1$.
- CV $= 0.3 \Rightarrow$ 3-fold ratio between 95th and 5th percentiles of a Gaussian trait distribution with positive mean.

Trait is offspring/yr (deterministic),CV=0.3



Trait is adult survival (CV=0.3), constant clutch size



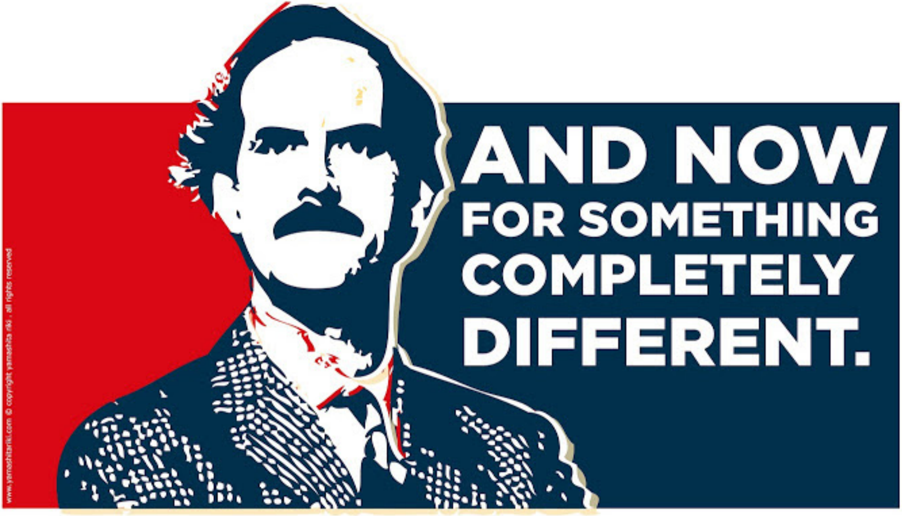
Trait is survival to adulthood

Trait variation accounts for under 10% of total variation in LRS, so long as trait $CV < 1$.

Trait variation dominates Var(LRS) if survival to adulthood is high, and trait effectively is adult LRS.

- LRS $\approx$ Lifespan $\times$ Mean clutch size.
- If one of those is $\approx$constant, and the other one is the trait, then trait variation dominates LRS.

Otherwise, so many forking paths through life that becoming big and fecund is mostly *sheer dumb luck*.


AND NOW
FOR SOMETHING
COMPLETELY
DIFFERENT.

Typically we model transitions using densities: transition probabities are absolutely continuous w.r.t. underlying measure.

For trait space, not always reasonable:

- Deterministic transitions of some trait components (genotype, breeding value).
- Constraints: allocations to growth $+$ reserves $=$ total energy intake.

Resulting models are very different, very little theory.

Simplest possible case:

- $z = (x, y) \in \mathbf{Z} = \mathbf{X} \times \mathbf{Y}$
- x has deterministic transitions
  $x' = \omega(x)$, ω smooth with smooth inverse α
- y has smooth stochastic transitions:
  $P(y'|x, y) = s(x, y)G(y'|x, y)$

$$n(x', y', t+1) = \int_{\mathbf{Z}} F(x', y', x, z) n(x, y, t)\, dxdy$$
$$+ 1_{\omega(\mathbf{X})}(x') \left|\alpha'(x')\right| \int_{\mathbf{Y}} G(y'|x'_*, y) s(x'_*, y) n(x'_*, y, t)\, dy$$
where $x'_* = \alpha(x'), n \equiv 0$ off $\mathbf{Z}$

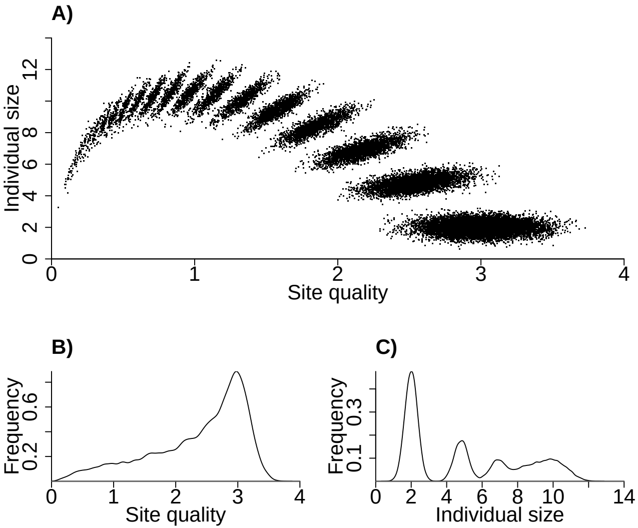
Example:

Individuals classified by size y, site quality $x \geq 0$ that decreases over time.

$$\begin{aligned} x' &= \delta x, \quad 0 < \delta < 1 \\ \text{Growth: } y' &\sim \text{Normal}(\mu = x + 0.9y, \sigma = \sigma_g) \end{aligned}$$

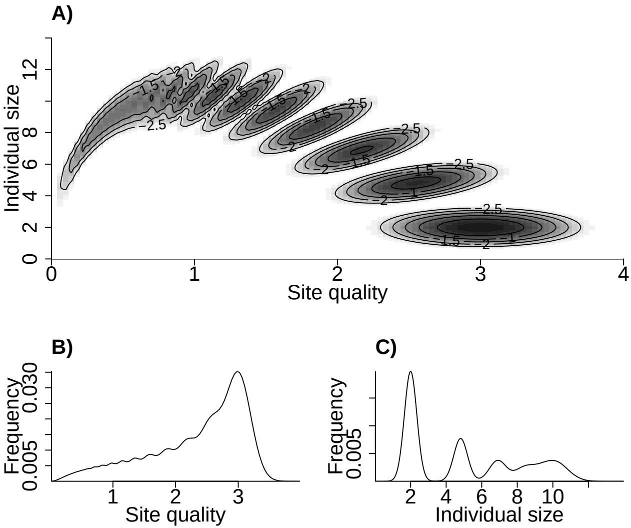
$$\begin{aligned} \text{Survival: logit } s(y) &= A + By, B > 0 \\ \text{Number of offspring: } b(x, y) &= by \\ x \text{ at birth} &\sim \text{Normal}(\mu_x, \sigma_x) \\ y \text{ at birth} &\sim \text{Normal}(\mu_y, \sigma_y) \end{aligned}$$

Agent-based simulations (to stable distribution)



Individuals grow at first but then shrink, because their site quality has dropped.

Numerical iteration of IPM



Individuals grow at first but then shrink, because their site quality has dropped.

$$n(x', y', t+1) = \phi(x'; \mu_x, \sigma_x)\phi(y'; \mu_y, \sigma_y) \int_{\mathbf{Z}} byn(x, y, t)\, dydx$$
$$+ \frac{1}{\delta} \int_{\mathbf{Y}} \phi(y'; x'/\delta + 0.9y, \sigma_g) s(y) n(x'/\delta, y, t)\, dy$$

- What function space does this "live on"?
- Does n stay smooth, or can it develop "shock waves"?
- All the basic theory: stable stage distribution, eigenvalue sensitivity formulas, etc.

Conclusions

1. IDEs are models for the lives of individuals. We can extract from them much more information than we have been.
2. IDEs based on individual-level processes may not have transition densities. We know very little about such models.

Questions?

Graduate diversity recruitment weekend, E&EB Cornell and NB&B Cornell
April 21-23, 2007

An event to connect students from under-represented backgrounds with faculty, before they apply for graduate school.

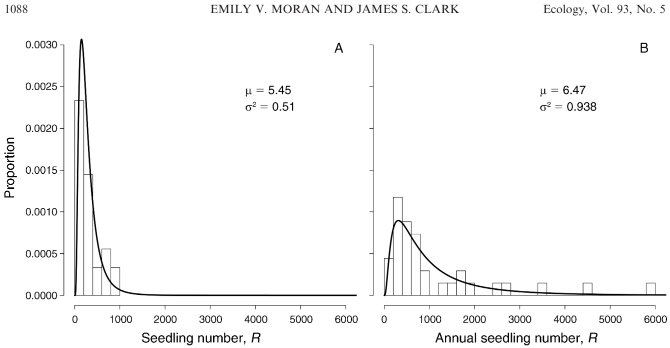
For college Junior or Seniors, or students who have graduated and are considering graduate school.

Application at cudiverisityrecruitment.weebly.com

Application deadline December 1, 2016.

Attendees will get $400 for travel, housing/meals for the weekend.

Even among the lucky few, LOTS of skew



Seedlings/yr, trees (Moran & Clark 2012)

(A) Duke Forest: top 5% make 29% of seedlings

(B) Coweeta: top 5% make 47% of seedlings

Competition kernel: splines (B. Teller et al. 2016, Methods in Ecology and Evolution)