

Population Extinction on a Random Fitness Seascape

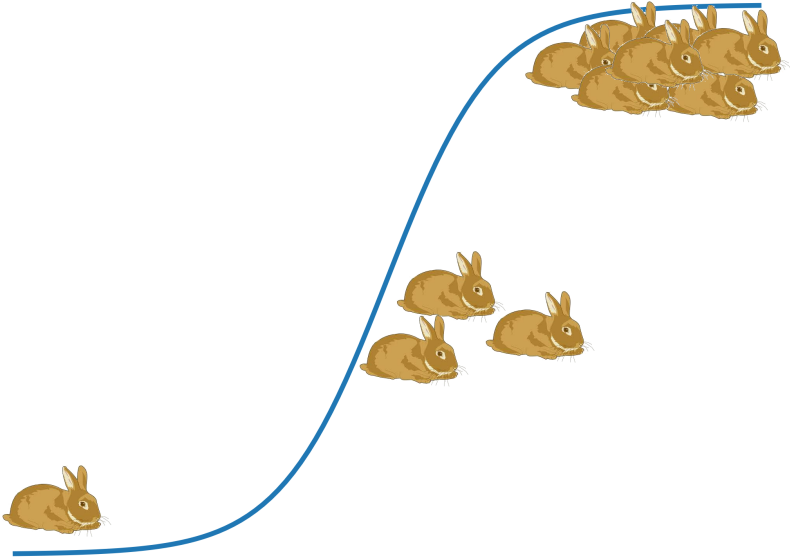
Bertrand Ottino-Löffler & Mehran Kardar

MIT

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Population Growth



Why Are There So Many Population Models?

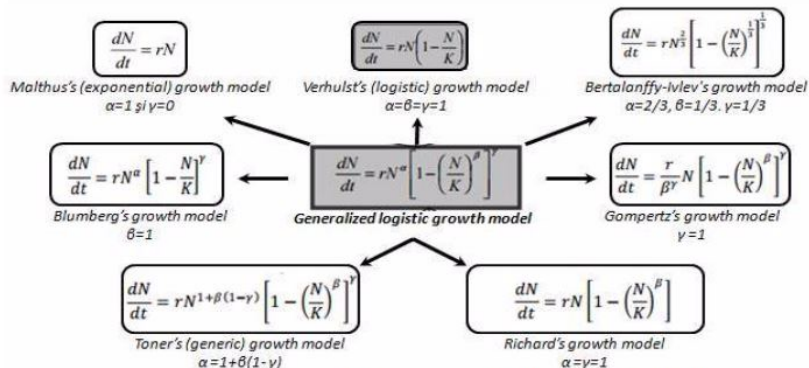


FIG. 3. The generalized logistic curve and its derivative models [11]

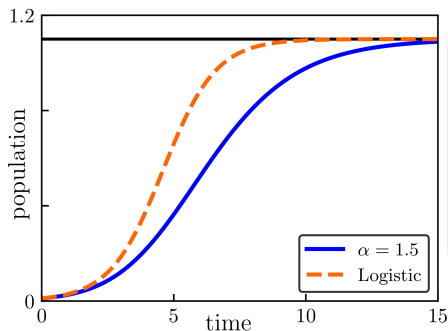
Figure: Cioruța (2016)

Richards' Equation

The **Richards' Equation** generalizes the logistic equation's second-order term, so

$$\partial_t y = \mu y - ay^\alpha.$$

This is commonly used in forestry and epidemics, but the value of α isn't always motivated.



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A Spatial Population Model As An Origin

The Fisher Equation

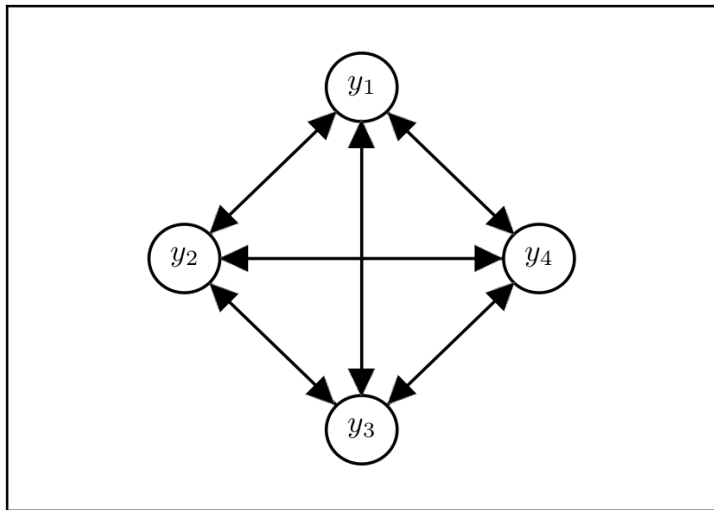
The **Mean-Field Fisher Equation** is given by

$$\partial_t y = \mu y - ay^2 + D(\bar{y} - y),$$

where

- μ sets growth rate,
- a sets saturation population,
- D sets diffusion rate, and
- \bar{y} is the spatial average.

A Mean-Field Model



Fitness is Time Dependent



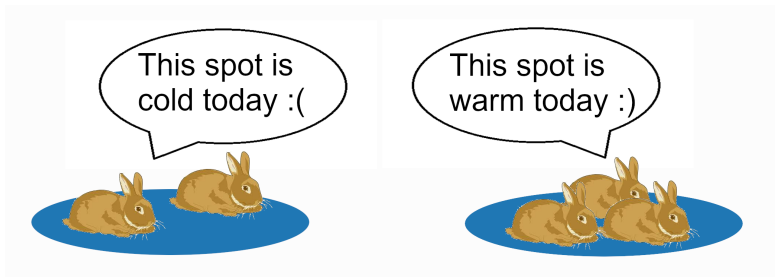
Figure: Merrell (1994)

Randomness in Fitness is Seascape Noise

We represent seascape noise by treating the fitness parameter μ as noisy. So,

$$\mu \rightarrow \mu + \sigma\eta,$$

where η is a stochastic term with unit variance and zero mean.



Seascape Noise

The Mean-Field Seascape Fisher Equation

The Fisher Equation with seascape noise is written as

$$\partial_t y = \mu y - ay^2 + D(\bar{y} - y) + \boxed{\sigma y \eta},$$

where $y\eta$ represents randomness in fitness and environment

Stationary State First

Good News:

- If a stationary state exists, then the spatial average pop. \bar{y} should be the same as the ensemble averaged pop. $\langle y \rangle$ via the Law of Large Numbers.

Bad News:

- In the absence of noise, the Fisher equation converges to $\bar{y} \rightarrow \mu/a$.

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- In the absence of noise, the Fisher equation converges to $\bar{y} = \mu/a$.
- However, $\bar{y} \not\rightarrow \mu/a$ in the presence of noise.
- \bar{y} must be obtained through self-consistency.

Self-Consistent

To be self consistent, we need

$$\partial_t \langle y \rangle = 0$$

Therefore, we need

$$\begin{aligned} 0 &= \langle \mu y - ay^2 + D(\bar{y} - y) + \sigma y \eta \rangle \\ &= \mu \bar{y} - a \langle y^2 \rangle \end{aligned}$$

So our condition is

$$\boxed{\mu \bar{y} = a \langle y^2 \rangle}$$

Distribution Solution

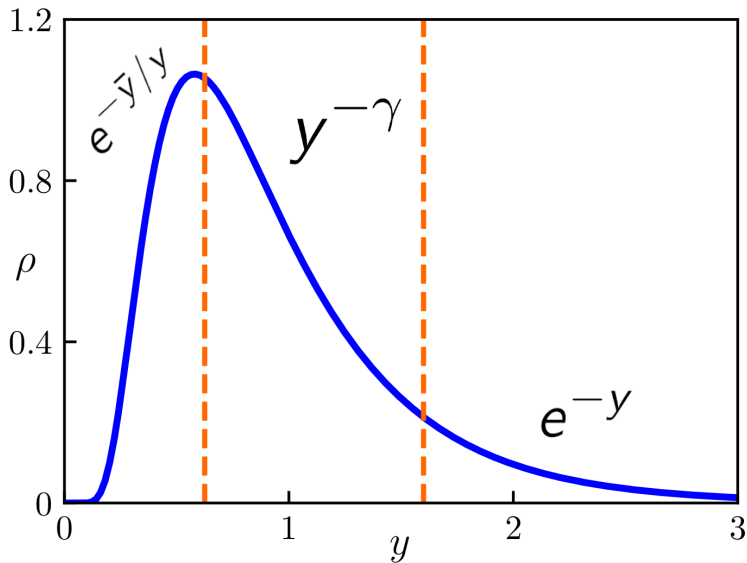
Distribution in the Growth Case

When $\mu > 0$, the population distribution under seascape noise is proportional to

$$\hat{\rho}(y, \bar{y}) = e^{-c_D \bar{y}/y} y^{-2-c_D+c_\mu} e^{-c_a y} .$$

where $c_D = 2D/\sigma^2$, $c_\mu = 2\mu/\sigma^2$, and $c_a = 2a/\sigma^2$, and \bar{y} is chosen self-consistently.

$$\hat{\rho}(y, \bar{y}) = e^{-\bar{y}/y} y^{-\gamma} e^{-y}$$



Self-Consistent mean

Using the cutoffs in $\hat{\rho}$, we can estimate

$$\mu\bar{y} = a\langle y^2 \rangle = a \frac{\int_0^\infty y^2 \hat{\rho}(y, \bar{y}) dy}{\int_0^\infty \hat{\rho}(y, \bar{y}) dy},$$

and solve the self-consistency condition.

Mean Pop at Small Fitness

Scaling Law for Seascape Noise

In the extinction limit, the population mean scales with the fitness as:

$$\bar{y} \propto \begin{cases} \mu, & 2D > \sigma^2; \\ \mu\sigma^2/(2D), & 2D < \sigma^2. \end{cases}$$

Notice that when $2D/\sigma^2 < 1$, we have an anomalous scaling exponent.

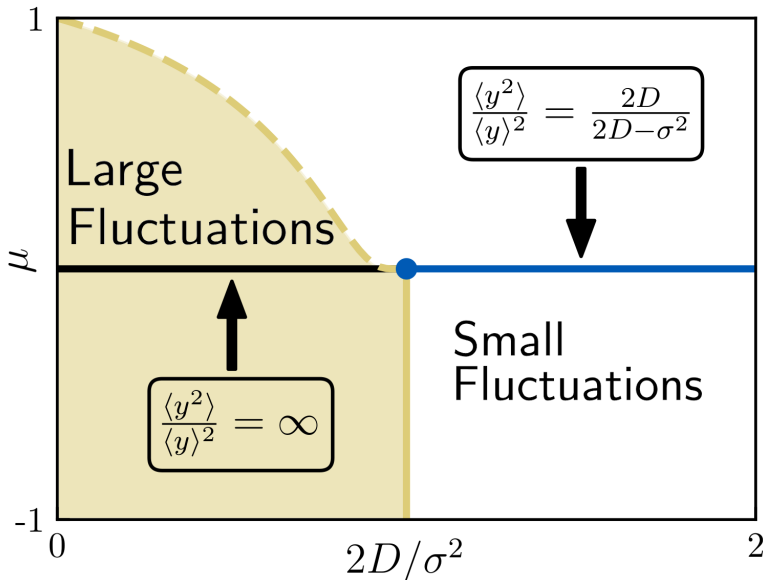
Moment Ratio with $\mu > 0$

Because we know the correct value of \bar{y} , we can calculate higher moments, and find that

$$\frac{\langle y^2 \rangle}{\langle y \rangle^2} = \frac{2D}{2D - \sigma^2}, \quad 2D > \sigma^2 ;$$
$$\frac{\langle y^2 \rangle}{\langle y \rangle^2} \propto \mu^{-\sigma^2/(2D)+1}, \quad 2D < \sigma^2 .$$

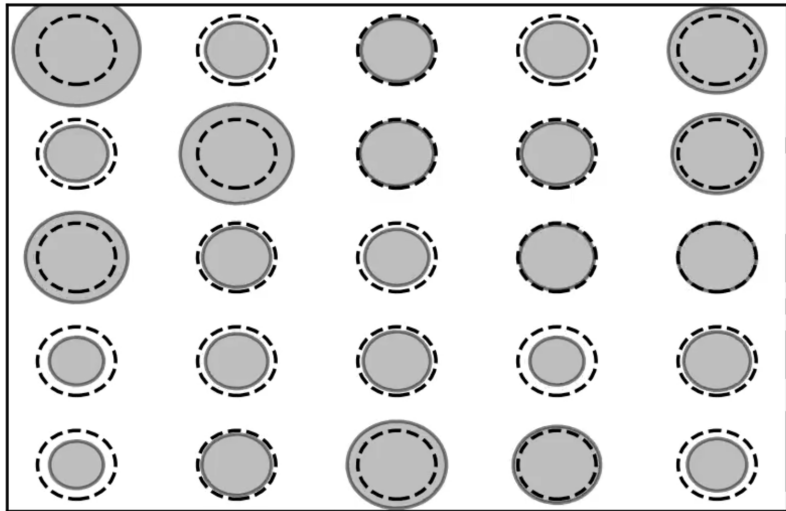
So as μ gets small, the variance may or may not get large compared to the mean.

Phase Diagram for Seascape Noise



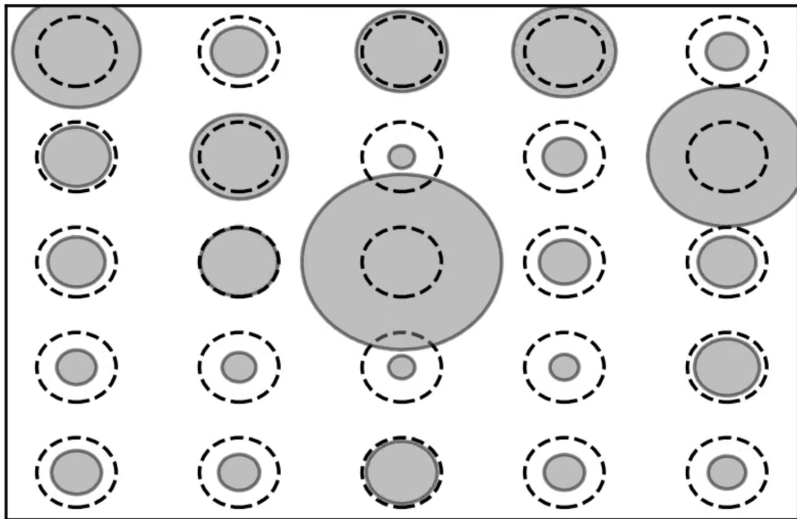
High $D \implies$ Low Variance

$$c_\mu = c_a = 0, c_D = 4.0, \sigma = 1.0, t = 5.0$$



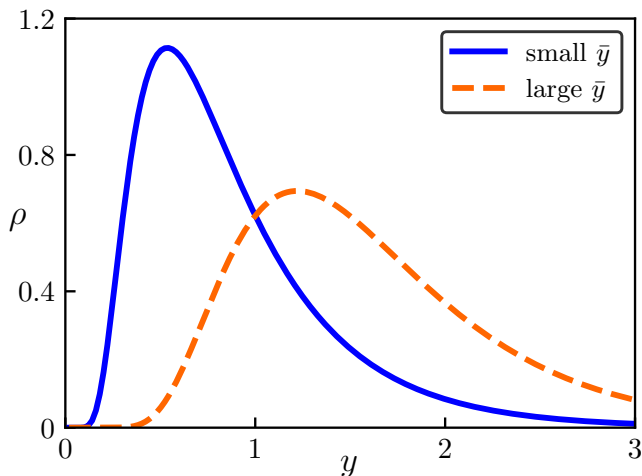
Low $D \implies$ High Variance

$$c_\mu = c_a = 0, c_D = 0.5, \sigma = 1.0, t = 5.0$$



Taking Stationary Solution into Dynamics....

Assume the distribution still looks like $\hat{\rho}$, but for a time-varying \bar{y} ...



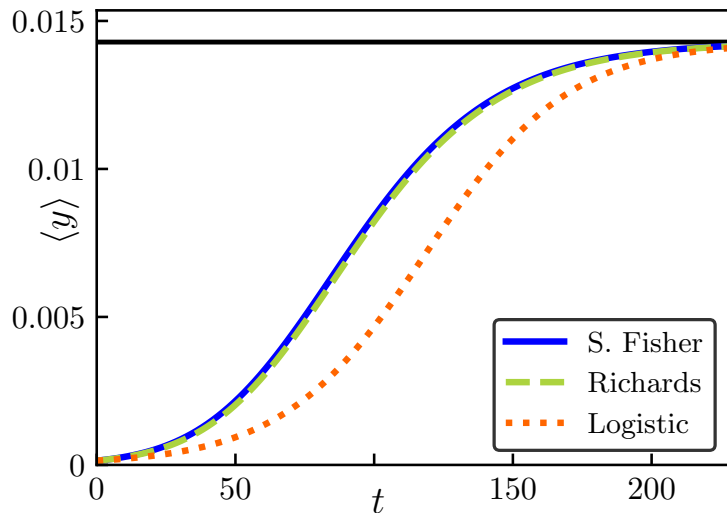
Fisher Averaged leads to Richards' Equation

Near extinction, the mean of the Stochastic Fisher Eq. behaves as

$$\begin{aligned}\partial_t \langle y \rangle &= \mu \langle y \rangle - a \langle y^2 \rangle + D \langle \bar{y} - y \rangle + \langle \sigma y \eta \rangle \\ &= \mu \langle y \rangle - a \langle y^2 \rangle \\ &\approx \mu \langle y \rangle - a \bar{y}^{1+\beta},\end{aligned}$$

which is a Richards' Equation!

Dynamics of the Mean



Final Summary

Seascape Noise + Spatial Diffusion



Anomalous, Nonuniversal Power Laws



Richards' Equation!

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Different Kinds of Noise

Tails	y small	y intermediate	y large
Seascape	$\exp[1/y]$	$y^{-\eta}$	$\exp[-y]$
Demographic	$y^{-\eta}$	$\exp[-y]$	$\exp[-y^2]$
Mixed	$y^{-\eta}$	$(y+r)^{-\gamma}$	$\exp[-y]$