

A Seascape Origin of Richards Growth

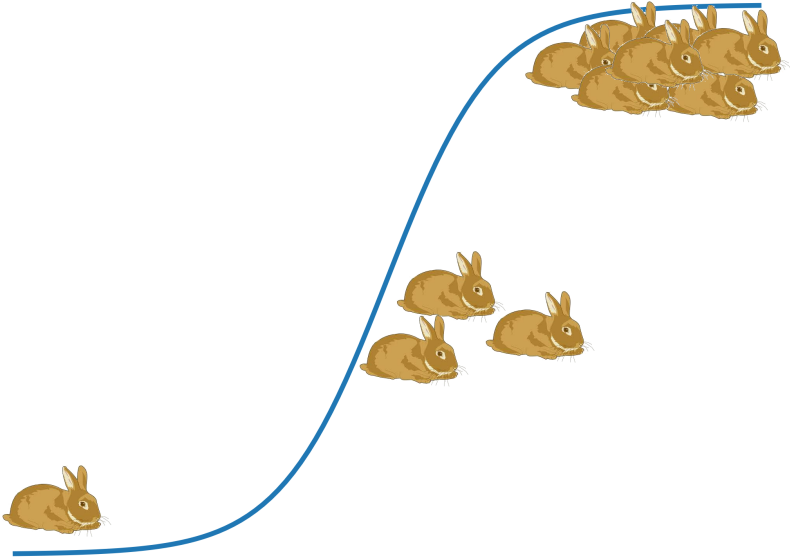
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Rockefeller University

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Population Growth



Why Are There So Many Population Models?

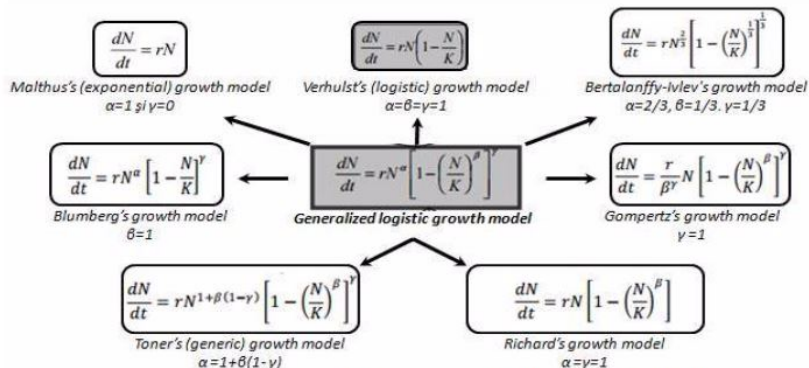


FIG. 3. The generalized logistic curve and its derivative models [11]

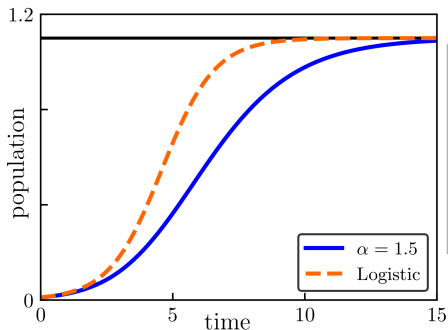
Figure: Cioruța (2016)

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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- 1 Generalised logistic differential equation
- 2 Gradient of generalized logistic function
- 3 Modeling COVID-19 infection trajectory
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Where Does It Come From?

Previous explanations have been to...

- Do a detailed manipulation of SIR, or
- Assume a fractal spatial structure, neither of which are particularly general.

How about a Spatial Population Model?

The Fisher Equation

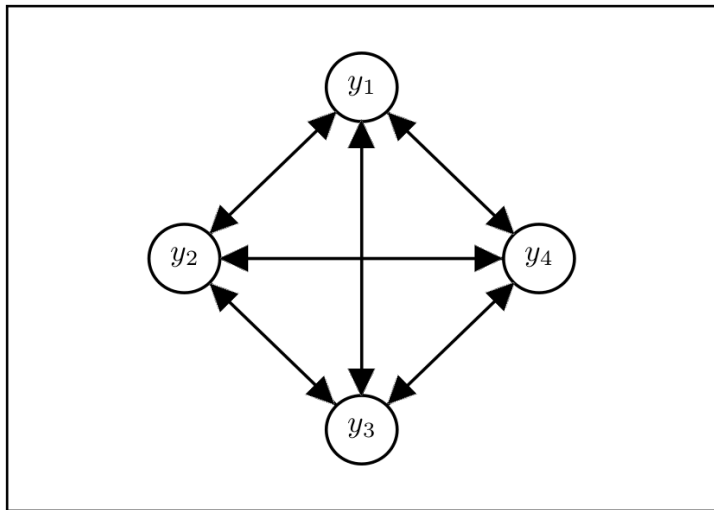
The Mean-Field Fisher Equation is given by

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

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

The Mean-Field Seascape Fisher Equation

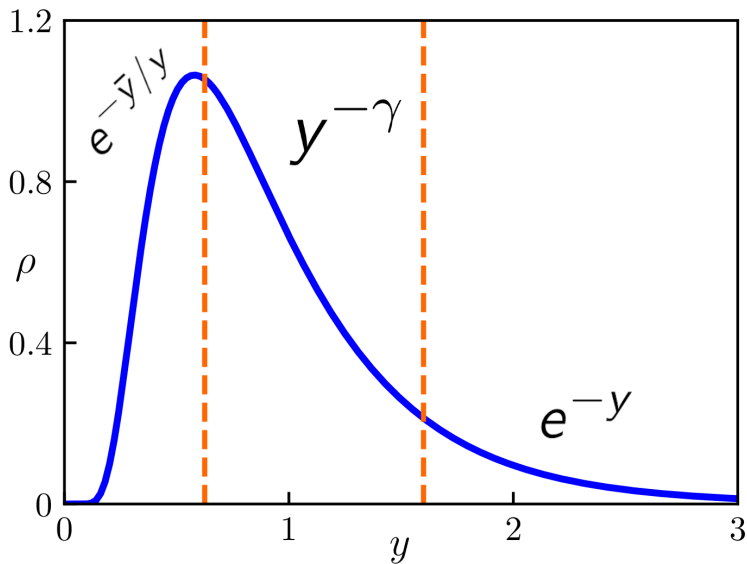
The Fisher Equation with seascape noise is written as

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

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

- This has a known steady-state solution!

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



How Do We Make The Stationary Solution into Dynamics?

Dynamics?

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

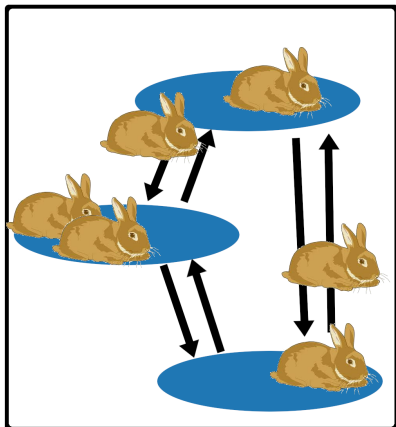
- Simultaneous growth and exploration is difficult to analyze...

Just Split Them!

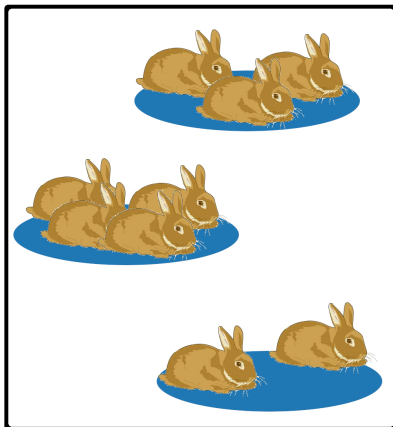
- Explore, then grow, then explore, then grow, and so on, and so on....

Seasonal Growth Model

Exploratory Phase



Growth Phase



Explore, Grow, Repeat...

Exploratory Phase Dynamics

$$\partial_t y = D(\bar{y} - y) + \sigma y \eta$$

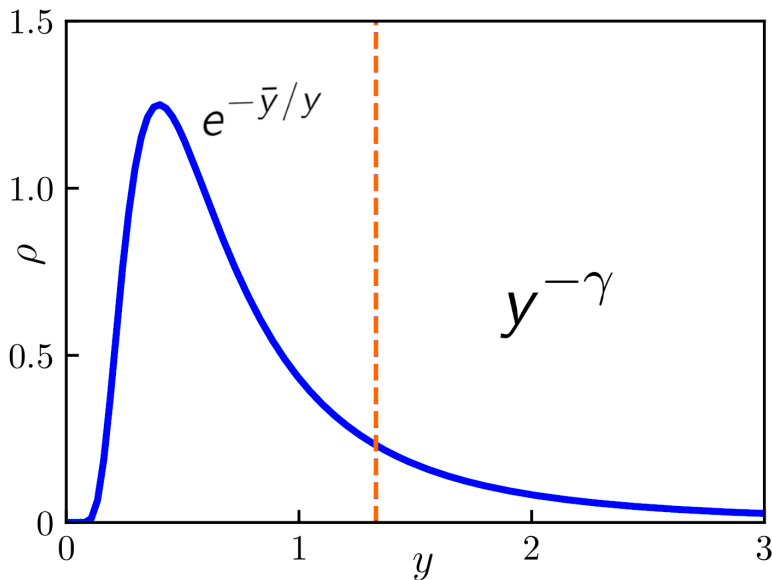
⇒ *Diffusion with seascape noise.*

Growth Phase Dynamics

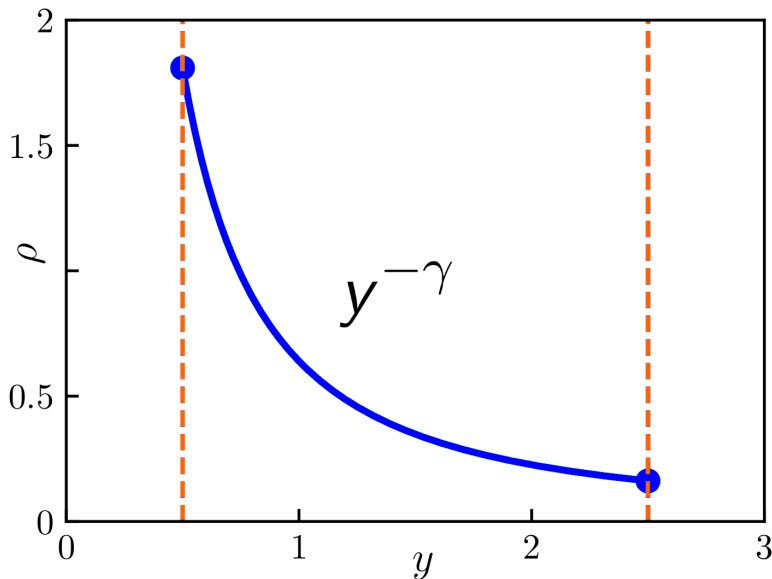
$$\partial_t y_i = \mu y_i - a y_i^2$$

⇒ *Logistic growth*

Problem With Exploring: No Upper Cutoff



Time is Finite, so Simplify



Time is Finite, so Simplify

Given this, we expect

$$\langle y^2 \rangle \propto \langle y \rangle^{1+2D/\sigma^2},$$

leading to a spatially dependant power law¹.

¹So long as $2D < \sigma^2$

Logistic Growth

The growth phase is deterministic, so each node goes like

$$y_i(t) = \frac{\mu y_i e^{\mu t}}{a y_i (e^{\mu t} - 1) + \mu}.$$

Short Growth Phase

If the timescale of growth Δt is small, then we can average over the exponential steady state and Taylor expand:

$$\langle y(t + \Delta t) \rangle = (1 + \mu \Delta t) \langle y(t) \rangle - a \langle y^2(t) \rangle \Delta t.$$

Short Growth Phase

If the upper cutoff Λ in the expository phase is sufficiently large compared to its mean, then

$$\frac{\langle y(t) + \Delta t \rangle - \langle y(t) \rangle}{\Delta t} = \mu \langle y(t) \rangle - \tilde{a}(\Lambda) \langle y(t) \rangle^\gamma + O\left(\left(\langle y(t) \rangle / \Lambda\right)^{2D/\sigma^2}\right)$$

Combined Dynamics

Combining the two phases leads to an averaged dynamics of

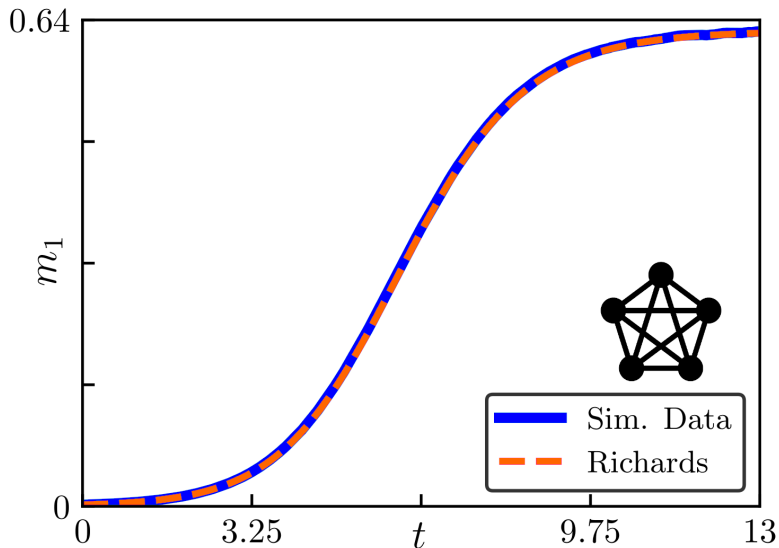
$$\partial_t \langle y \rangle = \tilde{\mu} \langle y \rangle - \tilde{a} \langle y \rangle^\gamma,$$

where $\tilde{\mu}$ and \tilde{a} depend on the time spent in each phase.

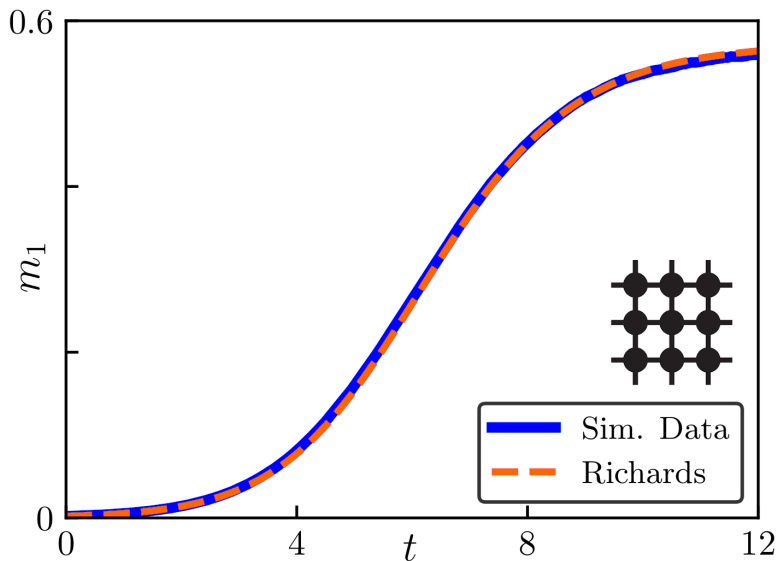
An Origin of Richards Growth

- 1 Diffusion under seascape noise produces power law distributions in space.
- 2 Under logistic growth, this power law shows up in the dynamics of the averages.

Mean Field



Shows up for 2D too



Universality

- Because the derivation is insensitive to perturbation in the growth phase, we get **Universality** that other approaches lack.

Final Summary

Seascape Noise + Spatial Diffusion



Anomalous, Nonuniversal Power Laws



Richards' Equation!

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First proposed as an empirical rule over half a century ago, the Richards growth equation has been frequently

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