Metapopulations: Part I

EFB 370: Population Ecology

Dr. Elie Gurarie

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Blowing up N_t in space

Simple population:

$$N(t)$$

Age/stage-structured:

$$N_i(t) = \{N_1(t), N_2(t), \ldots, N_k(t)\}$$

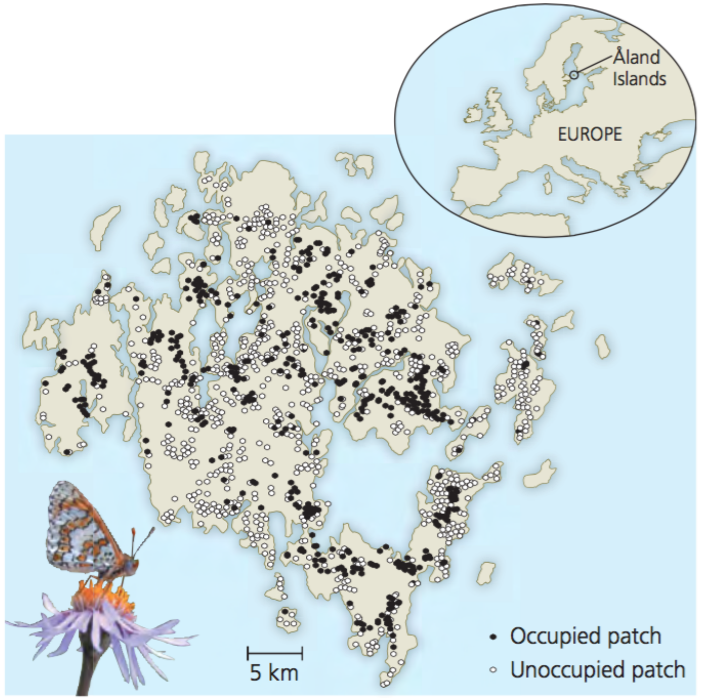
- where i represents structure, with k age/stage classes

Spatial structure:

$$N_i(t) = \{N_1(t), N_2(t), \ldots, N_k(t)\}$$

- where i is location, with k locations

A metapopulation is a **population of populations**



▲ Figure 53.21 The Glanville fritillary: a metapopulation. On the Åland Islands, local populations of this butterfly (filled circles) are found in only a fraction of the suitable habitat patches (open circles) at any given time. Individuals can move between local populations and colonize unoccupied patches.

Ribwort plantain (Plantago lanceolata)

Spiked speedwell (Veronica spicata)

1. The local populations MUST be somehow connected via **dispersal**.
2. There must be areas of (near) zero density in between. The "in-between" is referred to as the **matrix**.

Canonical examples

- **Fragmented habitats**
- Island populations

Population vs. Metapopulation

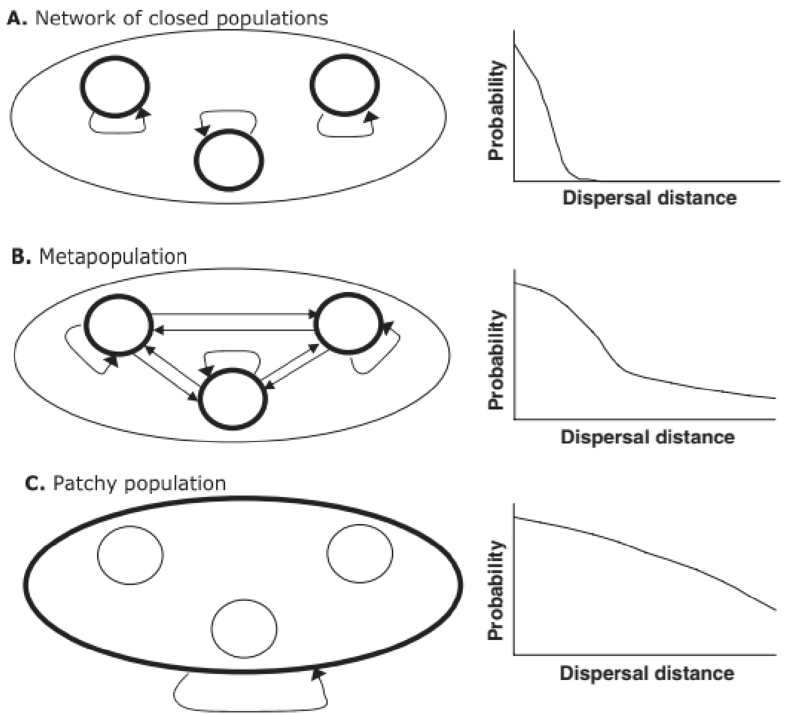
WA sea otters

- Closed population
  - only **Birth** and **Death**
- Questions:
  - growth | dynamics | age structures
- **Extinction** of interest mainly due to stochasticity, low numbers

ALL sea otters

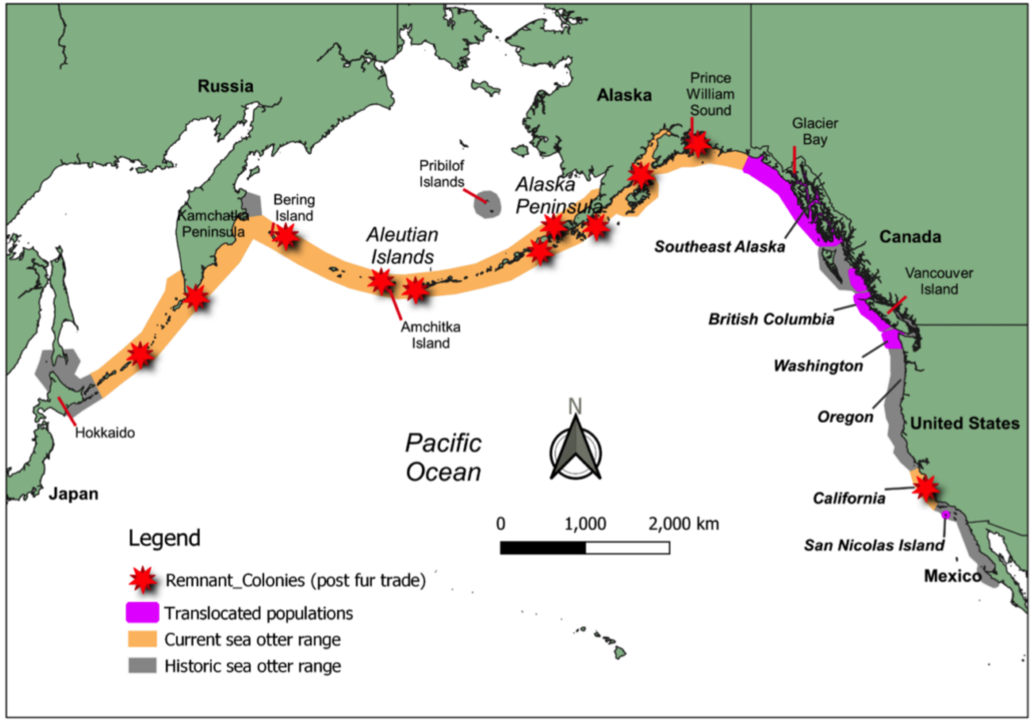
- Open population
  - **Immigration! Emigration!**
- Questions:
  - given that a local population might go **extinct**, will the metapopulation go **extinct**?
  - what is the proportion of occupied patches?

What makes it a metapopulation? **Dispersal distance**



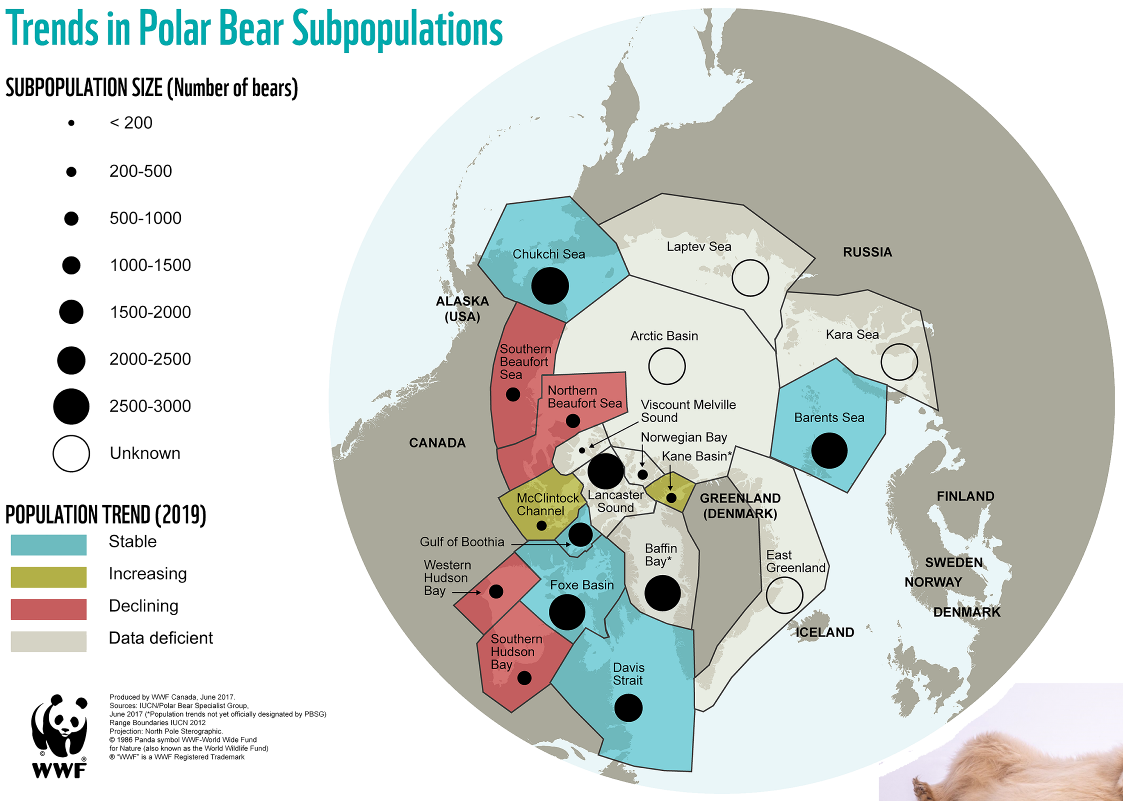
Sale, Hanski, Kritzer 2006

As long as there is *some* local connectivity among populations.

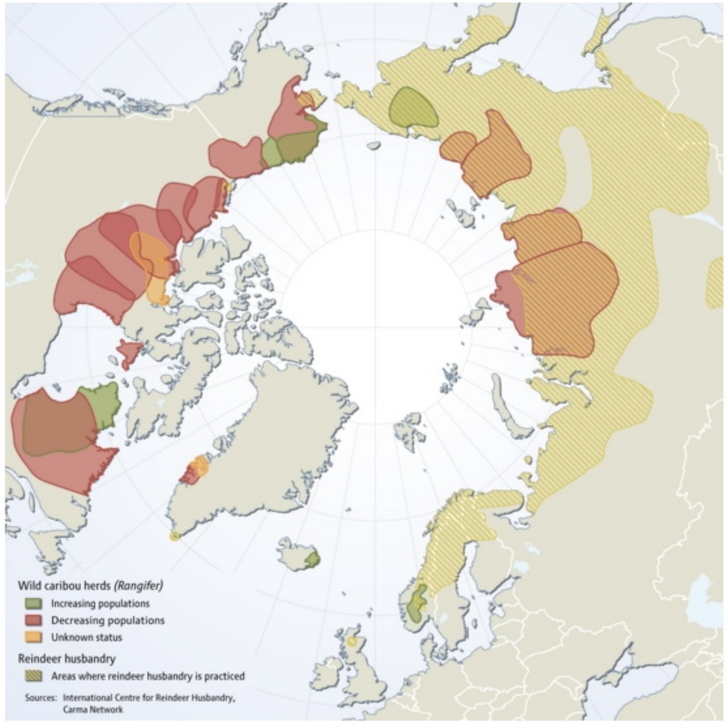


By that metric ...

Polar bear (*Ursus maritimus*)



and caribou / reindeer (*Rangifer tarandus*)

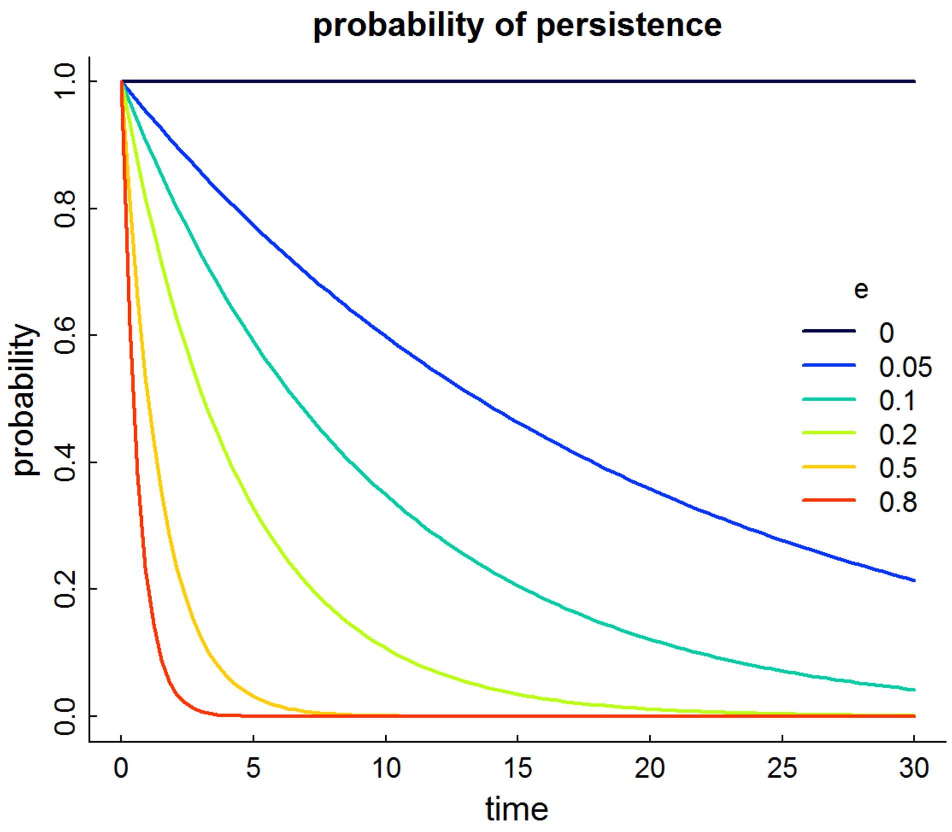


Are also **metapopulations**

Population persistence of a single population?

e = *local* probability of extinction

time steps	Prob. persistence
1:	$1-e$
2:	$(1-e)(1-e)$
3:	$(1-e)(1-e)(1-e)$
4:	$(1-e)(1-e)(1-e)(1-e)$
…	
t:	$(1-e)^t$

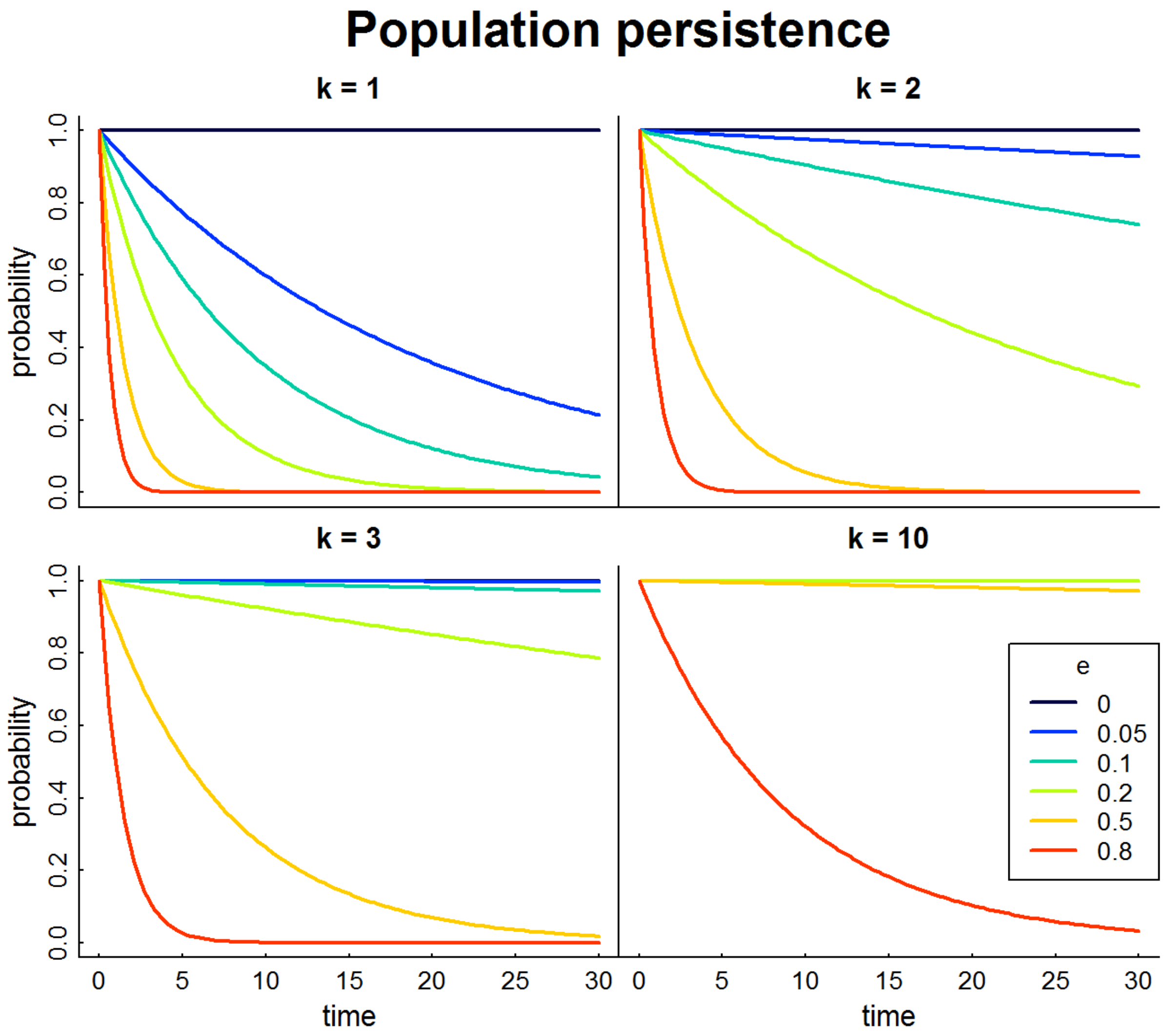


Take away: Even with very LOW probability of extinction, you WILL go extinct.

M0: Population persistence of a **metapopulation**

k populations, t time steps

Pops:	1 time step	t steps
1:	$1 - e$	$(1 - e)^t$
2:	$1 - e \times e$	$(1 - e^2)^t$
3:	$1 - e \times e \times e$	$(1 - e^3)^t$
...	...	...
k:	$1 - e^k$	$(1 - e^k)^t$

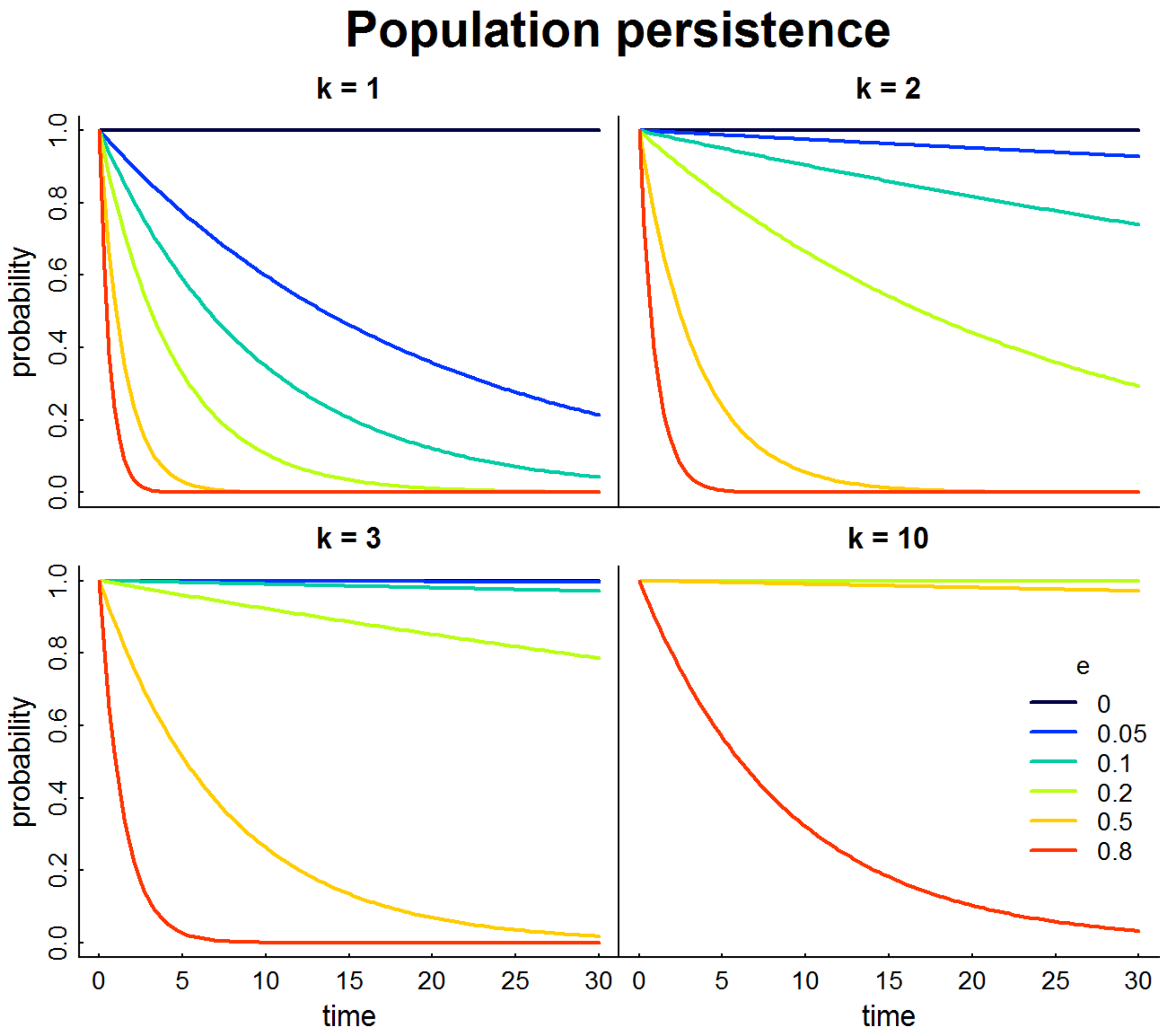


Metapopulations are resistant to extinction!

$$P(k,t) = (1 - e^k)^t$$

Metapopulations **dramatically** spread out / buffer the risk of extinction!

But still ... if the ONLY process is extinction, you **will go extinct** (sorry!)

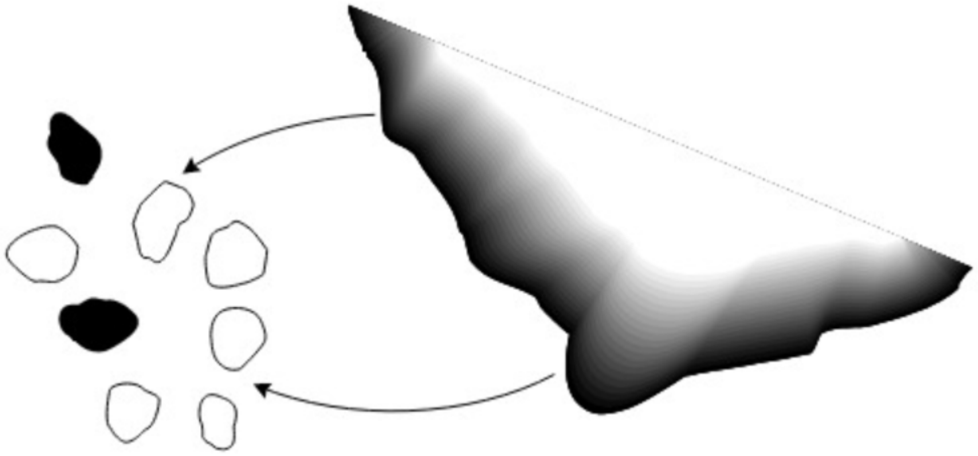


M1: Let's add colonization

Island-Mainland model

- Every (local) population has a probability of going extinct: p_e
- But every empty location has a probability of getting colonized: p_c

> Note - there is an important (implicit) assumption that population very quickly hits **carrying capacity**, so essentially *instant* saturation.



The mainland is a constant, independent source of potential colonizers. Also known as **propagule rain**.

(echoes of *biogeography*).

M1: Island-Mainland Model

Q: How many occupied patches might we expect?

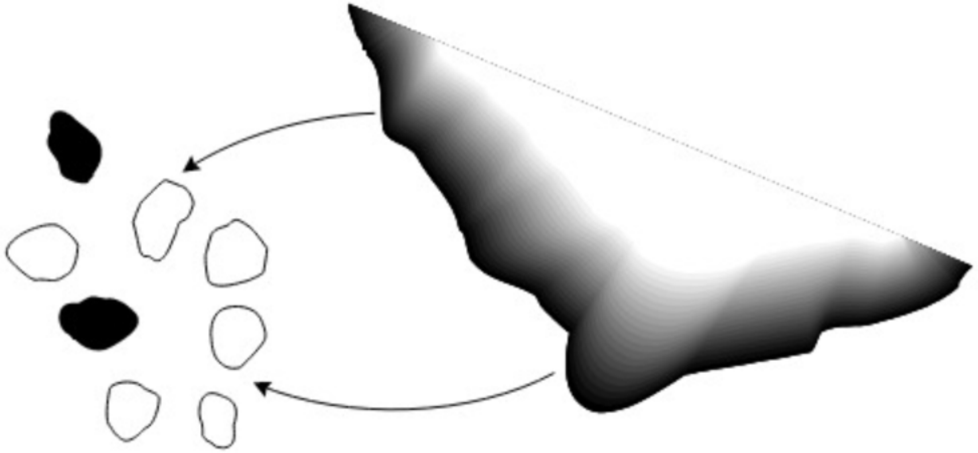
$$E(N_{t+1}) = N_t - p_e N_t + (K - N_t)\, p_c$$

define proportion of populated patches: $f_t = E(N_t)/K$, and define *equilibirum*:

$$f^* := f_{t+1} = f_t$$

...then some math happens...

$$f^* = \frac{p_c}{p_c + p_e}$$



The equilibrium is a balance between colonization and extinction rate.

Continuous time formulation

Very general metapopulation model:

$$\frac{df}{dt} = c(f) - e(f)$$

Where c = colonization rate, e = extinction rate. Can be (often are!) functions of `(f)` (occupied proportion).

Note: this is similar to

$$\frac{dN}{dt} = b(N) - d(N).$$

which is the foundation of population growth models)

Assumptions:

- Deterministic (i.e. $k \to \infty$)
- Continuous-time, unstructured extinction / colonization process
- "Rates" are like infinitesemal probabilities

But - lots of elegant analyses can be made messing with this model.

M1: Mainland-Island

$$\frac{df}{dt} = c - e$$

Colonization is constant, so proportional to **available** patches:

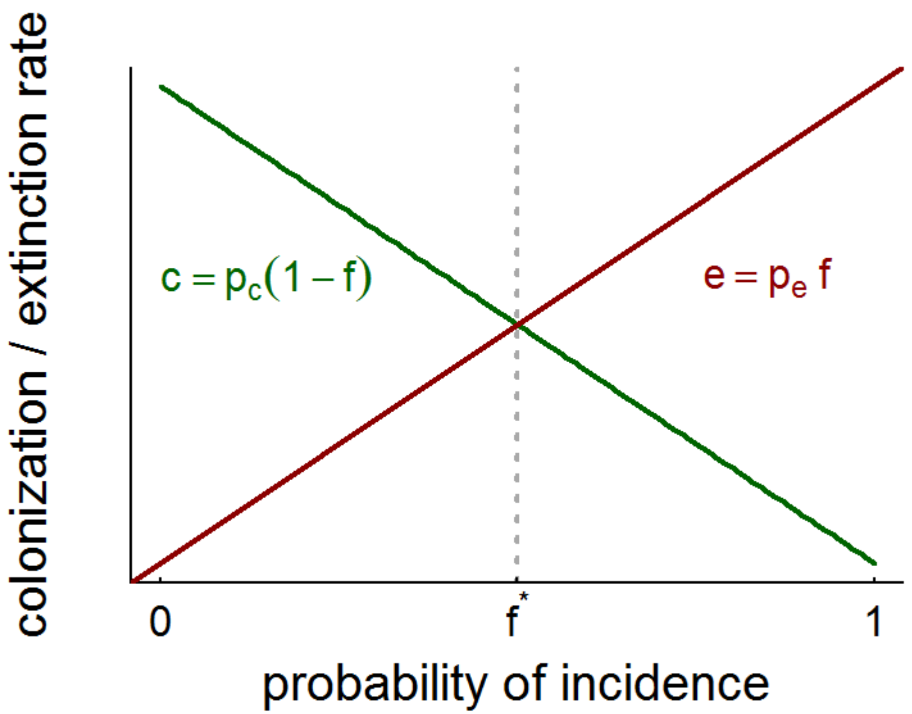
$$c = p_c(1 - f)$$

Extinction is constant, so proportional to **occupied** patches:

$$e = p_e f$$

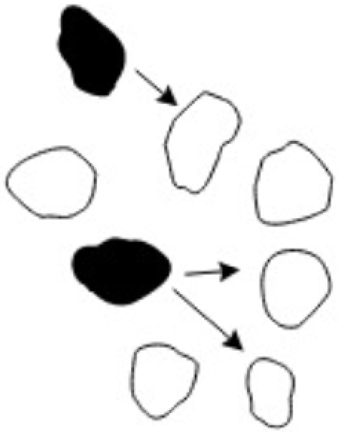
so:

$$\frac{df}{dt} = p_c(1 - f) - p_e f$$



The rate of change of the occupied patches GROWS in proportion to unoccupied patches and FALLS in proportion with occupied patches.

M2: Internal Colonization



$$\frac{df}{dt} = p_c f(1 - f) - p_e f$$

Extinction *rate* is constant, as before:

$$e = p_e f$$

Colonization can only come from **occupied** patches:

$$c = p_c\, f\,(1 - f)$$

If no patch is colonized ($f = 0$), nothing can colonize.

If the population is 100% occupied ($f = 1$), there is nothing to colonize.

M2: Internal Colonization - with Schematic

$$\frac{df}{dt} = p_c f(1-f) - p_e f$$

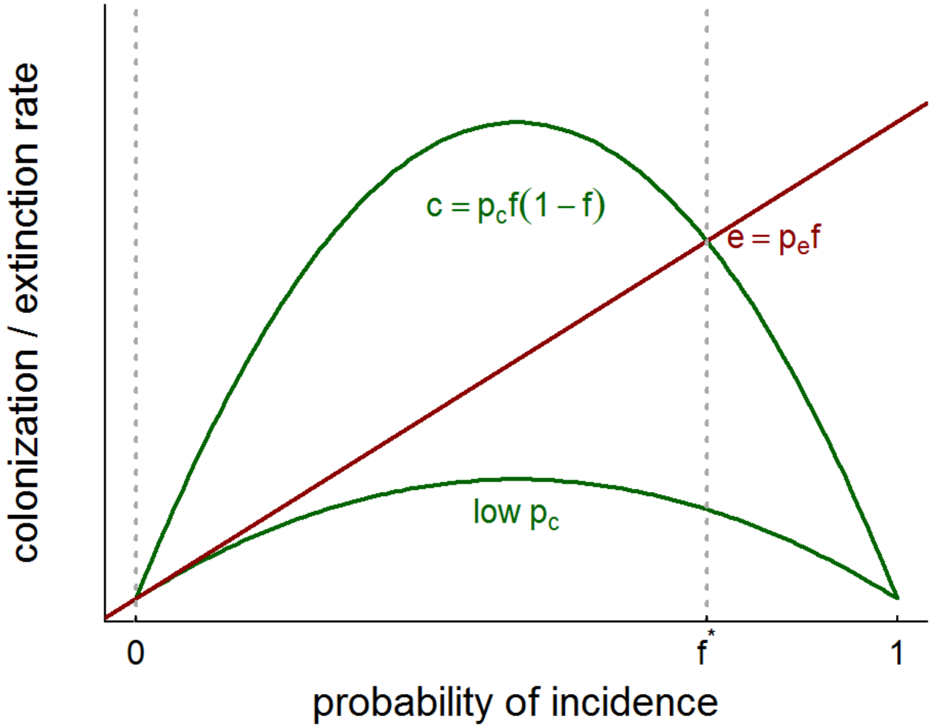
Extinction is constant, as before:

$$e = p_e f$$

Colonization can only come from **occupied** patches:

$$c = p_c\, f\,(1-f)$$

The maximum rate of colonization occurs when $f = 1/2$.



Equilibrium occurs when:

$$f^* = \begin{cases} 1 - p_e/p_c & \text{when} \quad p_e < p_c \\ 0 & \text{when} \quad p_e \geq p_c \end{cases}$$

M3: Rescue Effect

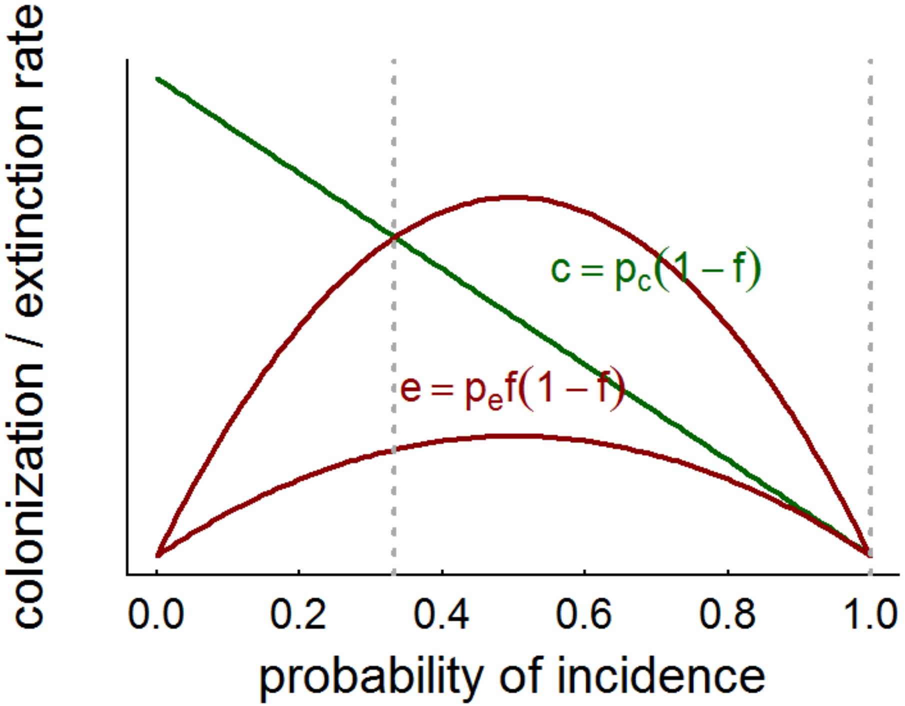
$$\frac{df}{dt} = p_c(1-f) - p_e f(1-f)$$

Assumes that if you have a lot of neighbors some loose "propagules" will buffer you from extinction.

Equilibrium states:

$$f^* = \begin{cases} p_c/p_e & \text{when} \quad p_e > p_c \\ 1 & \text{when} \quad p_e \leq p_c \end{cases}$$

Even with higher extinction rate than colonization rate, there will always be some occupied patches!



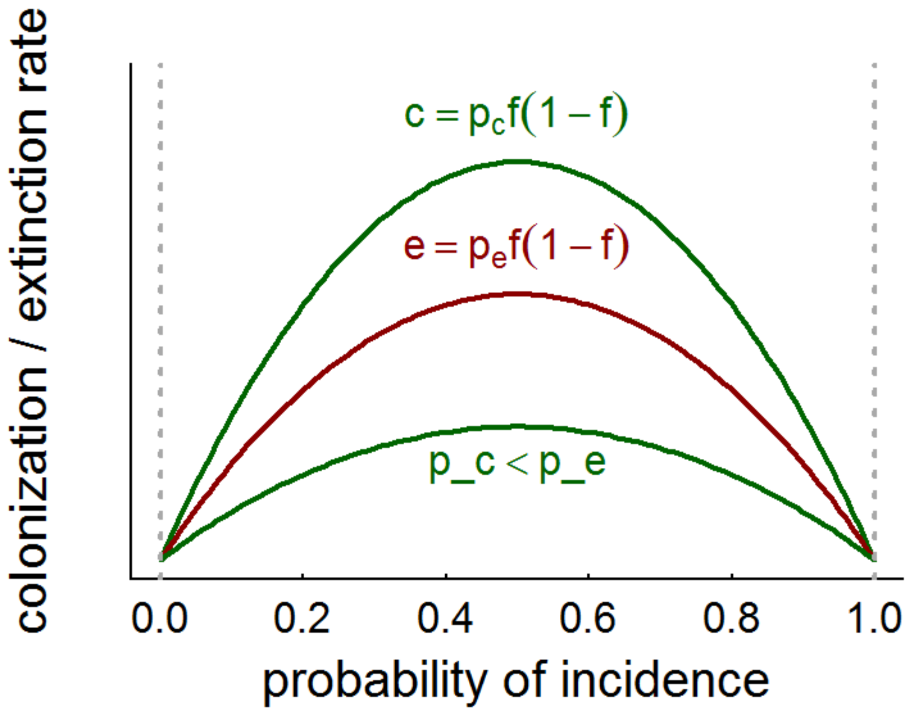
M4: Rescue Effect with Internal Colonization

$$\frac{df}{dt} = p_c f(1-f) - p_e f(1-f)$$

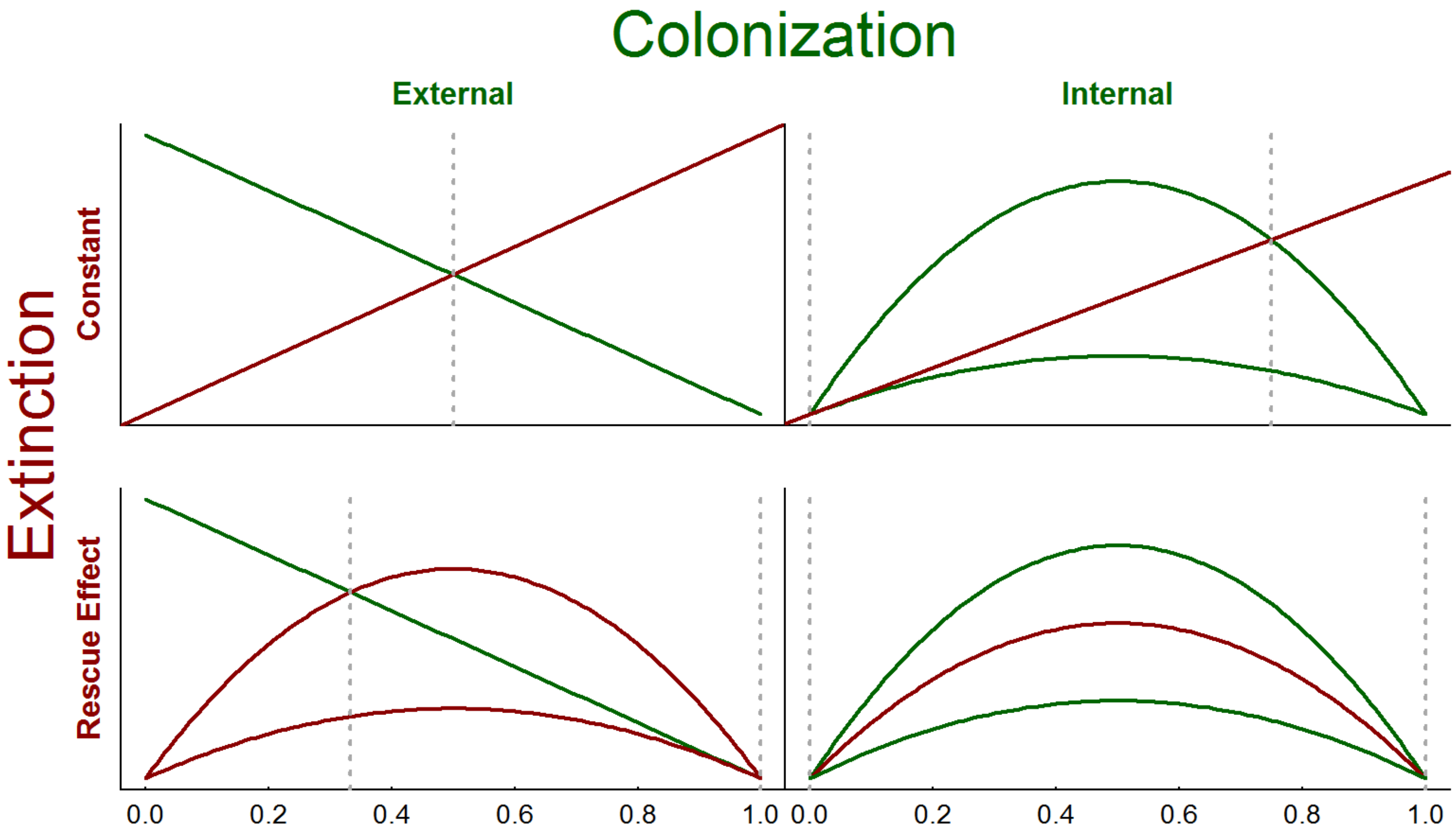
Only equilibria: 0, if $p_e > p_c$ or 1, if $p_e \leq p_c$.

Fundamental conclusions:

> **metapopulation** under equilibrium MUST be rare! Either everything colonizes or nothing colonizes.**



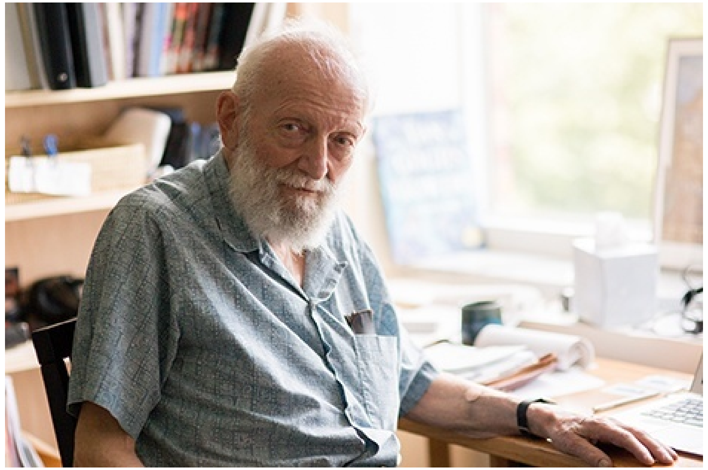
Four models



With rather different predictions! (Nice synthesis - mainly due to Gotelli.)

Some characters

Richard Levins (1930-2016)



- "Scholarship that is indifferent to human suffering is immoral."
- "Our truth is the intersection of independent lies."

Ilkka Hanski (1953-2016)