Population Ecology: Spatial questions and methods to model them

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B) Spatial problems and methods for modeling them

How do you think about ‘space’ ?

How is ‘space’ structured for problems in your field ?

Methods for spatial problems in ecology and socio-environmental science

In ecology, different conceptualizations point to different spatial methods

- Explicit vs. Implicit Space
- One Patch vs. ‘Outside’
- Small sets of homogeneous patches vs. Large networks with heterogeneity
- Large, continuous regions with gradients

Methods for spatial problems in ecology and socio-environmental science

In ecology, different conceptualizations point to different spatial methods

Alphabet Soup:

PM: Patch Models
BBA: Bin, Bucket, and Array Models
: Metapopulation Models
: Network Models
CA: Cellular Automata
IP: Interacting Particle Models
PDE: Partial Differential Equations
IDE: Integro-Difference Equations

→ The kinds of questions we can ask (and the kinds of answers & insights we can get) can hinge on spatial methods we use

Conceptual Overview of Metapopulations

What is a metapopulation really?

→ Buzzword used to describe a variety of spatially-structured populations

Think of a landscape broken up into patches

→ patches obey local population dynamics

→ patches are connected by dispersal

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Moving from population dynamics
To sets of populations

Conceptual Overview of Metapopulations

Represent larger spatial scale dynamics

→ focus on patch states (occupied vs. empty)

→ focus on abstraction (useful because we can't always keep all the details)

Time scale argument

→ population dynamics on local patches are changing faster than patch states

Quantitative Representation of Metapopulation Dynamics

$$\frac{dp}{dt} = cp(1-p) - ep$$

$p =$ proportion of patches occupied at time t

$c =$ rate of patch colonization

$e =$ rate of patch extinction

[equation structure]

Equilibrium:

$$\text{set } \frac{dp}{dt} = 0$$

$$p^* = 1 - \frac{e}{c}$$

↑

Equilibrium fraction of patches occupied

[Check is it a stable or unstable equilibrium?]

Conservation Issues:

What happens if you destroy (make uninhabitable) some patches?

Modify Equation:

$$\frac{dp}{dt} = cp(1 - p - \underline{D}) - ep$$

↑

Fraction destroyed

New $p^* = 1 - \frac{e}{c} - D$

⇒ What value of D guarantees extinction?

⇒ Do you have to destroy all the patches to cause extinction?

C) Integrodifference equations as a robust platform

Starting with Kot et al. 1996. *Ecology* _or_
Hastings et al. 2005. *Ecology Letters*

- Overview and Equation Structure
- Application to Spatial Spread of Invasive Species
- Application to Central Place Foraging
- Application to Conservation Planning: Average Dispersal Success

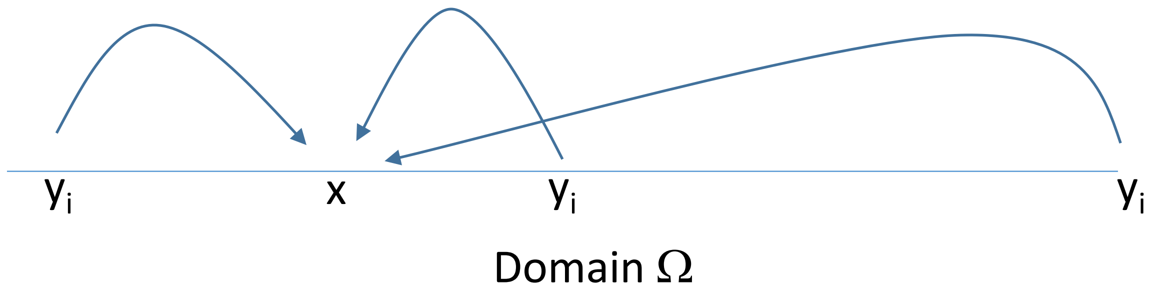
Integrodifference Equations

→Discrete time
→But space is continuous

Domain Ω
"the patch"
"the landscape"

Integrodifference Equations

→Discrete time
→But space is continuous



Focus on local dynamics at each position x

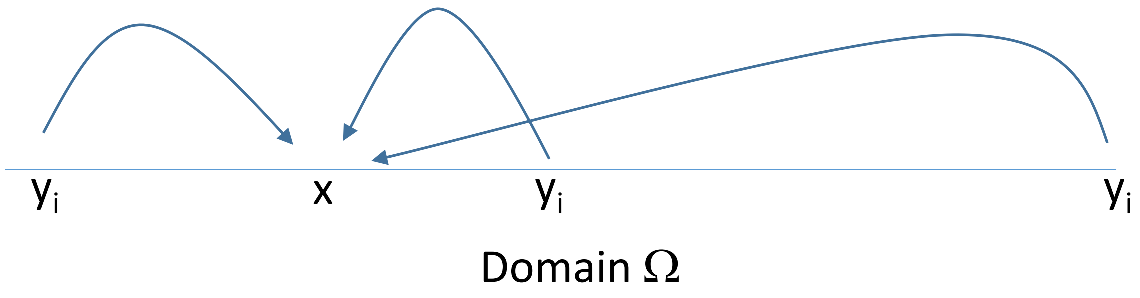
Population growth at all possible positions y

Individuals get redistributed and some arrive at x

→Integrate growth across all positions (y) & redistributions (from y) to quantify local change at x

Integrodifference Equations

→Discrete time
→But space is continuous



$$N(t+1,x)=\int_{\Omega}k(x,y)N(t,y)dy$$

Note: y is still a position in 'space' just like x

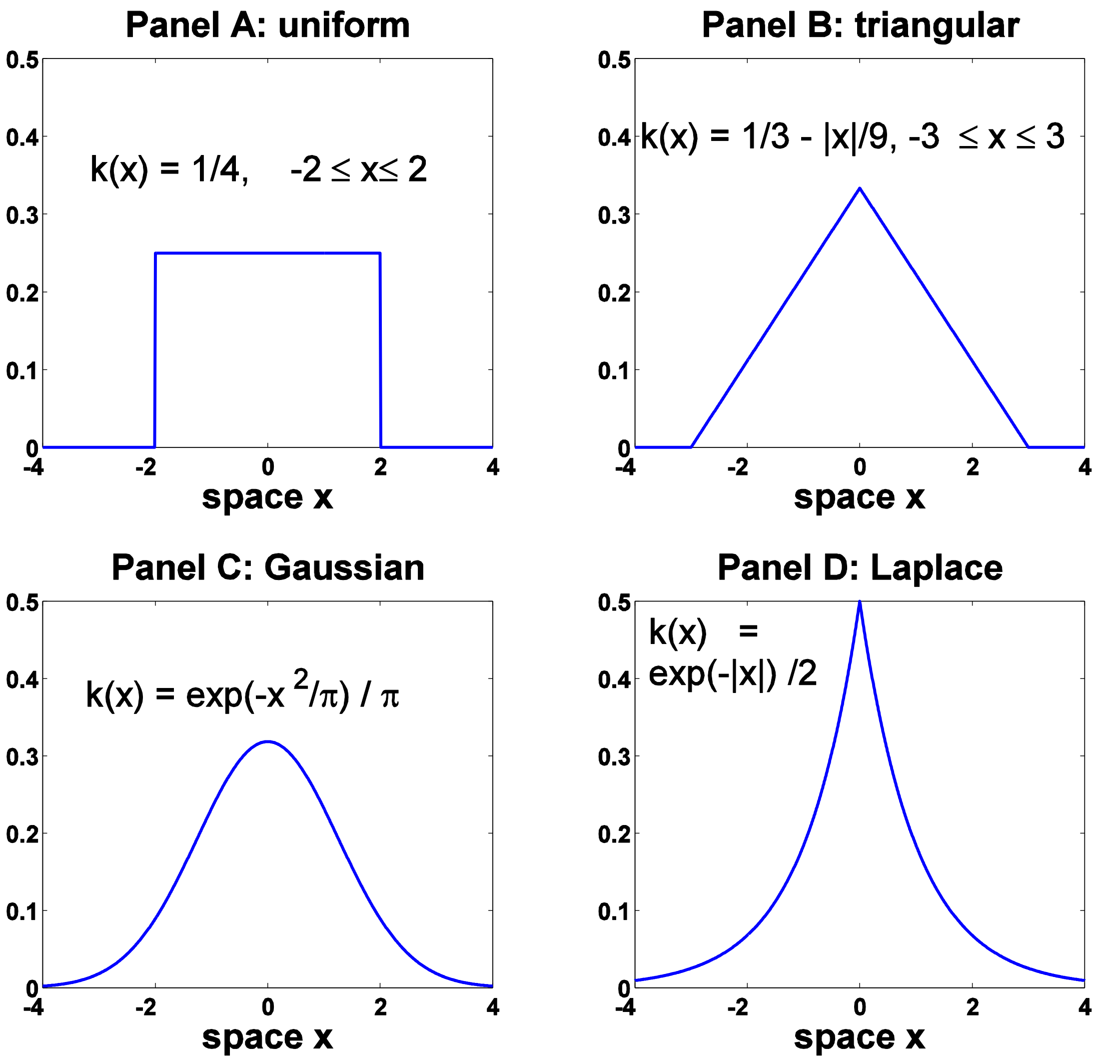
Integrodifference Equations

→ Dynamics depend on form of the dispersal kernel *k(x,y)* ← Kernel is a probability density function

$$N(t+1,x)=\int_{\Omega} k(x,y)N(t,y)dy$$

Spatial Foraging Pattern (Kernels)

k(x) : distribution of foraging locations, $\int |x| k(x) dx = 1$



Integrodifference Equations

→ Dynamics depend on form of the dispersal kernel *k(x,y)* ← Kernel is a probability density function

$$N(t+1,x)=\int_{\Omega} k(x,y)N(t,y)dy$$

What are the advantages ?

Integrodifference Equations

→ Dynamics depend on form of the dispersal kernel *k(x,y)* ← Kernel is a probability density function

$$N(t+1,x) = \int_{\Omega} k(x,y) N(t,y) dy$$

What are the advantages ?

1) Discrete time structure (e.g., annual) provides a good match to many ecological (and SE) data
2) Build from well-understood population dynamics platform to add important complexities
3) Statistically estimable parameterizations
4) Analytically tractable
5) Strong mathematical / theoretical foundation
6) ‘Interesting’ to mathematicians / theoreticians

Integrodifference Equations

→ Dynamics depend on form of the dispersal kernel *k(x,y)* ← Kernel is a probability density function

$$N(t+1,x)=\int_{\Omega}k(x,y)N(t,y)dy$$

Some questions to ask:

1) How fast will a species spread through a landscape ?

2) How does foraging away from a "home-base" influence resources and population dynamics of the foragers ?

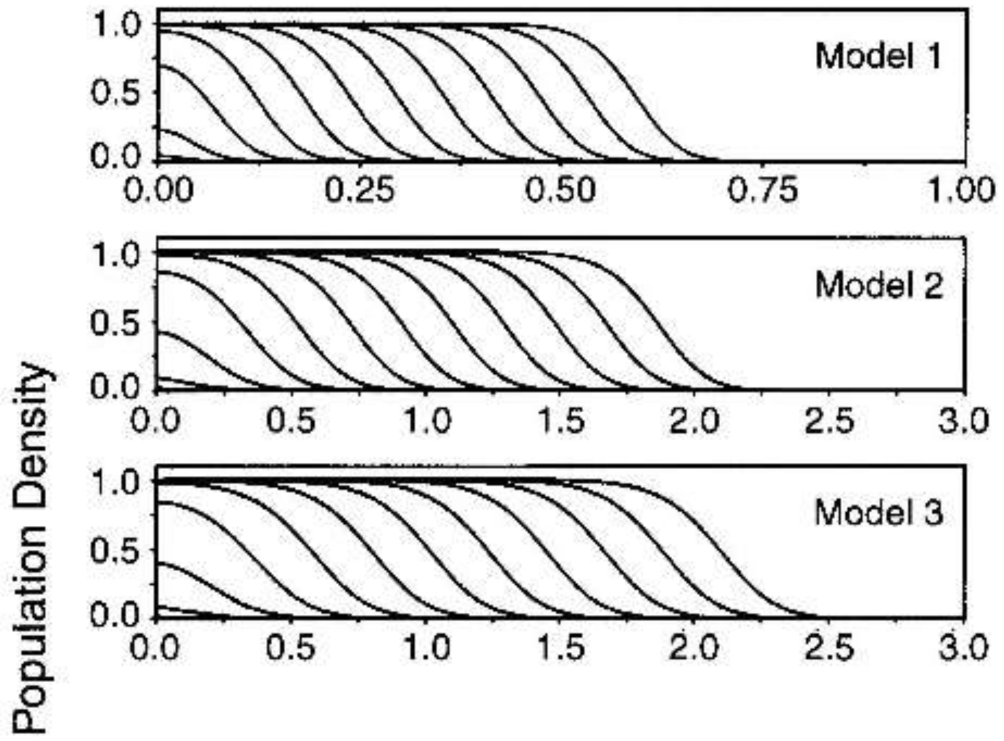
3) How much of a population is lost out of a patch into unsuitable habitat ?

1) How fast will a species spread through a landscape ?

See: Kot, M., M.A. Lewis, P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. Ecology. 77 (7): 2027-2042

For some kernels:

Can get an asymptotically constant 'spreading speed'
Can get 'traveling wave' phenomenon where shape of wavefront is stable



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See: Kot, M., M.A. Lewis, P. van den Driessche. 1996. Dispersal data and the spread of invading organisms.

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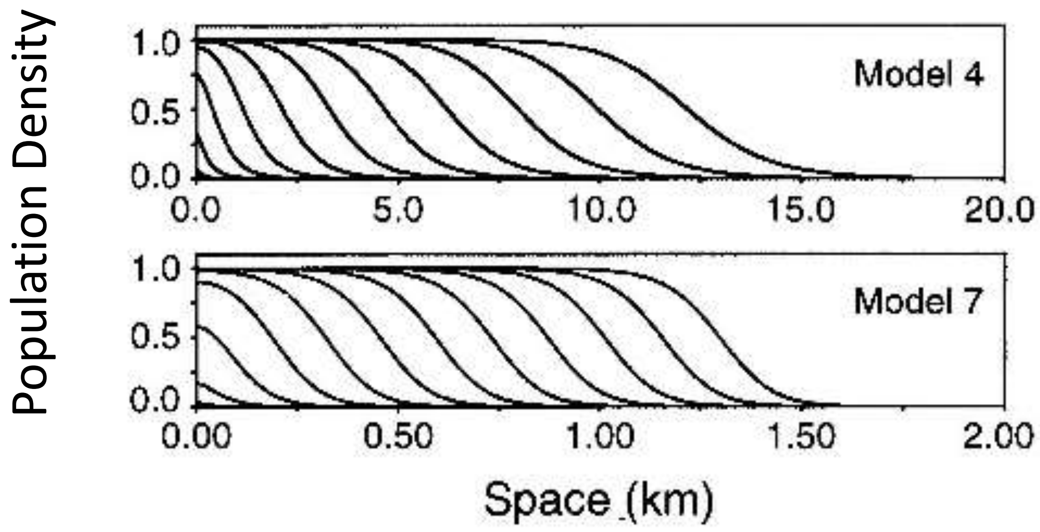
For ‘heavy-tailed’ kernels:

Can get accelerating spread
Amount of long-distance dispersal is critical to expansion

Relevance to

S – E systems ?

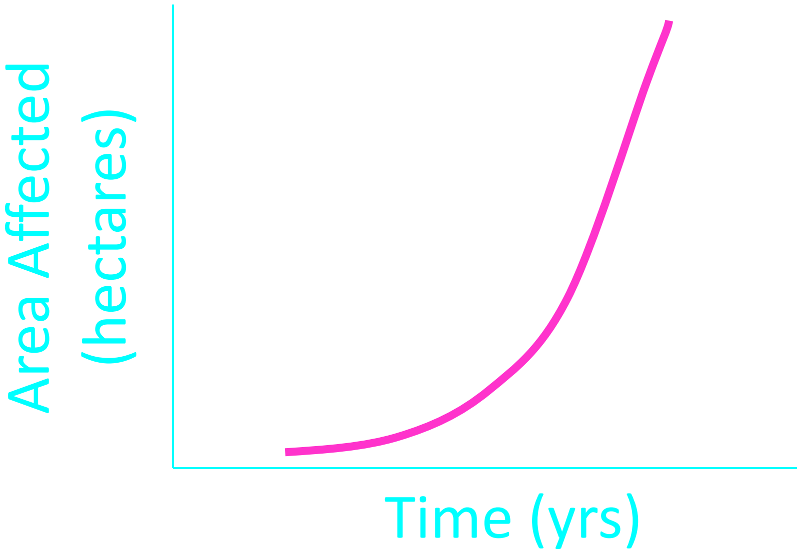


Biological control as a problem in spatial ecology

Spatial Spread of Pests

Total area affected

Rate of spread



Spatial Control

How many releases of control agents ?

Where to release control agents ?
- Areas of high damage
- New outbreaks

Area of control vs. Rate of spread

Biological Control and the Mathematics of Invasive Spread

- Theoretical perspective:

  What does it take to stop the spread of a pest ?

  ➔ Building models of spatial spread

- Empirical perspective

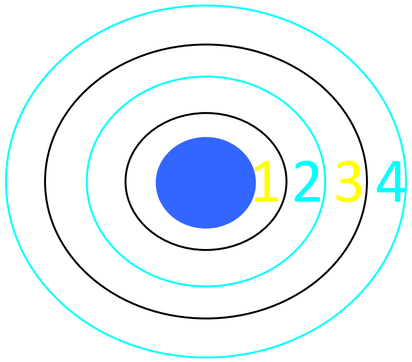
  What can plant-herbivore "co-invasions" teach us about biological control ?

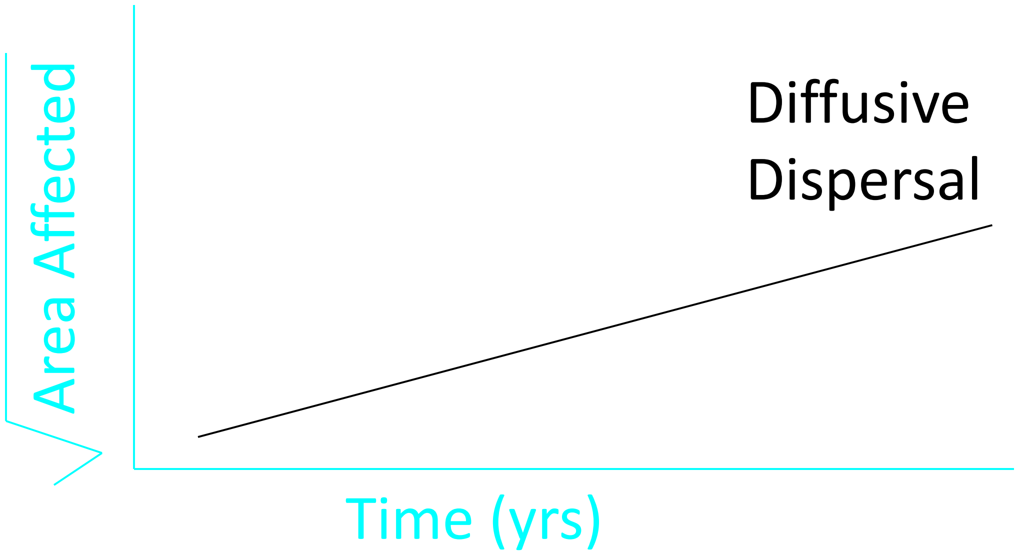
Early mathematical models of spreading populations

$$\frac{\partial u}{\partial t} = D_u \frac{\partial^2 u}{\partial x^2} + u f(u)$$

Predict a constant rate of invasion (eventually)

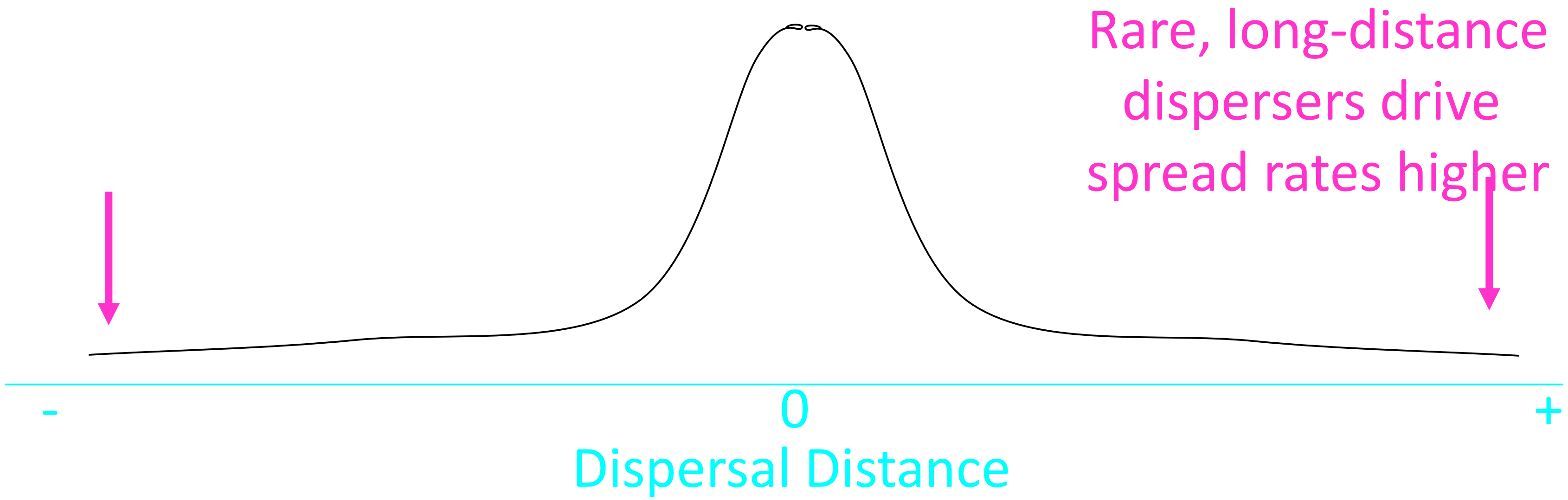
$$c_u = 2\sqrt{D_u f(0)}$$



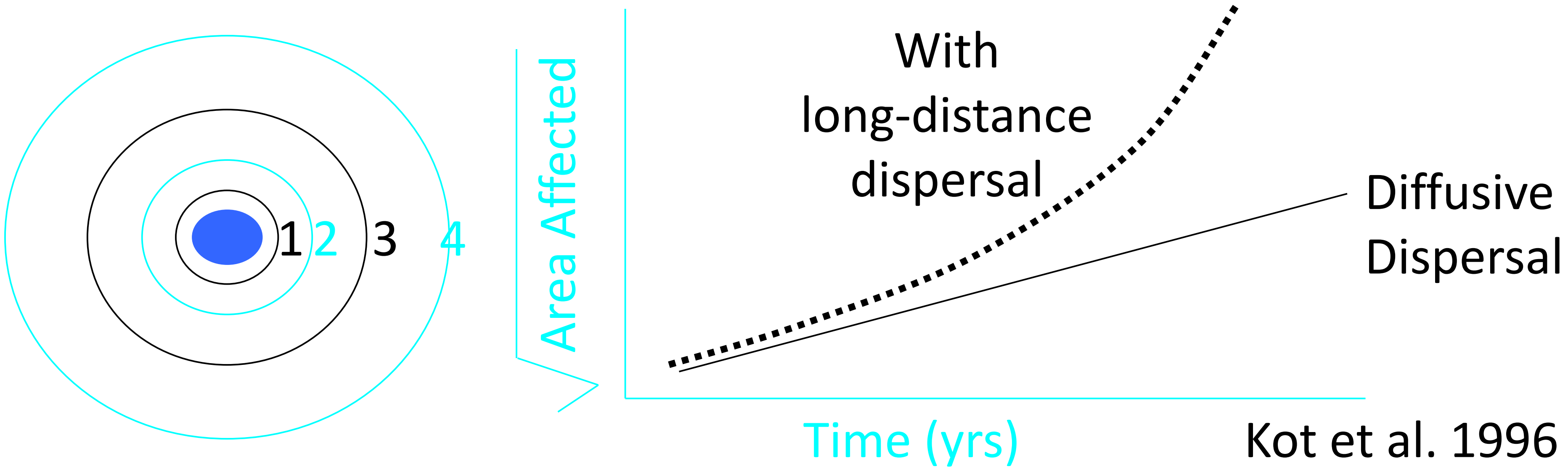


Integro-difference equation models of spreading populations

→ Highlight importance of long distance dispersal

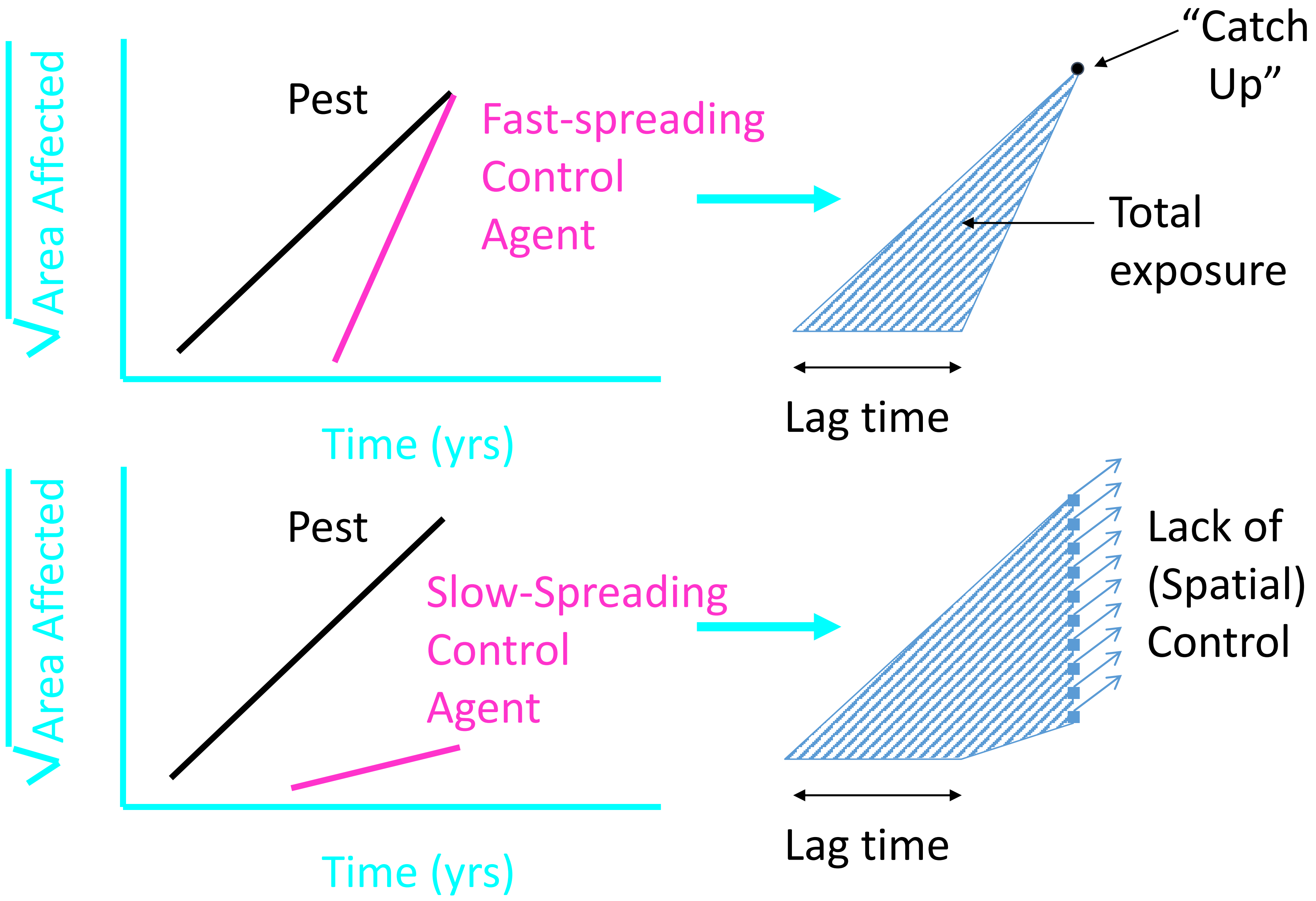


→ And demonstrate that spread rates can actually increase over time

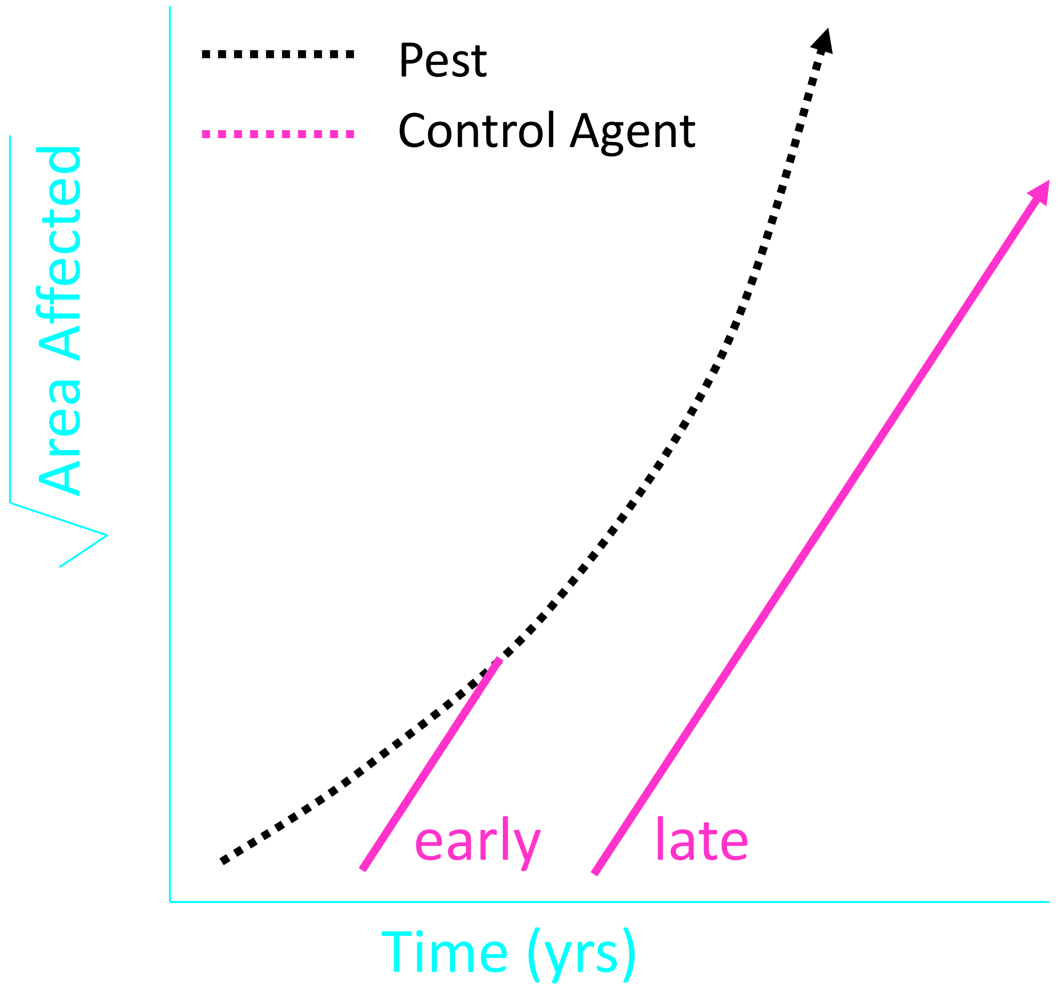


Kot et al. 1996

So we need control agents that can “catch-up” to pests



“Catch-up” is a major concern for fast-spreading pests



- Relative dispersal abilities of pest and control agent
- Timelag before agent is released

Issues in Spatial Biological Control:

1) Reduce spread rate of pest
    - Importance of monitoring
    - Reduce human-aided transport

2) Enhance spread rate of control agent
    - Choice of species
    - Multiple release sites
    - Positioning of release sites

What happens at "catch-up" depends on the pest, control agent, and landscape

1) Population dynamics of the pest

   → Pest growth rates and "Allee effects"

2) Feeding ecology of the control agent

   → Generalist vs. specialist control agents

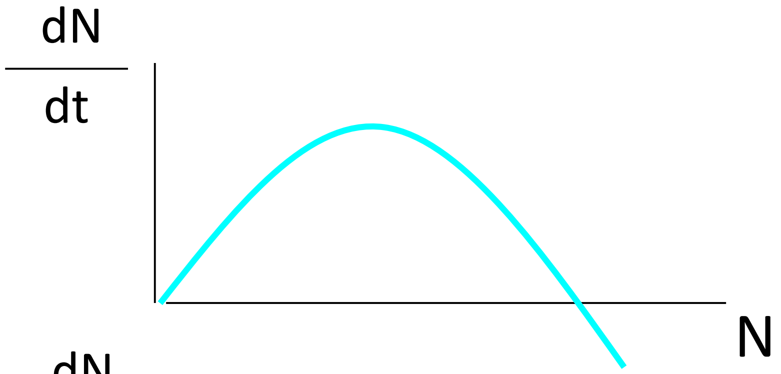
3) "Patchiness" of the landscape

   → The importance of nascent foci

What Happens at Catch-Up ?

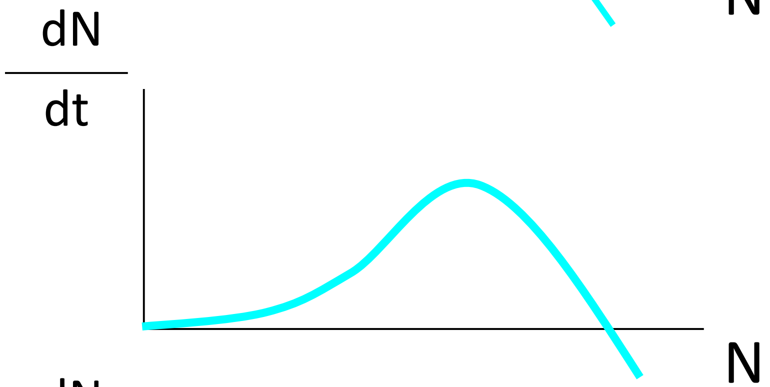
1) Pest Population Dynamics (with a specialist predator)

a) logistic growth



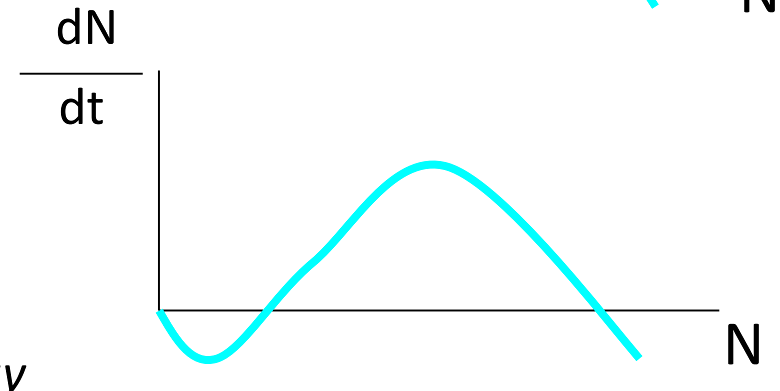
pest outruns control agent

b) weak Allee effect



control agent can slow pest's spread

c) strong Allee effect



control agent can shrink area of impact

Owen and Lewis. 2001. *Bull. Math. Biology*

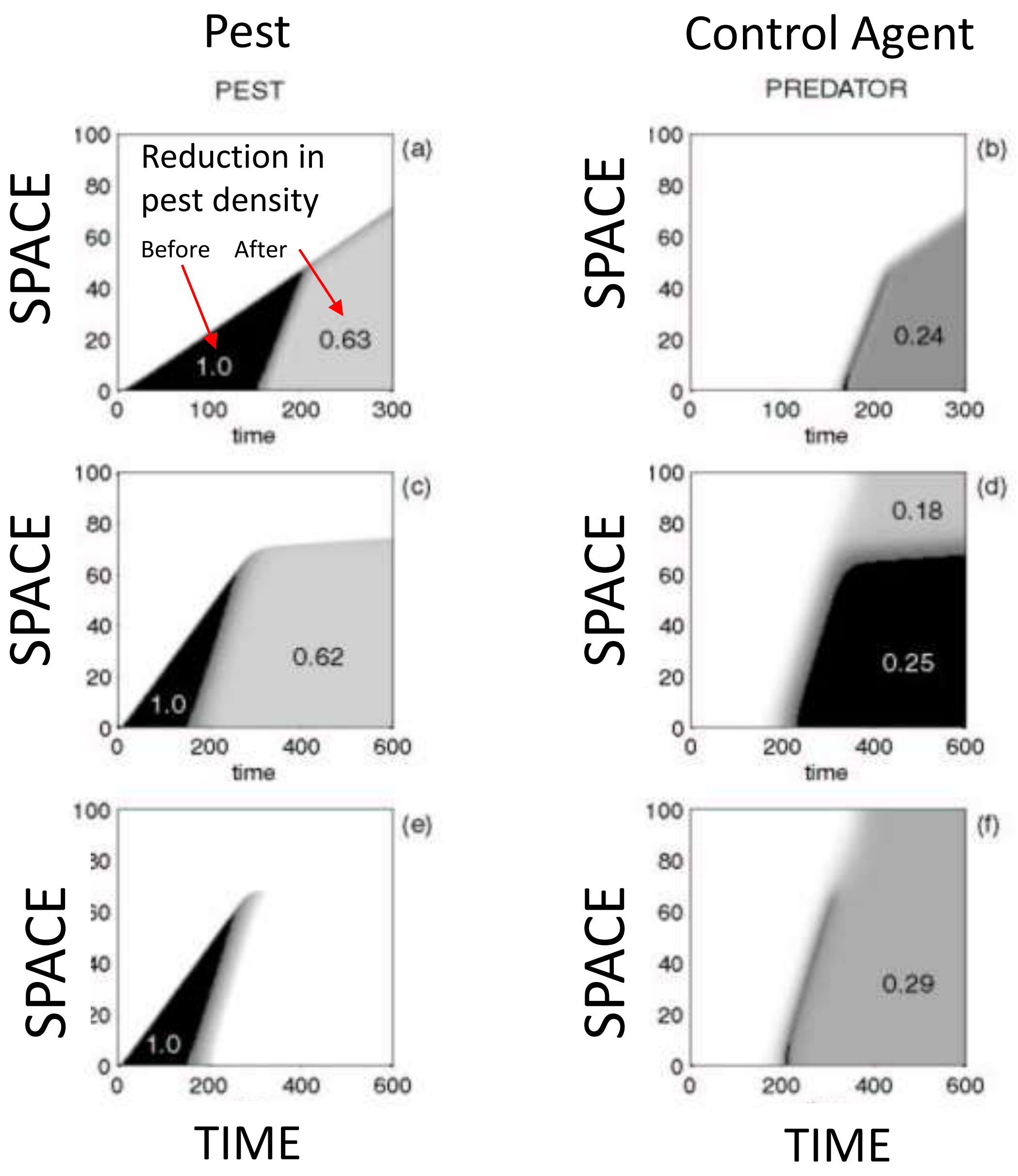
What Happens at Catch-Up ?

2) Feeding ecology of the control agent

Specialist control agent ➔ (spread continues)

Weakly generalized control agent ➔ (spread slowed)

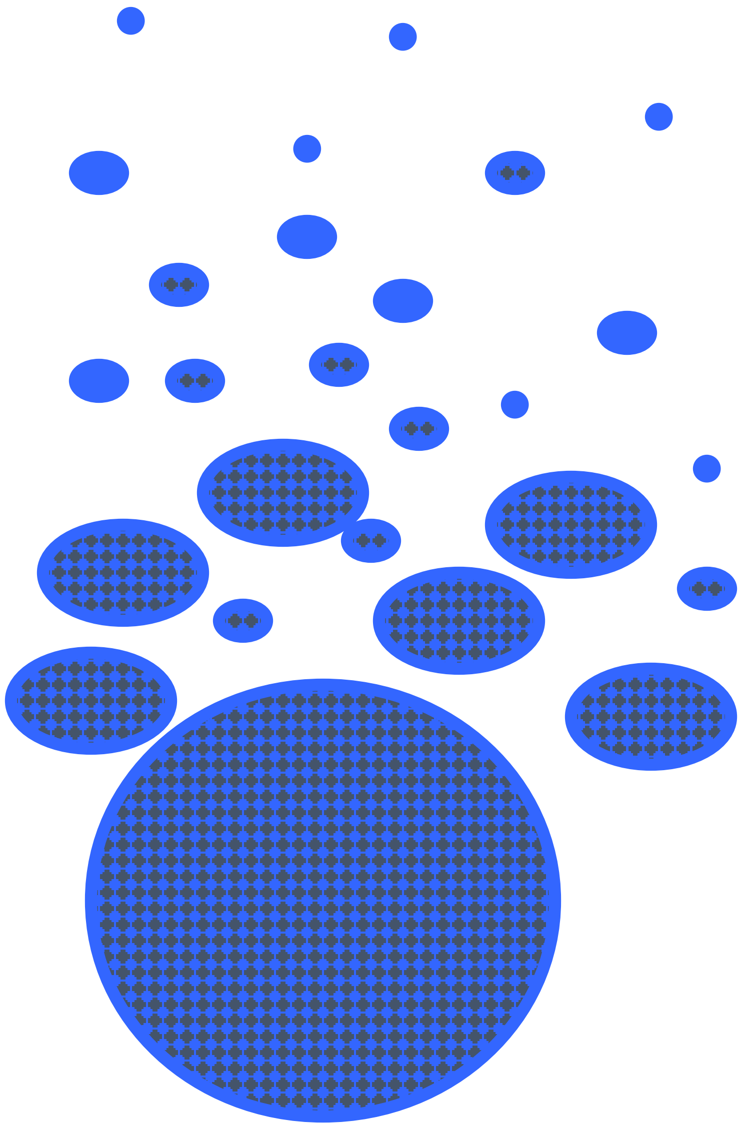
Highly generalized control agent ➔ (pest eliminated)



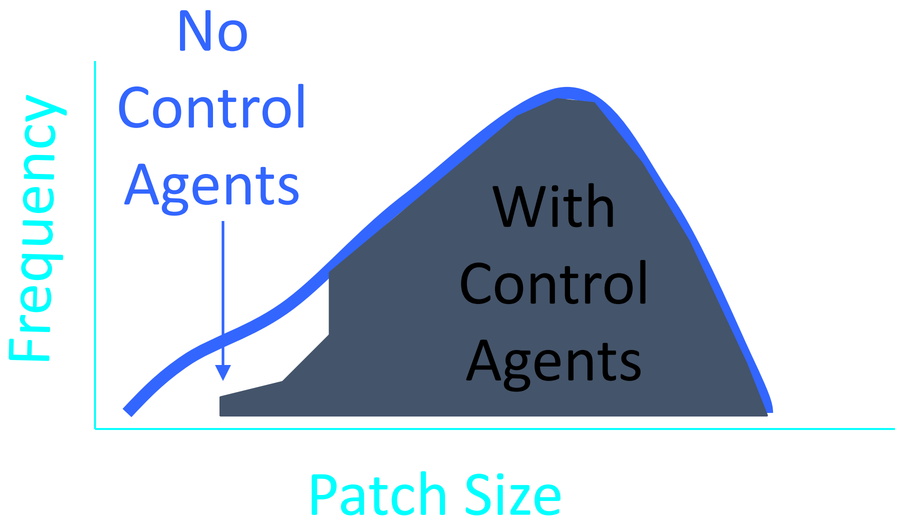
Fagan et al. 2001. *Ecology Letters*

What Happens at Catch-Up ?

3) "Patchiness" of the landscape

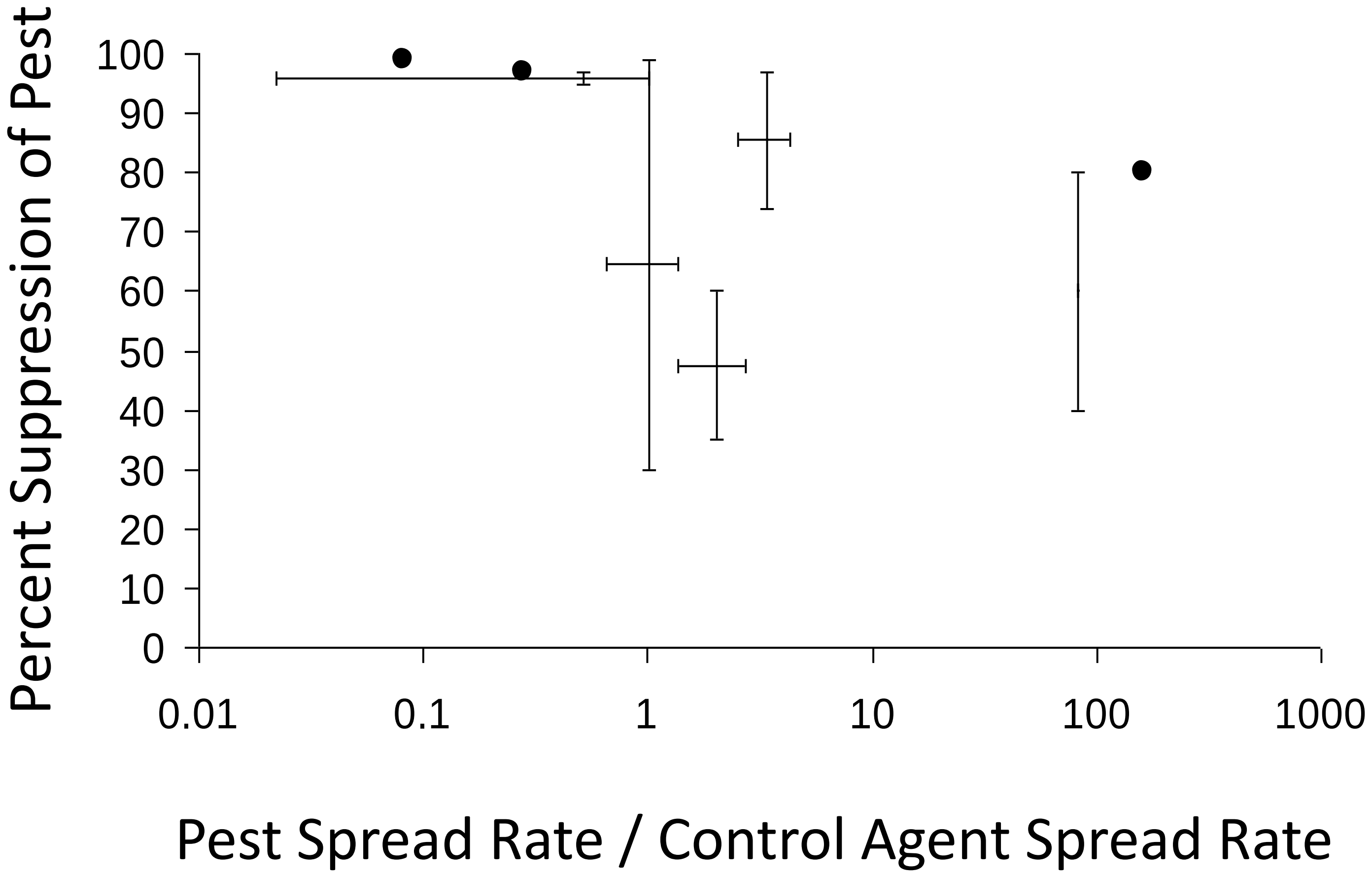


- Nascent foci facilitate spread
- Patchy, discontinuous spread facilitates pest escape from control agents



Fast spread is important, but doesn't necessarily mean good control

→ Possible relationship between dispersal ability and local suppression



Fagan et al. 2001. *Ecology Letters*

2) How does foraging away from a "home-base" influence resources and population dynamics of the foragers ?

→ "Central place foraging"

What are some ecological examples of central place foragers ?

What is relevance of central place foraging for S-E systems ?

Central Place Foraging

Individuals reside in one area ('the central place')
but forage in surrounding areas

- **-- nesting birds**
- **-- pikas**
- **-- beavers**
- **-- fence lizards**



Central place foragers often live communally

- **-- ants**
- **-- seabirds**
- **-- bats**
- **-- cave crickets**




Orians and Pearson 1979
Chase 1998

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Villages ?

Mega-Cities ?




Orians and Pearson 1979
Chase 1998

Population and Community Consequences of Spatial Subsidies Derived From Central Place Foraging

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Published in: American Naturalist 2007

Spatial Subsidies

Movement of individuals or resources from one area to another

Net ‘enhancement’ in recipient community

Relevance to S – E Systems ?

Emphasis on subsidies of basal resources that support consumers
(e.g., sea wrack, dead leaves, salmon carcasses)

Spatial subsidies especially important in resource-poor habitats
(e.g., desert islands, deep sea floor, caves)

Polis et al. 1997
Naiman et al. 2002

Central Place Foraging

Human agents ?

Animals as conduits for allochthonous resources

- -- facilitate local population growth
- -- recycling of waste products

Supports local communities

- -- inquilines in ant nests
- -- guanophilic species at seabird colonies
- -- troglobitic species in cave interiors

Central Place Foraging

Animals as conduits for allochthonous resources
- **-- facilitate local population growth**
- **-- recycling of waste products**

Kernel $k(x,y)$ becomes $k(x)$ because all resources go back to central place

Supports local communities
- **-- inquilines in ant nests**
- **-- guanophilic species at seabird colonies**
- **-- troglobitic species in cave interiors**



Central Place Foraging Theory

Classically, a branch of optimal foraging theory

How should individuals search for food near their central place ?

-- selectivity in taking food as a function of distance
-- risk / reward tradeoffs
-- energetics / travel time constraints

Discrete patches vs. continuum of resources

Orians and Pearson 1979
Schoener 1979
Elliott 1988

Modeling Approaches

Discrete-time reproductive events

Spatially distributed resource

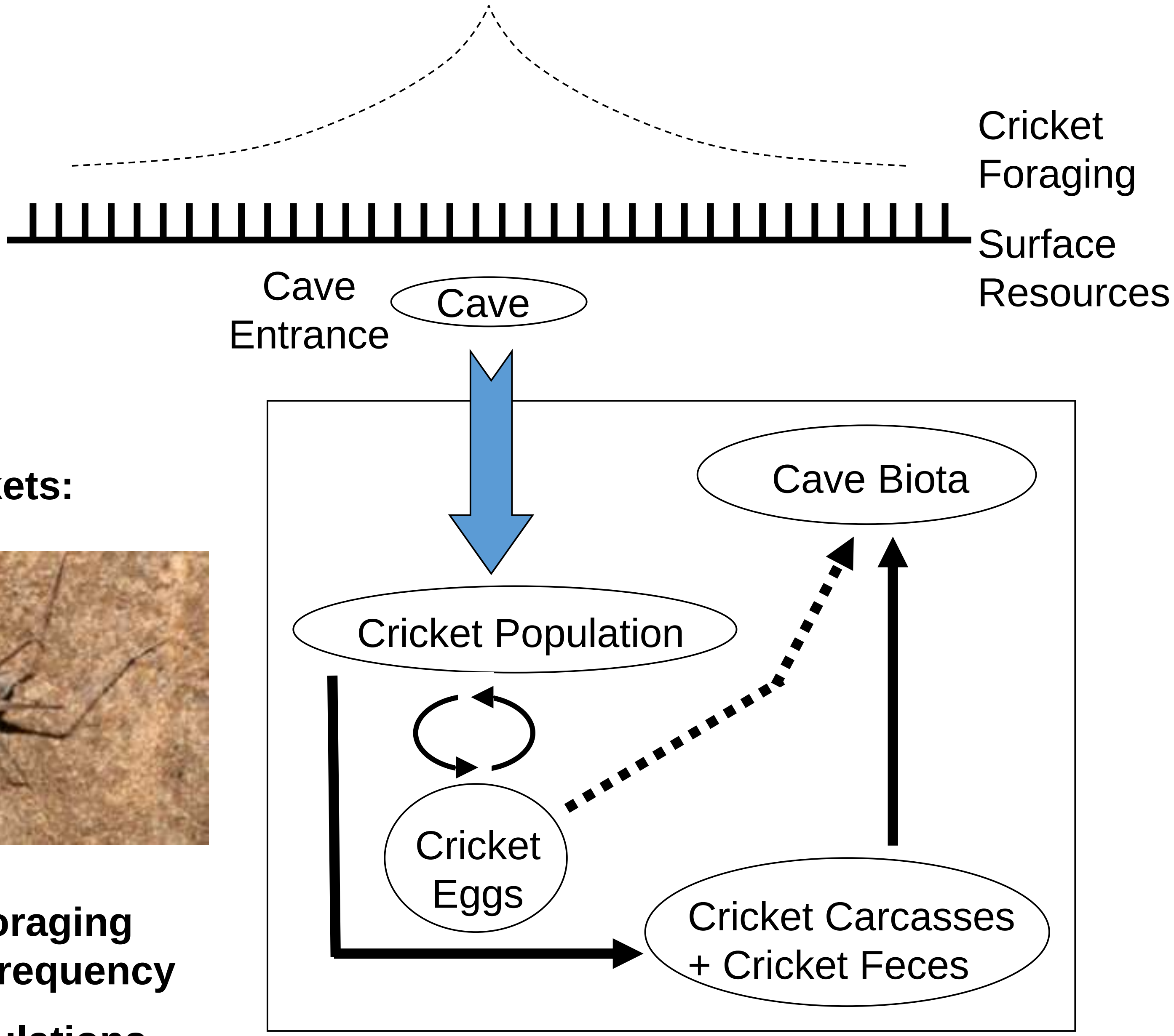
Foraging strategies in space and time

→ Population-level approach
to central place foraging

Biological Context: Cave ecology

Extreme dependence on
allochthonous inputs

Biological Setup



Cave Crickets:

Variable Foraging Foray Frequency

Large Populations

Nonspatial Consumer-Resource Model

Resource

$$f_{t+1} = G(f_t)(1 - P(c_t))$$

Total consumption

$$e_t = G(f_t)P(c_t)$$

Consumer

$$c_{t+1} = s_c c_t + \beta e_t$$

G : Recruitment function (compensatory Beverton-Holt)

P : probability of finding resource $P(c) = 1 - exp(-c)$

s_c : Survival of consumers to next generation

β : conversion coefficient

Hassell 2000
Kot 2001

Spatial Model

Resource

$$f_{t+1}(x) = G(f_t(x))(1 - P(c_t k(x)))$$

Total consumption

$$e_t = \int_{-L/2}^{L/2} G(f_t(x)) P(c_t k(x)) dx$$

Consumer

$$c_{t+1} = s_c c_t + \beta e_t$$

Consumers may forage outside the patch *L*.
No resources outside, but no foraging-related mortality (yet)

Critical Patch Size

Critical patch size for consumer persistence, *L**

$$\int_{-L/2}^{L/2} k(x)\,dx = \frac{1-s_c}{\beta}$$

Consumer extinction if

$$s_c + \beta < 1$$

S_c = Consumer survival
β = Consumer conversion efficiency

$$L^*_{Laplace} < L^*_{Gaussian} < L^*_{triangle} < L^*_{uniform}$$