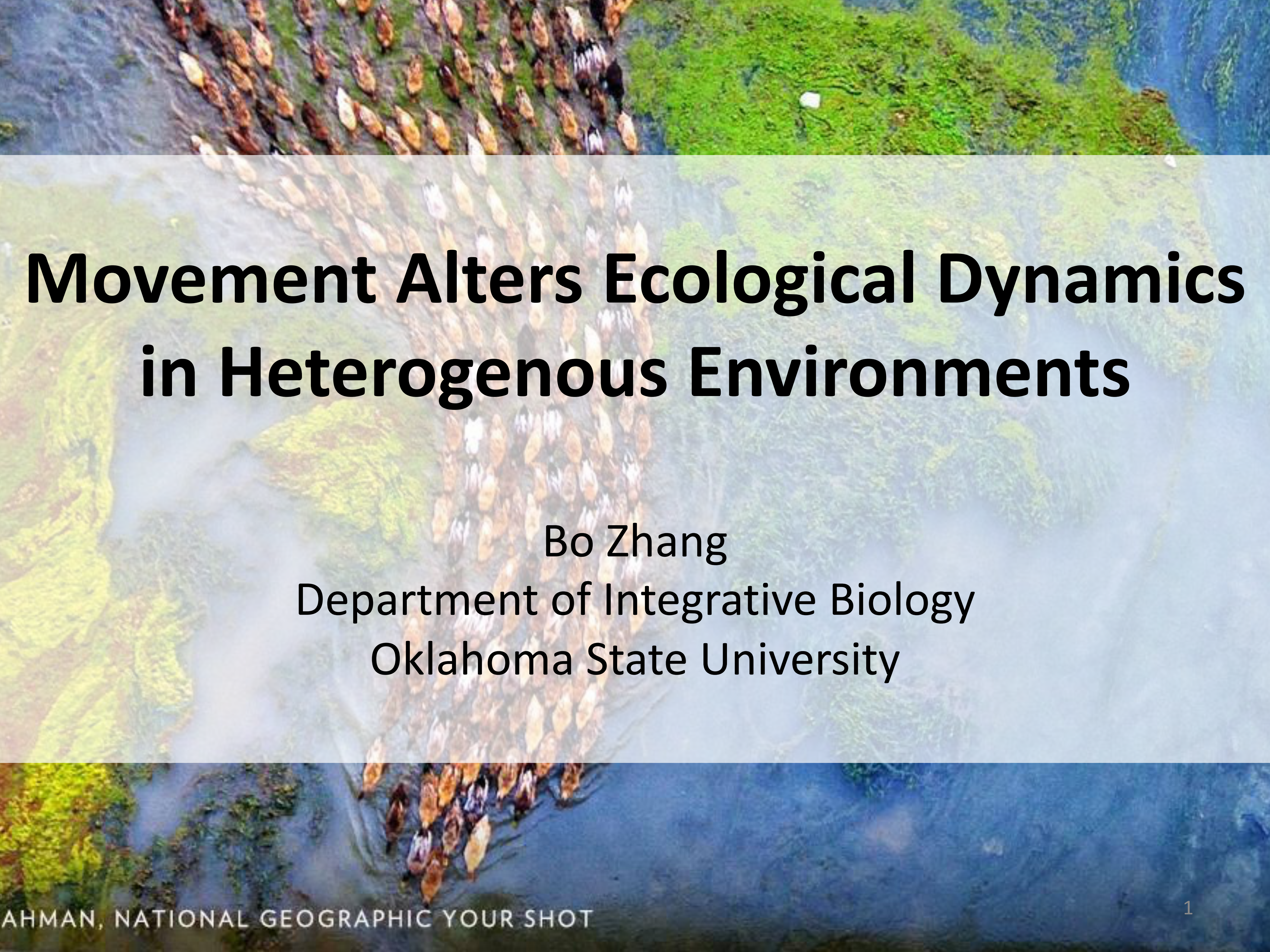

AHMAN, NATIONAL GEOGRAPHIC YOUR SHOT

Movement Alters Ecological Dynamics in Heterogenous Environments

Bo Zhang
Department of Integrative Biology
Oklahoma State University

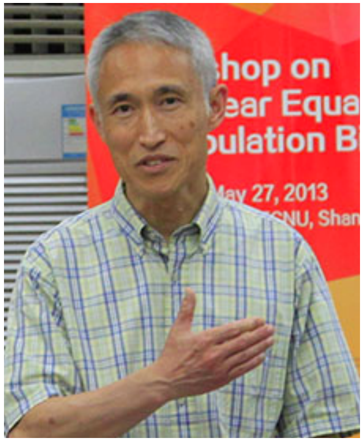
Everything *disperses* to Miami

2012

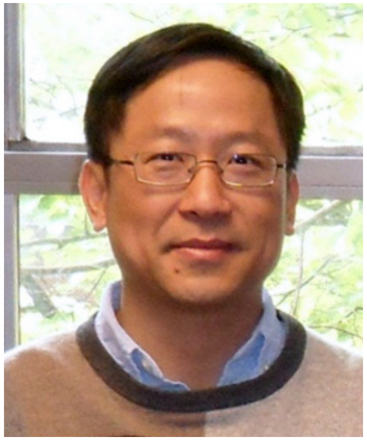
Acknowledgements

Donald DeAngelis
(PhD advisor)

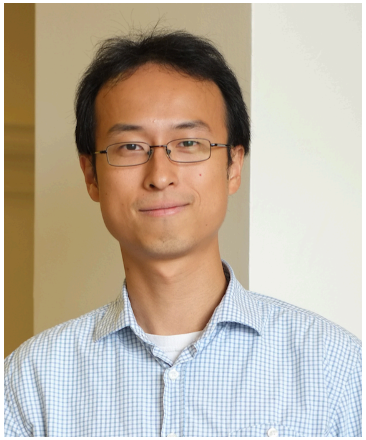
Alan Hastings
(Postdoc advisor)



Wei-Ming Ni



Yuan Lou

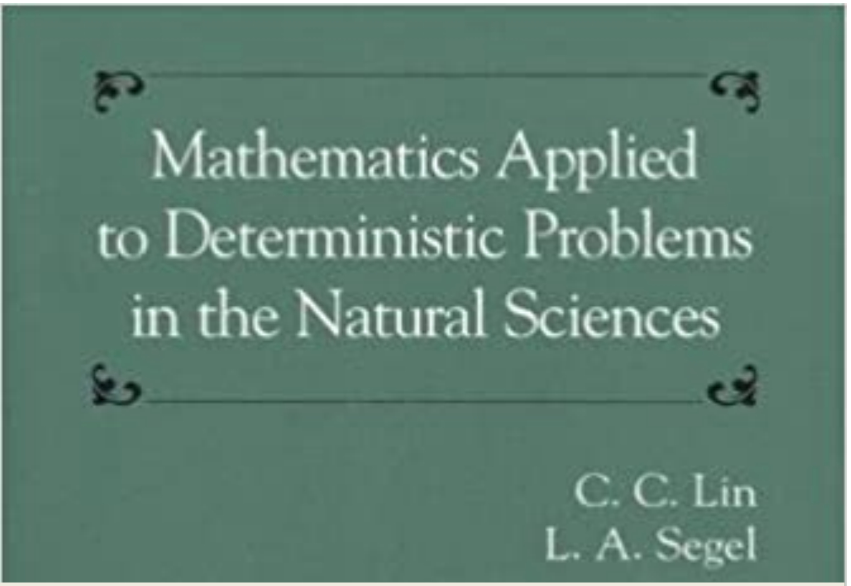


King-Yeung Lam

David Van Dyken
(Postdoc advisor)

Kevin Collins

How to develop mathematical theories to predict biological dynamics in the real world?



Mathematics Applied
to Deterministic Problems
in the Natural Sciences

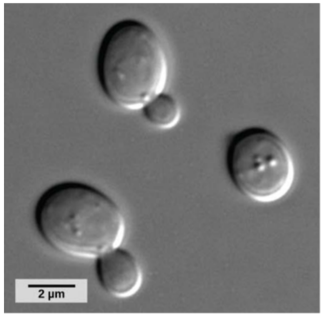
C. C. Lin
L. A. Segel

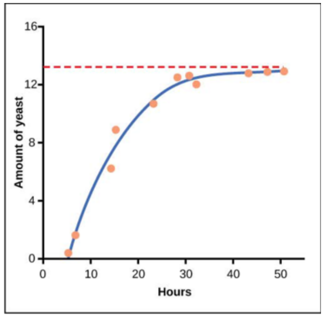
"In applied mathematics, empirical verification is a necessary and powerful judge."
"Being creative."

C · L · A · S · S · I · C · S
In Applied Mathematics
siam
1

Examples of using logistic equation model in simple systems

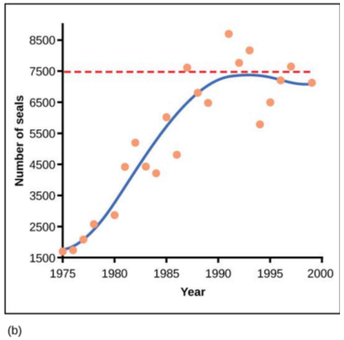
Micro-system





Yeast

Macro-system



Harbor seals

Environmental Biology

How to predict biological dynamics in complex systems?

NSF'S 10 BIG IDEAS

"Life on our planet is arranged in levels of organization ranging from the molecular scale through to the biosphere. There exists a remarkable amount of complexity in the interactions within and between these levels of organization and across scales of time and space."

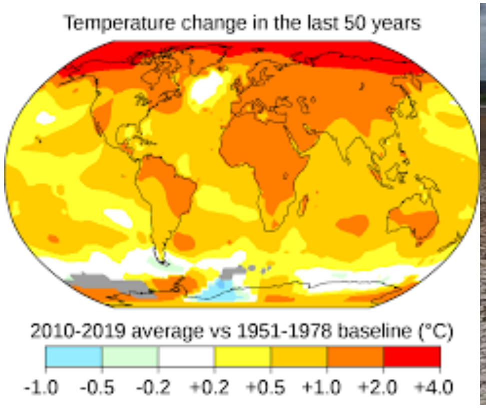
Scaling up is challenging.

Challenging factor: Environmental heterogeneity

Environmental heterogeneity changes across scales of time and space.

Caused by human disturbance

Caused by climate change



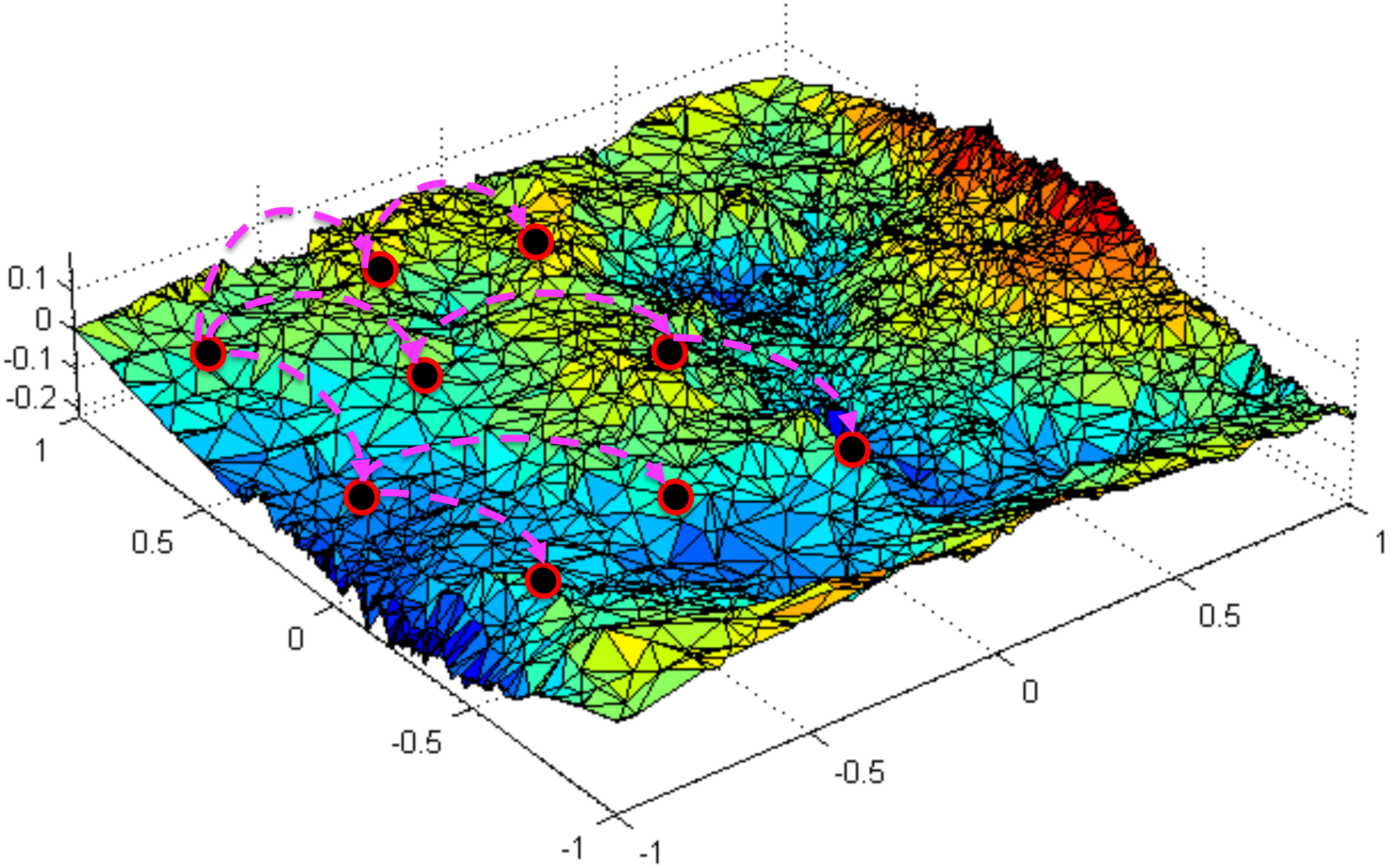
Warming temperature

Drought

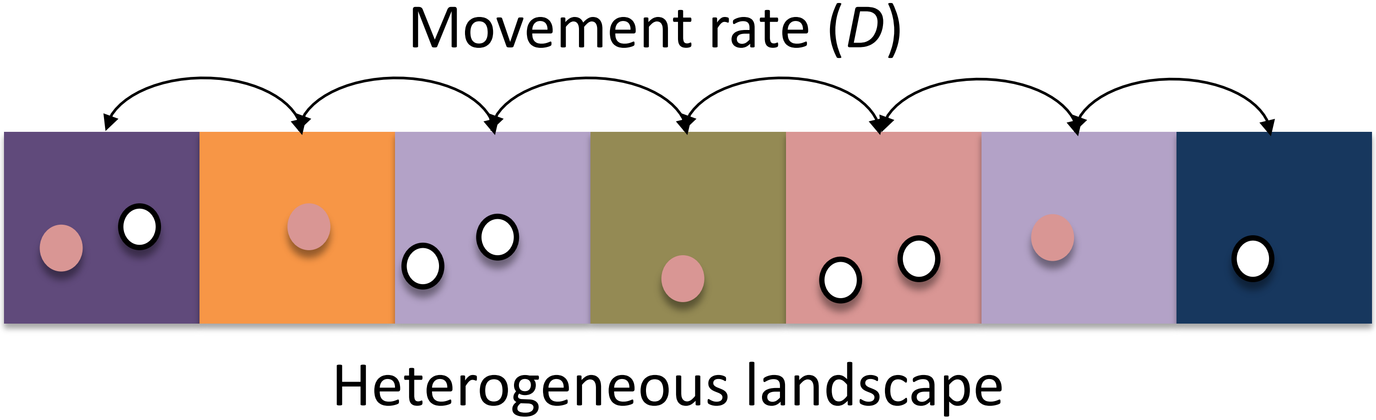
Fragmentation

Credit: Andy Gonzalez

Another challenging factor: Movement

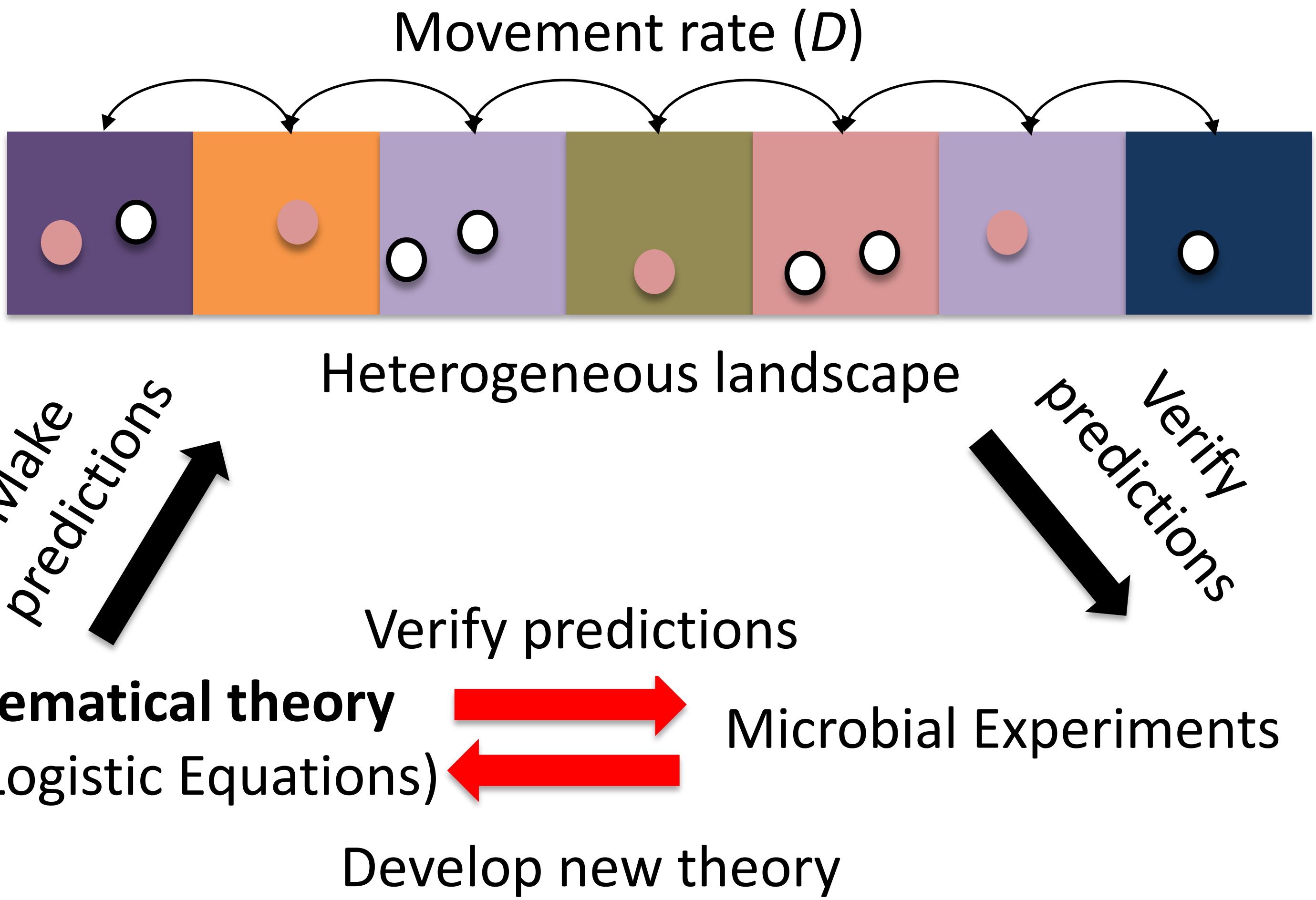


How does one accurately model the integrative effect of environmental heterogeneity and movement?



Knowledge gap: Current biological models have generally made very simple assumptions on the movement impact, or ignored the feedback between the organisms and their environment, which could significantly mislead some predictions.

How to develop mathematical theories to predict biological dynamics in the real world?



Movement rate (*D*)

Heterogeneous landscape

Make predictions

Verify predictions

Verify predictions

Mathematical theory
(e.g., Logistic Equations)

Microbial Experiments

Develop new theory

Talk Outline

1: How does movement alter population dynamics in heterogeneous environments? (Single species)

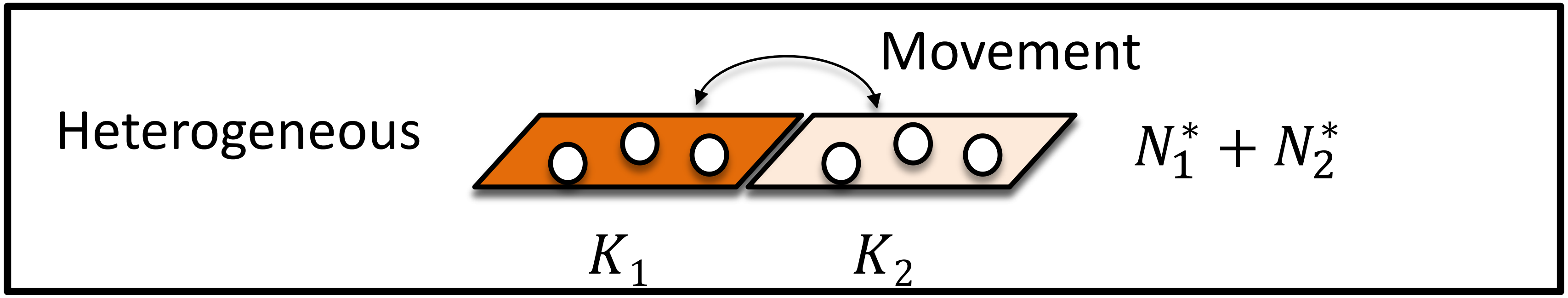
2: How does movement alter competition outcomes in heterogeneous environments? (Two species)

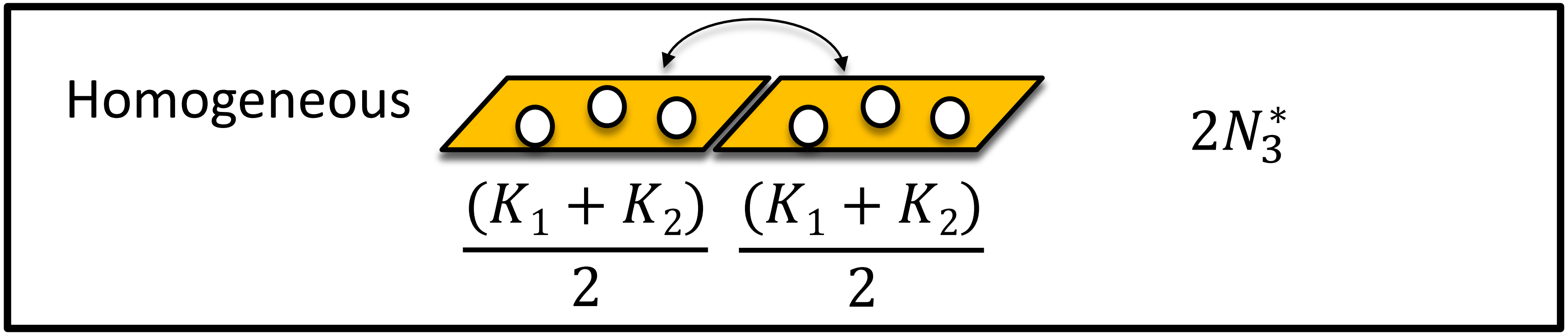
Part I

Meta-population dynamics (Single species)

Q: How can one attribute the **same total** carrying capacity in an environment to **maintain a larger population**?

Q: Will **movement** change the total population size?





Can we just add carrying capacities?

Previous model results of population diffusion in heterogeneous spatial regions with fixed *r* and *K*;

Environmental heterogeneity changes *r* and *K* in the system;

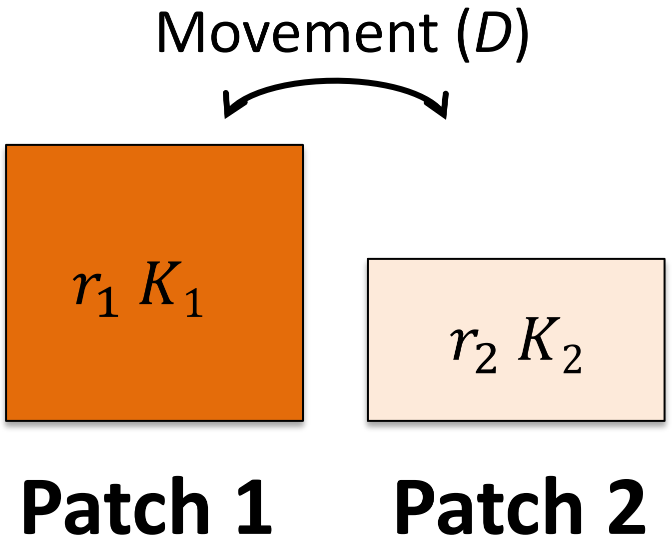
$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - DN_1 + DN_2$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - DN_2 + DN_1$$

Change in population density

Logistic growth term

Population Movement



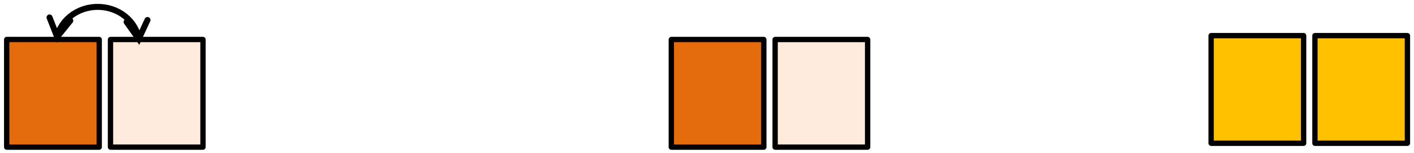
***No feedback effect of the population on the resource.**

Is feedback important to biological dynamics?

References:
Freedman and Waltman 1977; Holt 1985; Lou 2006; He and Ni 2013; Arditi et al., 2015; Zhang et al. 2015; DeAngelis, Ni, and Zhang 2016

“Surprising” theoretical predictions (Logistic equations)

*$TP_{\text{heterogeneous, movement}} \geq TP_{\text{heterogeneous,nomovement}} \geq TP_{\text{homogeneous}}$



Total population (TP)

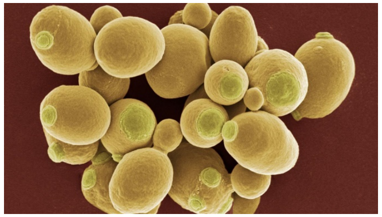
*When *r(x)* and *K(x)* are positively related;

*When the **same total** carrying capacity is distributed heterogeneously *VS.* homogeneously in the environment;

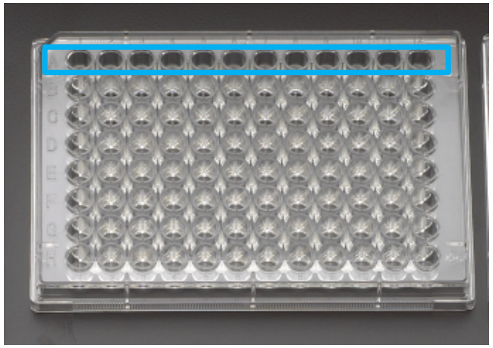
Is this true? No empirical verification existed!

References:
Freedman and Waltman 1977; Holt 1985; Lou 2006; He and Ni 2013; Arditi et al., 2015; Zhang et al. 2015; DeAngelis, Ni, and Zhang 2016

Experimental verification

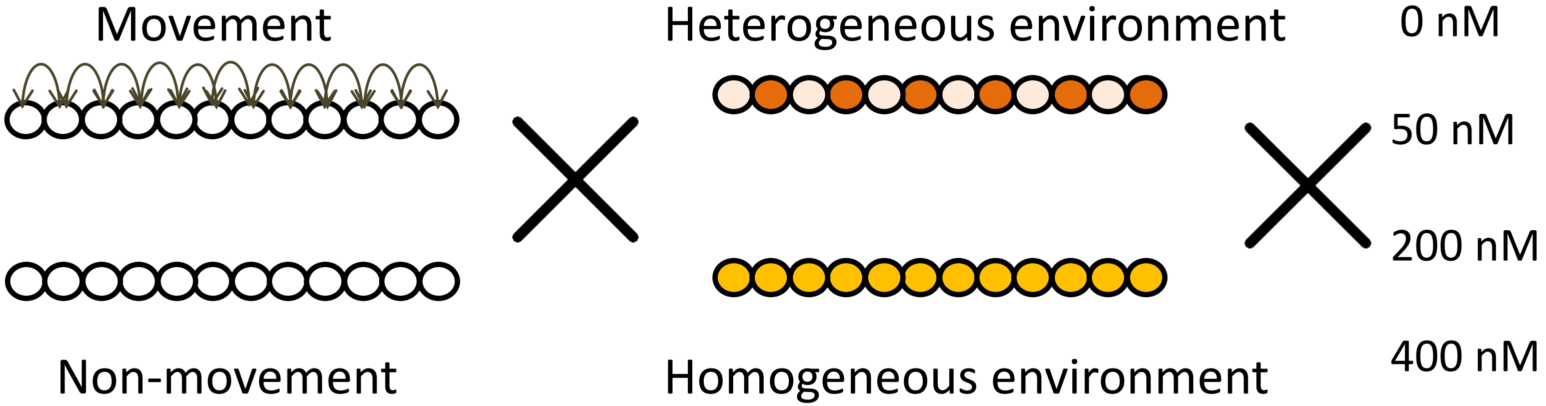


Yeast



1 row (12 wells) = 1 meta-population

To manipulate the correlation of *r* and *K*



Movement

Non-movement

Heterogeneous environment

Homogeneous environment

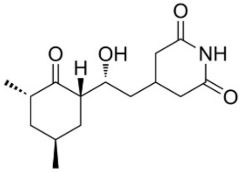
0 nM

50 nM

200 nM

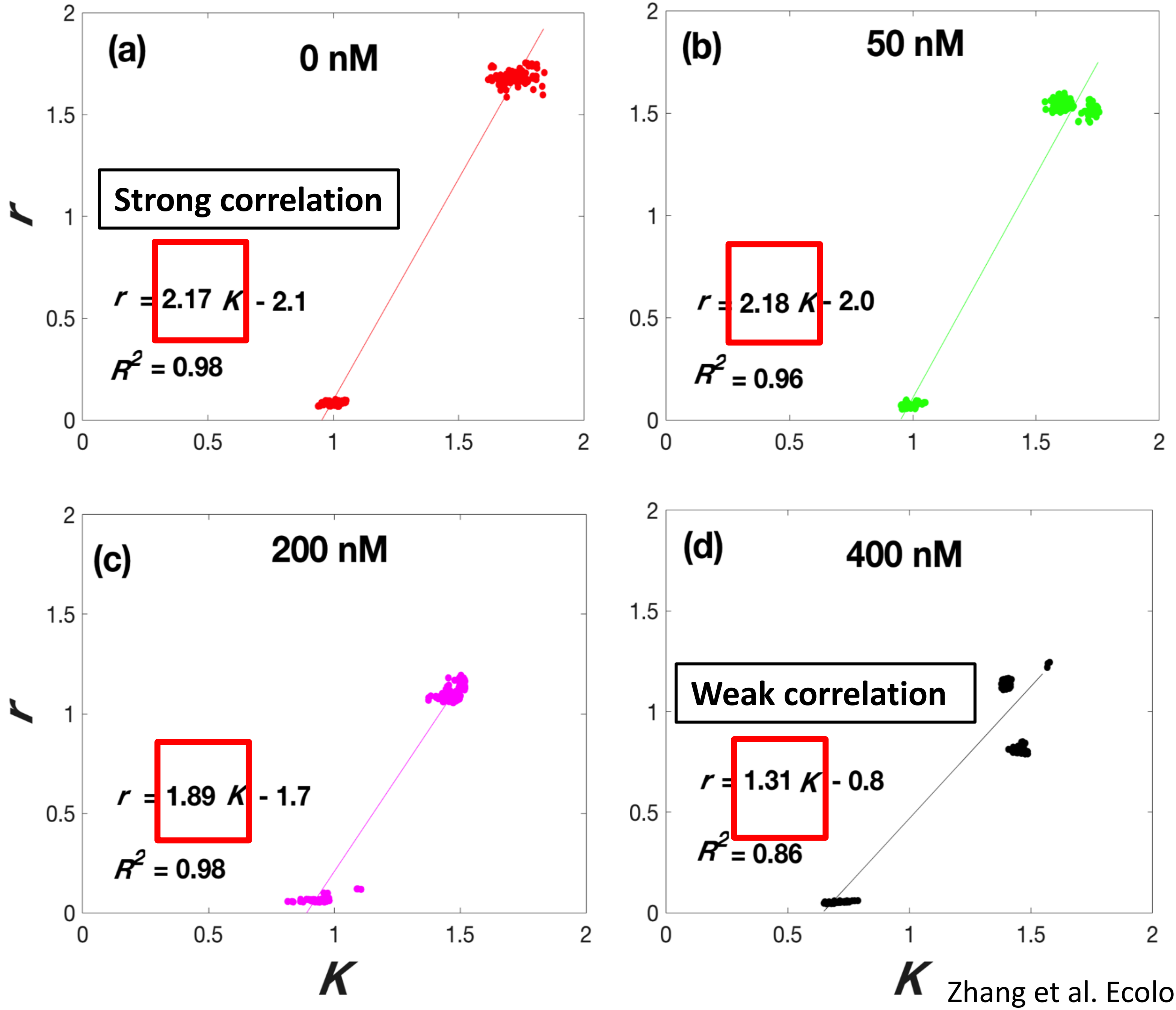
400 nM

Growth inhibiting antibiotic (Cycloheximide)

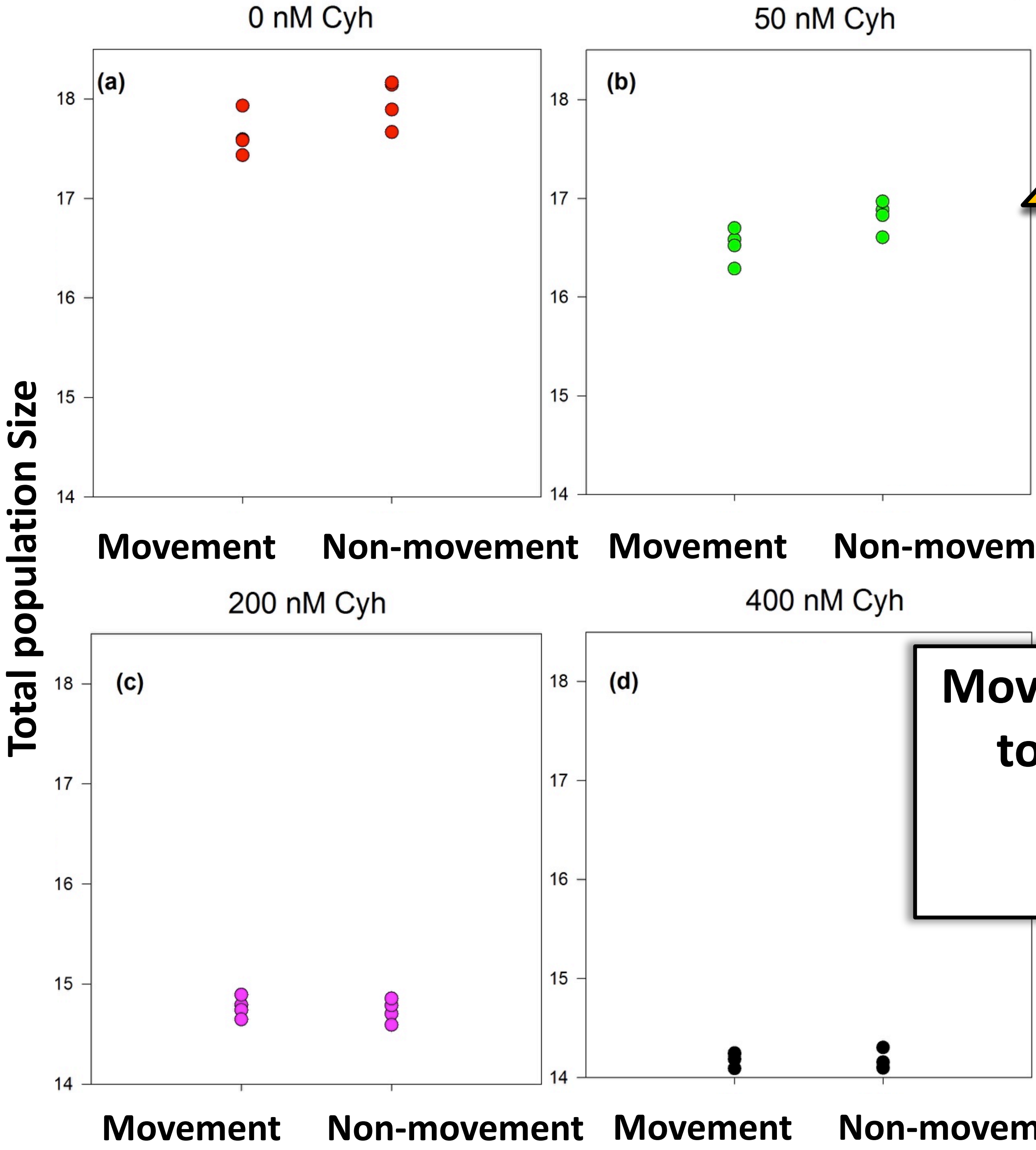


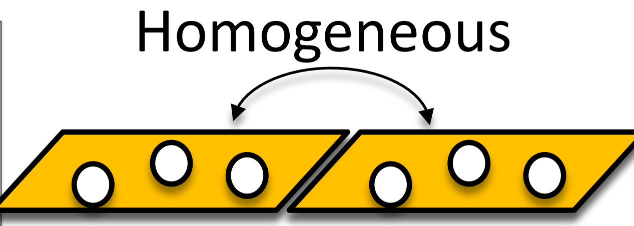
Full factorial design with 4 replicates.

Growth inhibiting antibiotic



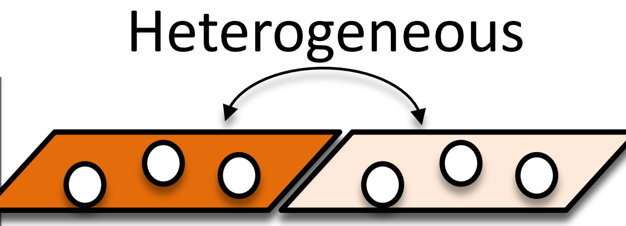
Zhang et al. Ecology Letters 2017

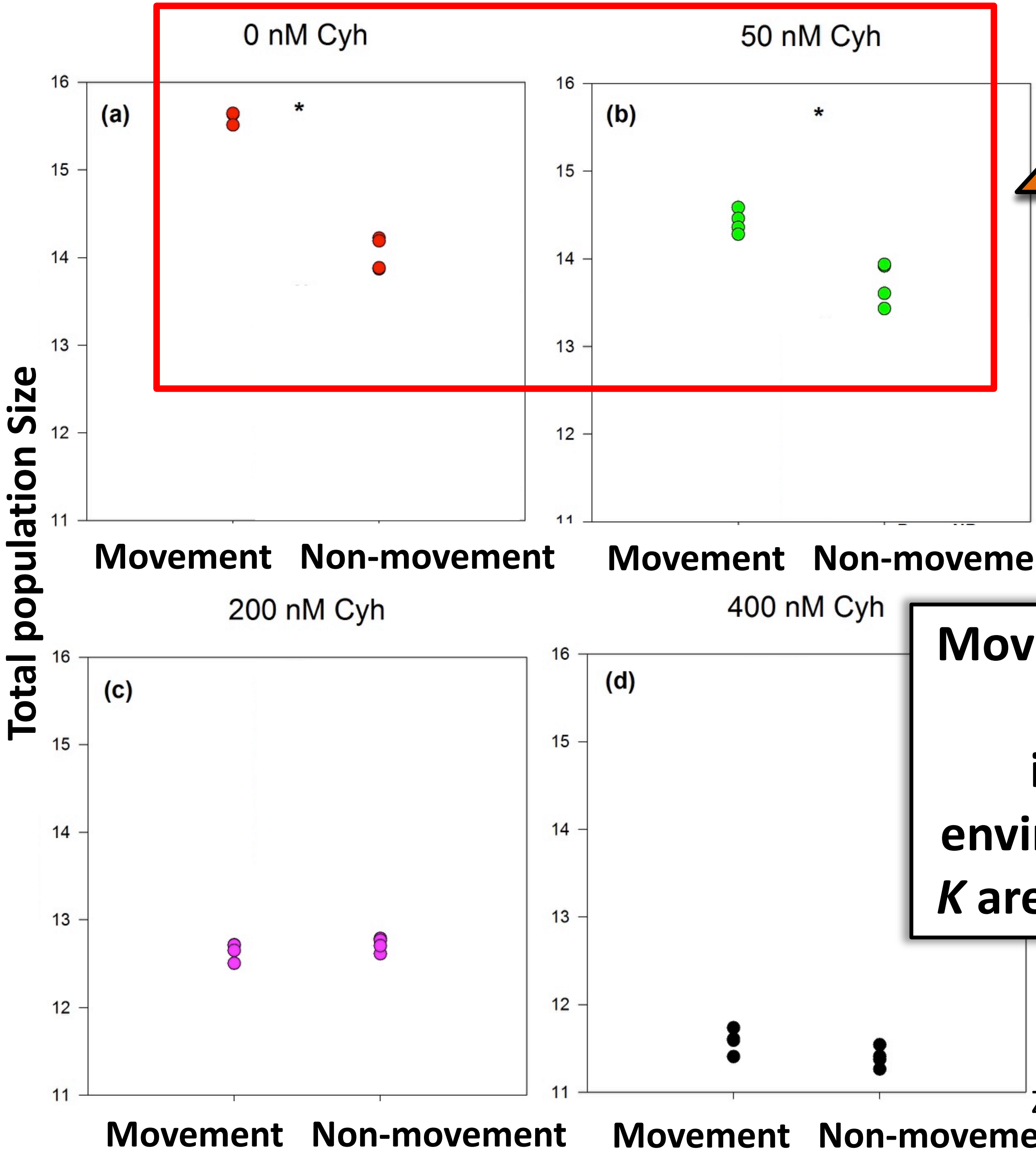




Movement does not alter total population size in homogeneous environments

Zhang et al. Ecology Letters 2017

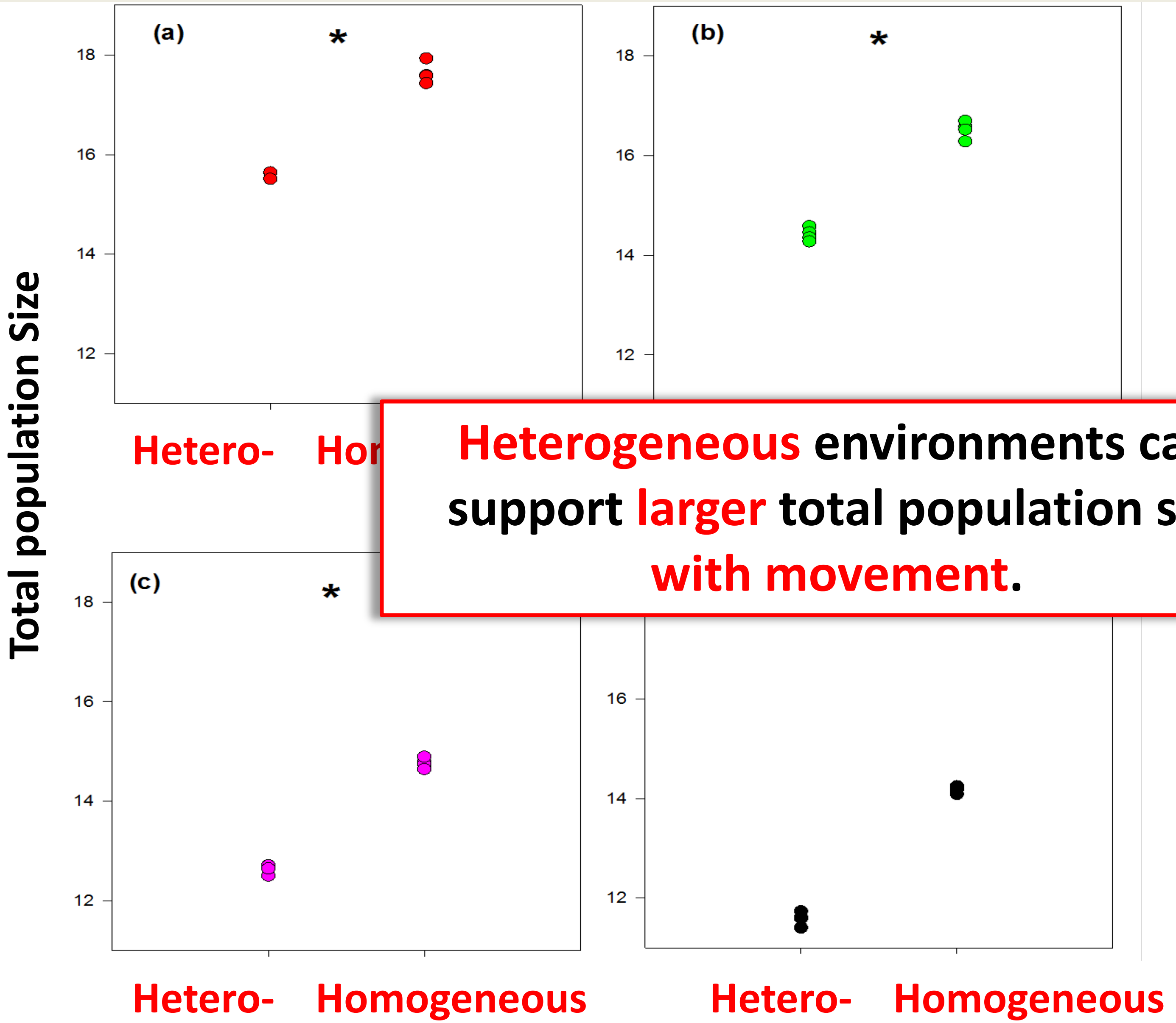




Movement increases total population size in heterogeneous environments when *r* and *K* are positively correlated

Zhang et al. Ecology Letters 2017

Heterogeneity *VS.* Homogeneity



Heterogeneous environments can support larger total population size with movement.

Limitations of Logistic equation models

> *"Logistic models do not explicitly consider* ***feedbacks*** *between the organisms and their abiotic environment."*
>
> – Wilkinson 2007

Resource Dynamics

To avoid setting fixed constants r_i and K_i

*Logistic equation models only cover a particular kind of feedback (i.e., resource dynamics are much faster than the consumer dynamics).

Therefore, population growth is best modeled using a mechanistic, bottom-up approach with **feedbacks** between the organisms and their environment.

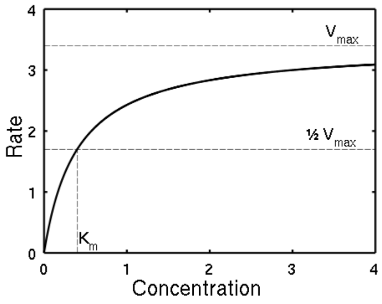
Model feedbacks by using the Consumer-Resource model

Consumer dynamics

$$\frac{dN_i}{dt} = r_{max}N_i\left(\frac{S_i}{k+S_i}\right) - mN_i - gN_i^2 + D\left[\frac{N_{i+1}}{2}+\frac{N_{i-1}}{2}-N_i\right]$$

- Change in consumer density
- Monod (non-linear) term
- Mortality
- Density-dependent mortality
- Population Movement

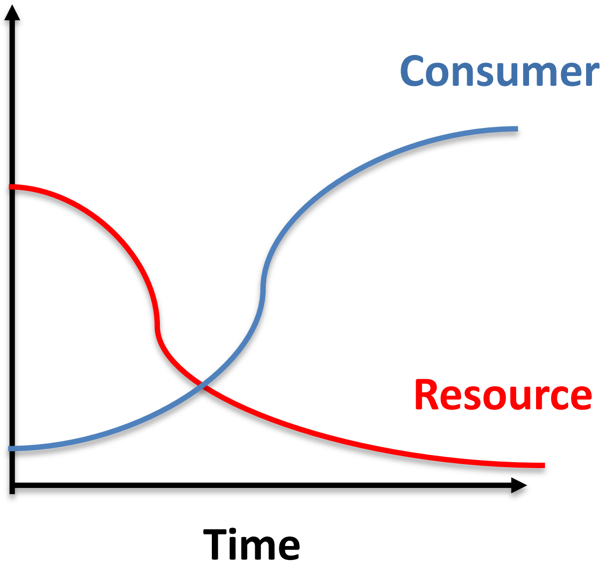
Monod curve



Resource dynamics

$$\frac{dS_i}{dt} = S_{IN,i} - \delta S_i - \frac{1}{\gamma}r_{max}N_i\left(\frac{S_i}{k+S_i}\right)$$

- Change in resource density
- Input
- Dilution/ death
- Consumption by consumer species



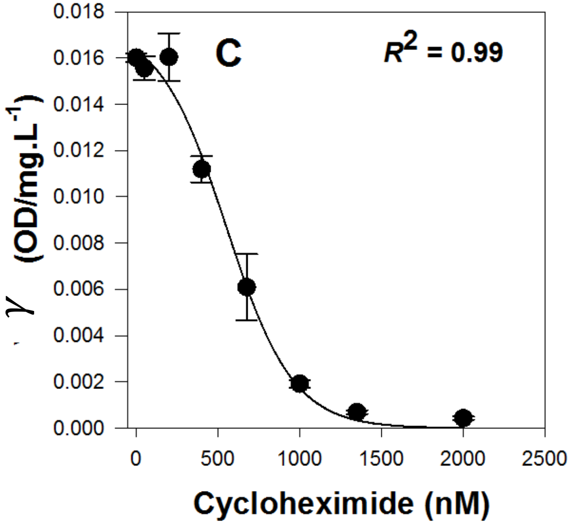
i: Patch number

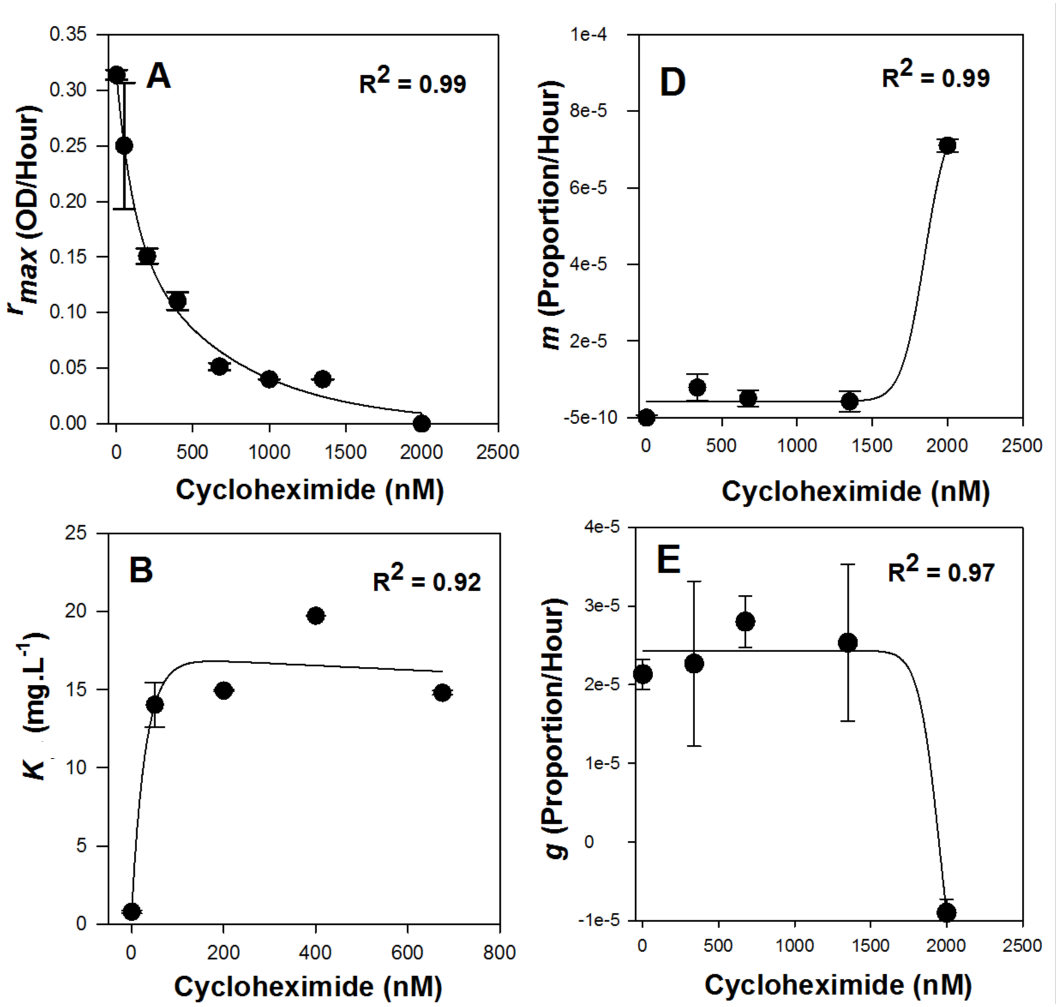
Tilman *Resource Competition and Community Structure* 1982

Parameter estimation based on experiments

$$\frac{dN_i}{dt} = \boxed{r_{max}} N_i \left(\frac{S_i}{\boxed{k} + S_i}\right) - \boxed{m} N_i - \boxed{g} N_i^2 + D\left[\frac{N_{i+1}}{2} + \frac{N_{i-1}}{2} - N_i\right]$$

$$\frac{dS_i}{dt} = S_{IN,i} - \delta S_i - \frac{1}{\boxed{\gamma}} r_{max} N_i \left(\frac{S_i}{k + S_i}\right)$$

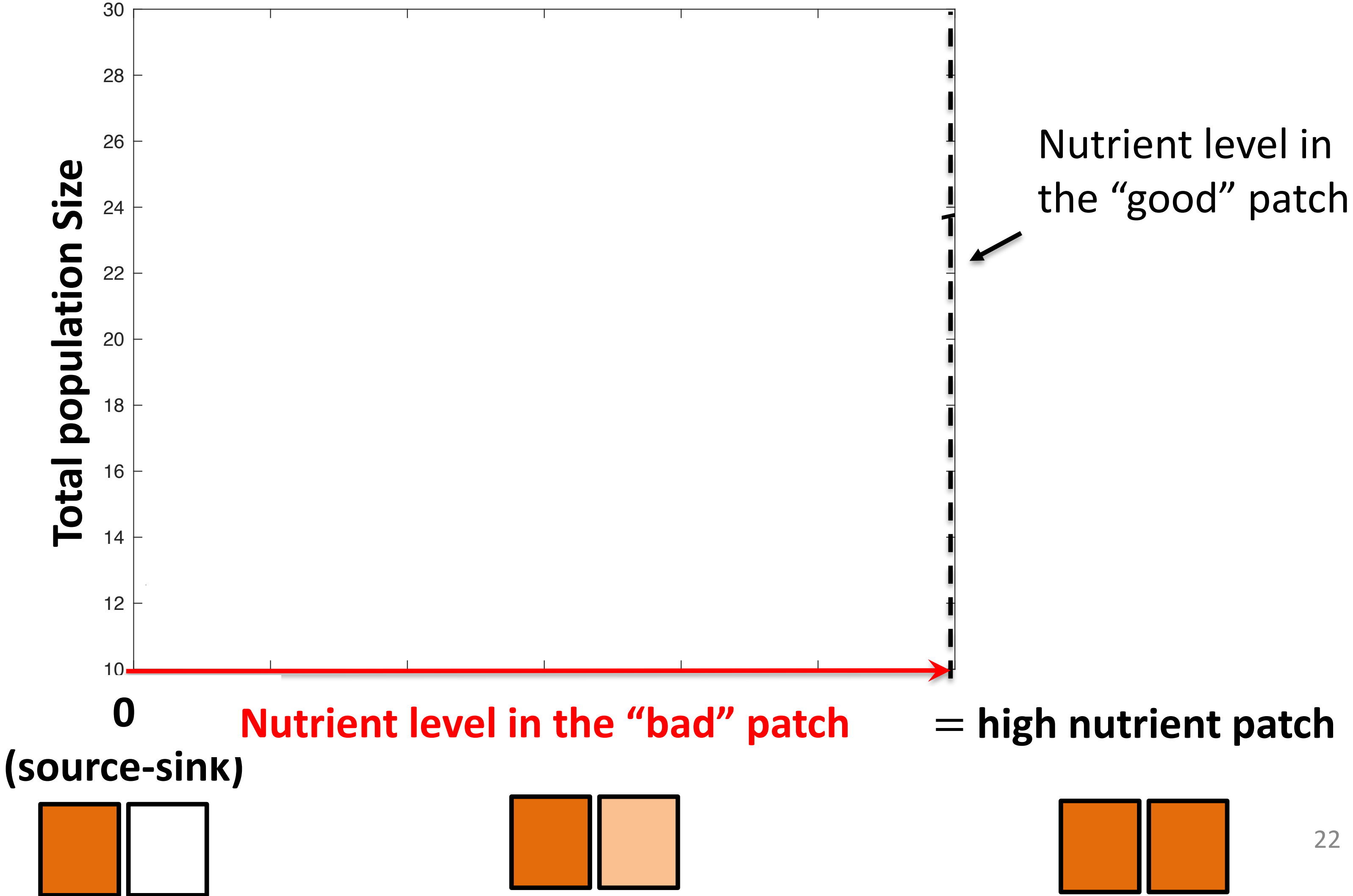




Zhang et al. American Naturalist 2020

New predictions based on the Consumer-Resource model

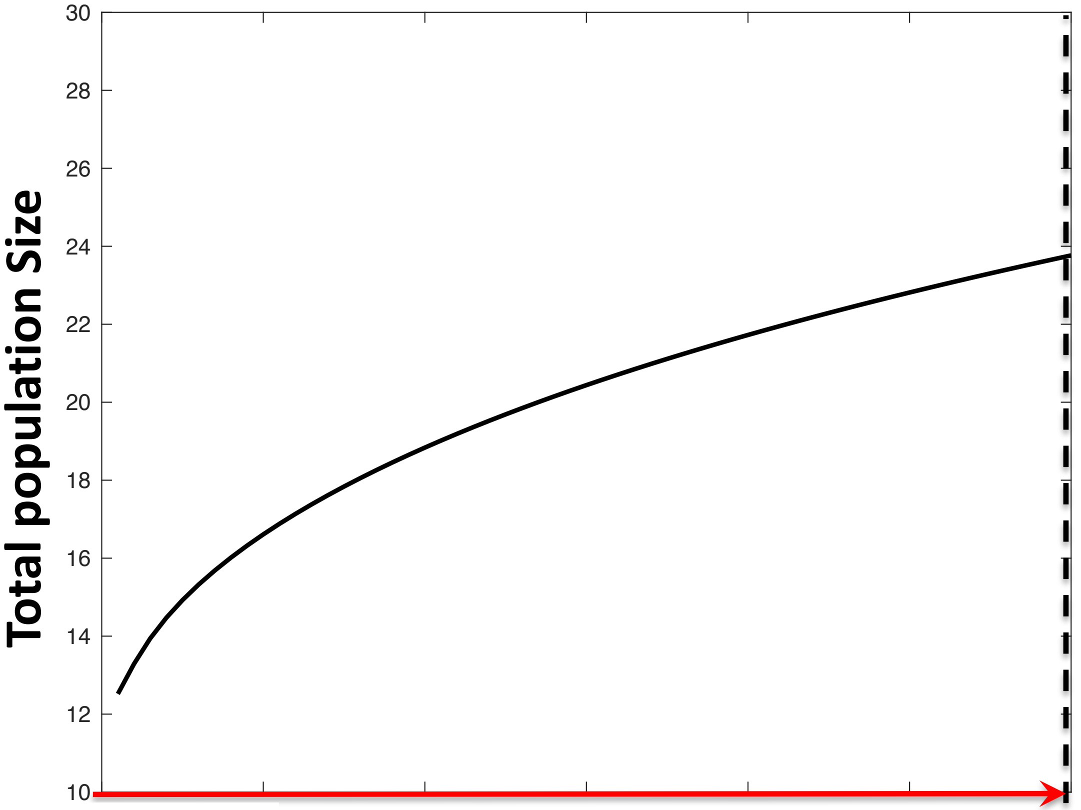
Heterogeneous environment **without** movement



Nutrient level in the "good" patch

New predictions based on the Consumer-Resource model

Heterogeneous environment without movement



Nutrient level in the “good” patch

0
(source-sink)

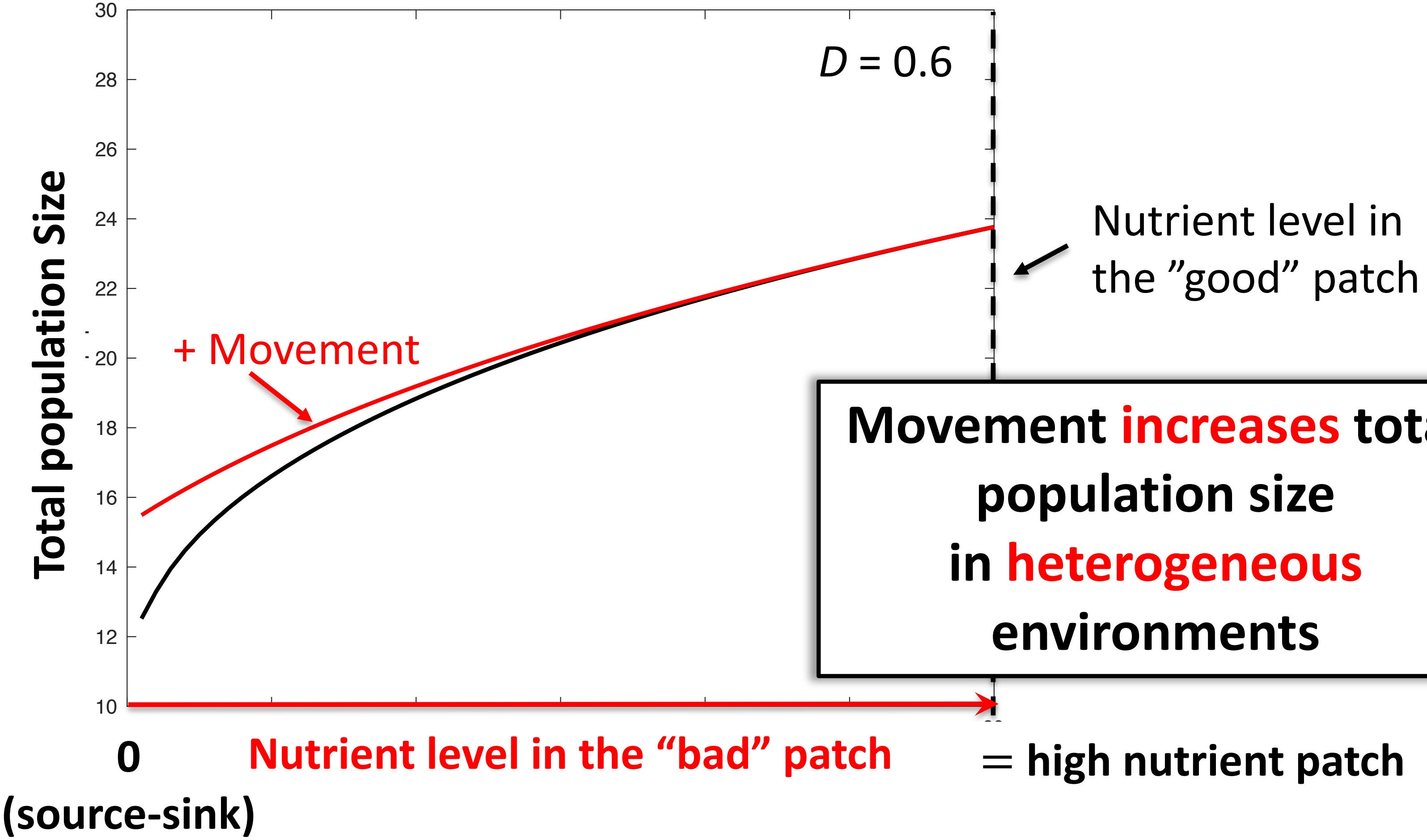
Nutrient level in the “bad” patch

= high nutrient patch

Zhang et al. Ecology Letters 2017

New predictions based on the Consumer-Resource model

Heterogeneous environment **with** movement

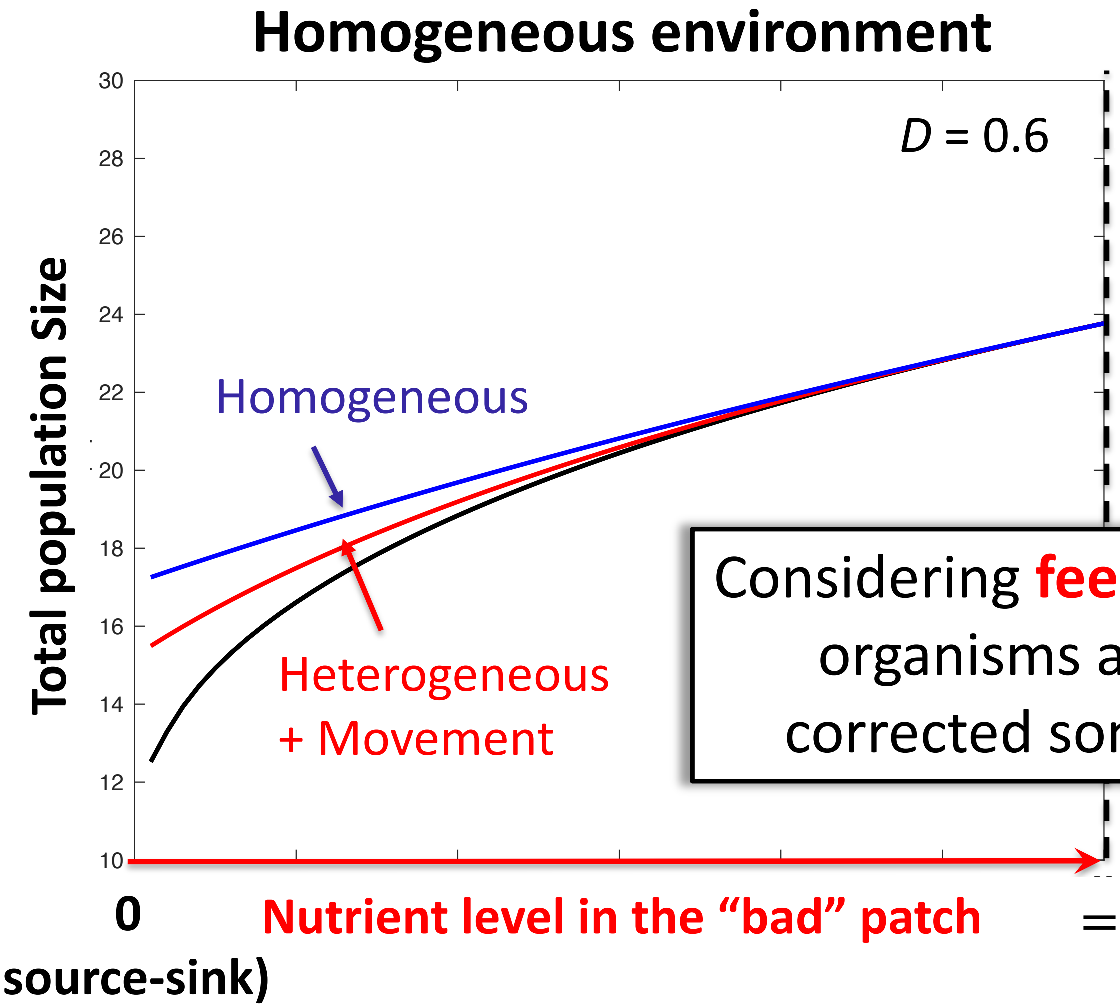


Movement increases total population size in heterogeneous environments

Zhang et al. Ecology Letters 2017

New predictions based on the Consumer-Resource model

*The homogeneous case has the same total resource input.



Nutrient level in the “good” patch

Considering **feedbacks** between the organisms and environment corrected some earlier results.

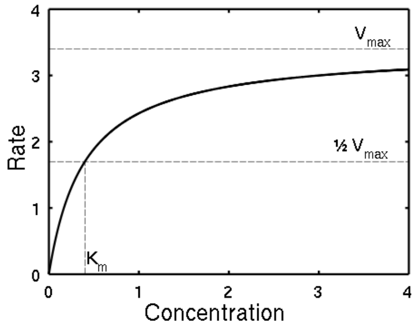
= **high nutrient patch**

Zhang et al. Ecology Letters 2017

Take home message

When feedbacks between organism growth and resource dynamics are modeled, some earlier results are better understood;

Non-linearity is important to consider.



Monod curve

Part II

Competition between two species

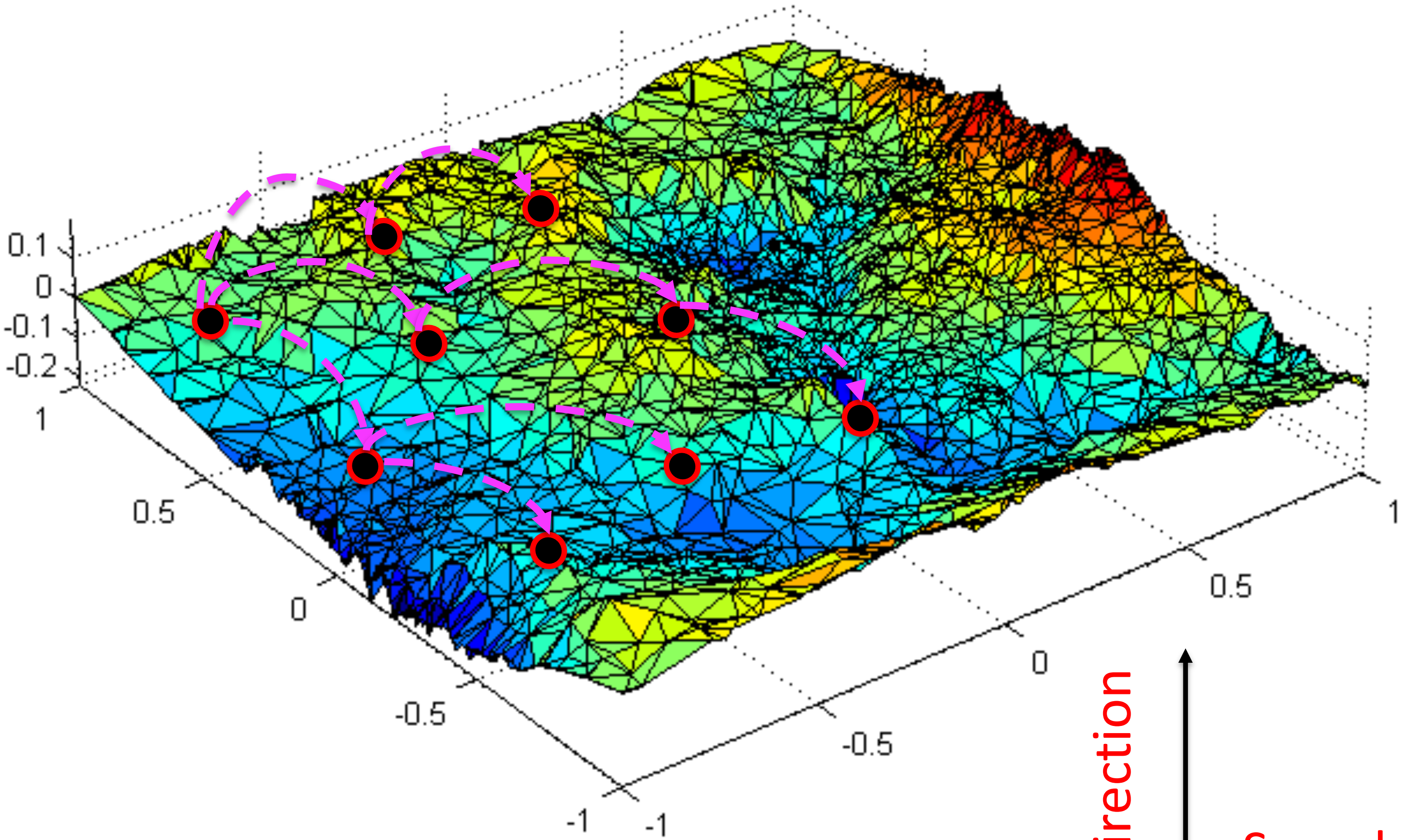
Q: How do movement strategies alter competition outcomes in heterogeneous environments?

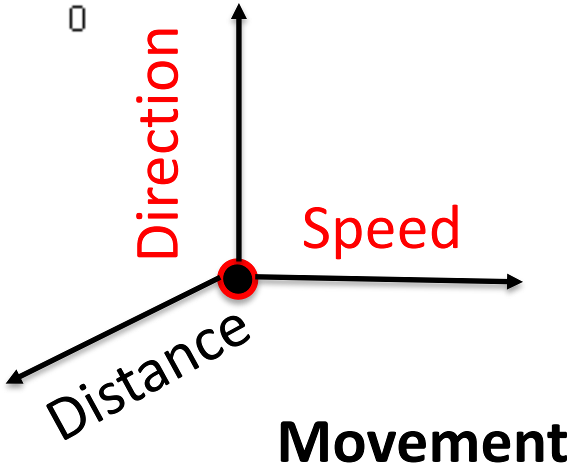
Q: How should an organism move in a changing environment?

Foundation: Gause (1934); Hutchinson (1959)

Theory based on the competition for a common resource (Chesson 2000, Amarasekare 2003);

Optimal movement strategy

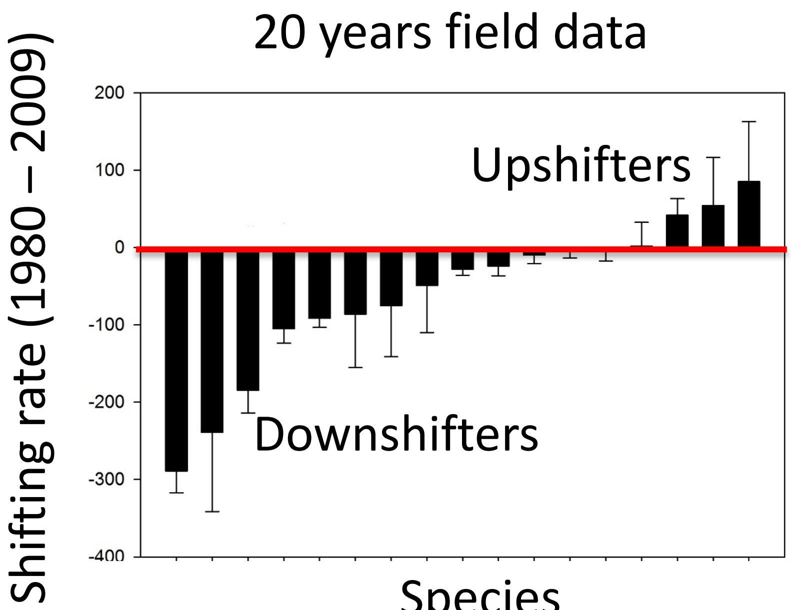




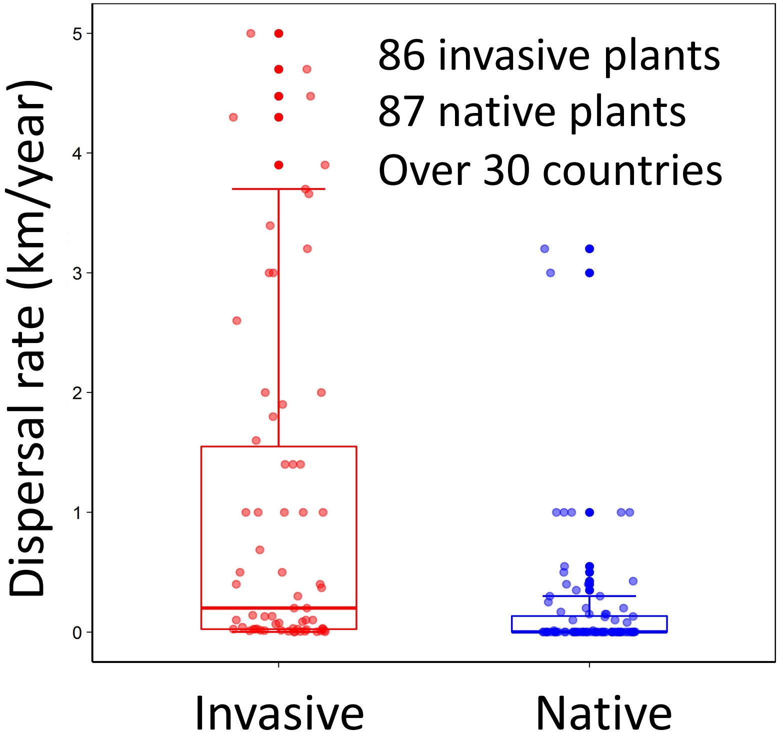
Species could have different moving rates

Divergent distribution shifting rates under deforestation and warming temperature.

Invasive species had significantly faster dispersal rates than native ones.



Zhang *et al.* (2019)
Environmental Research Letter



Zhang et al. under review

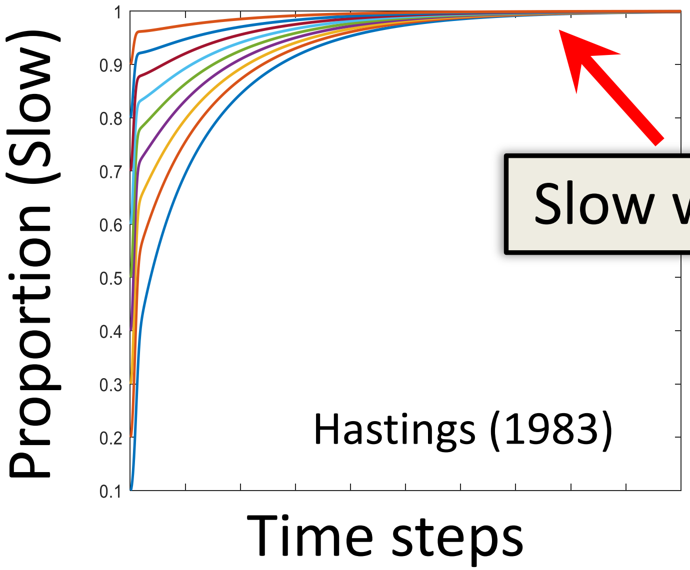
Which moving strategy is better?
Slower or faster?

Theoretically speaking…

Slower movement is better - The slower mover outcompetes the faster one in spatially heterogeneous but temporally constant environments (Logistic model).

The species with fast-moving strategy could go extinct.

(Hastings (1983) *Theoretical Population Biology*)



Slow wins

Is this true? No empirical verification existed!

Experimental verification

C. elegans

A free-living, transparent nematode

≈ 1 mm in length

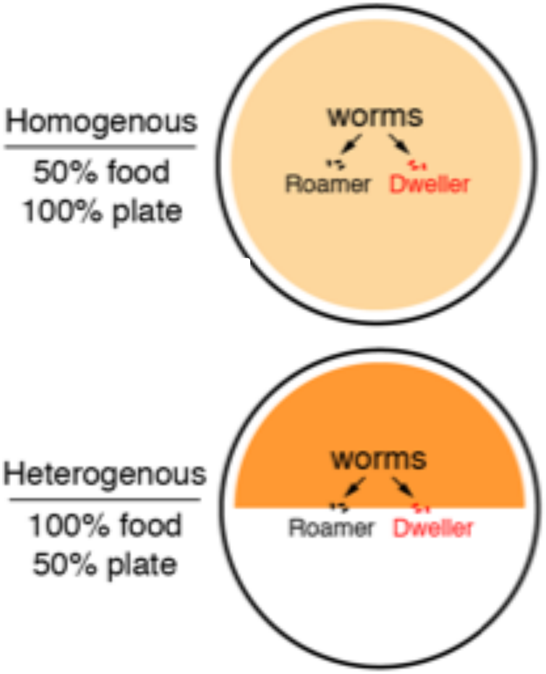
Strains: Roamer > Control > Dweller by dispersal rate

Fluorescently labeled

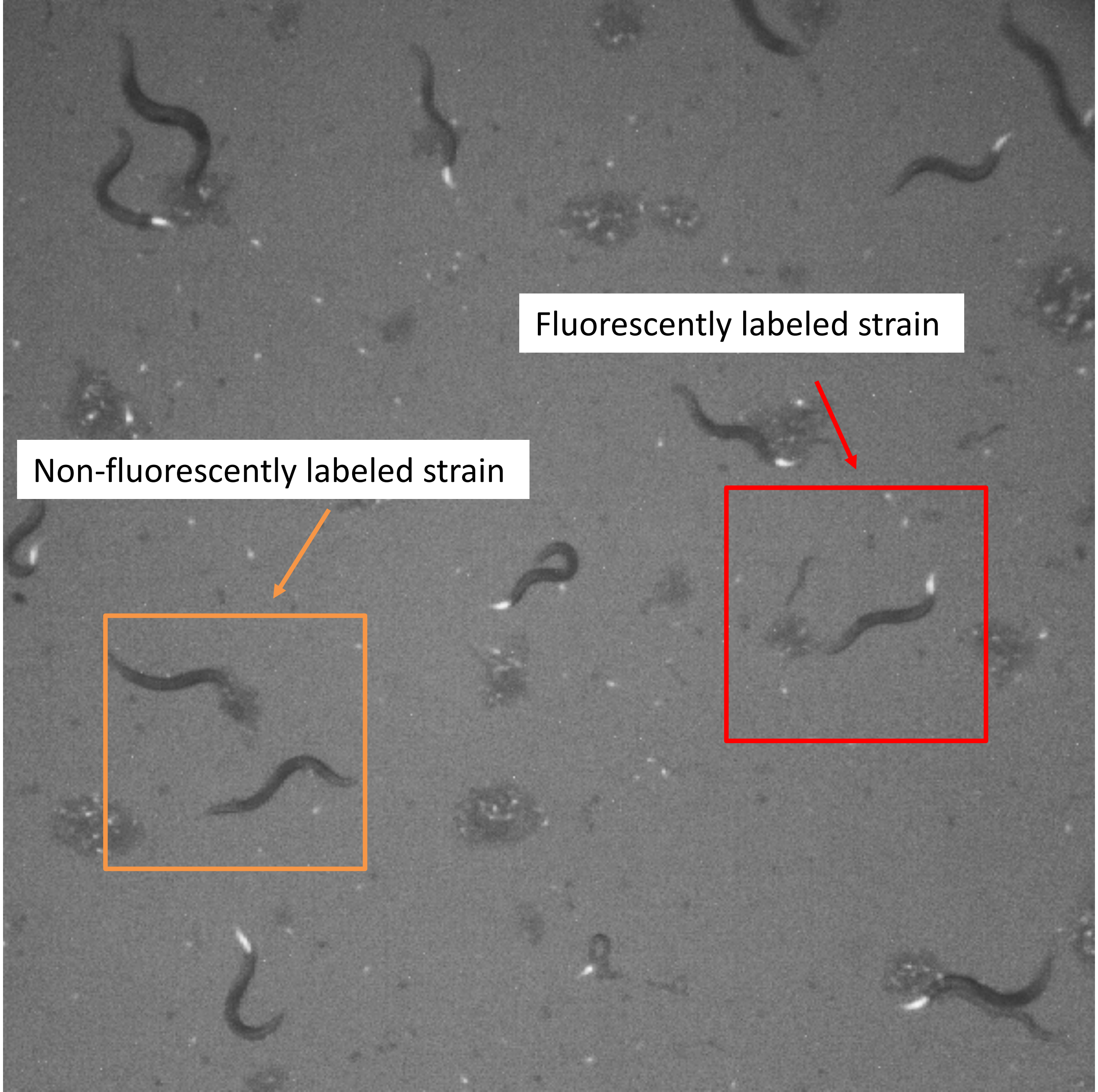
Control *vs.* Roamer

Control *vs.* Dweller

×

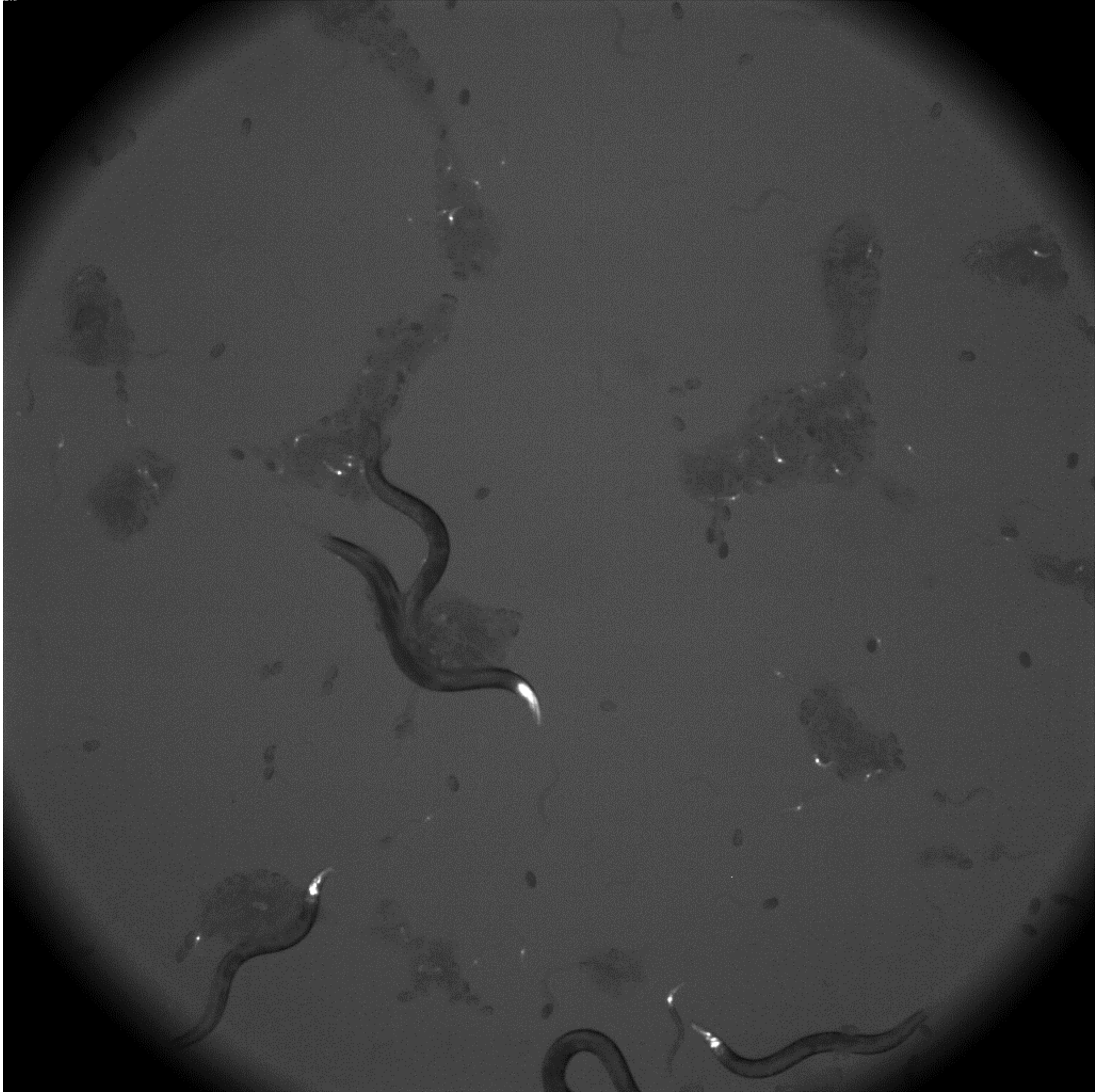


(Five replicates of each)

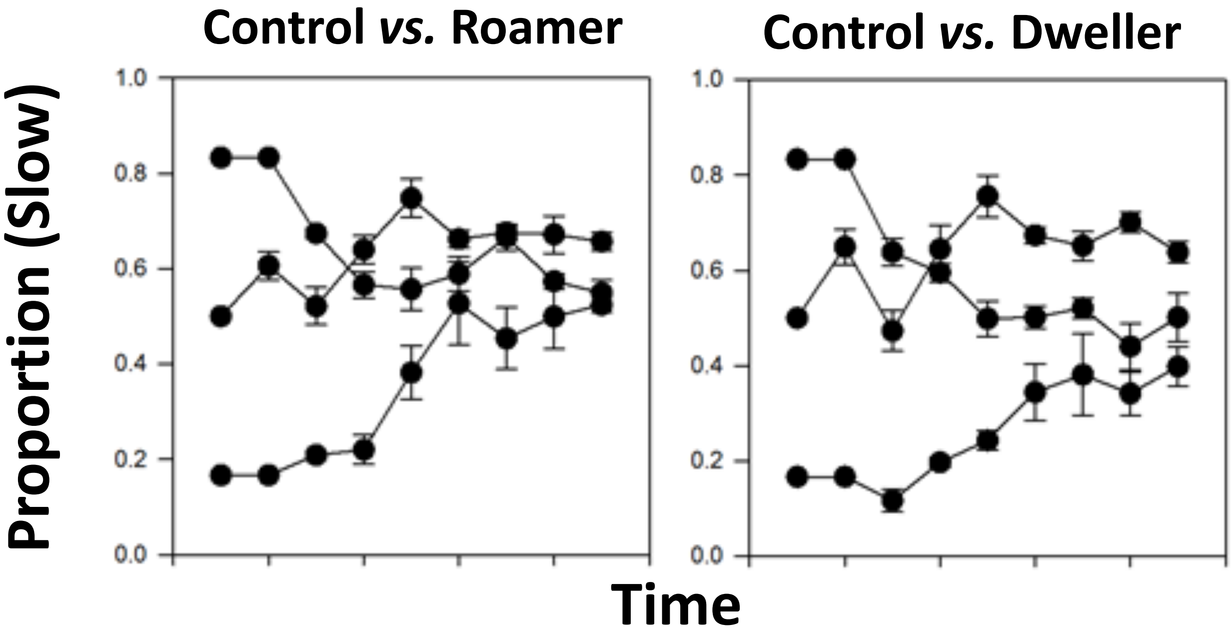


Fluorescently labeled strain

Non-fluorescently labeled strain



Experimental results



Coexistence

Slower movement is better

- (Logistic model).

Limitations of the logistic model:

It has not explicitly considered **resource dynamics** caused by **individual organisms**.

Zhang et al. (2021) *Trends in Ecology and Evolution*

Zhang et al. Ecology Letters, 2021

Resource dynamics can be better considered using Consumer-Resource models

Consumer (U) *same for another species (V)

i: Patch number

$$\frac{dU_i}{dt} = \frac{r_{max}N_iU_i}{k + N_i} - (mU_i + gU_i{}^2) + d_1\left(\frac{U_{i+1}}{2} + \frac{U_{i-1}}{2} - U_i\right)$$

Consumer dynamics

Growth

Mortality

Movement among neighbor patches

Resource (N)

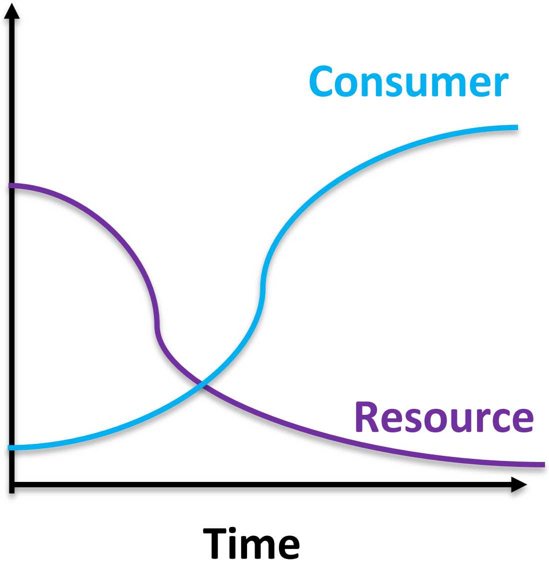
$$\frac{dN_i}{dt} = N_{input,i} - \theta Ni - \left(\frac{r_{max}N_iU_i}{\gamma(k + Ni)} + \frac{r_{max}N_iV_i}{\gamma(k + Ni)}\right)$$

Resource dynamics

Input

Dilution/ death

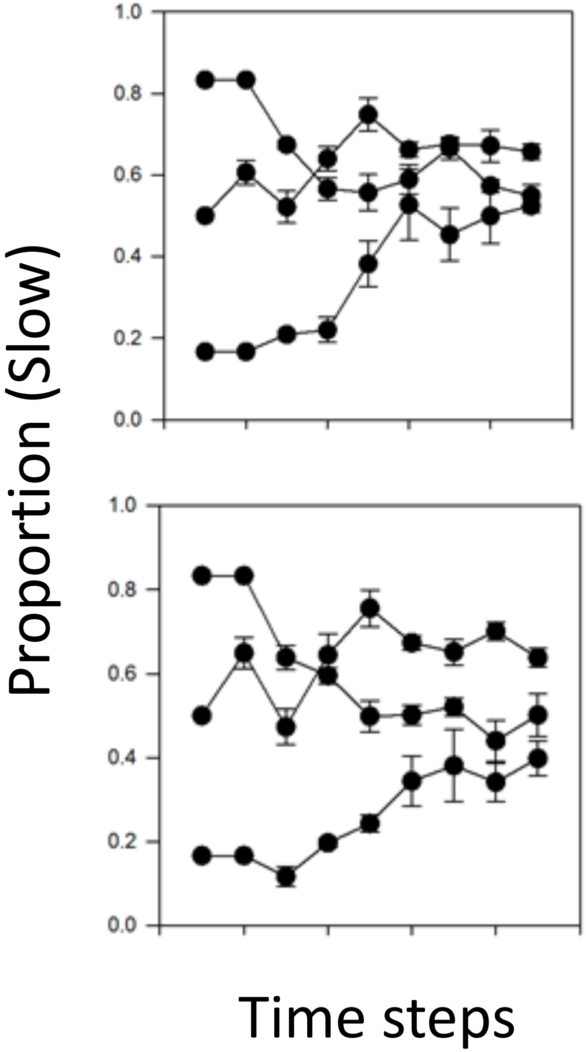
Resource dynamics caused by consumption



Tilman (1982) *Resource Competition and Community Structure;*

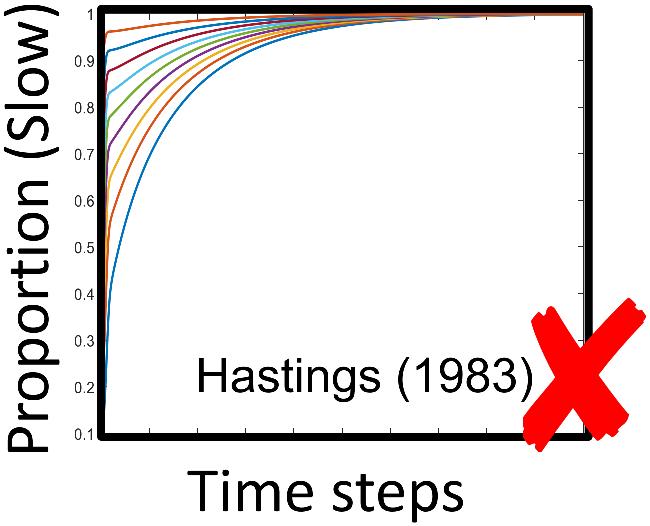
Mismatch between data and theory

Data



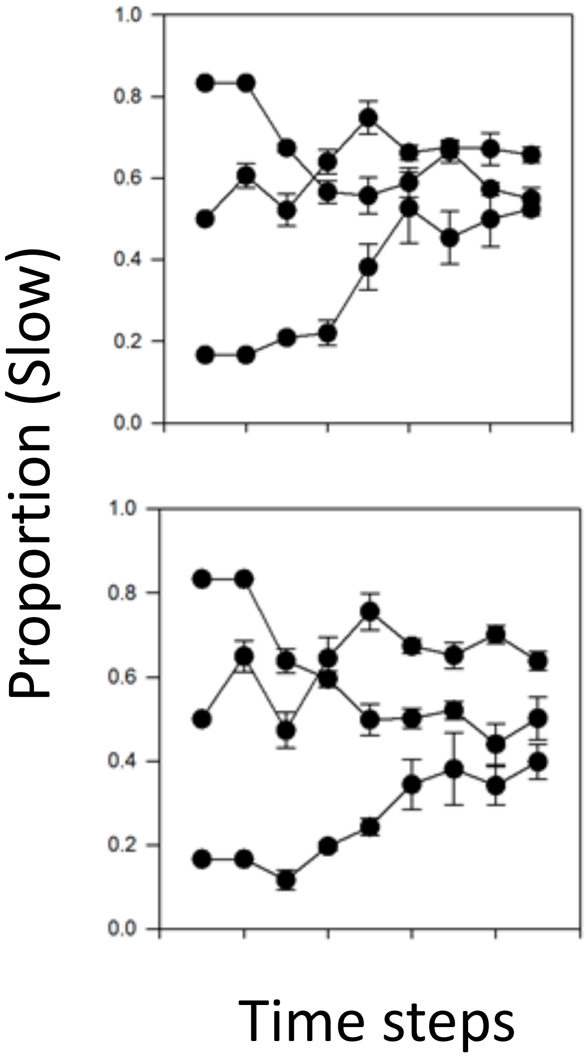
Simulations

1. Logistic model



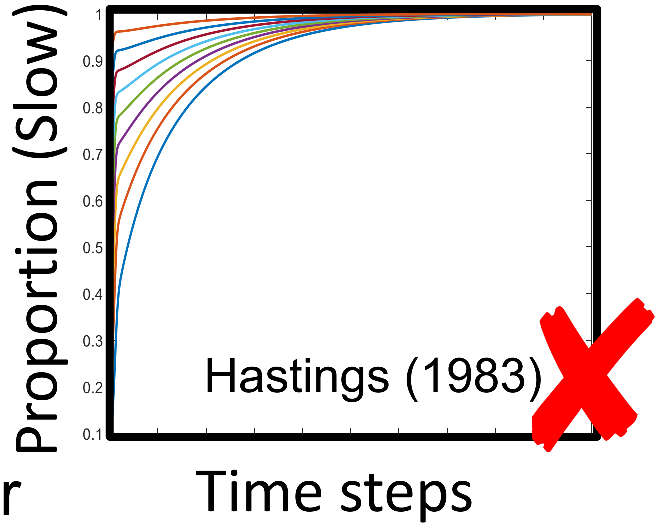
A little bit better: Consumer-Resource model

Data



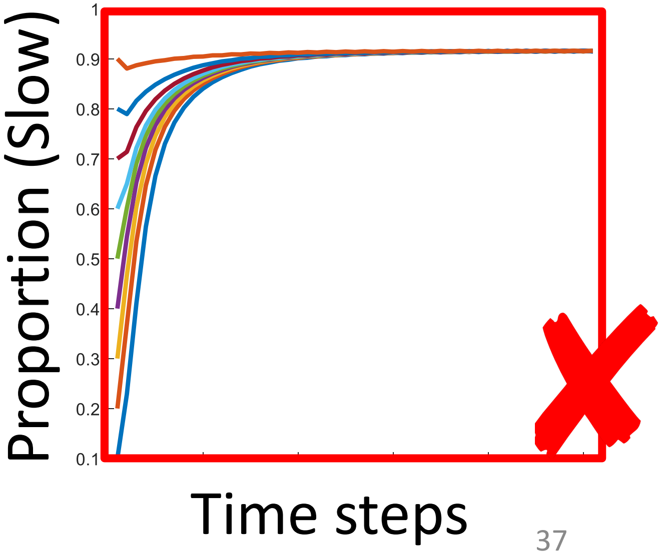
Simulations

1. Logistic model



A little bit better

2. Resource dynamics



Why Just ‘a little bit’ better?

The Consumer-Resource models do not consider **directed movement** towards to different resource levels.

C. Elegans

Meisel and Kim *Trends in Immunology* 2014

Directed dispersal by bird

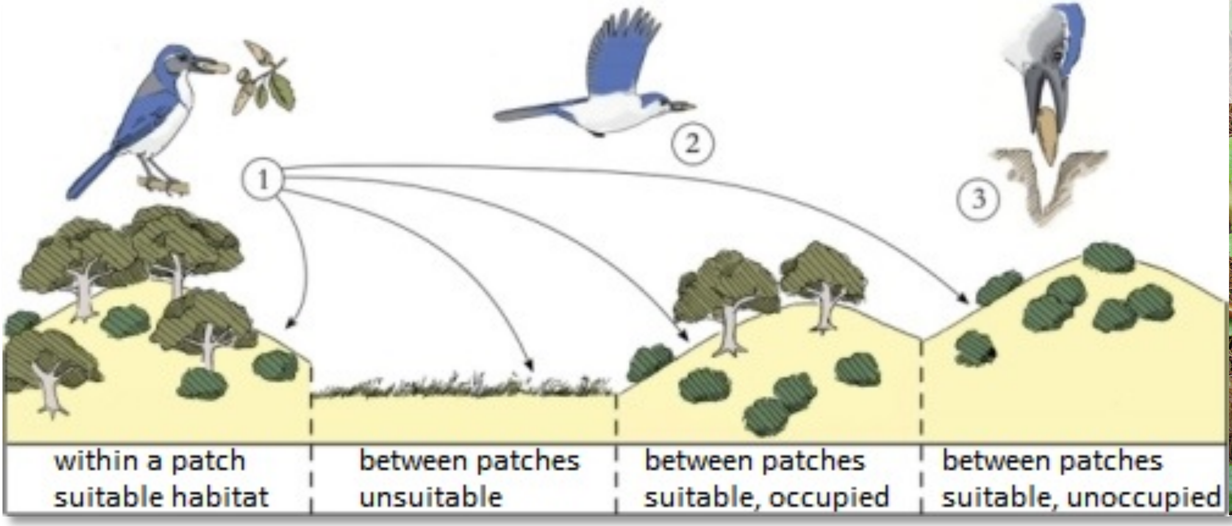


Photo credit: BOU

Foraging behavior of clonal plants

Hydrocotyle, Evans and Cain 1995

Consumer-Resource + directed movement

Consumer dynamics

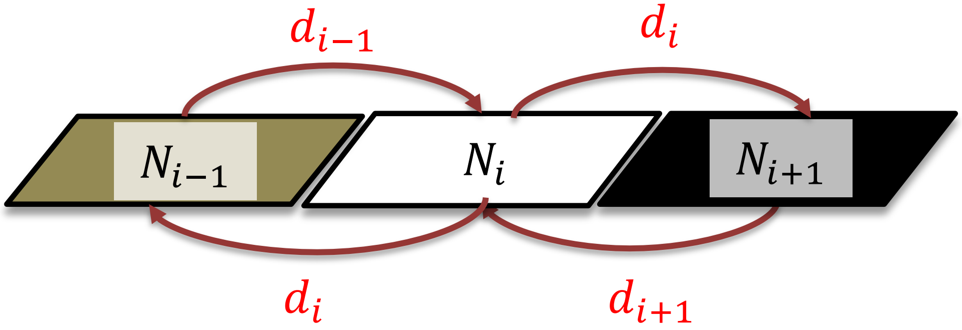
$$\frac{dU_i}{dt} = \frac{r_{max}N_iU_i}{(k+N_i)} - (mU_i + gU_i{}^2) + d1(U_{i-1} - 2U_i + U_{i+1})$$

The same coefficient (d_1)

↓

different ones $(d_i \neq d_{i-1} \neq d_{i+1}$

$$\frac{dU_i}{dt} = \frac{r_{max}N_iU_i}{(k+N_i)} - (mU_i + gU_i{}^2) + (d_{i-1}U_{i-1} - 2d_iU_i + d_{i+1}U_{i+1})$$



N_i : Resource

$$d_i = d + \alpha\frac{N_{i-1} - N_i}{N_i + \beta}$$

↓ Random diffusion

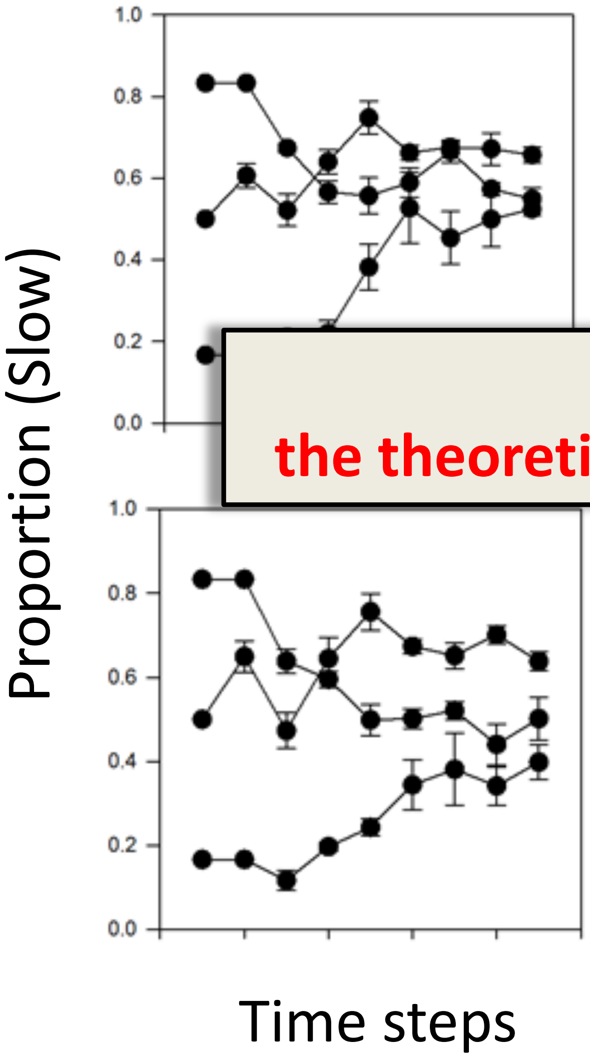
↓ Directed movement

* Both competing species have the same directed dispersal asymmetry (α). So they are totally identical except for their rates of random diffusion.

*Directed movement = 0 when dispersing from a low resource patch to a high resource patch

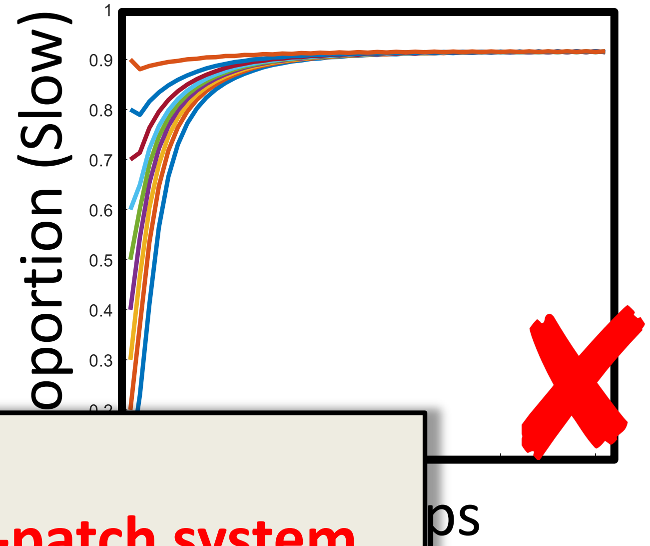
Much better with directed movement

Data



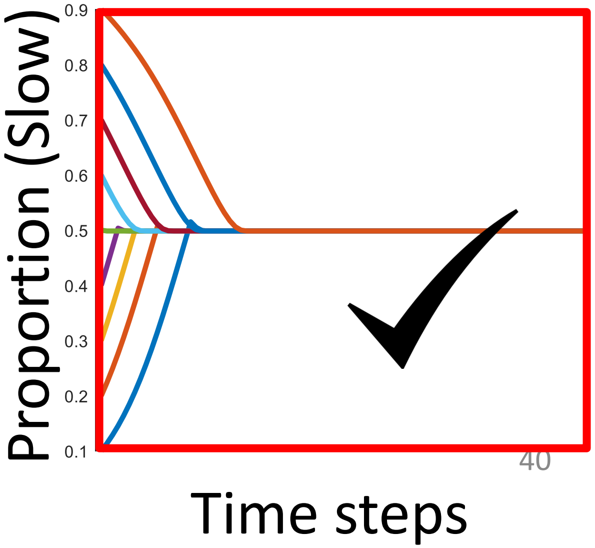
Simulations

2. Resource dynamics

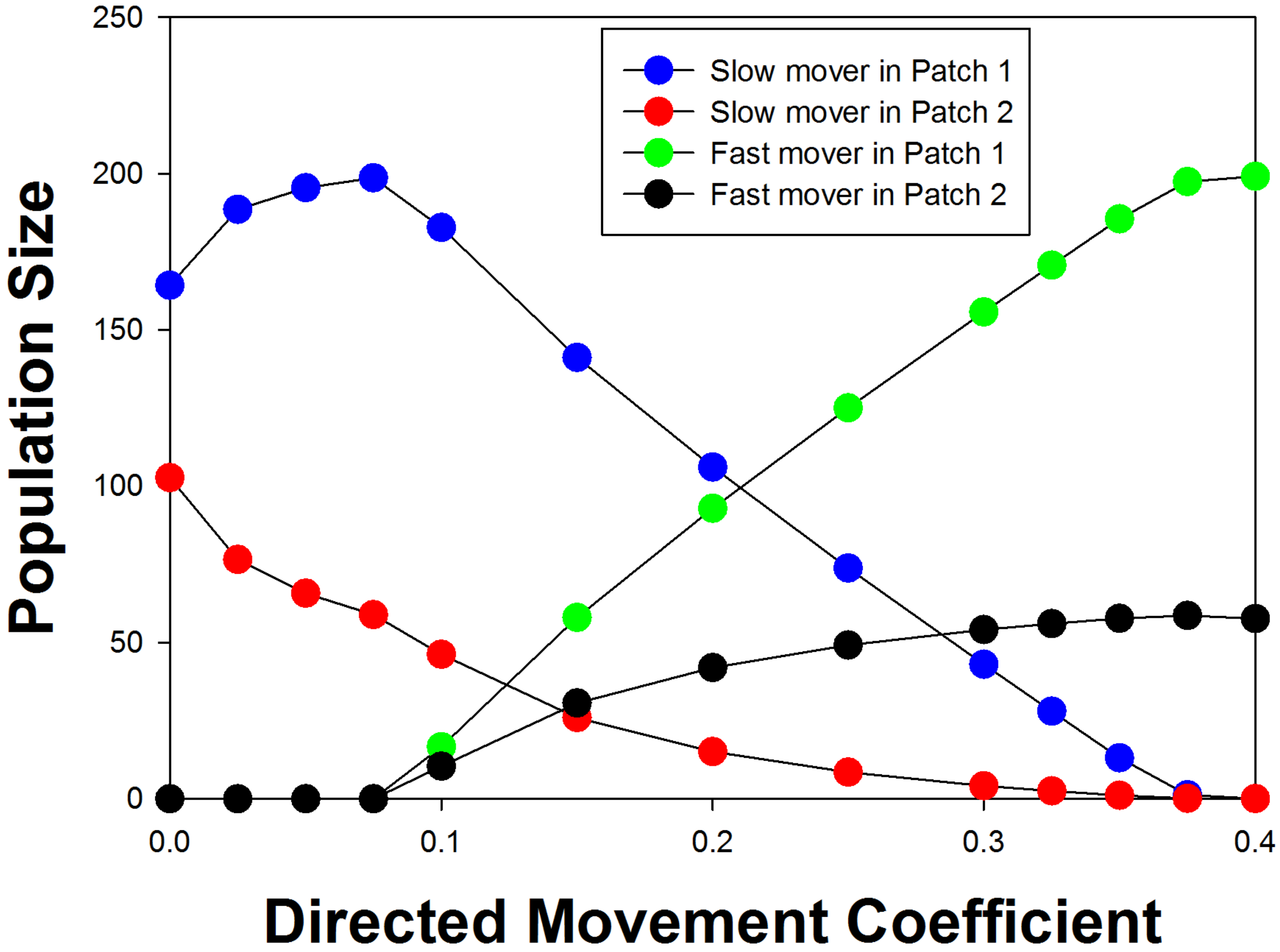


More importantly,
the theoretical results hold in a N-patch system.

3. Resource dynamics + directed movement

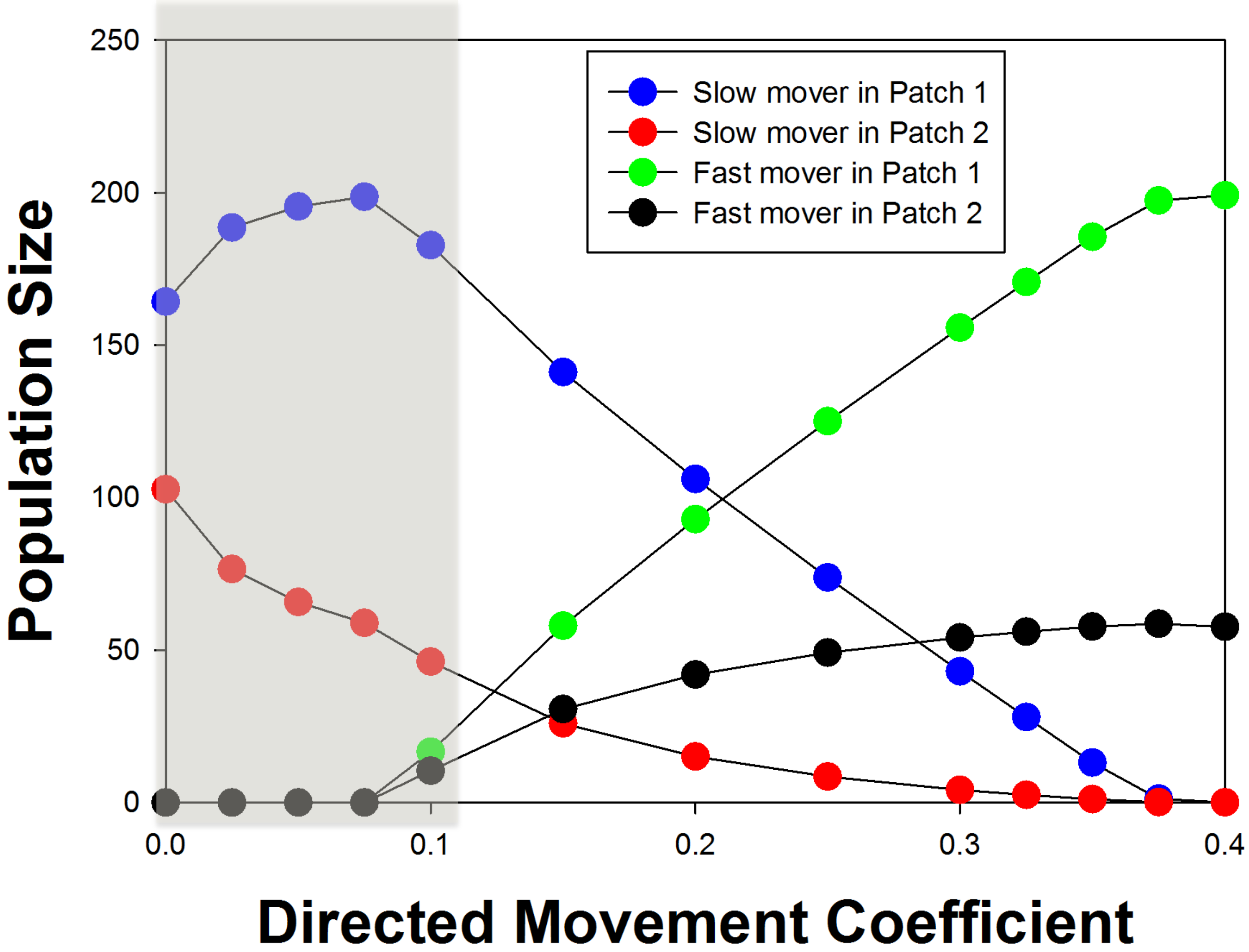


The directed movement coefficient MATTERS



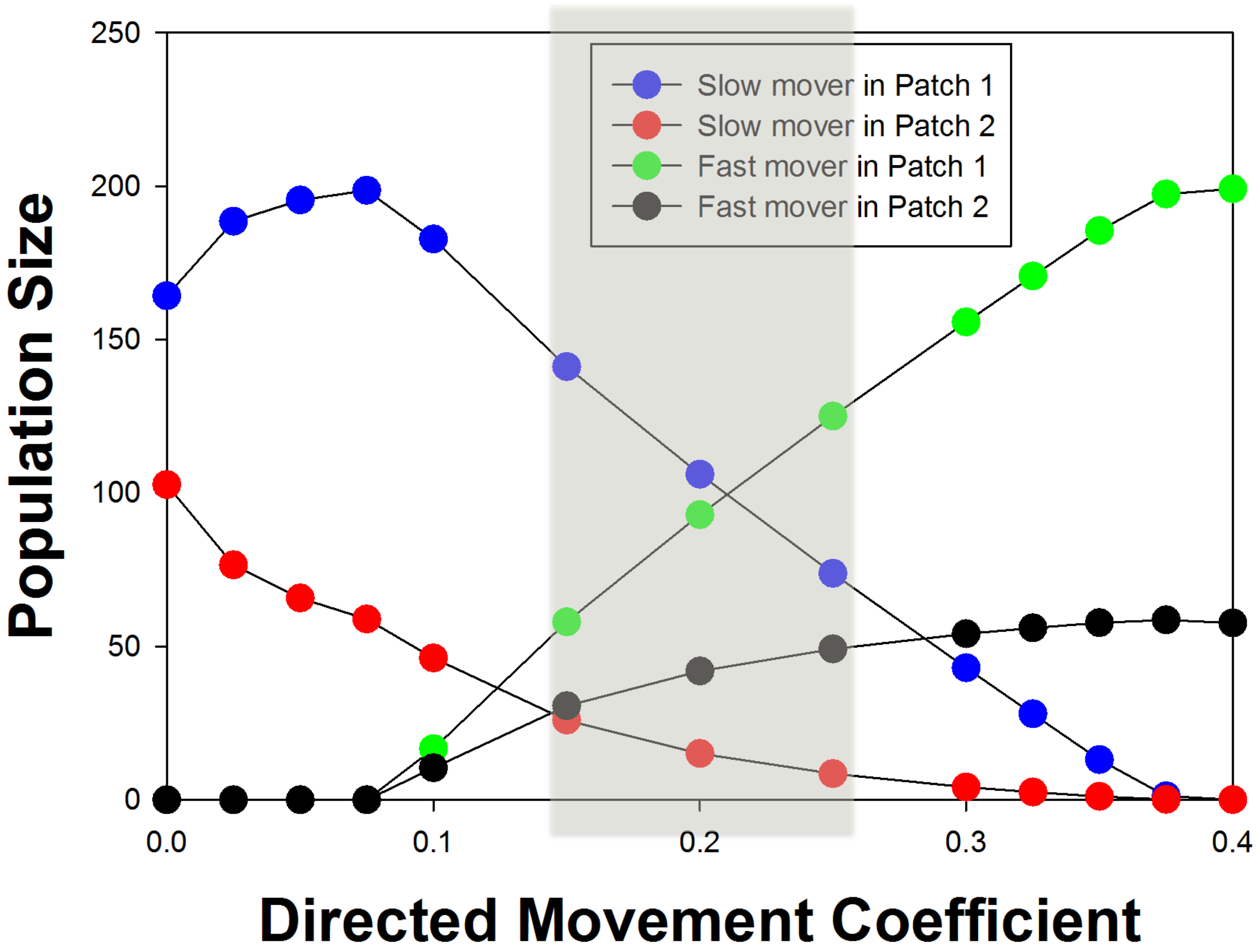
Zhang et al. Ecology Letters, 2021

Slow wins



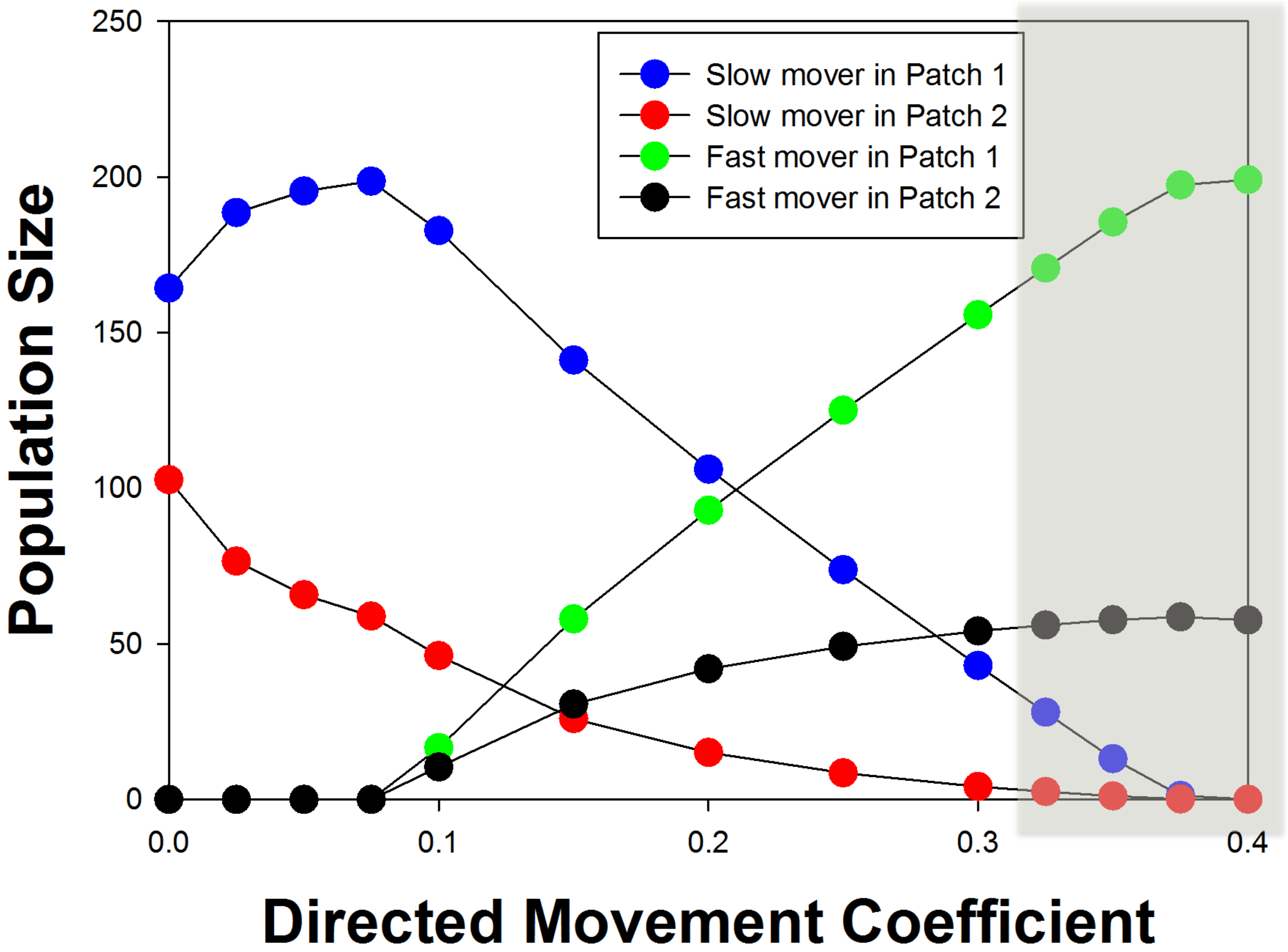
Zhang et al. Ecology Letters, 2021

Coexistence



Zhang et al. Ecology Letters, 2021

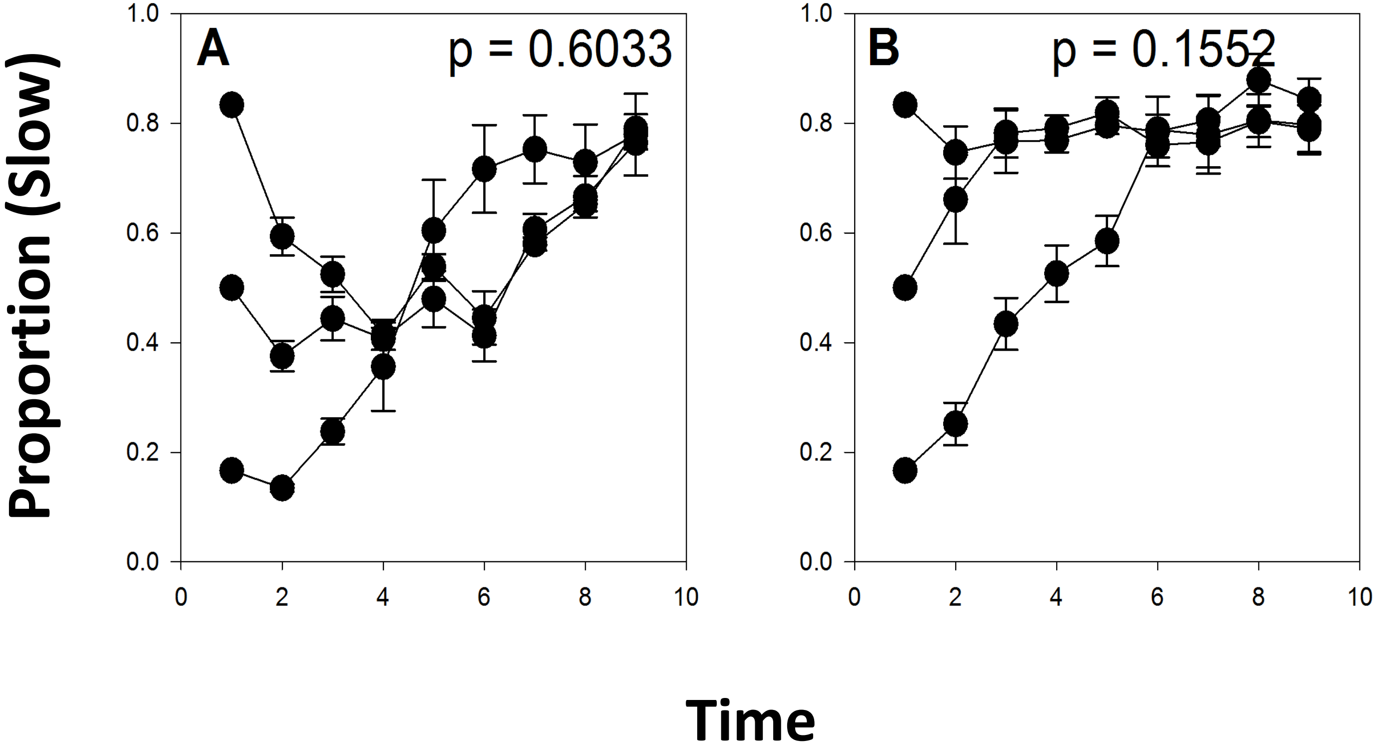
Fast wins



Zhang et al. Ecology Letters, 2021

Experimental results without directed movement

Heterogeneous Environment



Control *vs.* Roamer

Control *vs.* Dweller

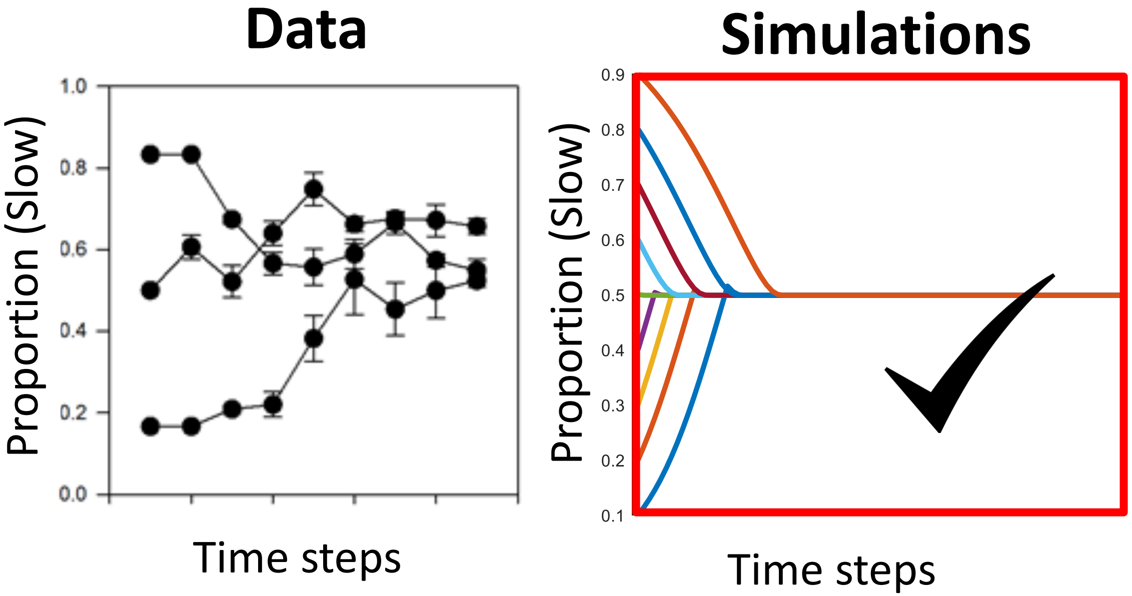
Slow wins

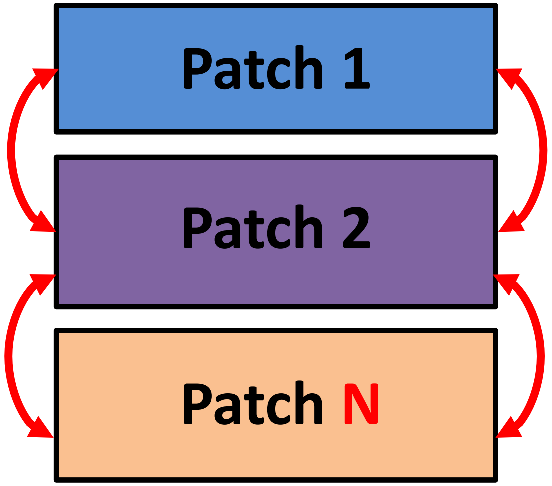
Zhang et al. Ecology Letters, 2021

Summary and implications

1. The organism-environment feedbacks, including resource dynamics and directed movements, determine the cross-patch dynamics (i.e., ecological dynamics at a large scale).

2. The spatial Consumer-Resource model could be a promising approach to model complex dynamics at a large scale.





QUESTIONS?

Contact Information:

Email: bozhangophelia@gmail.com