Population Carrying Capacity in Heterogeneous and Temporally Periodic Systems

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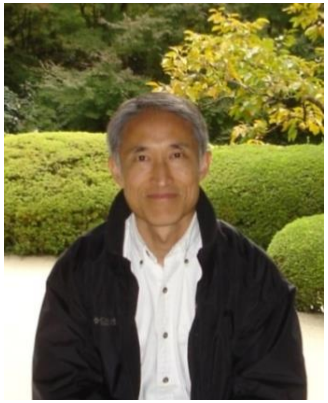

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Outline

- Carrying capacity, a confusing concept
- Extension of carrying capacity to heterogeneous space
- Extension of carrying capacity to a temporally periodic environment
- Experimental testing of predictions from logistic model for carrying capacity extended to heterogeneous space
- Interpretation with consumer-resource model
- Conclusions and future work

Carrying Capacity:
A Confusing Concept

Carrying Capacity: A Confusing Concept

‘Carrying capacity’ was introduced in the early 20th century by wildlife biologists as a tool in wildlife management.

While commonly defined as the ‘upper limit on the size of the population at equilibrium’, many different definitions became attached to the concept; e.g., subsistence density, optimum density, security density, and tolerance density.

Andre’ Dhondt (1989) reviewed the multiplicity of views of carrying capacity and called it “confusing”, concluding that, at least for wildlife biology, the term should be avoided.

Carrying Capacity: A Confusing Concept

But carrying capacity had already become formalized mathematically.

Odum (1953) represented carrying capacity as a mathematical parameter. He defined it as the constant *K* in the Pearl-Verhulst form of the logistic population equation;

$$\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right)N$$

where *N* is population size and *r* is the intrinsic population growth rate. This equation defines the carrying capacity as an equilibrium, or steady state, point of the population.

Critiques of Pearl-Verhulst Logistic Model

The logistic model itself has been widely criticized

“it has never been observed in nature“ (Botkin 1990)
“shown to be poor representation of populations” (C. A. S. Hall 1988)
density-vague regulation more realistic, (Strong 1986).

Leads to mathematical awkwardness (Ginzburg1992)
Misleading for evolutionary theory (Mallet 2012).

Nevertheless, the Pearl-Verhulst form of the logistic equation, with carrying capacity *K*, has been standard in ecology textbooks since the 1970's, and has a central place in theoretical ecology.

Extending Carrying Capacity in Space and Time

Beyond those criticisms, attempts to extend carrying capacity to spatially heterogeneous or temporally varying environments also raises issues.

A population in a spatial region with a heterogeneously distributed K can have steady state size either greater or smaller than the sum of local carrying capacities, depending on movement rates and heterogeneity of growth rates.

A population in an environment with K varying periodically between two values, K_1 and K_2, measures of the population size can be greater or smaller than the sum $K_1 + K_2$, again depending on growth rates.

Therefore, we assert that 'upper limit on the size of a population at equilibrium', or 'carrying capacity', is more of an emergent than a fundamental quantity. That can be shown by simple modeling.

Extension to Heterogeneous Space

Extension to Heterogeneous Space

It can be shown analytically that population at equilibrium can exceed the sum of local carrying capacities

Poggiale et al. (2005)

$$\frac{dN_1}{d\tau} = m_{12}N_2 - m_{21}N_1 + \varepsilon r_1 N_1\left(1 - \frac{N_1}{K_1}\right)$$

$$\frac{dN_2}{d\tau} = m_{21}N_1 - m_{12}N_2 + \varepsilon r_2 N_2\left(1 - \frac{N_2}{K_2}\right)$$

where ε is a small time-parameter and m_{ij} are movement rates. Letting

$$u_1 = \frac{m_{12}}{m_{12} + m_{21}} \qquad u_2 = \frac{m_{21}}{m_{12} + m_{21}}$$

Poggiale, J.C., et al, 2005. Global production increased by spatial heterogeneity in a population dynamics model. *Acta Biotheoretica*, *53*(4), pp.359-370.

Extension to Heterogeneous Space

Poggiale et al. found in the limit ε → 0

$$N_1^* + N_2^* \rightarrow \frac{K_1 K_2 (r_1 u_1 + r_2 u_2)}{K_2 r_2 u_1^2 + K_1 r_2 u_2^2}$$

Then, assuming $K_1 = K_2$ they showed that, if

$$1 < \frac{m_{21}}{m_{12}} < \frac{r_1}{r_2} \quad \text{then} \quad N_{total} = N_1^* + N_2^* > K_1 + K_2$$

But one can also make alternative assumptions; such as

$$K_1 \neq K_2, \quad r_1 \neq r_2 \quad \text{and } m_{12} = m_{21} = m$$

Extension to Heterogeneous Space

Then the same result as Freedman and Waltman (1977) Holt (1985) and (in more detail with minor correction), Arditi et al. (2015) follows

When the two patches are well-mixed by **rapid diffusion** (*D* → ∞*)*, equivalent to ε → 0.

$$N_1^* + N_2^* = K_1 + K_2 + (K_1 - K_2)\frac{(r_1 K_2 - r_2 K_1)}{r_1 K_2 + r_2 K_2} > K_1 + K_2$$

$$\text{if } K_1 > K_2 \quad \text{and} \quad r_1/r_2 > K_1/K_2$$

Also, Lou (2006) studied a population of biomass *u*, and growth rate, *g(x)*, reaction-diffusion equation

$$\frac{\partial u}{\partial t} = D\Delta u + [g(x) - u]u$$

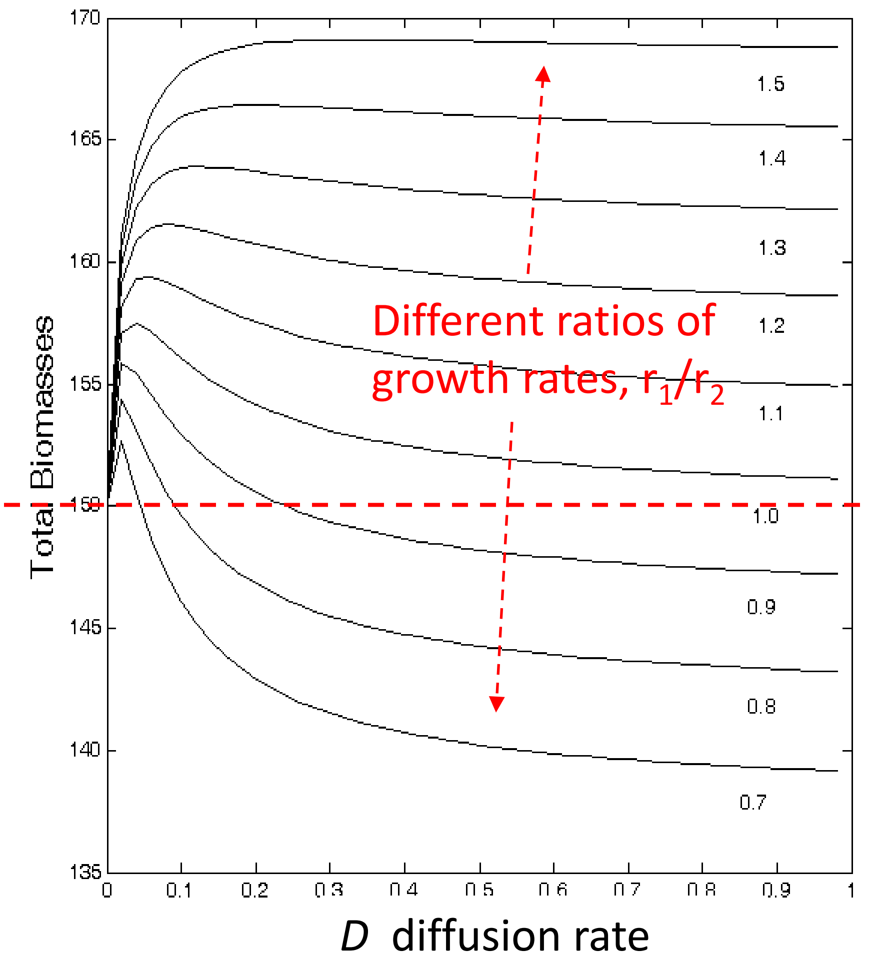
$$D\int_\Omega \frac{|\nabla u|}{u^2} + \int_\Omega [g(x) - u(x)]dx = 0 \qquad D\int_\Omega \frac{|\nabla u|}{u^2} > 0 \qquad \int_\Omega [u(x) - g(x)]dx > 0 \qquad \text{for all } D > 0$$

Arditi, R., Lobry, C., & Sari, T. (2015). Is dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation. Theoretical population biology, *106*, 45-59.

Pearl-Verhulst Growth Equation: Two Patches

Total population size N_{total} for each value of growth rate as a function of diffusion rate .

Total carrying capacity of two patches with no diffusion



This shows both that total population size initially increases as D increases from 0.

Can be generalized beyond Pearl-Verhulst and beyond two-patch

Extension to Temporally Periodic Variation

Extension of Logistic to Temporally Periodically Varying Environment

The population is described by

$$\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right)N$$

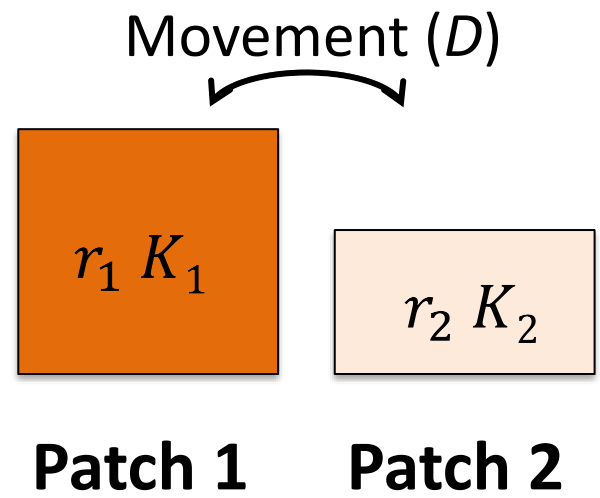
where, within a given time period (0, T)

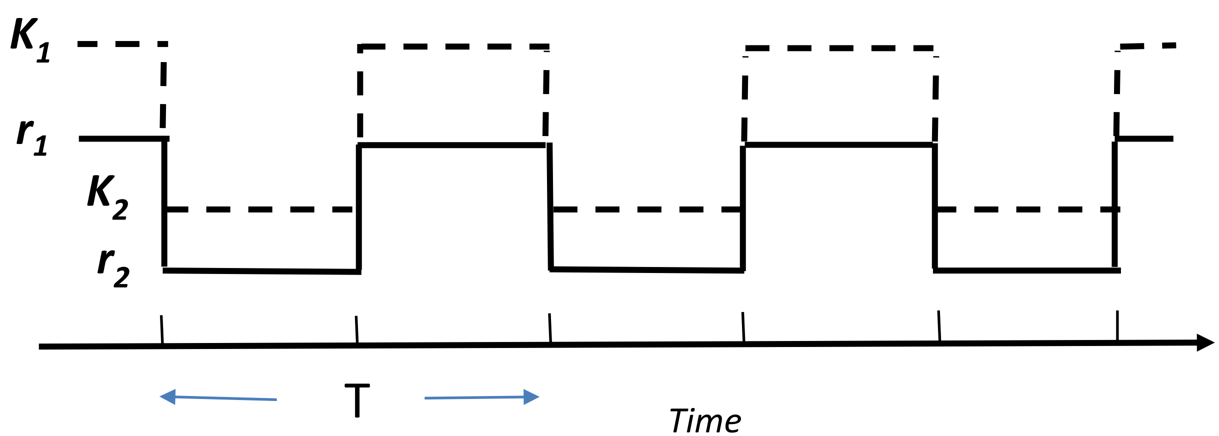
$$K, r = K_1, r_1 \quad \text{when} \quad 0 \leq t < (1/2)T$$

$$K, r = K_2, r_2 \quad \text{when} \quad (1/2)T \leq t \leq T$$

Temporally Periodic Environment

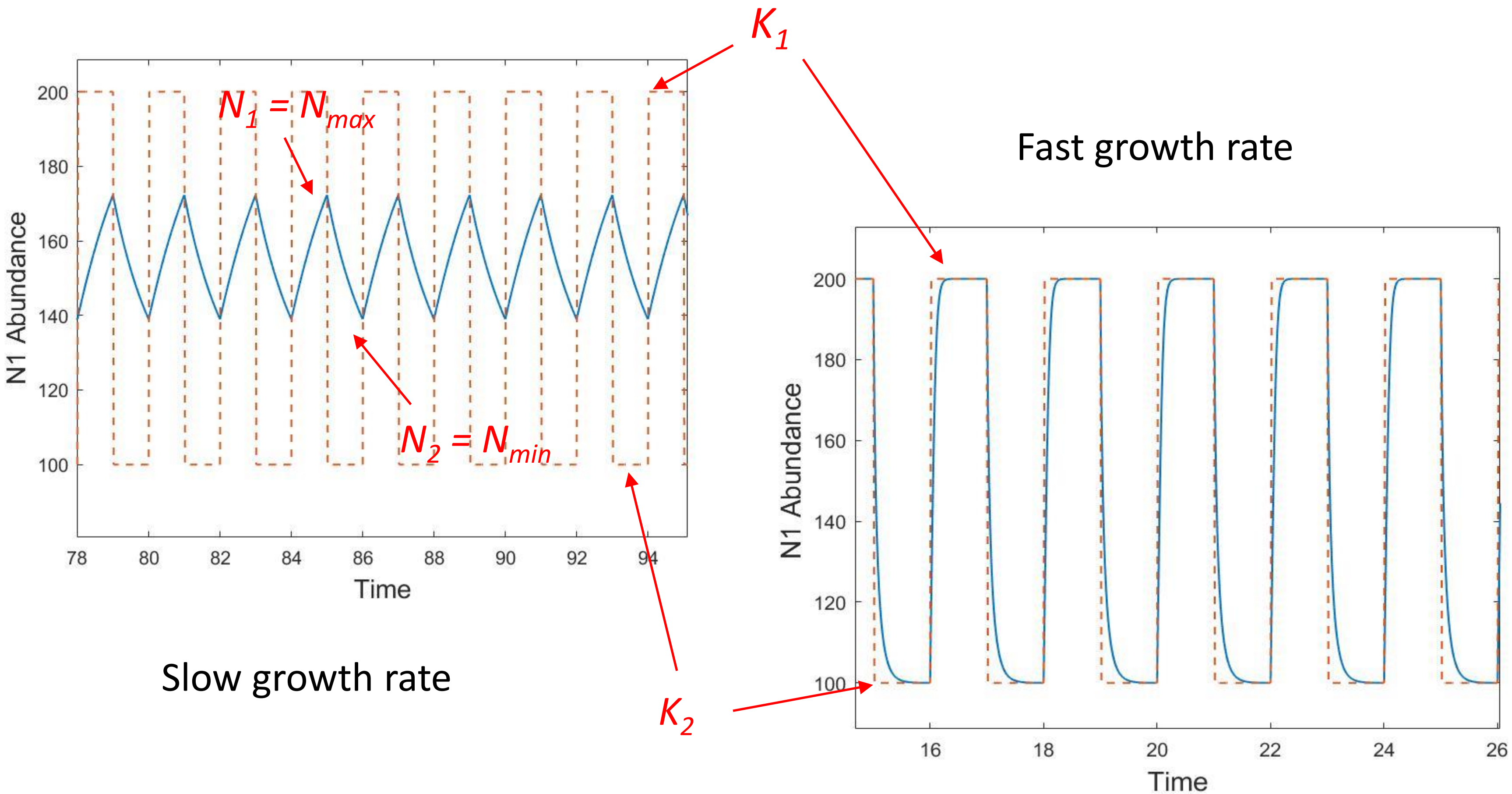
There is a parallel between the heterogeneous spatial two-patch logistic model and the periodically temporally varying logistic model.





Temporally Periodic Environment

The effect of temporal variability on the population depends on the temporal period and the two growth rates.



Temporally Periodic Environment

By solving for the values of N_1 and N_2 at the ends of the respective intervals, we find

$$N_1 = N_{max} = \frac{K_1 K_2\left(e^{0.5(r_1+r_2)T} - 1\right)}{K_1(e^{0.5r_2T} - 1) + K_2 e^{0.5r_2T}(e^{0.5r_1T} - 1)}$$

$$N_2 = N_{min} = \frac{K_1 K_2\left(e^{0.5(r_1+r_2)T} - 1\right)}{K_2(e^{0.5r_1T} - 1) + K_1 e^{0.5r_1T}(e^{0.5r_2T} - 1)}$$

Then, for both r_1 and r_2 very small (small growth rate),

$$N_1 \to \frac{K_1 K_2 (r_1 + r_2)}{K_1 r_2 + K_2 r_1} \qquad N_2 \to \frac{K_1 K_2 (r_1 + r_2)}{K_2 r_1 + K_1 r_2}$$

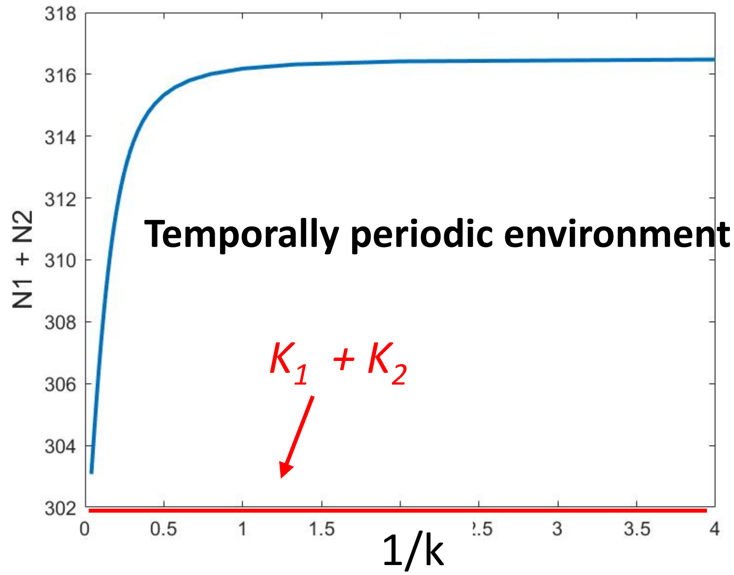
$$Sum\ of\ Populations \to N_1 + N_2 = K_1 + K_2 + (K_1 - K_2)\frac{r_1 K_2 - r_2 K_1}{r_1 K_2 + r_2 K_1}\ .$$

Same as two-patch spatial model for *D* →∞

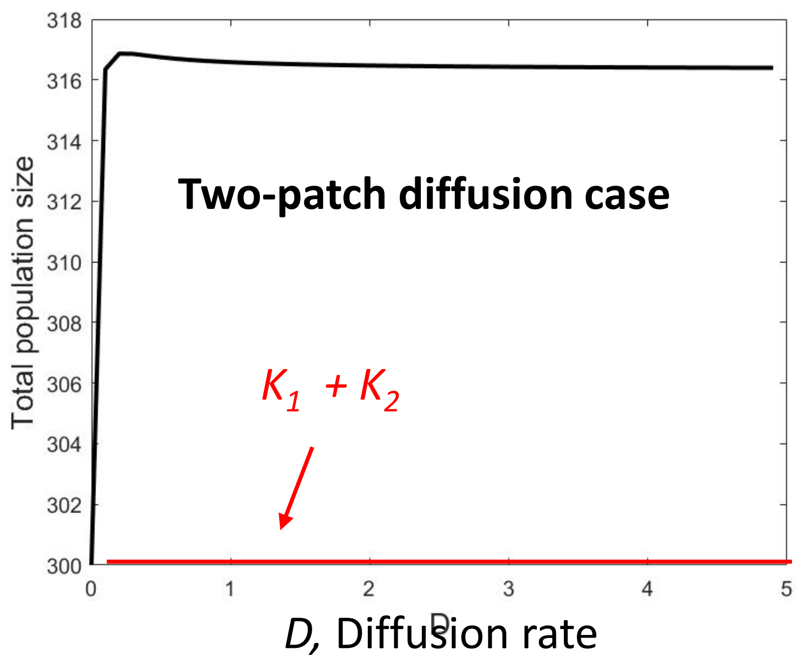
The similarity of the spatial and temporal models extends to the whole axes.

Let k be a common scaling factor for r_1 and r_2 .

Then $N_1 + N_2 > K_1 + K_2$ over the whole range of k



Above. Temporally varying case. K_1 = 200, K_2 = 100, r_1 = 0.75, r_2 = 0.25, T=1.5, r_1/r_2 = 3. Sum of maximum and minimum values of N_1 and N_2



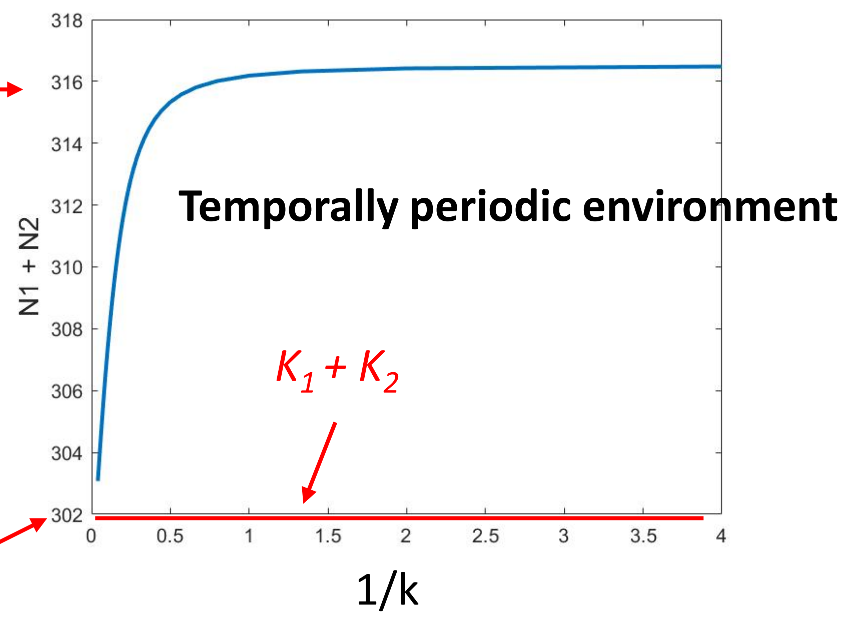
Left. Two-patch case with symmetric dispersal using Eqs. (1a,b). Total population vs. D for K_1 = 200, K_2 = 100, r_1 = 0.75, r_2 = 0.25, r_1 / r_2 = 3

Explanation of Results

When $1/k \to \infty$, this is equivalent to low relative growth rate relative to temporal period (similar to a high diffusion rate in the two-patch case).

So the temporally periodic case resembles the two-patch diffusion in that limit.

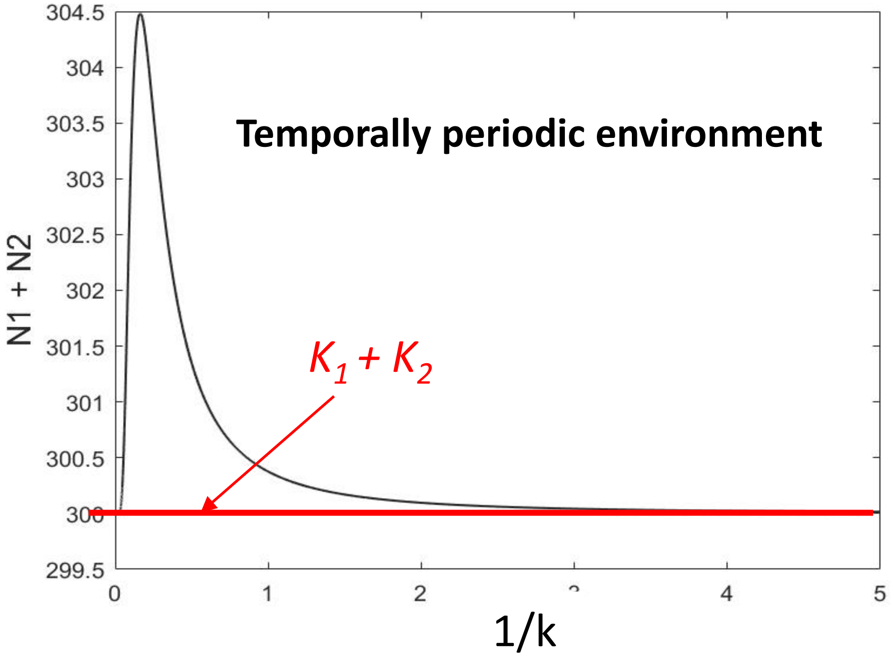
At the opposite end of the spectrum, when k (scaling r_1 and r_2) is large, so that $1/k << 1$, growth rate is very large and $N_{max} + N_{min} \to K_1 + K_2$.



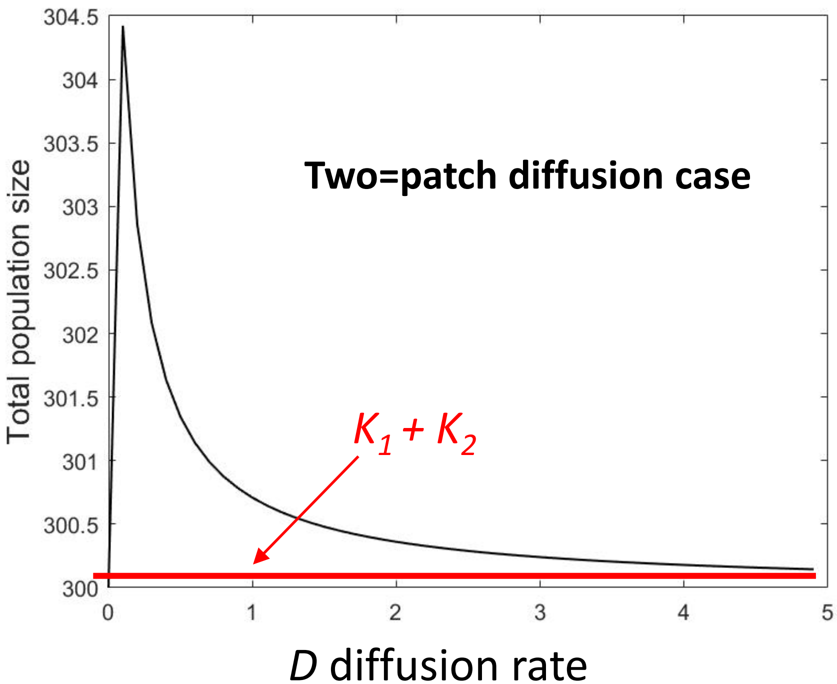
Repeat with the special case of $r_1/r_2 = K_1/K_2$

Let k be a common scaling factor for r_1 and r_2 .

Then $N_1 + N_2 > K_1 + K_2$ over the whole range of k



Above. Temporally varying case. K_1 = 200, K_2 = 100, r_1 = 0.5, r_2 = 0.25. Sum of maximum and minimum values of N_1 and N_2



Left. Two-patch case with symmetric dispersal using Eqs. (1a,b). Total population vs. D for K_1 = 200, K_2 = 100, r_1 = 0.07, r_2 = 0.035, r_1 / r_2 = 2

Temporally periodic environment

Above, we have just added the minimum and maximum values of N, that is, $N_{max} + N_{min}$ to get the above results.

To get another measure of total N, we can also integrate over N over the whole time period

$$\frac{dN}{dt} = r\left(\left(1 - \frac{N}{K}\right)N\right)$$

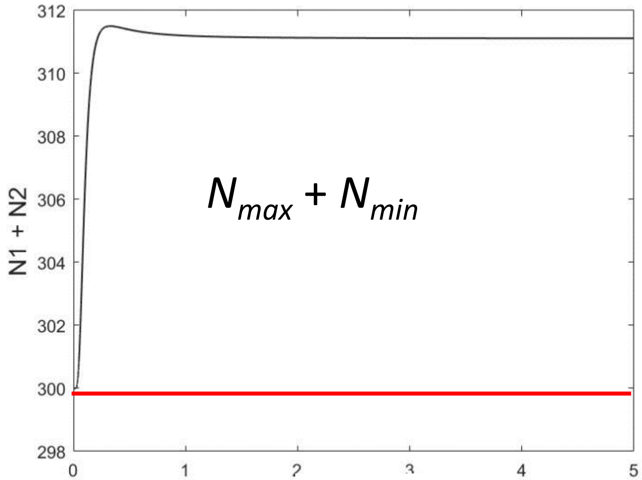
to obtain

$$\int_0^{\mathrm{T}} N(\mathrm{t}) \; = 0.5(K_1 + \; K_2) + \frac{1}{T}\left(\frac{K_1}{r_1} - \frac{K_2}{r_2}\right)(\ln(N_2/N_1),$$

The two different expressions, $N_1 + N_2$ (or $N_{max} + N_{min}$) and $2\int_0^1 N(t)$ somewhat agree for $K_1 r_2 - \; K_2 r_1 \; \neq 0$, but not when $K_1 r_2 - \; K_2 r_1 = 0$, see next slides.

Both $N_{max} + N_{min}$ and $2\int_0^T N(t)$ can give total population $> K_1 + K_2$

$K_1 = 200$, $K_2 = 100$, $r_1 = 0.5$, $r_2 = 0.2$.

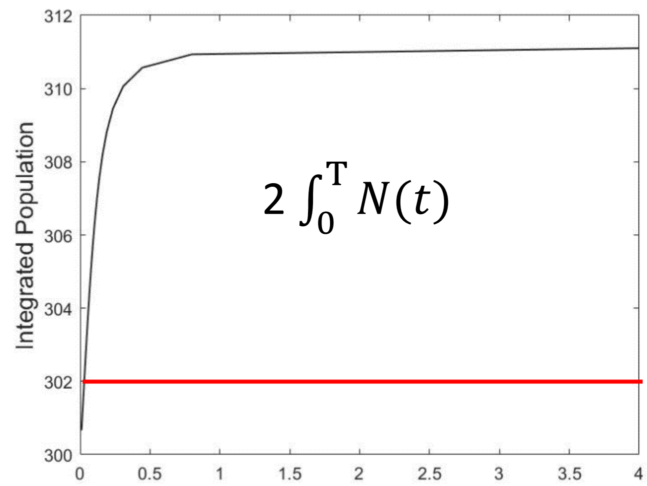


$K_1 + K_2$

$1/k$

Sum of maximum and minimum values of N

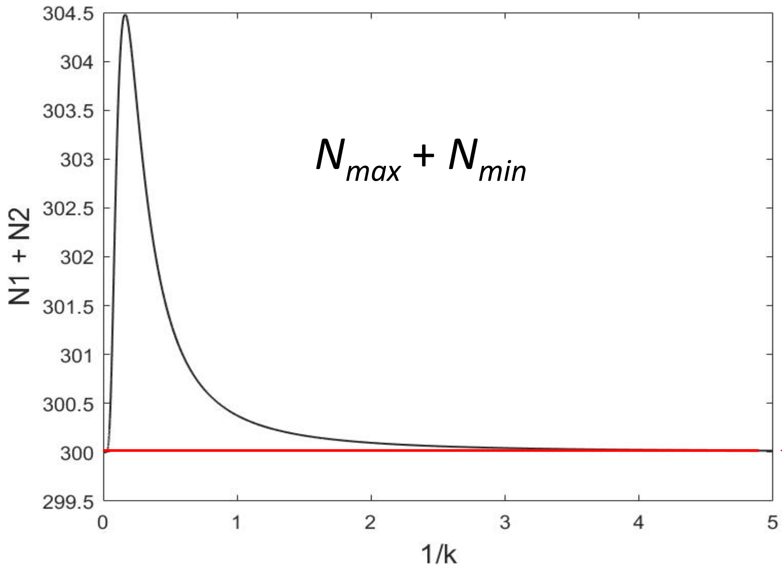
Integral of N over the period, $2\int_0^T N(t)dt$ over the interval $(0,T)$, vs. $1/k$, $T = 1.5$.



$K_1 + K_2$

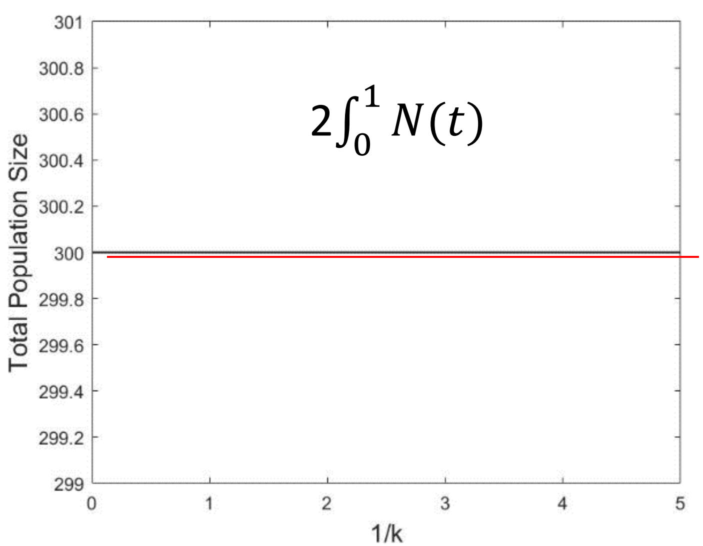
$1/K$

The peak is crushed in the $\mathrm{r_1 K_2 - r_2 K_1} = 0$ case



$K_1 + K_2$

K_1 = 200, K_2 = 100,
r_1 = 0.5, r_2 = 0.25.



Thus, when $r_1 K_2 = r_2 K_1$
the hump disappears

Experimental Testing of Predictions

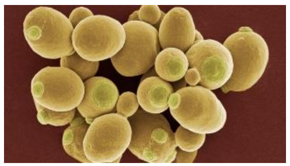
Predictions Arising from the Logistic Model Extended to Heterogeneous Space

Prediction 1: A population in a spatially heterogeneous environment (K_is and r_is differ) can reach a higher (or lower) steady state size when it diffuses than when it does not.

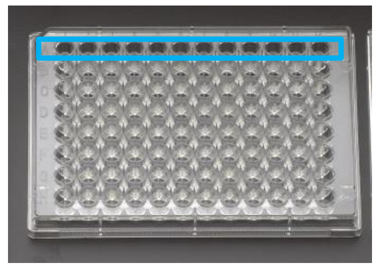
Prediction 2: A convex positive relationship of growth rate and carrying capacity is associated with the population reaching a higher level.

Prediction 3: If $K_1 + K_2$ is kept the same in both a homogeneous and heterogeneous two-patch case, a diffusing population can reach a higher size in the heterogeneous than in the homogeneous case.

Experimental testing using yeast



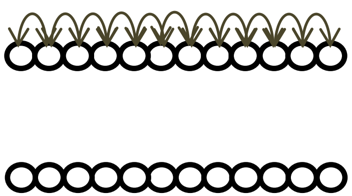
Yeast



1 row (12 wells) = 1 meta-population

To manipulate the correlation of r and K

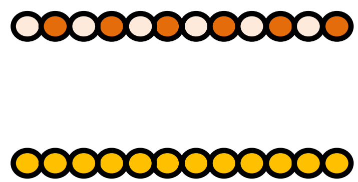
Movement



Non-movement

×

Heterogeneous environment



Homogeneous environment

×

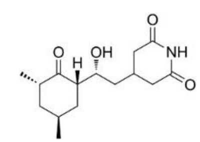
0 nM

50 nM

200 nM

400 nM

Growth inhibiting antibiotic (Cycloheximide)

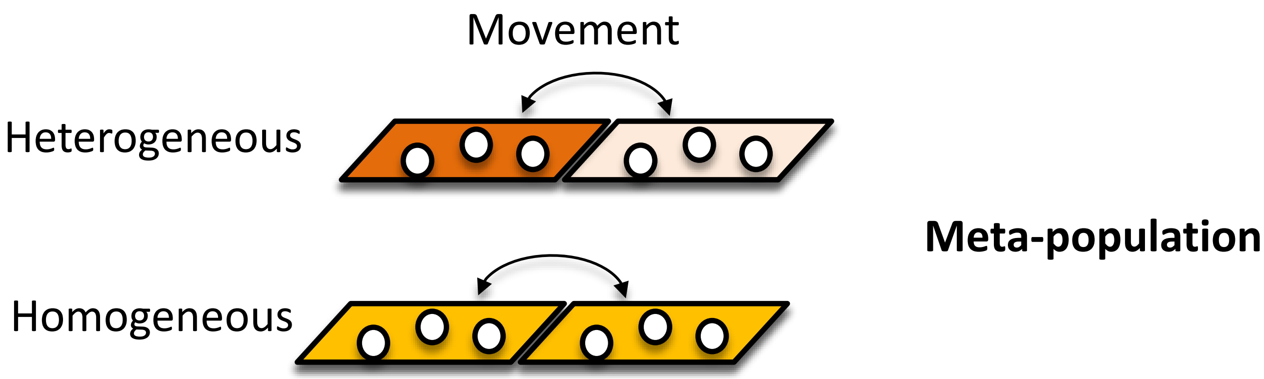


Limiting nutrient tryptophan

Full factorial design with 4 replicates.

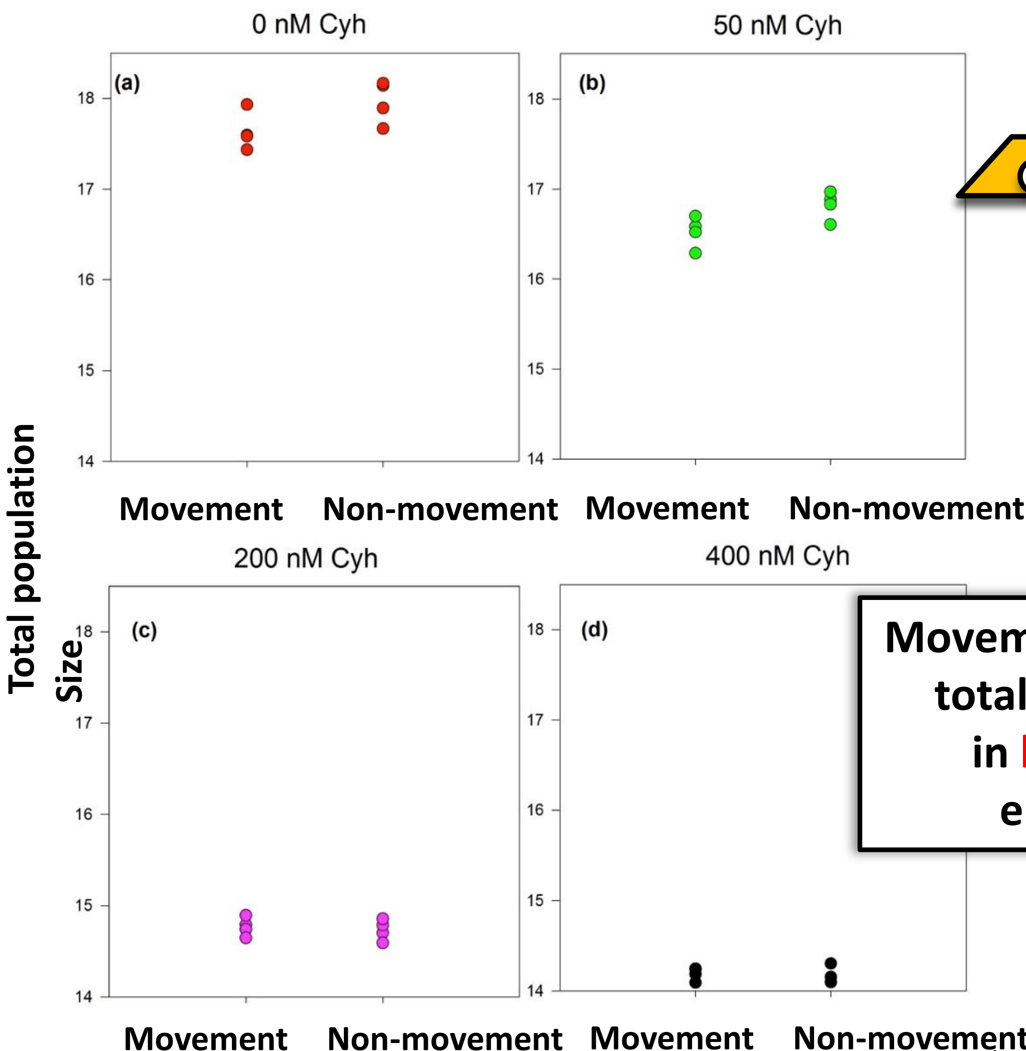
Zhang et al *Ecology letters* 20, no. 9 (2017): 1118-1128.

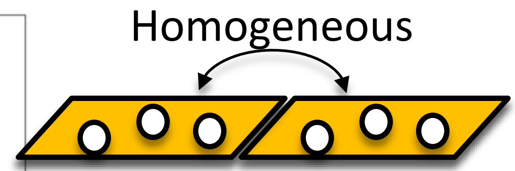
Patch population dynamics (Single species)



Different predictions can be tested by varying both the heterogeneity of the patch system and varying the movement rate between patches.

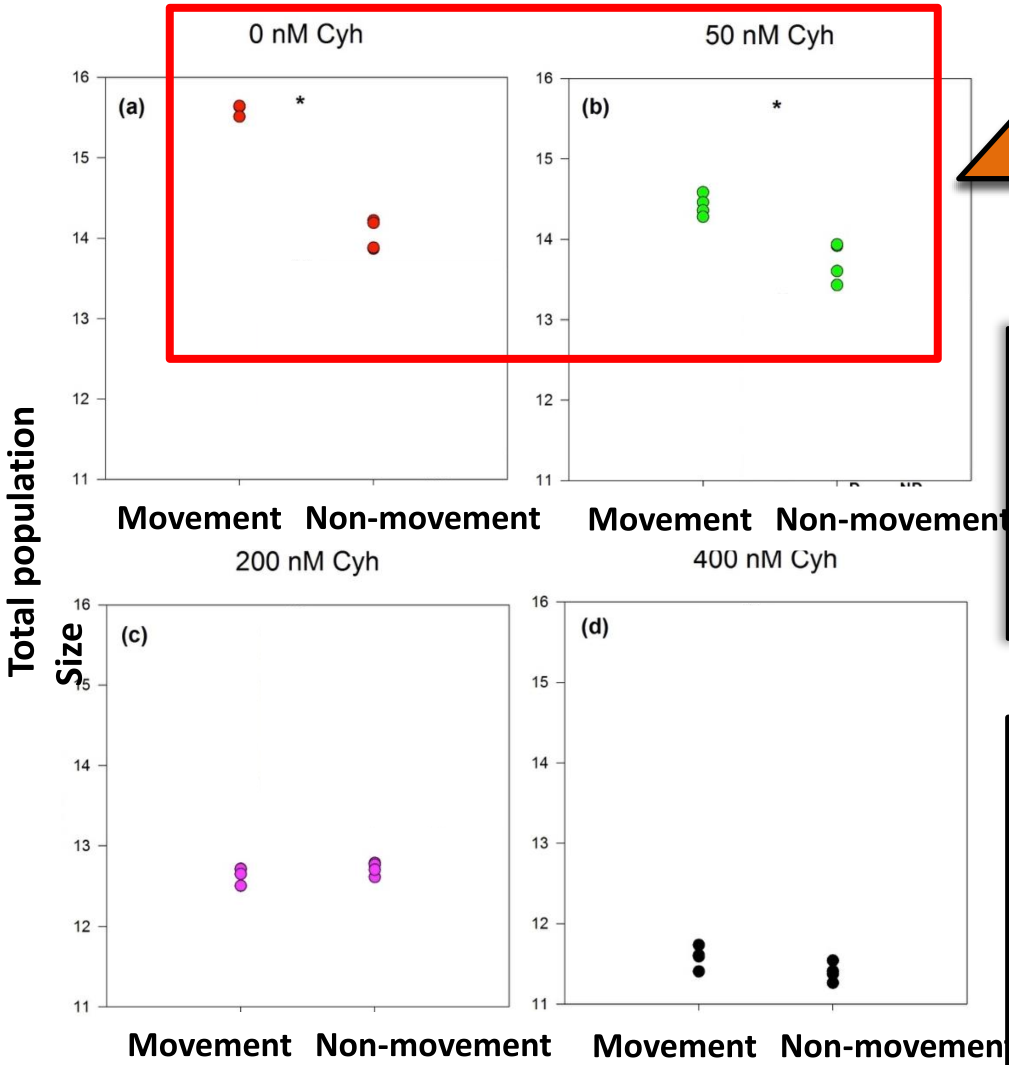
Four different levels of growth inhibitor Cycloheximide

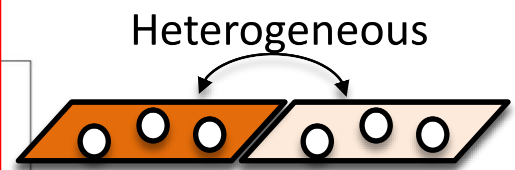




Movement does not alter total population size in homogeneous environments

Zhang et al. Ecology Letters 2017



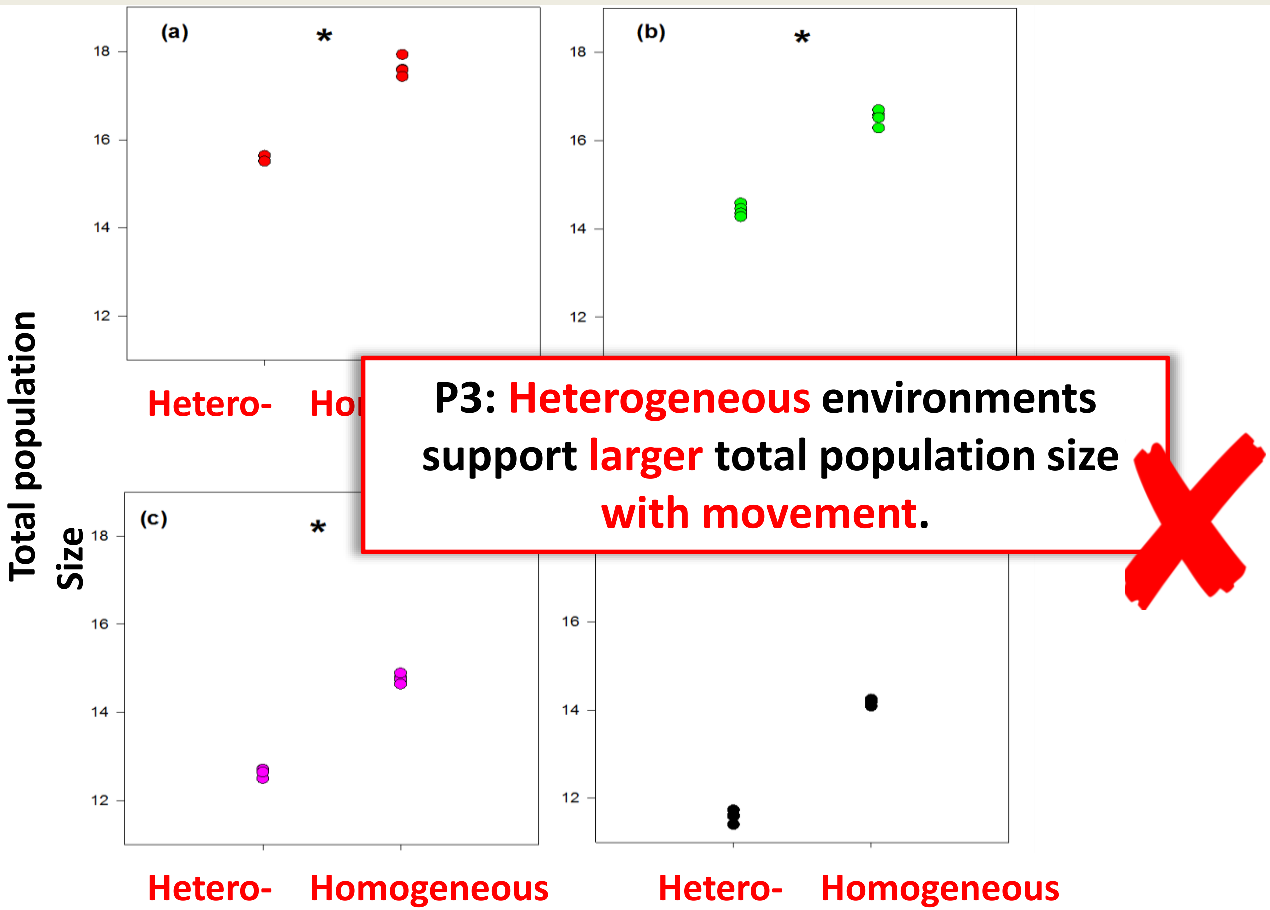


P1: Movement increases total population size in heterogeneous environments when *r* and *K* are positively correlated

P2: Characterized by a convex positive relationship of growth rate and carrying capacity (upper left is most convex, as Cyh is growth inhibitor)

Zhang et al. Ecology Letters 2017

Heterogeneity *VS.* Homogeneity



P3: Heterogeneous environments support larger total population size with movement.

Problem with Prediction 3

Prediction 3: The logistic model shows that keeping $K_1 + K_2$ is kept the same in both a homogeneous and heterogeneous two-patch case can lead to higher total biomass in the latter – if the values of r_1 and r_2 differ in appropriate ways.

However, in the experiment the nutrient input rate was kept the same between the homogeneous and heterogeneous systems, and, in that case, it can be proven that the homogeneously spread input rate will always lead to a higher total population.

Wang, Y. and DeAngelis, D.L., 2019.. *Theoretical Population Biology*, *125*, pp.30-37.

Consumer-Resource Model as a Basis for Theory

Limitations of Logistic Equation Models

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

– Wilkinson 2007

To include this feedback, population growth can be modeled using a mechanistic, bottom-up approach with a population of consumers utilizing variable resources.

But also, this allows both growth rate and carrying capacity to be determined from the more basic driver of resource (energy or limiting nutrient) input.

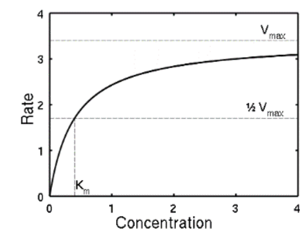
Consumer-Resource (Chemostat) Model

Consumer dynamics

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

- $\frac{dN_i}{dt}$: Change in consumer density
- $r_{max} N_i \left(\frac{S_i}{k + S_i} \right)$: Monod (non-linear) term
- mN_i: Density-independent mortality
- gN_i^2: Density-dependent mortality
- $D \left[\frac{N_{i+1}}{2} + \frac{N_{i-1}}{2} - N_i \right]$: Population Movement

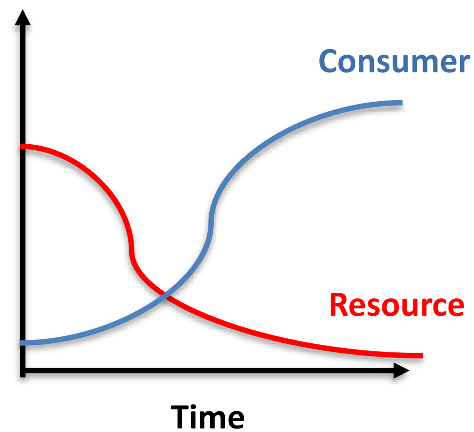
Monod curve



Resource dynamics

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

- $\frac{dS_i}{dt}$: Change in resource density
- $S_{IN,i}$: Input
- δS_i: Dilution/ death
- $\frac{1}{\gamma} r_{max} N_i \left(\frac{S_i}{k + S_i} \right)$: Consumption by consumer species

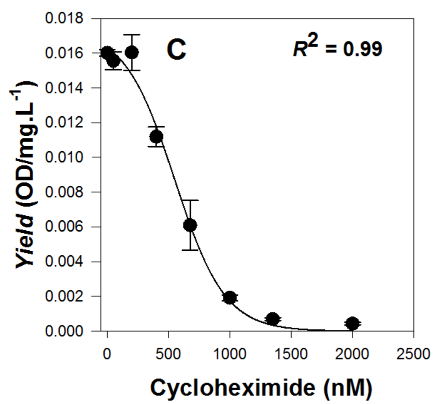


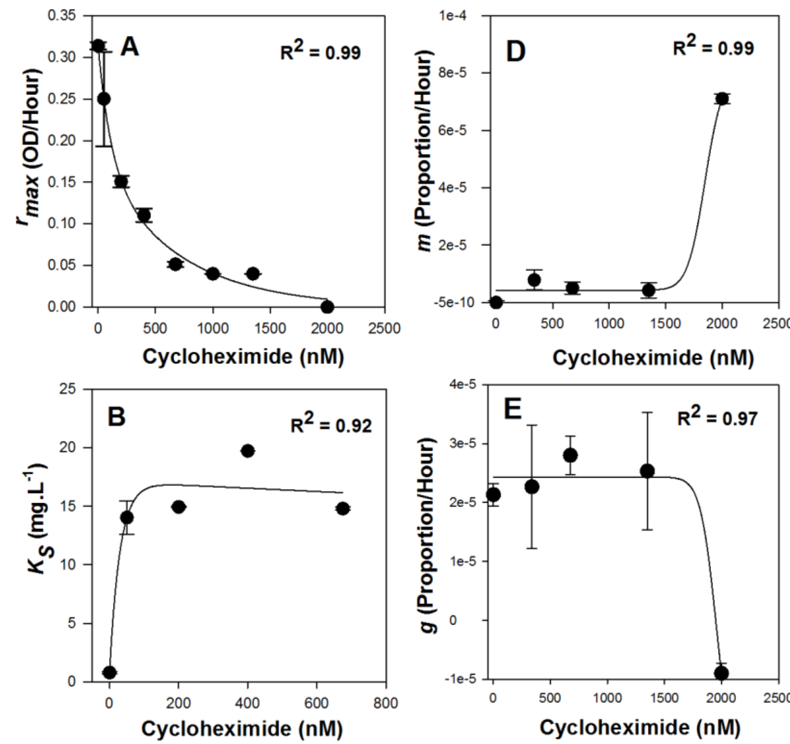
Tilman *Resource Competition and Community Structure* 1982

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

Interpretation of Experiments Based on Consumer-Resource Model

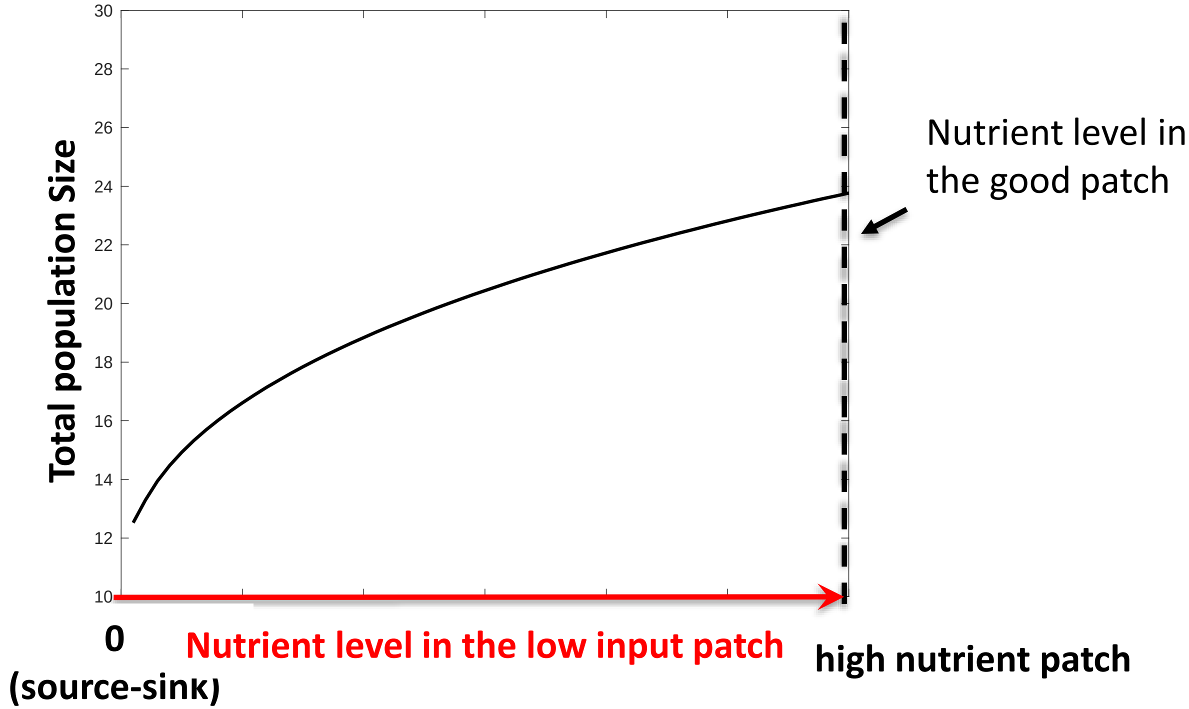
Assume two patches, with different nutrient input rates; a ‘high input’ patch and a ‘low input’ patch.

Using simulations, we compared three situations across values of nutrient input in the low input patch.

The simulations showed the following

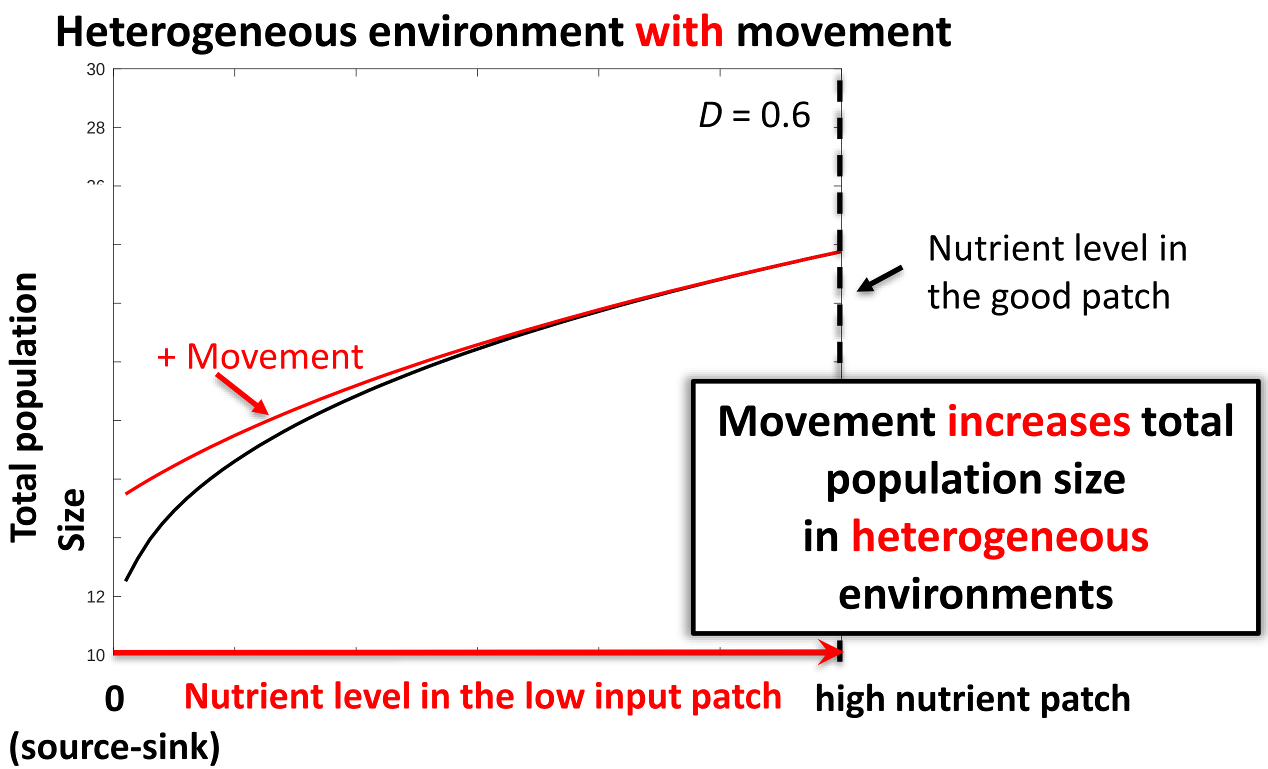
Predictions Based on the Consumer-Resource Model for Two Patches with Different Nutrient Inputs

Heterogeneous environment without movement



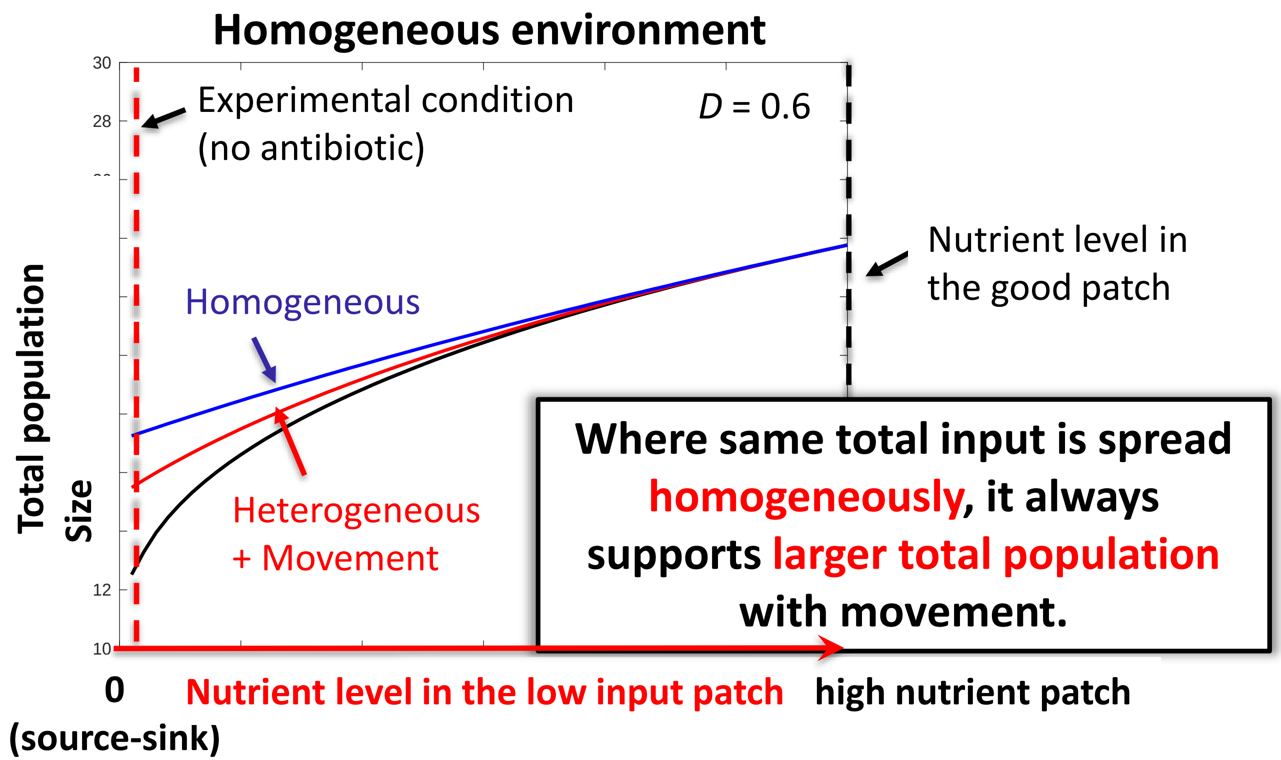
Zhang et al. Ecology Letters 2017

Predictions based on the Consumer-Resource model



Zhang et al. Ecology Letters 2017

Predictions based on the Consumer-Resource model

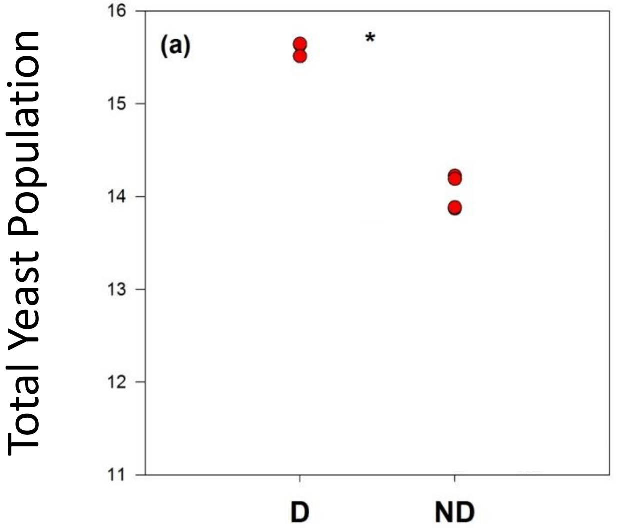


Zhang et al. Ecology Letters 2017

Experimental Tests

Test of Prediction 1

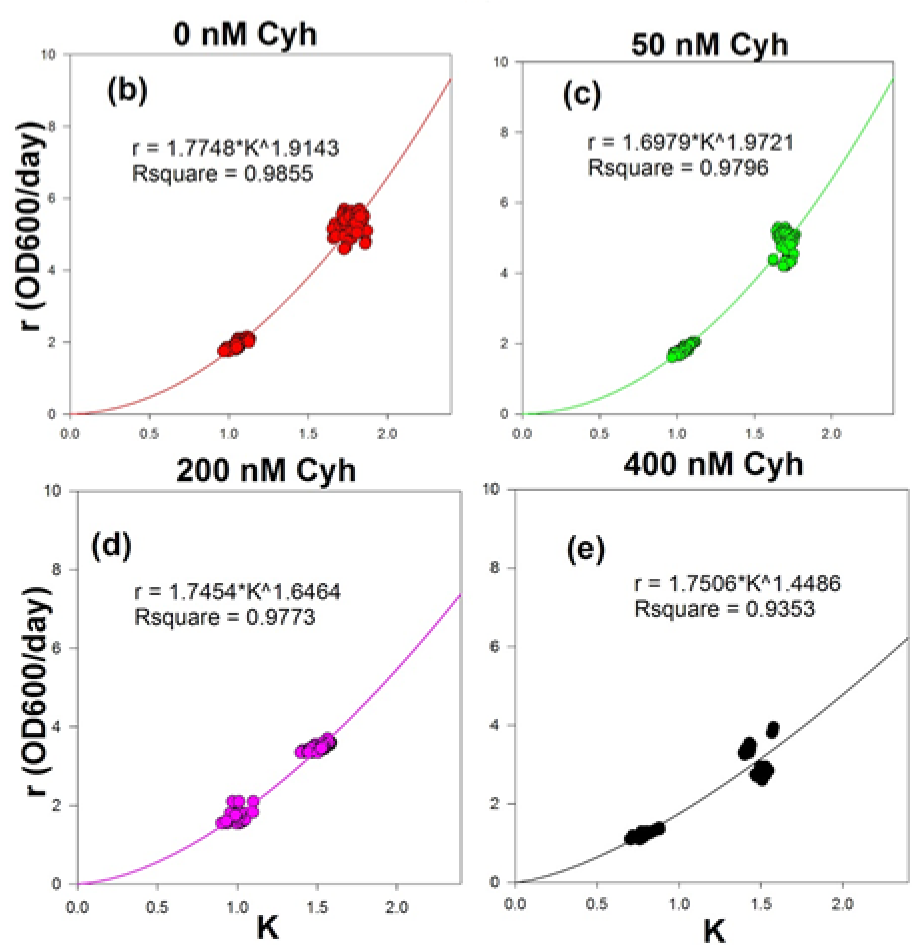
Prediction 1: When a consumer exists in a spatial region with a heterogeneously distributed input of exploitable limiting resource, the steady state population can reach a greater size when it diffuses than when it does not.



Total Pop$_D$ > Total Pop$_{ND}$

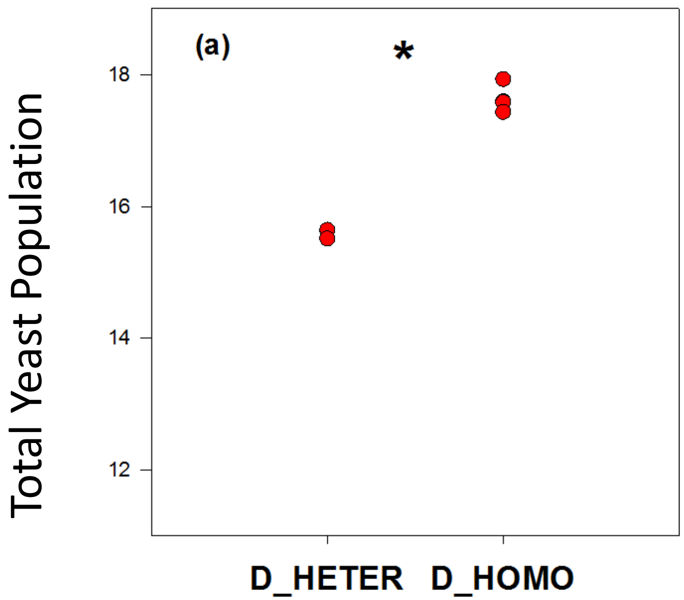
Test of Prediction 2

Prediction 2: The higher population in a heterogeneous environment with diffusion is characterized by a convex positive relationship of growth rate and carrying capacity.



Test of Prediction 3

Prediction 3: A consumer population diffusing in a spatial region with a homogeneously distributed input of exploitable limiting resource can reach a greater steady state size than a population diffusing (or not) in the spatial region with the same total input of resources spread heterogeneously.



Total $Pop_{D,Het.} < TotalPop_{D,Hom}$

Logistic Model with Carrying Capacity K
vs.
Consumer-Resource Model with Resource Input Rate

In the Pearl-Verhulst logistic model implicitly carrying capacity is a fundamental quantity.

In the Consumer-Resource model input rate (energy or nutrient) fundamental. This is consistent with literature arguing ‘power’ to be the fundamental quantity in ecology

Power as a Fundamental Quantity

“Metabolism provides a basis for using first principles of physics, chemistry, and biology to link the biology of individual organisms to the ecology of populations, communities, and ecosystems.”

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. and West, G.B., 2004. Toward a metabolic theory of ecology. Ecology, 85(7), pp.1771-1789.

Lotka’s maximum power principle restated: “Given N systems interacting both among themselves and with a common environment ....the systems that shall prevail … are those capable of tapping the highest possible amount of such exergy surplus … in accordance with the three Laws of Thermodynamics"

Sciubba, E., 2011. What did Lotka really say? A critical reassessment of the “maximum power principle”. Ecological Modelling, 222(8), pp.1347-1353.

“Energy is the currency of economic exchange and value, but power – the rate at which energy and raw materials are used – is the measure of economic performance”

Vermeij, G.J., 2009. Nature: an economic history. Princeton University Press.

Conclusions and Future Work

Conclusions

In the Logistic model, *K*, *r*, and *D* are all involved in total population size in heterogeneous space.

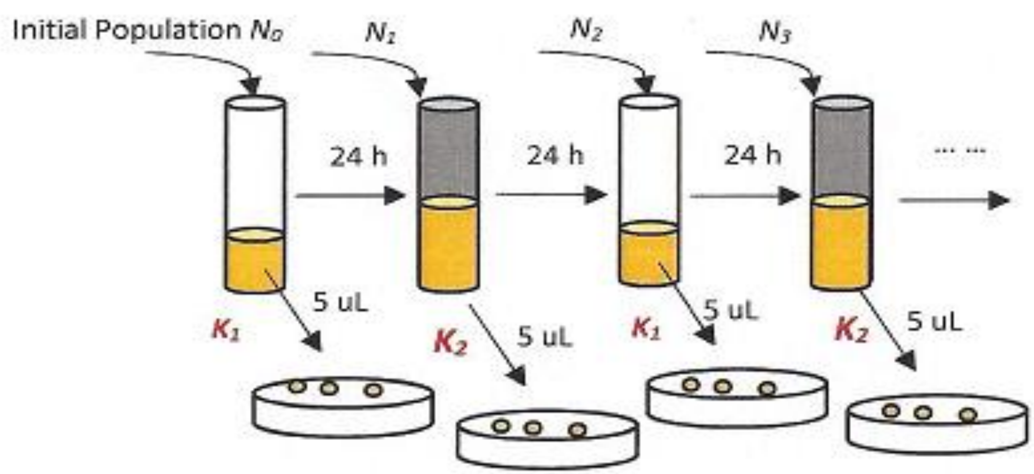
In the Logistic model, K, r. and time period T are all involved in measures of population size in a time-periodic environment.

These two situations are strongly analogy

The consumer-resource (or chemostat) model may be a better tool for studying populations in heterogeneous space, as power is a fundamental property.

Carrying capacity is emergent property of ecological systems.

Future work will include testing the effects of a periodically temporally varying environment on average population size over the period. Also using consumer-resource theory.



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Thanks! Questions?