Patterns of abundances in niche models

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ICTP (Trieste) 24/10/2010

Competition

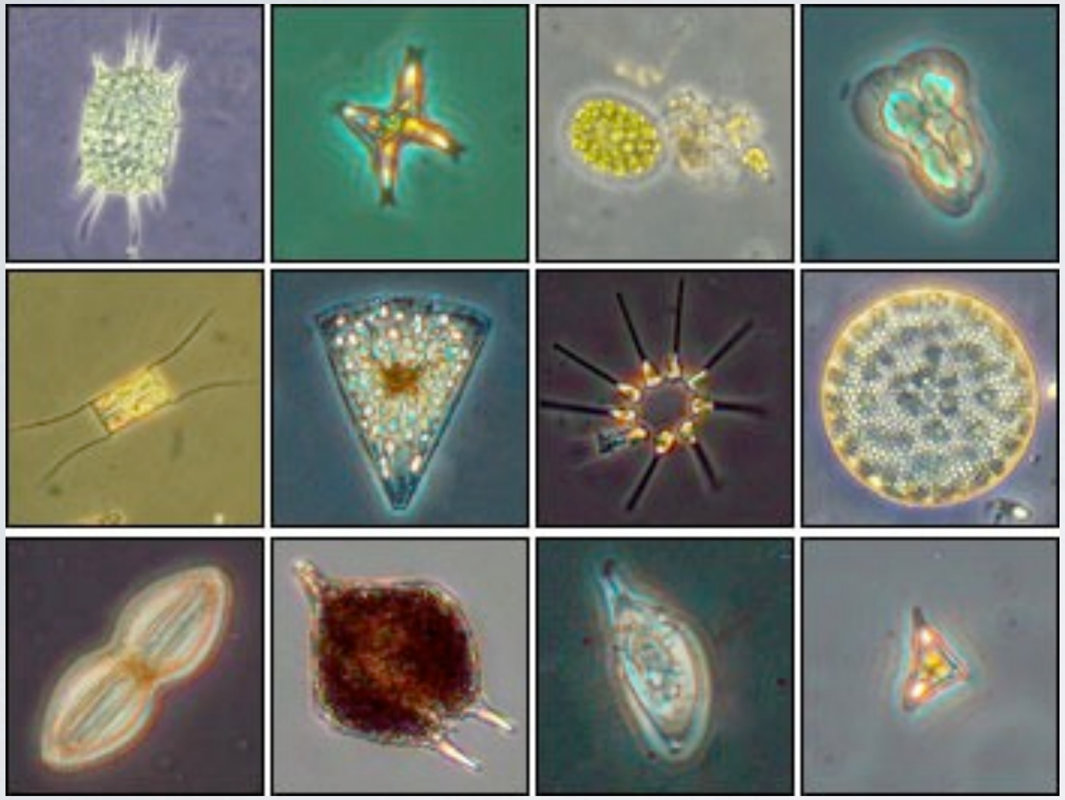
from: www.alexanderwild.com

for: preys, nutrients, space

Outline

- trait-based competition
- neutral theory in space

Competition, diversity, exclusion



from: Smithsonian Environmental Research Lab

classical result:

$$N_{competitors} \leq N_{resources}$$

Plankton Paradox (Hutchinson Am. Nat. 1961)

many ways out: shared predators, time dependence, space, flows, food webs, neutrality

this lecture: what if resources are continuous?
(food of different size)

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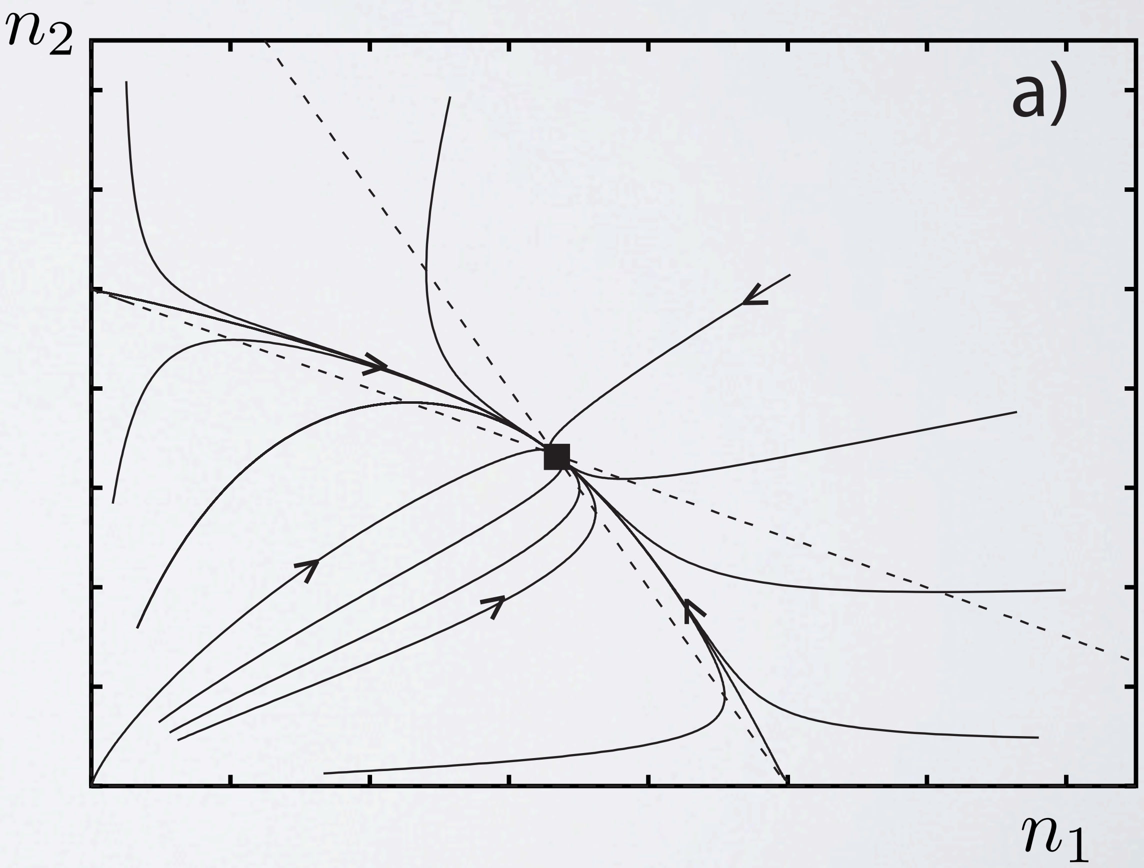
Basic model: 2 species

competitive Lotka-Volterra system:

$$\begin{aligned}\frac{d}{dt}n_1 &= n_1(r_1 - a_{11}n_1 - a_{12}n_2)\\ \frac{d}{dt}n_2 &= n_2(r_2 - a_{21}n_1 - a_{22}n_2)\end{aligned}$$



unique coexistence fixed point, stable if:

$$a_{12}/a_{22} < r_1/r_2 < a_{11}/a_{21}$$

intraspecific > interspecific

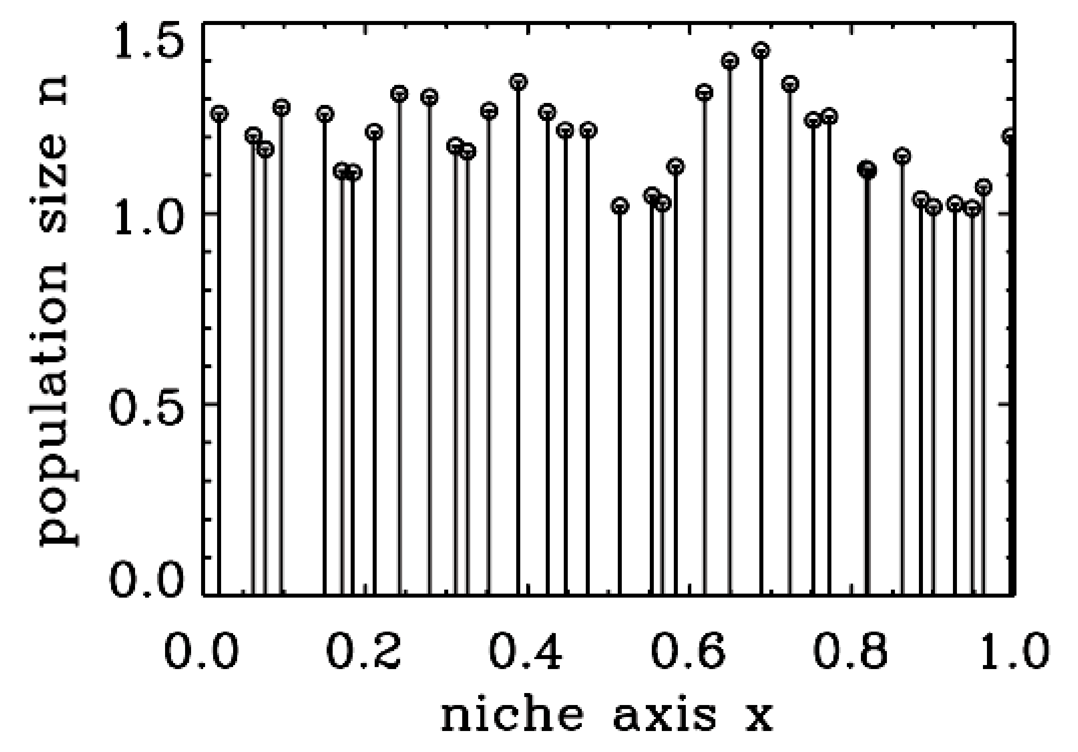
Basic model: many species

$$\frac{d}{dt}n_i \quad = \quad n_i\left(r_i - \sum_j a_{ij}n_j\right) \qquad i,j = 1\ldots N$$

- also in this case: unique fixed point
- stable if eigenvalues of matrix are positive
- too many parameters: N x (N+1)
- how does competition depend on traits?

Niche model

$$\frac{d}{dt}n_i \quad = \quad n_i \left(r(x_i) - \sum_j a(|x_i - x_j|) n_j \right) \qquad i,j = 1 \ldots N$$



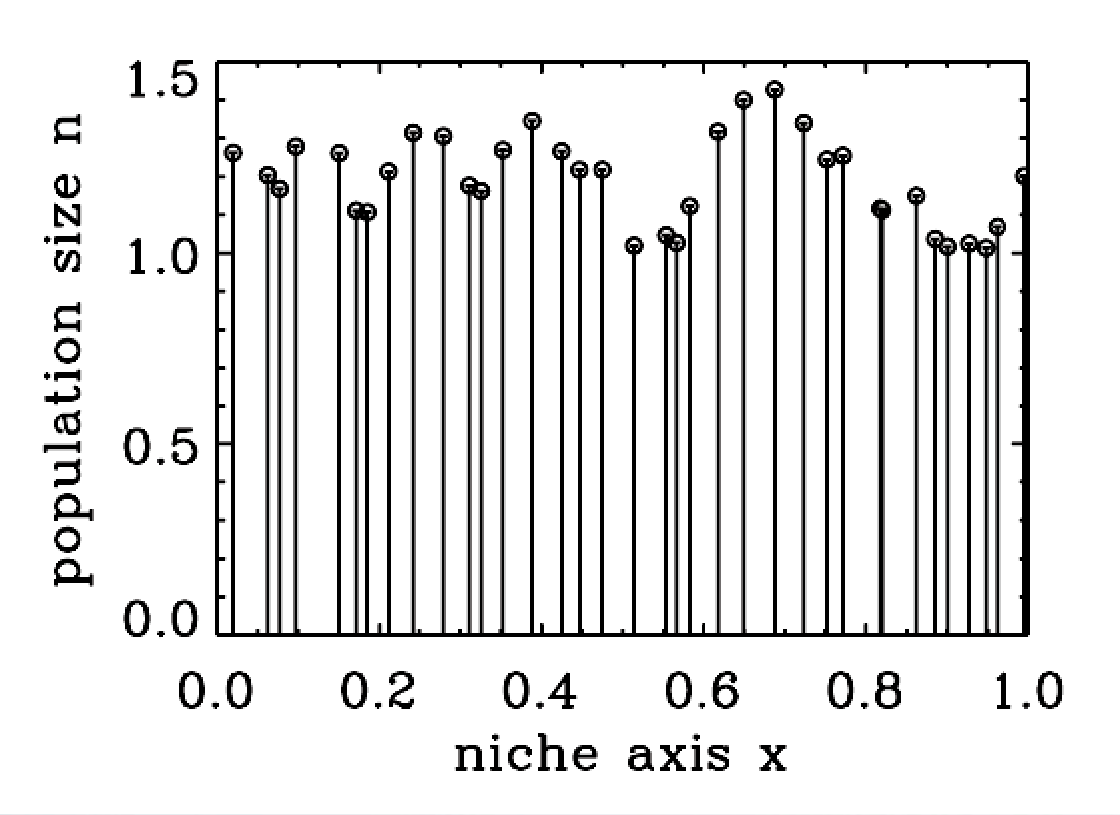
- species are characterized by trait x (body mass, beak size etc)

- growth depend on trait

- competition intensity decays with increasing trait difference

Niche model - protocols

$$\frac{d}{dt}n_i \quad = \quad n_i \left(r(x_i) - \sum_j a(|x_i - x_j|) n_j \right) \qquad i,j = 1 \dots N$$



- fixed number of species (regular/irregular spacing)

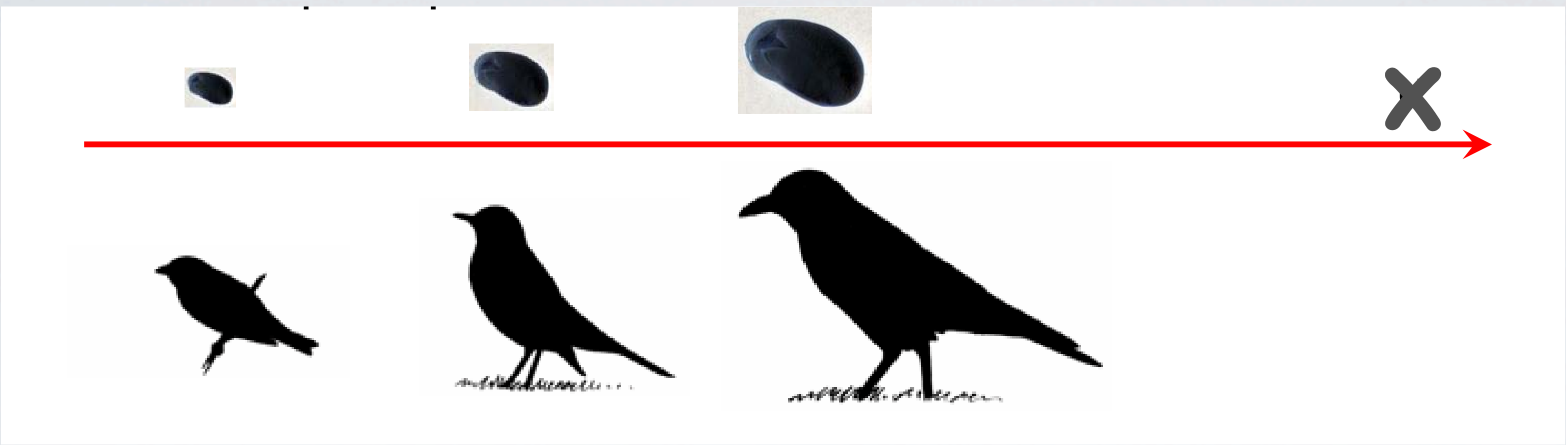
- assembly (random rare invasion)

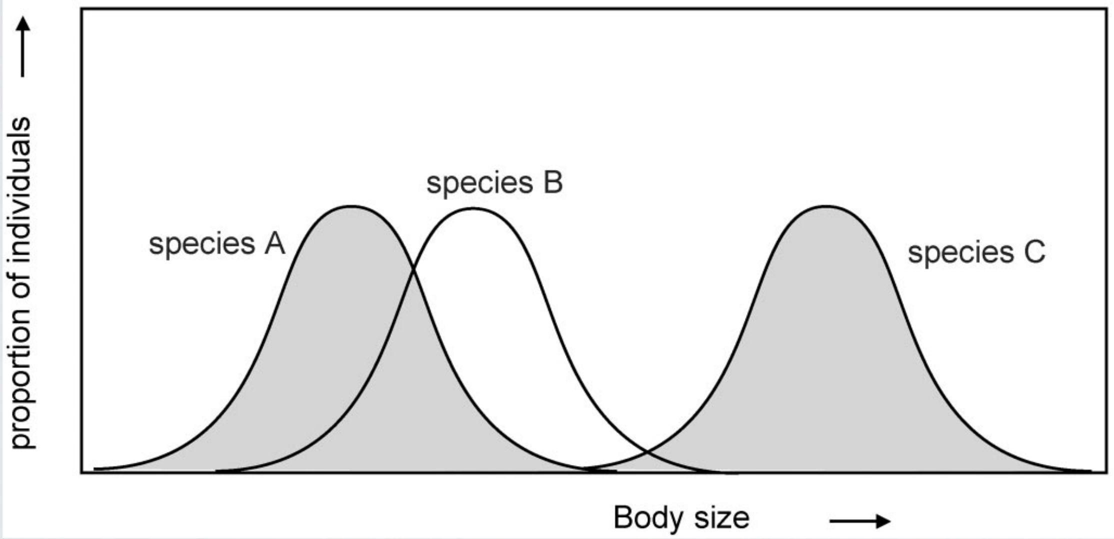
- mutation (diffusion in niche axis)

- extinction threshold

Multiple solution -> the answer depends on the question
(invasibility vs stability of the "diverse" state)

Wait a minute: where are the resources?





- to each trait value x correspond a distribution of preferred resources -> utilization function

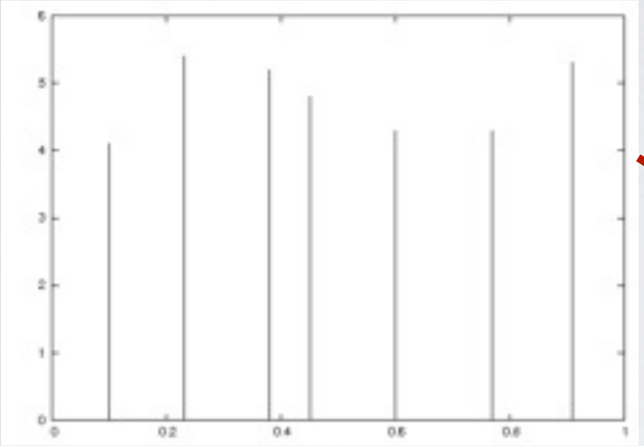
- competition intensity is proportional to the overlap of the utilization functions

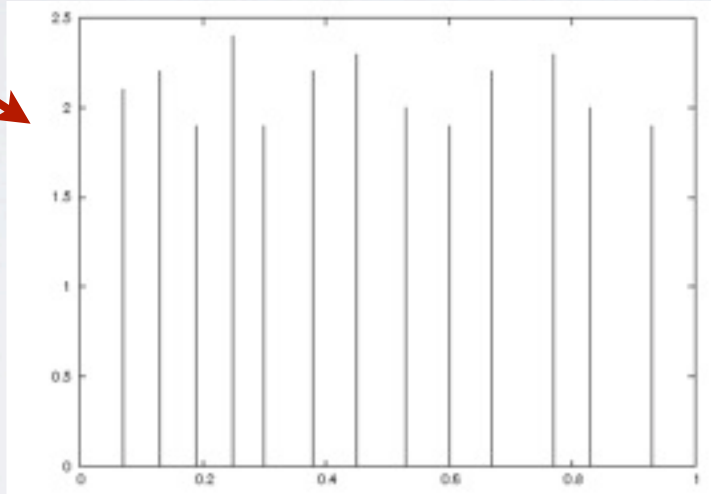
- two different interpretations: distribution of traits or distribution of preferences

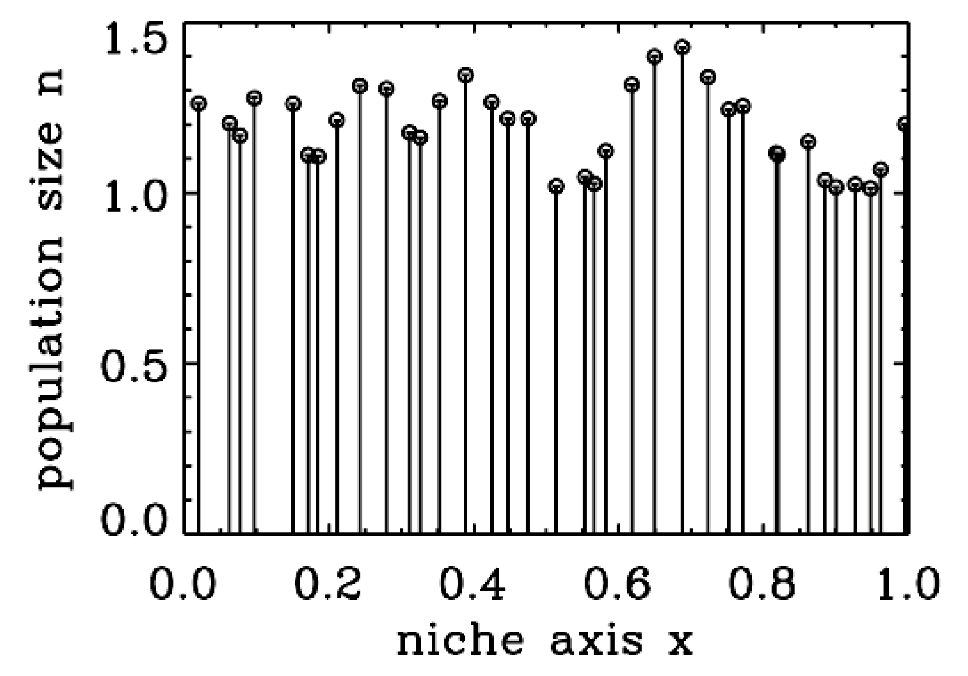
- popular assumption: everything is Gaussian

Limiting similarity

$$\frac{d}{dt}n_i = n_i\left(r - \sum_j a(|x_i - x_j|)n_j\right) \qquad i,j = 1\dots N$$







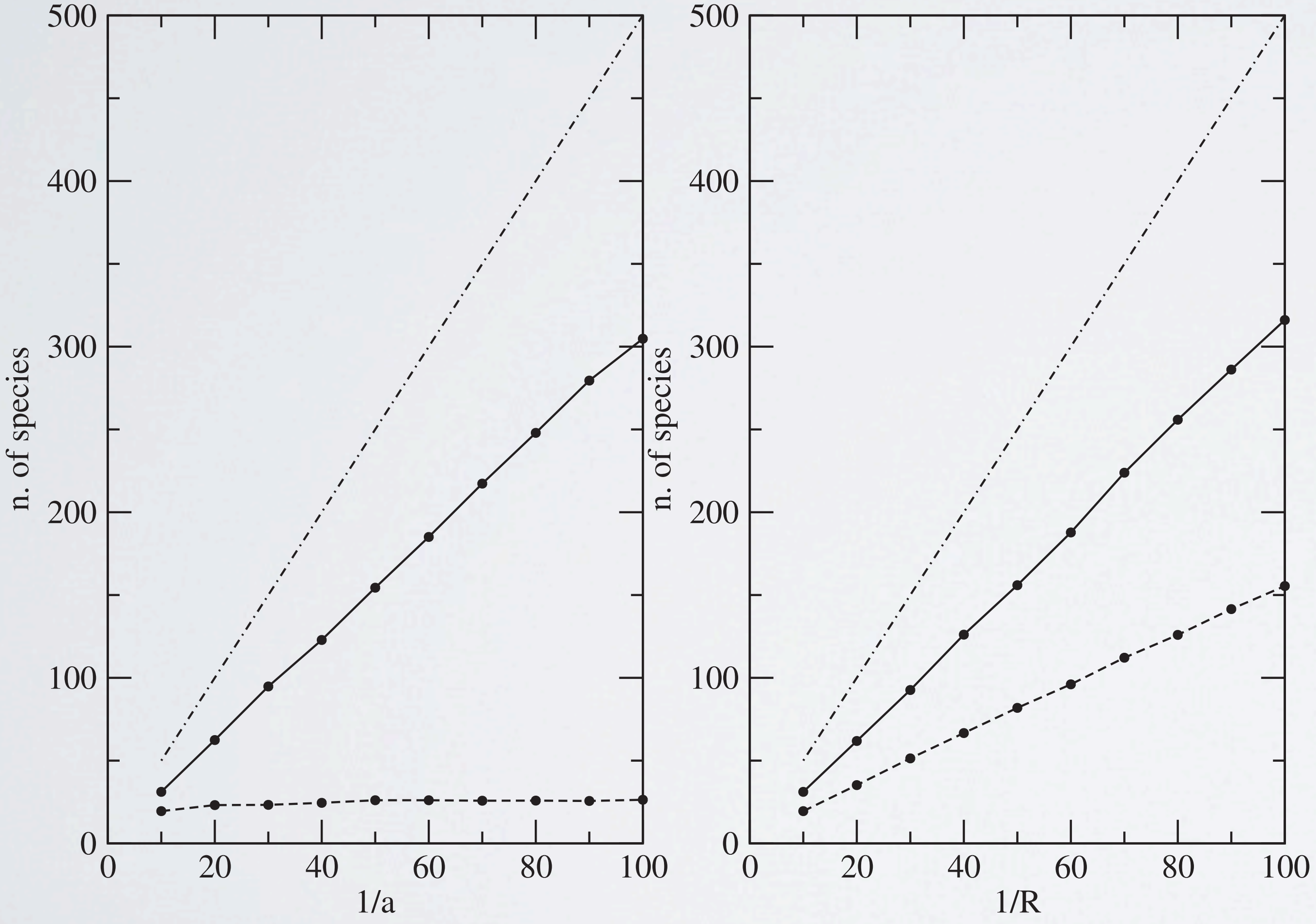
- in this model, competition does not set a limit to similarity

- threshold and/or diversity will result in limiting similarity

Invasibility vs Coexistence

Limiting similarity

$$\frac{d}{dt}n_i = n_i\left(r - \sum_j a(|x_i - x_j|)n_j\right) \qquad i,j = 1\ldots N$$

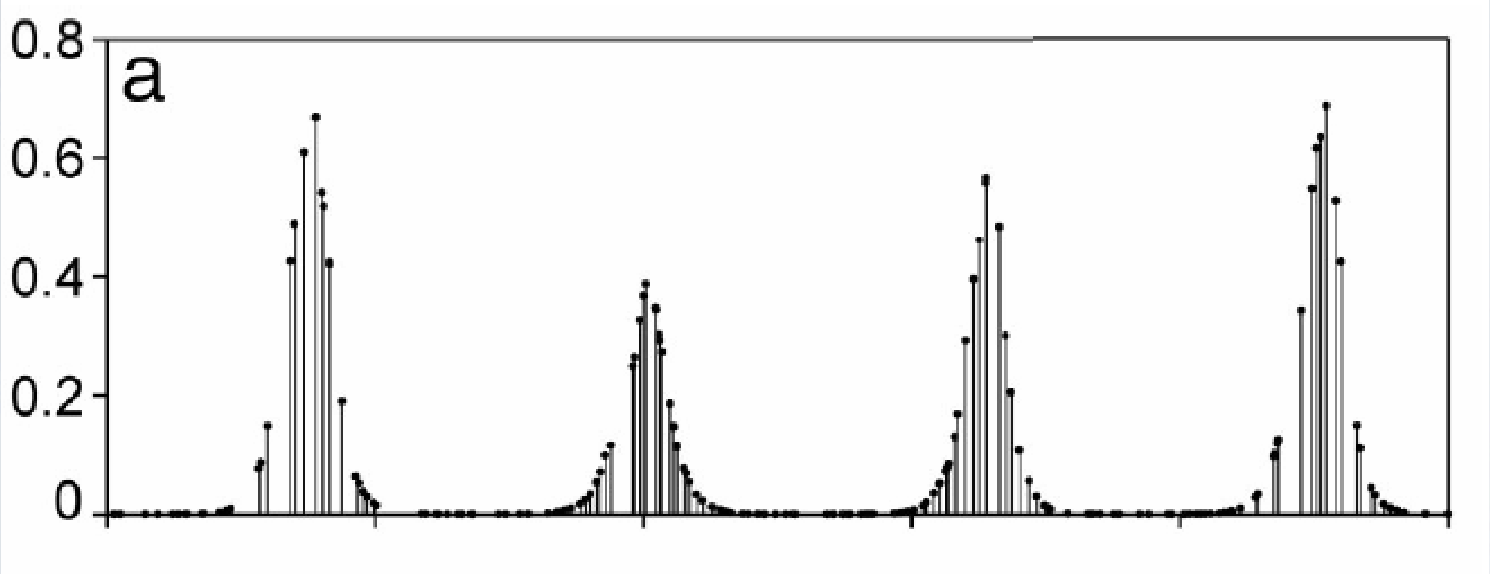


a(x)=a exp(-x/L), threshold=1

left: varying a, L=0.1
right: varying L, a=0.1

continuous: no heterogeneity
dashed: 10% heterogeneity
dot-dashed: upper bound

Clumps in niche models

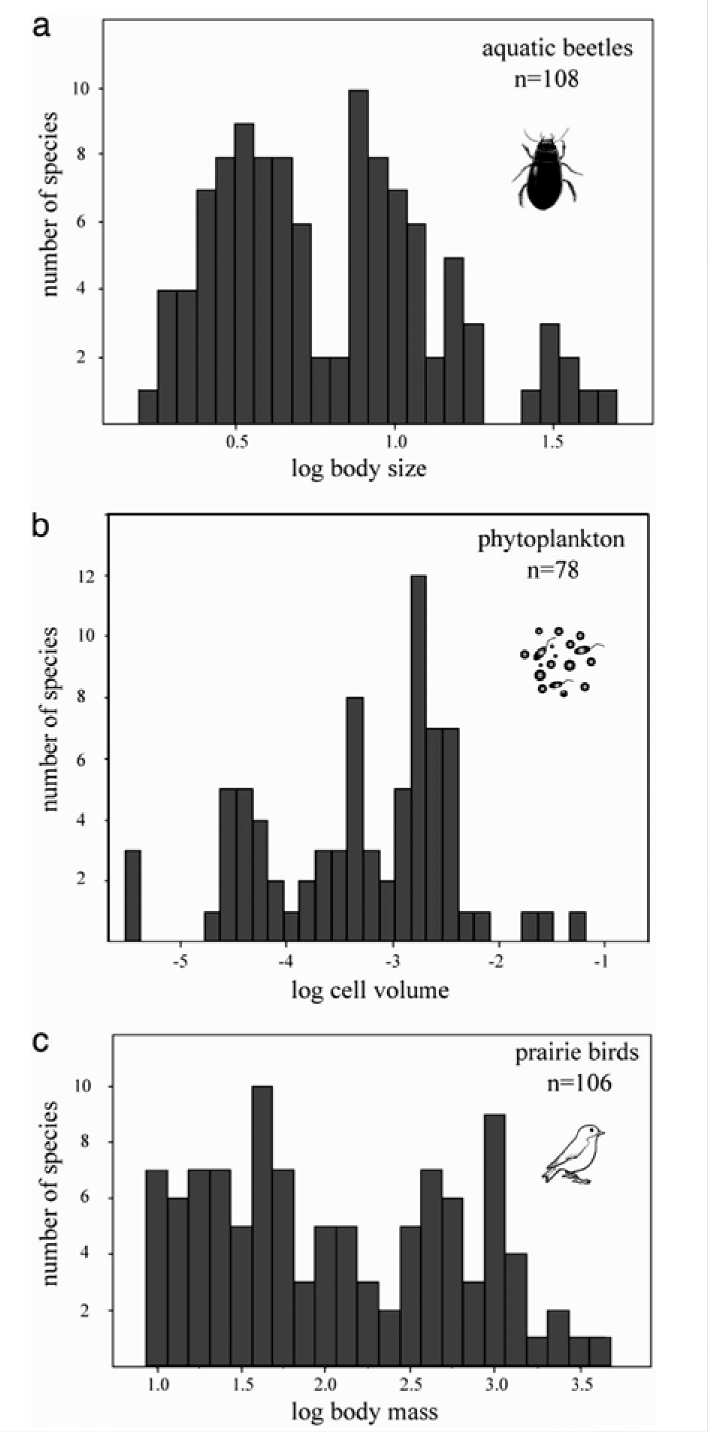


from: Scheffer and Van Nes (2005)

$$G(x) = a \exp\left(-X^2/L^2\right)$$

for large L (0.2 ~ 0.3) and periodic boundary condition, clumps of species separated by exclusion zones

clumps shrink to single peaks (over long times) and are stable if intraspecific competition is enhanced



From species to distributions

$$\frac{d}{dt}n_i = n_i\left(r(x_i) - \sum_j a(|x_i - x_j|)n_j\right) \qquad i,j = 1 \dots N$$

$n(x,t)$ density of individuals at trait x and time t

$$\partial_t n(x,t) = n(x,t)\left[r(x) + a\int G(|x-y|)n(y,t)\right]$$

G(x) kernel function, $\int G(x)dx = 1$

if growth rate constant r(x)=r then homogeneous solution n(x,t) = r/a

stability of homogeneous state

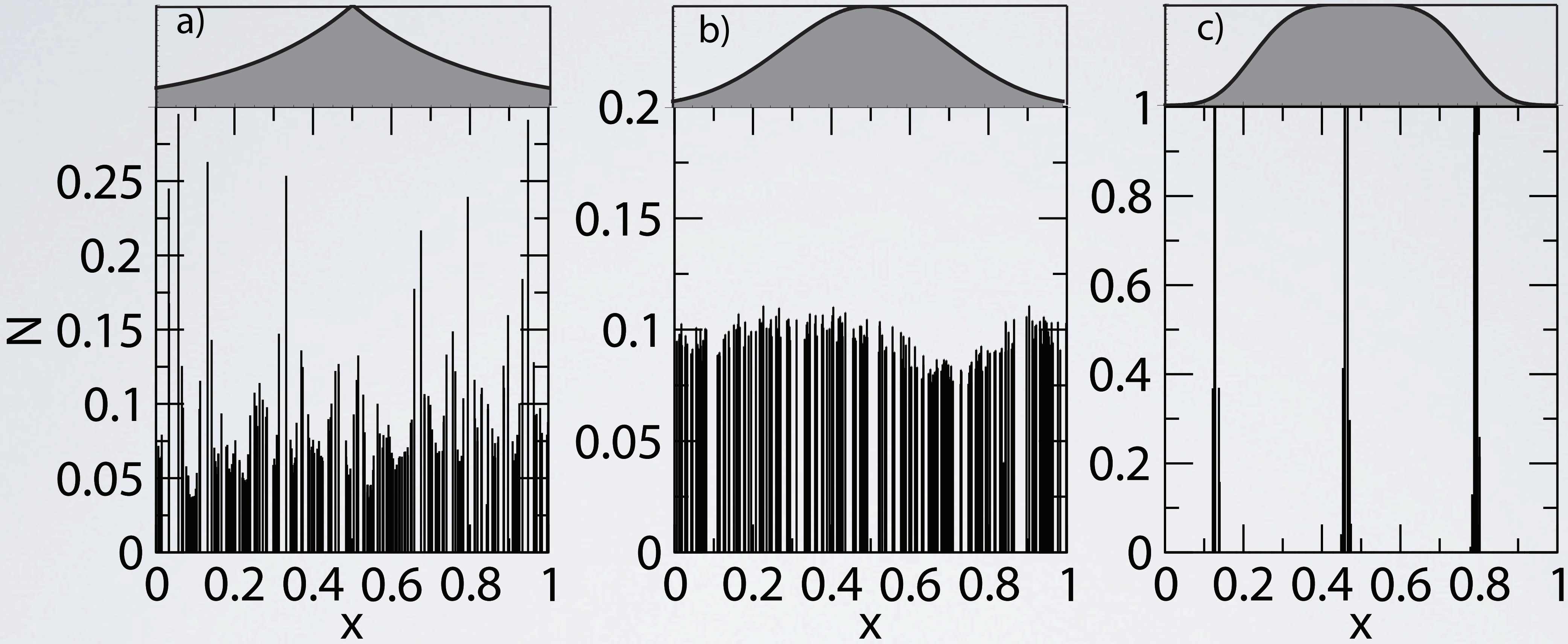
$$\partial_t n(x,t) = n(x,t) \left[r + a \int dy \; G(|x-y|) \; n(y,t) \right]$$

$n(x,t) = r/a$ **stable when:** $\tilde{G}(k) = \int \exp(ikx) G(x) > 0 \qquad \forall k$

- which competition functions satisfy this condition?

Pigolotti, Lopez, Hernandez-Garcia, Phys. Rev. Lett. (2007)

Playing with G(x)

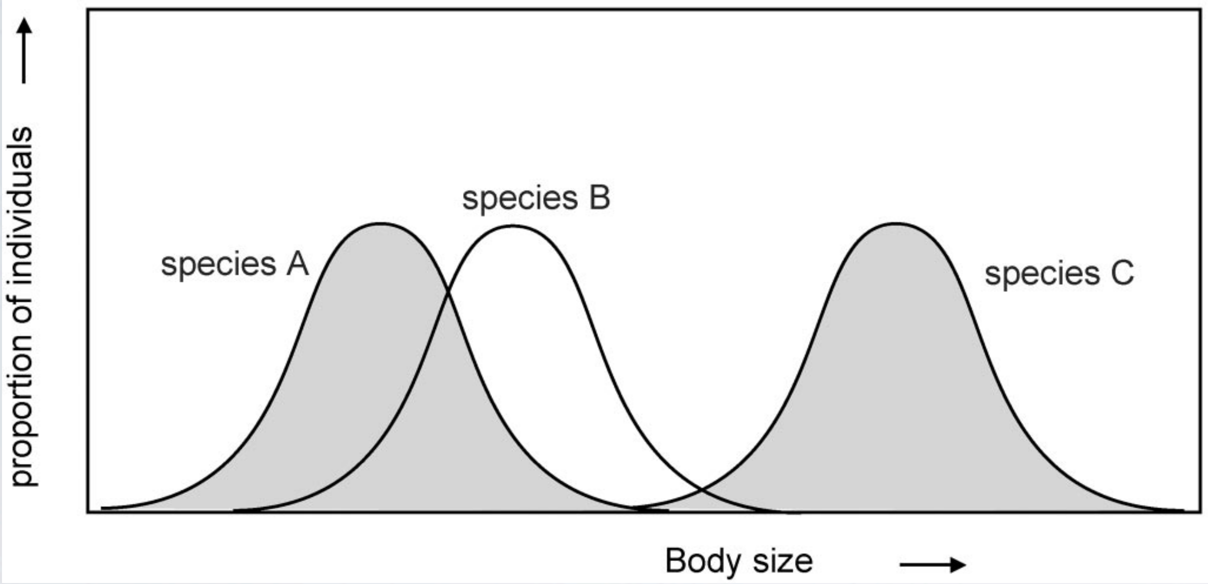


a) Exponential b) Gaussian c) Quartic

general family of kernels: $G(x) = \exp[-(x/L)^\sigma]$

stable when $\sigma \leq 2$ Gaussian is borderline!

utilization functions -> no clumps



any competition function constructed as an overlap:

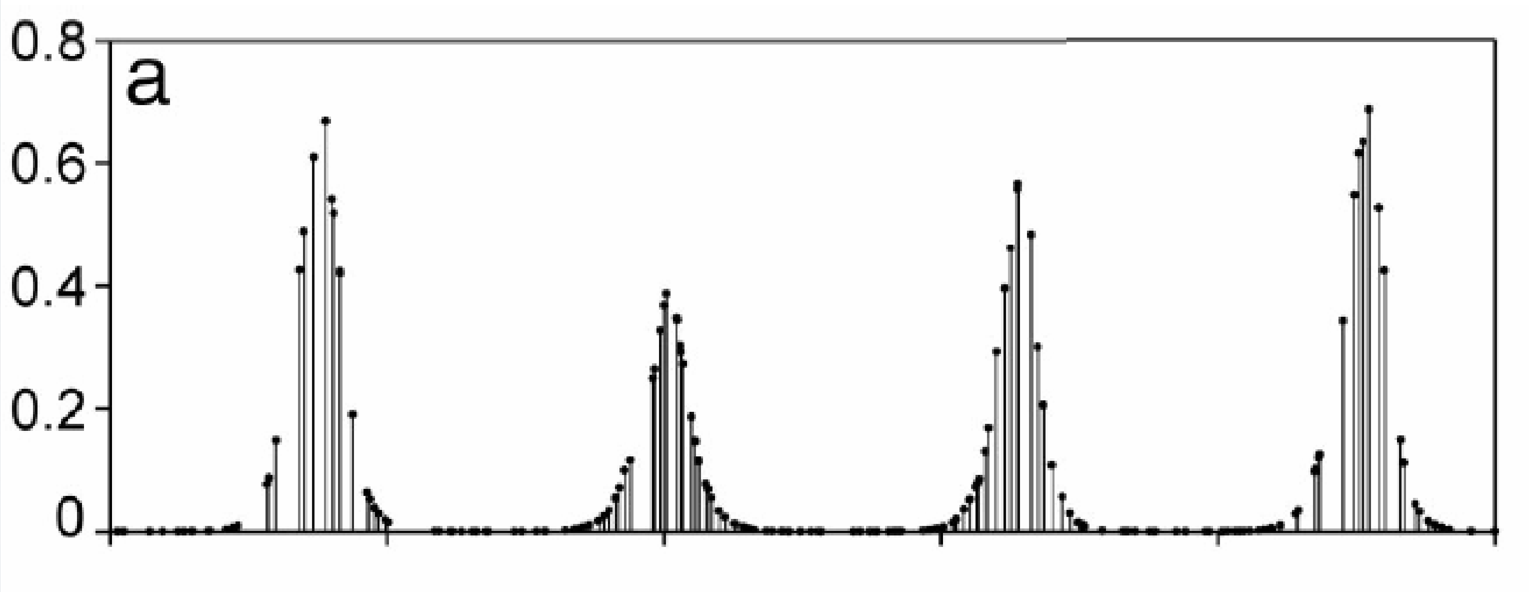
$$G(x-y) \propto \int u(x-z)u(y-z)dz$$

never leads to clumps (Roughgarden 1979)

- one can construct more general utilization function (e.g. depending on trait) resulting in unstable kernels

$$G(x-y) \propto \int u(x,z)u(y,z)dz$$

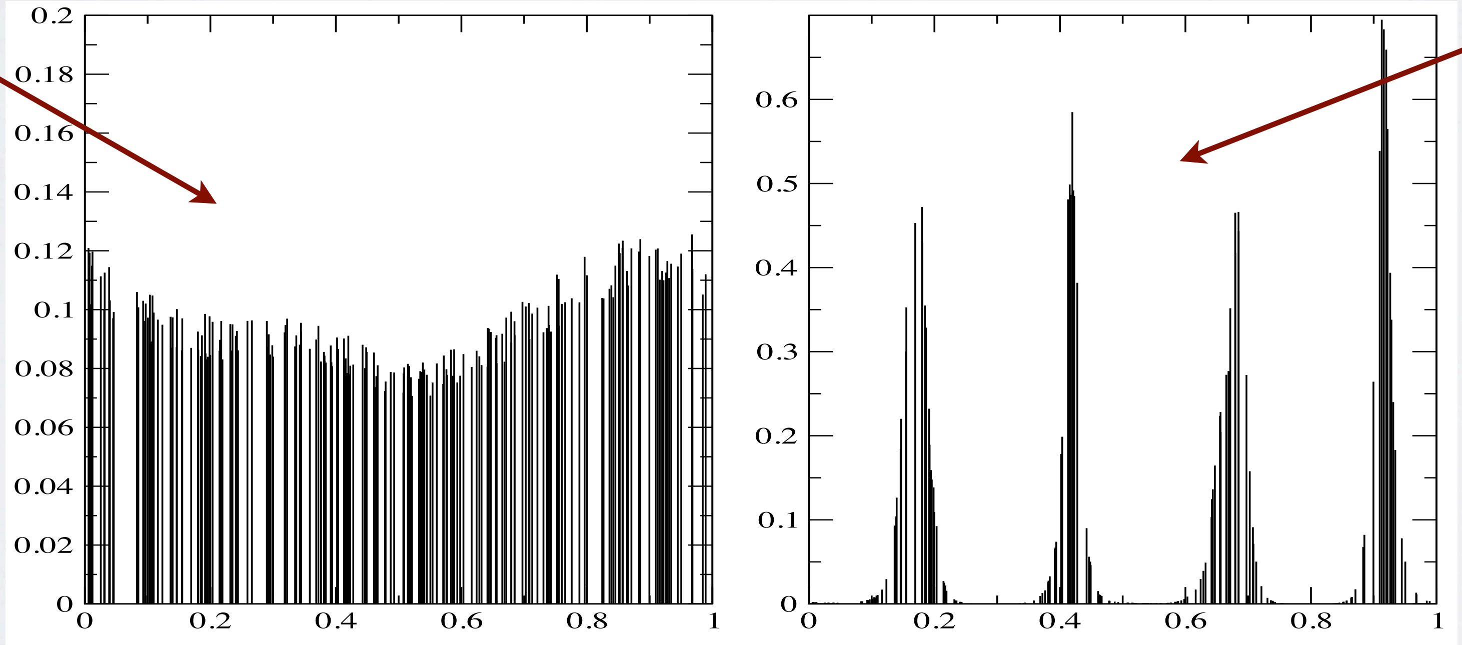
The clumps revisited



Gaussian is marginal, role of boundary condition

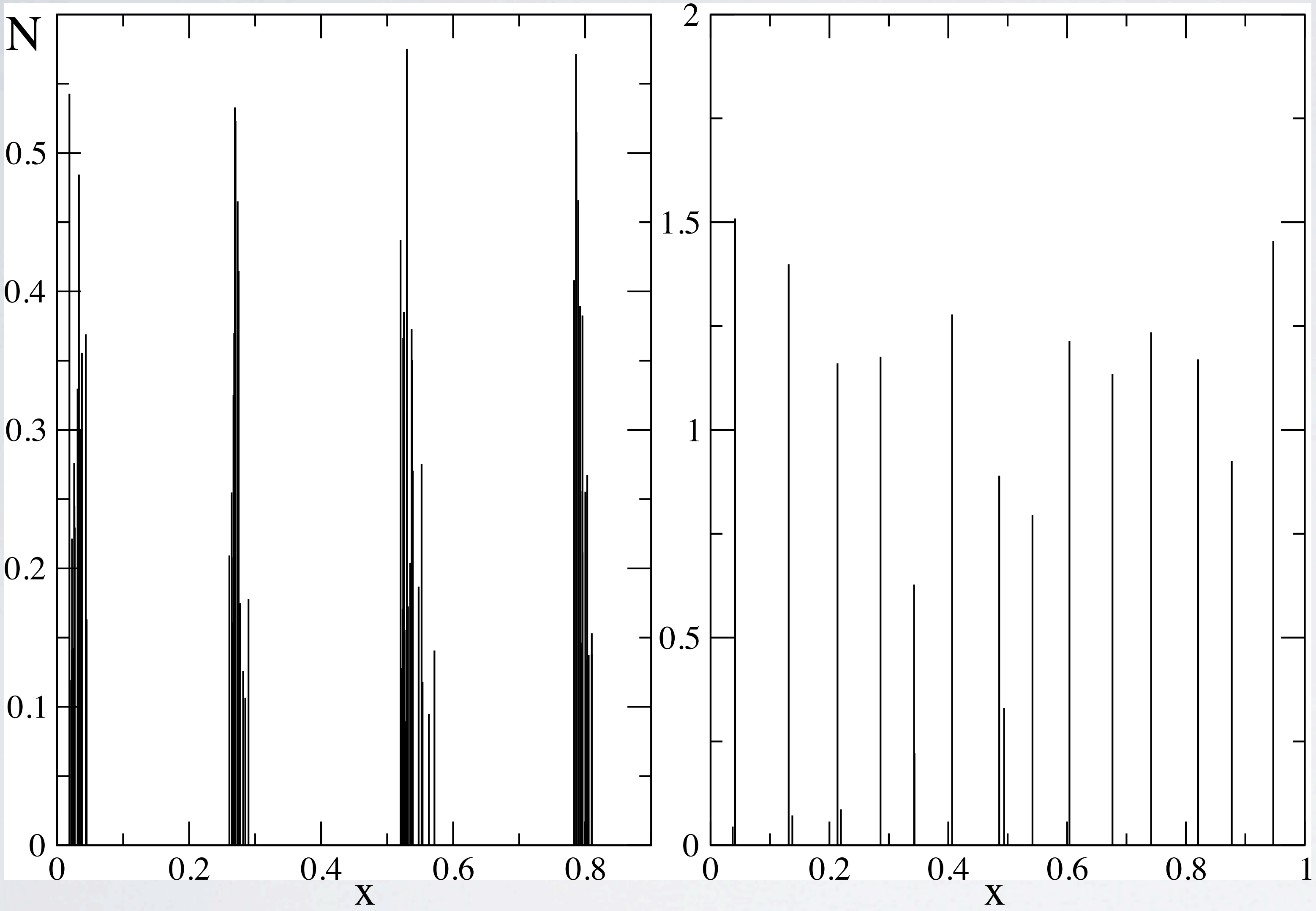
no truncation

truncation



Pigolotti, Lopez, Hernandez-Garcia, Andersen, Theo. Ecol. (2010)

Gaussian + evolution



- species with small population go extinct

- new species are placed close to existing ones

left: Gaussian, right: Exponential

Pigolotti, Lopez, Hernandez-Garcia, Andersen, Theo. Ecol. (2010)

Take home message

- The good side:

Gaussian competition leads to interesting phenomenology

- The bad side:

Gaussian competition is risky and unrobust

Fitness landscape

$$\frac{d}{dt}n_i = n_i \left(r(x_i) - \sum_j a(|x_i - x_j|)n_j \right) \qquad i, j = 1 \dots N$$

- now r(x) is not constant, example: preferred phenotype (r(x) peaked)

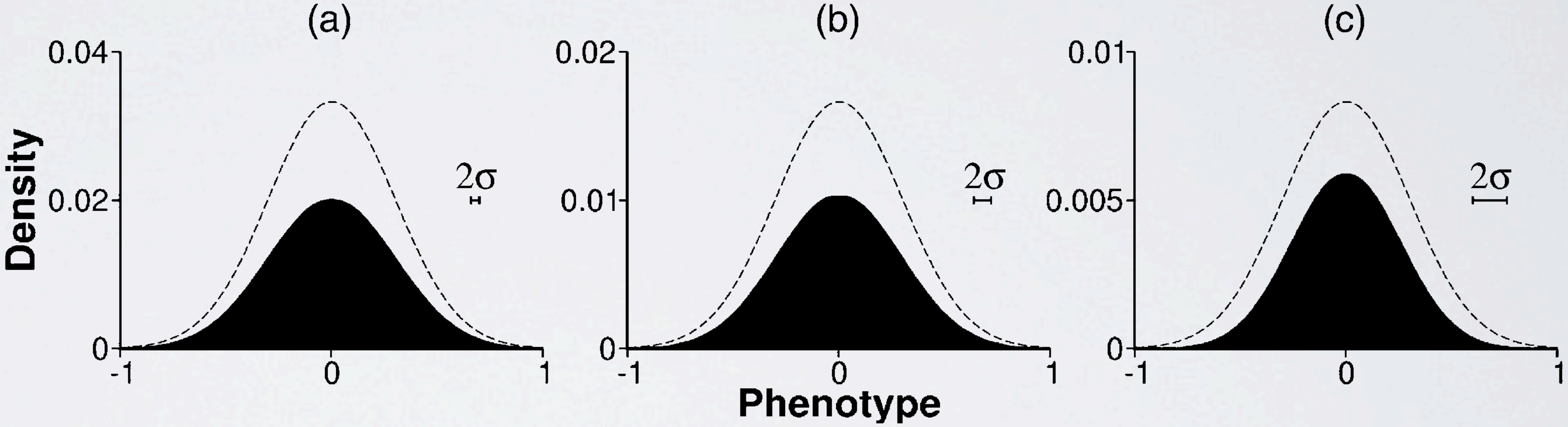
- result: if a coexistence solution exists, the stability still depends on a(x) not having negative Fourier modes

Hernandez-Garcia, Pigolotti, Lopez, Andersen, Phyl. Trans. Roy. Soc. A (2009)

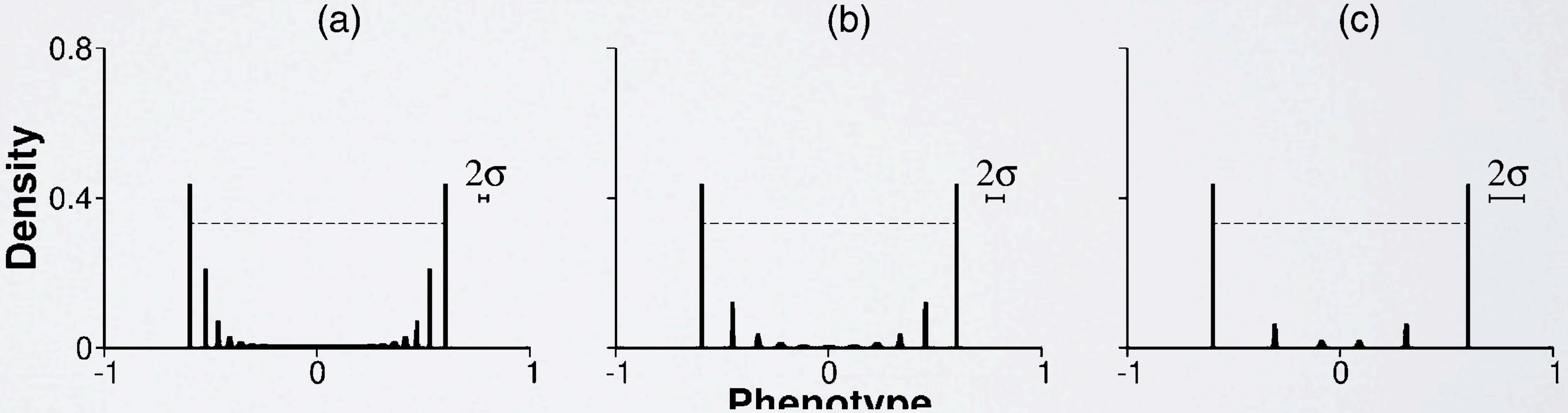
Fitness landscape

$$\frac{d}{dt}n_i \quad = \quad n_i\left(r(x_i) - \sum_j a(|x_i - x_j|)n_j\right) \qquad i,j = 1\ldots N$$

Gaussian competition, Gaussian r(x) (continuous coexistence)



Gaussian competition, Box r(x) (no continuous coexistence)



Roughgarden (1972), Szabo and Meszena (2006)

Summary

Three ways of breaking down continuous coexistence

- limiting similarity mechanism (heterogeneity, thresholds

- “sharp” r(x) (or K(x)) breaks down the solution like in the box function case

- instability coming from the choice of the kernel

(open) questions

- Functional response?

$$\frac{d}{dt} n_i \quad = \quad n_i \left(r(x_i) - \sum_j a(|x_i - x_j|) \frac{n_j}{k(x) + n_j} \right) \qquad i, j = 1 \dots N$$

(open) questions

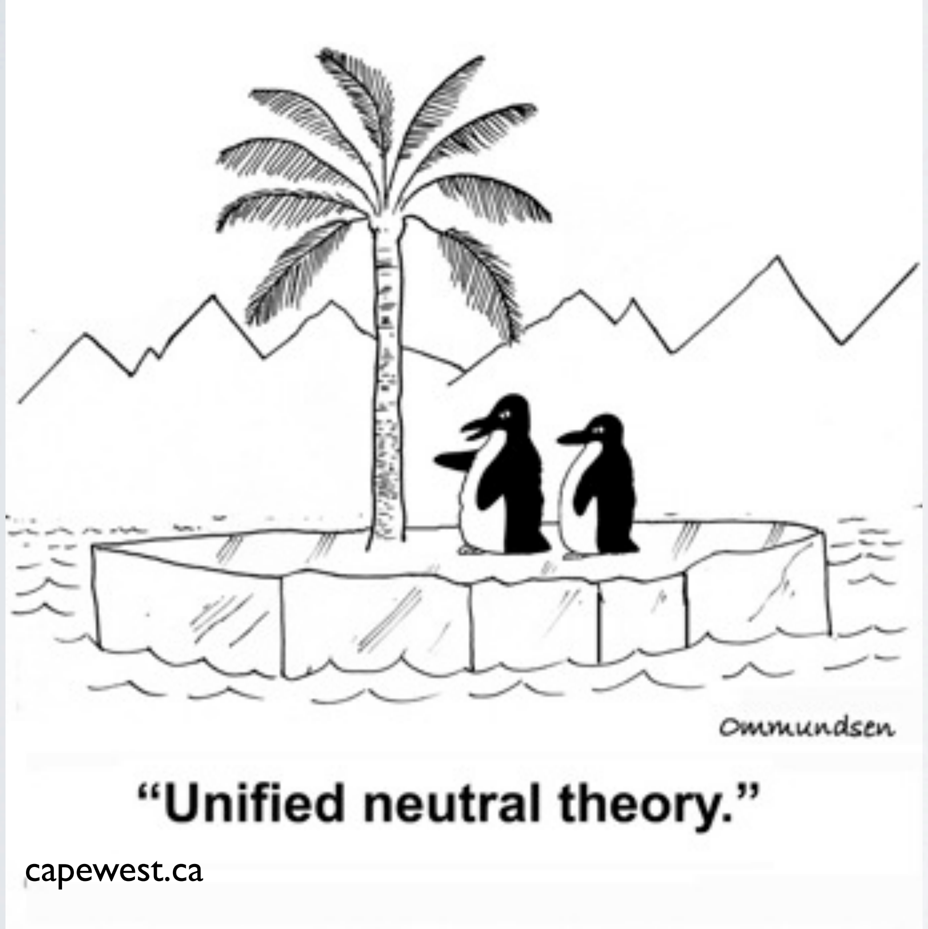
- Functional response?

$$\frac{d}{dt}n_i = n_i \left(r(x_i) - \sum_j a(|x_i - x_j|) \frac{n_j}{k(x) + n_j} \right) \qquad i,j = 1 \ldots N$$

- More trophic levels?

Neutral competition

ecological equivalence: all individuals have the same birth rate, death rate, immigration rate…



"Unified neutral theory."

capewest.ca

in analogy with Kimura's genetic theory, but harder to justify (equalizing mechanisms?) -> working hypothesis

- Ingredients:
- lottery dynamics + immigration (speciation)
- spatial (lattice) models: variations of voter models

S.P. Hubbell, *The unified neutral theory of biodiversity and Biogeography* (2001)

Species-Area Relations: Phenomenology

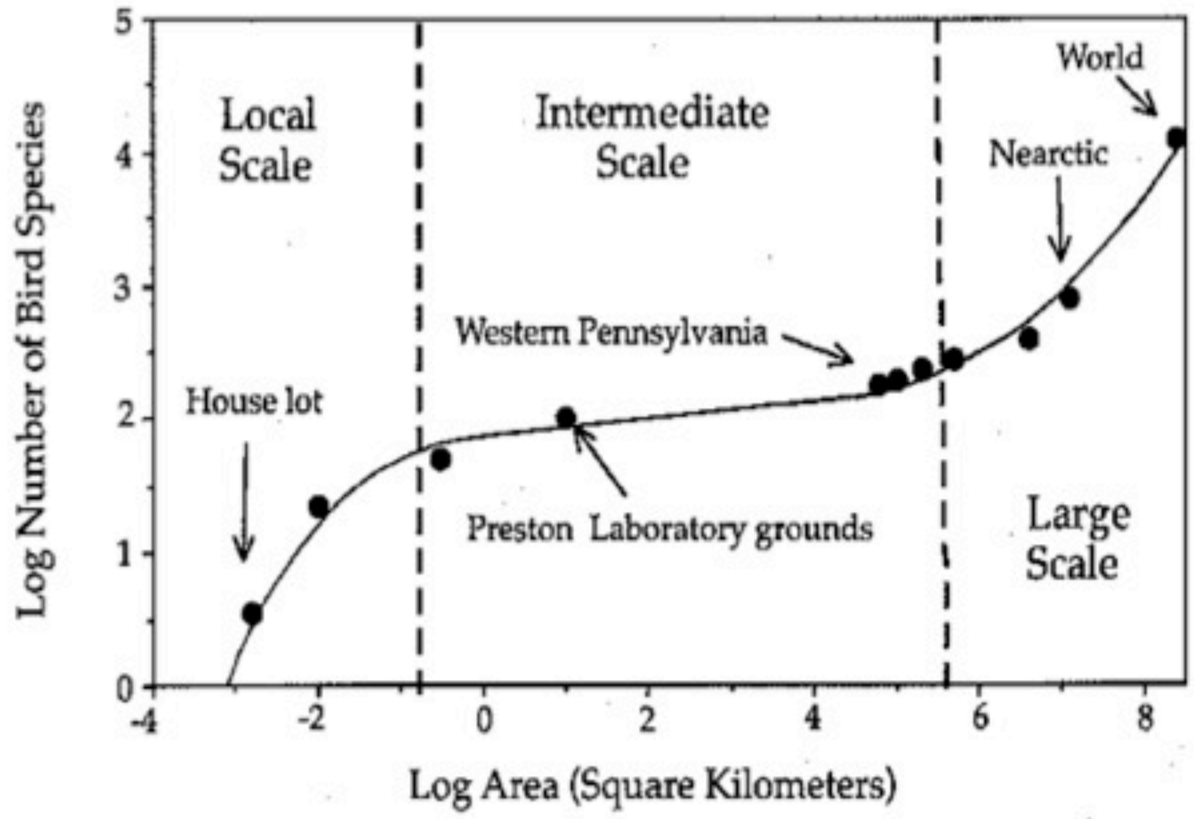
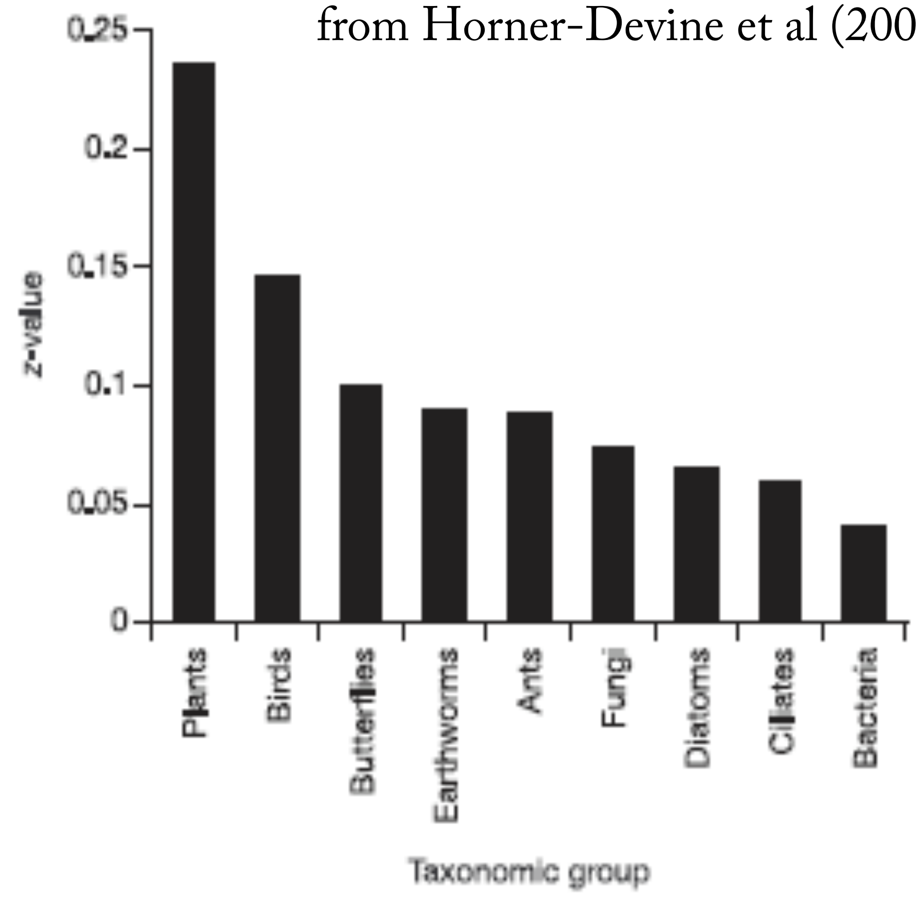


FIG. 6.2. Species-area curve for the world's avifauna, spanning spatial scales from less than one acre to the entire surface of the Earth. The S-shaped curve suggests that the sampling units change as area is increased, from individuals, to species ranges, and finally to different biogeographic realms at local, regional to subcontinental, and finally to intercontinental spatial scales. Data from Preston (1960).



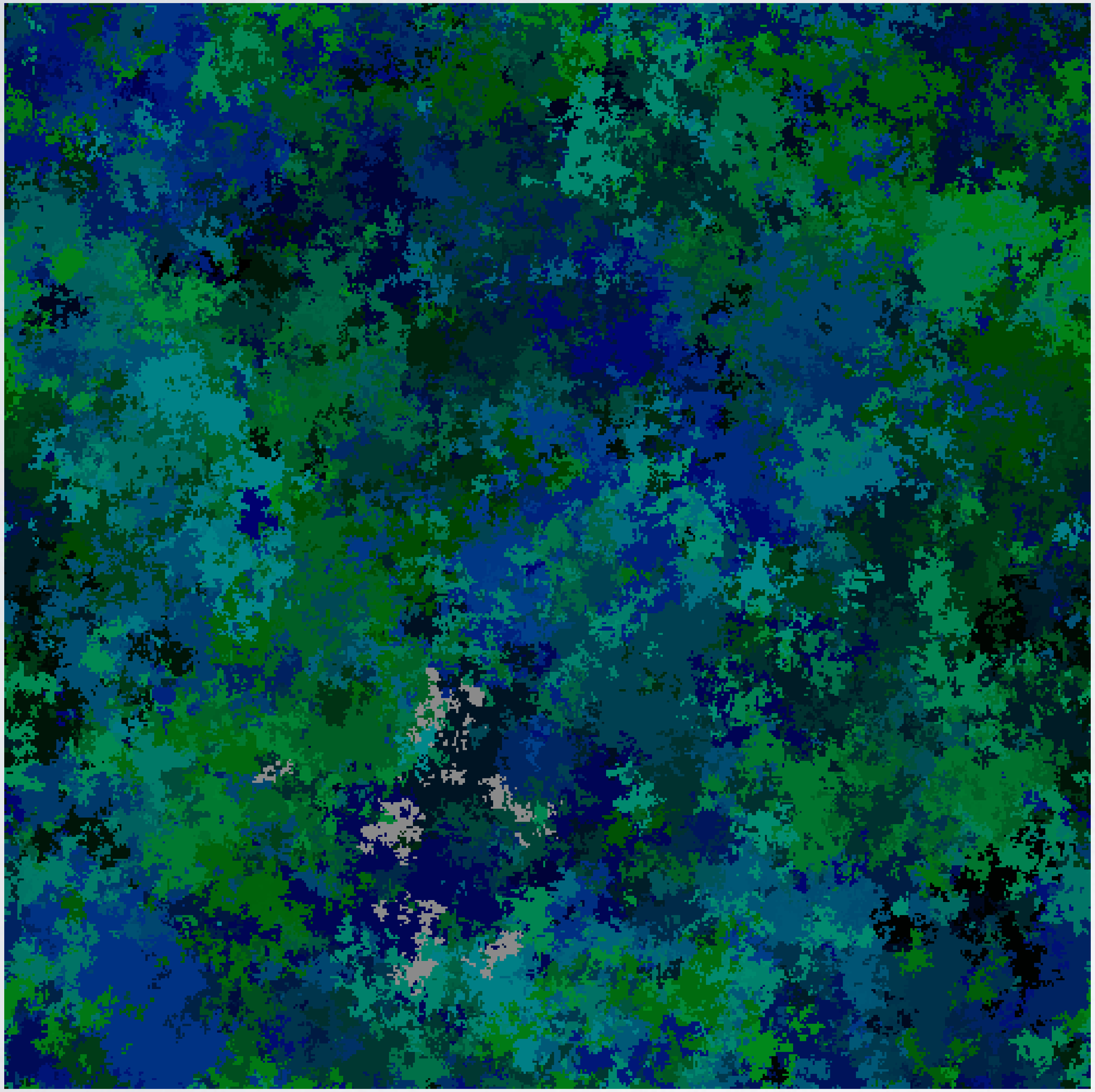
from Horner-Devine et al (2004)

$S \propto cA^z$ z is scale-dependent

$z \approx 1$ for small & large scales

$z < 1$ non-trivial (intermediate scales)

A neutral IBM



2d LxL-lattice, one individual per site

Dynamics: pick a random site, kill the resident

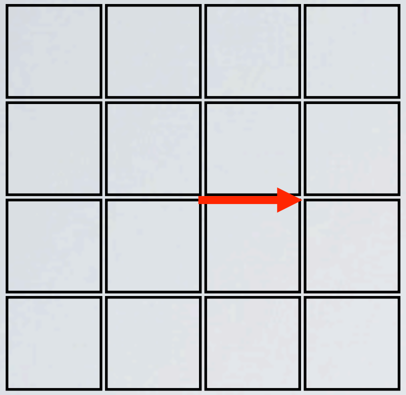
individual; then with probability

$1-\nu$ copy an individual in the "neighborhood"

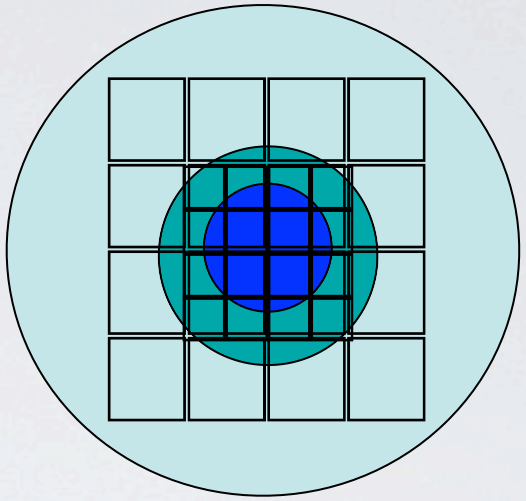
ν place an individual from a

"new" species **(immigration/speciation)**

Dispersal



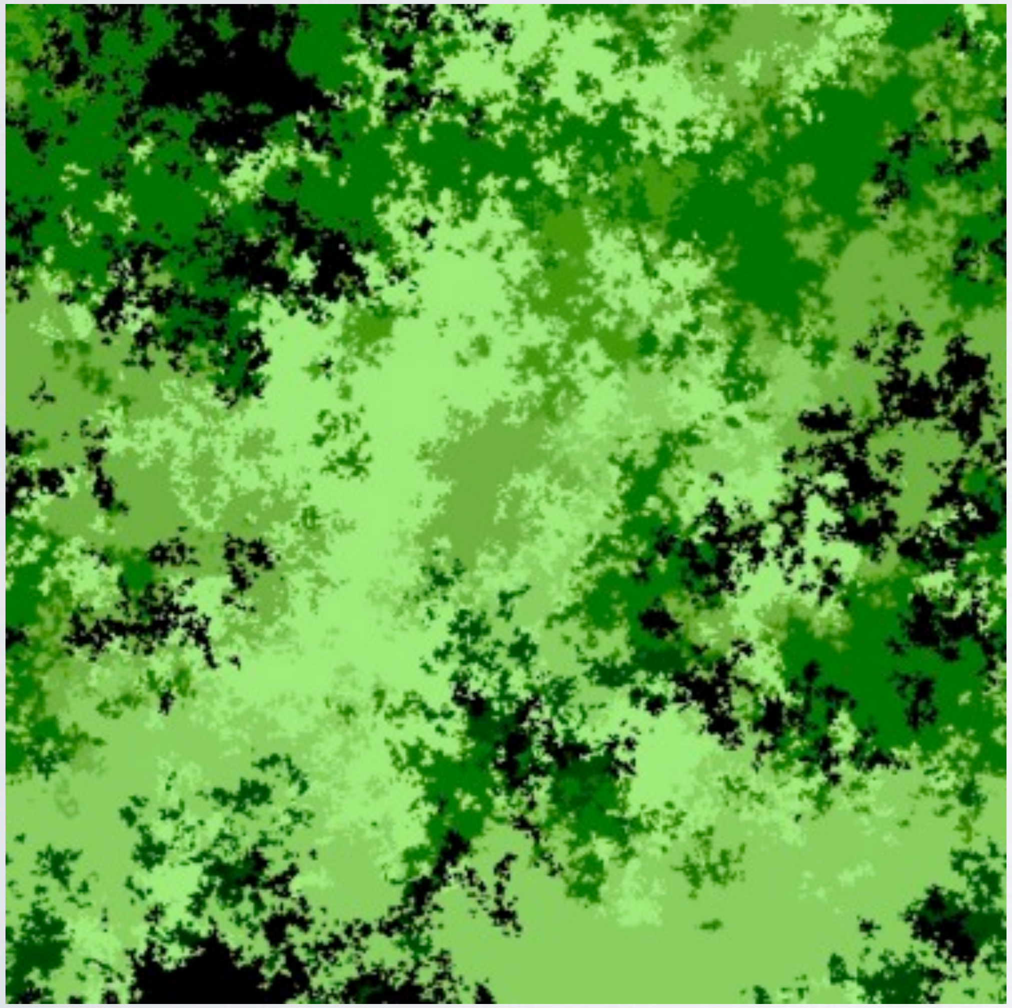
Nearest-Neighbor

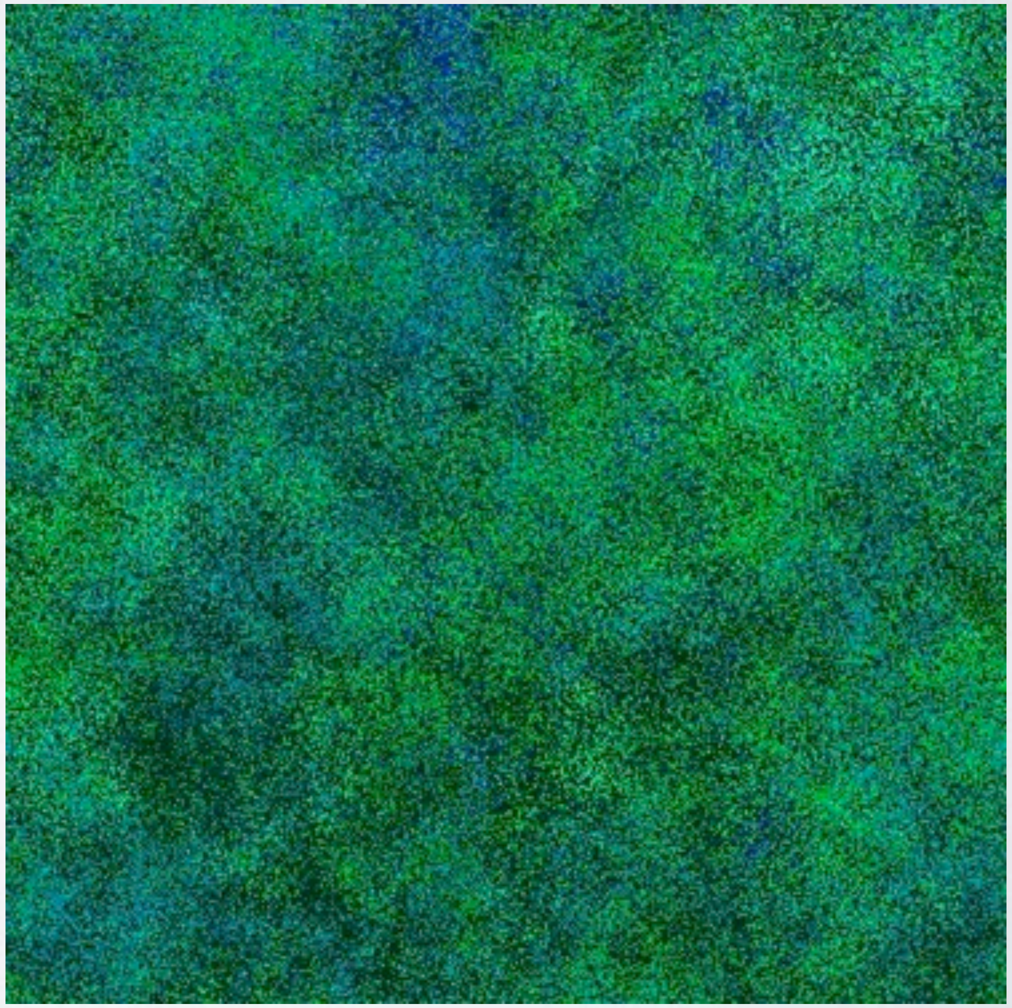


General Kernel

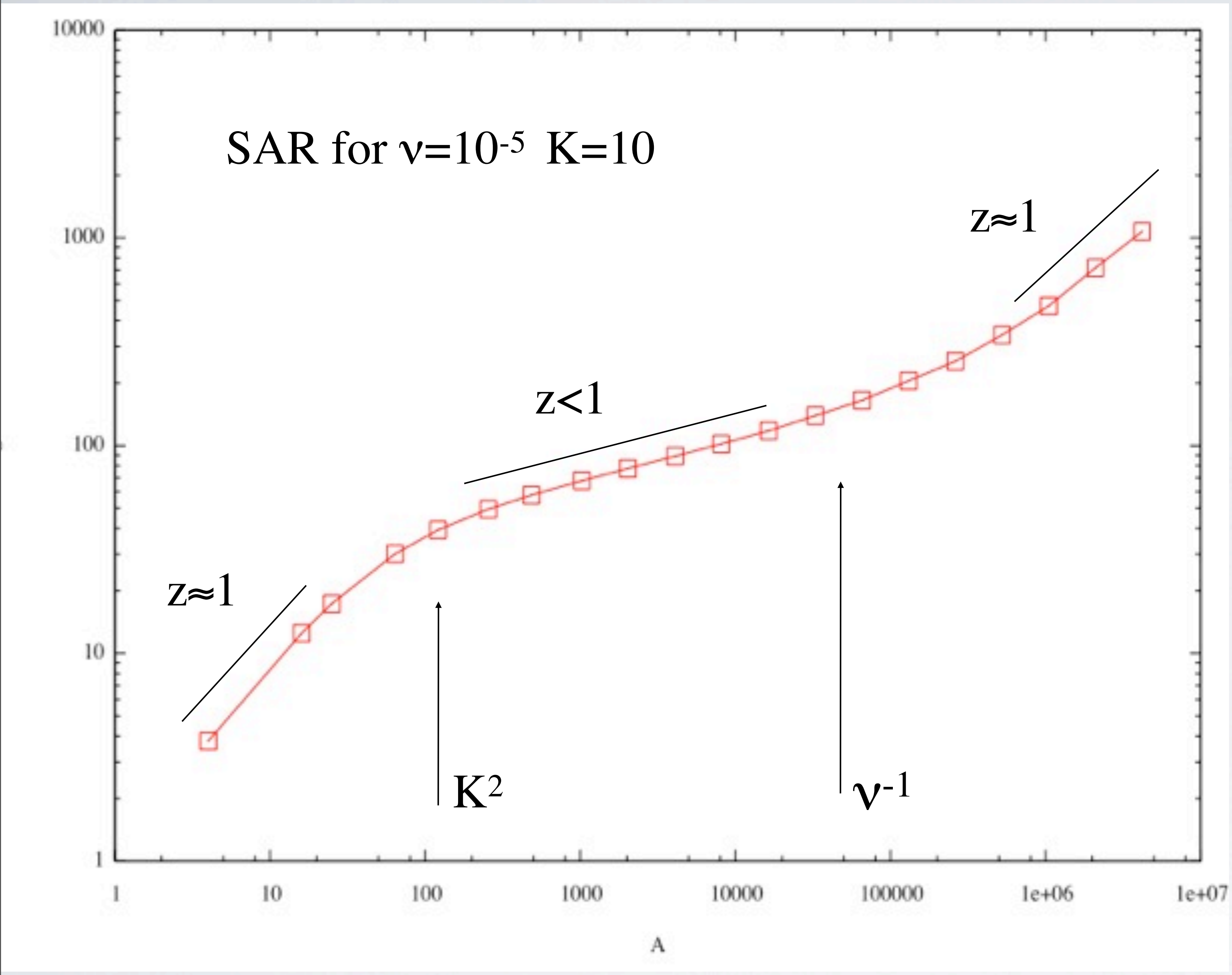
of range K

(e.g. Gaussian, Square)





Result: SAR with voter model



SARs features are well reproduced by the model

(Durrett and Levin 1996, Hubbell 2001, Chave et al. 2002, Rosindell et al 2007)

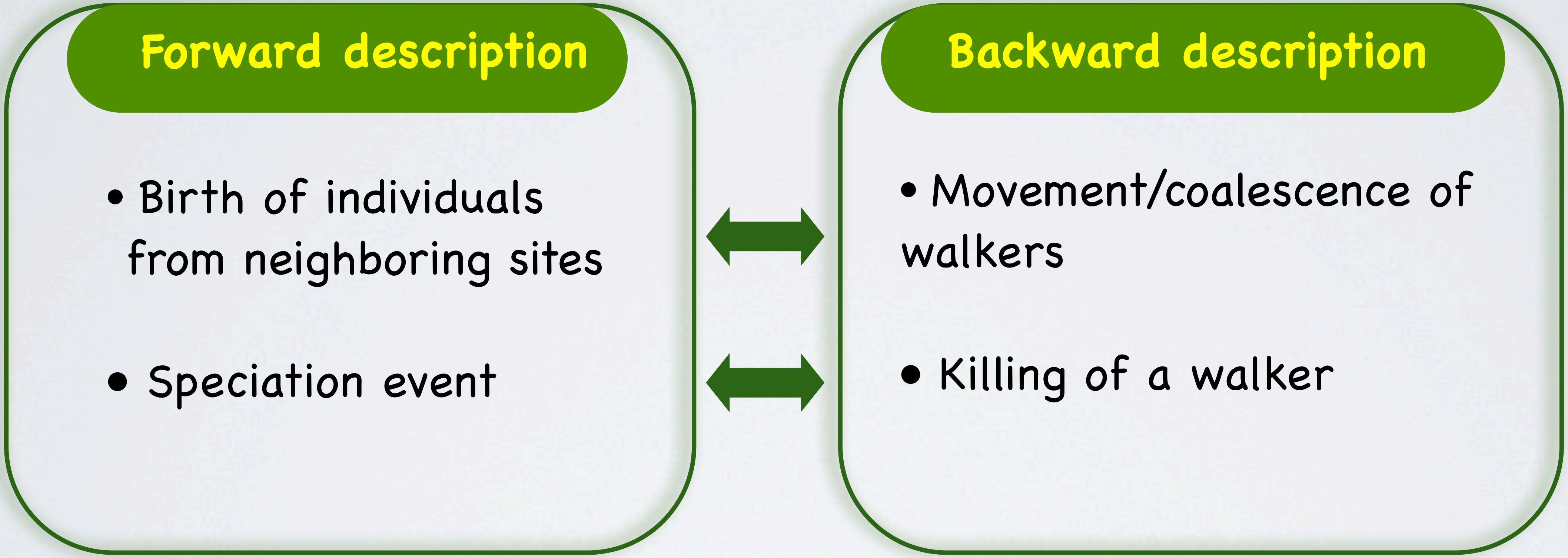
Intermediate range:

1. How z depends on the dispersion kernel?
2. How z depends on the speciation rate?

SP and M. Cencini, Jour. Theo. Biol. 260:83-89 (2009), arXiv:0902.3906

Coalescent approach

The multitype voter model (backward in time) maps onto a problem of coalescing random walker with a killing rate (Liggett, 1985)



Forward description

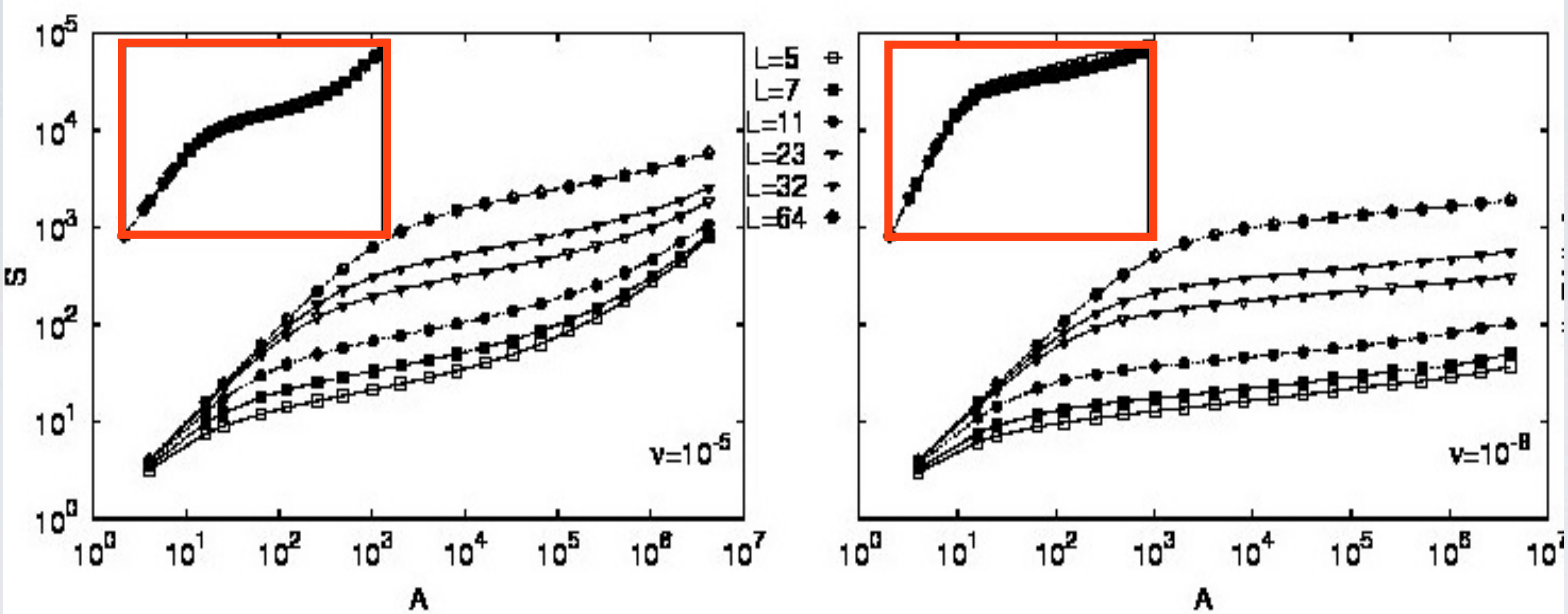
- Birth of individuals from neighboring sites
- Speciation event

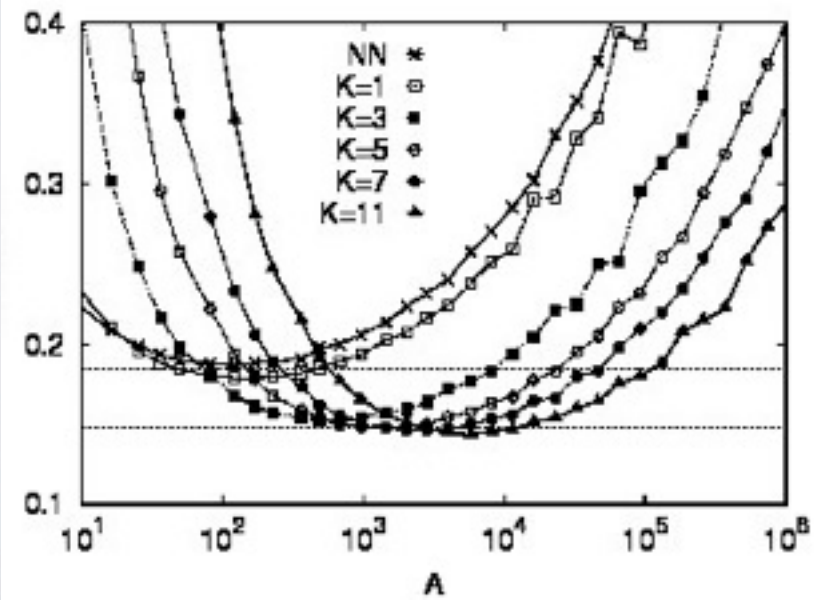
Backward description

- Movement/coalescence of walkers
- Killing of a walker

Advantages: MUCH faster simulations, open boundaries, helps physical insight

Results: dispersal range





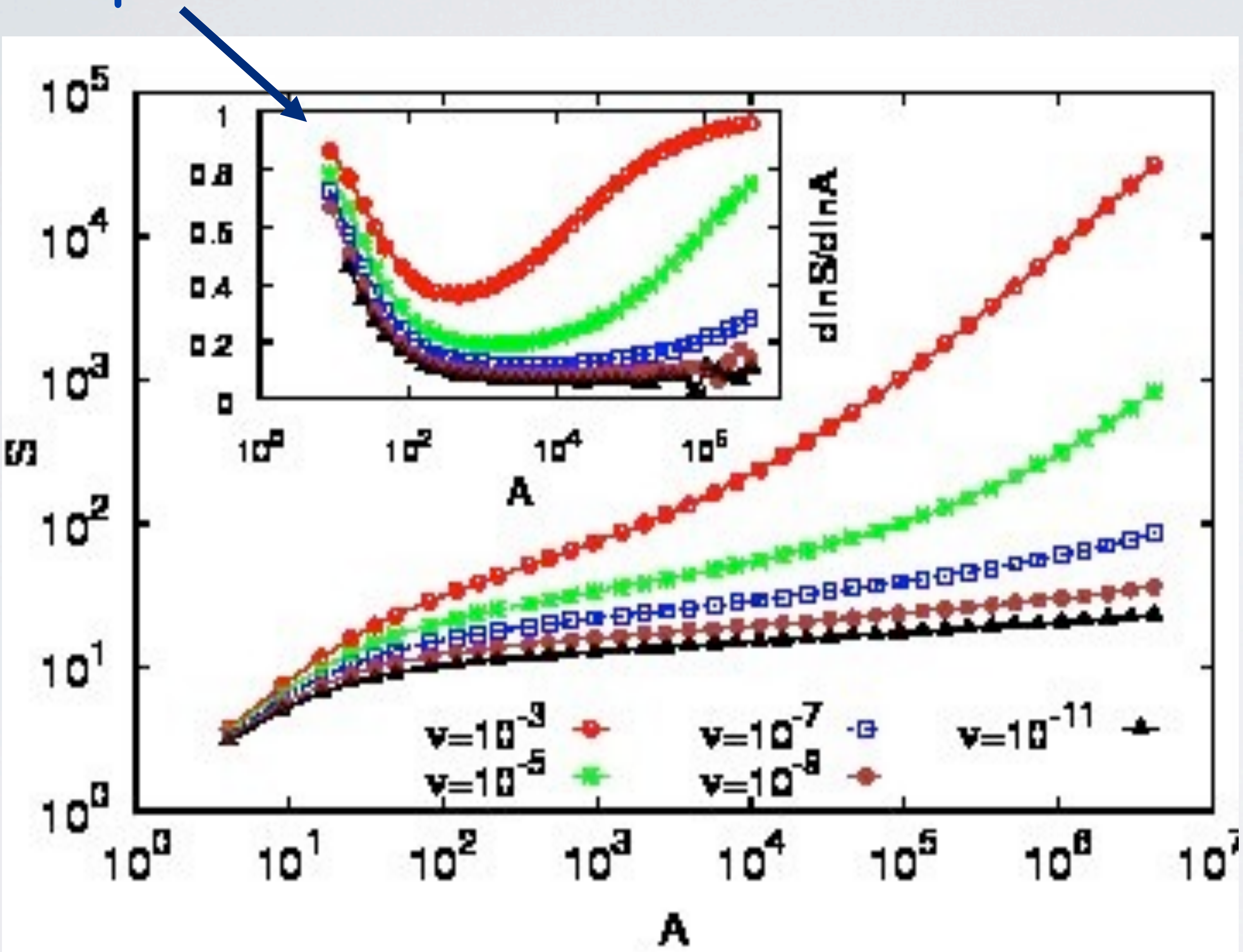
The exponent is independent on the dispersal range

$$\boxed{f(A,\nu,K) = K^r\phi(A/K^r,\nu)}$$

$r \sim 1.93$ (Rosindell et al 2007)

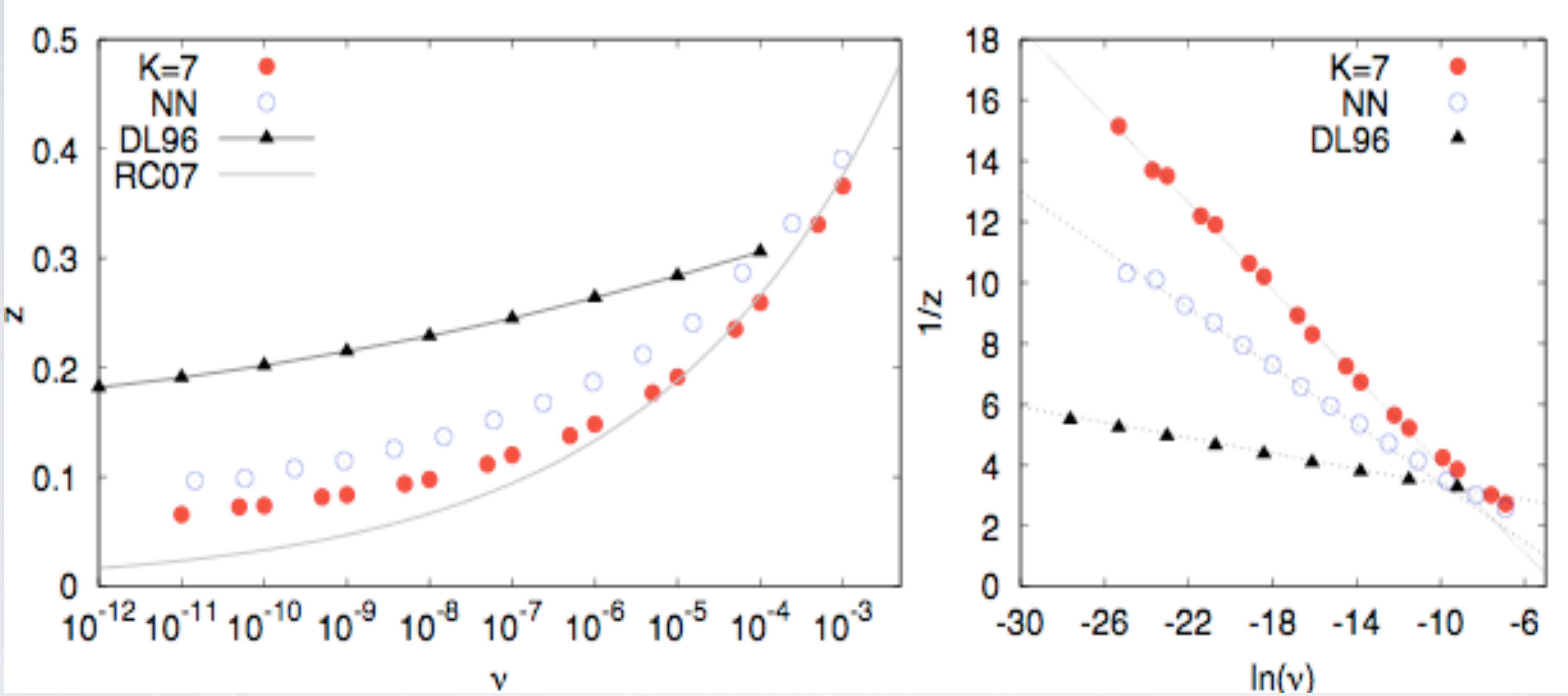
🡐 Corrections for small K only (like NN case)

Results: speciation


Local exponent

Which kind of functional dependence?

z vs speciation



$$z = \frac{1}{q + m\ln(\nu)}$$

Simulations confirm DL96 logarithmic scaling but with a different prefactor (pre-asymptotic effects?)

with q=-3.3 m=-0.72

Do we have data?

A difficult comparison: no realiable data on speciation rates

We look at the definition of the adimensional speciation rate

$$\boxed{\nu = \frac{t}{t_s}}$$

t=lifespan of the individual of a specie
t_s=waiting time for a new specie

Realiable estimate of t are possible!

how does z depend on lifespan?

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ICTP, 24/10/2010

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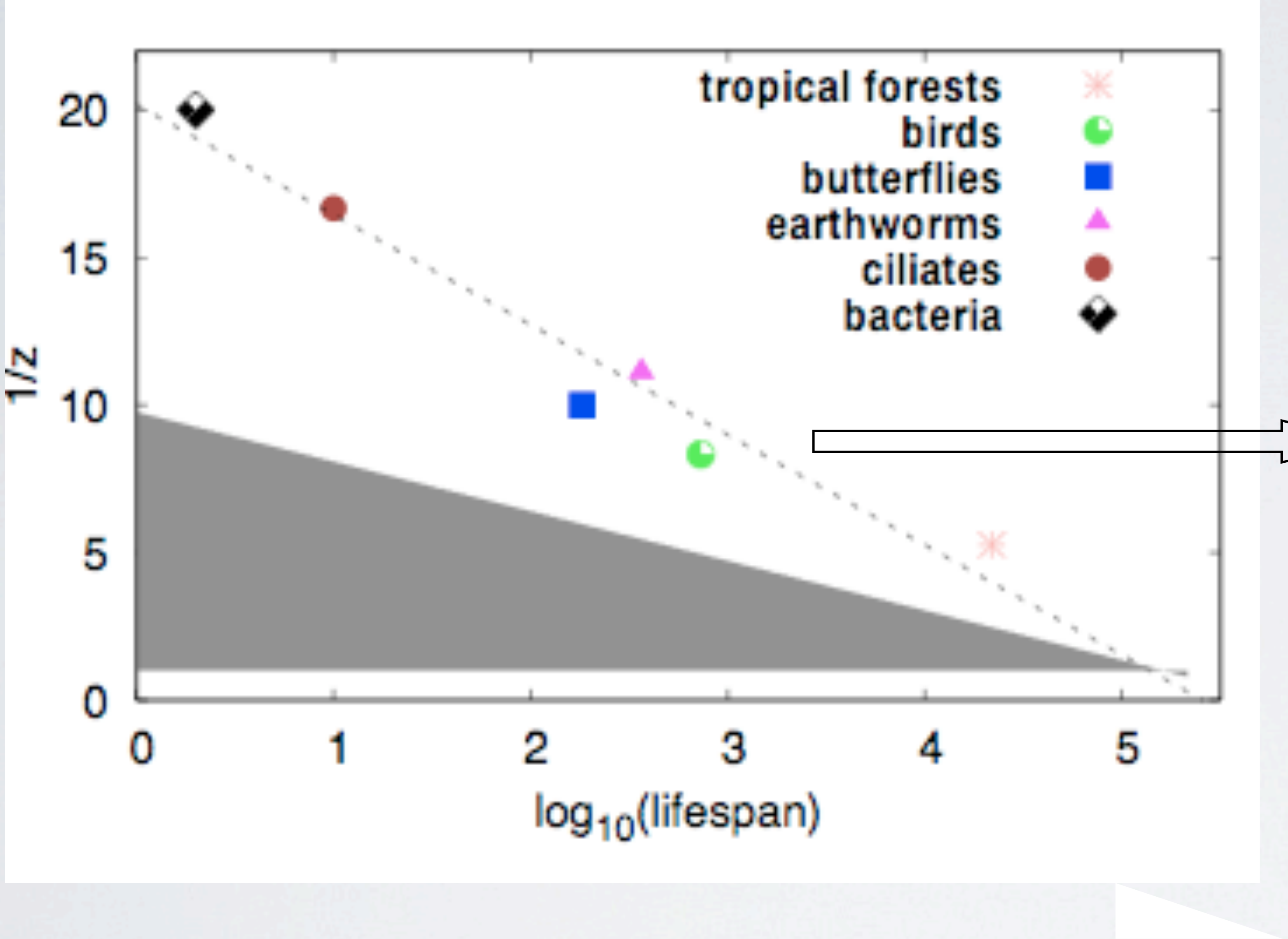
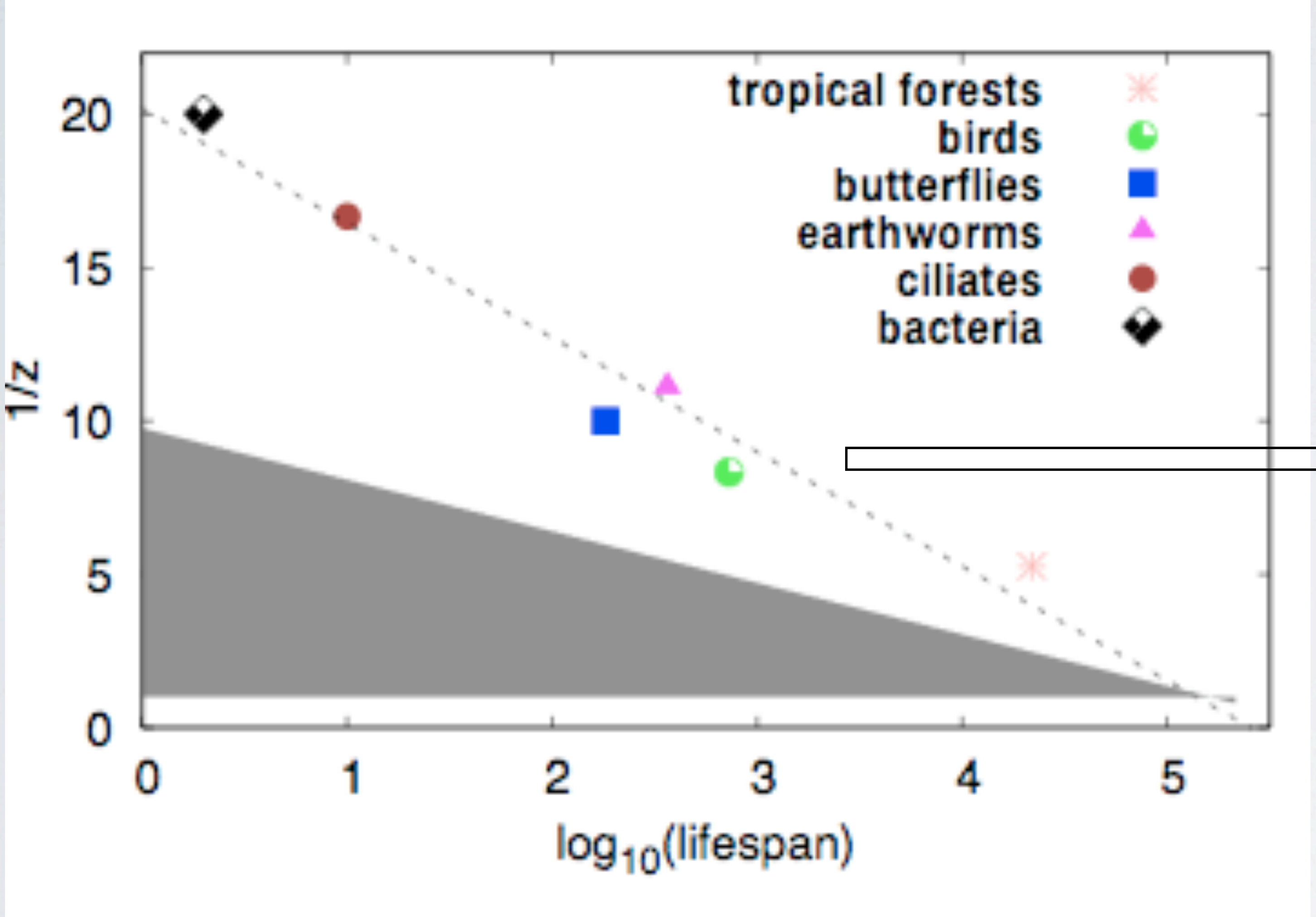
A conjecture



$1/z \propto \log(t)$

A conjecture



From the voter model

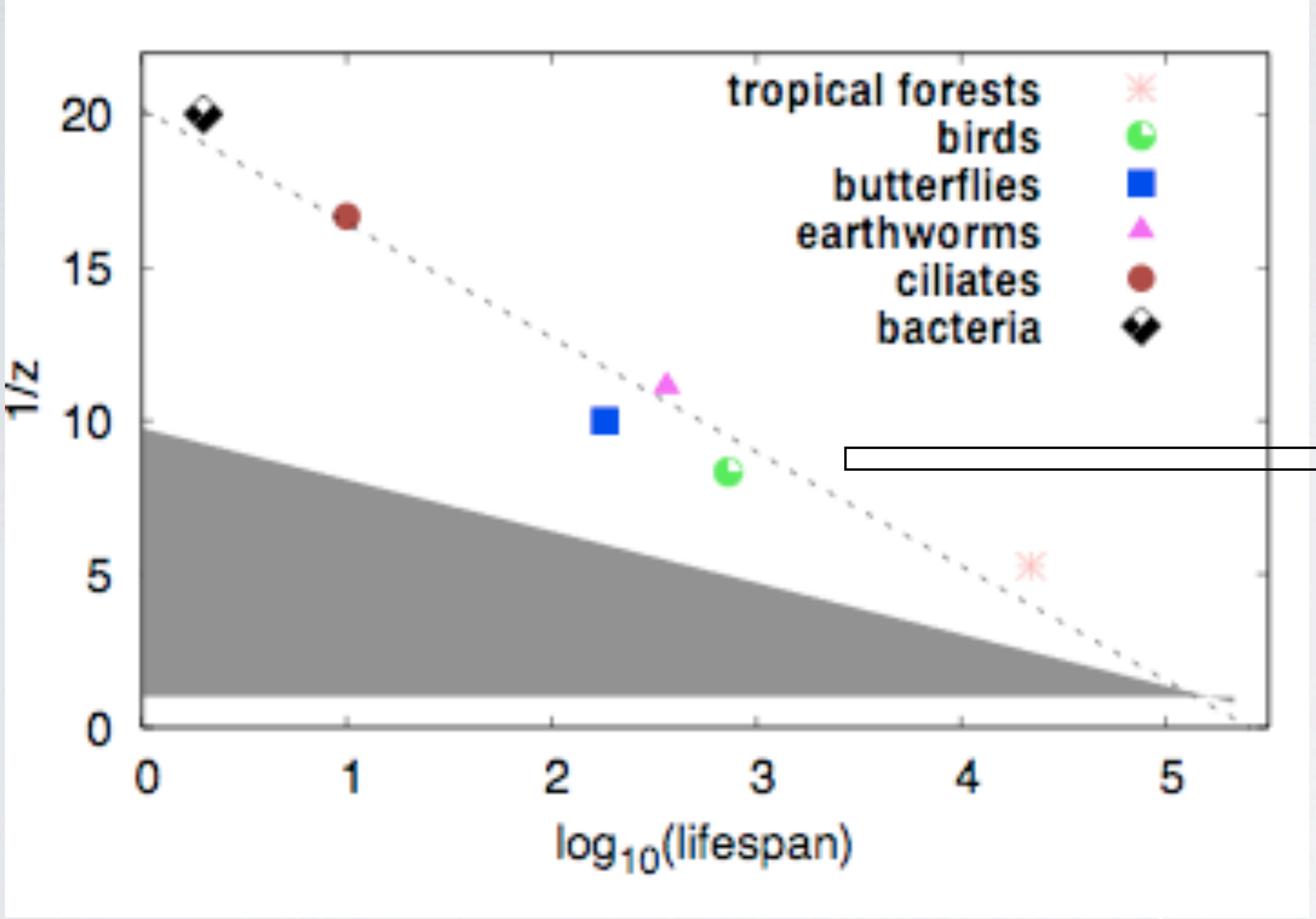
$1/z = m \log(\nu) = m(\log(t) - \log(t_s))$

$+$

$1/z \propto \log(t)$

$t_s \propto t^w$

A conjecture



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$1/z = m \log(\nu) = m(\log(t) - \log(t_s))$

$+$

$1/z \propto \log(t)$

$t_s \propto t^w$

The observed slope implies $w<0$ which is unreasonable
(bacteria's speciation time would be much longer than that of trees)

References

NICHES:

- MacArthur and Wilson, Am. Nat. (1967), Roughgarden, "Theory of population genetics and evolutionary ecology: an introduction"" (1979), Scheffer and Van Nes, PNAS (2005), Szabo and Meszena, Oikos (2006), Pigolotti, Lopez, Hernandez-Garcia, Phys. Rev. Lett. (2007), Pigolotti, Lopez, Hernandez-Garcia, Andersen, Theo. Ecol. (2010), Hernandez-Garcia, Pigolotti, Lopez, Andersen, Phil. Trans. Roy. Soc. A (2009)

NEUTRAL:

Durrett and Levin, J. Theo. Biol (1996), Rosindell and Cornell Ecol. Lett. (2007), Pigolotti and Cencini J. Theo. Biol. (2009)

APPLETS:

http://www.nbi.dk/~pigo/competition.html
http://www.nbi.dk/~pigo/niche.html