

Intraspecific niche flexibility facilitates species coexistence in a competitive community with a fluctuating environment

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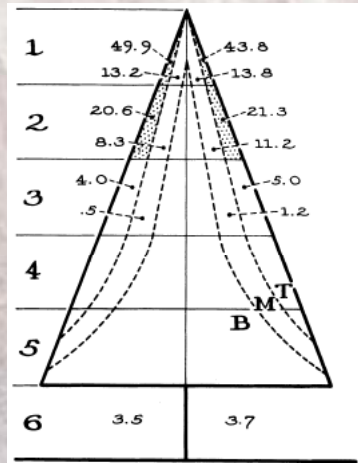
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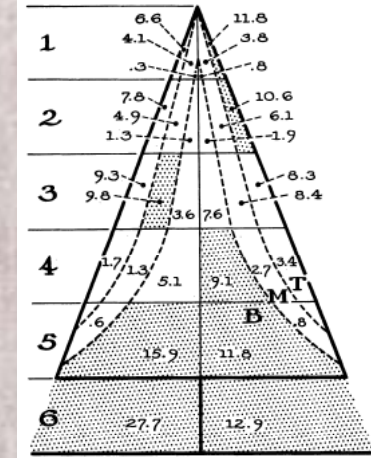


Coexistence on one-dimensional niche space

- Feeding positions of warblers (MacArthur, 1958)



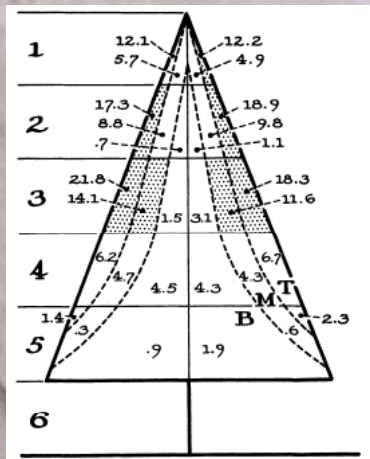
Cape May warbler



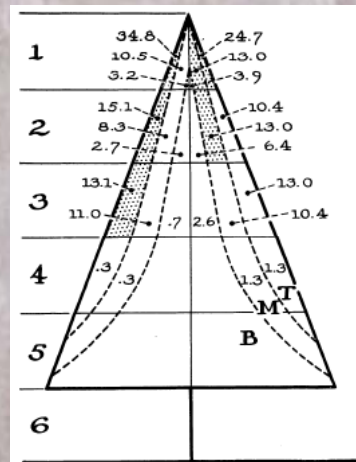
Myrtle warbler

Time of observation | Number of observation

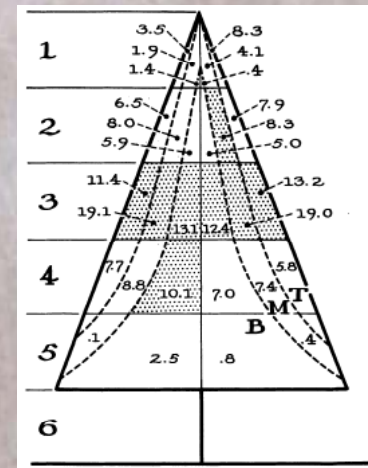
niche
(生態的地位)



Black-throated green warbler



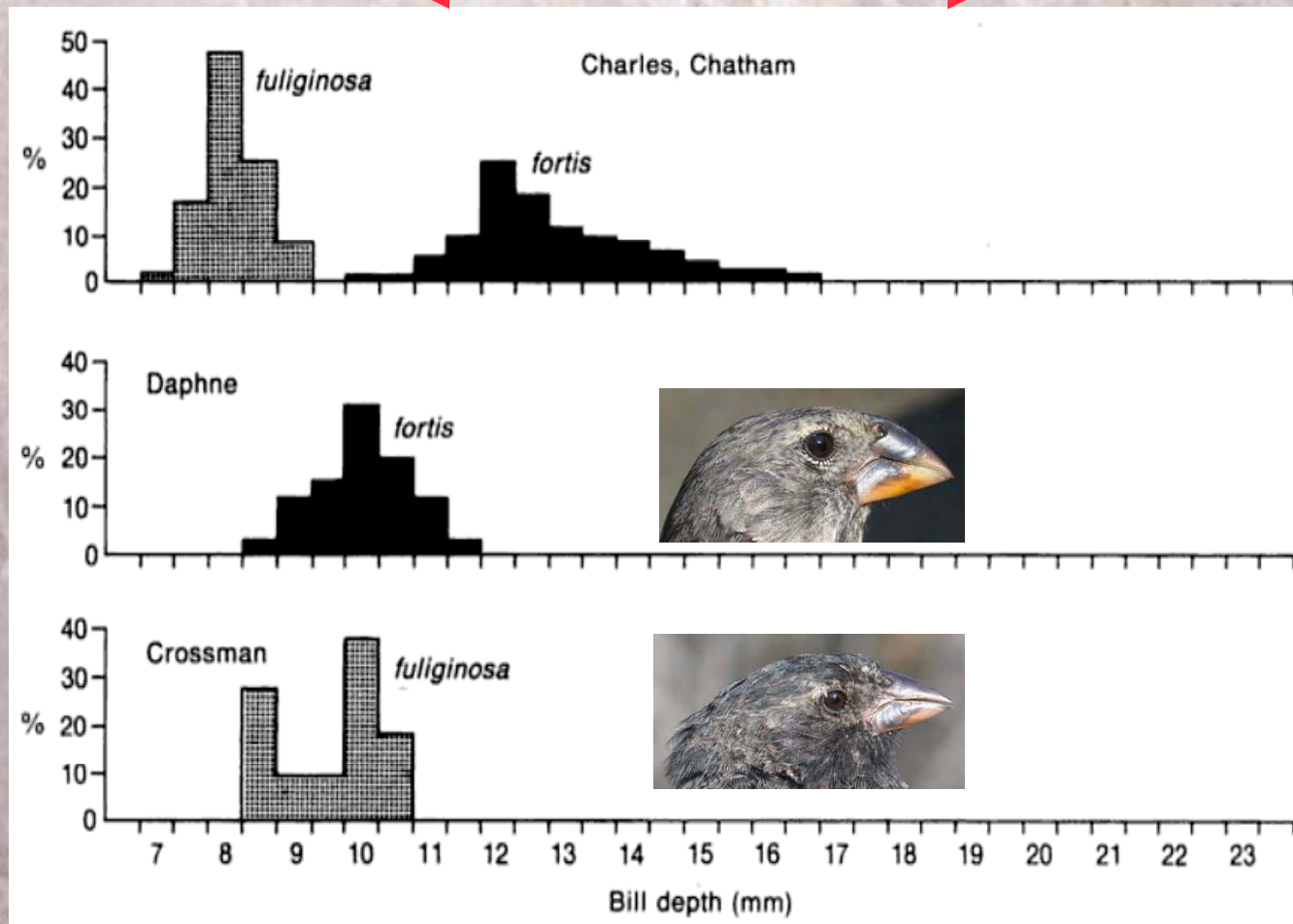
Blackburnian warbler



Bay-breasted warbler

- Bill depth of Darwin finch in Galapagos islands (Lack, 1947)

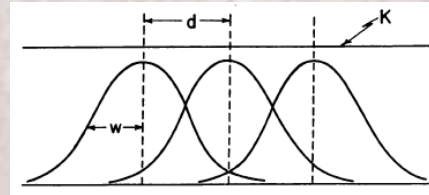
niche (生態的地位)



→ Character displacement

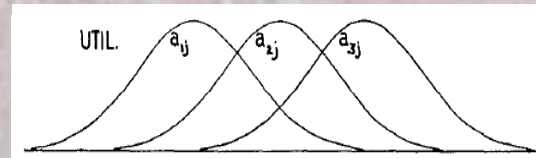
Theory of species coexistence on a niche space

Limiting Similarity (MacArthur and Levins 1967, May and MacArthur 1972)



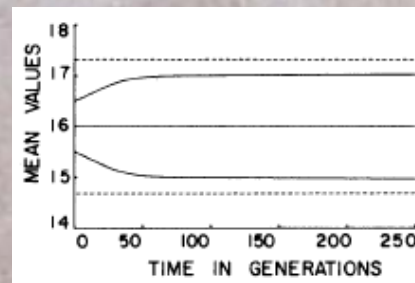
Conditions for coexistence

Species Packing (MacArthur 1969, 1970)



Number of coexisting species

Character displacement (Slatkin 1980, Taper and Case 1985)



Coexistence by evolution



Recent development of coexistence on niche space

- Importance of **functional form of fitness kernel**

(Sasaki and Ellner 1995, Szabó and Meszéna

- Importance of **intraspecific diversity**

(Vellend 2005)

- Importance of **stochasticities**

(Tillman 2004)

Study Subject

Analysis of effects of intraspecific diversity (niche flexibility) on species diversity under fluctuating environmental

Keywords:

- Competition kernel
- Flexibility (intraspecific diversity)
- Stochasticity

Model

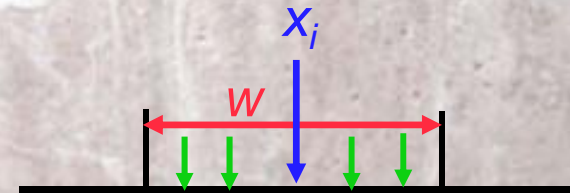
Species i is characterized by

Different among species

- specific niche position ($x_i : 0 \leq x_i \leq 100$)

Same for all species in the community

- specific niche width (w) (= flexibility)
 - potential variation of individual niche position
- intrinsic growth rate (r)
- vulnerability to intraspecific competition
- vulnerability to interspecific competition
- competition kernel



Population growth phase

$$n'(i, j) = n(i, j) + \left\{ r - \sum_k \sum_l \alpha_{i,j,k,l} n(k, l) + \omega_{j,t} \right\} n(i, j)$$

$n(i, j)$: density of species i at niche position j

$\alpha_{i,j,k,l}$: competition coefficient between subpopulations of species i at niche position j and species k at niche position l

$$\alpha_{i,j,k,l} = \begin{cases} \alpha_1 f(j, l) & \text{if } i = k \\ \alpha_2 f(j, l) & \text{if } i \neq k \end{cases}$$

$f(j, l)$: competition kernel between niche positions j and l

$\omega_{j,t}$: environmental fluctuation on position j at time t

Inheritance phase

Sexual inheritance

Approximate hypergeometric phenotypic model

(Shpak and Kondrashov 1999)

$${}_{2n}^{\text{app}}R_{p_1, p_2}(q) = \sum_{s=0}^{p_1} {}_{p_1}^{\text{app}}R_{p_1}(s) {}_{p_2}^{\text{app}}R_{p_2}(q-s)$$

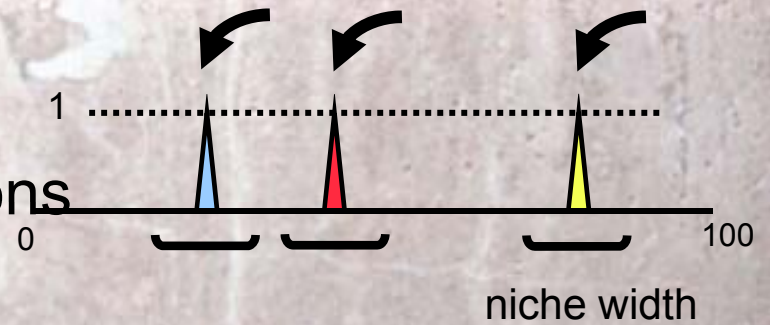
$${}_{p_1}^{\text{app}}R_{p_1}(s) = H(p, \max[p, s + p - 2n])$$

$$H(u, v) = \frac{\binom{u}{v} \binom{u}{v-u}}{\binom{2u}{u}}$$

- Diploid organisms
- Individual niche position is coded by 6 loci (13 genotypes)

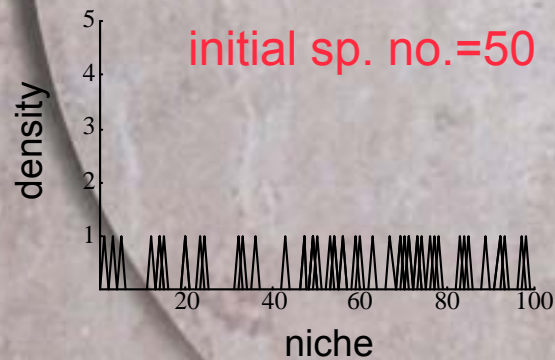
Initial species assemblage

Randomly selected N species are introduced to specific niche positions (center of niche) with density 1

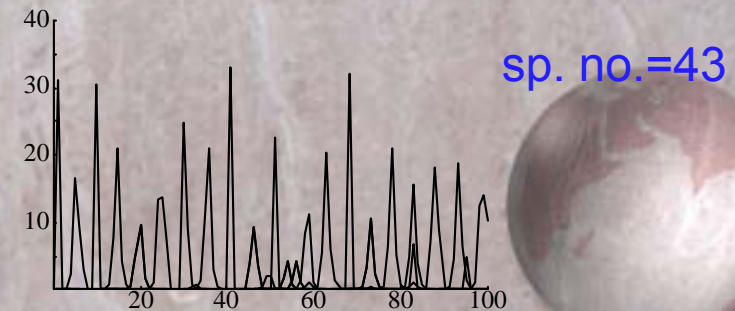
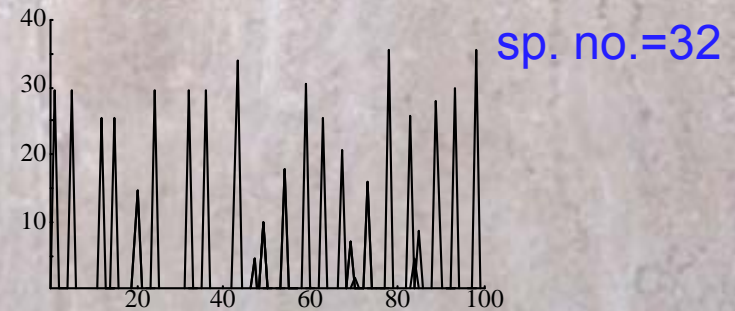
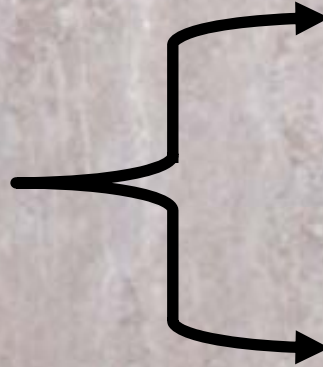


→ Diversity results from segregations of alleles and recombinations among loci

Subsequent dynamics

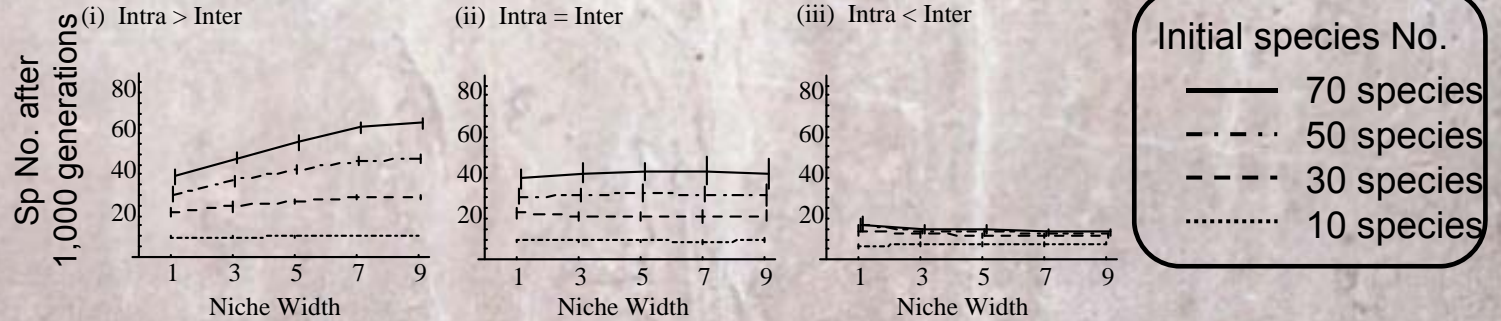


niche width = 1

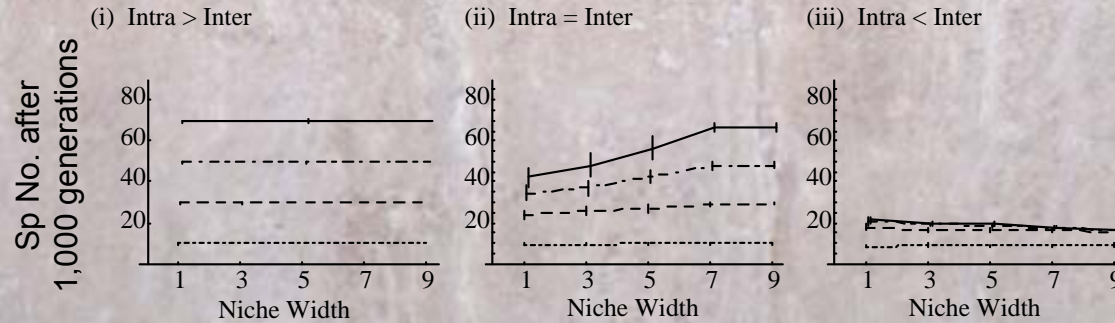


Sexual inheritance under constant environment

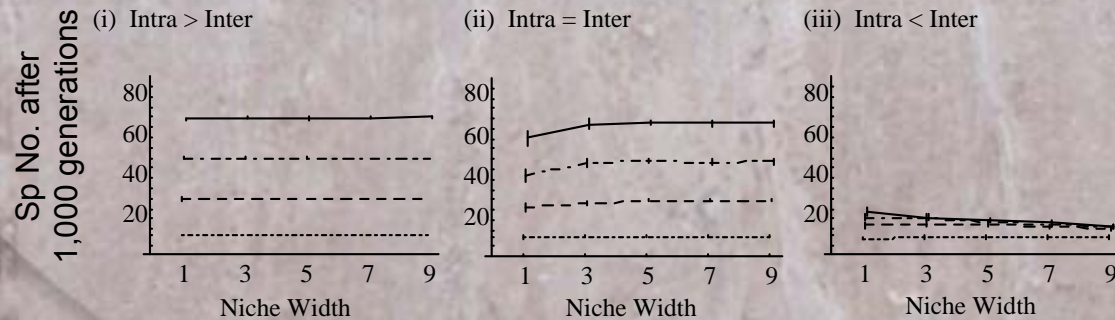
(a) Rectangle Kernel Model : Constant environment ($\sigma_r = 0$)

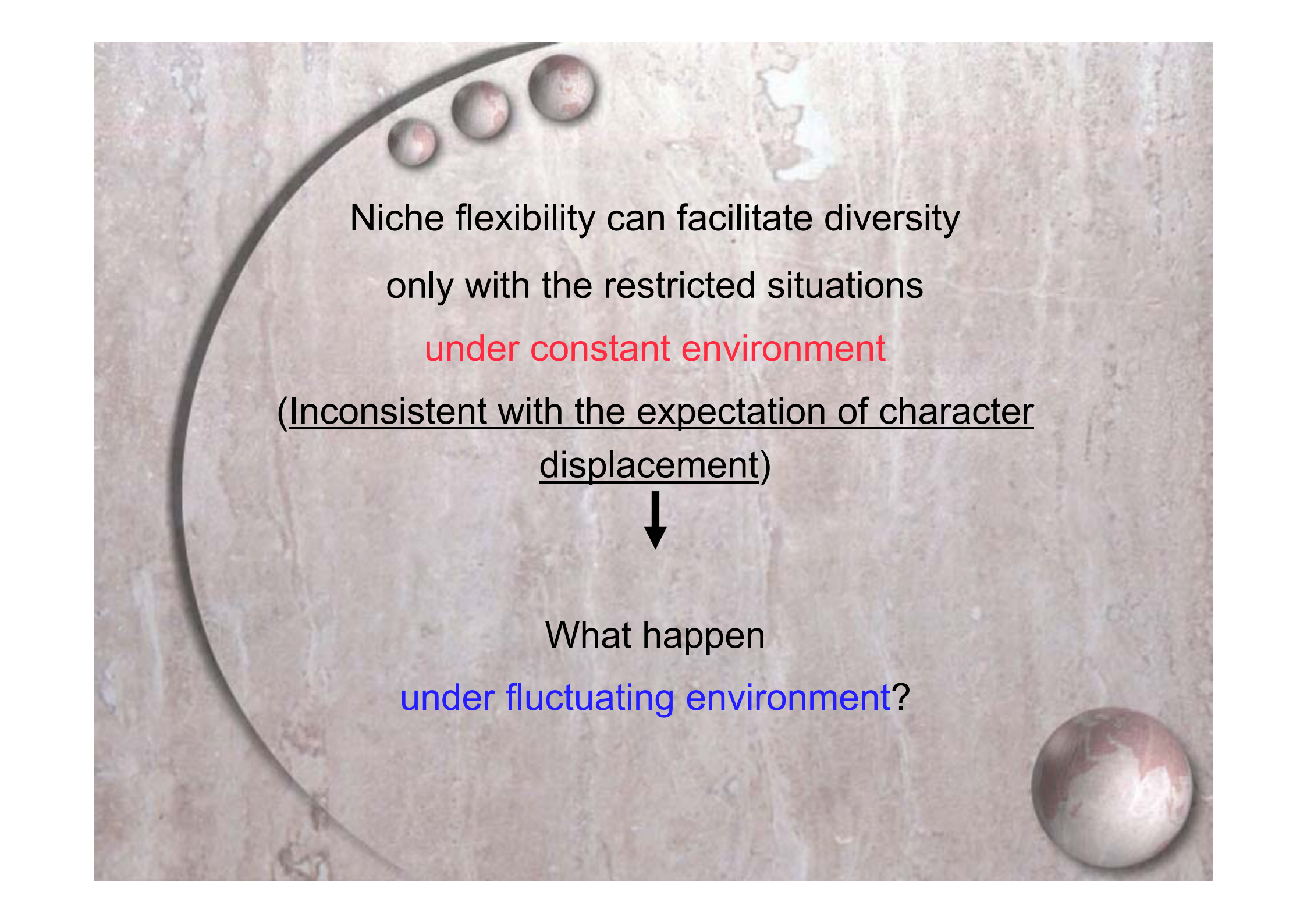


(b) Gaussian Kernel Model with Truncation at $2\sigma_c$: Constant environment ($\sigma_r = 0$)



(c) Gaussian Kernel Model with Truncation at $3\sigma_c$: Constant environment ($\sigma_r = 0$)





Niche flexibility can facilitate diversity
only with the restricted situations

under constant environment

(Inconsistent with the expectation of character
displacement)



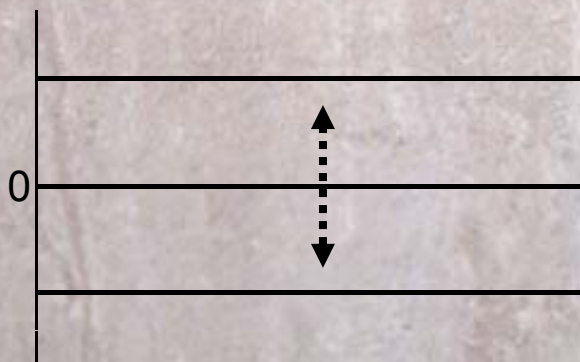
What happen

under fluctuating environment?

Two types of environment fluctuation, $\omega_{j,t}$

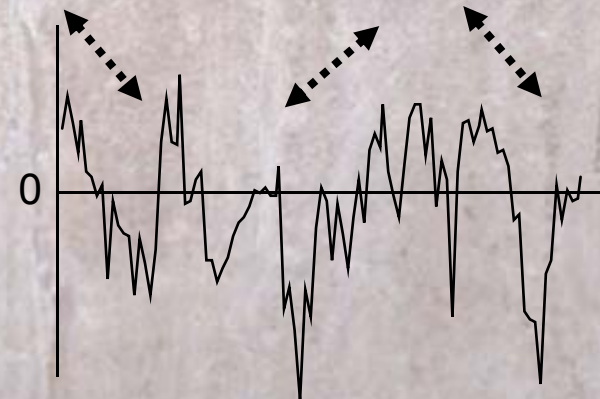
niche-independent fluctuation
(temporal)

niche-dependent fluctuation
(spatial)



niche position j

+



niche position j

autocorrelation

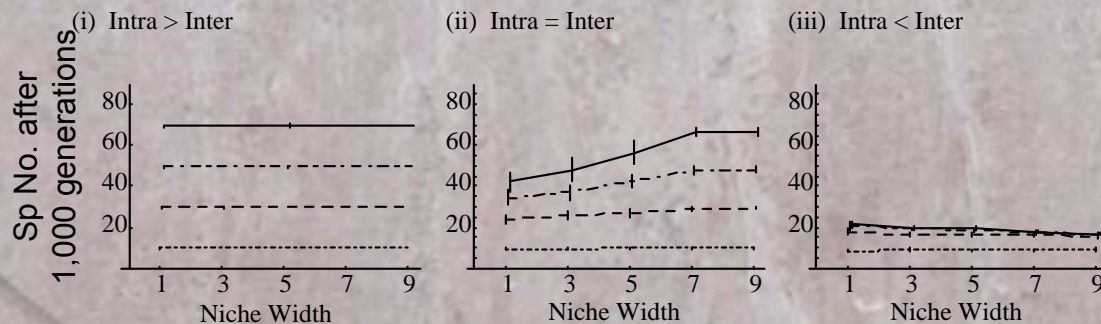


Examining four cases

- (a) niche-independent fluctuation
- (b) niche-dependent fluctuation without correlation
- (c) niche-dependent fluctuation with correlation
- (d) both niche-independent fluctuation and
niche-dependent fluctuation with correlation

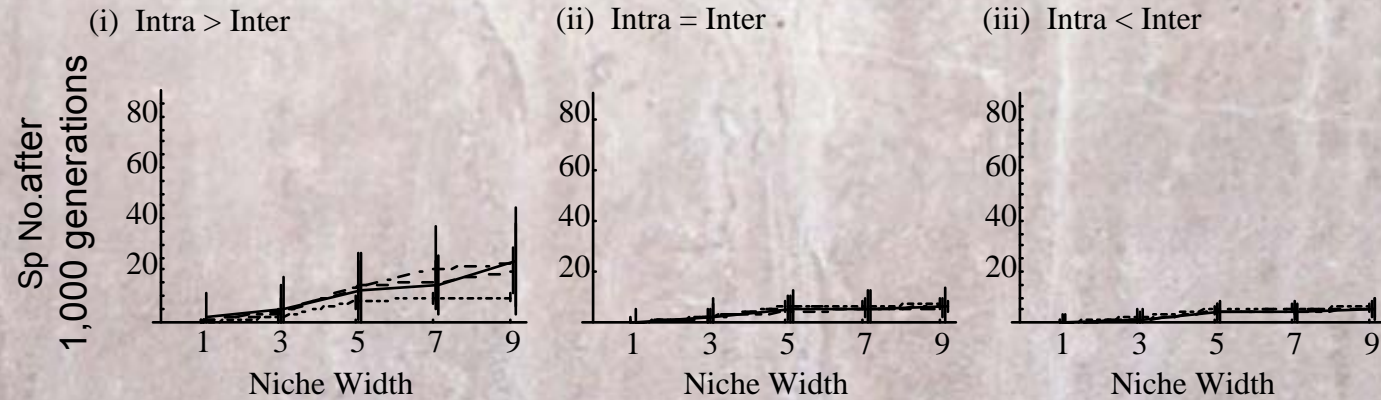
In all cases, $E[\omega] = 0$ and $V[\omega] = 0.08$

(b) Gaussian Kernel Model with Truncation at $2\sigma_c$: Constant environment ($\sigma_r = 0$)

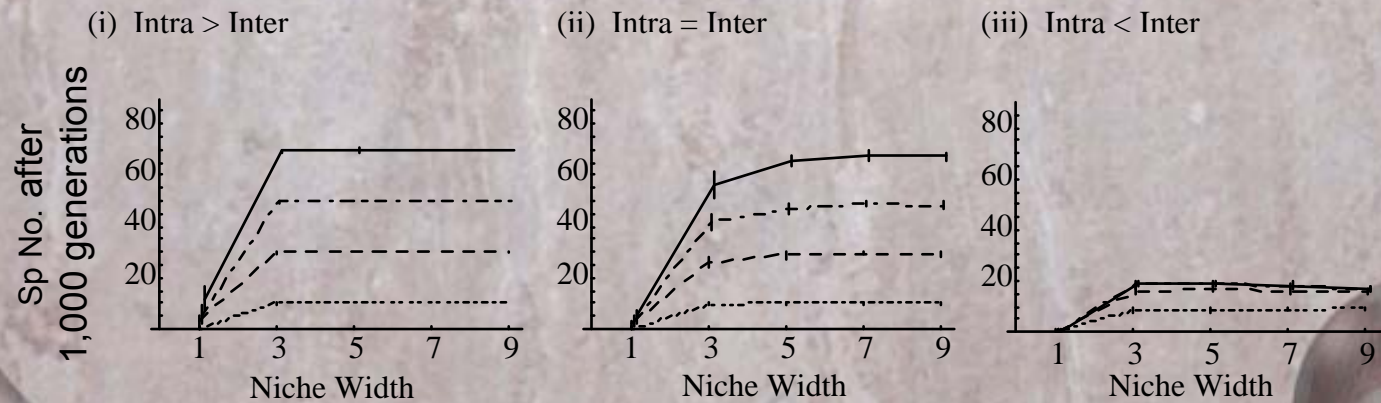


Sexual inheritance under fluctuating environment (1)

(a) **Niche-independent** fluctuation ($\sigma_r^2 = 0.08$)



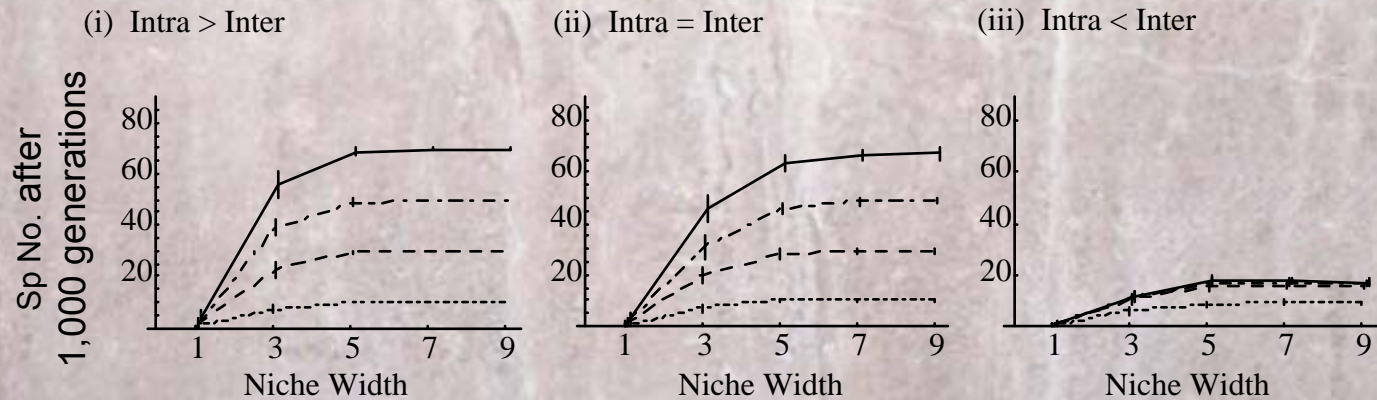
(b) **Niche-dependent** fluctuation without correlation ($\sigma_r^2 = 0.08, c = 0$)



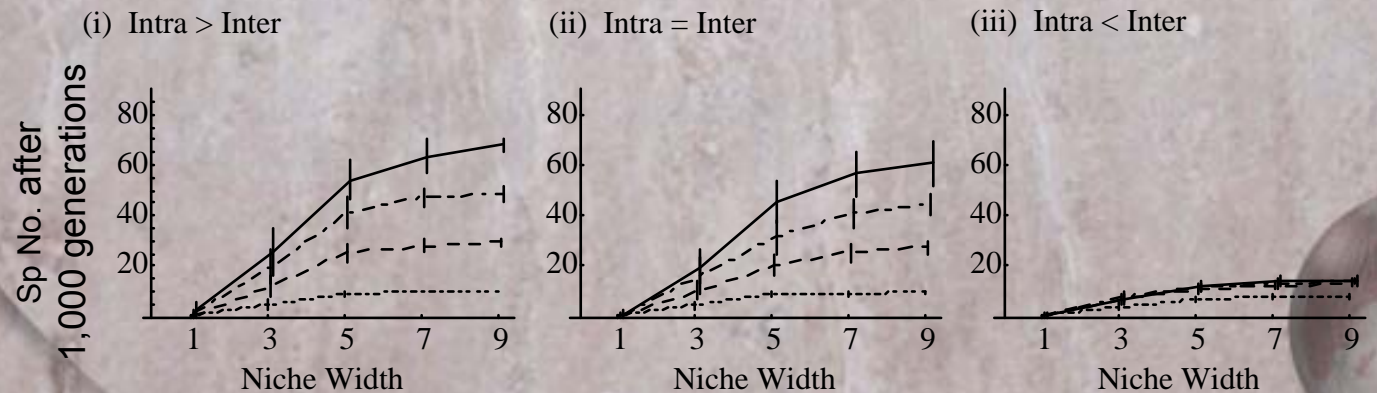
... bet-hedging!

Sexual inheritance under fluctuating environment (2)

(c) **Niche-dependent** fluctuation with **correlation** ($\sigma_r^2 = 0.08$, $c = 0.7$)




(d) Both **niche-independent** and **niche-dependent** fluctuations with **correlation**
($\sigma_r^2 = 0.08$, $\sigma_\omega^2 = 0.04$, $c = 0.7$)



Conclusions

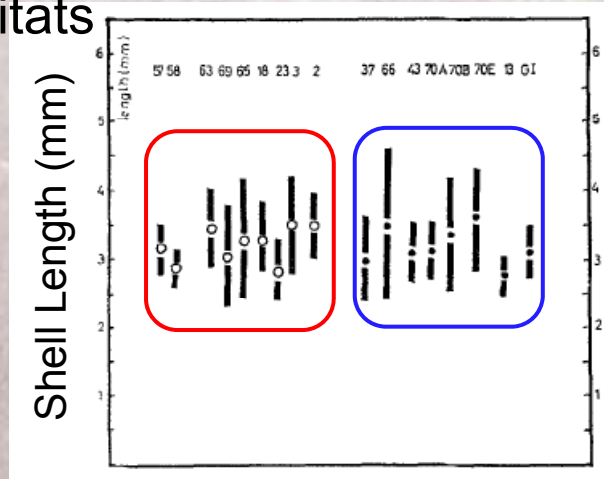
- Flexibility of niche usage possibly promotes species diversity under fluctuating environment
- Even if variance of fluctuation is same, an extent of promotion depends on pattern of fluctuation
- Positive correlation is most significant with both **niche-independent** and **niche-dependent** fluctuation **with autocorrelation**
- The promotion is notable when the initial species number is large, and when intraspecific competition is more intense

The background is a textured, light brown surface, possibly paper or fabric. A large, thick black arc curves from the top left towards the bottom left. In the top left corner, three small, semi-transparent globe icons are arranged in a slight curve. In the bottom right corner, a single larger semi-transparent globe icon is positioned. The text "大謝!" is centered in the middle of the page.

大謝！

- Shell length of Mud Snails (Hydrobiidae) (Fenchel, 1975)

Alone
habitats



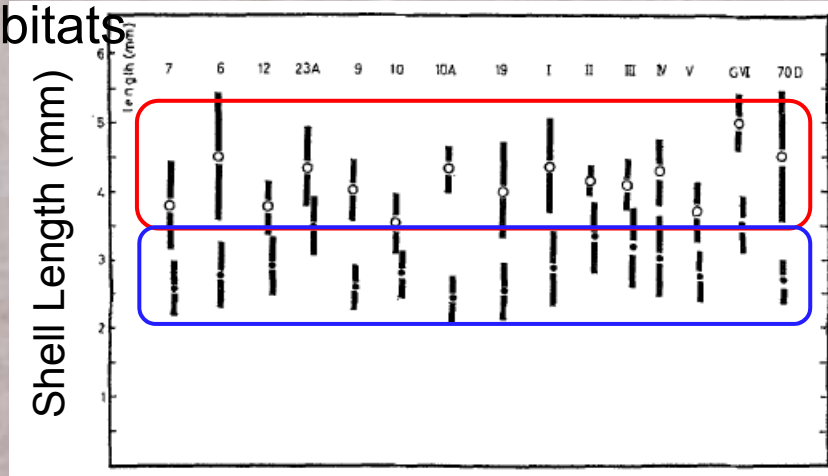
Hydrobia ulvae



Hydrobia ventros



Coexisting
habitats



→ Character displacement

Life history of organisms

- Inheritance phase

Inheritance of individual niche position

- Population growth phase

Change of density due to growth and

competitions

Inheritance phase

- System with sexual inheritance

- Approximate hypergeometric phenotypic model

for diploid organisms

(Shpak and Kondrashov

1999)

- Individual niche position is coded by 6 loci (13

- System without inheritance (genotypes)

- No genetic difference among individuals

- Phenotypic plasticity

Competition kernel

competition between individuals
on distant niche positions

Each individual utilizes
resources on some niche
range



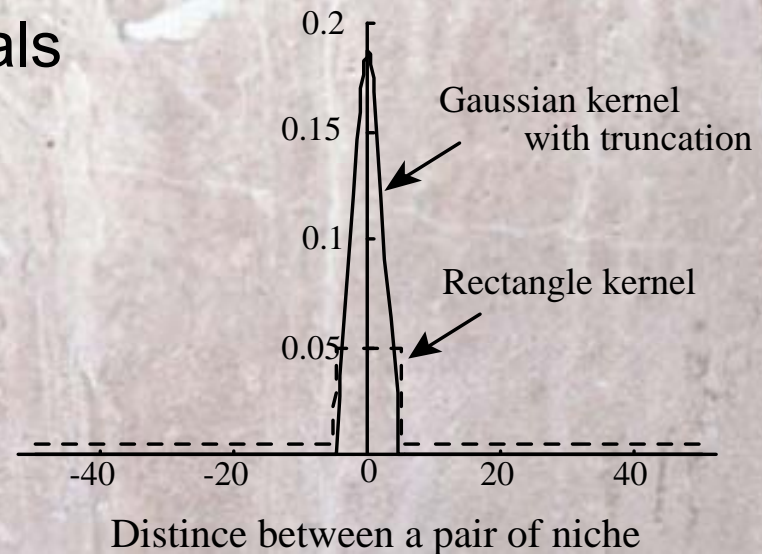
Overlap of resource
utilization

results in competition

Two types of intraspecific variations in niche usage

- **Niche width** ... variation of **individual niche position**
(reflecting individual genotypes)
- **Resource utilization range** ... individual range of resource
usage

(determining competition kernel;
non-genetic character)



Implications

- If the niche flexibility is constant,
the level of species diversity tends to follow the order;
 - (i) constant environment
 - (ii) **niche-dependently** fluctuating environment **without correlation**
 - (iii) **niche-dependently** fluctuating environment **with correlation**
 - (iv) both **niche-dependently** and **niche-dependently** fluctuating environment **with correlation**
 - (v) **niche-independently** fluctuating environment
- A correlation between neighbor niches is also a determinant of regional variations of species diversity