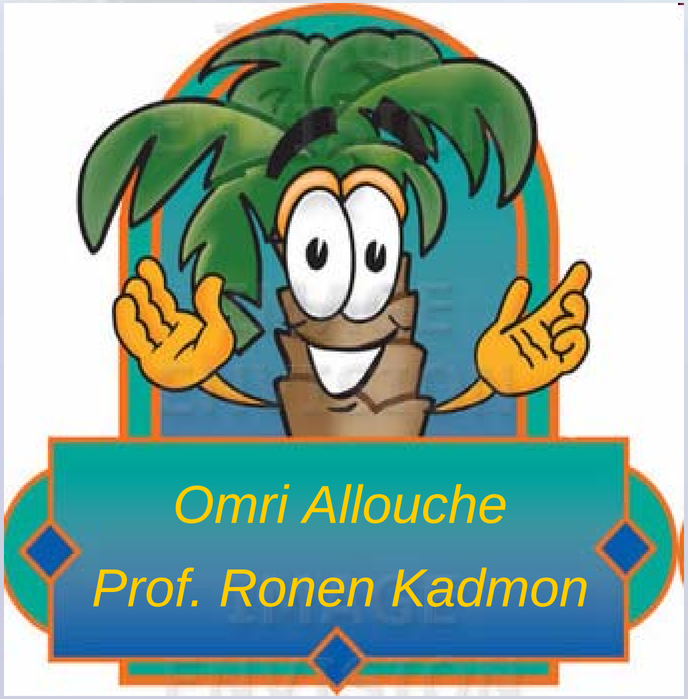
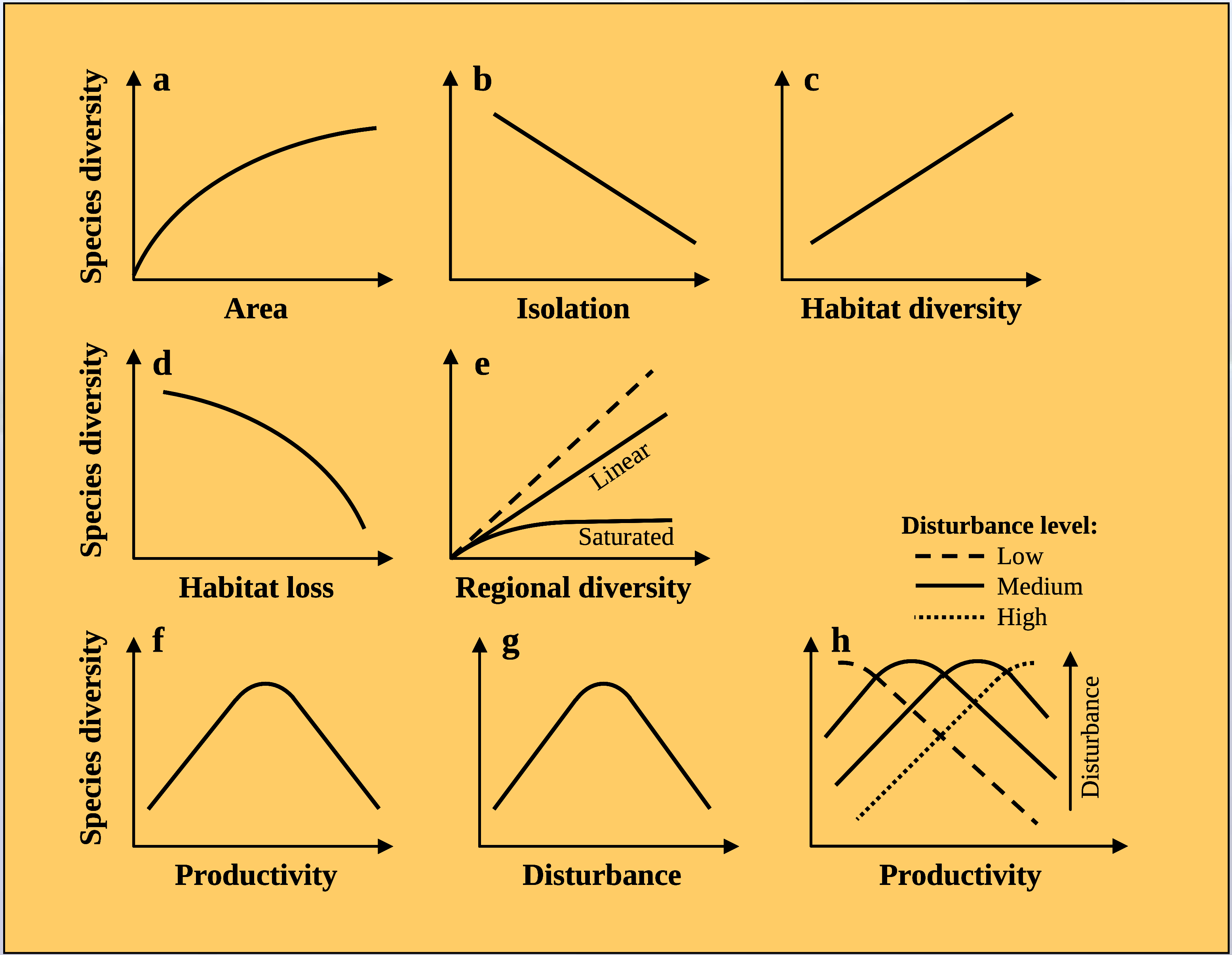
The Markovian Patch-Occupancy (MPO) framework in Community Ecology



Sep 2008

Photos taken from Life, the science of biology, WH Freeman

Semi-universal patterns



The Aim

Develop a general framework for modeling ecological communities:

- *Elementary community dynamics*
- *Simplified representation of communities*
- *Analytic solution*
- *Able to qualitatively produce known patterns of species-diversity*
- *Useful for the study of complex ecological phenomena*

The importance of Demography

- *Species richness is determined by species extinctions and colonizations*

- *Species extinctions and colonizations result from actions of **individuals***

- *The basic elements of ecological communities are individuals*

- *Individuals go through demographic processes of birth, death and migration*

The MPO Framework

General Framework for Modeling Ecological Communities

- *Individual-based*
- *Island receiving immigrants from a mainland*
- *Multiple species*
- *Basic demographic processes:*

  Local Reproduction

  Mortality

  Immigration + Emigration

The MPO Framework

- In a small-enough time interval dt only a single event can take place

- A Markov chain:

$$P\{X_{n+1}=i_{n+1}\,|\,X_n=i_n,\ldots,X_0=i_0\}=P\{X_{n+1}=i_{n+1}\,|\,X_n=i_n\}$$

- Implicit space - Global dispersal

- We wish to find the steady state probability of

$$\vec{N}=(N_1,\ldots,N_S)$$

The Master Equation:

$$\frac{dP(\vec{N})}{dt} = \sum_{k=1}^{S_M} \left(P\left(\vec{N} + \vec{e}_k\right) r^k_{\vec{N}+\vec{e}_k} + P\left(\vec{N} - \vec{e}_k\right) g^k_{\vec{N}-\vec{e}_k} - P\left(\vec{N}\right)\left(g^k_{\vec{N}} + r^k_{\vec{N}}\right)\right)$$

$$(\vec{e}_k)_l = \begin{cases} 1 & \text{if } k = l \\ 0 & \text{otherwise} \end{cases}$$

Possible events:

Increase in the number of individuals of species k

$g^k_{\vec{N}}$ — *Local reproduction*; *Immigration from the mainland*

Decrease in the number of individuals of species k

$r^k_{\vec{N}}$ — *Mortality*; *Emigration*

Analytic Solution

The transition rates are highly flexible, and can incorporate complex ecological phenomena.

We only require that:

$$\frac{g^k_{\vec{N}+\vec{e}_i}}{g^k_{\vec{N}}}\frac{r^i_{\vec{N}+\vec{e}_k+\vec{e}_i}}{r^i_{\vec{N}+\vec{e}_i}}=\frac{g^i_{\vec{N}+\vec{e}_k}}{g^i_{\vec{N}}}\frac{r^k_{\vec{N}+\vec{e}_k+\vec{e}}}{r^k_{\vec{N}+\vec{e}_k}}$$

This holds for many interesting cases, and can be easily checked for any transition rates.

Analytic Solution

The steady-state probability

of state

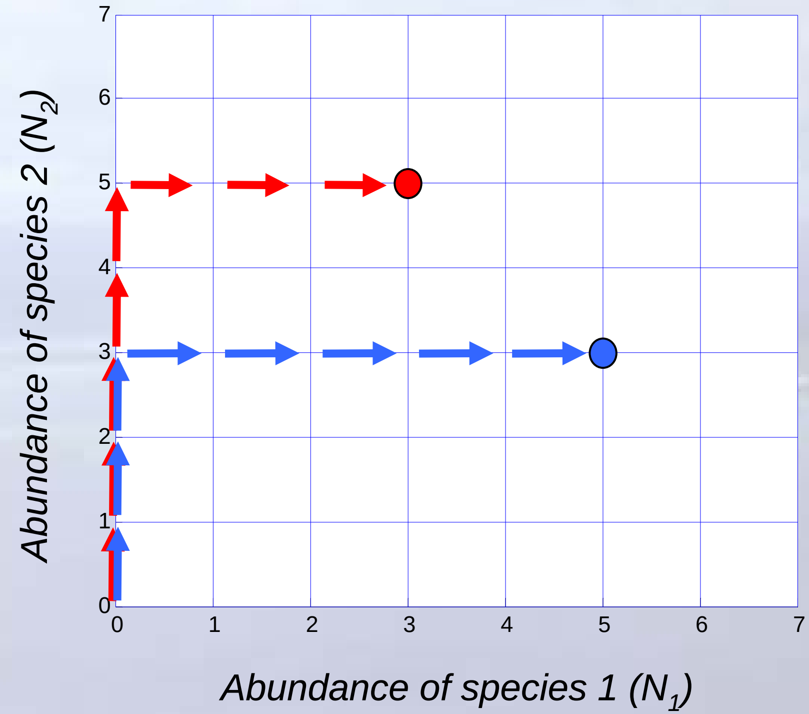
$$\vec{N} = (N_1, \ldots, N_{S_M})$$

is given by:

$$P_{MPO}(\vec{N}) = \left(\sum_{\vec{N}} X(\vec{N}) \right)^{-1} X(\vec{N})$$

$$X(\vec{N}) = \prod_{k=1}^{S_M} \prod_{m=0}^{N_k - 1} \frac{g^k_{\vec{N}_{\{1,\ldots,k-1\}} + m * \vec{e}_k}}{r^k_{\vec{N}_{\{1,\ldots,k-1\}} + (m+1) * \vec{e}_k}}$$

$$X((0,0,\ldots,0)) \square 1$$



$$\vec{N}_{\{1,\ldots,n\}} = \begin{cases} N_k & \text{if k} \le \text{n} \\ 0 & \text{otherwise} \end{cases}$$

$$\frac{P_{MPO}(\vec{N}+\vec{e}_k)}{P_{MPO}(\vec{N})} = \frac{g^k_{\vec{N}_{\{1,\dots,k-1\}}+N_k*\vec{e}_k}}{r^k_{\vec{N}_{\{1,\dots,k-1\}}+(N_k+1)*\vec{e}_k}} * \prod_{i=k+1}^{S_M}\prod_{m=0}^{N_i-1}\left(\frac{g^i_{\vec{N}_{\{1,\dots,i-1\}}+\vec{e}_k+m*\vec{e}_i}}{r^i_{\vec{N}_{\{1,\dots,i-1\}}+\vec{e}_k+(m+1)*\vec{e}_i}} \Bigg/ \frac{g^i_{\vec{N}_{\{1,\dots,i-1\}}+m*\vec{e}_i}}{r^i_{\vec{N}_{\{1,\dots,i-1\}}+(m+1)*\vec{e}_i}} \right) = \frac{g^k_{\vec{N}_{\{1,\dots,k\}}}}{r^k_{\vec{N}_{\{1,\dots,k\}}+\vec{e}_k}} * \prod_{i=k+1}^{S_M}\prod_{m=0}^{N_i-1} \frac{g^i_{\vec{N}_{\{1,\dots,i-1\}}+\vec{e}_k+m*\vec{e}_i}}{g^i_{\vec{N}_{\{1,\dots,i-1\}}+m*\vec{e}_i}} \frac{r^i_{\vec{N}_{\{1,\dots,i-1\}}+(m+1)*\vec{e}_i}}{r^i_{\vec{N}_{\{1,\dots,i-1\}}+\vec{e}_k+(m+1)*\vec{e}_i}}$$

$$\prod_{i=k+1}^{S_M}\prod_{m=0}^{N_i-1} \frac{g^i_{\vec{N}_{\{1,\dots,i-1\}}+m*\vec{e}_i+\vec{e}_k}}{g^i_{\vec{N}_{\{1,\dots,i-1\}}+m*\vec{e}_i}} \frac{r^i_{\vec{N}_{\{1,\dots,i-1\}}+(m+1)*\vec{e}_i}}{r^i_{\vec{N}_{\{1,\dots,i-1\}}+(m+1)*\vec{e}_i+\vec{e}_k}} = \prod_{i=k+1}^{S_M}\prod_{m=0}^{N_i-1} \frac{g^k_{\vec{N}_{\{1,\dots,i-1\}}+(m+1)*\vec{e}_i}}{g^k_{\vec{N}_{\{1,\dots,i-1\}}+m*\vec{e}_i}} \frac{r^k_{\vec{N}_{\{1,\dots,i-1\}}+m*\vec{e}_i+\vec{e}_k}}{r^k_{\vec{N}_{\{1,\dots,i-1\}}+(m+1)*\vec{e}_i+\vec{e}_k}} =$$

$$\prod_{i=k+1}^{S_M} \frac{g^k_{\vec{N}_{\{1,\dots,i-1\}}+N_i*\vec{e}_i}}{g^k_{\vec{N}_{\{1,\dots,i-1\}}}} \frac{r^k_{\vec{N}_{\{1,\dots,i-1\}}+\vec{e}_k}}{r^k_{\vec{N}_{\{1,\dots,i-1\}}+N_i*\vec{e}_i+\vec{e}_k}} = \frac{g^k_{\vec{N}}}{g^k_{\vec{N}_{\{1,\dots,k\}}}} \frac{r^k_{\vec{N}_{\{1,\dots,k\}}+\vec{e}_k}}{r^k_{\vec{N}+\vec{e}_k}}$$

$$P_{MPO}(\vec{N})g^k_{\vec{N}} = P_{MPO}(\vec{N}+\vec{e}_k)r^k_{\vec{N}+\vec{e}_k}$$

"detailed balance"

$$P(a)P_{a\to b} = P(b)P_{b\to a}$$

Analytic Solution

Steady-state distribution:

$$P_{MPO}(\vec{N}) = \left(\sum_{\vec{N}} X(\vec{N}) \right)^{-1} X(\vec{N}) \qquad X(\vec{N}) = \prod_{k=1}^{S_M} \prod_{m=0}^{N_k - 1} \frac{g^k_{\vec{N}_{\{1,\dots,k-1\}} + m * \vec{e}_k}}{r^k_{\vec{N}_{\{1,\dots,k-1\}} + (m+1) * \vec{e}_k}}$$

Community size distribution:

$$p(J) = \sum_{\vec{N}:\ \sum_k N_k = J} P_{PO}(\vec{N})$$

Abundance distribution:

$$P_k^{local}(n) = \sum_{\vec{N}:\ N_k = n} P_{PO}(\vec{N})$$

Species Richness:

$$SR = \sum_{k=1}^{S_M} (1 - P_k^{local}(0))$$

Multispecies community with competition for space

- *Island of area A*
- *Multiple species*
- *Rates of:*

    Birth ⇨ b_k

    Death ⇨ d_k

    Immigration ⇨ i_k

- *Relative regional abundance* P_k^{reg}
- *Individuals only establish in vacant sites*

Mortality:

$$d_k N_k dt$$

$$r_{\vec{N}}^k = d_k N_k$$

Local reproduction:

$$b_k N_k \frac{A-J}{A} dt$$

Immigration from the regional pool:

$$i_k P_k^{reg} (A-J) dt$$

$$g_{\vec{N}}^k = \left(b_k N_k + i_k P_k^{reg} A\right) \frac{A-J}{A}$$

The solution:

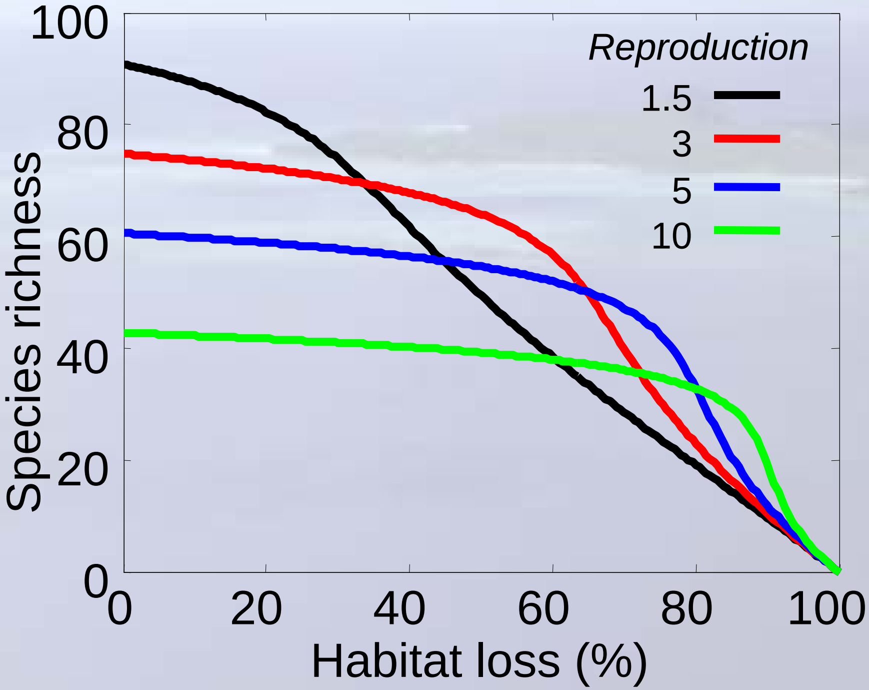
$$X(\vec{N}) = \frac{(A-J+1)_J}{A^J} \prod_{k=1}^{S_M} \left(\frac{b_k}{d_k}\right)^{N_k} \frac{\left(\beta_k P_k^{reg}\right)_{N_k}}{N_k!}$$

$$\beta_k = \frac{i_k}{b_k} A$$

$$(x)_y = \prod_{i=0}^{y-1} (x+i)$$

Habitat Loss

“The greatest existing threat to biodiversity “



$$g_{\vec{N}}^{k} = (b_k N_k + i_k P_k^{reg} A)\frac{A - A_D - J}{A}$$

$$r_{\vec{N}}^{k} = d_k N_k$$

A_D = *The number of destroyed sites*

$$X(\vec{N}) = \frac{(A - A_D - J + 1)_J}{A^J} \prod_{k=1}^{S_M} \left(\frac{b_k}{d_k}\right)^{N_k} \frac{\left(\beta_k P_k^{reg}\right)_{N_k}}{N_k!}, \quad \beta_k = \frac{i_k}{b_k} A$$

Habitat Heterogeneity and niche partitioning

1. *An island consisting of A sites, divided among H habitats*
2. *Each species is able to establish and persist in only one habitat*
3. *Individuals disperse and immigrate to random sites*

Habitat Heterogeneity

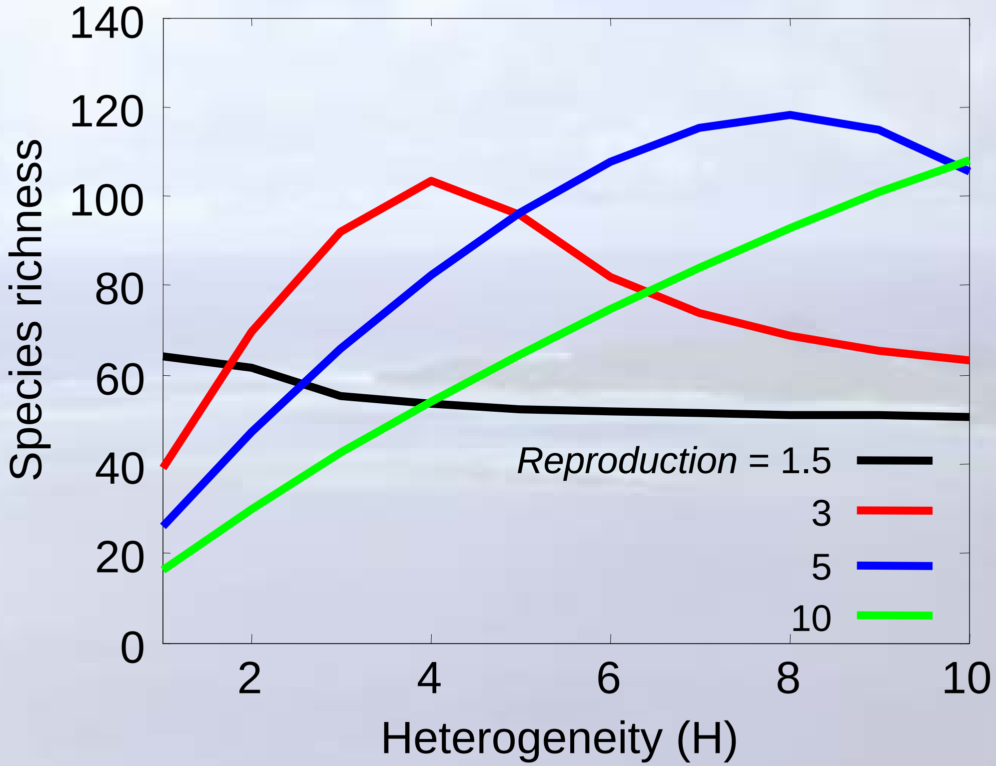
$$g_{\vec{N}}^{k} = (b_k N_k + i_k P_k^{reg} A)\frac{A_{H_k} - J_{H_k}}{A}$$

$$r_{\vec{N}}^{k} = d_k N_k$$

A_{H_k} total area

J_{H_k} community size

in habitat of species *k*



$$X(\vec{N}) = \frac{1}{A^J}\prod_{h=1}^{H}\left(A_h - J_h + 1\right)_{J_h}\prod_{k=1}^{S_M}\left(\frac{b_k}{d_k}\right)^{N_k}\frac{\left(\beta_k P_k^{reg}\right)_{N_k}}{N_k\,!} \qquad \beta_k = \frac{i_k}{b_k}A$$

and *H* is the total number of habitats

Kadmon and Allouche 2007 Am Nat

Habitat Preference

Offspring arrive in suitable habitats more than in unsuitable habitats

due to active site selection or environmental autocorrelation and limited dispersal

$$g_{\vec{N}}^{k} = (b_k N_k + i_k P_k^{reg} A) \frac{A_{H_k} - J_{H_k}}{A_{H_k}} \frac{v_k A_{H_k}}{v_k A_{H_k} + (A - A_{H_k})}$$

$$r_{\vec{N}}^{k} = d_k N_k$$

$$X(\vec{N}) = \prod_{h=1}^{H} \left(A_h - J_h + 1\right)_{J_h} \prod_{k=1}^{S_M} \left(\frac{b_k}{d_k}\right)^{N_k} \left(\frac{v_k}{A_{H_k}(v_k - 1) + A}\right)^{N_k} \frac{\left(\beta_k P_k^{reg}\right)_{N_k}}{N_k!}$$

$$\beta_k = \frac{i_k}{b_k} A$$

Non-random Dispersal

Offspring tend to arrive to vacant sites more than to occupied sites

$$g_{\vec{N}}^{k} = (b_k N_k + i_k P_k^{reg} A)\frac{v(A-J)}{v(A-J)+J}$$

$$r_{\vec{N}}^{k} = d_k J_k$$

$$X(\vec{N}) = \frac{(A-J+1)_J}{(\gamma A)_J}\gamma^J \prod_{k=1}^{S_M}\left(\frac{b_k}{d_k}\right)^{N_k}\frac{\left(\beta_k P_k^{reg}\right)_{N_k}}{N_k!}$$

$$\beta_k = \frac{i_k}{b_k}A \qquad \gamma = \frac{v}{1-v}$$

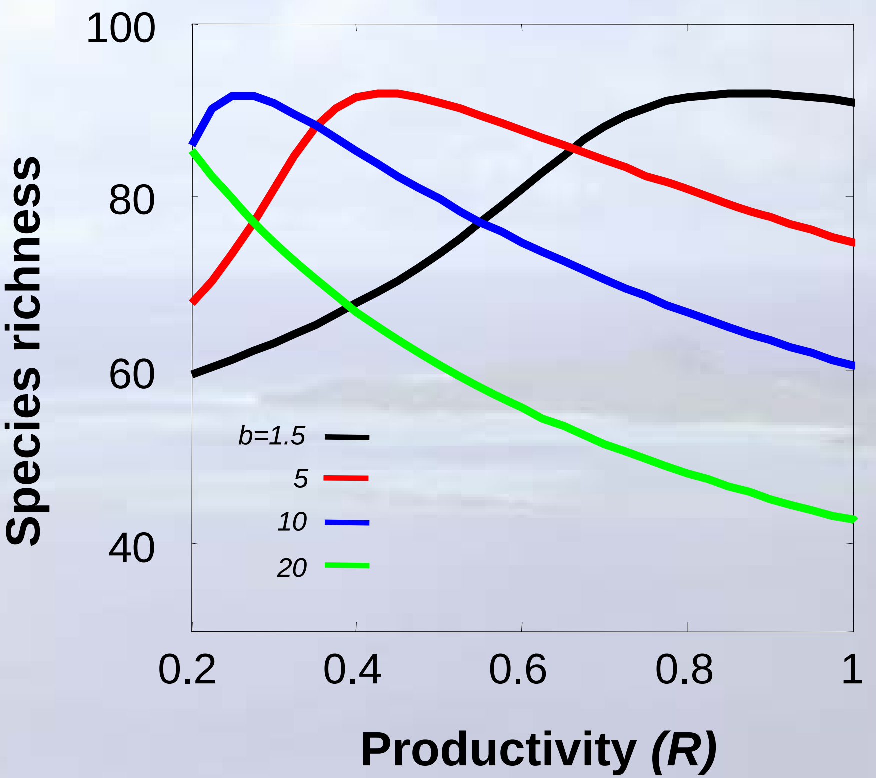
Productivity

Increased reproduction due to more resources

$$g^k_{\vec{N}} = (Rb_k N_k + i_k P^{reg}_k A)\frac{A-J}{A}$$

$$r^k_{\vec{N}} = d_k J_k$$

R = Productivity



$$X(\vec{N}) = \frac{(A-J+1)_J}{A^J}\prod_{k=1}^{S_M}\left(\frac{b_k}{d_k}\right)^{N_k}\frac{\left(\beta_k P^{reg}_k\right)_{N_k}}{N_k!}$$

$$\beta_k = \frac{i_k}{b_k}A$$

$$(x)_y = \prod_{i=0}^{y-1}(x+i)$$

Allee Effect

Reduced reproduction of small populations

due to mate finding, predation, aggregation, environmental modification…

$$g_{\vec{N}}^{k} = (b_k N_k \frac{N_k}{N_k + \mu_k} + i_k P_k^{reg} A)\frac{A-J}{A}$$

$$r_{\vec{N}}^{k} = d_k N_k$$

$$X(\vec{N}) = \frac{(A-J+1)_J}{A^J} \prod_{k=1}^{S_M} \left(\frac{b_k}{d_k}\right)^{N_k} \frac{\prod_{m=0}^{N_k-1}\left(m^2 + \beta_k P_k^{reg} m + \beta_k P_k^{reg} \mu_k\right)}{N_k!(\mu_k)_{N_k}}$$

$\beta_k = \frac{i_k}{b_k} A,\quad \mu_k$ the level of Allee effect for species *k*

Population-Level Density Dependence

Increased mortality of large populations

due to parasites and diseases, predation, environmental modification…

$$g_{\vec{N}}^{k} = (b_k N_k + i_k P_k^{reg} A)\frac{A-J}{A}$$

$$r_{\vec{N}}^{k} = \left(d_k + (b_k - d_k)\frac{N_k}{K_k} \right) N_k$$

$$X(\vec{N}) = \frac{(A-J+1)_J}{A^J} \prod_{k=1}^{S_M} \left(\frac{b_k}{\gamma_k}\right)^{N_k} \frac{\left(\beta_k P_k^{reg}\right)_{N_k}}{N_k!\left(\frac{d_k}{\gamma_k}+1\right)_{N_k}} \qquad \beta_k = \frac{i_k}{b_k}A, \quad \gamma_k = \frac{b_k - d_k}{K_k}$$

Community-Level Carrying Capacity

Increased mortality of large communities

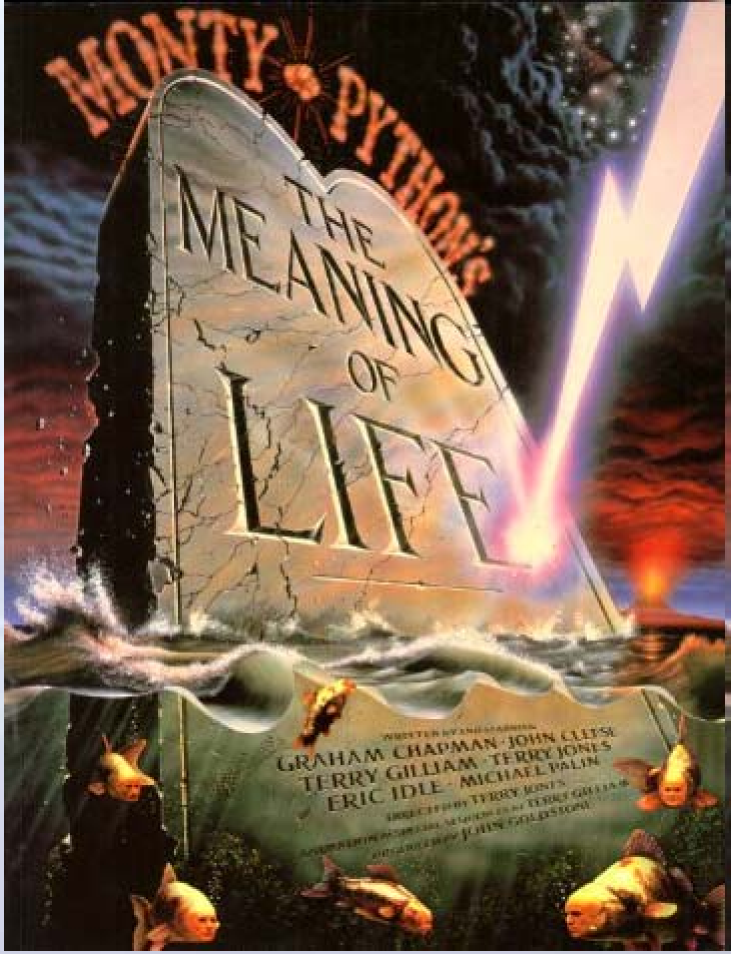
due to parasites and diseases, predation, environmental modification…

$$g^k_{\vec{N}} = b_k N_k + i_k P_k^{reg} A$$

$$r^k_{\vec{N}} = d_k N_k \frac{J}{K}$$

$$X(\vec{N}) = \frac{K^J}{J!} \prod_{k=1}^{S_M} \left(\frac{b_k}{d_k} \right)^{N_k} \frac{\left(\beta_k P_k^{reg} \right)_{N_k}}{N_k!} \qquad \beta_k = \frac{i_k}{b_k} A$$

The Meaning of Life

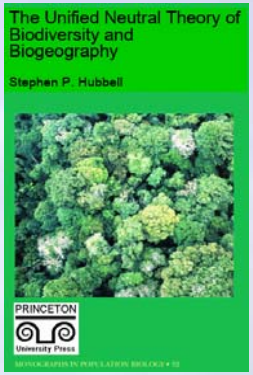


$$g^k_{\vec{N}} = \iint_{\$@\#\$!} (b_k N_k + i_k P_k^{reg} A) \lim_{x \to \infty}\left(\frac{\sqrt[5.14]{N_k \pi \otimes \hat{\theta}}}{Bugs\_Bunny}\right) \frac{A - A_D - J}{A} \frac{n!}{r!(n-r)!} \frac{-b \pm \sqrt{b^2 - 4ac}}{2a} dt$$

$$r^k_{\vec{N}} = d_k N_k$$

42

General Framework for Neutral Models



Hubbell’s mainland-island model *(Hubbell 2001)*

$$g_{\vec{N}}^{k} = (bN_k + iP_k^{reg} A)\frac{A - J}{A}$$

$$r_{\vec{N}}^{k} = dN_k$$

where: $b \propto dA$, $i \propto dA$

$$m = \frac{iA}{iA + b(A-1)}$$

Independent neutral species *(Volkov et al. 2003, 2005 Nature, He 2005 Func Ecol., Etienne et al. 2007 JTB)*

$$g_{\vec{N}}^{k} = bN_k + iP_k^{reg}$$

$$r_{\vec{N}}^{k} = dN_k$$

Community-Level Density-Dependence *(Haegeman & Etienne 2008 JTB)*

$$g_{\vec{N}}^{k} = b(J)N_k + i(J)P_k^{reg}$$

$$r_{\vec{N}}^{k} = d(J)N_k$$

The MPO Framework - Summary

- General framework for modeling ecological communities
  - Individual-based
  - Basic demographic processes
- Demographic differences among species
- Analytically tractable
- A general framework for neutral null models
- Extends patch-occupancy theory

The MPO Framework

- *Highly flexible*
- *Useful for the study of complex ecological phenomena*
- *Able to qualitatively produce leading patterns of species-diversity*
- *Useful for other fields (???)*