Chapter 10: Co-existence in large communities

We have derived resource competition models from consumption models.

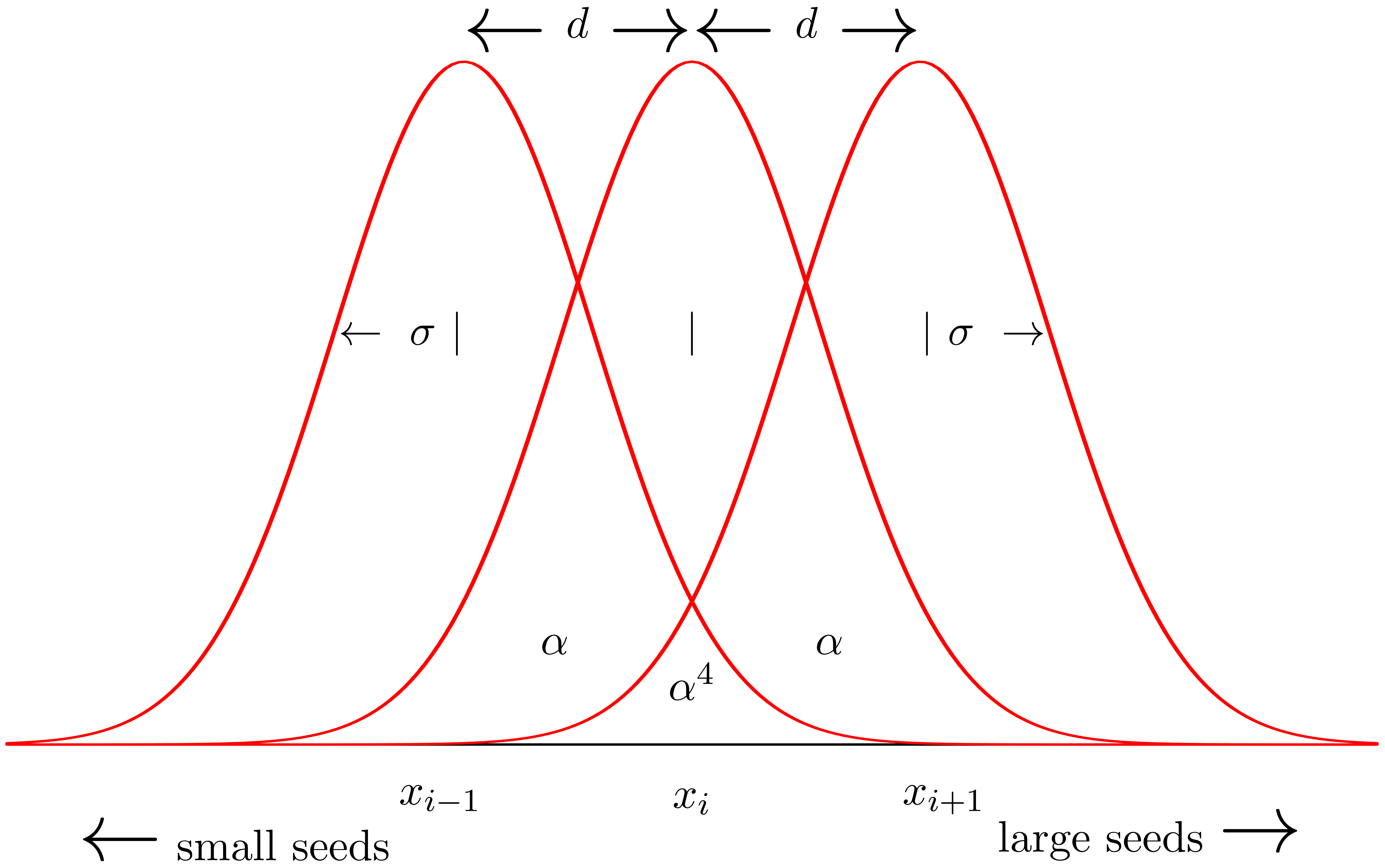
This lead to competitive exclusion: no more than n consumers on n resources.

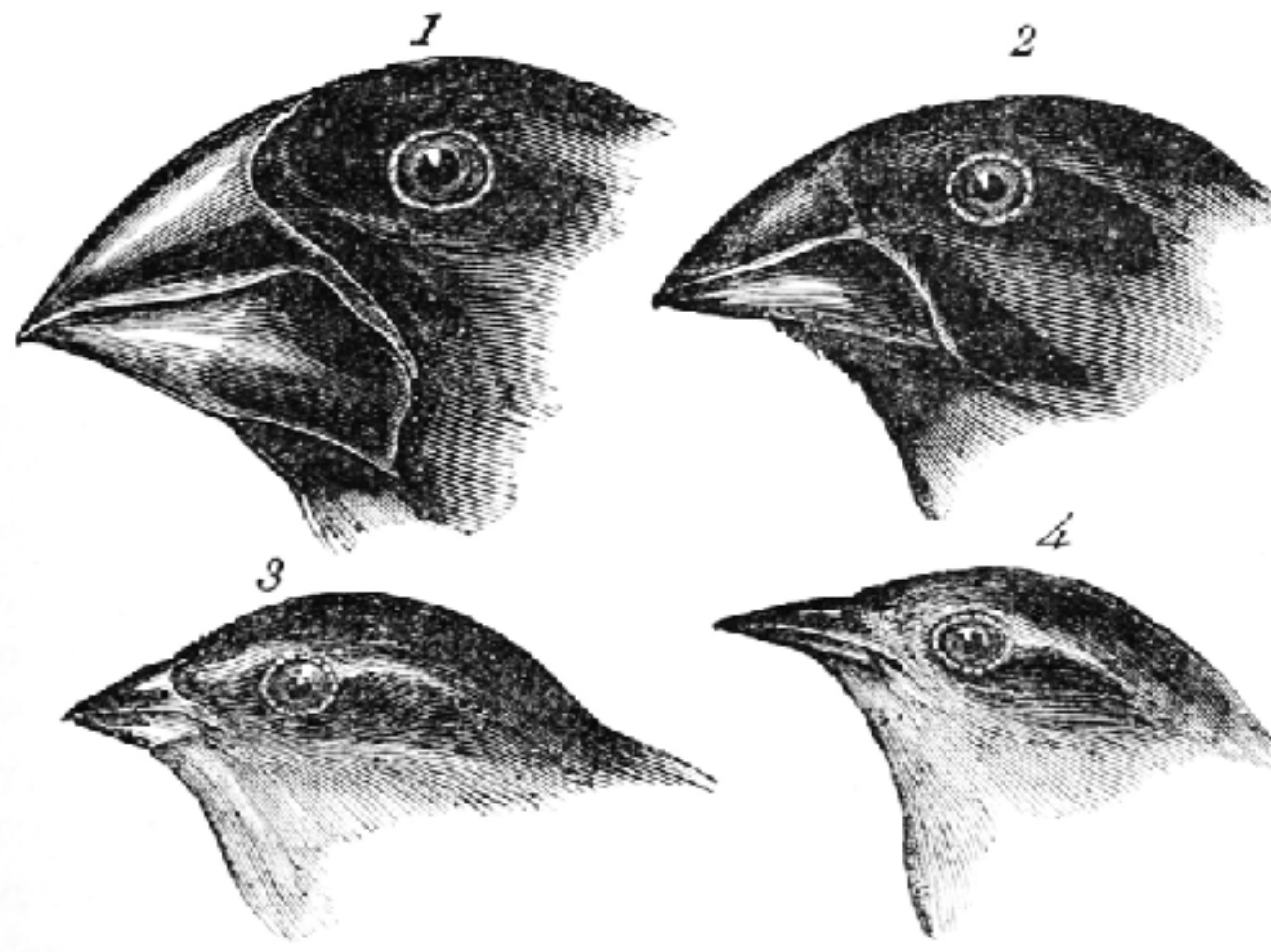
Steady state result: non-equilibrium co-existence.

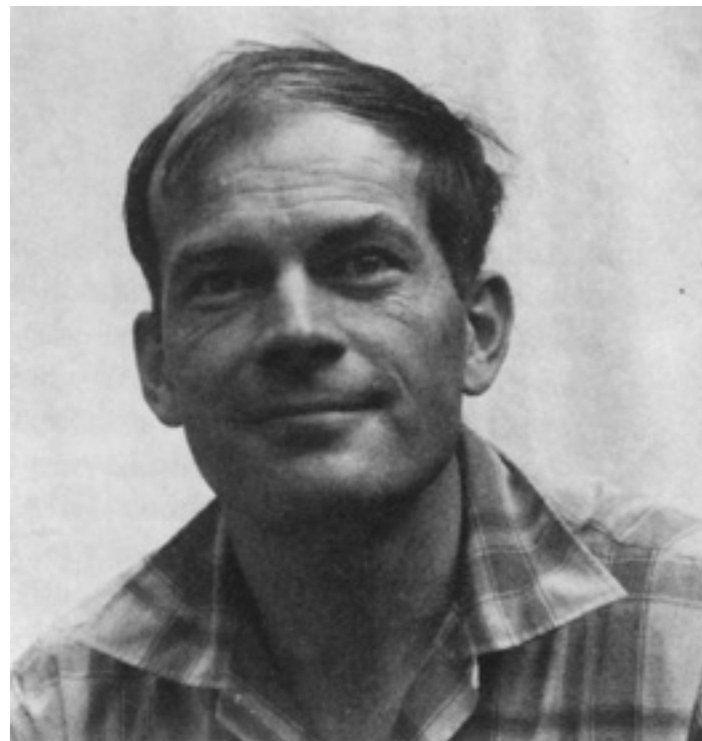
Chapter 10: various examples of high-dimensional models.

Chemostats and Lotka-Volterra models will be the starting point.

Niche space models







Robert MacArthur

Niche space model

$$\alpha = \frac{\int_{-\infty}^{\infty} \mathrm{e}^{-\frac{x^2}{2\sigma^2}} \times \mathrm{e}^{-\frac{[x-d]^2}{2\sigma^2}}\,\mathrm{d}x}{\int_{-\infty}^{\infty} \mathrm{e}^{-\frac{x^2}{2\sigma^2}} \times \mathrm{e}^{-\frac{x^2}{2\sigma^2}}\,\mathrm{d}x} = \mathrm{e}^{-\left(\frac{d}{2\sigma}\right)^2}$$

hence $\mathrm{e}^{-\left(\frac{2d}{2\sigma}\right)^2} = \mathrm{e}^{-4\left(\frac{d}{2\sigma}\right)^2} = \alpha^4$

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = rN_i\left(1 - \sum_{j=1}^{n} A_{ij}N_j\right)$$

with

$$A = \begin{pmatrix} 1 & \alpha & \alpha^4 & \alpha^9 & \alpha^{16} & \dots & \\ \alpha & 1 & \alpha & \alpha^4 & \alpha^9 & \dots & \\ \alpha^4 & \alpha & 1 & \alpha & \alpha^4 & \dots & \\ \alpha^9 & \alpha^4 & \alpha & 1 & \alpha & \alpha^4 & \dots \\ \dots & & & & & & \end{pmatrix}$$

n=2, 3, 4, ….

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = rN_1(1 - N_1 - \alpha N_2) \quad \text{and} \quad \frac{\mathrm{d}N_2}{\mathrm{d}t} = rN_2(1 - N_2 - \alpha N_1)$$

$$\begin{aligned}
\frac{\mathrm{d}N_1}{\mathrm{d}t} &= rN_1(1 - N_1 - \alpha N_2 - \alpha^4 N_3) \ , \\
\frac{\mathrm{d}N_2}{\mathrm{d}t} &= rN_2(1 - N_2 - \alpha[N_1 + N_3]) \ , \\
\frac{\mathrm{d}N_3}{\mathrm{d}t} &= rN_3(1 - N_3 - \alpha N_2 - \alpha^4 N_1) \ .
\end{aligned}$$

$$\bar{N}_{1/3} = \frac{1}{1+\alpha^4}$$

Test invasion:

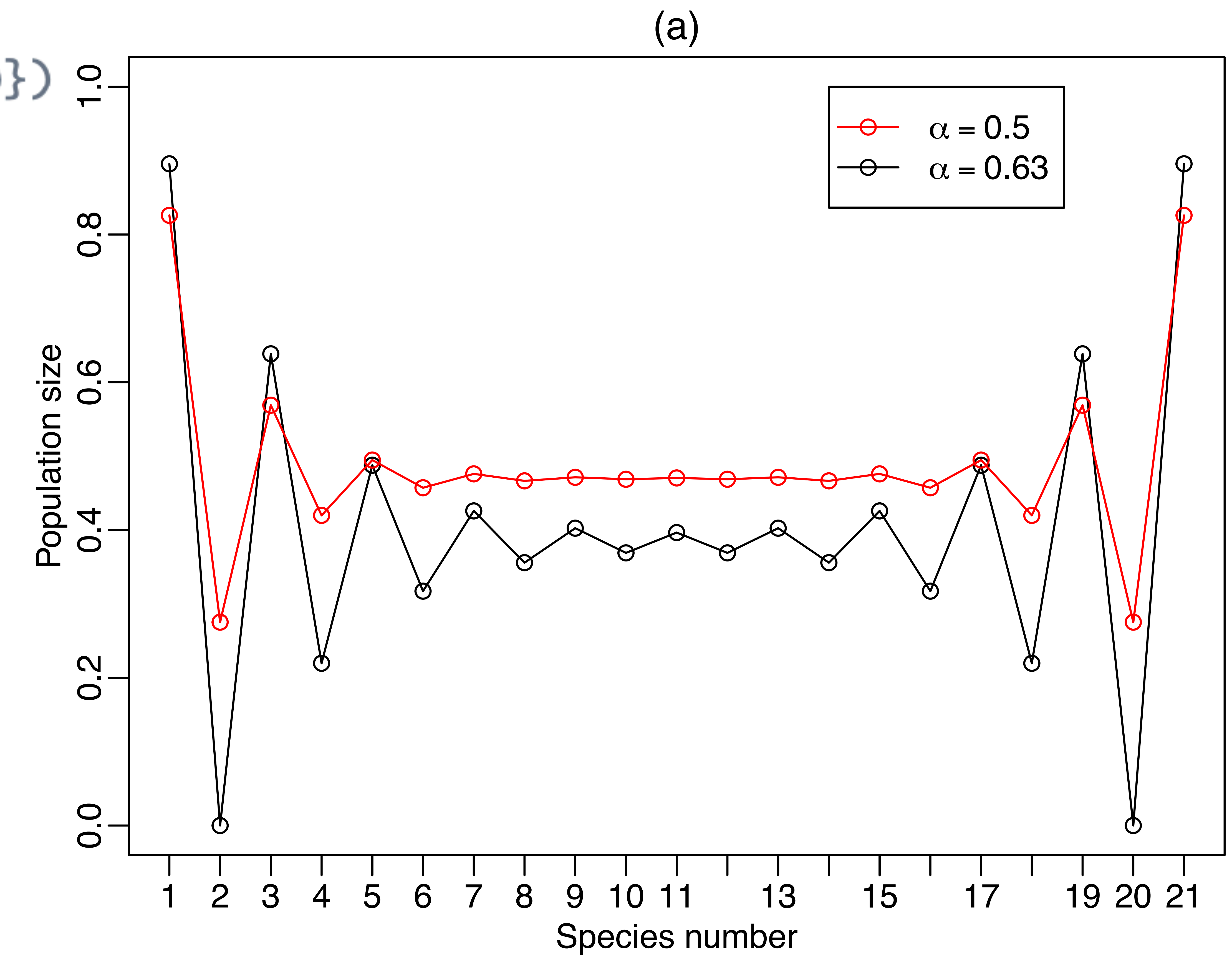
$$\frac{\mathrm{d}N_2}{\mathrm{d}t} \simeq rN_2(1 - \alpha 2\bar{N})$$

$$1 - \frac{2\alpha}{1+\alpha^4} > 0 \quad \text{or} \quad 1 + \alpha^4 - 2\alpha > 0$$

R-script: niche.R

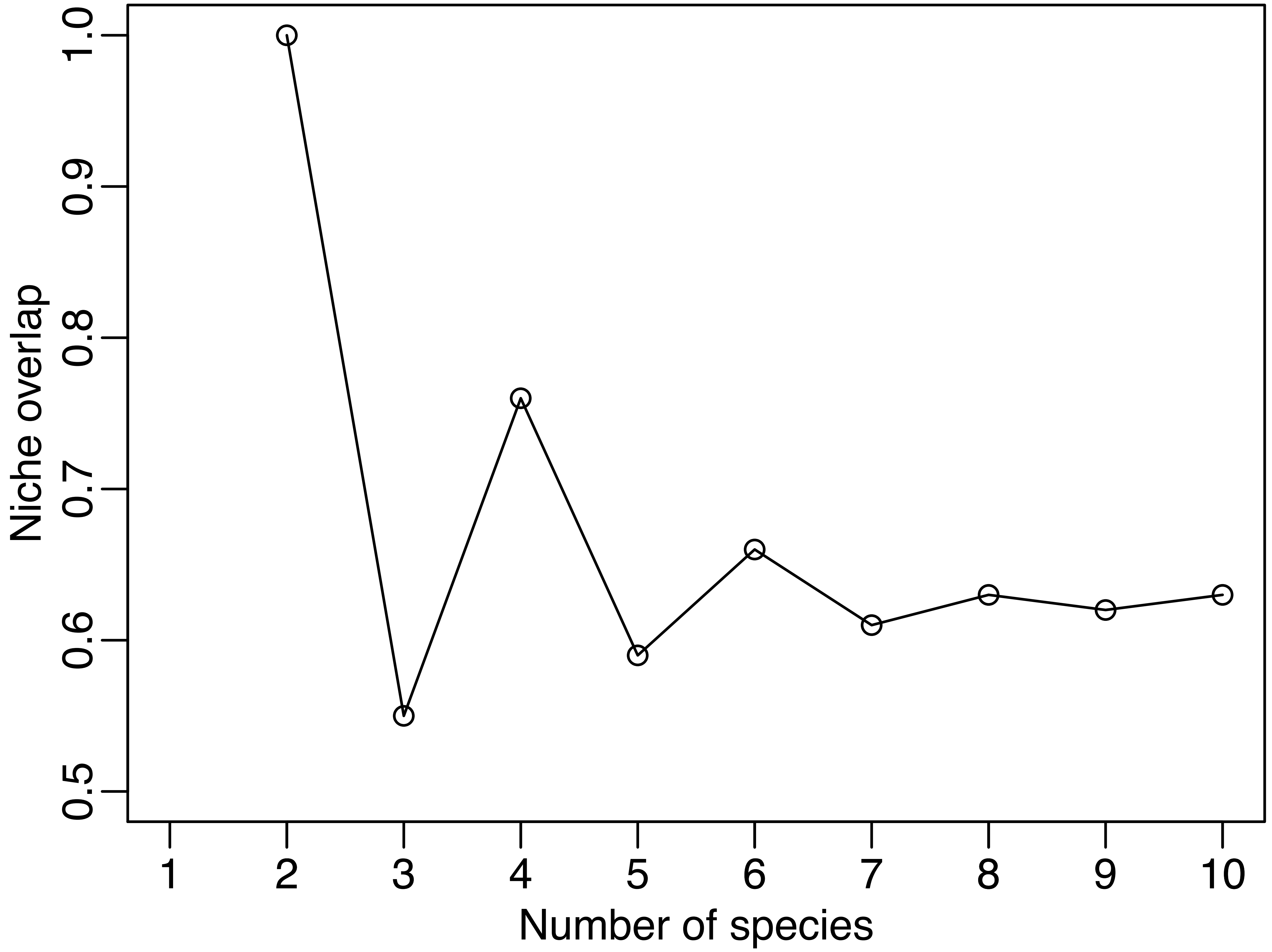
```r
model <- function(t, state, parms) {
  with(as.list(c(state,parms)), {
    N <- state
    S <- A %*% N  # R code for matrix x vector multiplication
    dN <- r*N*(1 - S)
    return(list(dN))
  })
}

makeMatrix <- function(alpha) {
  seqAlpha <- sapply(seq(from=0,n-1),function(i){alpha^(i^2)})
  A <- matrix(0,nrow=n,ncol=n)
  for (i in seq(n)) {
    A[i,i:n] <- seqAlpha[1:(n-i+1)]
    A[i,1:i] <- rev(seqAlpha)[(n-i+1):n]
  }
  return(A)
}
```

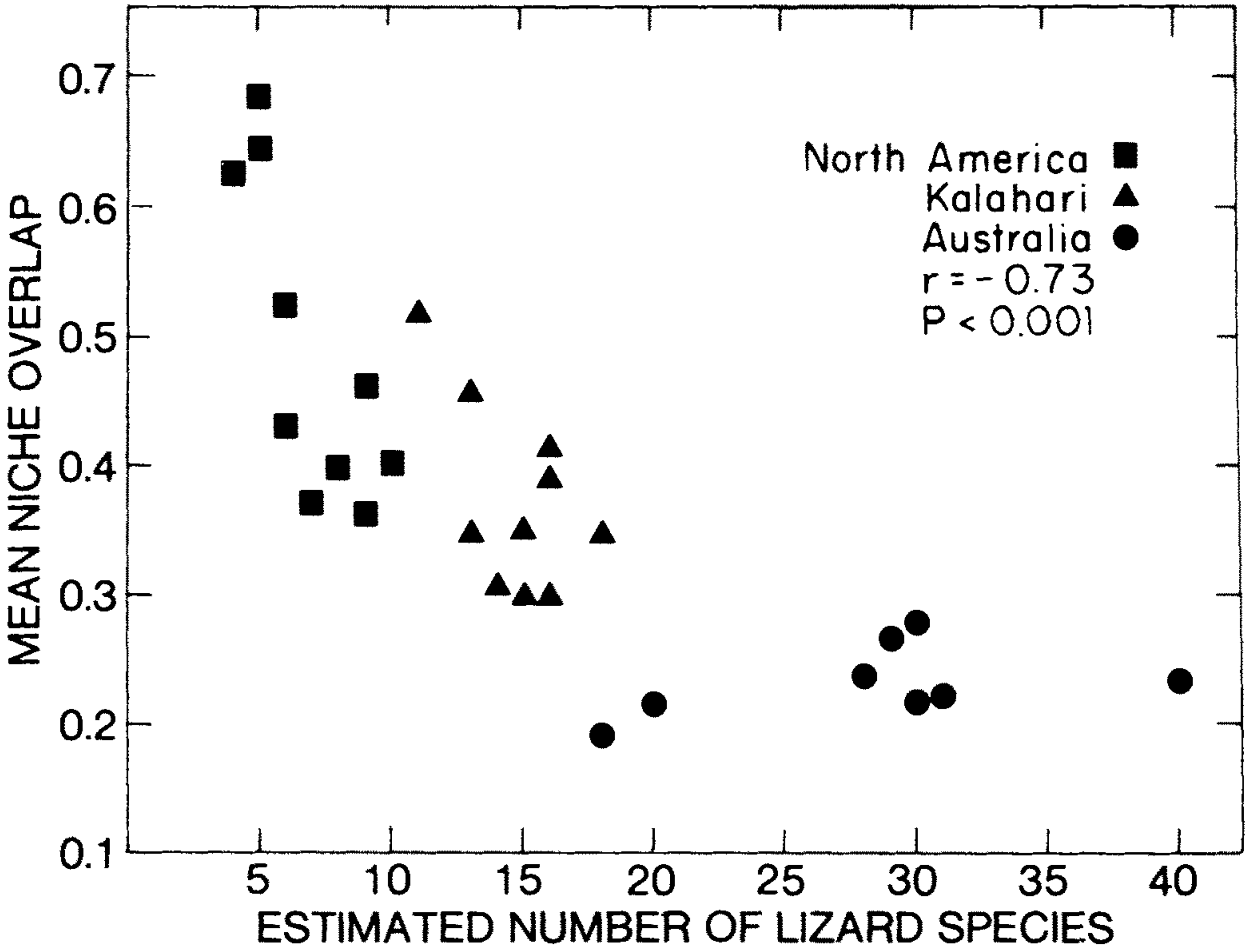
$$A = \begin{pmatrix} 1 & \alpha & \alpha^4 & \alpha^9 & \alpha^{16} & \dots & \\ \alpha & 1 & \alpha & \alpha^4 & \alpha^9 & \dots & \\ \alpha^4 & \alpha & 1 & \alpha & \alpha^4 & \dots & \\ \alpha^9 & \alpha^4 & \alpha & 1 & \alpha & \alpha^4 & \dots \\ \dots & & & & & & \end{pmatrix}$$



R-script: niche.R

```
findMaxAlpha <- function(n) {
  n <<- n
  s <- rep(0.1,n)
  names(s) <- paste("N",seq(1,n),sep="")
  for (alpha in seq(0,1,0.01)) {
    A <<- makeMatrix(alpha)
    f <- newton(run(state=s,timeplot=FALSE),atol=1e-20)
    if (min(f) <= 0) return(alpha)
  }
  return(1)
}
```





Pianka 1974

Why $\alpha \to 0.63$?

$$A = \begin{pmatrix} 1 & \alpha & \alpha^4 & \alpha^9 & \alpha^{16} & \dots & \\ \alpha & 1 & \alpha & \alpha^4 & \alpha^9 & \dots & \\ \alpha^4 & \alpha & 1 & \alpha & \alpha^4 & \dots & \\ \alpha^9 & \alpha^4 & \alpha & 1 & \alpha & \alpha^4 & \dots \\ \dots & & & & & & \end{pmatrix}$$

Consider the boundary:

$$\begin{aligned} \frac{\mathrm{d}N_1}{\mathrm{d}t} &= N_1(1 - N_1 - \alpha N_2) \ , \\ \frac{\mathrm{d}N_2}{\mathrm{d}t} &= N_2(1 - \alpha N_1 - N_2 - \alpha N_3) \ , \\ \frac{\mathrm{d}N_3}{\mathrm{d}t} &= N_3(1 - \alpha N_2 - N_3 - \alpha N_4) \simeq N_3(1 - \alpha N_2 - N_3 - \alpha \bar{N}) \ , \end{aligned}$$

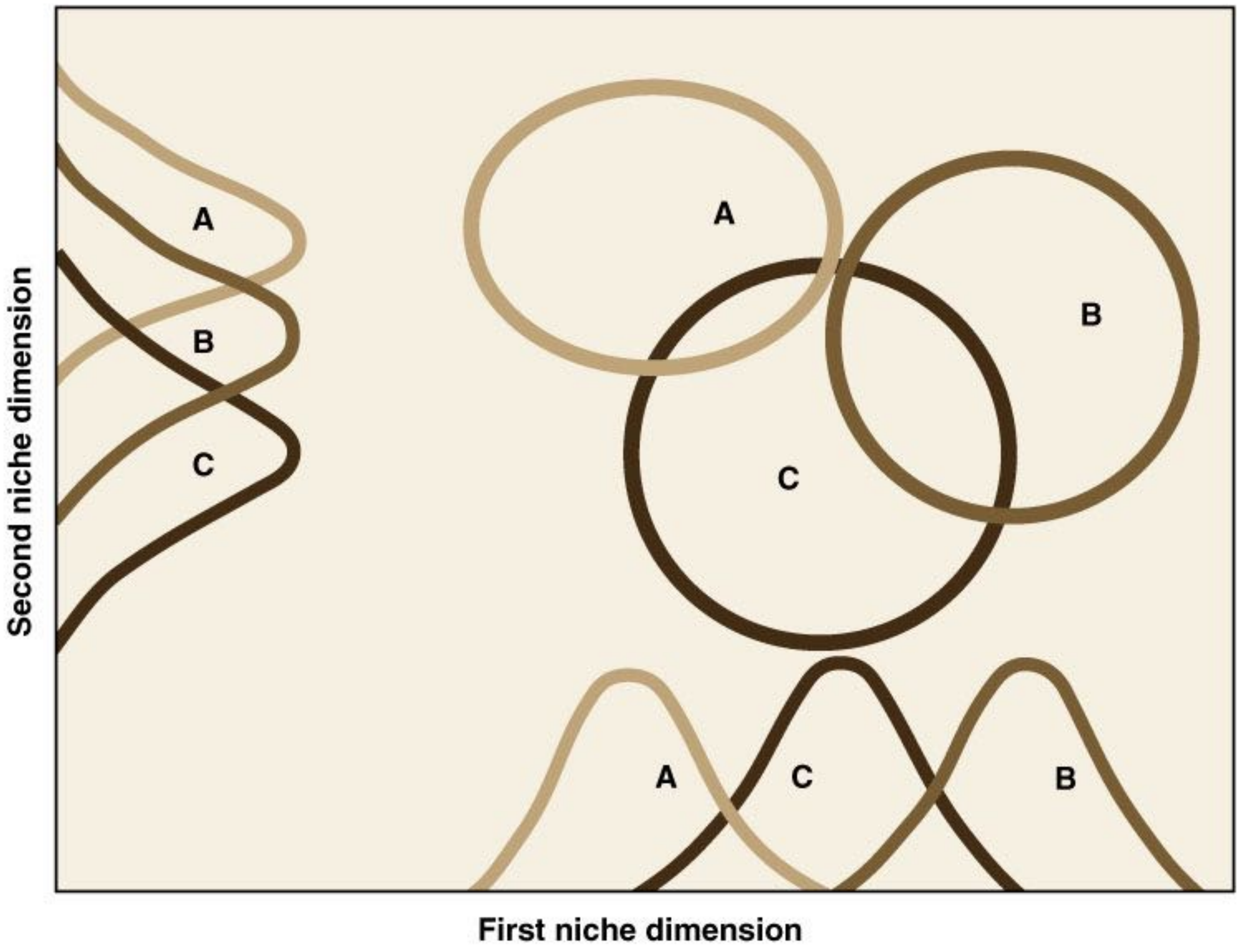
where the average $\bar{N}$ can be solved from

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N(1 - \sum_j A_{ij} N) = N(1 - N \sum_j A_{ij}) \quad \text{or} \quad \bar{N} = \frac{1}{\sum A_{ij}} = \frac{1}{1 + 2\alpha + 2\alpha^4 + 2\alpha^9 + \dots} \simeq \frac{1}{1 + 2\alpha}$$

Solving $N_1' = N_2' = N_3' = 0$ for the α at which $\bar{N}_2 = 0$ corresponds to

$$\bar{N}_2 = \frac{3\alpha^2 - 1}{(1 + 2\alpha)(2\alpha^2 - 1)} = 0 \qquad \text{or} \qquad \alpha = \frac{1}{\sqrt{3}} \simeq 0.58$$

Niche space models: 2-dimensional



Rappoldt and Hogeweg 1980

Stability and complexity

Consider the Jacobian of an arbitrary steady state:

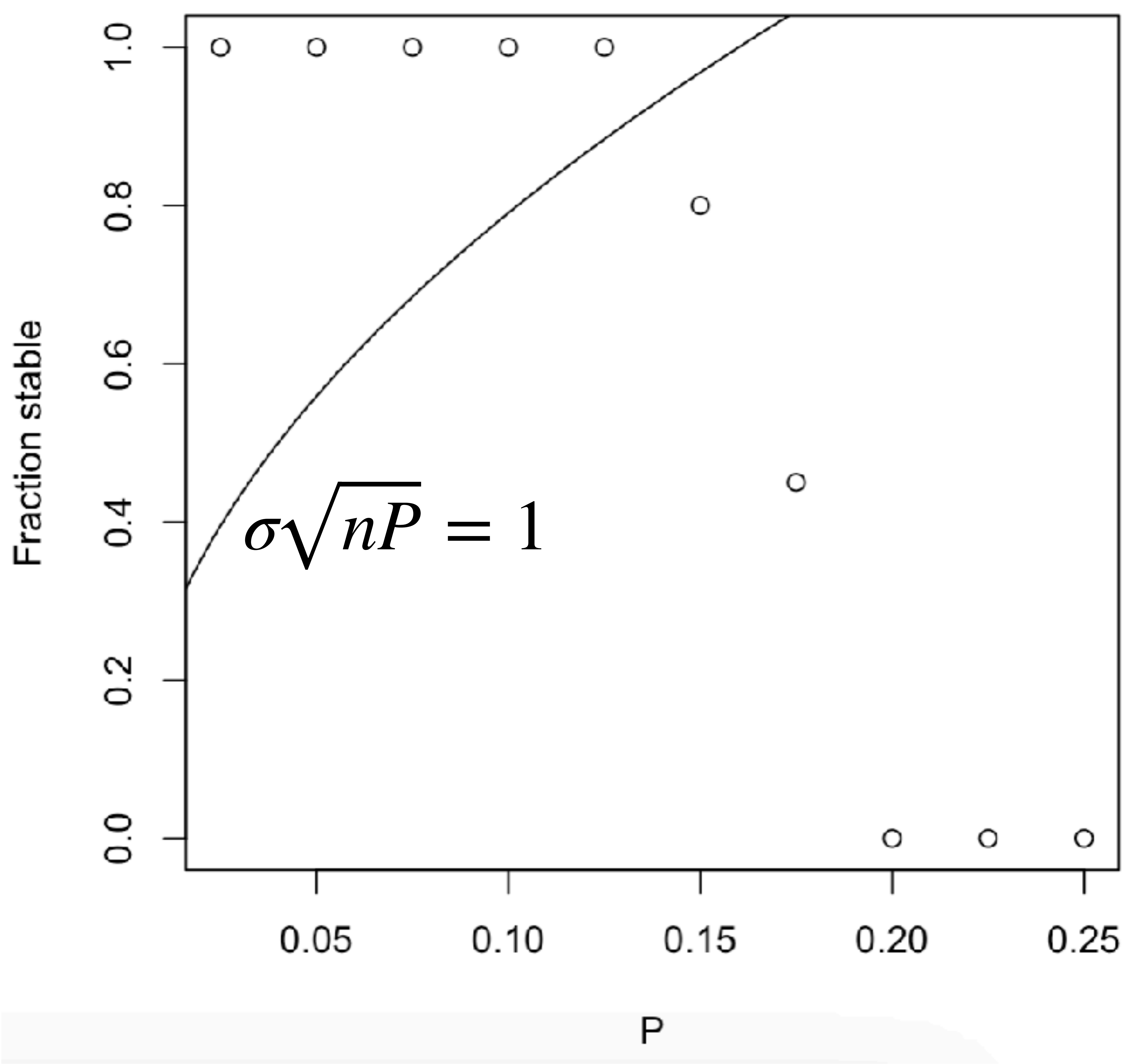
1. Every species a carrying capacity with the same return time
2. Set elements with some probability *P*, i.e., $P(1-n)$ connections per row
3. Draw interaction strength form normal distribution with mean 0 and sd σ

$$J = \begin{pmatrix} -1 & 0 & 0 & a & 0 & 0 & -b & 0 & \dots \\ 0 & -1 & 0 & 0 & 0 & c & \dots & & \\ 0 & 0 & -1 & 0 & \dots & & & & \\ -d & \dots & & -1 & \dots & & & & \end{pmatrix}$$

Largest eigenvalue is expected to be negative when $\sigma\sqrt{nP} < 1$

R-script: gardner.R

```r
maxEigen <- function(n,p,sd) {
  A <- matrix(0,nrow=n,ncol=n)
  for (i in seq(n))
    for (j in seq(n)) {
      if (i != j && runif(1) < p) A[i,j] <- rnorm(1,0,sd)
    }
  diag(A) <- -1
  return(max(Re(eigen(A)$values)))
}

n <- 100
p <- 1
s <- 0.25
maxEigen(n,p,s)
s*sqrt(n*p)
```



Random Lotka-Volterra models

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i(r_i - \sum_j^n A_{ij}N_j)$$

Roberts (1974): set $A_{ij} = \pm z$ where z is some random number (and all $A_{ii} = -1$)

Solve the algebraic system $\vec{r} - A\ \vec{N} = 0$, i.e., $N = A^{-1}\ \vec{r}$

Not all $N_i > 0$

He accused Gardner, Ashby and May of considering unfeasible systems

Random Lotka-Volterra models

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i(r_i - \sum_j^n A_{ij}N_j)$$

Modernize this by drawing random A_{ij} values

Compare this analytic solution with numerical solution

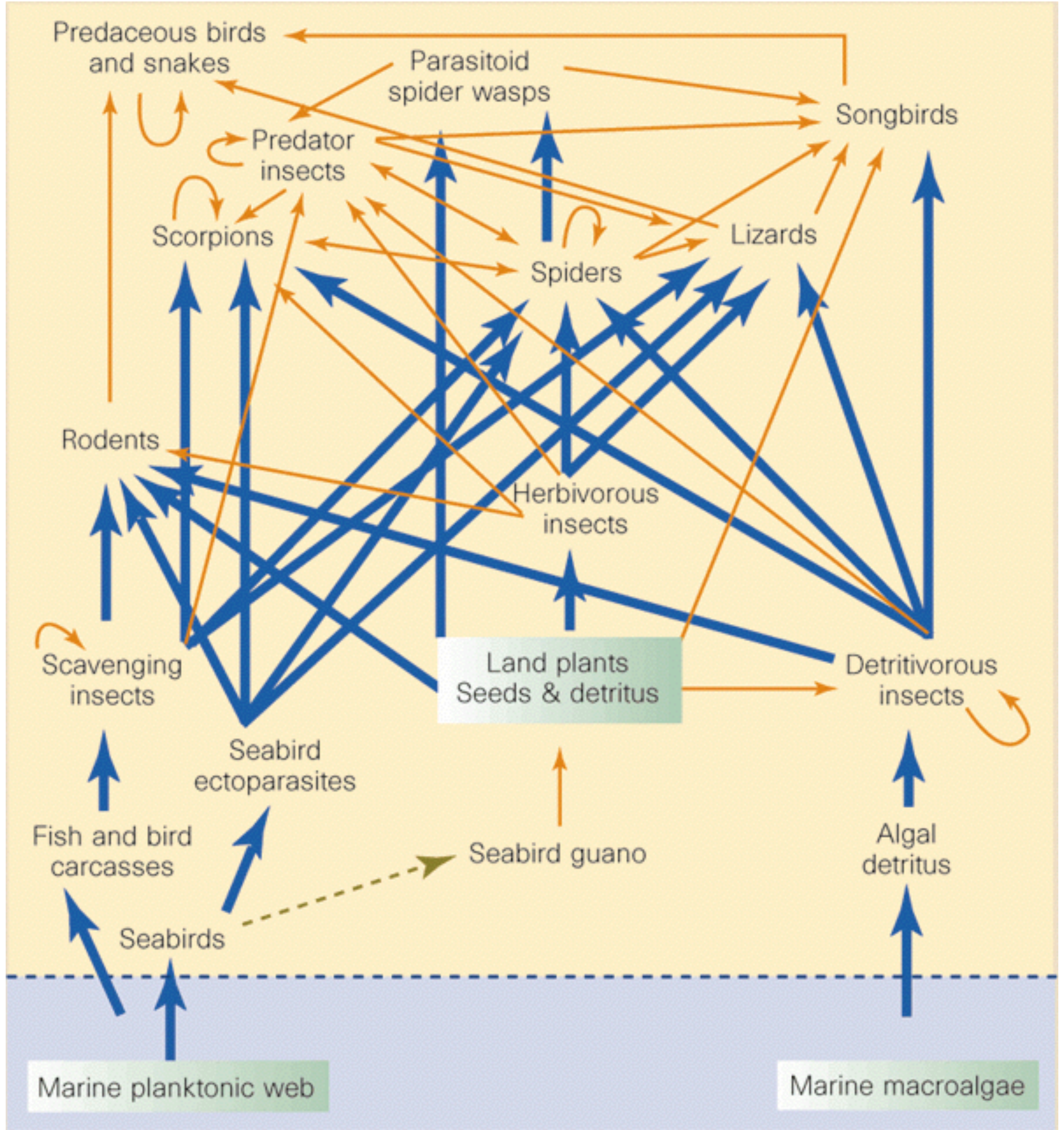
Study Lotka-Volterra competition model

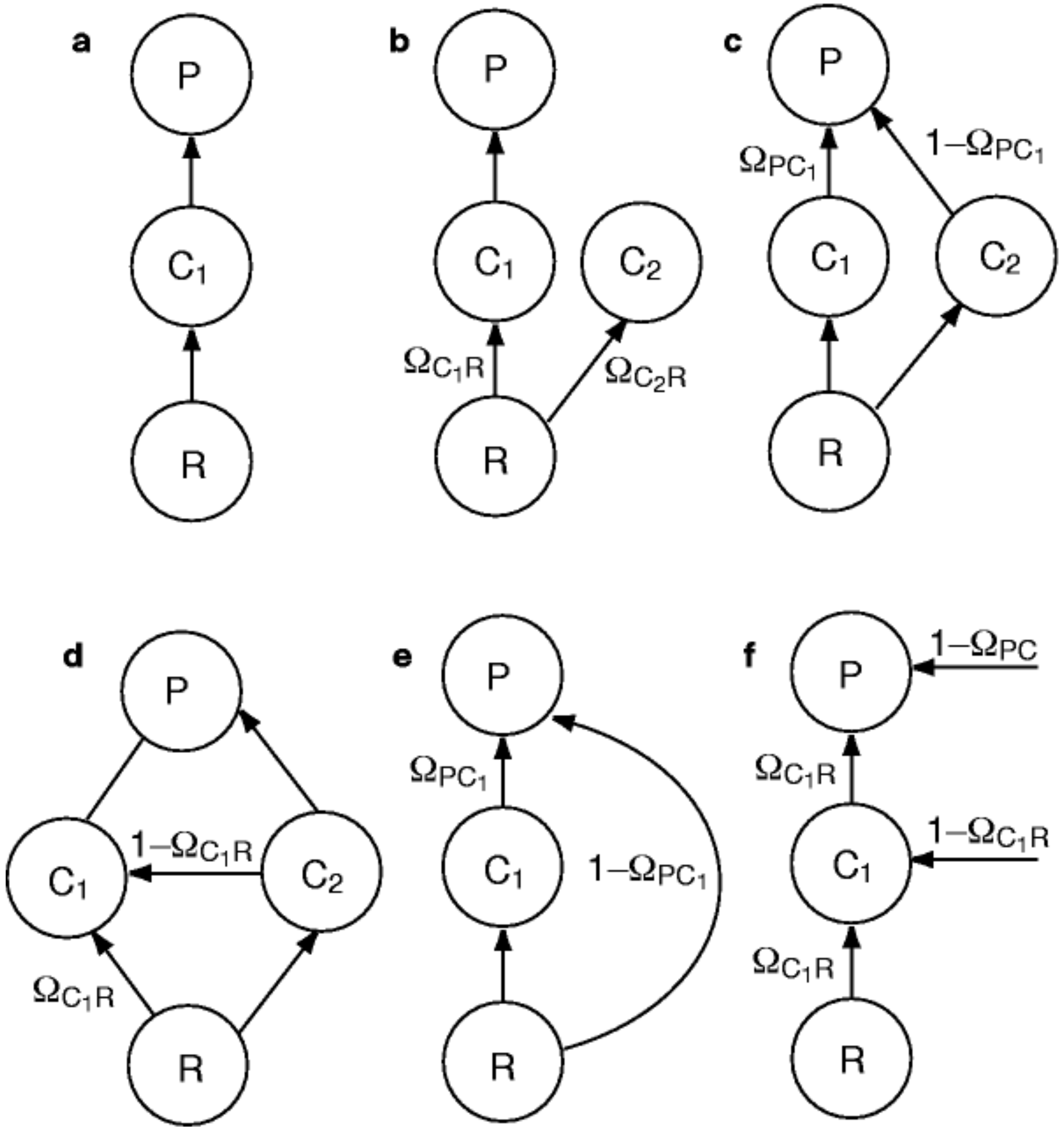
```
model <- function(t, state, parms) {
  state <- ifelse(state < 0, 0, state)
  N <- state
  S <- A %*% N
  dN <- N*(r - S)
  return(list(dN))
}

n <- 5
s <- rep(0.1,n)
r <- rep(1,n)
p <- NULL
names(s) <- paste("N",seq(1,n),sep="")
zmean <- 0.1
z <- rnorm(n*n,zmean,zmean/10)
k <- ifelse(runif(n*n)<0.5,1,-1)
A <- matrix(k*z,nrow=n,ncol=n)
diag(A) <- 1
```

```
frun <- run(); cat(frun)
AI <- solve(A)        # Compute the inverse of A
fsol <- AI %*% r      # Use this to solve A N = r
cat(fsol)
print(c(ReturnTime=-1/newton(frun,value=TRUE)))
```

```
> round(A,3)
       [,1]   [,2]   [,3]  [,4]   [,5]
[1,]  1.000  0.101 -0.109 0.110  0.104
[2,]  0.097  1.000  0.091 0.104  0.107
[3,] -0.105  0.093  1.000 0.103 -0.106
[4,] -0.109 -0.095 -0.107 1.000  0.090
[5,] -0.109 -0.091  0.106 0.075  1.000
```

Stability of food webs





From McCann, Nature 1998

Self-assembling food webs

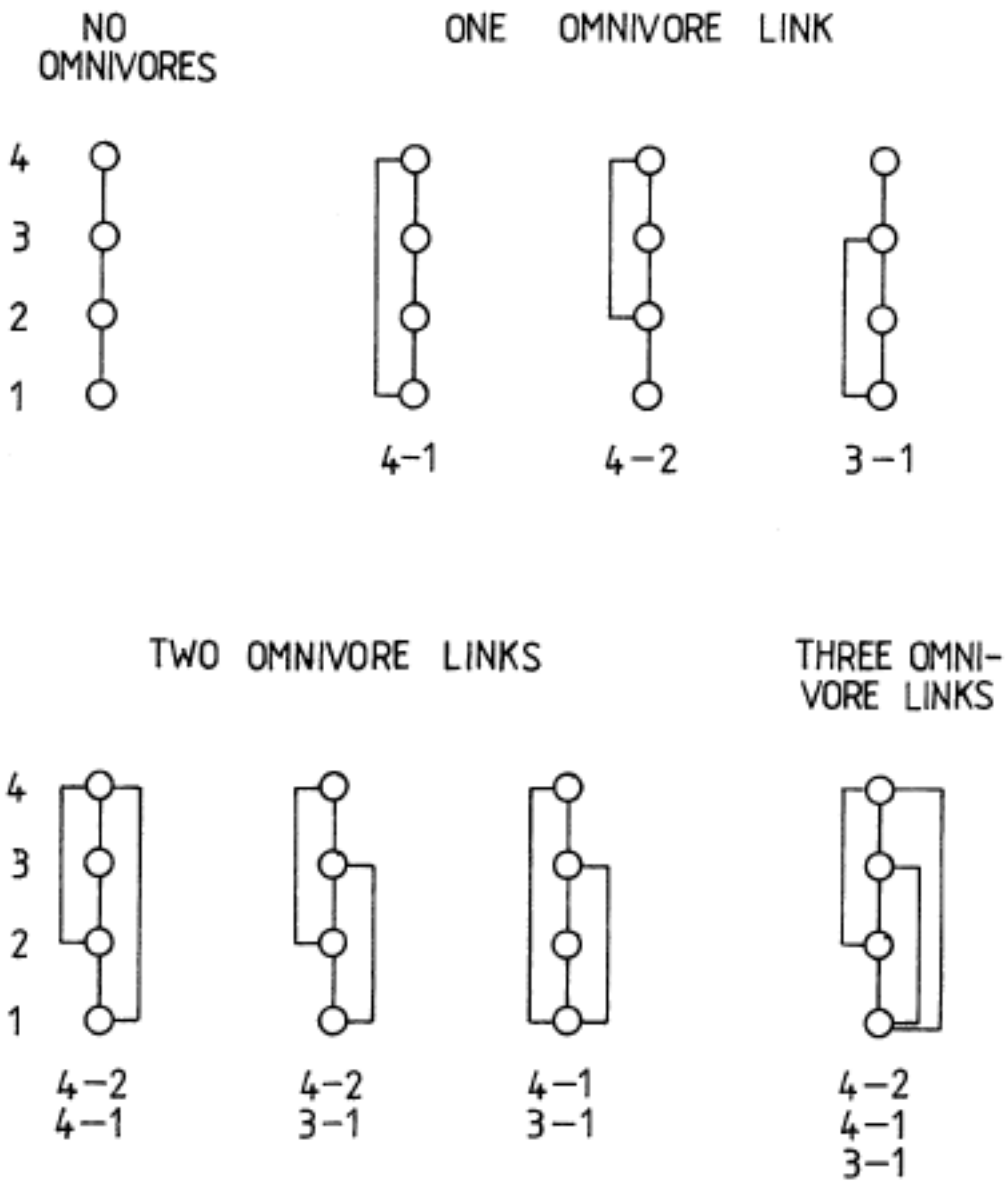


FIG. 2. Some food webs with contrasting degrees of omnivory (from Pimm and Lawton 1978). Species 1 is a self-supporting species at the base of the food web and is eaten by species higher up in the web; a line joining two species indicates that the upper one eats the lower one.

TABLE 1. Permanence and asymptotic stability of four-species food webs, based on 2 × 10^5 realizations of each configuration as described in the text (see *Permanence, asymptotic stability, and omnivory*). The results refer to realizations in which $f_{i,B} < 5$ for all species at all boundary equilibria.

Community configuration	Number with interior equilibrium	Number permanent	Number with asymptotic stability*
No omnivory	1107	1107	1107
One omnivore link:			
4–1†	1726	1726	959
4–2	914	796	456
3–1	660	636	400
Two omnivore links:			
4–2, 4–1	1062	1018	564
4–2, 3–1	917	499	287
4–1, 3–1	1173	1089	674
Three omnivore links:			
4–2, 4–1, 3–1	972	711	394

* This refers to asymptotic stability of the four-species interior equilibrium.

† Numbers refer to nonadjacent trophic levels with feeding links between them; e.g., 4–1: species at trophic level 4 feeds on the basal species at trophic level 1.

From: Law & Blackford, Ecology, 1992

Random assembly (Tilman chemostat models)

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i(f_i(R_1,\ldots,R_m) - d_i) \ , \quad \text{for } i = 1,\ldots,n$$

$$\frac{\mathrm{d}R_j}{\mathrm{d}t} = D(S_j - R_j) - \sum_i^n c_{ij} f_i(R_1,\ldots,R_m) N_i \ , \quad \text{for } j = 1,\ldots,m$$

$$\text{with} \quad f_i() = b_i \min\left(\frac{R_1}{h_{i1}+R_1},\ldots,\frac{R_m}{h_{im}+R_1}\right) \ ,$$

Consider a fixed number of resources and keep on adding random consumers (Huisman, et al, 1999, 2001). Matrix *c* defines contents, matrix *h* the consumption.

$$\frac{\mathrm{d}R}{\mathrm{d}t} = s - wR - \frac{aRN}{h+R} \quad \text{and} \quad \frac{\mathrm{d}N}{\mathrm{d}t} = \frac{caRN}{h+R} - (w+d)N = \frac{caRN}{h+R} - \delta N \ . \qquad (5.6)$$

Random assembly: Huisman papers

$$
\begin{aligned}
\frac{\mathrm{d}N_i}{\mathrm{d}t} &= N_i(\mu_i(R_1,\ldots,R_m) - D)\ , \quad \text{for } i = 1,\ldots,\infty \\
\frac{\mathrm{d}R_j}{\mathrm{d}t} &= D(S_j - R_j) - \sum_i^n c_{ij}\mu_i(R_1,\ldots,R_m)N_i\ , \\
\mu_i() &= r_i \min\left(\frac{R_1}{K_{i1}+R_1},\ldots,\frac{R_m}{K_{im}+R_1}\right)\ ,
\end{aligned}
$$

```r
model <- function(t, state, parms){
  state <- ifelse(state < 0, 0, state)
  R <- state[1:nr]
  if (nn == 0) return(list(D*(S-R)))
  N <- state[(nr+1):(nr+nn)]
  mu <- r*unlist(lapply(Ks,function(x){min(R/(x+R))}))
  co <- sapply(seq(nn),function(i){Cs[[i]]*mu[i]*N[i]})
  dR <- D*(S-R) - rowSums(co)
  dN <- 1e-3 + (mu - D)*N
  return(list(c(dR,dN)))
}
```

Fix the number of resources and keep on adding randomly drawing consumers. Add them when their $R_0 > 1$

Random interaction matrices: Scheffer exercise

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = \frac{egN_i \sum_j^m S_{ij} R_j}{h + \sum_j^m S_{ij} R_j} - dN_i \ ,$$

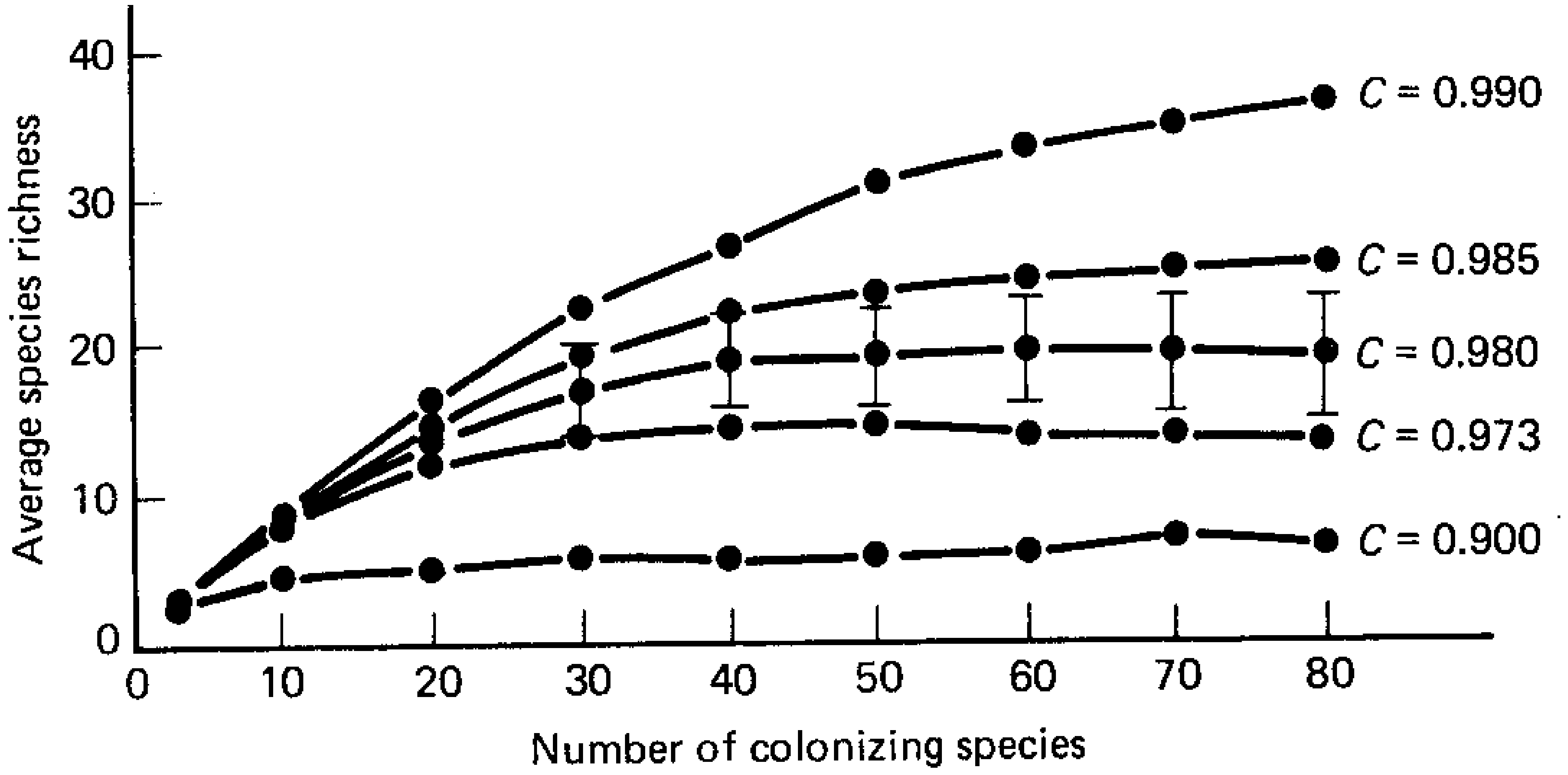
$$\frac{\mathrm{d}R_j}{\mathrm{d}t} = r_j R_j \Big(1 - \sum_i^m A_{ij} R_i / K\Big) - gR_j \sum_i^n \frac{S_{ij} N_i}{h + \sum_k^m S_{ik} R_k} \ ,$$

for $i = 1, \ldots, n$ consumers and $j = 1, \ldots, m$ resources, respectively.

High-dimensional Monod saturated model studied for different types of competition between resources (Rodriguez-Sanchez et al, 2020). How often do we obtain non-equilibrium co-existence with randomly chosen parameters?

Founder effects in space

$$\frac{\mathrm{d}N_{a_i}}{\mathrm{d}t} = N_{a_i}\left(1 - \sum_{j=1}^{n} A_{ij} N_{a_j}\right) + \sum_{b=1}^{m} D_{ab}(N_{b_i} - N_{a_i})$$

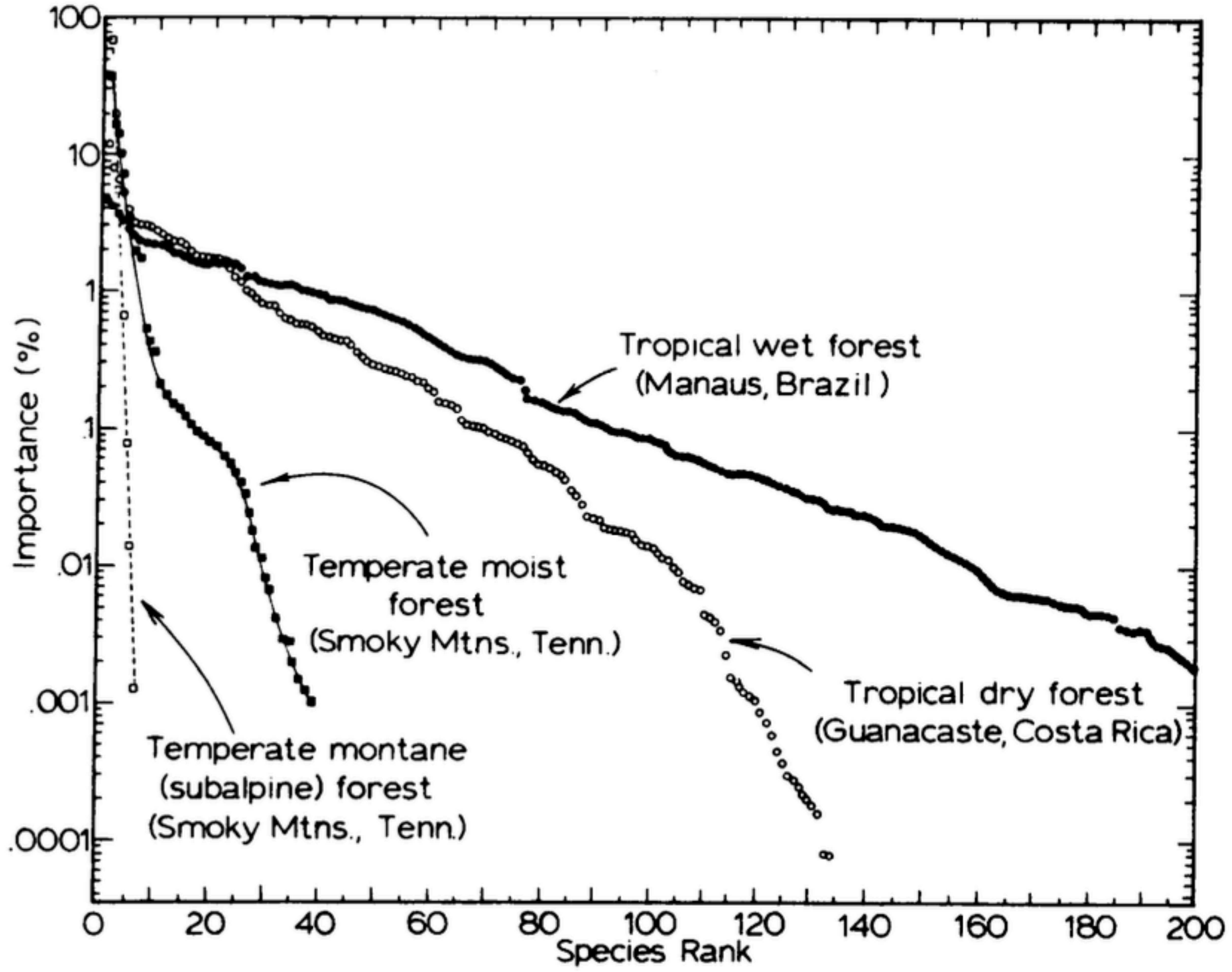


Neutral coexistence: Hubbell, Science, 1979

Tree Dispersion, Abundance, and Diversity in a Tropical Dry Forest

That tropical trees are clumped, not spaced, alters conceptions of the organization and dynamics.

Stephen P. Hubbell



Relative species abundance in forests are explained by a simple stochastic model based on random-walk immigration and extinction set in motion by periodic community disturbance.

Cross-feeding models for microbiomes

Dal Bello (2021): one consumer per resource:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = (1-\alpha_i)b_i R_i N_i - wN_i \ ,$$
$$\frac{\mathrm{d}R_i}{\mathrm{d}t} = w(\hat{R}_i - R_i) - b_i R_i N_i + \sum_j S_{ij}\alpha_j b_j R_j N_j \ ,$$

Leakage vector α_i creating novel resources.
With $\hat{R}_j = 0$ and invasion of novel N_j

Goldford (2018) several consumers per resource

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\left(\sum_j C_{ij}A_{ij}R_j - w\right) \ ,$$
$$\frac{\mathrm{d}R_j}{\mathrm{d}t} = w(\hat{R}_j - R_j) - \sum_i A_{ij}N_i R_j + \sum_i \sum_k S_{i,jk}A_{ik}N_i R_k \ ,$$

$$C_{ij} = c_j - \sum_k S_{i,jk}c_k,$$

Three matrices: interactions, *A*, content *C*, and stoichiometry S_i

Typo's

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\Big(\sum_j C_{ij}A_{ij}R_j - w\Big) ,$$

$$\frac{\mathrm{d}R_j}{\mathrm{d}t} = w(\hat{R}_j - R_j) - \sum_i A_{ij}N_iR_j + \sum_i\sum_k S_{i,jk}A_{ik}N_iR_k , \qquad (10.19)$$

where C is a matrix defining the conversion rates from resource j into species i, S_i is a species-specific stoichiometric matrix, with $S_{i,jk}$ defining the number of molecules of resource j secreted by species i per molecule of resource k it has taken up. The interaction matrix A collects the mass-action consumption rates of species i on resources j. $\hat{R}_i$ is the concentration of resource i in the supply, which is zero for all novel metabolic byproducts, and w is the dilution rate of the chemostat. The energy (or biomass) of the resource is conserved because the conversion rates, C_{ij}, are scaled by the secretion rates, i.e., $C_{ij} = c_j - \sum_k S_{i,jk}c_k$, where c_j is the maximum energy (or biomass) supplied by resource j (Goldford *et al.*, 2018). These matrixes were defined

Book says resource *j* and c_j