# Novel asymptotic expansions of hypergeometric functions enable the mechanistic modeling of large ecological communities

Andrew Noble
with Nico Temme

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# A sampling theory for asymmetric communities

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# Outline

- Origins of the Project
- Niche and Neutral Coexistence Mechanisms
- Breaking the Symmetry of Neutral Theory
- Asymptotic Expansions of Hypergeometric Functions

# Motivation for Quantitative Modeling in Ecology

Current extinction rates are ~1000 times higher than the expected background.

At this rate, ~50% of present-day species will be extinct by 2100.

(UN Convention on Biological Diversity)

# Quantitative Modeling of Community Ecology

- Goal: Predict observed patterns of species abundance and distribution based on a dynamical model prescribing interactions among the individuals of the coexisting species in a given area.

- Central method: Specify rates of birth, death, migration, and speciation for a master equation where allowed abundances are the non-negative integers and the timing of demographic events are stochastic.

# The Appearance of Hypergeometric Functions

Univariate master equations with birth and death rates that are polynomial in the number of individuals yield stationary distributions with a normalization given by a hypergeometric function.

Adrienne Kemp (1968)

$$_2F_1$$

that depends on

$$J - \text{Community size} \;> 10{,}000 \text{ individuals}$$

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Journal of Computational and Applied Mathematics 153 (2003) 441–462

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# Large parameter cases of the Gauss hypergeometric function

Nico M. Temme*

*CWI, P.O. Box 94079, 1090 GB Amsterdam, Netherlands*

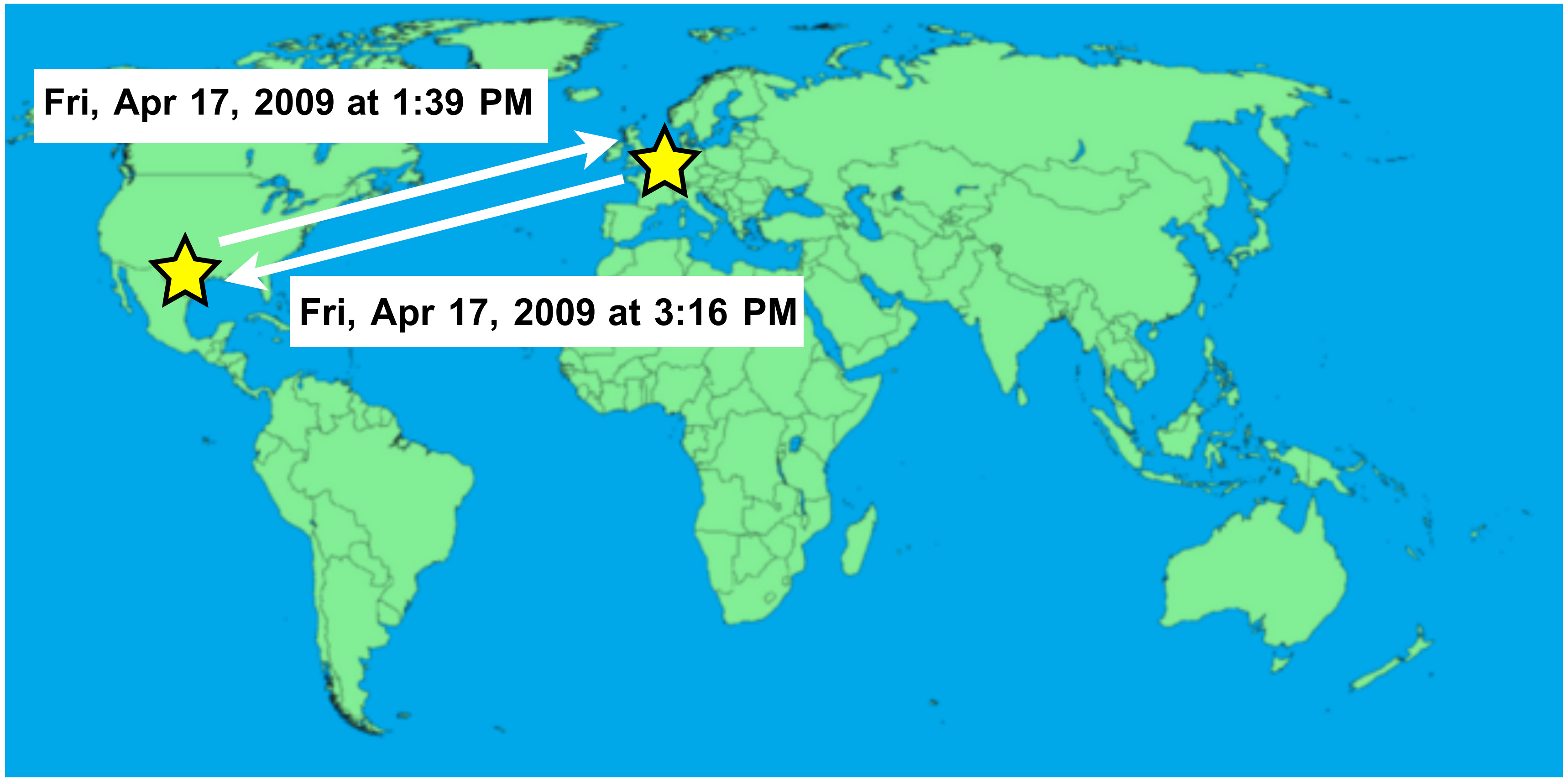
Received 7 November 2001


Dear Professor Temme,

In the course of my research, I came across your 2003 paper "Large parameter cases of the Gauss hypergeometric function."  If you have any suggestions on my current problem, they would be greatly appreciated.

I am attempting to find an asymptotic expansion of the Gauss hypergeometric function,
_2F_1( \alpha - \lambda, \beta + m \lambda, \gamma + n \lambda; z ),
for large \lambda and generic m, n, where all parameters are real valued.  Is this a known case?

Thanks you very much for considering this,
Andrew




Dear Andrew,

this is certainly not a known case; I will see what can be said about this. Are m and n positive? Perhaps integers? Also the value of the ratio m/n may be important. And is $z < 1$?

With best regards,

Nico.

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# Two-Species Phenomenological Niche Theory

Volterra-Lotka Equations:

$$\frac{dn_1}{dt} = n_1(r_1 - a_{11}n_1 - a_{12}n_2)$$
$$\frac{dn_2}{dt} = n_2(r_2 - a_{22}n_2 - a_{21}n_1)$$

$r_i$ – intrinsic growth rate
$a_{ij}$ – competition strength

Criteria for a Stable Coexisting Fixed Point:

$$r_2 \frac{a_{12}}{a_{22}} < r_1$$
$$r_1 \frac{a_{21}}{a_{11}} < r_2$$

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Diversity requires species asymmetries.

# Consumer-Resource Niche Theory

- Diversity requires species asymmetries.
- The number of species at equilibrium is equal to the number of limiting resources.

# Origins of Niche Theory

THE INFLUENCE OF BIOLOGICALLY CONDITIONED MEDIA ON THE GROWTH OF A MIXED POPULATION OF *PARAMECIUM CAUDATUM* AND *P. AURELIA*

BY G. F. GAUSE, O. K. NASTUKOVA AND W. W. ALPATOV.

(*Zoological Institute, Moscow University.*)

1934

# Origins of Niche Theory

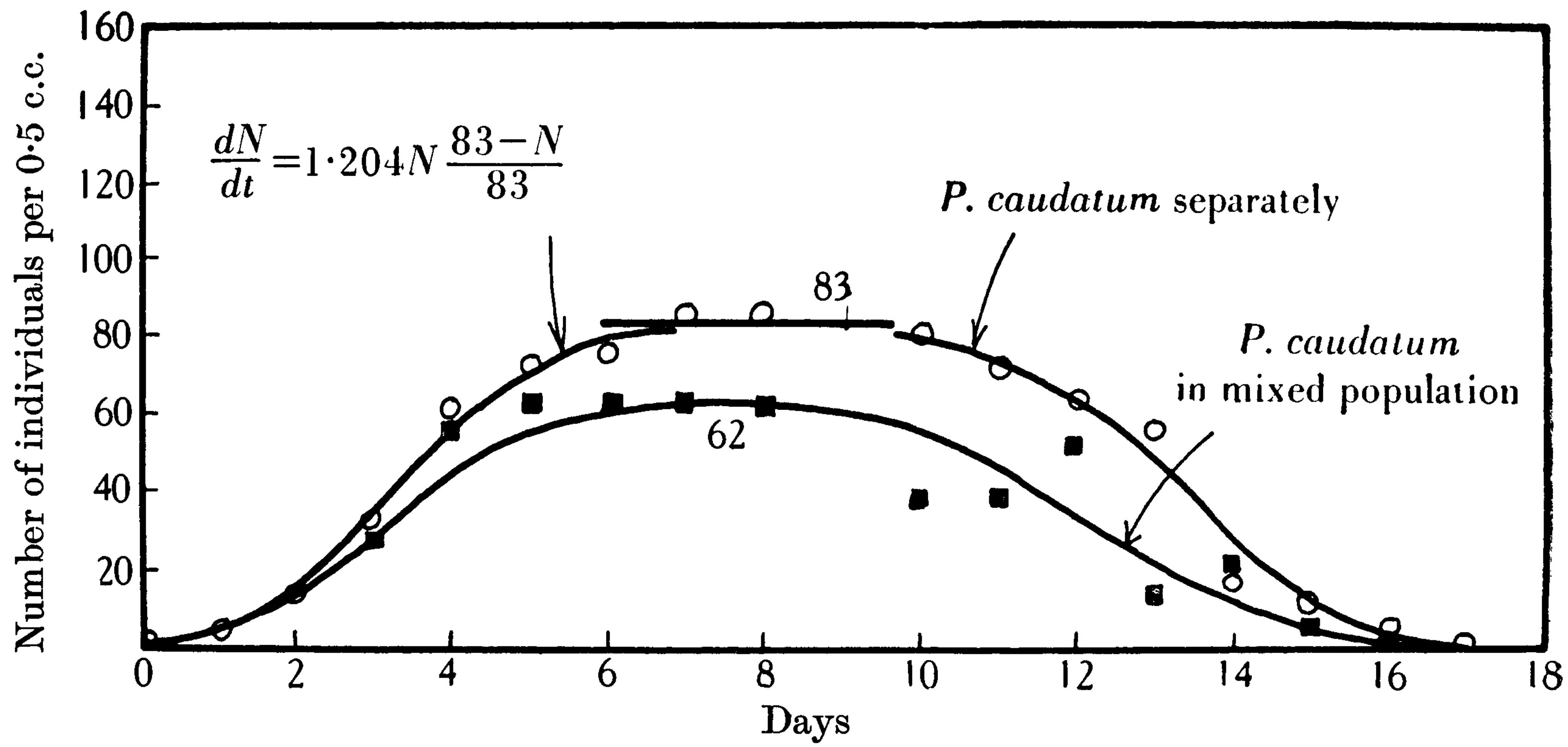



Fig. 3. The growth of *P. caudatum* in pure and mixed populations (medium of *P. aurelia*).

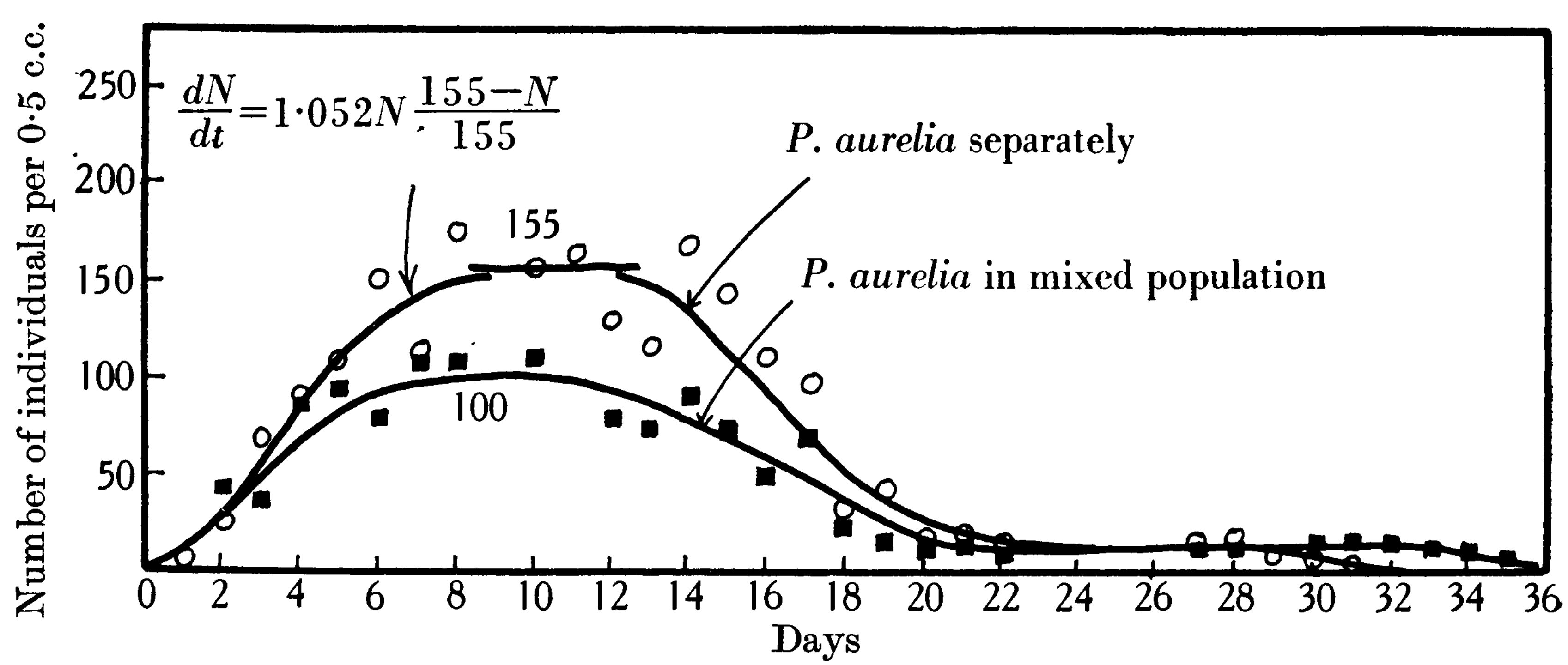
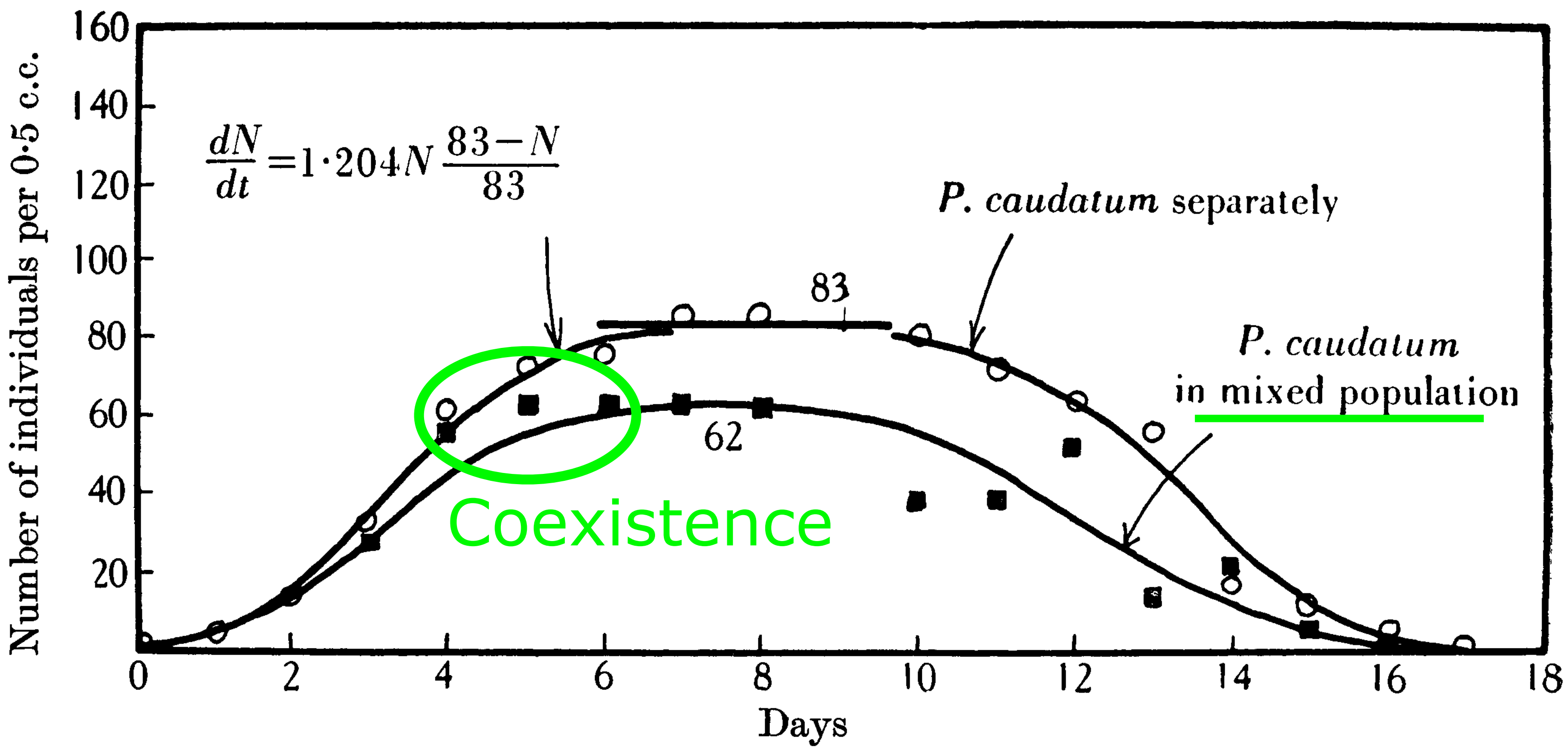



Fig. 4. The growth of *P. aurelia* in pure and mixed populations (medium of *P. aurelia*).

# Origins of Niche Theory

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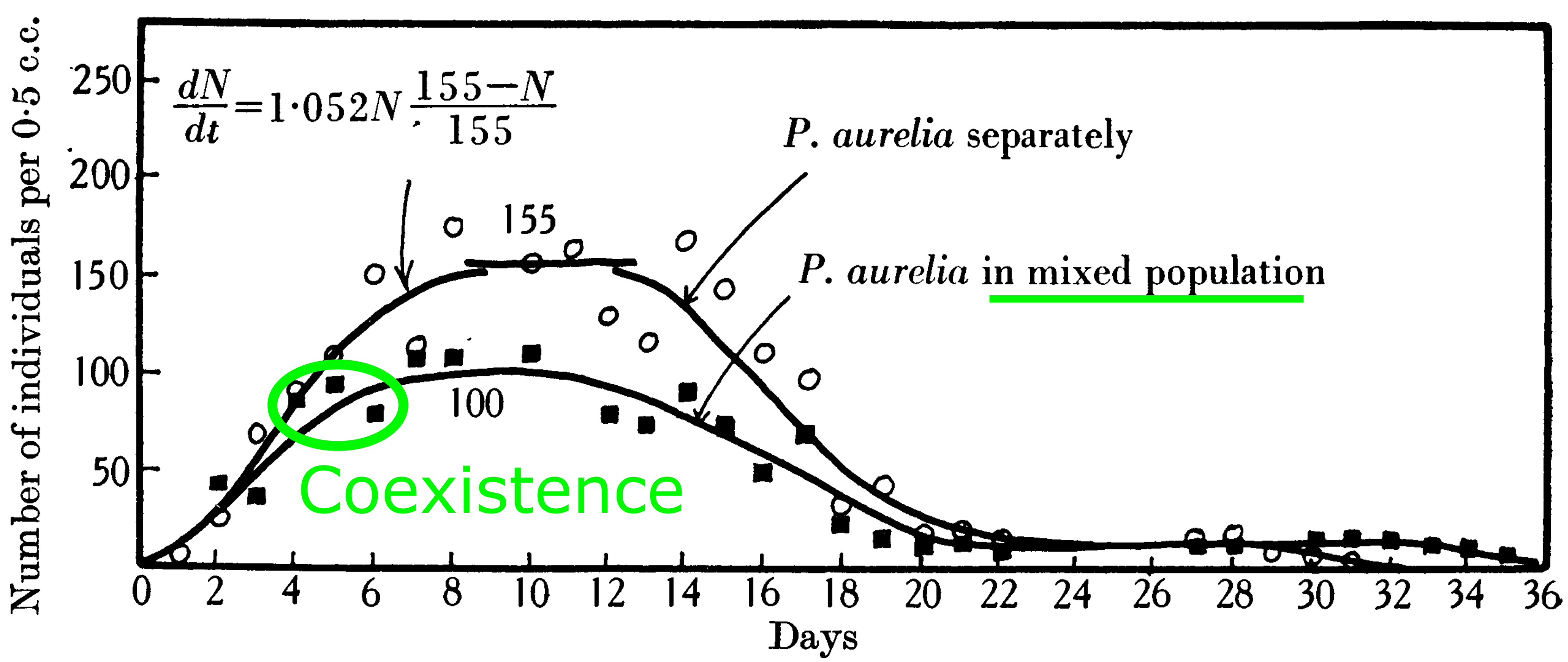


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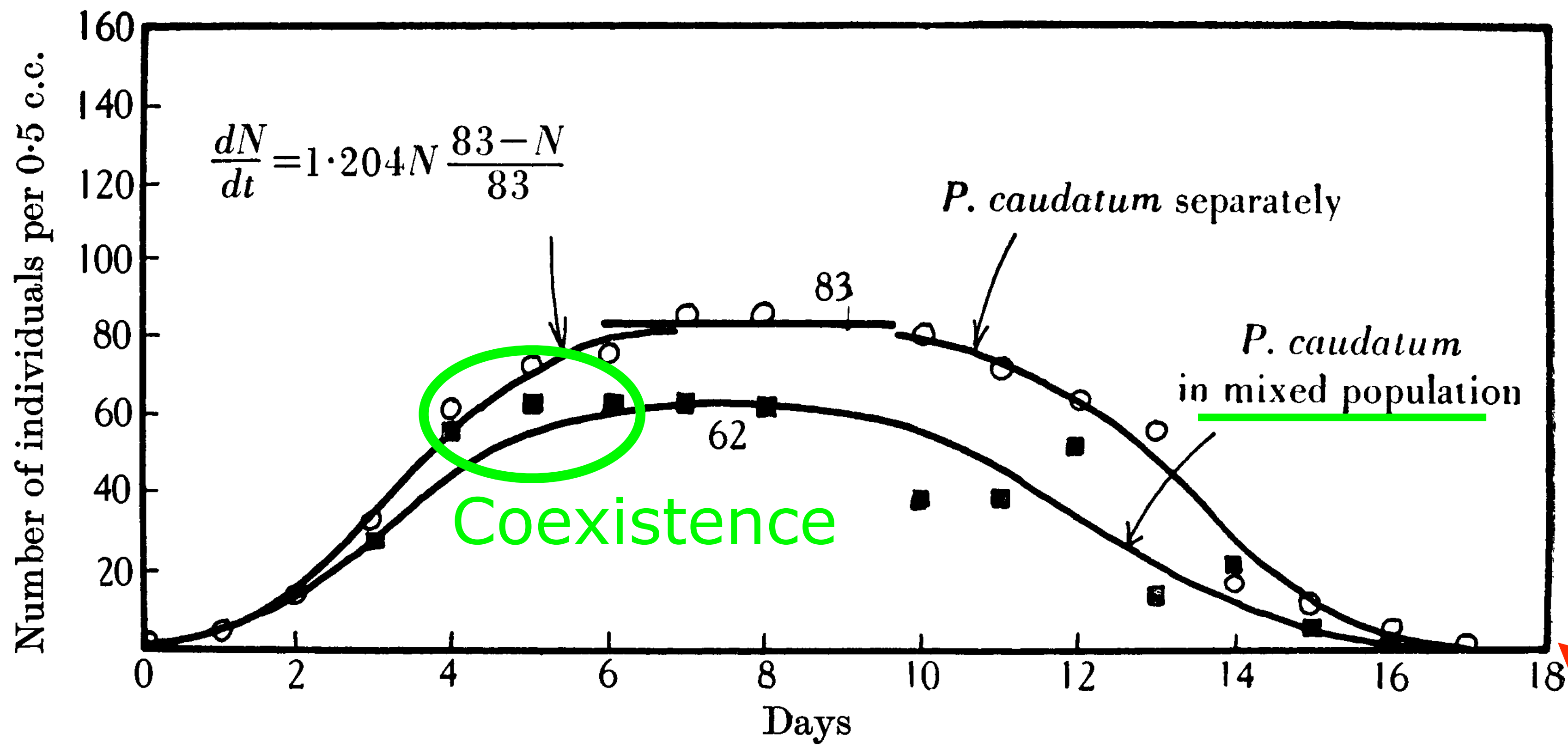
# Origins of Niche Theory

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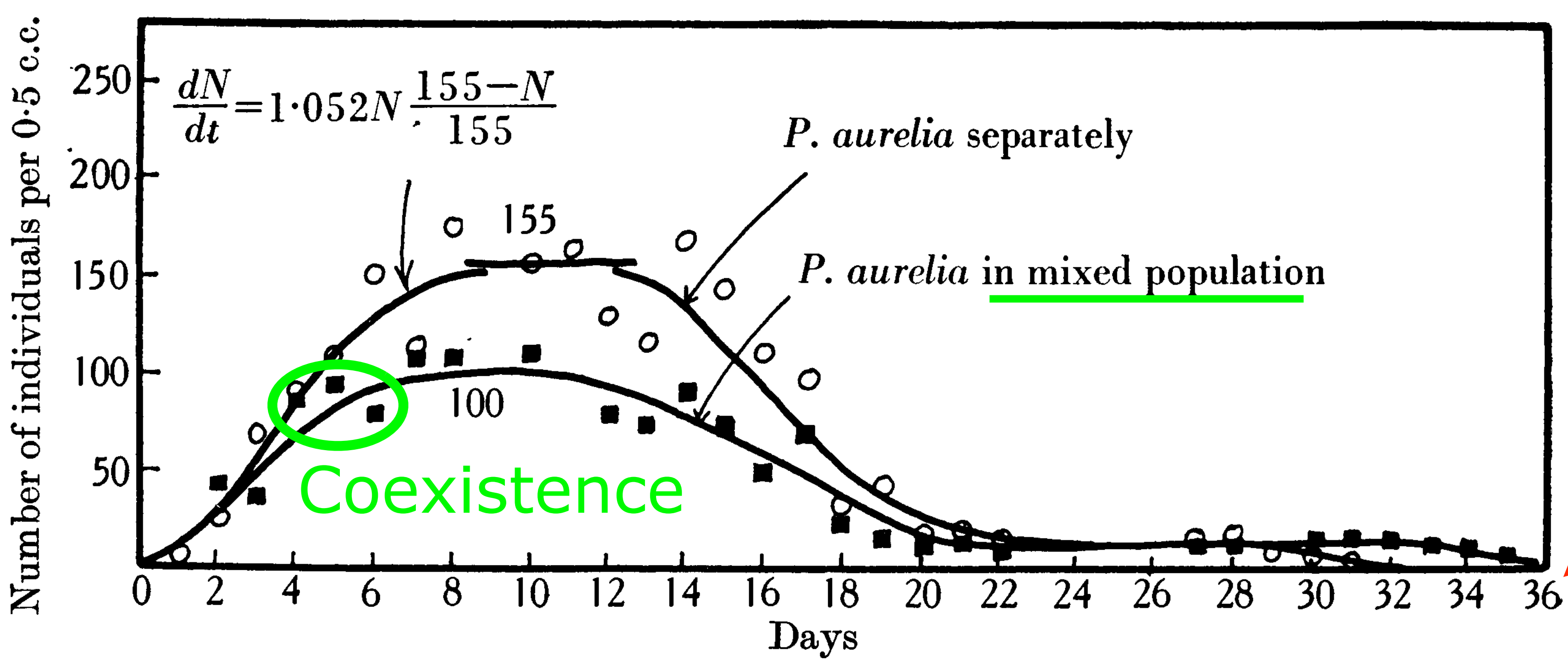
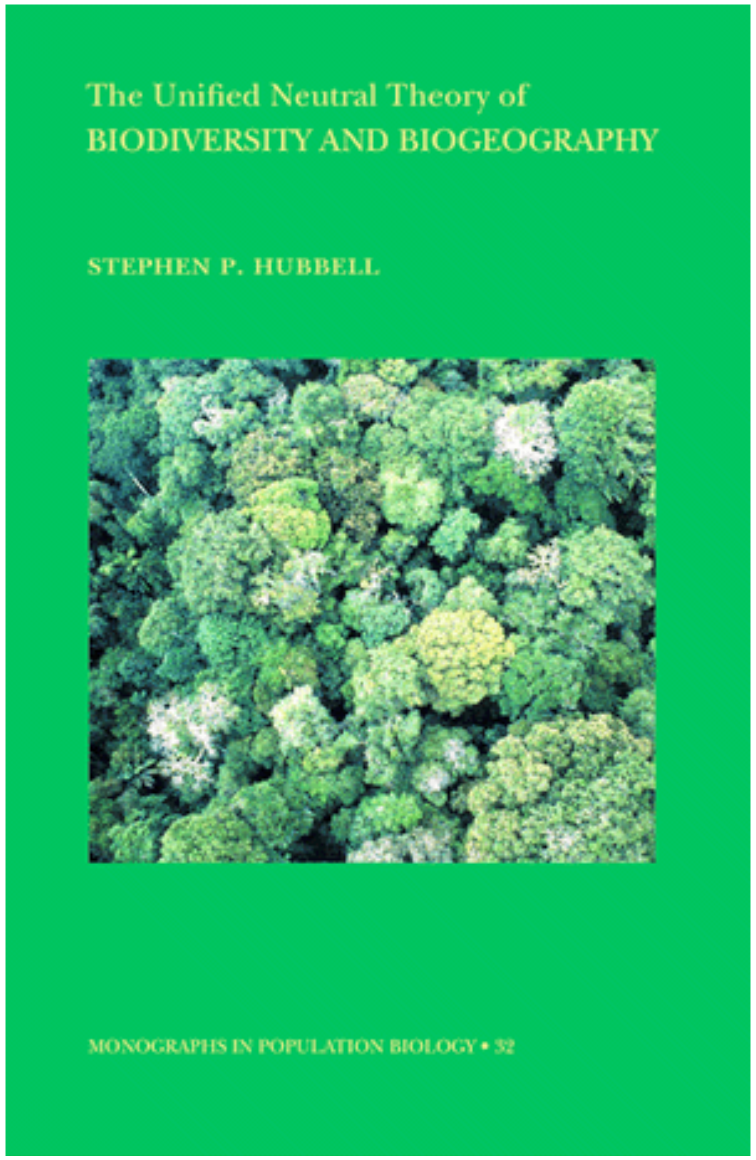



Fig. 4. The growth of *P. aurelia* in pure and mixed populations (medium of *P. aurelia*).

Eventual Extinction?

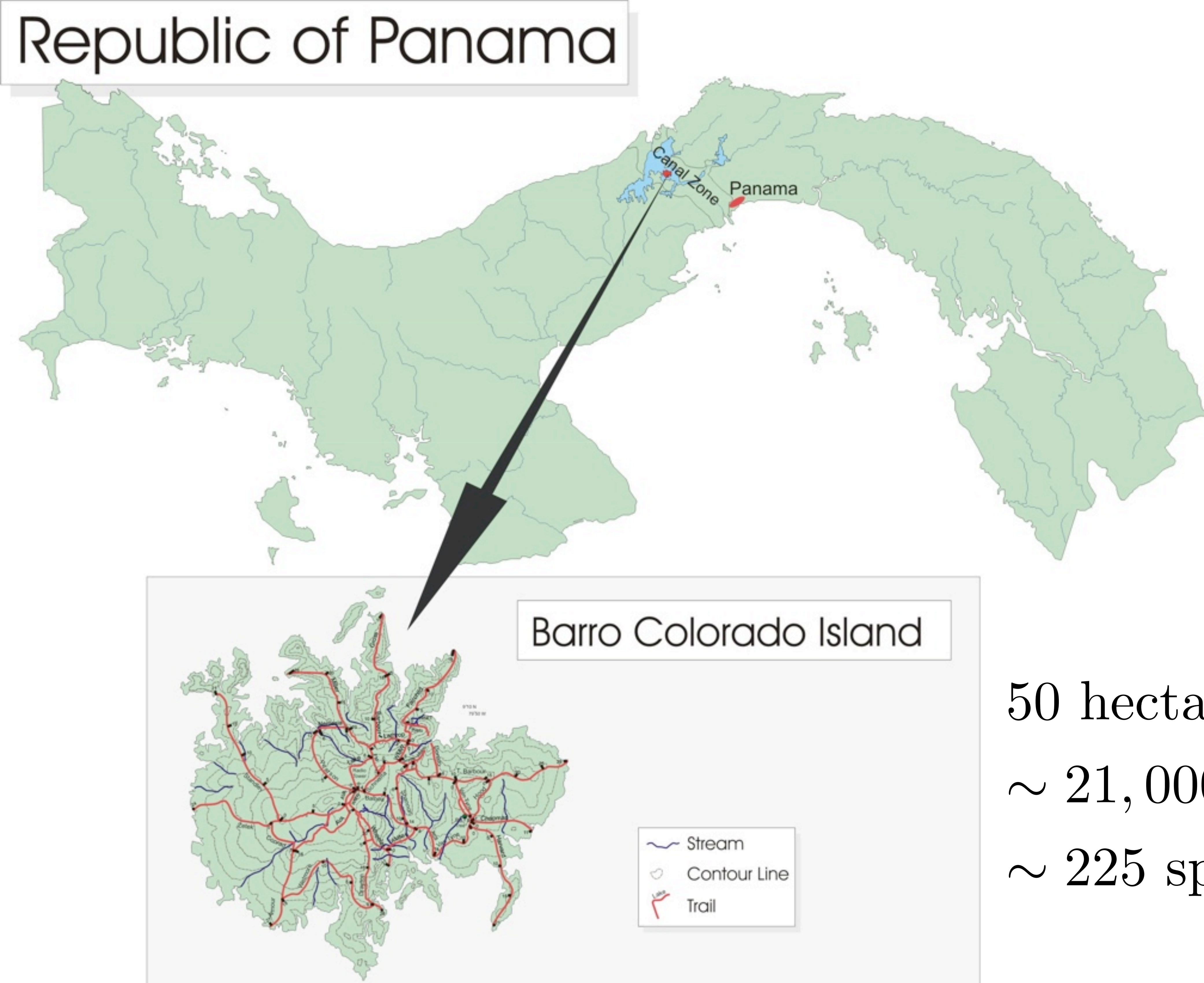
# Neutral Theory




2001

- Speciation and extinction events balance over evolutionary time scales to maintain species diversity despite an incessant turnover in species composition.

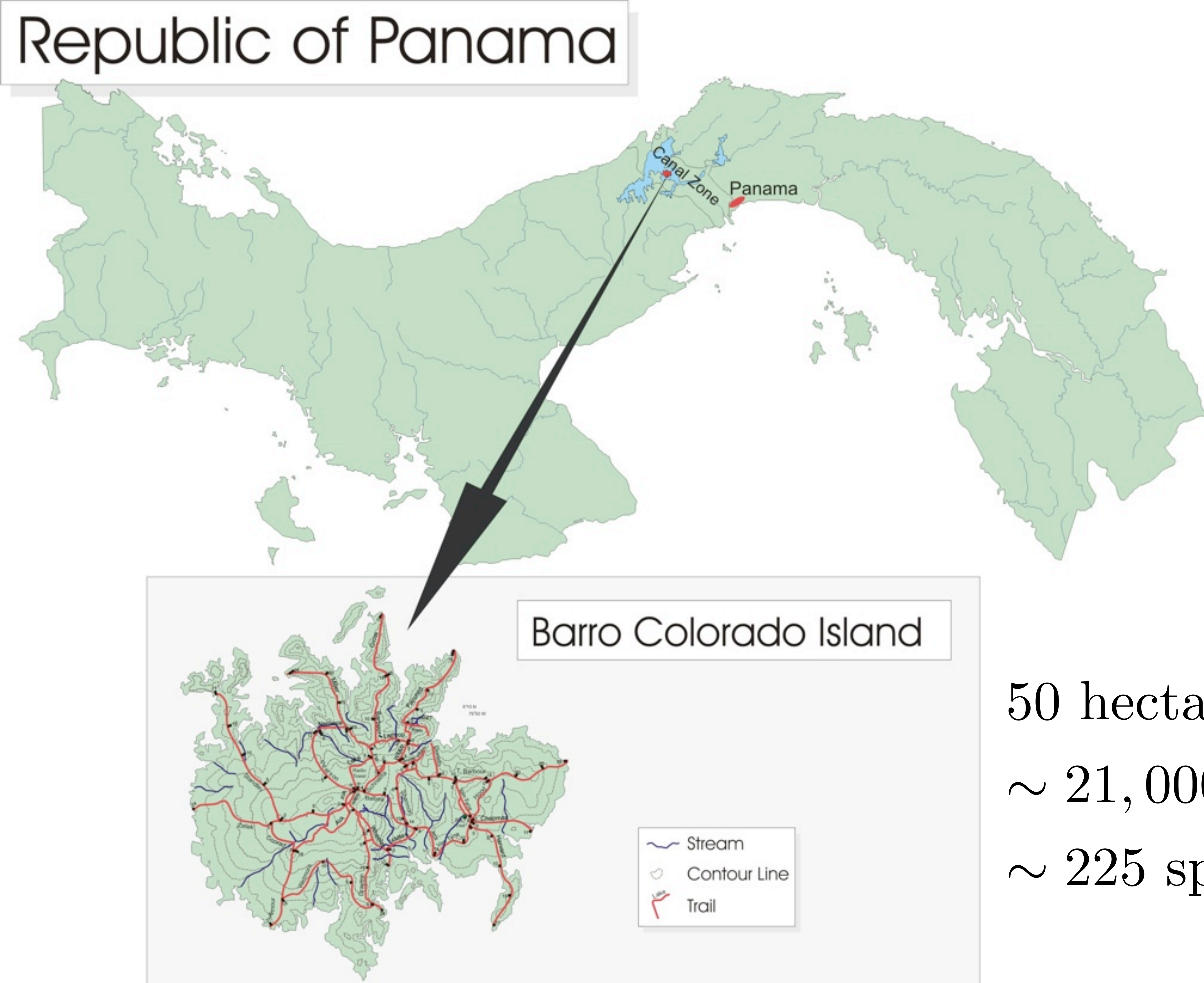
- This mechanism for maintaining diversity does not require species asymmetries, and neutral theory assumes that birth and death rates are independent of species identity.




50 hectares

$\sim 21,000$ canopy trees

$\sim 225$ species




50 hectares

$\sim 21,000$ canopy trees

$\sim 225$ species

Could there be 225 limiting resources for canopy trees?

# Neutral Theory Extends the Moran Model

Transition Rates for Each of the Symmetric Species

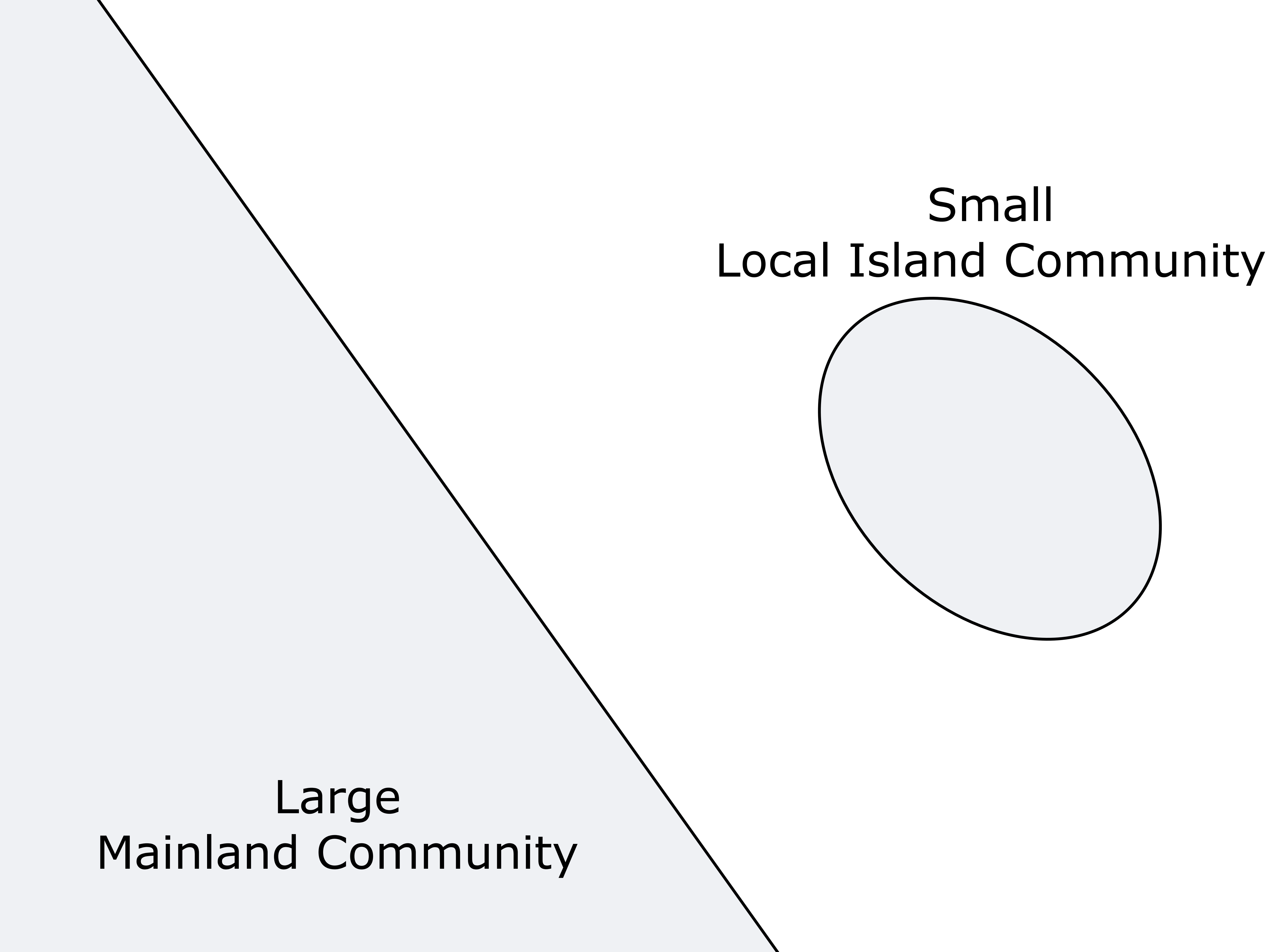
$$g_n = \frac{J-n}{J}\left(\frac{n}{J-1}\right)$$ Rate of gain

$$r_n = \frac{n}{J}\left(\frac{J-n}{J-1}\right)$$ Rate of reduction

Marginal Dynamics Given by a Univariate Master Equation

$$\frac{dP_n}{dt} = g_{n-1}P_{n-1} + r_{n+1}P_{n+1} - (g_n + r_n)P_n$$

# Local Community Dynamics for Any Given Species



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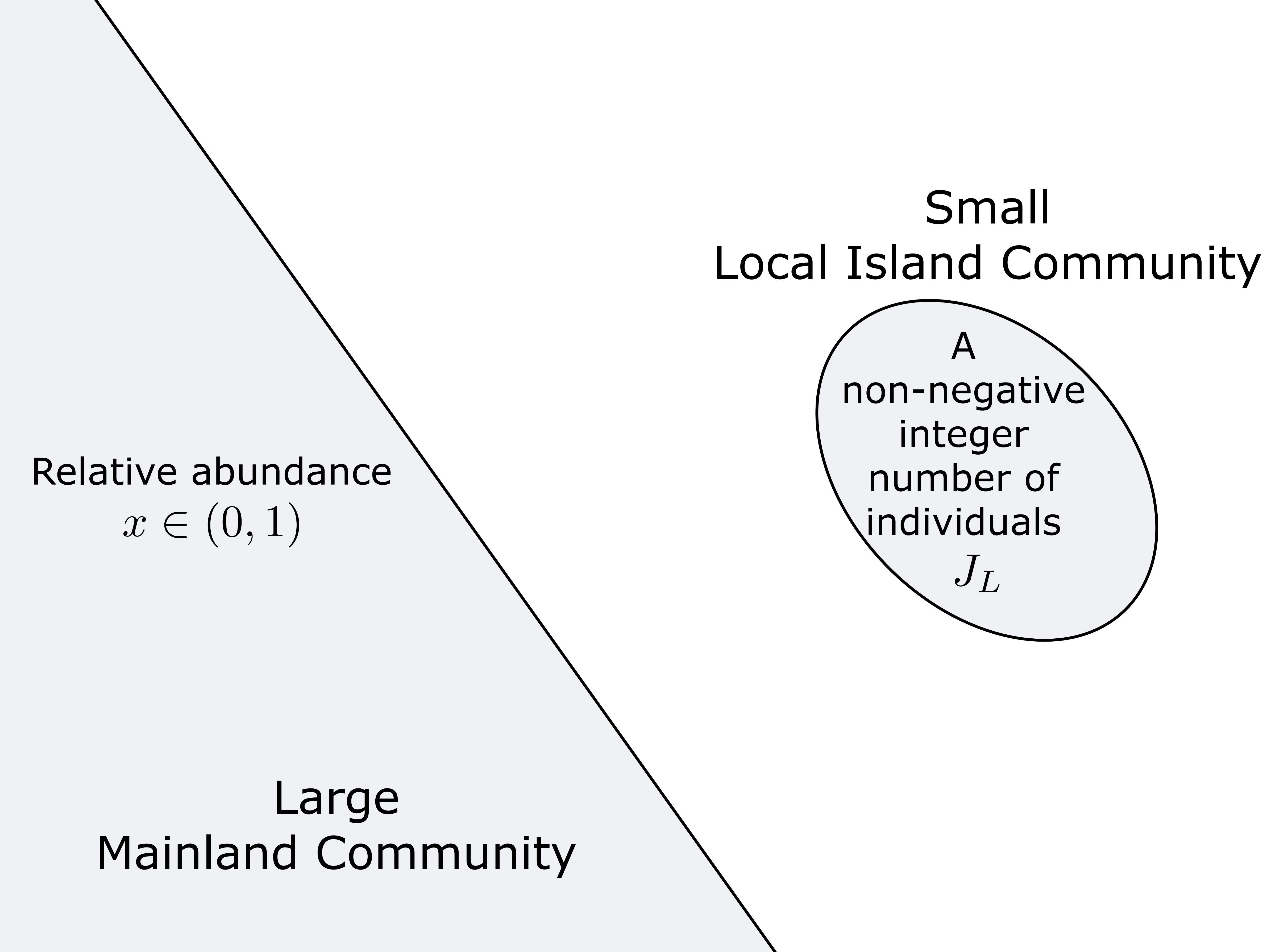

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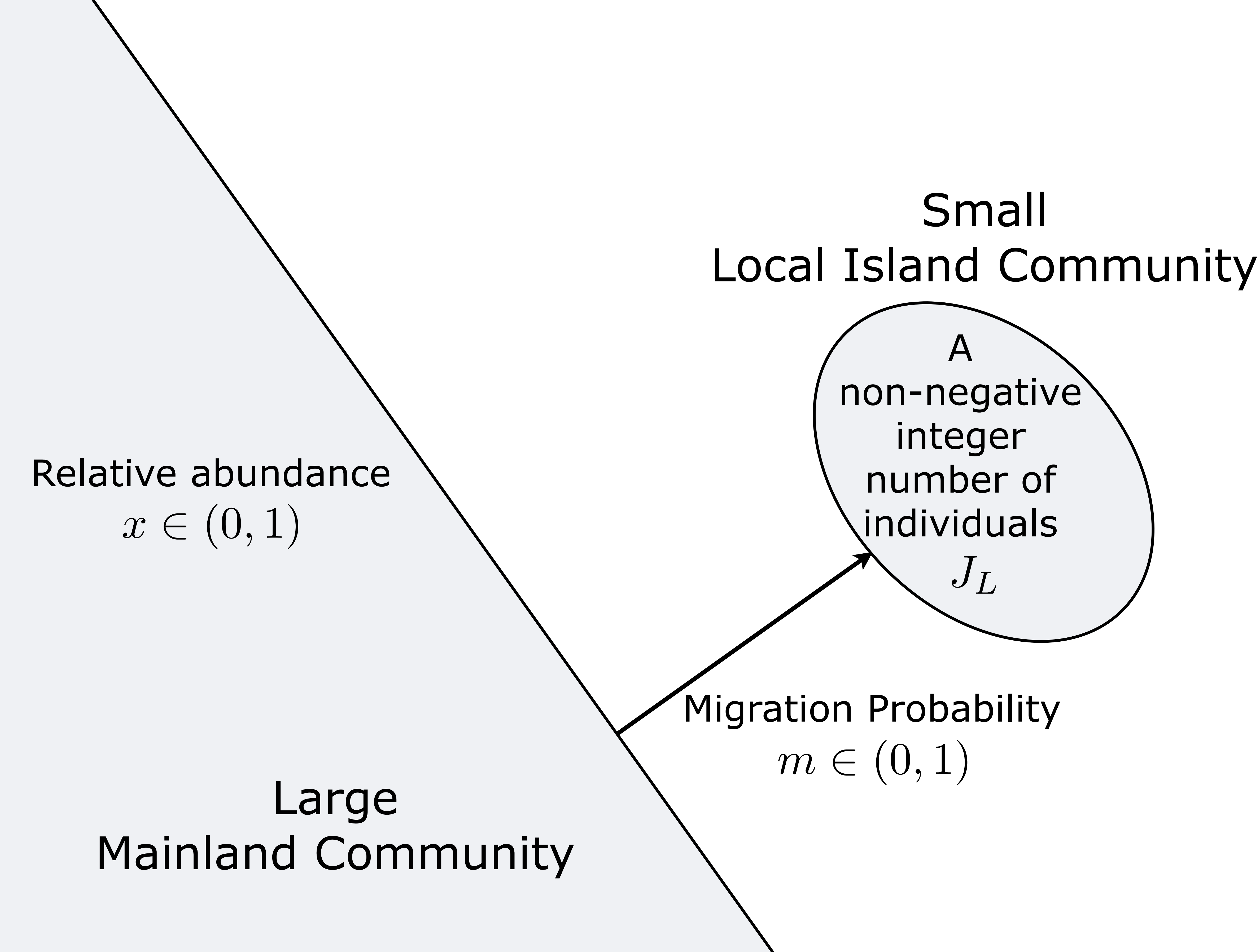


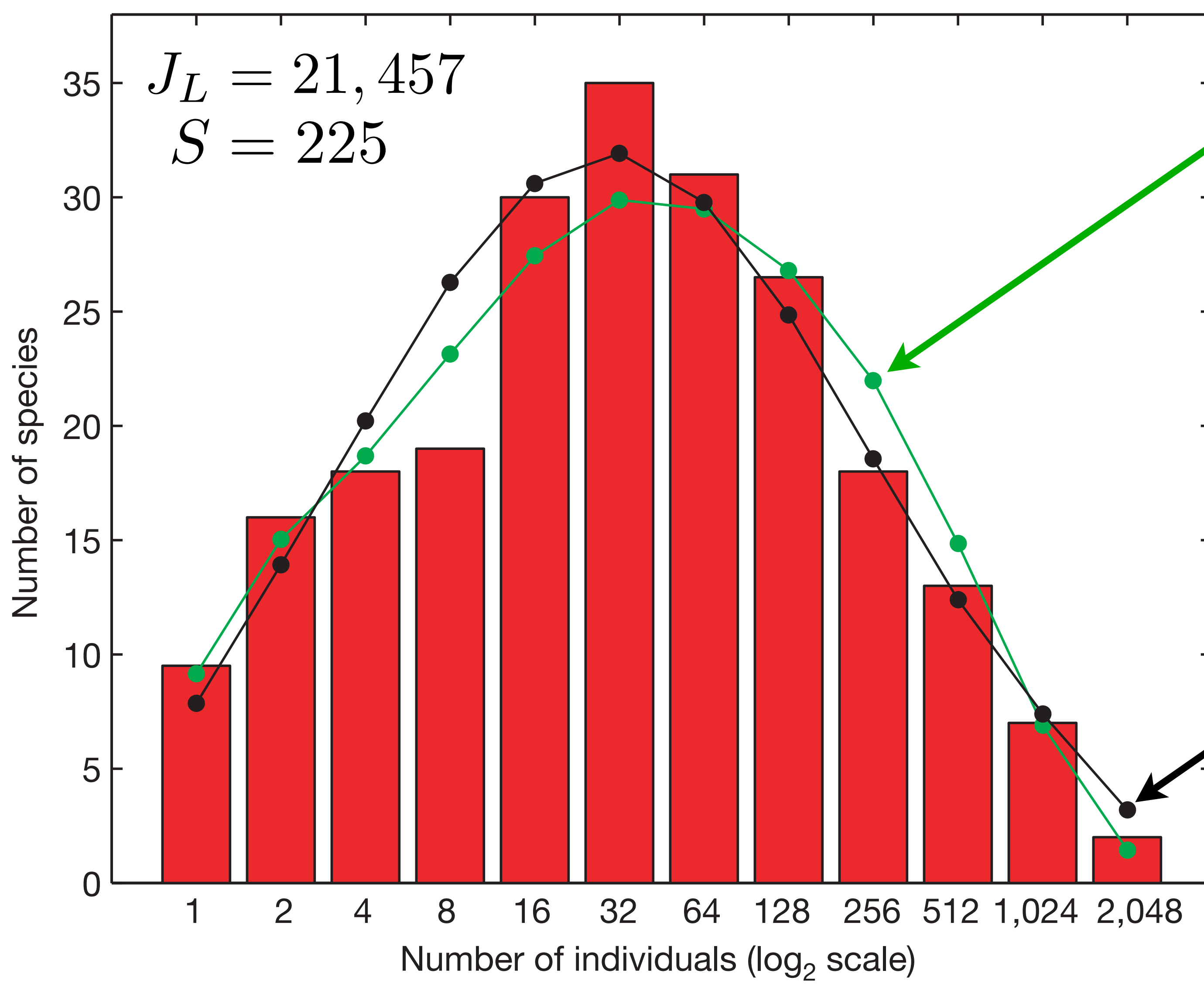
# Neutral Theory

**letters to nature**

## Neutral theory and relative species abundance in ecology

**2003**

Igor Volkov[1], Jayanth R. Banavar[1], Stephen P. Hubbell[2,3] & Amos Maritan[4,5]




Neutral Fit

Lognormal Distribution

# Outline

- Origins of the Project
- Niche and Neutral Coexistence Mechanisms
- Breaking the Symmetry of Neutral Theory
- Asymptotic Expansions of Hypergeometric Functions

# Objectives

- Allow for asymmetries in demographic rates as the first step towards unifying niche and neutral theory.
- Retain neutral theory as the symmetric limit.
- Fit stationary distributions that emerge from the asymmetric theory to data and test for departures from neutrality.

# Extending the Moran Model

## Transition Rates

$$T_{ij\vec{n}} = \frac{n_i}{J}\left(\frac{w_j n_j}{\sum_{k=1}^{S} w_k n_k - w_i}\right)$$

Rate of gaining species j after losing species i

## Community Dynamics from a Multivariate Master Equation

$$\frac{dP_{\vec{n}}}{d\tau} = \sum_{i=1}^{S} \sum_{j=1, j\neq i}^{S} \left(T_{ij\vec{n}+\vec{e}_i-\vec{e}_j} P_{\vec{n}+\vec{e}_i-\vec{e}_j} - T_{ji\vec{n}} P_{\vec{n}}\right) \Theta_{ij}$$

# A Nearly Neutral Local Community

## Stationary Distribution for the Asymmetric Species

$$P_n^* = {}_2F_1(-J_L, \lambda; 1-\xi; \eta)^{-1} \binom{J_L}{n} \eta^n \frac{\mathrm{B}(\lambda+n, \xi-n)}{\mathrm{B}(\lambda, \xi)}$$

## Moments

$$\mathrm{E}[N^*] = \frac{J_L \lambda \eta}{\xi - 1} \frac{{}_2F_1\left(1-J_L, 1+\lambda; 2-\xi; \eta\right)}{{}_2F_1\left(-J_L, \lambda; 1-\xi; \eta\right)}$$

$$\mathrm{E}[N^{*2}] = \frac{J_L \lambda \eta}{\xi - 1} \frac{{}_3F_2\left(1-J_L, 1+\lambda, 2; 2-\xi, 1; \eta\right)}{{}_2F_1\left(-J_L, \lambda; 1-\xi; \eta\right)}$$

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# Statement of the Problem

We write

$$a = \alpha - J_L, \quad b = \alpha + \beta + \mu J_L, \quad c = \alpha + \gamma + \rho J_L,$$

with $\alpha = 0, 1, 2$ and $J_L$ a positive integer. In terms of $w$, $m$, $x$, and $m_o$ we have

$$\beta = -\frac{mx}{1 - m + x(w-1)}, \quad \mu = -\beta,$$

and

$$\gamma = \frac{1 - xwm_o + x(w-1)}{1 - wm_o + x(w-1)}, \quad \rho = -\gamma.$$

The asymptotic behaviour will be considered of the Gauss hypergeometric function

$$F = {}_2F_1(a, b; c; \eta),$$

for large–$J_L$, where

$$\eta = w\frac{1 - m + x(w-1)}{1 - wm_o + x(w-1)},$$

and

$$w \in (0, \infty), \quad x, m, m_o \in (0, 1).$$

# Critical Values

$$\mu = \frac{mx}{1 - m + x(w-1)}, \qquad \rho = -\frac{1 - xwm_o + x(w-1)}{1 - wm_o + x(w-1)}$$

Considered as functions of $w$, $\mu$ and $\rho$ become unbounded at $w = w_{c_\mu}$ and $w = w_{c_\rho}$, respectively, where

$$w_{c_\mu} = \frac{m + x - 1}{x}, \quad w_{c_\rho} = \frac{1 - x}{m_o - x}.$$

# The Case of $w \longrightarrow w_{c_\mu}$

In this case $\eta$ becomes small, $b$ becomes unbounded, but the product $b\eta$ remains finite. The $k$th term of the standard power series of $F$ becomes

$$\frac{(a)_k(b)_k}{k!(c)_k}\eta^k \sim \frac{(a)_k}{k!(c_0)_k}z^k,$$

with

$$z = \lim_{w\to w_{c_\mu}} b\eta = u + vJ_L, \quad c_0 = \lim_{w\to w_{c_\mu}} c = \gamma_0 + \rho_0 J_L,$$

where

$$u = -\frac{mx(m+x-1)}{mx - m_o(m+x-1)}, \quad v = -u,$$

and

$$\gamma_0 = \frac{x(m(1-m_o) + m_o(1-x))}{mx - m_o(m+x-1)}, \quad \rho_0 = -\gamma_0.$$

It follows that $F$ approaches a confluent hypergeometric function:

$${}_2F_1(a,b;c;\eta) \to {}_1F_1(a;c_0;z).$$

Further action is needed to obtain an asymptotic approximation of the ${}_1F_1$–function.

# The Case of $w \longrightarrow w_{c_\rho}$

In this case $\eta$ and $c$ become unbounded, but the ratio $\eta/c$ remains finite. The $k$th term of the standard power series of $F$ becomes

$$\frac{(a)_k(b)_k}{k!(c)_k}\eta^k \sim \frac{(a)_k(b_0)_k}{k!\, z^k},$$

with

$$z = \lim_{w\to w_{c_\rho}} c/\eta = u + vJ_L, \quad b_0 = \lim_{w\to w_{c_\rho}} b = \beta_0 + \mu_0 J_L,$$

where

$$u = \frac{m_o(m_o - x)(1-x)}{mx - m_o(m+x-1)}, \quad v = -u,$$

and

$$\beta_0 = -\frac{mx(m_o - x)}{mx - m_o(m+x-1)}, \quad \mu_0 = -\beta_0.$$

It follows that $F$ approaches a ${}_2F_0$ hypergeometric function

$${}_2F_1(a, b; c; \eta) \to {}_2F_0(a, b_0; -; 1/z) = \sum_{k=0}^{-a} \frac{(a)_k(b_0)_k}{k!\, z^k},$$

because $a$ is a negative integer. This function can be expressed in terms of the Kummer $U$–function

$${}_2F_0(a, b_0; -; 1/z) = (-z)^a U(a, 1 + a - b_0, -z).$$

Further action is needed to obtain an asymptotic approximation of the $U$–function.

# The Remaining Cases

## Expansion A

An integral representation is

$$ {}_2F_1(a,b;c;\eta) = \frac{\Gamma(c)}{\Gamma(b)\Gamma(c-b)} \int_0^1 t^{b-1}(1-t)^{c-b-1}(1-t\eta)^{-a}\,dt, $$

valid for $c > b > 0, \eta < 1$. This integral can be used when $\rho > \mu > 0, \eta < 1$.

# The Remaining Cases

## Expansion B

Another integral representation is

$$ {}_2F_1(a,b;c;\eta) = \frac{\Gamma(1+b-c)}{\Gamma(b)\Gamma(1-c)} \int_0^\infty t^{b-1}(t+1)^{c-b-1}(1+t\eta)^{-a}\,dt, $$

which is only valid for $a = 0, -1, -2, \ldots$ and $c < a+1$. It can be verified by expanding $(1+t\eta)^{-a}$ in powers of $\eta$. We have $\mu > 0$ and $\rho < -1$, and because

$$ \eta = -\frac{mx}{(1-m_o x)}\,\frac{\rho}{\mu}, $$

we see that $\eta \geq 0$.

## Expansion C

If $\mu < \rho < -1$ and $\eta < 0$, apply the transformation

$$ {}_2F_1(a,b;c;\eta) = (1-\eta')^a\,{}_2F_1(a,b';c;\eta'), $$

where

$$ b' = c - b = \beta' + \mu' J_L, \quad \beta' = \gamma - \beta, \quad \mu' = \rho - \mu, \quad \eta' = \frac{\eta}{\eta - 1}. $$

Now,

$$ \mu' > 0, \quad \rho < -1, \quad \eta' > 0, $$

so use Expansion B.

# The Remaining Cases

1. $w_{c_\mu}, w_{c_\rho} < 0$

   For all $w > 0$, we have $\mu > 0$, $\rho < -1$, and $\eta > 0$, so use Expansion B.

2. $w_{c_\mu} > 0$, $w_{c_\rho} < 0$

   For all $w_{c_\mu} > w > 0$, we have $\mu < -1$, $\rho < -1$, and $\eta < 0$, so use Expansion C.

   For all $w > w_{c_\mu}$, we have $\mu > 0$, $\rho < -1$, and $\eta > 0$, so use Expansion B.

3. $w_{c_\mu} < 0$, $w_{c_\rho} > 0$

   For all $w_{c_\rho} > w > 0$, we have $\mu > 0$, $\rho < -1$, and $\eta > 0$, so use Expansion B.

   For all $w > w_{c_\rho}$, we have $\rho > \mu > 0$ and $\eta < 0$, so use Expansion A.

4. $w_{c_\rho} > w_{c_\mu} > 0$

   For all $w_{c_\mu} > w > 0$, we have $\mu < -1$, $\rho < -1$, and $\eta < 0$, so use Expansion C.

   For all $w_{c_\rho} > w > w_{c_\mu}$, we have $\mu > 0$, $\rho < -1$, and $\eta > 0$, so use Expansion B.

   For all $w > w_{c_\rho}$, we have $\rho > \mu > 0$ and $\eta < 0$, so use Expansion A.

# Additional Work for the Mainland Model

Expanding ${}_2F_1(1 - J_M, 1; 2 - \xi_M; \eta_M)$ and ${}_3F_2(1 - J_M, 1, 1; 2, 2 - \xi_M; \eta_M)$.

# Summary

- For a problem in ecological modeling, we have derived a great number of expansions of hypergeometric functions by identifying critical parameter values and enumerating special cases.
- In a few cases, the asymptotics can only be described by using their limits in the form of confluent hypergeometric functions.
- Future research is needed to develop uniform transitions among the great number of special cases.