Non-linearity * Variability ➡ Diversity

Non-linearity

Arises when biotic interactions generate density/frequency-dependence in fitness

Variability

Abiotic variation cannot generate density/frequency-dependence in fitness

Modify non-linearities in space and time, generate large-scale patterns

1. Non-linearity in the absence of variability ✓

2. Interplay between non-linearity and variability

Interplay between non-linearity and variability

Spatial

Temporal

Interplay between non-linearity and spatial variation

Spatial structure of the landscape

Local scale: community

Local dynamics

species interactions

(R^*, P^* rules)

Dispersal

Variability

Regional scale: metacommunity

Spatial dynamics

Interplay between local dynamics and spatial variation $\Rightarrow$ emergent properties at the regional scale

Local dynamics

Density-dependent feedback loops generated by species interactions **within local communities**

Spatial variation ≠ variation in abiotic environment (temperature, rainfall)

Spatial variation ⇒ spatial heterogeneity in *biotic* environment

Spatial variation in abiotic environment matters only if it generates variance in fitness

Spatial heterogeneity in biotic interactions

Spatially heterogeneous **biotic** environment

Spatial variation in the environment generates spatial variance in density-dependent feedback loops

⇒ density-/frequency dependence not the same everywhere

When the biotic environment is spatially heterogeneous, individual will respond by dispersing between habitats in a way that maximizes fitness.

The resulting interplay between local non-linearity and spatial variation can allow coexistence of species that would otherwise exclude each other

Interplay between local dynamics and spatial variation

1. Exploitative competition

2. Mutualistic interactions

Interplay between local dynamics and spatial variation

1. Exploitative competition in spatially varying environments

Spatially heterogeneous **competitive** environment

Spatial environmental variation ⇒ spatial heterogeneity in competitive interactions (strength of intra- and inter-specific competition not same everywhere)

Spatially heterogeneous **competitive** environment

Locality 1

$a_{11} < 1$

$a_{21} > 1$

Favorable to Species 1

Species 2 excluded

Source for Species 1

Sink for Species 2

Locality 2

$a_{12} > 1$

$a_{22} < 1$

Unfavorable to Species 1

Species 1 excluded

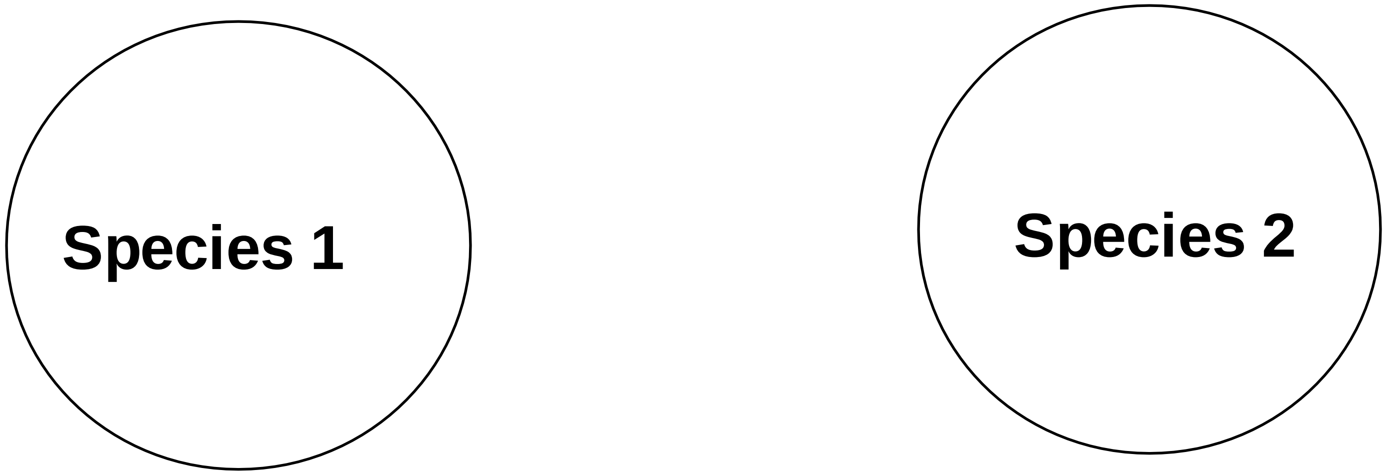
Sink for Species 1

Source for Species 2

Spatially heterogeneous **competitive** environment

Locality 1

Locality 2



Favorable to Species 1

Species 2 excluded

Unfavorable to Species 1

Species 1 excluded

Regional coexistence of competing species

Local scale: community

Local dynamics — species interactions (R^*, P^* rules)

Dispersal ↓

Variability ↓

Regional scale: metacommunity

Regional dynamics

Local dynamics*spatial variation ⇒ regional dynamics

Spatially variation in competitive ability across the landscape ⇒ regional coexistence

Local scale: community

Local dynamics

species interactions

(R^*, P^* rules)

Dispersal

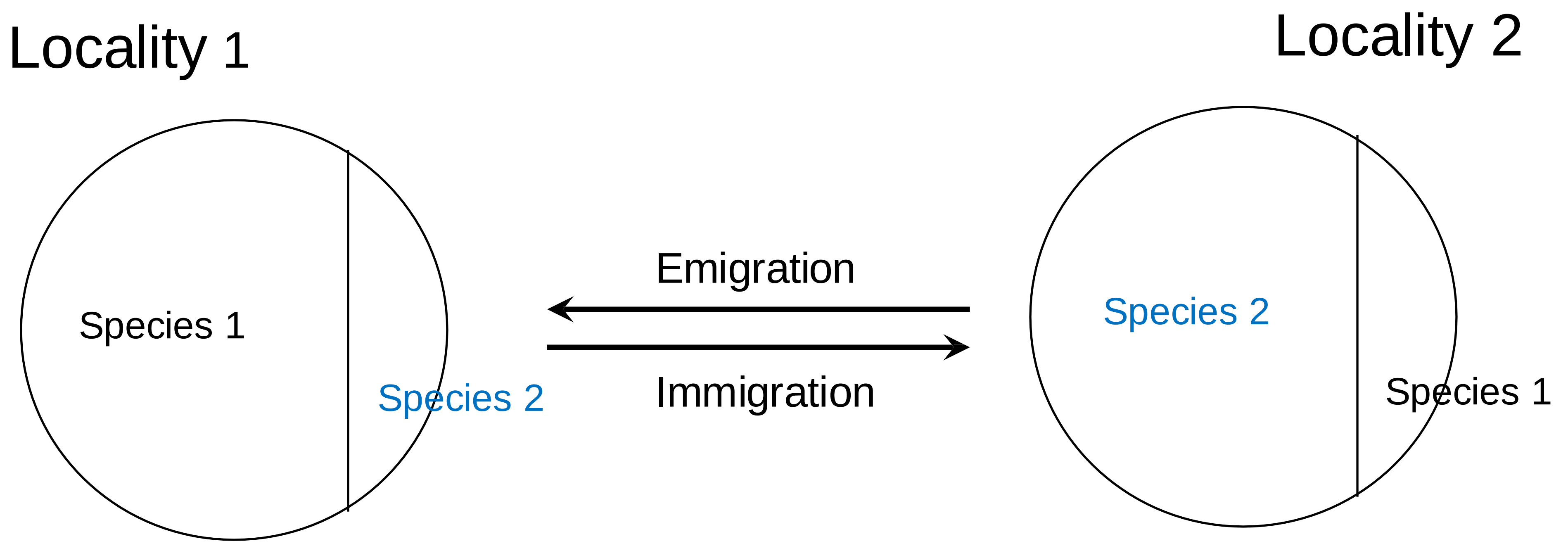
Variability

Regional scale: metacommunity

Regional dynamics

Local dynamics*spatially variation ⇒ regional coexistence

Local dynamics*spatially variation*dispersal ⇒ local coexistence?



Local coexistence

Given spatial variation in competitive ability, dispersal between localities can lead to **local** coexistence via **source-sink dynamics**

Spatial dynamics of exploitative competition

Patchy environment

Spatial variation in competitive ability

Emigration and immigration between patches
on the same time scale as local dynamics

Spatial dynamics of exploitative competition

Point of departure: two-patch, two-species metacommunity

Generalizable to *n*-patch, *m*-species metacommunity

Mathematical model of competition and dispersal

$$\frac{dX_i}{dt} = r_X X_i \left(1 - \frac{X_i}{K_{X_i}} - \alpha_{X_i} \frac{Y_i}{K_{X_i}}\right) - d_X X_i + d_X X_j$$

$$\frac{dY_i}{dt} = r_Y Y_i \left(1 - \frac{Y_i}{K_{Y_i}} - \alpha_{Y_i} \frac{X_i}{K_{Y_i}}\right) - d_Y Y_i + d_Y Y_j$$

$$(i, j = 1, 2, i \neq j)$$

Competition Emigration Immigration

$$x_i = \frac{X_i}{K_{X_i}} \qquad y_i = \frac{Y_i}{K_{Y_i}} \qquad a_{x_i} = \alpha_{X_i}\frac{K_{Y_i}}{K_{X_i}}$$

$$a_{y_i} = \alpha_{Y_i}\frac{K_{X_i}}{K_{Y_i}} \qquad k_x = \frac{K_{X_j}}{K_{X_i}} \qquad k_y = \frac{K_{Y_j}}{K_{Y_i}}$$

$$\rho = \frac{r_Y}{r_X} \qquad \beta_X = \frac{d_X}{r_X} \qquad \beta_Y = \frac{d_Y}{r_Y}$$

$$\tau = r_X t \qquad (i, j = 1, 2, i \neq j)$$

Species differ in competitive and dispersal abilities, but are otherwise similar:

$$\rho = 1 \qquad k_x = k_y = 1 \qquad K_{X_i} = K_{Y_i}$$

$$\Rightarrow \ a_{x_i} = \alpha_{x_i} \qquad a_{y_i} = \alpha_{x_i}$$

Non-dimensionalized model of competition and dispersal

$$\frac{dx_i}{d\tau} = x_i\left(1 - x_i - \alpha_{x_i} y_i\right) - \beta_x x_i + \beta_x x_j$$

$$\frac{dy_i}{d\tau} = y_i\left(1 - y_i - \alpha_{y_i} x_i\right) - \beta_y y_i + \beta_y y_j$$

Competition Emigration Immigration

$$(i, j = 1, 2, i \neq j)$$

Compute invasion criteria

Within a given patch, can the inferior competitor increase when rare when the superior competitor is at carrying capacity?

Construct the Jacobian matrix for the competition-dispersal model

$$\begin{bmatrix} 1-2{x_1}^\star-\alpha_{x,1}{y_1}^\star-\beta_x & \beta_x & -\alpha_{x,1}{x_1}^\star & 0 \\ \beta_x & 1-2{x_2}^\star-\alpha_{x,2}{y_2}^\star-\beta_x & 0 & -\alpha_{x,2}{x_2}^\star \\ -\alpha_{y,1}{y_1}^\star & 0 & 1-2{y_1}^\star-\alpha_{y,1}{x_1}^\star-\beta_y & \beta_y \\ 0 & -\alpha_{y,2}{y_2}^\star & \beta_y & 1-2{y_2}^\star-\alpha_{y,2}{x_2}^\star-\beta_y \end{bmatrix}$$

Evaluate the Jacobian matrix at the boundary equilibrium $(x_1^\star, x_2^\star, y_1^\star, y_2^\star) = (1, 1, 0, 0)$

Inferior competitor can invade when rare if the dominant eigenvalue is positive

Dominant eigenvalue is positive if

$$b + \frac{\sqrt{b^2 - 4c}}{2} > 0$$

where

$$b = (1 - \alpha_{y,1} - \beta_y) + (1 - \alpha_{y,2} - \beta_y)$$

and

$$c = (1 - \alpha_{y,1} - \beta_y)(1 - \alpha_{y,2} - \beta_y) - {\beta_y}^2$$

This gives us the invasion criterion for the inferior competitor:

$$(1 - \alpha_{y,1})(1 - \alpha_{y,2}) - \beta_y\Big((1 - \alpha_{y,1}) + (1 - \alpha_{y,2})\Big) < 0$$

where $1 - \alpha_{y,i}$ $(i = 1, 2)$ is the initial per capita growth rate of the inferior competitor in patch i in the absence of dispersal

$$(1-\alpha_{y,1})(1-\alpha_{y,2}) - \beta_y\Big((1-\alpha_{y,1}) + (1-\alpha_{y,2})\Big) < 0$$

$(1-\alpha_{y,1})(1-\alpha_{y,2})$: product of the initial per capita growth rates in the two patches

$(1-\alpha_{y,1}) + (1-\alpha_{y,2})$: sum of the initial per capita growth rates in the two patches

Invasion is possible only in a spatially heterogeneous competitive environment

Consider first, invasion in a spatially homogeneous competitive environment

Invasibility in a spatially homogeneous competitive environment

Species 1 is the superior competitor across the metacommunity:

$$\Rightarrow \alpha_{x,1} = \alpha_{x,2} = \alpha_x < 1$$

Species 2 is the inferior competitor across the metacommunity:

$$\Rightarrow \alpha_{y,1} = \alpha_{y,2} = \alpha_y > 1$$

By simplifying the invasion criterion,

$$(1-\alpha_{y,1})(1-\alpha_{y,2}) - \beta_y\Big((1-\alpha_{y,1}) + (1-\alpha_{y,2})\Big) < 0$$

We arrive at the inferior competitor's invasion criterion in a spatially homogeneous competitive environment:

$$(1 - \alpha_y)^2 - 2\beta_y(1 - \alpha_y) < 0.$$

$$(1-\alpha_y)^2 - 2\beta_y(1-\alpha_y) < 0$$

Recall that $(1-\alpha_y) < 0$ i.e., the inferior competitor cannot maintain a positive per capita growth rate when rare.

This means that,

(i) the sum of the initial growth rates $2(1-\alpha_y) < 0$ and

(ii) the product of the initial growth rates $(1-\alpha_y)^2 > 0$.

Since the sum of the initial growth rates $2(1-\alpha_y) < 0$,

and the product of the initial growth rates $(1-\alpha_y)^2 > 0$,

$(1-\alpha_y)^2 - 2\beta_y(1-\alpha_y) > 0$

$\Longrightarrow$ the inferior competitor cannot invade when rare in a spatially **homogeneous** competitive environment.

No local coexistence in a spatially homogeneous *competitive* environment

Relative strengths of intra-specific and inter- specific density-dependence are the same everywhere in the landscape

Local coexistence in a spatially heterogeneous *competitive* environment

In a spatially heterogeneous environment, initial per capita growth rate is positive in the favorable locality, and negative in the unfavorable locality.

$$(1-\alpha_{y,i})<0,(1-\alpha_{y,j})>0 \quad (i,j=1,2,i\neq j).$$

This means that the product of the initial growth rates $(1-\alpha_{y,i})(1-\alpha_{y,j})$ is always negative.

Invasibility depends on the sum of the initial growth rates

$$(1-\alpha_{y,1})(1-\alpha_{y,2})-\beta_y\Big((1-\alpha_{y,1})+(1-\alpha_{y,2})\Big)<0$$

Case 1. Strong spatial variation in competitive ability

$$(1-\alpha_{y,1})(1-\alpha_{y,2})-\beta_y\Big((1-\alpha_{y,1})+(1-\alpha_{y,2})\Big)<0$$

If the positive initial growth rate in the favorable locality is high relative to the negative growth rate in the unfavorable locality, the sum of the initial growth rates is positive.

This makes the LHS negative, thus satisfying the condition for inferior competitor's invisibility.

Invasion is possible under any level of dispersal, i.e., magnitude of dispersal rate does not matter if spatial variance in competitive ability is high

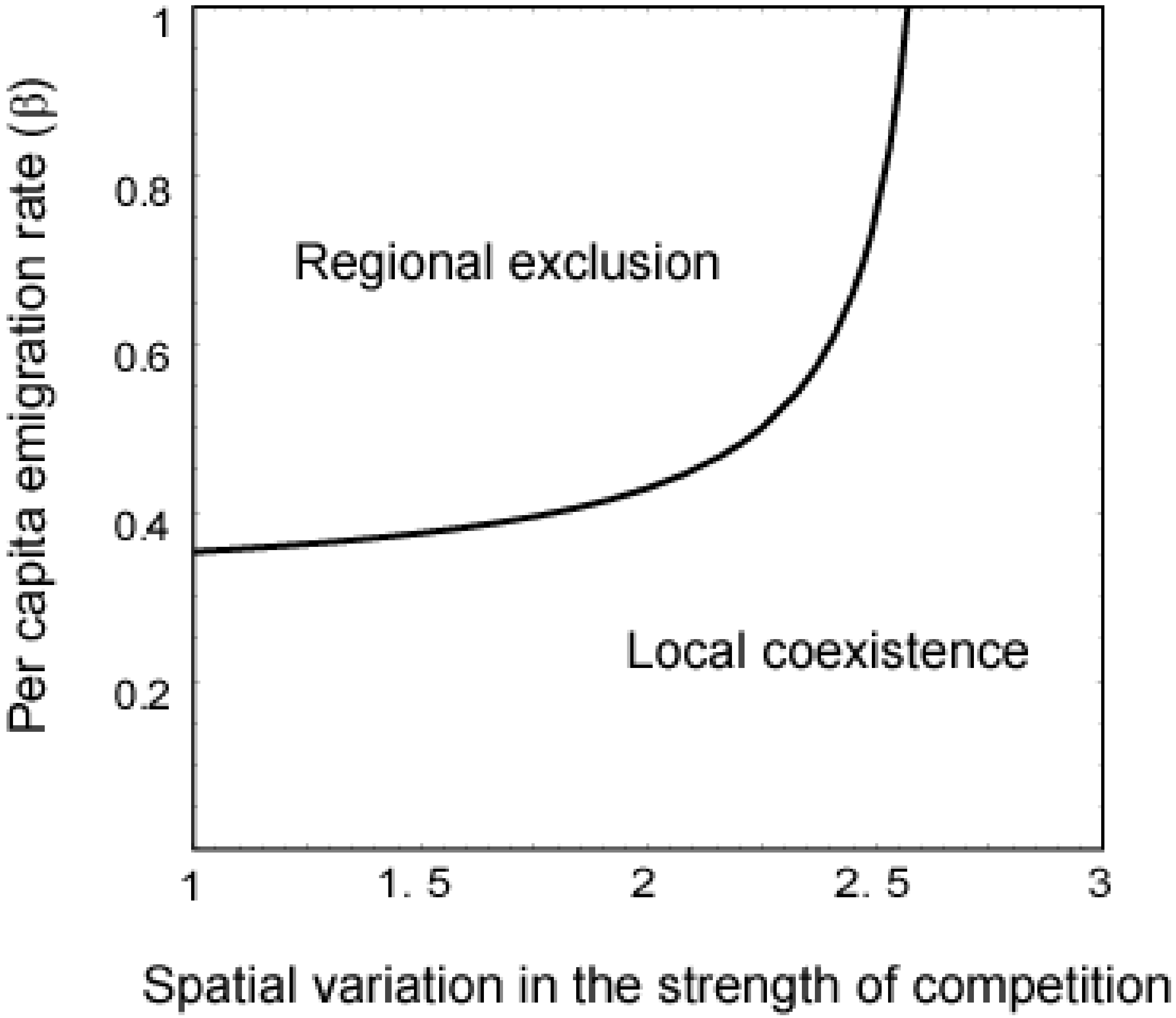
Coexistence equilibrium is stable when it is feasible, and therefore, invasibility guarantees long-term coexistence.

Case 2. Weak spatial variation in competitive ability

$$(1-\alpha_{y,1})(1-\alpha_{y,2}) - \beta_y\Big((1-\alpha_{y,1}) + (1-\alpha_{y,2})\Big) < 0$$

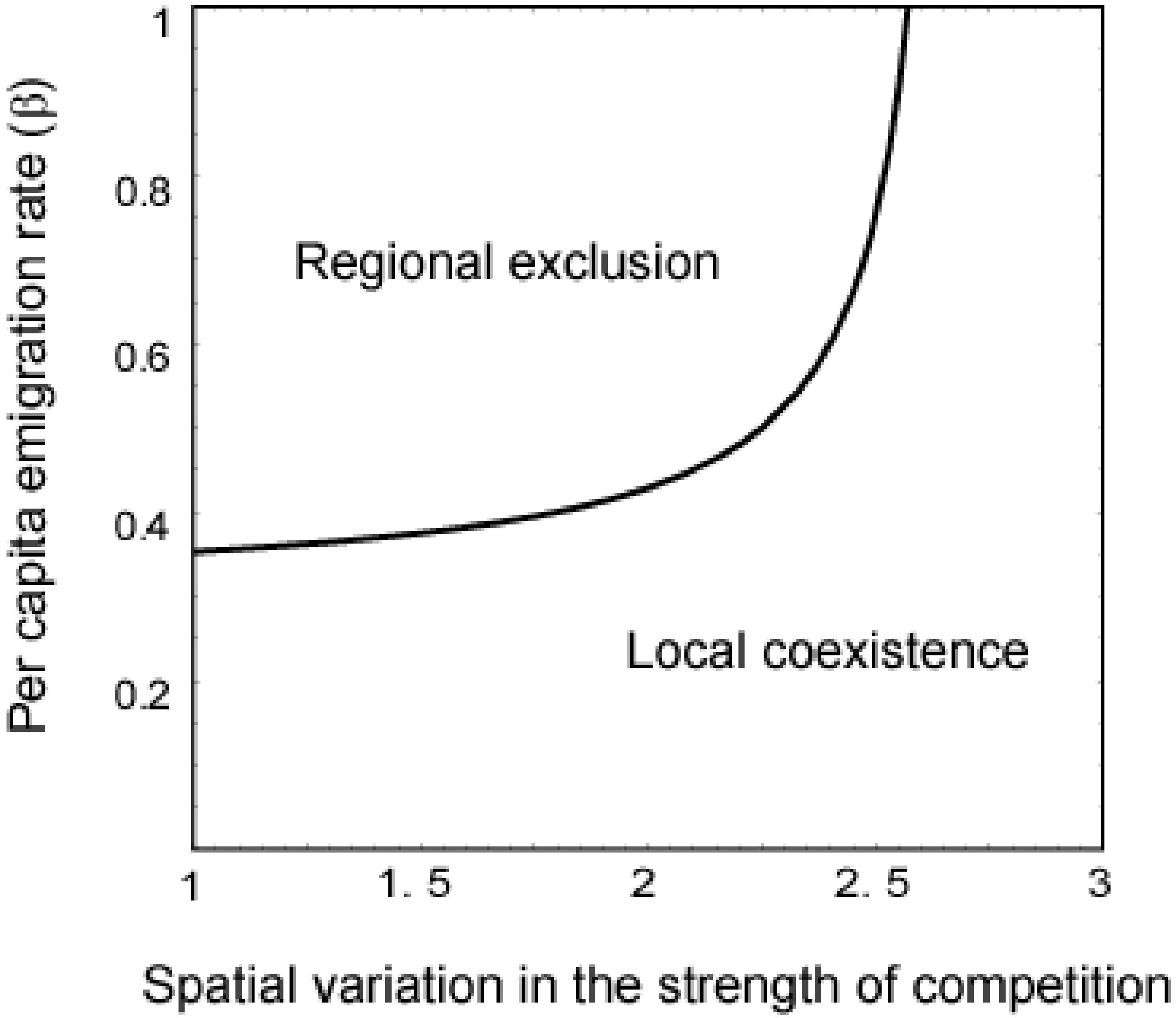
If the positive growth rate in the favorable locality is small in magnitude relative to the negative growth rate in the unfavorable locality, the sum of the initial growth rates can be negative.

Now, invasibility depends on the relative magnitudes of competition and dispersal.



High spatial variation: competitive advantage in source very high relative to competitive disadvantage in sink

Low spatial variation: competitive advantage in source low relative to competitive disadvantage in sink



When spatial variation is high, coexistence possible as long as β >0.

When spatial variation is low, coexistence only if β below critical threshold

High dispersal is detrimental to coexistence

1. When spatial variation in competitive ability is high, coexistence is possible regardless of the dispersal rate.

2. When spatial variation in competitive ability is low, high dispersal can eliminate competitive differences between patches and cause competitive exclusion at the regional scale.

How does dispersal allow local coexistence?

Simple answer: inferior competitor can persist as long as there is immigration from other localities

Coexistence: species must limit themselves more than they do others (intra-specific competition > inter-specific competition)

If dispersal allows coexistence, …??

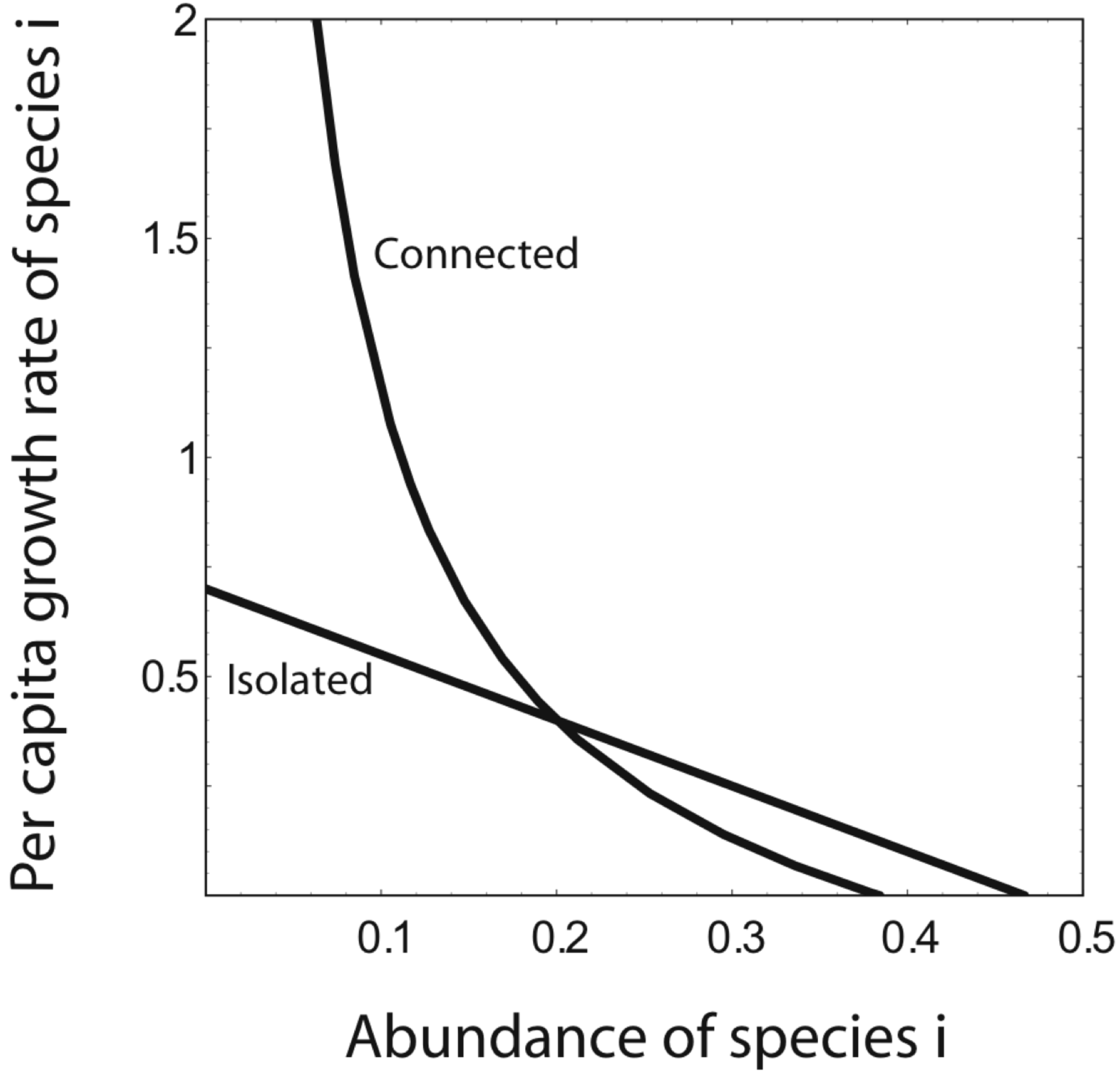
Coexistence: species must limit themselves more than they do others (intra-specific interactions > inter-specific interactions)

If dispersal allows coexistence, it must be by increasing the strength of intra-specific interactions relative to inter-specific interactions

Coexistence requires negative feedback (negative DD in per capita growth rates)

Compare per capita growth rates in isolated and connected communities

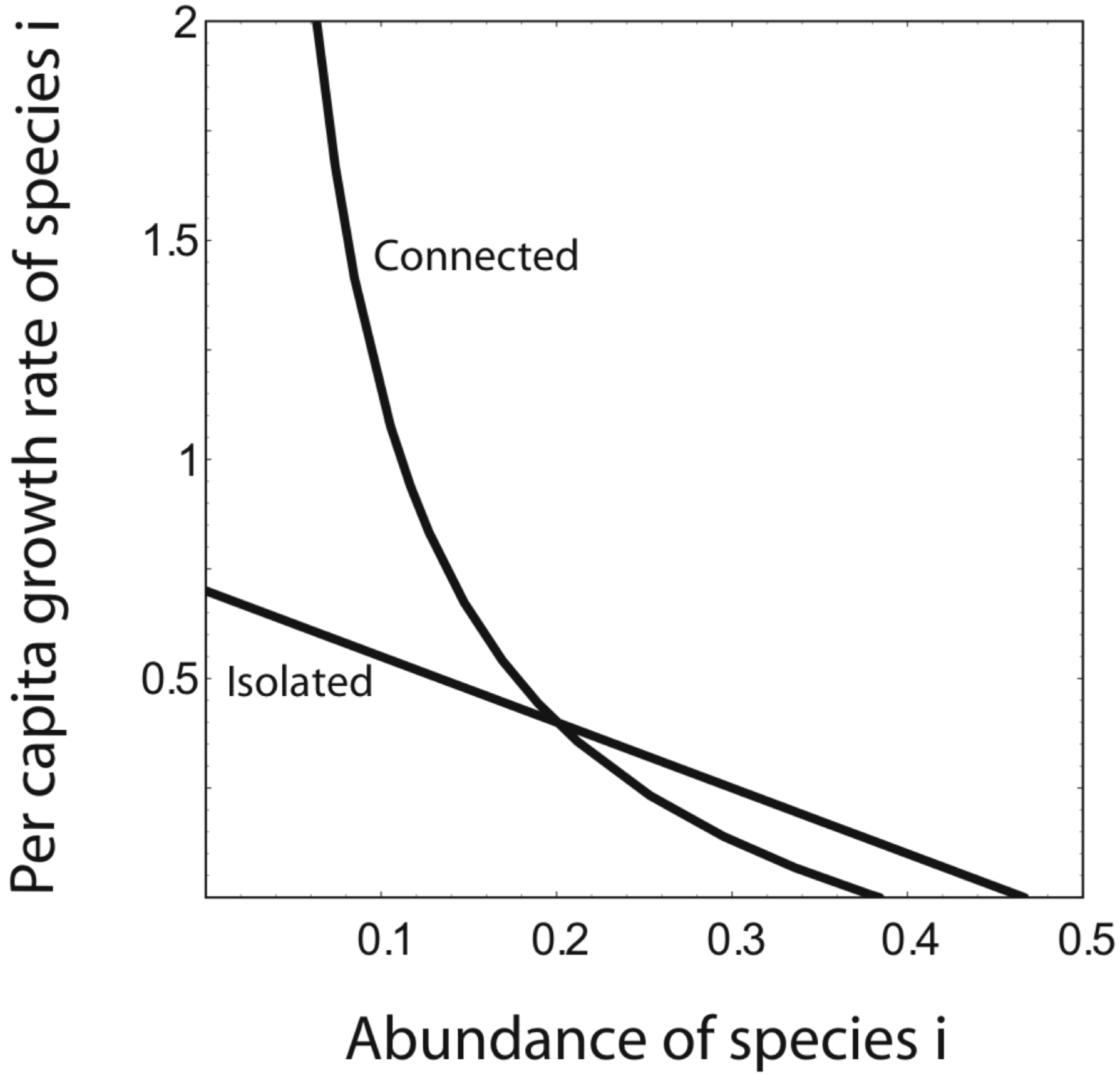
Mechanism of spatial coexistence



Non-linear density-dependence: dispersal generates negative feedback

Enhances negative DD in the growth rate

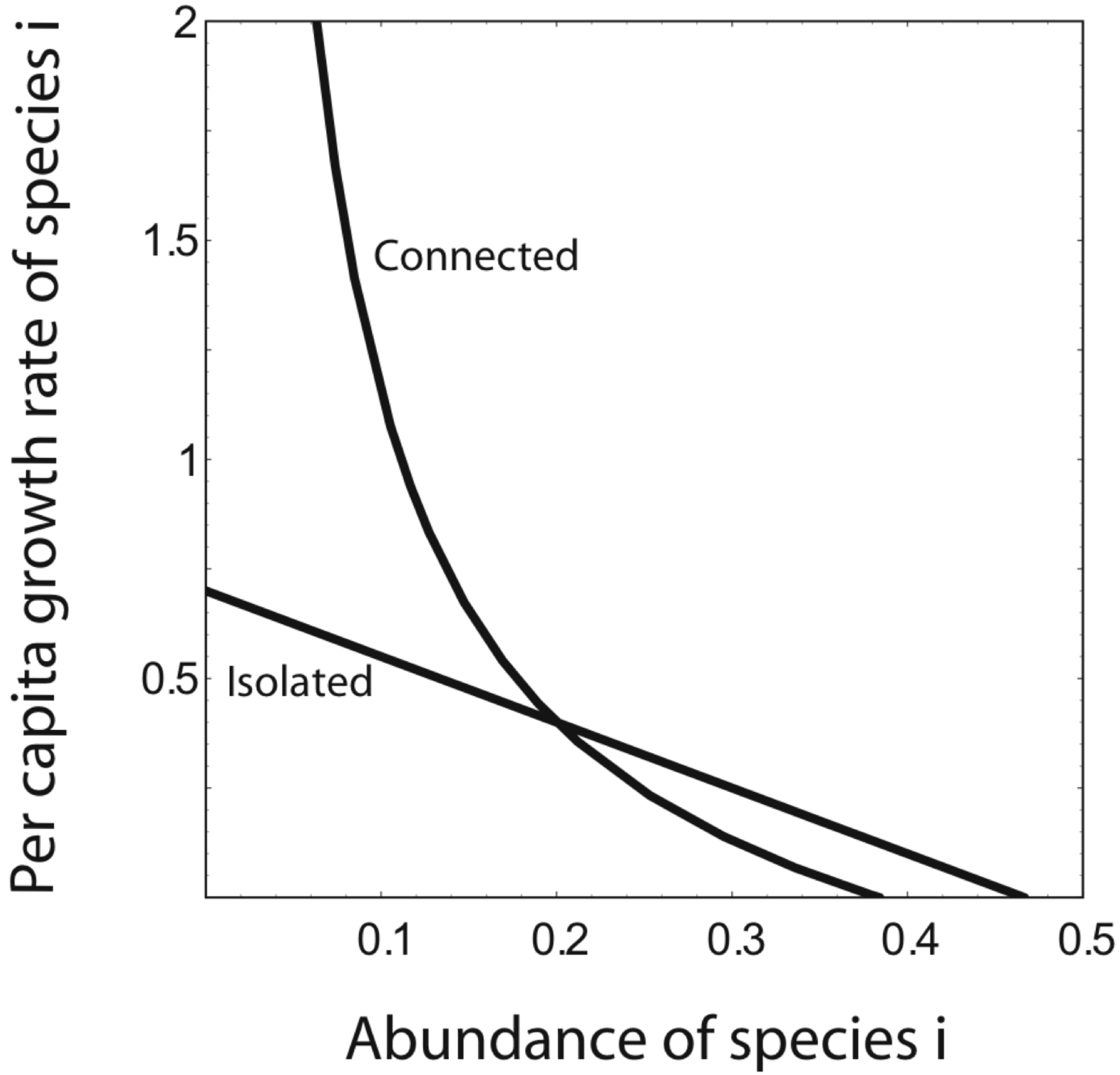
Mechanism of spatial coexistence



Higher growth rate at low abundances: enhances ability of species to recover from low density

Lower growth rate at high abundances increases negative DD and the stability of coexistence equilibrium

Mechanism of spatial coexistence



Net result

Stable coexistence of species that would otherwise be excluded

Negative feedback due to dispersal

$$\frac{dx_i}{d\tau} = x_i\left(1 - x_i - \alpha_{x_i} y_i\right) - \beta_x x_i + \beta_x x_j$$

$$\frac{dy_i}{d\tau} = y_i\left(1 - y_i - \alpha_{y_i} x_i\right) - \beta_y y_i + \beta_y y_j$$

$$(i, j = 1, 2, i \neq j)$$

Focus on species i's per capita growth rate when rare:

$$\frac{dx_i}{dt}\frac{1}{x_i} = (1 - x_i - \alpha_{x_i} y_i) - \beta_x + \beta_x \frac{x_j}{x_i}$$

Per capita growth rate is a **non-linearly decreasing function of density** (x_i) through the immigration term.

This generates negative density-dependence over and above that due to intra-specific competition

Mechanism of spatial coexistence

Dispersal generates negative density-dependent effect

Increases strength of intra-specific interactions relative to inter-specific interactions

Promotes coexistence

Local dynamics*spatially variation ⇒ regional coexistence

Local dynamics*spatially variation*dispersal ⇒ local coexistence? YES

Interplay between local dynamics and spatial variation

1. Exploitative competition ✓
2. Mutualistic interactions

Mutualistic interactions

1. Local dynamics: positive feedback (Allee effects)

2. Allee effects: increase extinction risk due to perturbations (e.g., fragmentation)

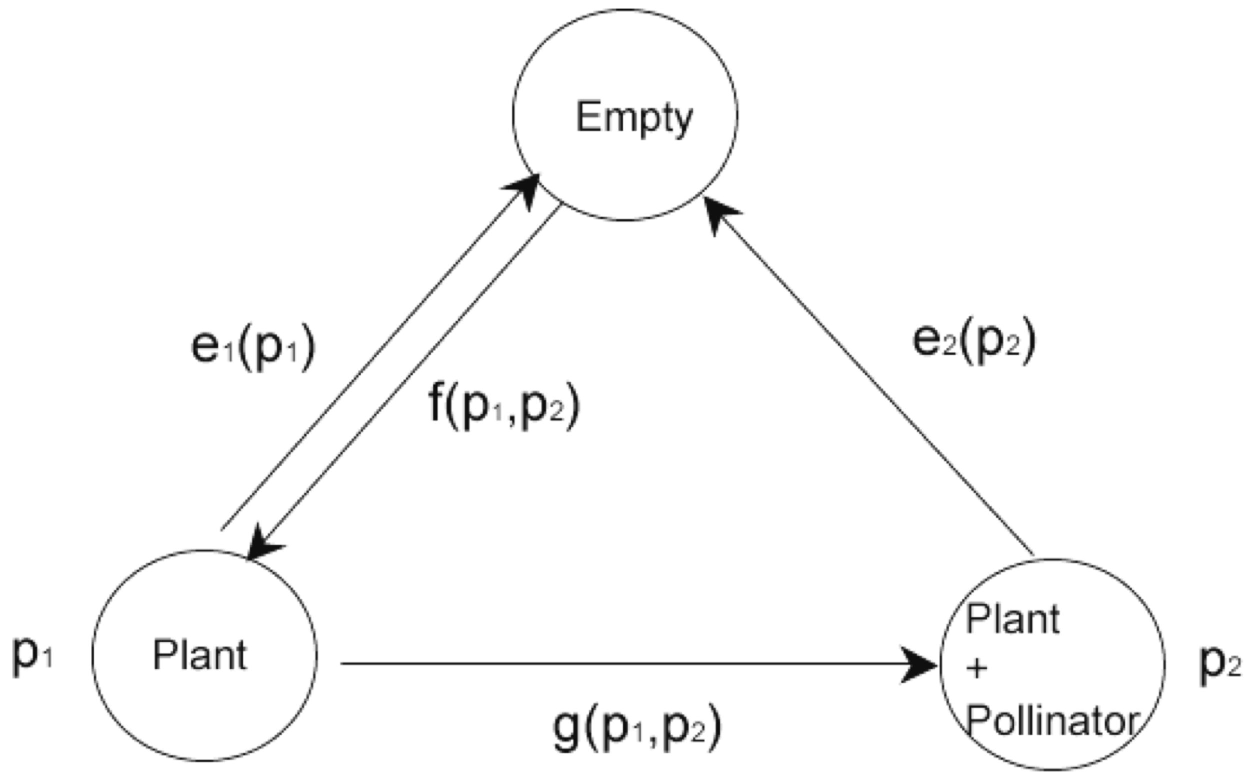
Mutualistic interactions in spatially heterogeneous environments

1. Obligate mutualism

2. Pairwise: mobile and non-mobile species

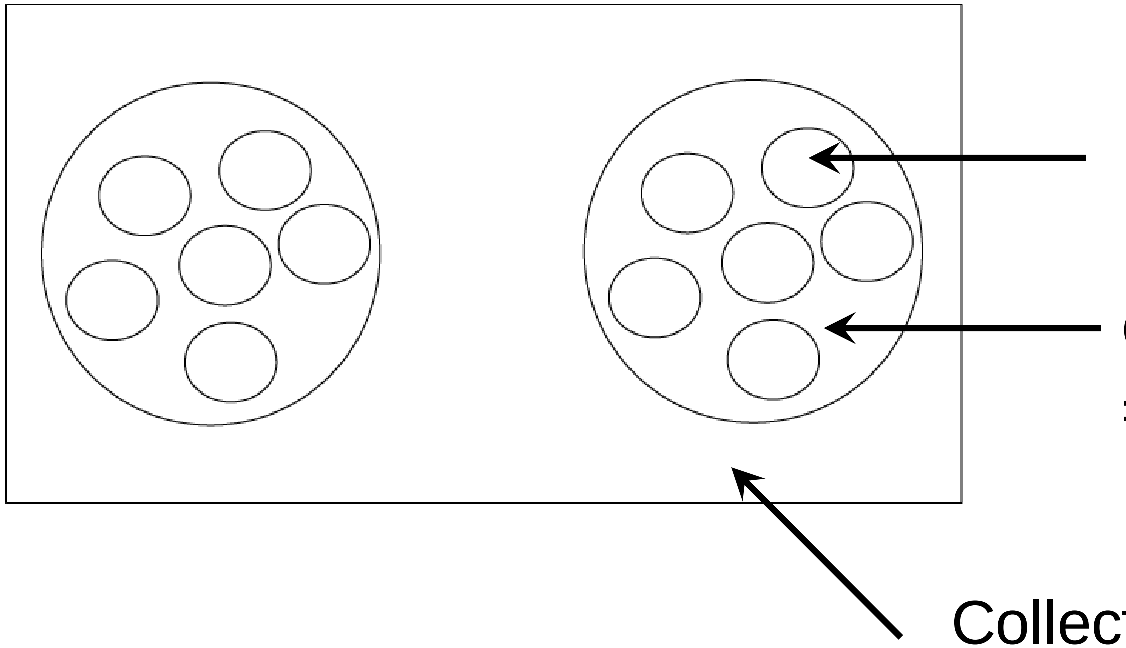
3. Dispersal of mobile mutualist

Local dynamics



$$\frac{dp_1}{dt} = f(p_1, p_2) - g(p_1, p_2) - e_1(p_1)$$
$$\frac{dp_2}{dt} = g(p_1, p_2) - e_2(p_2)$$

Hierarchical spatial structure

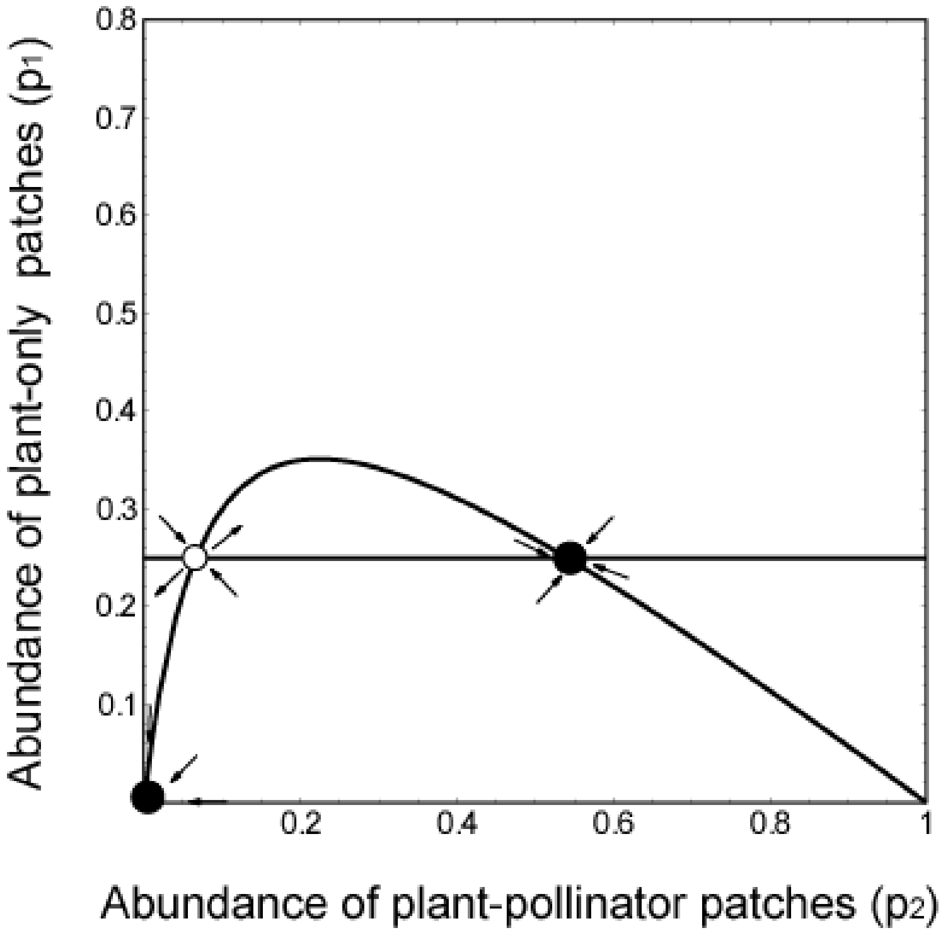


Patch = **Individual**

Collection of patches
= **Local community**

Collection of local
communities =
Metacommunity

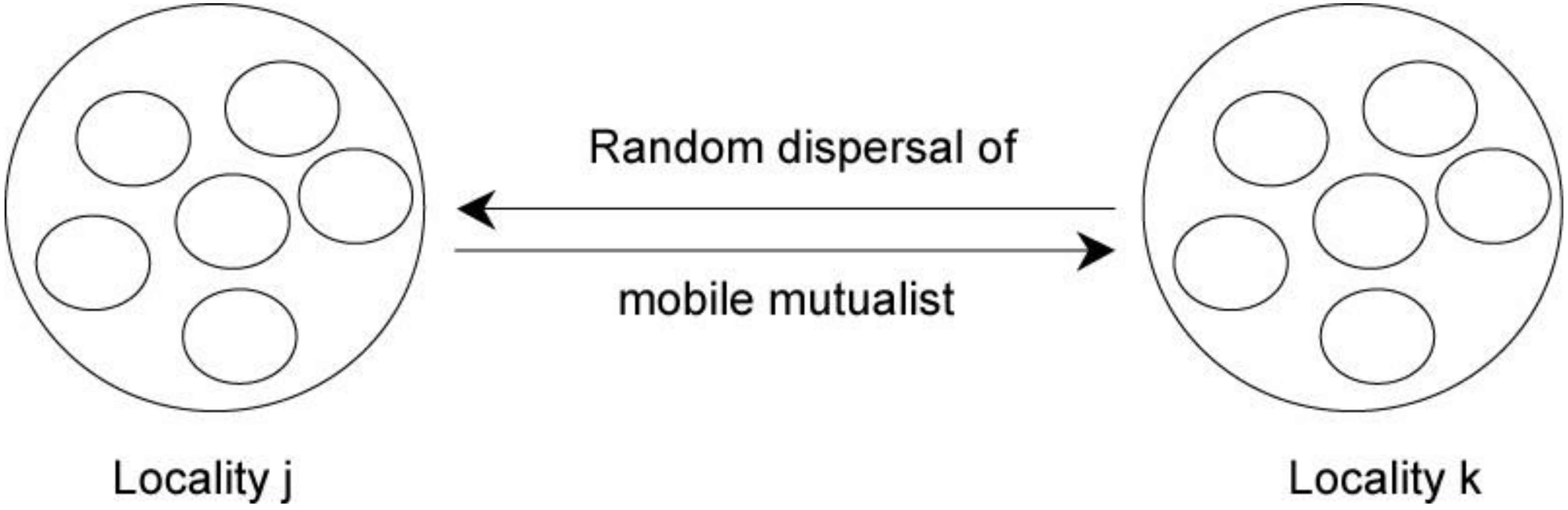
Local dynamics of an isolated locality



Allee effect ==> Species cannot increase when rare

Can spatial variation counteract the Allee effect and allow species to increase when rare?

Spatial dynamics: dispersal between localities



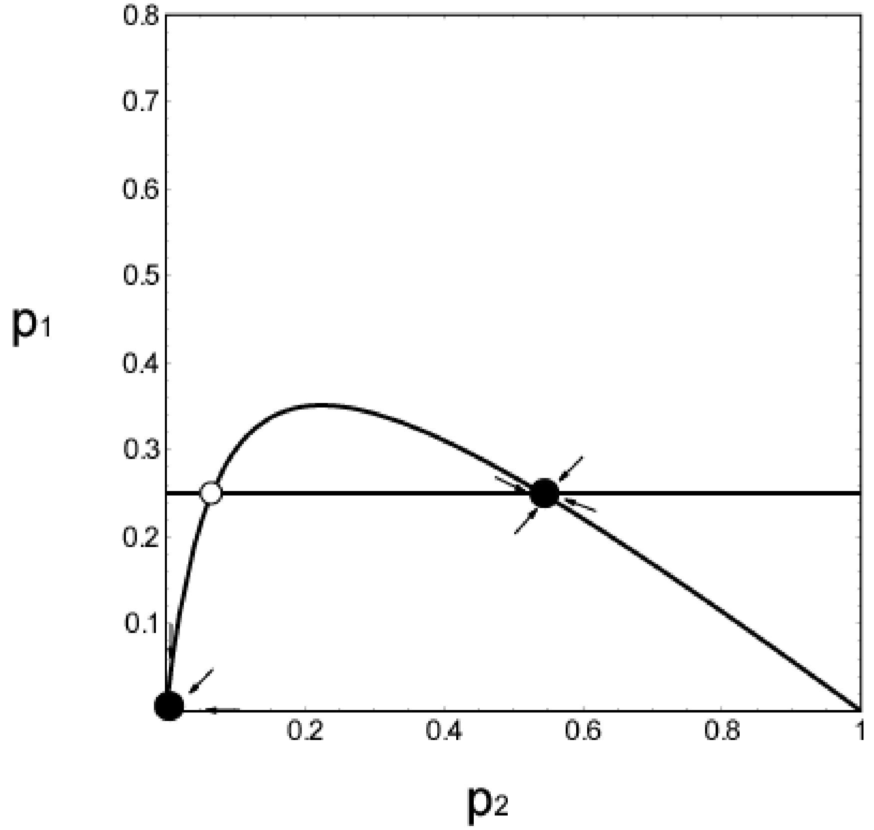
$$\frac{dp_{1j}}{dt} = f_j(p_{1j}, p_{2j}) - g_j(p_{ij}, p_{2k}, I) - e_{1j}(p_{1j})$$

$$\frac{dp_{2j}}{dt} = g_j(p_{ij}, p_{2k}, I) - e_{2j}(p_{2j}) \quad i, j, k = 1, 2;\ j \neq k$$

↑

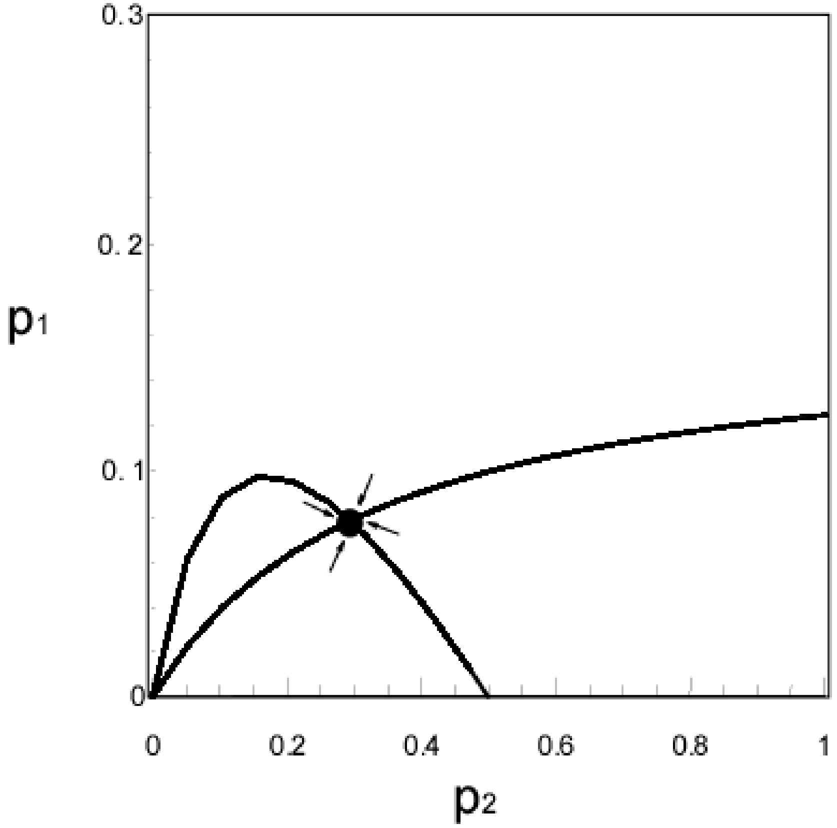
Production of plant-pollinator patches

Isolated



Species cannot increase when rare

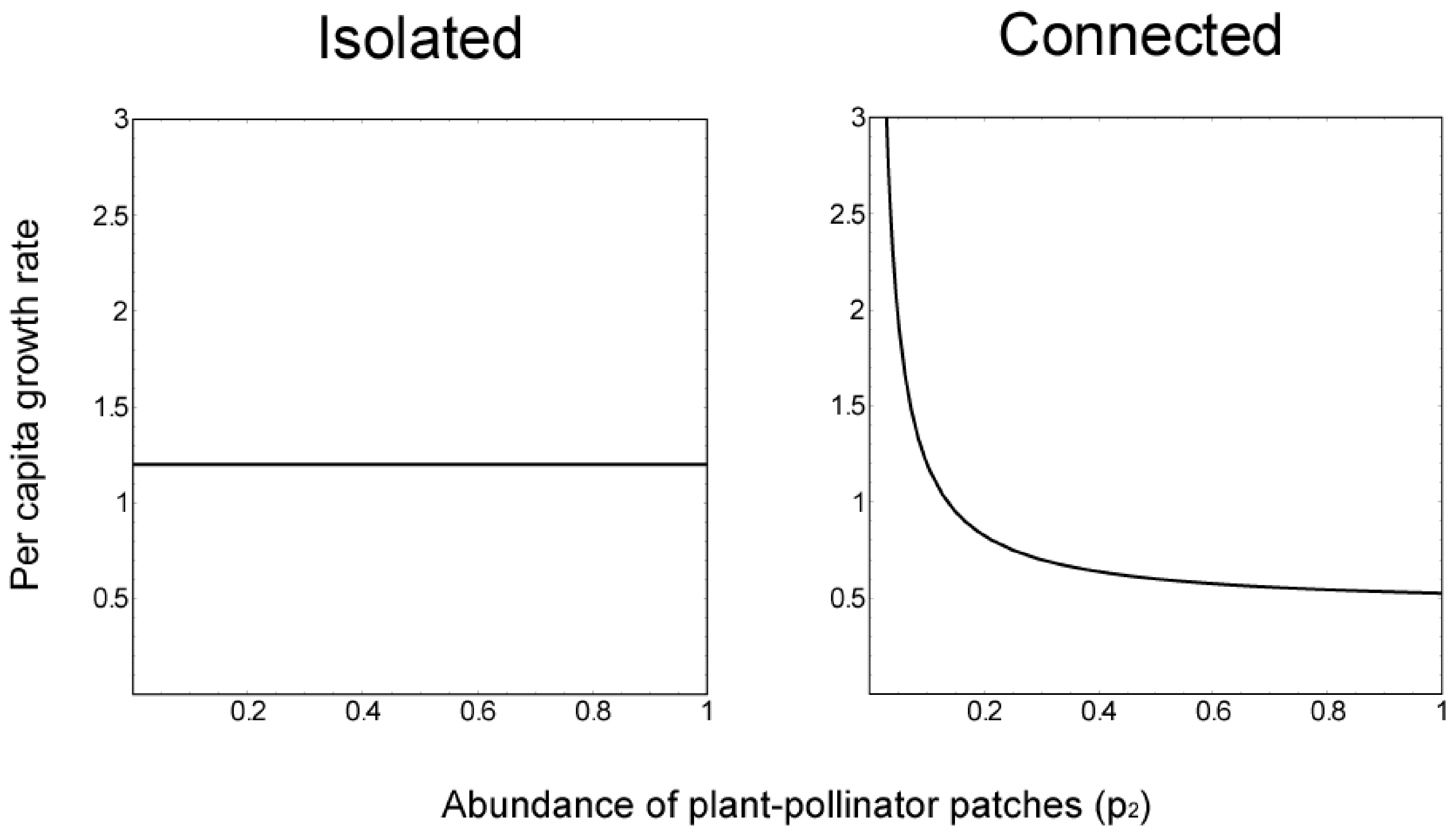
Connected

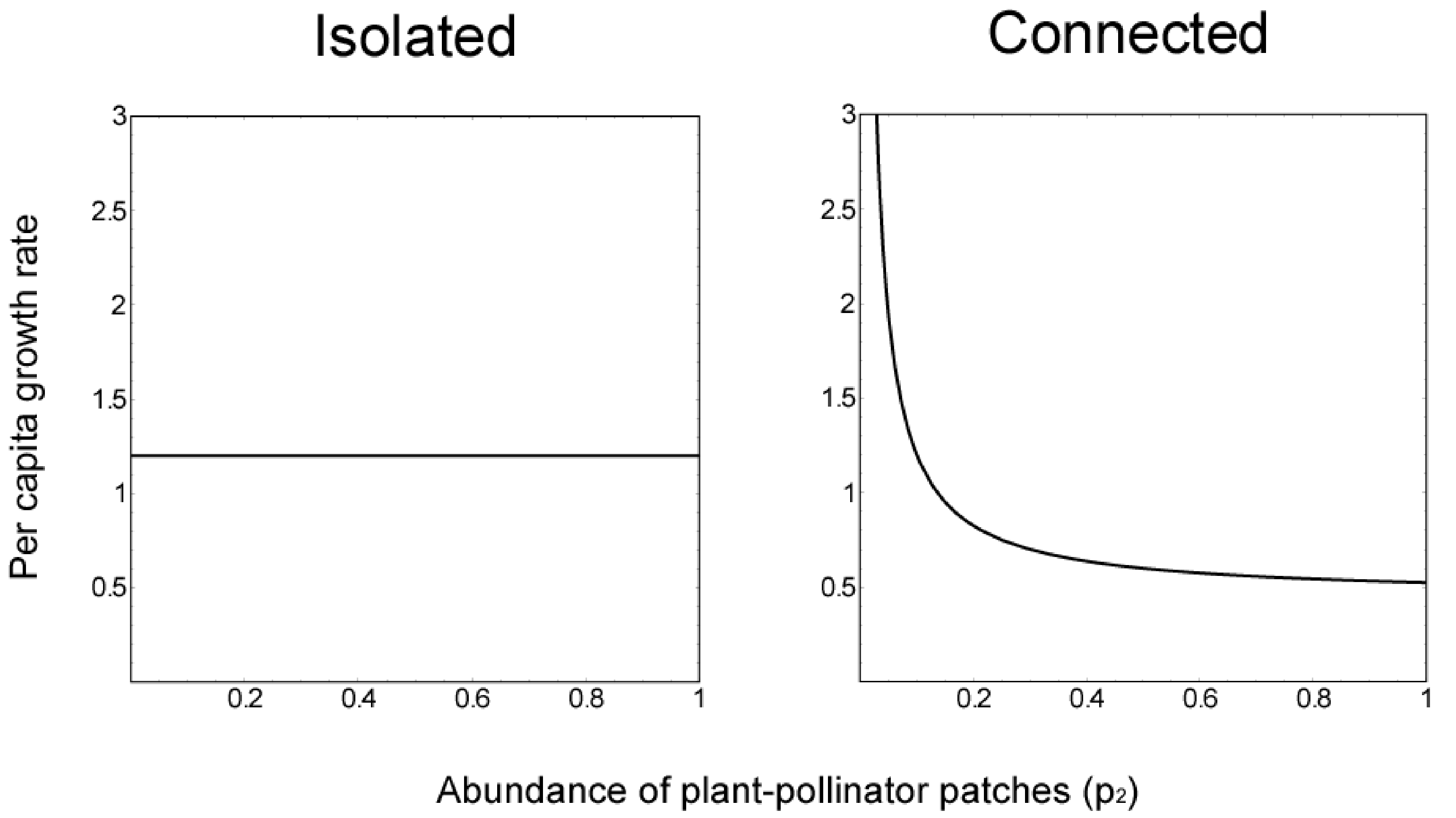


Species can increase when rare

Dispersal itself is density-independent, but it generates negative density-dependence that counteracts the positive density-dependence due to the Allee effect

Mechanism of the rescue effect: negative density-dependence due to dispersal





Dispersal generates a negative density- dependent effect similar to intra- specific competition. Per capita growth rate is high when abundance is low. This allows species to increase when rare.

Mechanistic basis of the rescue effect

Dispersal increases the strength of intra-specific interactions relative to inter-specific interactions.

Spatial coexistence of mutualistic species

Local dynamics (positive DD)

Spatial variation in fitness (per capita growth rate)

Dispersal (negative DD)

Spatial coexistence of mutualistic species

Negative density-dependence generated by dispersal counteracts positive density-dependence due to Allee effect, promotes coexistence

Interplay between local dynamics and spatial variation

1. Exploitative competition ✓

2. Mutualistic interactions ✓

Local dynamics can reduce diversity

1. Competitive interactions: R^* rule ==> competitive exclusion

2. Mutualistic interactions: Allee effects ==> extinction

Local dynamics*spatially variation ⇒ regional coexistence

Local dynamics*spatially variation*dispersal ⇒ local coexistence

1. When spatial variation is high, coexistence is possible regardless of the dispersal rate.

2. When spatial variation is low, coexistence is possible only if dispersal is low enough not to eliminate fitness differences between patches.

Interplay between non-linearity and variability

Spatial ✓

Temporal