Mechanisms that maintain diversity

Diversity: Species coexistence

Coexistence: Non-linear dynamics * Environmental heterogeneity

(density-dependence) (temporal, spatial)

Sources of non-linearity and heterogeneity

Non-linearity: resources, natural enemies

(**Species interactions**)

Heterogeneity: space, time

(Jensen's inequality)

Coexistence via interplay between non-linearity and heterogeneity

1. Coexistence via non-linearity alone ✓

2. Coexistence via non-linearity and environmental heterogeneity

Coexistence via interplay between non-linearity and heterogeneity

1. Non-linearity*spatial heterogeneity ==> **Spatial niche partitioning**

2. Non-linearity*temporal heterogeneity ==> **Temporal niche partitioning**

Coexistence via interplay between non-linearity and spatial heterogeneity

Local non-linearity*spatial heterogeneity

Local scale: single community

species interactions

(R^*, P^* rules)

Dispersal

Heterogeneity

Regional scale: metacommunity

Coexistence via interplay between non-linearity and spatial heterogeneity

1. Exploitative competition

2. Mutualistic interactions

Coexistence via interplay between non-linearity and spatial heterogeneity

1. Exploitative competition in a spatially heterogeneous environment

Spatial heterogeneity in competitive ability

Locality 1

$\alpha_{11} < 1$

$\alpha_{21} > 1$

Species 1

Source for Species 1

Sink for Species 2

Locality 2

$\alpha_{12} > 1$

$\alpha_{22} < 1$

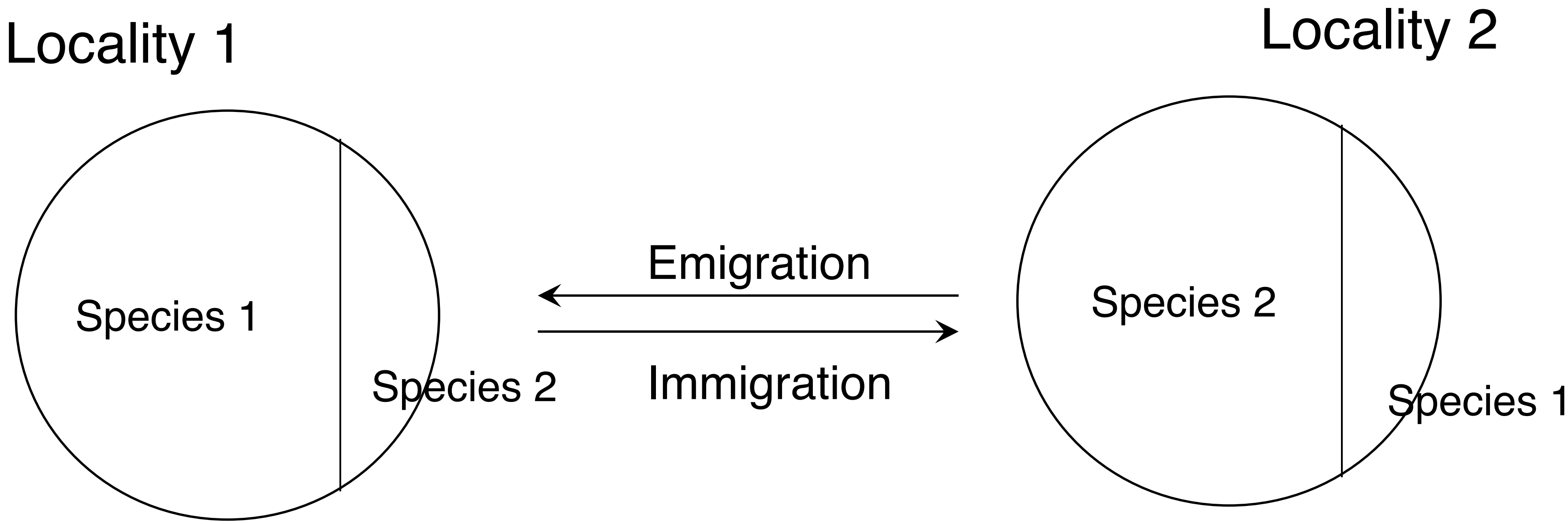
Species 2

Sink for Species 1

Source for Species 2

Regional coexistence

Spatial heterogeneity + dispersal



Local coexistence ?

Spatial dynamics of exploitative competition

Patchy environment

Spatial variation in competitive ability

Emigration and immigration between patches

Model of exploitative competition and dispersal

$$\frac{dX_{ij}}{dt} = r_i X_{ij}\left(1 - \frac{X_{ij} - \alpha_{ij} X_{kj}}{K_{ij}}\right) - D_i X_{ij} + D_i X_{il}$$

Competition **Emigration** **Immigration**

$$i, j, k, l = 1, 2 \;\; i \neq k, j \neq l$$

Two species, two localities

Simplify model via non-dimensionalization

$$x_{ij} = \frac{X_{ij}}{K_{ij}}, \qquad a_{ij} = \alpha_{ij}\frac{K_{kj}}{K_{ij}}, \qquad k_i = \frac{K_{il}}{K_{ij}}$$

$$\beta_i = \frac{D_i}{r_i}, \qquad \rho = \frac{r_2}{r_1}, \qquad \tau = r_1 t$$

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

$$k_i = 1, \qquad \rho = 1, \qquad a_{ij} = \alpha_{ij}$$

Non-dimensionalized model of competition and dispersal

$$\frac{dx_{ij}}{d\tau} = x_{ij}(1 - x_{ij} - \alpha_{ij}x_{kj}) - \beta_i x_{ij} + \beta_i x_{il}$$

Competition **Emigration** **Immigration**

$$i, j, k, l = 1, 2 \quad i \neq k, j \neq l$$

Two species, two localities

Invasibility

$$(1-\alpha_{ij})(1-\alpha_{il}) - \beta_y\left[(1-\alpha_{ij}) + (1-\alpha_{il})\right] < 0$$

$$i, j, l = 1, 2 \; j \neq l$$

$1-\alpha_{ij}$ = initial growth rate of species i in locality j in the absence of dispersal

Invasibility in a spatially homogeneous environment

Species 1 superior competitor across metacommunity:

$$\alpha_{kj} = \alpha_{kl} = \alpha_i < 1$$

Species 2 inferior competitor across metacommunity:

$$\alpha_{ij} = \alpha_{il} = \alpha_i > 1$$

Invasibility in a spatially homogeneous environment

Invasion criterion of inferior competitor:

$$(1-\alpha_i)^2 - \beta_y(2 - 2\ \alpha_i)$$

Sum of the initial growth rates:

$$2 - 2\alpha_i < 0$$

Product of the initial growth rates:

$$(1-\alpha_i)^2 > 0$$

Then: $(1-\alpha_i)^2 - \beta_y(2 - 2\ \alpha_i) > 0$

Inferior competitor cannot invade when rare

Invasibility in a spatially heterogeneous environment

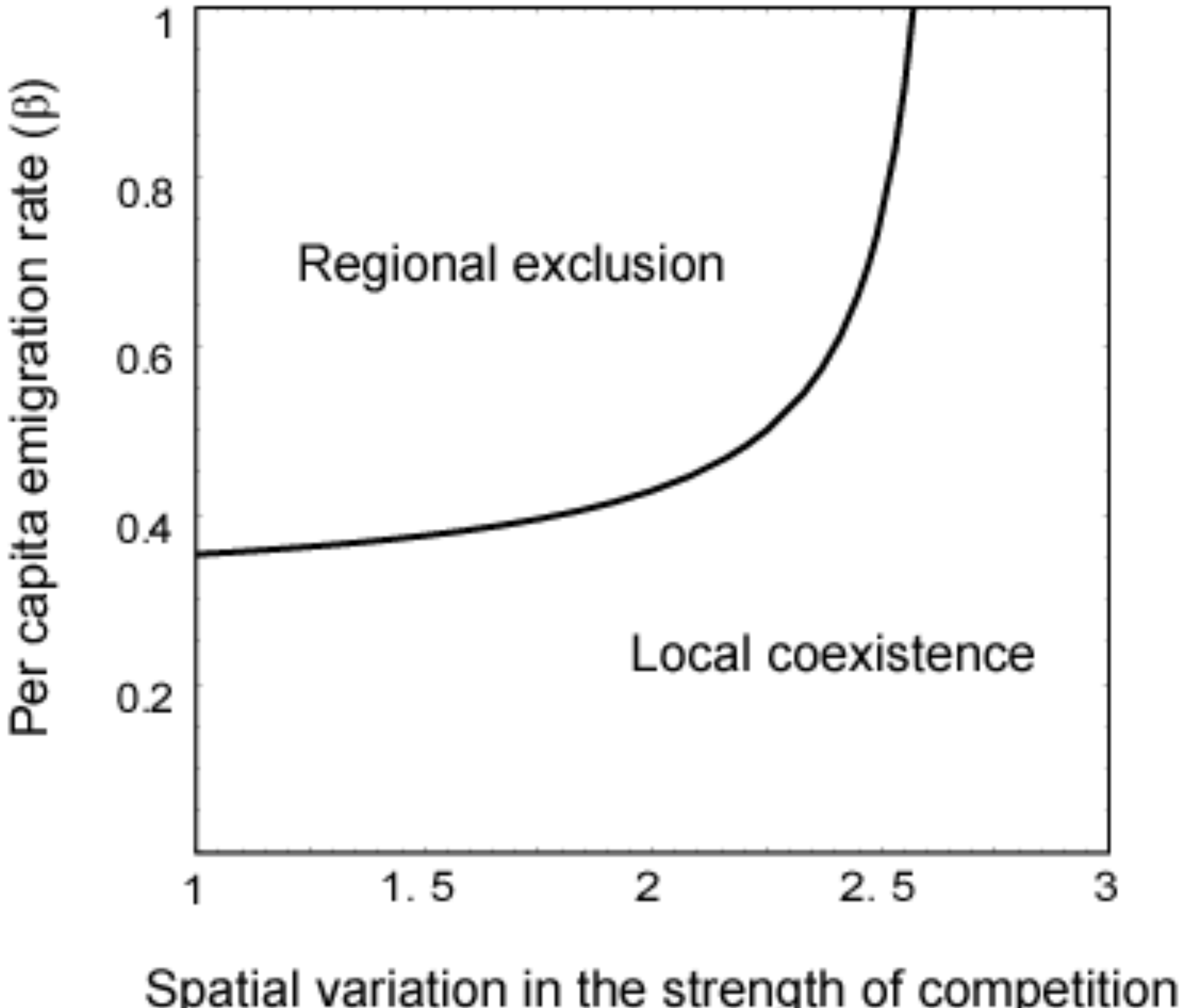
Spatial variation $\Rightarrow \quad 1 - \alpha_{ij} < 0, 1 - \alpha_{il} > 0$

Then:

$$(1 - \alpha_{ij})(1 - \alpha_{il}) - \beta_y \left[(1 - \alpha_{ij}) + (1 - \alpha_{il})\right] < 0$$

$$i, j, l = 1, 2 \; j \neq l$$

Inferior competitor can invade when rare



1
0.8
0.6
0.4
0.2
Per capita emigration rate (β)
Regional exclusion
Local coexistence
1
1. 5
2
2. 5
3
Spatial variation in the strength of competition

Mechanism of coexistence:

interplay between non-linearity and spatial heterogeneity

Coexistence:

Intra-specific competition stronger than inter-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

Mechanism of spatial coexistence

Per capita growth rate in the absence of dispersal:

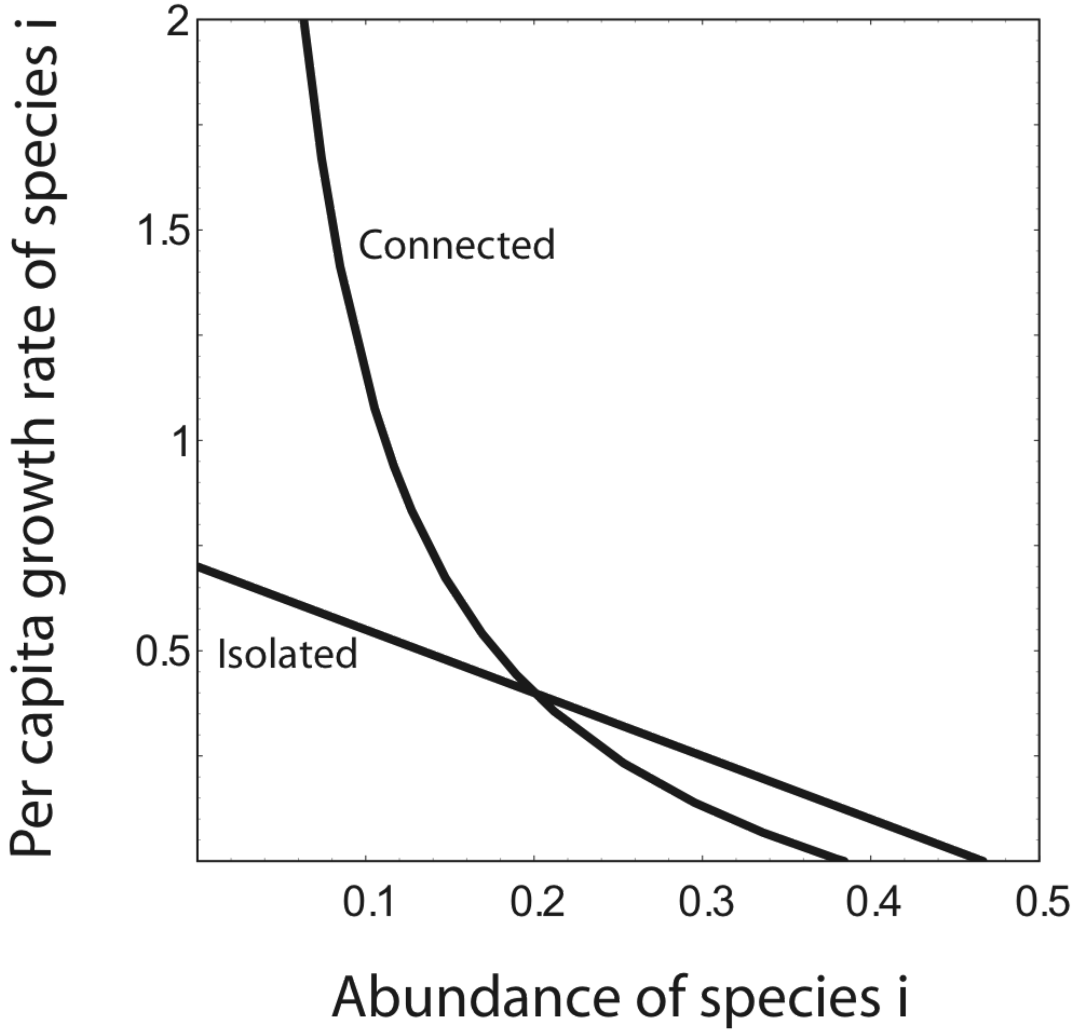
$$\frac{dx_{ij}}{d\tau}\frac{1}{x_{ij}} = 1 - x_{ij} - \alpha_{ij}x_{kj}$$

Per capita growth rate in the presence of dispersal:

$$\frac{dx_{ij}}{d\tau}\frac{1}{x_{ij}} = 1 - x_{ij} - \alpha_{ij}x_{kj} - \beta_i + \beta_i\frac{x_{il}}{x_{ij}}$$

Dispersal causes negative DD in per capita growth rate

Mechanism of spatial coexistence



Coexistence via interplay between non-linearity and spatial heterogeneity

Local dynamics (species interactions)

Spatial heterogeneity

Dispersal (sampling heterogeneity)

Local dynamics*dispersal: increases strength of intra-sp. interactions, promotes coexistence

Coexistence via interplay between non-linearity and spatial heterogeneity

1. Exploitative competition ✓

2. Mutualistic interactions

Coexistence via interplay between non-linearity and spatial heterogeneity

2. Mutualistic interactions in spatially heterogeneous environments

Mutualistic interactions

1. Local dynamics: positive feedback (Allee effects)

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

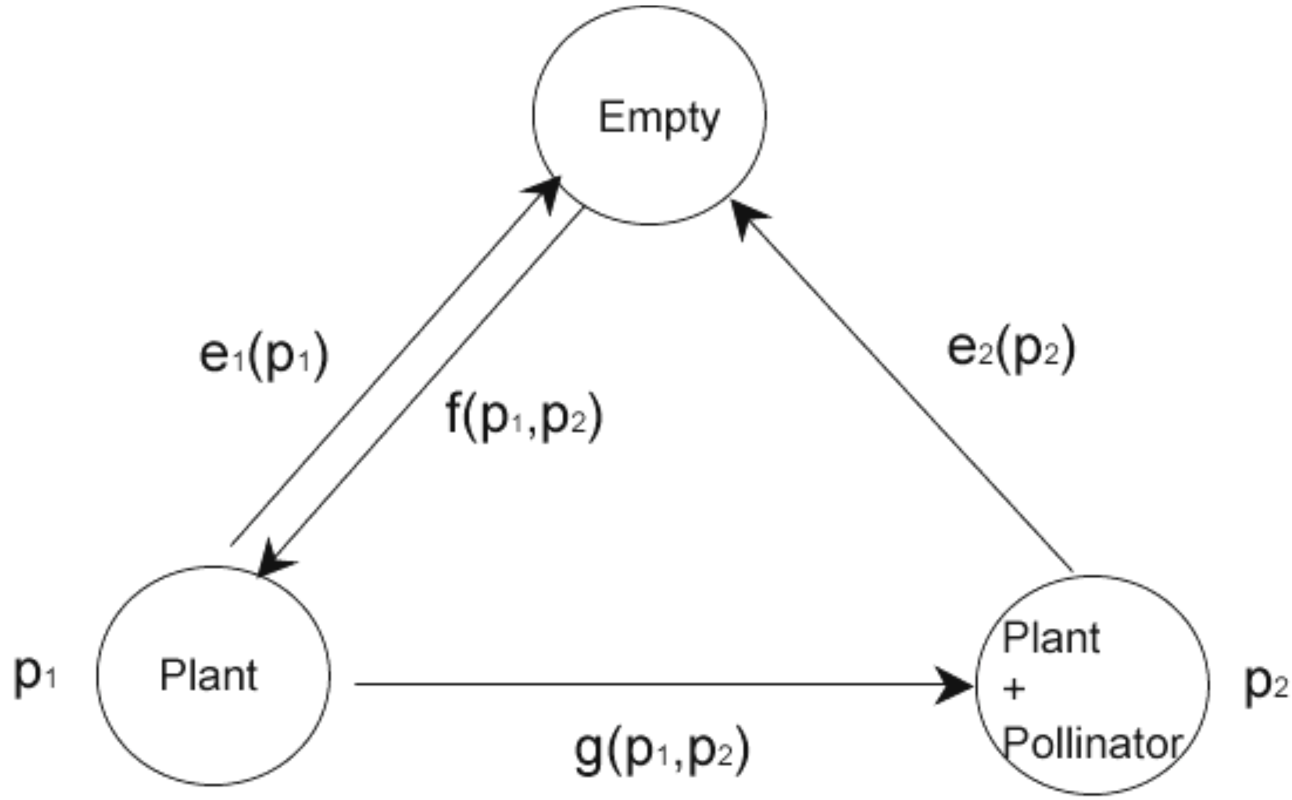
Mutualistic interactions in spatially heterogeneous environments

1. Obligate mutualism

2. Pairwise: mobile and non-mobile species

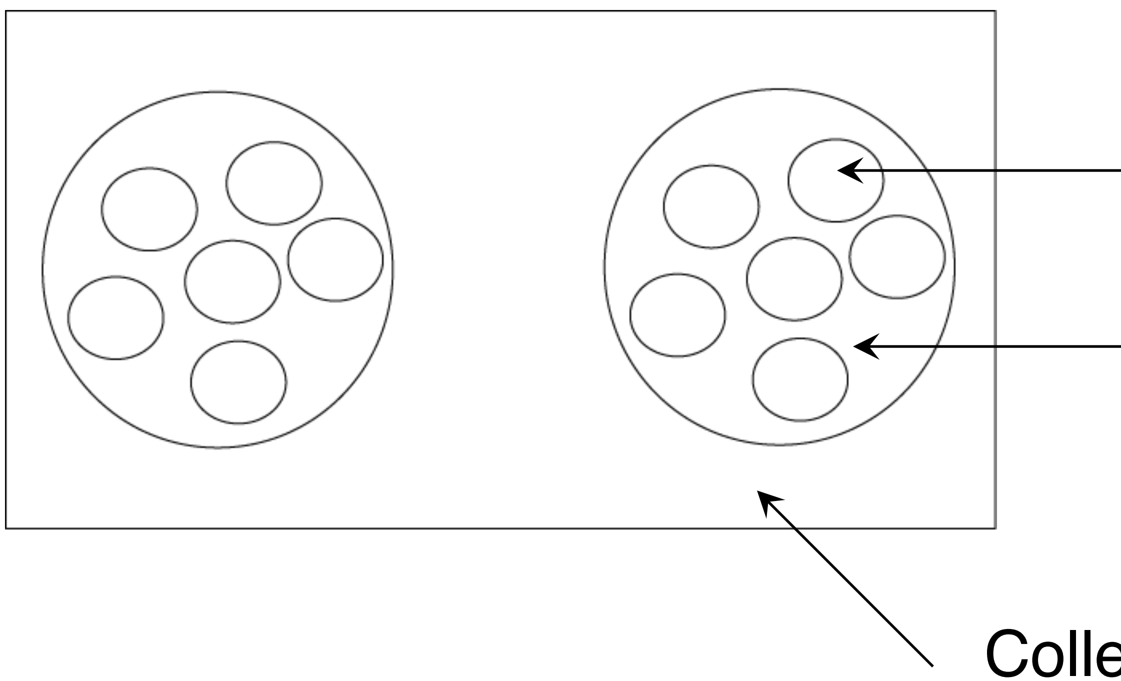
3. Dispersal of mobile mutualist

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

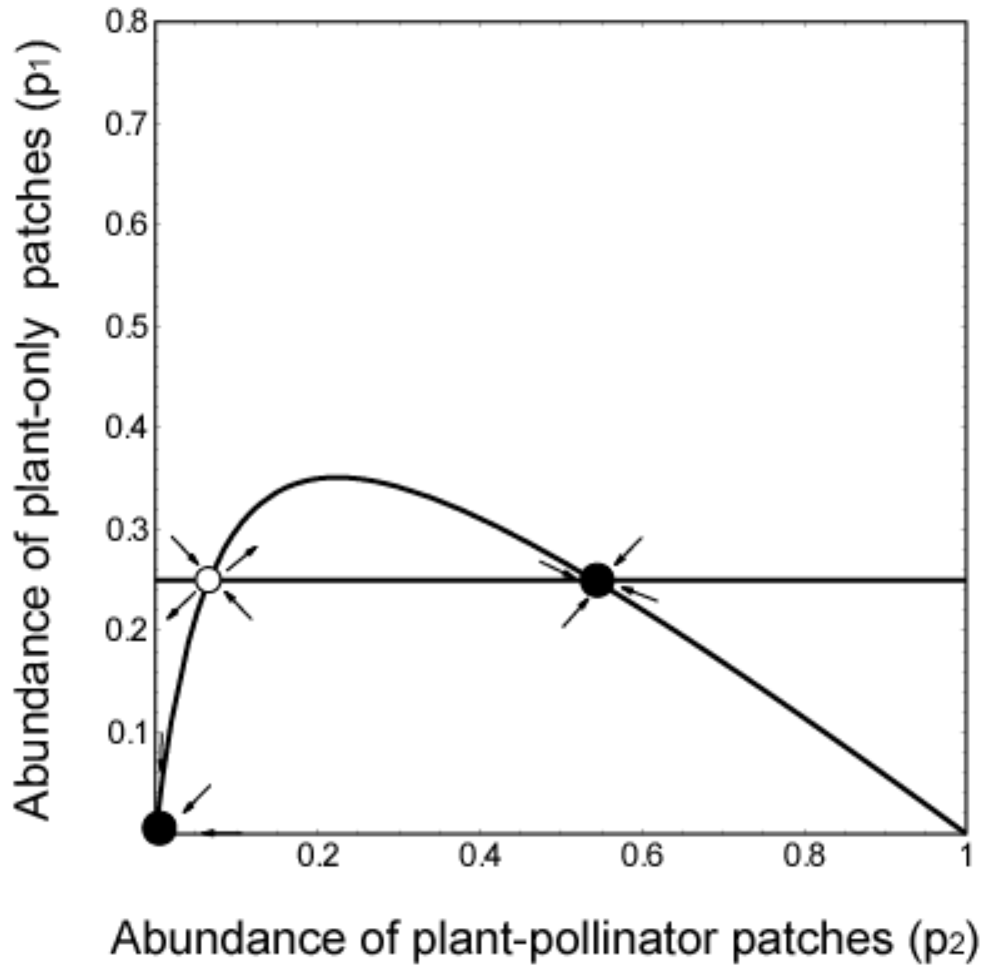


Patch = **Individual**

Collection of patches
= **Local population**

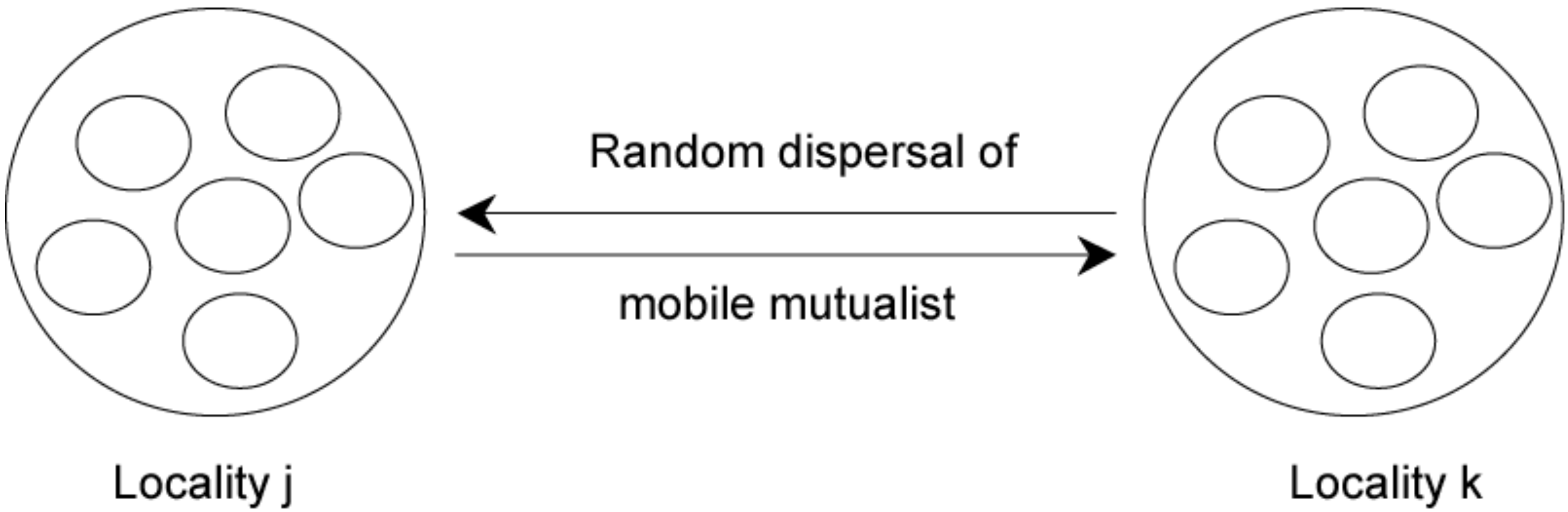
Collection of local
populations =
Metapopulation

Local dynamics of an isolated locality



Positive feedback (Allee effect) ==> Species cannot increase when rare

Spatial dynamics: dispersal between localities

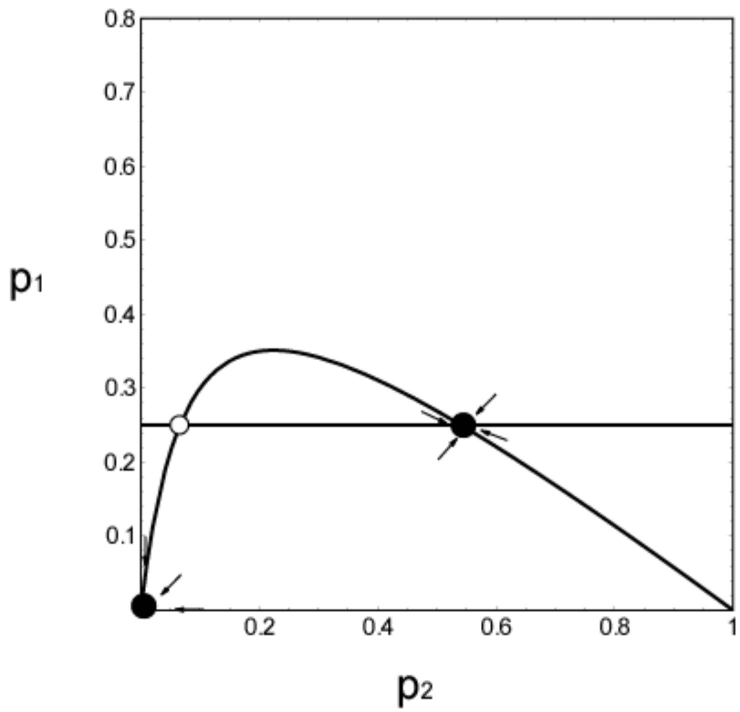


$$\frac{dp_{1j}}{dt} = f_j(p_{1j}, p_{2j}) - g_j(p_{ij}, p_{2k}, I) - e_{1j}(p_{1j})$$

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

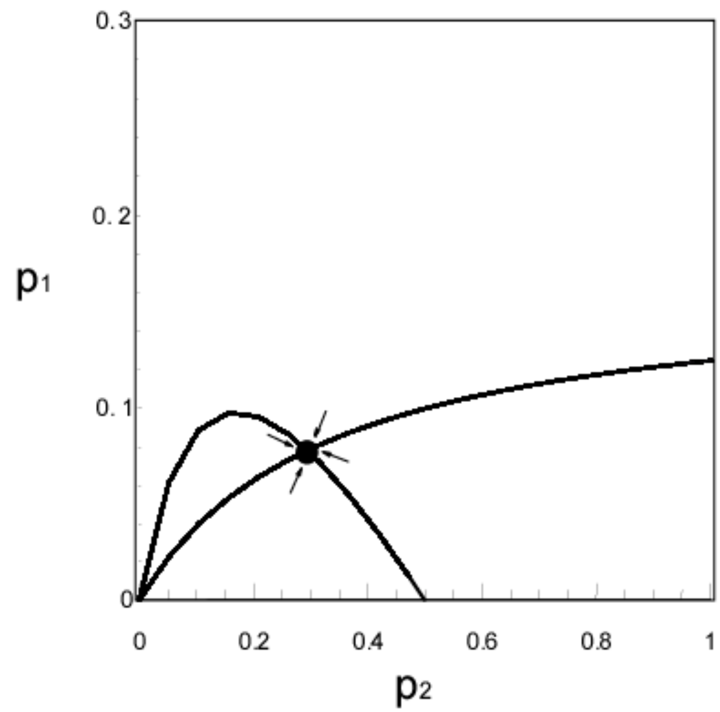
Production of plant-pollinator patches

Isolated



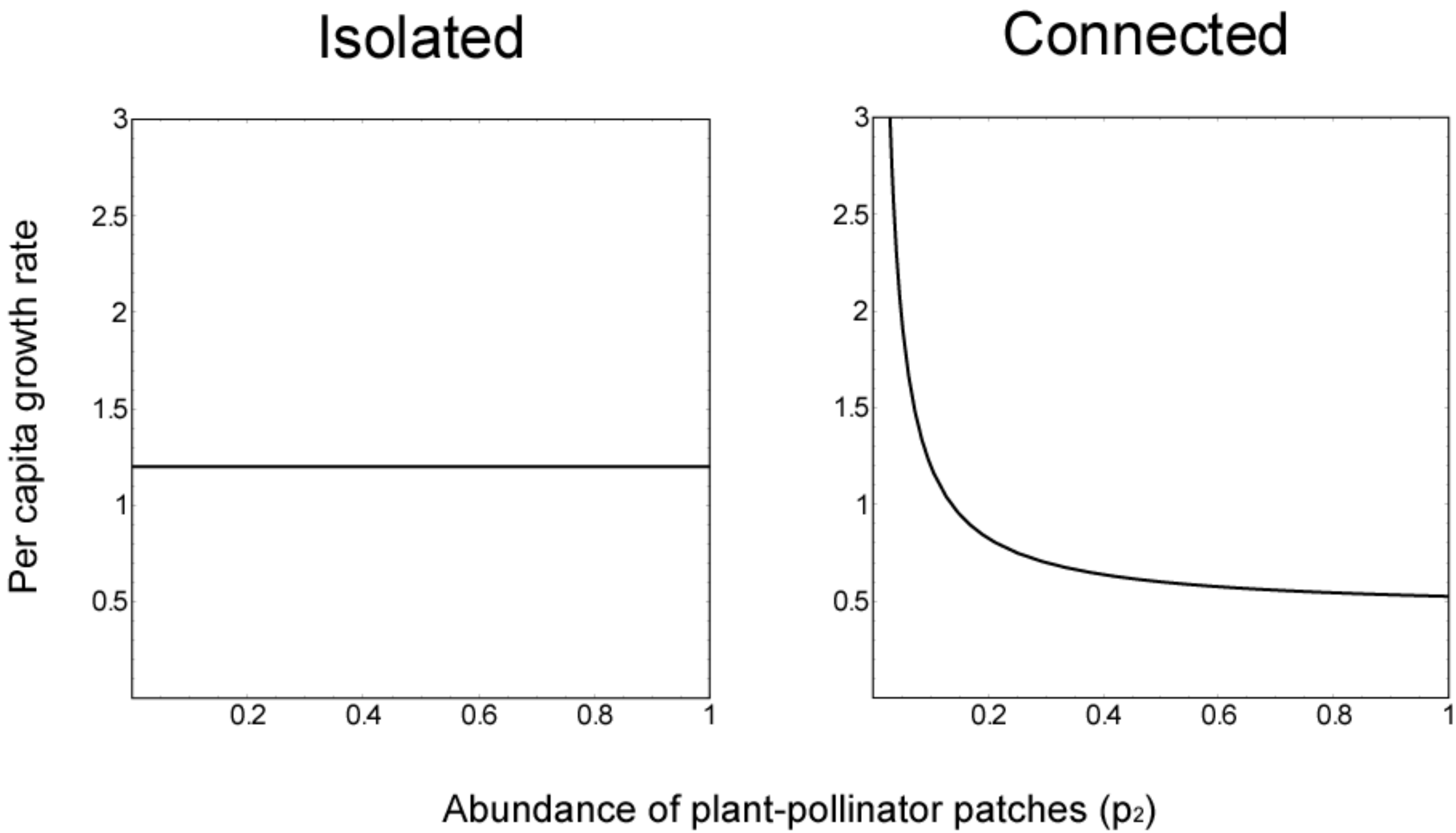
Species cannot increase when rare

Connected



Species can increase when rare

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



Mutualistic interactions in spatially heterogeneous environments

Local dynamics (positive DD)

Spatial heterogeneity

Dispersal (negative DD)

Negative DD due to dispersal counteracts positive DD due to Allee effect, promotes coexistence

Coexistence via interplay between non-linearity and spatial heterogeneity

Coexistence via interplay between non-linearity and spatial heterogeneity

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

2. Mutualistic interactions: Allee effects ==> extinction

3. Spatial heterogeneity+ dispersal --> coexistence

Mechanisms that maintain diversity

Diversity: Species coexistence

Coexistence: Non-linear dynamics * Environmental heterogeneity

Coexistence via interplay between non-linearity and heterogeneity

1. Coexistence via non-linearity alone ✓

2. Coexistence via non-linearity and spatial heterogeneity ✓

3. Coexistence via non-linearity and temporal heterogeneity

Coexistence via interplay between non-linearity and temporal heterogeneity