

Optimal network architectures for metapopulations with heterogeneous diffusion

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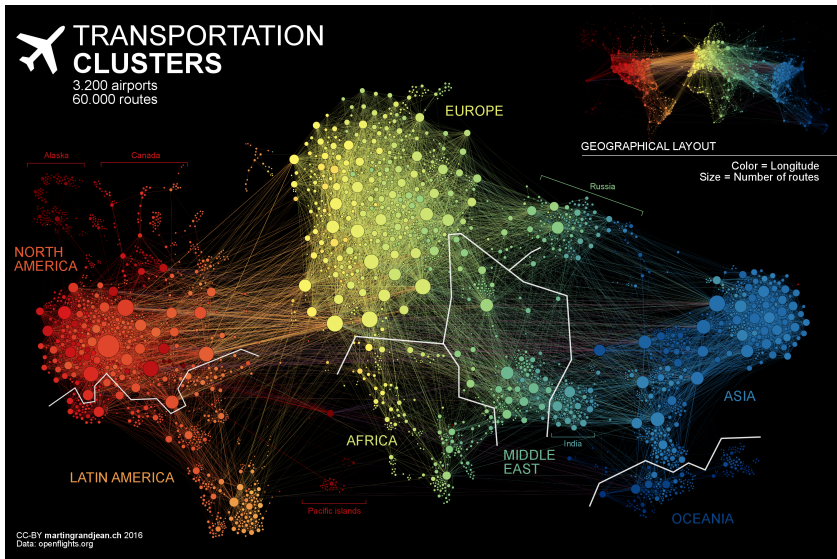
(Joint and on-going work with Alfonso Ruiz-Herrera)



Biological framework

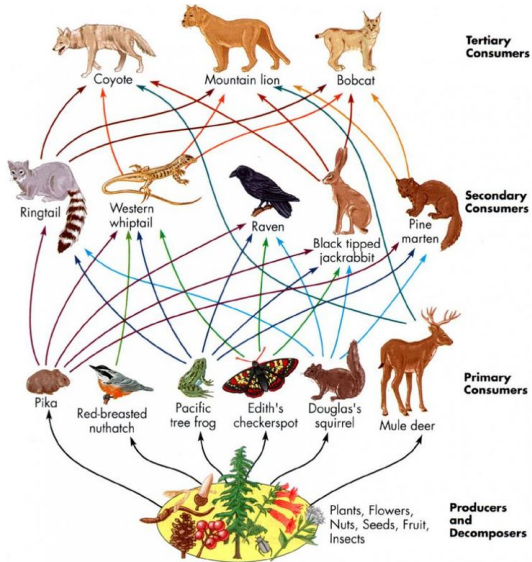
A network is any collection of units potentially interacting as a system.

Biological framework



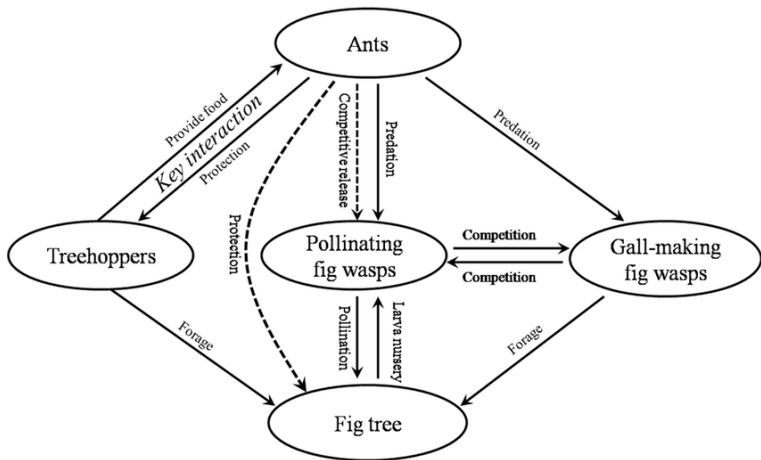
Biological framework

The typical example of network in Biology is a food web.



Biological framework

Mutualistic networks:

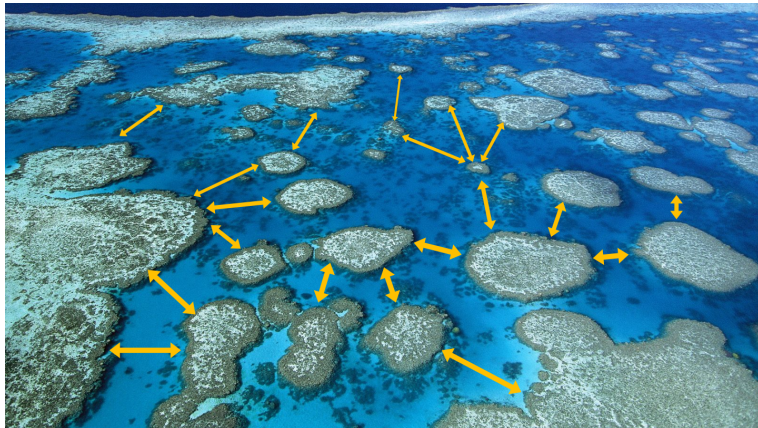


Metapopulation: a group of spatially separated populations of the same species that interact at some level.

Biological framework



Biological framework



Biological framework

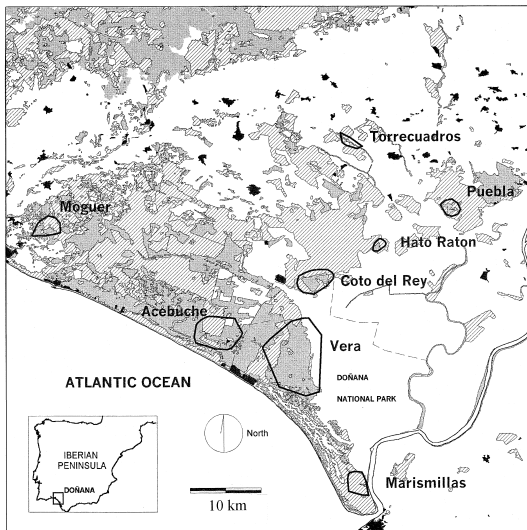


Figure: Fragmented habitat of the Iberian Linx

Biological framework



Figure: Ecological corridor

Biological framework



Figure: Patches of different qualities: sources and sinks

Biological framework



Figure: Sources and sinks: no-take zones

Objective: given a fragmented habitat, to design the optimal connection network to maximize the total population

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(Other objectives like synchronization are possible)

Mathematical model

Sources:

$$x'_i = r_i x_i (1 - x_i / K_i), \quad i = 1, \dots, m$$

Sinks:

$$x'_i = -r_i x_i, \quad i = m + 1, \dots, n$$

Mathematical model

Isolated nodes are connected through a *connectivity matrix* $A = (a_{ij})$, giving rise to the system

$$x_i' = f_i(x_i) + h \sum_{j=1}^n a_{ij} x_j,$$

where h is a parameter for the intrinsic mobility of the species.

Mathematical model

The connectivity matrix A verifies

- $a_{ij} \geq 0$ if $i \neq j$
- $\sum_{j=1}^n a_{ij} = 0$ (no cost of dispersal)

Let us denote this family of matrices by \mathcal{M} .

Mathematical model

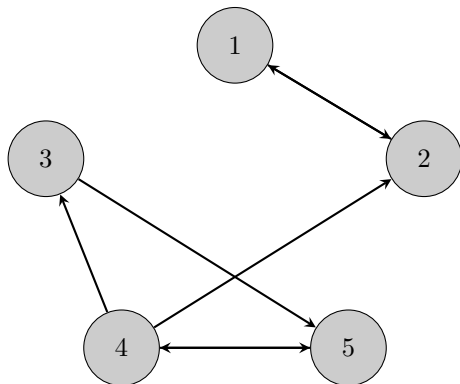


Figure: Representation of a network architecture with five patches. There exist many matrices associated with this network.

Mathematical model

Two matrices $A = (a_{ij})$ and $\tilde{A} = (\tilde{a}_{ij})$ represent the same network architecture when

$$a_{ij} > 0 \iff \tilde{a}_{ij} > 0$$

for all $i \neq j$.

A network architecture is **symmetric** when $a_{ij} > 0$ implies that $a_{ji} > 0$. In other words, if there exists a link from patch j to patch i , then there exists a link from patch i to patch j as well. Finally, the **movement is symmetric** if $a_{ij} = a_{ji}$, that is, an individual moves from patch i to patch j with the same probability as from j to i . Obviously, a symmetric movement implies a symmetric network architecture but not vice-versa.

Main problem

$$x'_i = f_i(x_i) + h \sum_{j=1}^n a_{ij} x_j$$

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For a given $A \in \mathcal{M}$, let $p(A) = (p_1, \dots, p_n)$ be the non-trivial equilibrium and $T(A) = p_1 + \dots + p_n$ the total population. How to maximize it?

$$\begin{cases} x_1' = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) + d_2 h x_2 - d_1 h x_1 \\ x_2' = -r_2 x_2 + d_1 h x_1 - d_2 h x_2. \end{cases}$$

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$$T(d_1, d_2) = k_1 \left(1 - \frac{r_2}{r_1} \frac{d_1 h}{r_2 + d_2 h}\right) \left(1 + \frac{d_1 h}{r_2 + d_2 h}\right)$$

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If $r_2 \geq r_1$, $T(d_1, d_2)$ is always less than the carrying capacity of the source.

$$\begin{cases} x_1' = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) + d_2 h x_2 - d_1 h x_1 \\ x_2' = -r_2 x_2 + d_1 h x_1 - d_2 h x_2. \end{cases}$$

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If $r_1 > r_2$, the maximum of $T(d_1, d_2)$ is achieved for any value of d_1, d_2 linked by the relation

$$\frac{d_1 h}{r_2 + d_2 h} = \frac{r_1 - r_2}{2r_2}$$

and it has the value

$$K_M = k_1 \frac{(r_1 + r_2)^2}{4r_1 r_2}. \quad (1)$$

We stress that $K_M > k_1$ for all $r_1, r_2 > 0$.

Source-sink

Define $\rho = \frac{r_1 - r_2}{2r_2}$.

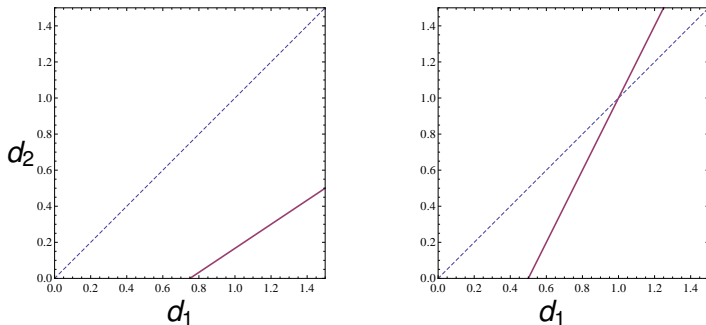


Figure: The thick line represents the values of d_1, d_2 for which K_M is achieved. (Left) We employed the parameters $r_1 = 2, r_2 = 0.5, k_1 = 3$ and $h = 1$. In this case, $\rho > 1$. Since the line does not cross the bisectrix, a symmetric movement can not produce the maximum value of the metapopulation. (Right) We used the parameters $r_1 = 2, r_2 = 1, k_1 = 3$, and $h = 1$. Now, $\rho < 1$ and K_M can be attained at a suitable symmetric movement, namely $d_1 = d_2 \approx 1$.

Source-sink

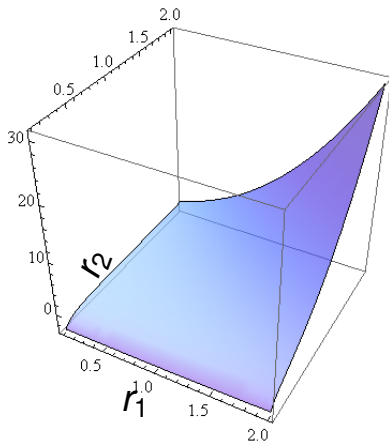


Figure: Representation of the difference between K_M and the maximum of $T(d, d)$ as a function of r_1 and r_2 . We employed the parameters $k_1 = 1$ and $h = 1$. Observe that the difference can be 30 times the carrying capacity of the source.

The general case: all the patches are sources

We consider the system

$$x_i' = r_i x_i (1 - x_i / K_i) + h \sum_{j=1}^n a_{ij} x_j, \quad i = 1, \dots, n \quad (2)$$

and denote by $p(h) = (p_1(h), \dots, p_n(h))$ the equilibrium (global attractor) and by

$$T(h) = p_1(h) + \dots + p_n(h).$$

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Lemma

$$T'(0) = \sum_{\substack{i,j=1, \\ i \neq j}}^n a_{ij} K_j \left(\frac{1}{r_i} - \frac{1}{r_j} \right). \quad (3)$$

The general case: all the patches are sources

The contribution of the route from the patch j to the patch i is

$$a_{ij} K_j \left(\frac{1}{r_i} - \frac{1}{r_j} \right).$$

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The recommendation to maximize $T'(0)$ is to use only routes from the patches of higher to lower growth rates.

The general case: all the patches are sources

Corollary

*For weak mobility, the optimal network architecture is a **maximal acyclic directed graph** with the arrows always pointing to the patch with the lowest growth rate.*

The general case: all the patches are sources

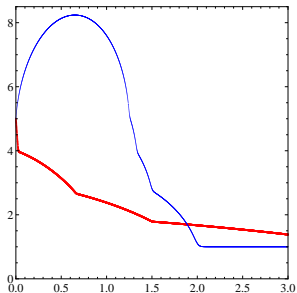
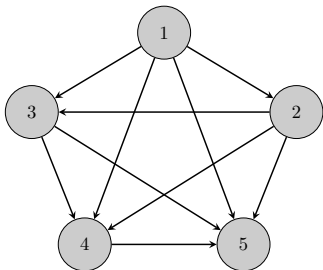


Figure: (Left) The optimal architecture for a network of 5 sources with decreasing value of the natural growth parameter, $r_i > r_j$ if $i < j$. (Right) Representation of the total population as a function of h . (Blue) The parameters employed are $r_1 = 5, r_2 = 4, r_3 = 3, r_4 = 2, r_5 = 1$ and $k_i = 1$ for all i . We use the network architecture given in the previous figure where the connectivity matrix A is given by $a_{ij} = 0$ if $i < j$ and $a_{ij} = 1$ if $i > j$. (Red) We use the architecture given by the maximal acyclic graph pointing to patch 1 (the worst choice). The connectivity matrix is $a_{ij} = 0$ if $i > j$ and $a_{ij} = 1$ if $i < j$.

The general case: sources and sinks

We assume that of a total of n patches, the first m patches are sources and the rest are sinks. Then,

$$T'(0) = \sum_{j=1}^m \sum_{i=1, j \neq i}^n a_{ij} K_j \left(\frac{1}{r_i} - \frac{1}{r_j} \right).$$

To maximize the total population size, the connection rule between sources remains the same, *i.e.* connections from higher to lower growth rates are beneficial and connections in the opposite sense are harmful. Meanwhile, a route from a source with growth rate r_j and a sink with mortality rate r_i is recommended only if $r_j > r_i$. Connections from a sink to a source or between sinks have no effect on the previous formula.

The general case: sources and sinks

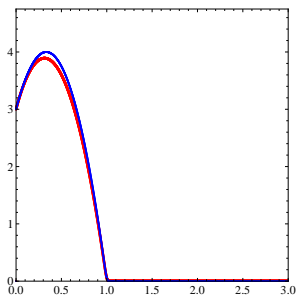
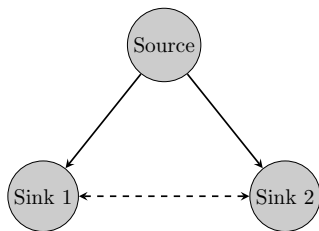


Figure: (Left) Pictorial illustration of a metapopulation with a source and two sinks. (Right) Representation of $T(h)$. Fixed parameters, $r_1 = 2, k_1 = 3$ (for the source); $r_2 = 0.5$ and $r_3 = 1$ (for the sinks).

Strong mobility

What happens if $h \rightarrow +\infty$? (perfect mixing)

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Let $p(h)$ the equilibrium of

$$x'_i = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + h \sum_{j=1}^n a_{ij} x_j,$$

and $T(h) = \sum_{i=1}^n p_i(h)$.

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and $T(h) = \sum_{i=1}^n p_i(h)$.

Proposition

For any $A \in \mathcal{M}$,

$$T(h) \leq \frac{1}{2} \left(\sum_{i=1}^n K_i + \sqrt{\sum_{i=1}^n k_i r_i \cdot \sum_{i=1}^n \frac{K_i}{r_i}} \right).$$

Strong mobility

Proof. Adding the equations, we have the restriction

$$\sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i}\right) = 0 \quad (4)$$

We have to maximize $F(x_1, \dots, x_n) = \sum_{i=1}^n x_i$ in the compact set

$$(x_1, \dots, x_n) \in K = \{(x_1, \dots, x_n) : \sum_{i=1}^n r_i x_i \left(1 - \frac{x_i}{K_i}\right) = 0\}.$$

By Lagrange's method, after simple computations, the maximum value of F is

$$\frac{1}{2} \left(\sum_{i=1}^n K_i + \sqrt{\sum_{i=1}^n K_i r_i \cdot \sum_{i=1}^n \frac{K_i}{r_i}} \right).$$



Strong mobility

Our next aim is to find a matrix $A \in \mathcal{M}$ such that

$$\lim_{h \rightarrow +\infty} T(h) = \frac{1}{2} \left(\sum_{i=1}^n K_i + \sqrt{\sum_{i=1}^n K_i r_i \cdot \sum_{i=1}^n \frac{K_i}{r_i}} \right).$$

Strong mobility

Lemma 1

Given any vector $v = (v_1, \dots, v_n) \in \mathbb{R}^n$ with $v_i > 0$ for all $i = 1, \dots, n$, there exists a matrix $A \in \mathcal{M}$ so that $v \in \text{Ker}(A)$.

Lemma 2

If $A \in \mathcal{M}$ is irreducible, then $\dim \text{Ker}(A) = 1$. Moreover, if $v = (v_1, \dots, v_n) \in \text{Ker}(A)$ with $v_i \geq 0$ for all $i = 1, \dots, n$, then $v_i > 0$ for all $i = 1, \dots, n$.

Lemma 3

For each irreducible $A \in \mathcal{M}$, there is a unique non-trivial vector $v = (v_1, \dots, v_n)$ with positive values so that $v \in \text{Ker}(A)$ and v satisfies (4).

Strong mobility

Lemma 1

Given any vector $v = (v_1, \dots, v_n) \in \mathbb{R}^n$ with $v_i > 0$ for all $i = 1, \dots, n$, there exists a matrix $A \in \mathcal{M}$ so that $v \in \text{Ker}(A)$.

Proof. Take $a_{1n} = 1$, $a_{11} = -\frac{v_n}{v_1}$, and $a_{1j} = 0$ for all $j = 2, \dots, n-1$. Take $a_{21} = \frac{v_n}{v_1}$, $a_{22} = -\frac{v_n}{v_2}$, and $a_{2j} = 0$ for $j = 3, \dots, n$. We repeat this methodology in each row. Specifically, in the i -th row, $a_{i,i-1} = \frac{v_n}{v_{i-1}}$, $a_{i,i} = -\frac{v_n}{v_i}$ and the rest of the entries equal to zero. By construction, $v \in \text{Ker}(A)$ and $A \in \mathcal{M}$. □

Strong mobility

For instance, taking the parameter values $r_1 = 5, r_2 = 4, r_3 = 3, r_2 = 2, r_1 = 0.1$ and $k_i = 1$ for $i = 1, 2, 3, 4, 5$, the optimal choice for A is

$$A \approx \begin{pmatrix} -9.95337 & 0 & 0 & 0 & 1 \\ 9.95337 & -9.51856 & 0 & 0 & 0 \\ 0 & 9.51856 & -8.87257 & 0 & 0 \\ 0 & 0 & 8.87257 & -8.83257 & 0 \\ 0 & 0 & 0 & 8.83257 & -1 \end{pmatrix}$$

Strong mobility

This cyclic network architecture has the virtue of being the minimal network for which the maximum can be attained, in the sense that the suppression of any of the links would break this property.

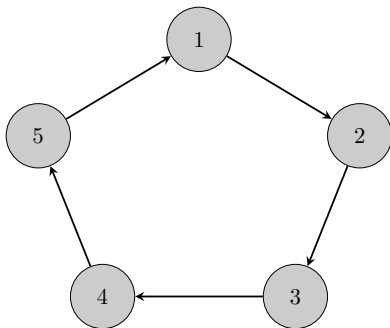


Figure: A cyclic network of 5 patches.

Strong mobility

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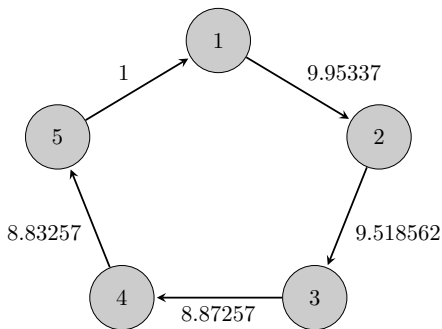


Figure: A cyclic network of 5 patches.

Strong mobility

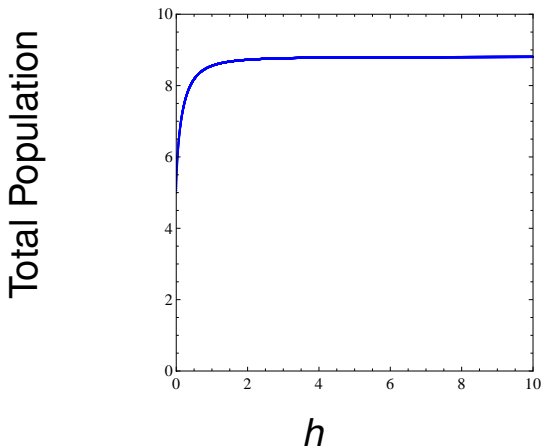


Figure: Total population size as a function of h (the limit is ≈ 8.80664)

Strong mobility

Assume that a network architecture is represented by $M_1 \subset \mathcal{M}$. Then it is possible to reach the maximum with this network architecture if and only for any vector $v = (v_1, \dots, v_n)$ with $v_i > 0$ for all $i = 1, \dots, n$, there is a matrix $A \in M_1$ so that $v \in \text{Ker}(A)$. A particular architecture with this property is

$$M_1 = \{A \in \mathcal{M} : a_{ij} \neq 0 \text{ for all } i = 1, \dots, n\}.$$

In fact, given (v_1, \dots, v_n) with $v_i > 0$ for all $i = 1, \dots, n$, we can take any matrix A such that $a_{ij}v_j = a_{ji}v_i$ for all $i \neq j$ and

$$a_{ii} = \frac{-1}{v_i} \sum_{\substack{j=1, \\ j \neq i}}^n a_{ij}v_j$$

for all $i = 1, \dots, n$.

Strong mobility

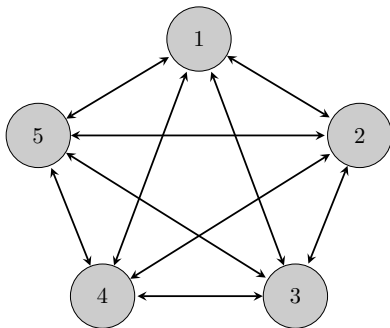


Figure: the complete bidirectional network of 5 patches.

Strong mobility: simmetric movement

Theorem

Assume that $A \in \mathcal{M}$ is a symmetric matrix. Then,

$$\lim_{h \rightarrow +\infty} T(h) = \frac{n \sum_{i=1}^n r_i}{\sum_{i=1}^n \frac{r_i}{K_i}}.$$

Strong mobility: symmetric movement

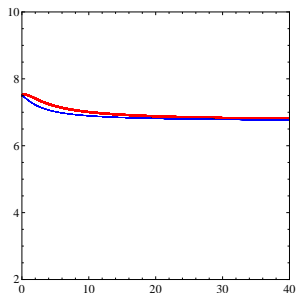
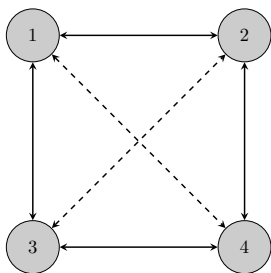


Figure: (Left) Pictorial description of the architectures employed in the simulations. (Right) Representation of the total population size as a function of h . The parameters in both curves are: $r_1 = 5$, $r_2 = 4$, $r_3 = 3$, $r_4 = 2$ and $k_1 = 3$, $k_2 = 1.5$, $k_3 = 1$, $k_4 = 2$.

Examples of practical recommendations for ecological management

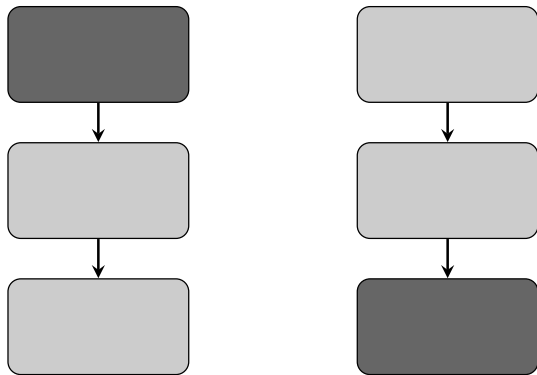


Figure: Optimal location of a protected area in a homogeneous landscape of three nodes and directional movement. (Left) Reduced mobility. (Right) Highly mobile species.

Examples of practical recommendations for ecological management

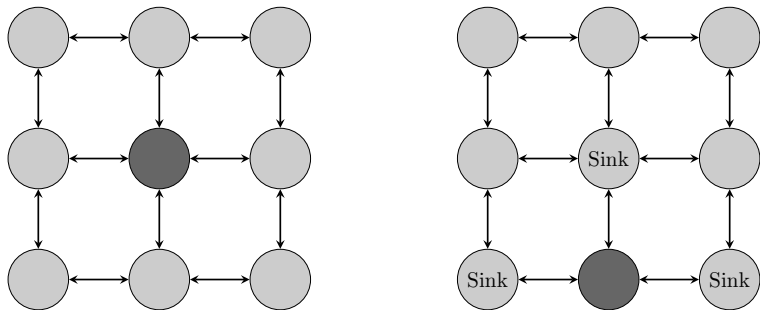


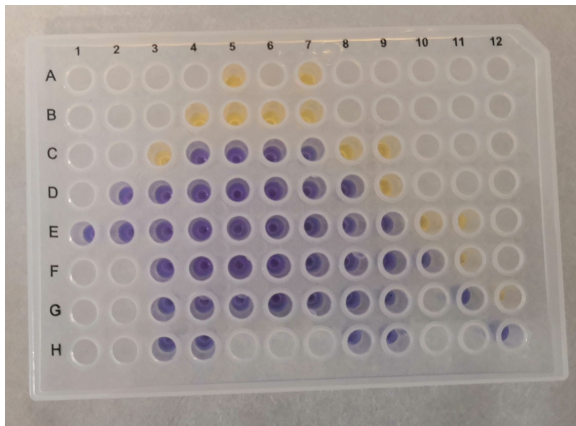
Figure: Optimal location of a protected area for species with reduced mobility in the absence of directional movement.

What more?

Experiment:

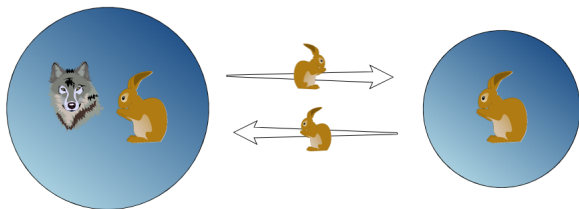
What more?

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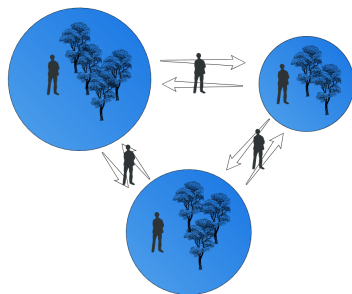


What more?

Many species interacting \implies Metacommunity



What more?



A. Ruiz-Herrera, P.J. Torres, Effects of diffusion on total biomass in simple metacommunities, *J. Theoretical Biology* 447 (2018), 12-24.

Epidemic models in networks

SIR Model:

$$S' = \lambda - \mu S - \beta SI$$

$$I' = \beta SI - (\gamma + \mu)I$$

$$R' = \gamma I - \mu R$$

Basic reproduction number:

$$R_0 = \frac{\beta \lambda}{\mu(\gamma + \mu)}.$$

If $R_0 > 1$, the endemic equilibrium $(\frac{\gamma + \mu}{\beta}, \frac{\mu}{\beta}(R_0 - 1))$ is a global attractor.

If $R_0 \leq 1$, the disease-free equilibrium $(\frac{\lambda}{\mu}, 0)$ is a global attractor.

Epidemic models in networks

SIR Model:

$$S'_i = \lambda_i - \mu S_i - \beta_i S_i I_i$$

$$I'_i = \beta_i S_i I_i - (\gamma_i + \mu_i) I_i$$

$$R'_i = \gamma_i I_i - \mu_i R_i$$

for $i = 1, \dots, n$.

Epidemic models in networks

SIR Model:

$$S'_i = \lambda_i - \mu S_i - \beta_i S_i I_i + h \sum_{j=1}^n a_{ij} S_j$$

$$I'_i = \beta_i S_i I_i - (\gamma_i + \mu_i) I_i + h \sum_{j=1}^n b_{ij} I_j$$

$$R'_i = \gamma_i I_i - \mu_i R_i + h \sum_{j=1}^n c_{ij} R_j$$

for $i = 1, \dots, n$, with $A, B, C \in \mathcal{M}$.

Infected cannot travel ($B \equiv 0$)

The relevant parameter is

$$\Delta_i = \frac{(\gamma_i + \mu)^2}{\beta_i}.$$

The connection from node i to node j is recommended if and only if

$$\Delta_i < \Delta_j.$$

Only infected travel ($A \equiv 0$)

The relevant parameter is

$$\Gamma_i = \frac{(\gamma_i + \mu)^2}{\lambda_i}.$$

The connection from node i to node j is recommended if and only if

$$\Gamma_i < \Gamma_j.$$

All the population can move

If $\Delta_i < \Delta_j$ and $\Gamma_i < \Gamma_j$, the link from i to j is recommended.

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If $\Delta_i < \Delta_j$ and $\Gamma_i > \Gamma_j$ (or viceversa), there is a balance to be studied.

Thank you for your attention!!