Quantifying metapopulation persistence across varying spatial networks
-
The temporal metapopulation capacity

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Hanski's legacy: Metapopulation theory

> *"Mathematical models of metapopulation are constructed in the hope that they will clarify our thinking, reveal unexpected and significant consequences of particular assumptions, and lead to interesting new predictions that could be tested with observational and experimental studies."*
>
> – Ikka Hanski

A world of fragmented habitats

Interactions between species and their habitat are crucial for biodiversity conservation and protection of natural habitats.

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Habitat are fragmented:

- Due to natural phenomena and land use by humans.
- Necessary migration for some species (birds, marine mammals).

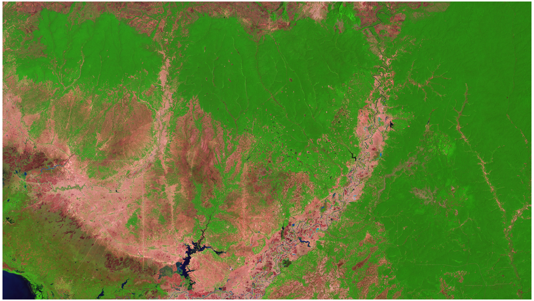
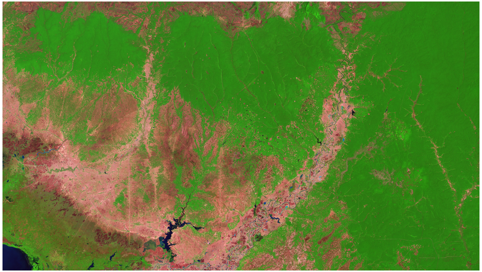
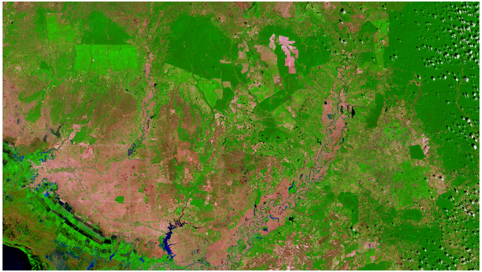


Figure 1: Example of a forest in Cambodia - February 20, 1999, NASA

A world of fragmented habitats and temporal variations

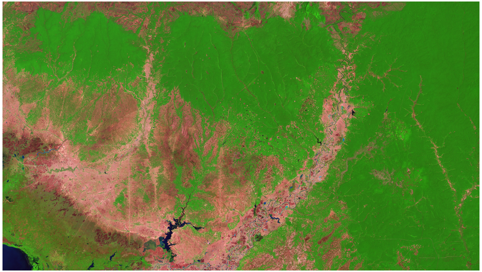


(a) February 20, 1999



(b) February 5, 2017

A world of fragmented habitats and temporal variations



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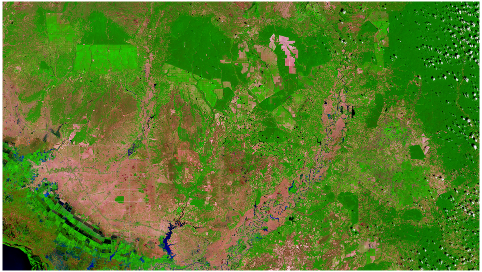

(b) February 5, 2017

Impacts of temporal habitat variations:

- Influence species persistence.
- Affect the movement of individuals, diseases, and disturbances.

The often overlooked dimension of time

Metapopulation models are created to help understand how a population persists in a given landscape.

- Stationary analyses and theories are insufficient.
- Need to integrate the temporal dimension into ecological networks.

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Fundamental questions:

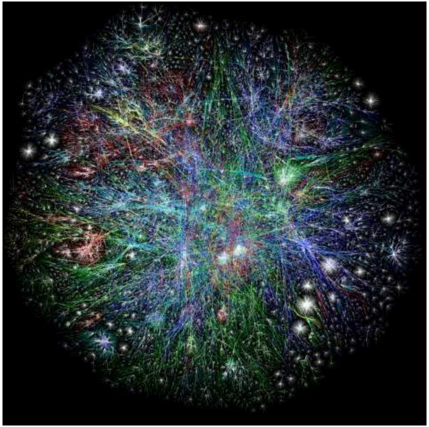
1. How does the temporal structure of the landscape or seasonal variations influence population persistence?
2. How do temporal metrics provide insights into the dynamic nature of ecological systems that stationary metrics might miss?

Network science: a framework for ecological dynamics

Applying network science to ecological systems:

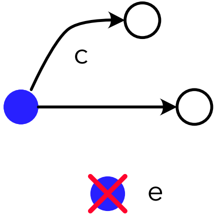
- SIS models: simulating disease spread in a given contact structure.
- Metapopulation models: Incorporating spatial structure.
- Temporal networks: Analyzing time-varying interactions.

Inspired by physics-based methods



Metapopulation: Levins model

Levins model[1](1969): a simple model to explain the dynamic of a species in a patchy environment.



Call $p(t)$ the proportion of patches occupied by the species of interest at time t and assume that

1. an empty patch is colonized by the populations in other patches with rate $cp(t)$ where c is the colonization rate,
2. that occupied patches become empty at rate $ep(t)$ where e is the extinction rate.

The proportion of patches occupied by the population at time t is:

$$\frac{dp(t)}{dt} = cp(t)(1 - p(t)) - ep(t)\,.$$

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[1] Levins (1969), *Bulletin of the Entomological Society of America*, **15-3**, 237–240

A network of 56 habitat patches

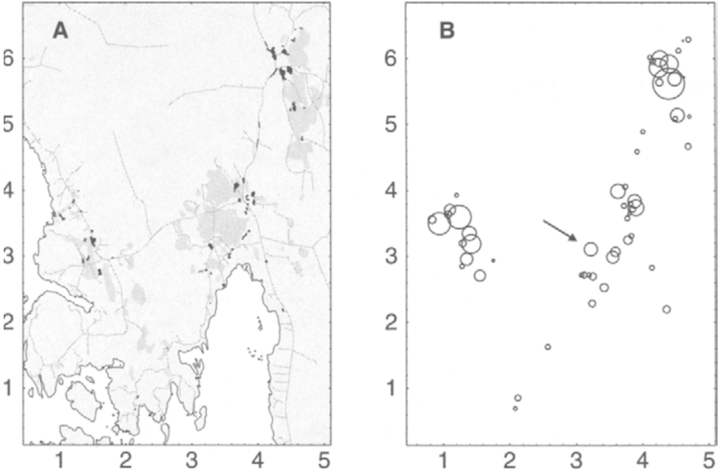

Figure 3: Glanville fritillary butterfly (Melitaea cinxia) in the Åland Islands in Finland.

Spatially realistic metapopulation model

Each patch (or node) is associated with a random variable $X_i(t)$ whose state can be either occupied $X_i = 1$ or empty $X_i = 0$.

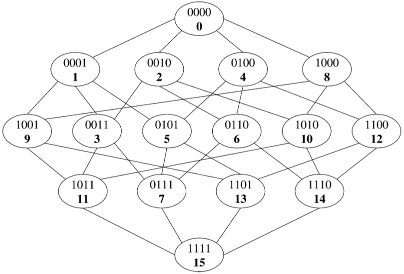

Figure 4: State diagram in a graph with 4 nodes and the binary numbering of the states.

Problem: to describe all potential states, a Markov process with 2^n states is necessary. The transition matrix among all these states cannot be written in general.

Van Mieghem *et al.* (2009) *IEEE/ACM Transactions on Networking* **17-1**, 1–14

Spatially realistic metapopulation model

We are interested in describing $p_i(t) = \mathbb{P}(X_i(t) = 1)$.

The dynamics of $\boldsymbol{p}(t) = (p_1(t), \dots, p_n(t))$ is given by the set of n differential equations:

$$\frac{dp_i(t)}{dt} = c \sum_{j=1}^{n} S_{ji} \mathbb{P}(X_i(t) = 0 \, \text{and} \, X_j(t) = 1) - e p_i(t) \,, \quad \forall i \in [n] \,.$$

where $S = (S_{ij})_{n \times n}$ is the connectivity matrix.

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where $S = (S_{ij})_{n \times n}$ is the connectivity matrix. To approximate the solution, we employ an individual-based approach, assuming independence between the states of different patches (reasonable approximation for large, well-mixed systems).

$$\mathbb{P}(X_i(t) = 0 \,\mathrm{and}\, X_j(t) = 1) \approx (1 - p_i(t)) p_j(t) \,.$$

This method tracks the quasi-stable state of the underlying Markov process

$$\frac{dp_i(t)}{dt} = c \sum_{j=1}^{n} S_{ji} (1 - p_i(t)) p_j(t) - e p_i(t) \,, \quad \forall i \in [n] \,.$$

Spatially realistic metapopulation model

$$\frac{dp_i(t)}{dt} = c_i(\boldsymbol{p})(1 - p_i(t)) - e_i(\boldsymbol{p})p_i(t)\,, \quad \forall i \in [n]\,,$$

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Colonization rate of an empty patch i:

$$c_i(\boldsymbol{p}) = c \sum_{j \neq i} A_j f(d_{ij}) p_j\,,$$

where:

c intrinsic colonization rate of the species,

f kernel function,

d_{ij} distance between sites i and j,

A_i area of site i.

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Colonization rate of an empty patch i:

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c	intrinsic colonization rate of the species,
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d_{ij}	distance between sites i and j,
A_i	area of site i.

Extinction rate of patch i:

$$e_i(\boldsymbol{p}) = e/A_i,$$

where:

e	extinction rate of the species,
A_i	area of site i.

Hanski & Ovaskainen (2000) *Nature* **404**, 755–758

Definition of the model

Each element of the connectivity matrix ($S = (S_{ij})_{n\times n}$) indicates the connectivity from patch i to patch j and is defined as:

$$S_{ij} = A_i f(d_{ij})\,.$$

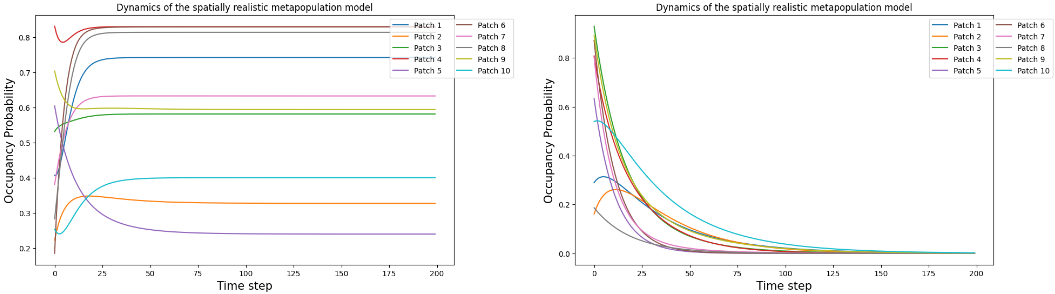
We define the vector of extinction rates as:

$$\boldsymbol{e} = (e_1, \dots, e_n) = (e/A_1, \dots, e/A_n)\,.$$

Ultimately, the dynamics of the probability of patch i being occupied over time can be described by the following differential equation:

$$\frac{dp_i(t)}{dt} = c\sum_{j\neq i} S_{ji}\, p_j(t)(1 - p_i(t)) - e_i p_i(t)\,, \quad \forall i \in [n]\,.$$

Dynamics of the metapopulation model


Dynamics of the spatially realistic metapopulation model

Dynamics of the spatially realistic metapopulation model

Figure 5: Dynamics of the metapopulation model for 10 patches and 2 different connectivity matrices.

Condition for the persistence of the metapopulation

$$\frac{dp_i(t)}{dt} = c \sum_{j \neq i} S_{ji} p_j (1 - p_i) - e_i p_i \, . \tag{1}$$

To compute the persistence threshold, one way is to linearize around the state where all species vanish. One obtains

$$\frac{d\boldsymbol{p}(t)}{dt} \approx (cS^\top - \mathrm{diag}(\boldsymbol{e}))\boldsymbol{p}(t) + o(\boldsymbol{p}(t)) \, .$$

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The existence of a positive equilibrium $p_i^* > 0$, is determined by the largest eigenvalue of the matrix $cS^T - \mathrm{diag}(\boldsymbol{e})$. Specifically, persistence occurs if and only if:

$$\rho(cS^T\mathrm{diag}(\mathbf{e})^{-1}) > 1\,.$$

This condition highlights the crucial role of local extinction rates in determining the overall persistence of the metapopulation.

The metapopulation capacity

When the extinction rate e is unique for each patch and the network structure S is fixed, we recover **the metapopulation capacity** λ_M

$$\lambda_M = \rho(M) > \frac{e}{c},$$

where $M_{ij} = A_i A_j f(d_{ij})$, $i \neq j$ and $M_{ii} = 0$, $\forall i \in [n]$.

Hanski & Ovaskainen (2000) *Nature* **404**, 755–758

- The condition can be derived via the Collatz-Wielandt formula and Perron Frobenius theorem, given that the matrix S is nonnegative.
- In epidemiological systems, this threshold is referred to as the epidemic threshold.

Discrete model of metapopulation

As in the continuous-time model, the problem may be analyzed as a model based on probabilistic discrete-time Markov chains.

Discrete model of metapopulation

As in the continuous-time model, the problem may be analyzed as a model based on probabilistic discrete-time Markov chains.

The discrete-time version of the dynamics of the probability of colonization is:

$$p_i(t+1) = (1 - q_i(t))(1 - p_i(t)) + (1 - e_i)p_i(t) + e_i(1 - q_i(t))p_i(t)$$

where $q_i(t) = \prod_j [1 - cS_{ji}p_j(t)]$ the probability that patch i is not colonized by one of its neighbors at time t.

Gómez (2010) *Europhysics Letters* **89**-**3**, 38009.

Discrete model of metapopulation

The equation can be written in the following form:

$$p_i(t+1) = 1 - [1 - (1 - e_i)p_i(t))] \prod_j [1 - cS_{ji}p_j(t)] \,. \tag{2}$$

where:

$$\boldsymbol{e} = (e_1, \dots, e_n) = (e/A_1, \dots, e/A_n)$$

and S is the connectivity matrix of the network given by

$$S_{ij} = A_i f(d_{ij}) \,.$$

Note that the equilibrium of the system (2) is given by:

$$p_i^* = 1 - q_i + (1 - e_i)p_i^* q_i \,,$$

and $p_i^* = 0, \forall i \in [n]$ is a solution.

Metapopulation capacity

Let's analyze the behavior around the equilibrium point, where $p_i^* = 0, \forall i \in [n]$.

Linearize the equation around $p_i^* = 0$:

$$p_i(t+1) = (1 - e_i)p_i(t) + c\sum_j S_{ji}p_j(t) + O(p_i^2).$$

This is due to the fact that when p_i is close to zero, it results to the approximation $(1-a)(1-b) = 1 - a - b$ when $a \ll 1$ and $b \ll 1$:

$$\prod_j [1 - cS_{ji}p_j(t)] \approx 1 - \sum_j cS_{ji}p_j(t)\,.$$

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$$\prod_j [1 - cS_{ji}p_j(t)] \approx 1 - \sum_j cS_{ji}p_j(t)\,.$$

The behavior of the model around $p_i(t) \approx 0$ is similar to the continuous case. In matrix form, this can be rewritten as

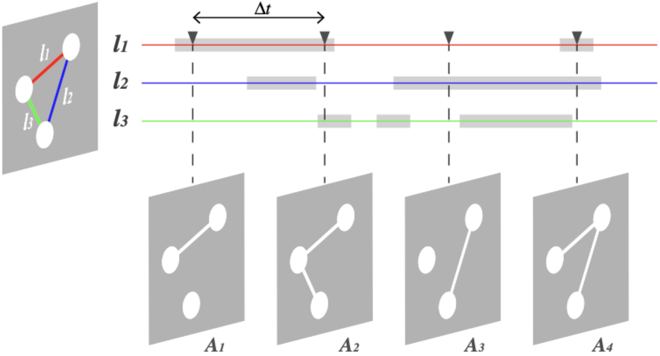
$$\boldsymbol{p}(t+1) = (\mathrm{diag}(\boldsymbol{e}) + cS^\top)\boldsymbol{p}(t)\,.$$

As a result, the metapopulation persist if and only if:

$$\rho(cS^T\mathrm{diag}(\boldsymbol{e}^{-1})) > 1\,.$$

Introduction to temporal networks

Temporal networks: networks where connections between nodes can change over time.



Valdano *et al.* (2015), *Physical Review X*, **5**, 021005

Annealed vs. Quenched regimes

Annealed Regime	**Quenched Regime**
• Rapid network dynamics compared to metapopulation dynamics. • Relevant network properties: average adjacency matrix, degree distribution. • **Degree-based mean-field theory (DBMF):** Assumes statistical equivalence of nodes with the same degree. • **Threshold computation:** Based on average connectivity and connectivity fluctuations.	

Annealed vs. Quenched regimes

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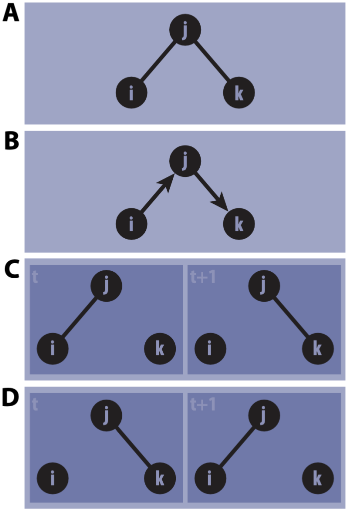
Static vs. Temporal network

- **Static network:** Connectivity is crucial as it determines colonization pathways.
- **Temporal network:** The timing of connections is essential. The sequence of connections over time must be considered.

Conclusion: the analysis of temporal networks more intricate.



Valdano (2015), *Computing the vulnerability of time-evolving networks to infections.*

The temporal metapopulation model

Let us assume that the size of each patch i, $A_i^{(t)}$ and the distances between patches $d_{ij}^{(t)}$ are time-dependent.

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Temporal metapopulation model is described by:

$$p_i(t+1) = 1 - [1 - (1 - e_i^{(t)}) p_i(t))] \prod_j [1 - c S_{ji}^{(t)} p_j(t)], \quad \forall i \in [n]\,,$$

where

$$\boldsymbol{e}^{(t)} = (e_1^{(t)}, \ldots, e_n^{(t)}) = (e/(A_1^{(t)}), \ldots, e/(A_n^{(t)}))\,,$$

and $S^{(t)}$ is the connectivity matrix at time t of the network given by

$$S_{ij}^{(t)} = A_i^{(t)} f(d_{ij}^{(t)})\,.$$

Assumptions and limitations

- **Time-Scale Considerations:**
    - Comparable timescales for fragmentation and ecological dynamics.
    - Intermediate regime between annealed and quenched regimes.

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  - Ensures asymptotic solution for generic temporal sequences.

Assumptions and limitations

- **Time-Scale Considerations:**
  - Comparable timescales for fragmentation and ecological dynamics.
  - Intermediate regime between annealed and quenched regimes.
- **Boundary Conditions:**
  - Periodic boundary conditions for network dynamics.
  - Ensures asymptotic solution for generic temporal sequences.
- **Impact of Temporal Dynamics:**
  - As T is an arbitrary parameter, this does not affect the model overall generality.
  - Estimation of epidemic/persistence threshold primarily influenced by short-term dynamics.
  - Findings from Valdano *et al.* support this observation.

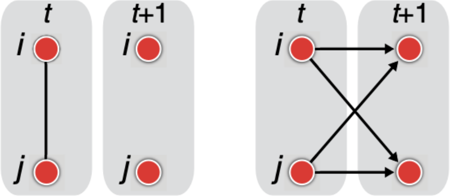
Valdano *et al.* (2015), *Physical Review X*, **5**, 021005

Multilayer representation of temporal networks

Snapshot representation of temporal network → the tensor representation of the weighted multilayer network.

$$\hat{M}_{ij}^{ts} = \delta^{t,s+1}[\delta_{ij} + M_{ij}^{(t)}]$$

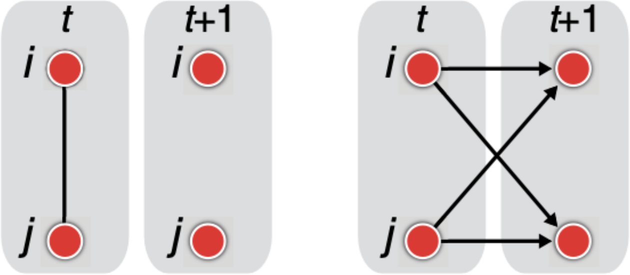
$\hat{M}_{ij}^{ts}$ is the entry of a fourth order tensor $\hat{M}$, called multilayer adjacency tensor and represents the connection strength between node i in layer t and node j in layer s where $i, j \in [n]$ and $t, s \in [T]$.



Multilayer representation of temporal networks

Ordinal coupling: linking each node at time t with its corresponding node at time $t+1$.

Representation of the extinction process, occurring at a rate of e_i for patch i between time steps t and $t+1$

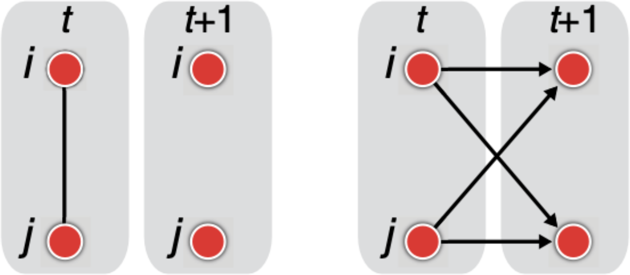


Valdano *et al.* (2015), *Physical Review X*, **5**, 021005

Multilayer representation of temporal networks

Non-diagonal coupling: introduces connections between different nodes across consecutive layers.
Representation of the colonization process, where individuals can disperse from one patch to another.

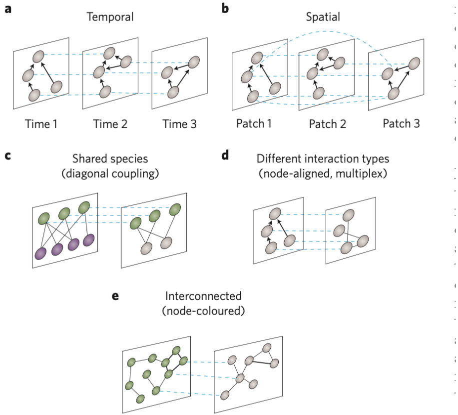
A link is established between node j at time t and node i at time $t+1$ with a strength of cS_{ji}.



Valdano *et al.* (2015), *Physical Review X*, **5**, 021005

Multilayer networks in ecology

In these toy examples, layers are represents different interaction types: trophic, non-trophic



Pilosof *et al.* (2017), *Nature Ecology & Evolution*, **1**-**4**, 0101

Multilayer for competitive metacommunity model

RESEARCH ARTICLE | ENVIRONMENTAL SCIENCES |

Landscape and environmental heterogeneity support coexistence in competitive metacommunities

Prajwal Padmanabha, Giorgio Nicoletti, Davide Bernardi, Samir Suweis, Sandro Azaele, Andrea Rinaldo, and Amos Maritan -3 Authors Info & Affiliations

Contributed by Andrea Rinaldo; received June 2, 2024; accepted September 10, 2024; reviewed by David Alonso and Silvia De Monte

October 22, 2024 | 121 (44) e2410932121 | https://doi.org/10.1073/pnas.2410932121

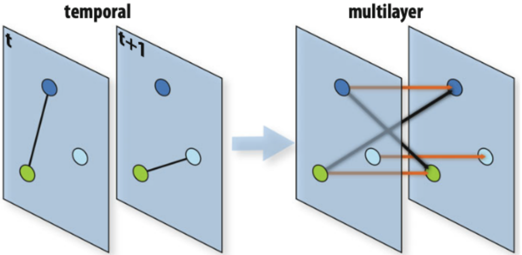
- Stable coexistence becomes possible in sufficiently heterogeneous environments.

Multilayer representation of temporal networks

Representation of the temporal metapopulation model as a tensor network incorporating both the colonization and extinction processes:

$$\hat{M}_{ij}^{ts} = \delta^{t,s+1}[(1 - e_i^{(t)})\delta_{ij} + cS_{ij}^{(t)}], \text{ with } S_{ij}^{(t)} = A_i^{(t)} f(d_{ij}^{(t)}) .$$

M provide all the information of the processes and the landscape structure through time.



Valdano *et al.* (2015), *Physical Review X*, **5**, 021005

Supra-adjacency matrix formulation

Use the supra-adjacency matrix formulation by mapping $(i, t) \to \alpha = nt + i$ where $\alpha \in [nT]$ which gives:

$$\hat{M} = \begin{pmatrix} 0 & (1-\boldsymbol{e}^{(1)})I + cS^{(1)} & 0 & \cdots & 0 \\ 0 & 0 & (1-\boldsymbol{e}^{(2)})I + cS^{(2)} & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & (1-\boldsymbol{e}^{(T-1)})I + cS^{(T-1)} \\ (1-\boldsymbol{e}^{(T)})I + cS^{(T)} & 0 & 0 & \cdots & 0 \end{pmatrix},$$

where $\hat{M}$ is a supra-adjacency matrix of size $nT \times nT$.

Asymptotic behavior of the dynamical system

Given the state vector $\hat{p}_\alpha(\tau)$ of size nT which represent the probability of each node to be occupied at each time step t included in a 1-period interval $[\tau T, (\tau+1)T]$.

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The dynamics of $\hat{p}_\alpha(\tau)$ is given by the Markov process:

$$\hat{p}_\alpha(\tau+1) = 1 - \prod_{\beta}^{nT}\left[1 - \hat{M}_{\beta,\alpha}\hat{p}_\beta(\tau)\right].$$

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$$\hat{p}_\alpha(\tau+1) = 1 - \prod_{\beta}^{nT} [1 - \hat{M}_{\beta,\alpha} \hat{p}_\beta(\tau)] \, .$$

The T-periodic asymptotic state of model given by:

$$\hat{p}^*_\alpha = 1 - \prod_{\beta}^{nT} [1 - \hat{M}_{\beta,\alpha} \hat{p}^*_\beta] \, .$$

Asymptotic behavior of the dynamical system

From this by linearizing the system around $\hat{p}^*_\alpha = 0$, we recover the system:

$$\hat{p}_\alpha(\tau+1) = \sum_\beta \hat{M}_{\beta\alpha}\hat{p}_\beta(\tau)\,,$$

which is formally

$$\hat{\boldsymbol{p}}(\tau+1) = \hat{M}\hat{\boldsymbol{p}}(\tau)\,,$$

where we recover the necessary and sufficient condition for the asymptotic persistence of the metapopulation:

$$\rho(\hat{M}) > 1\,.$$

Temporal metapopulation capacity

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The temporal metapopulation capacity is describe by the threshold condition

$$\rho(\hat{M}) = 1\,,$$

where $\hat{M}$ is the supra-adjacency matrix.

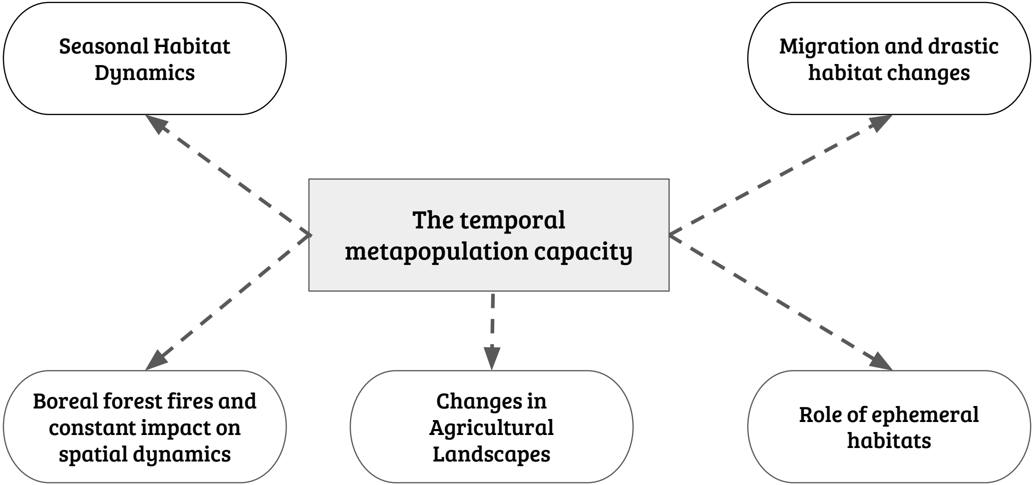
The block structure of the supra-adjacency matrix permits to simplify the computation of the spectral radius of $\hat{M}$:

$$\rho(\hat{M}) = \rho(P)^{1/T}\,,$$

where

$$P = \prod_{t=1}^{T} (1 - \mathrm{diag}(\boldsymbol{e}^{(t)}) + cS^{(t)})\,.$$

Practical applications


The temporal metapopulation capacity

Seasonal Habitat Dynamics

Migration and drastic habitat changes

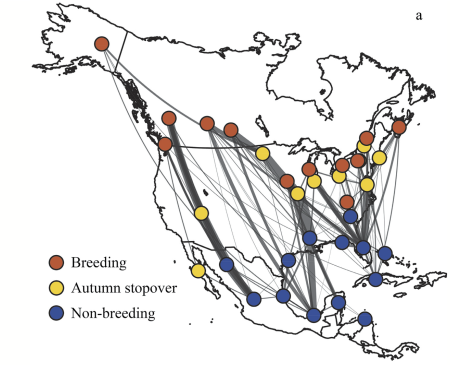
Boreal forest fires and constant impact on spatial dynamics

Changes in Agricultural Landscapes

Role of ephemeral habitats

Perspective 1: Migratory network

Migratory network for Tree Swallows showing breeding, autumn stopover, and non-breeding nodes:



(a) Migratory network

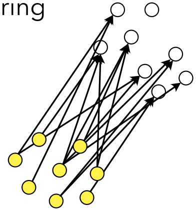
(b) A tree swallow

Knight *et al.* (2018), *Ecological Monographs*, **88-3**, 445–460

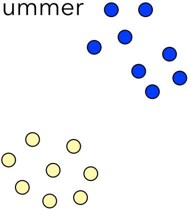
Perspective 1: A toy model

$$\begin{pmatrix} 0 & 0 \\ S_{\text{Winter}\to\text{Summer}} & 0 \end{pmatrix} \quad \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix} \quad \begin{pmatrix} 0 & S_{\text{Summer}\to\text{Winter}} \\ 0 & 0 \end{pmatrix} \quad \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}$$

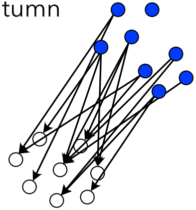
Spring



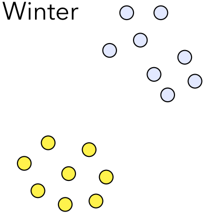
Summer



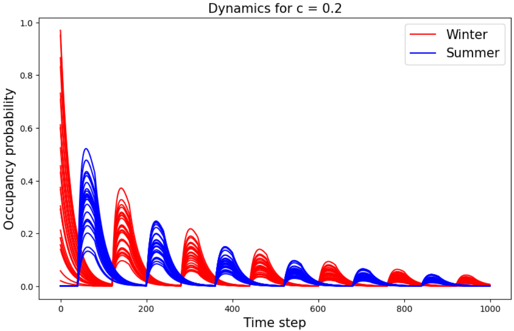
Autumn



Winter

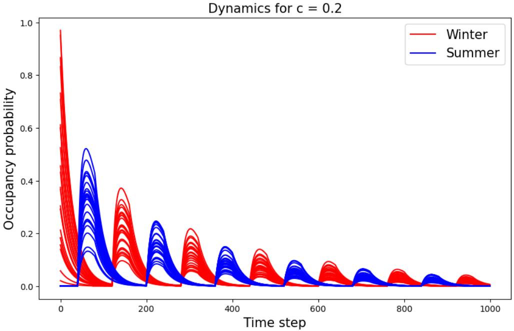


Perspective 1: Preliminary simulations



(a) Colonization rate $c = 0.2$

Perspective 1: Preliminary simulations



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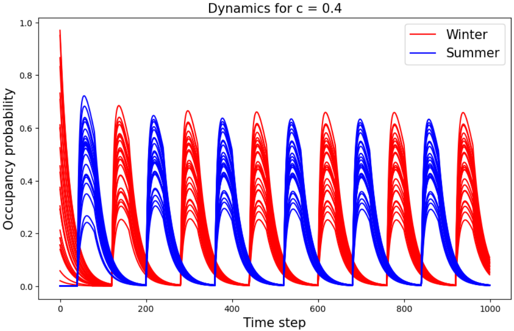
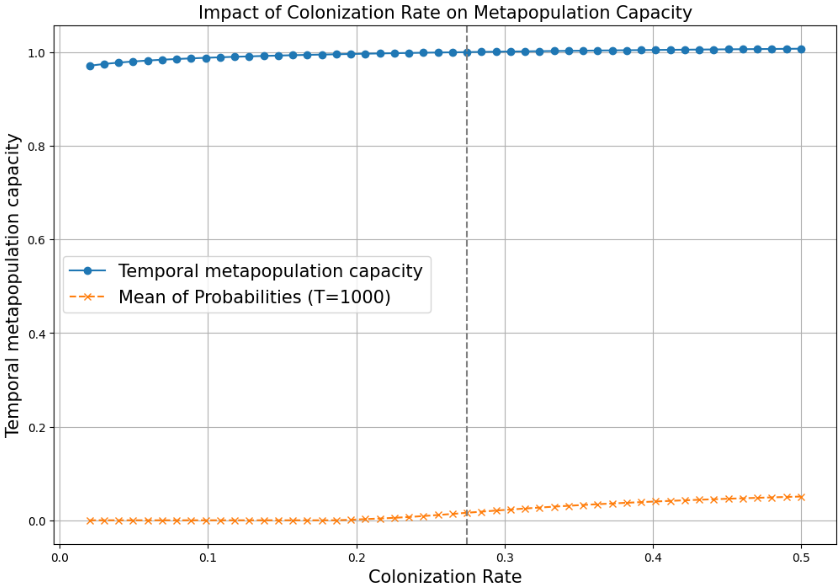


(b) Colonization rate $c = 0.4$

Perspective 1: Preliminary simulations

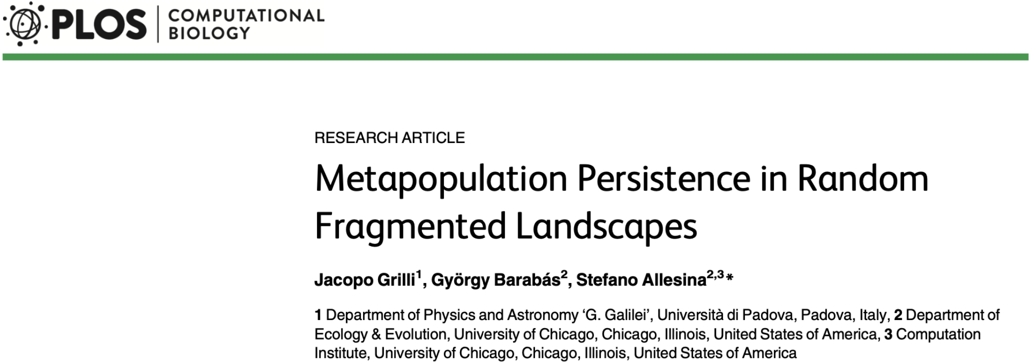


Perspective 2: Random matrix theory

The supra-adjacency matrix M:

$$M = \begin{pmatrix} 0 & (1-\boldsymbol{e}^{(1)})I + cS^{(1)} & 0 & \cdots & 0 \\ 0 & 0 & (1-\boldsymbol{e}^{(2)})I + cS^{(2)} & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & (1-\boldsymbol{e}^{(T-1)})I + cS^{(T-1)} \\ (1-\boldsymbol{e}^{(T)})I + cS^{(T)} & 0 & 0 & \cdots & 0 \end{pmatrix}.$$

Perspective 2: Random matrix theory



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RESEARCH ARTICLE

Metapopulation Persistence in Random Fragmented Landscapes

Jacopo Grilli[1], **György Barabás**[2], **Stefano Allesina**[2,3]*

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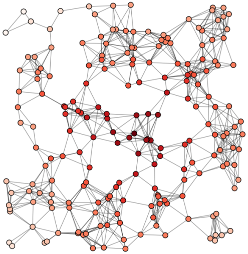
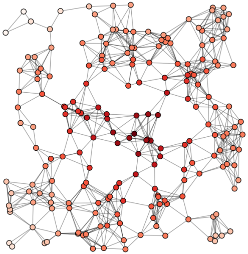
Perspective 2: Random matrix theory

Framework:

- Random landscape using random matrices theory.
- Dispersal kernel matrix belongs to the class of Euclidean random matrices (in particular Random Geometric Graphs).



Perspective 2: Random matrix theory



Framework:

- Random landscape using random matrices theory.
- Dispersal kernel matrix belongs to the class of Euclidean random matrices (in particular Random Geometric Graphs).

Results:

- Significance of hubs in maintaining the persistence of the metapopulation.
- The density of habitat patches, their variability, the shape of the dispersal kernel, and the dimensionality of the landscape all play crucial roles in determining the fate of the metapopulation.

Take-Home Message

- **Climate change, wildfires, human activities, and seasonal variations in habitat** all underscore the importance of considering the temporal dimension of ecosystems.

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- New metric: the "**temporal metapopulation capacity**" to quantify the ability of a metapopulation to persist in a dynamically changing landscape.

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- Time-varying interaction networks: Analyze how changes in species interactions over time influence ecological patterns and processes.

Thank you for your attention!

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