Linear Stability Invariant Metapopulations
Network Partitioning

Dinesh Kumar∗  Soumyendu Raha

Department of Computational & Data Sciences,
Indian Institute of Science, Bangalore, India

Abstract: Metapopulations is a multi-patch habitat system, where populations live and interact in habitat patches, and individuals disperse from one patch to other via dispersal connections. The loss of dispersal connections among habitat patches can impact negatively on the stability of the system. This paper aims to determine some necessary and sufficient mathematical conditions for an appropriate metapopulations network partitioning (spatial cut) such that populations remain linearly stable in the partitioning induced daughter subnetworks. For that, metapopulations stability analyzed and role of the Fiedler value of a metapopulations induced graph Laplacian described first. Our study suggests, sufficiently connected metapopulations network (having the Fiedler value greater than or equal to some threshold level) along with the constrained internal patch dynamics always results in stable metapopulations dynamics around its co-existential equilibrium solution.

Keywords: Metapopulations; Linear Stability; Graph Partitioning

1 Introduction

Metapopulations structures of species are prevalent in the nature. Theoretical and experimental studies (for instance, [see 1, and references therein]) suggest that metapopulation structures and dispersal are important in the persistence of species. Thus, the distribution of the populations over a range of spatially discrete patches and the dispersal of individuals of species among these patches are very crucial for populations’ interactions and persistence in the ecological system.

Any interference (by nature or enforced) with the metapopulations structure have the risk of disruptive dynamics of metapopulations. It is well known that habitat destruction is the biggest cause of extinction for many species. Habitat fragmentation either by nature or human activities such as transportation routes, cross-border fencing and agriculture etc., leads to both lower dispersal

∗Email: kdinesh@iisc.ac.in
rates (as distances between patches are not easily crossed) and higher extinction rates (as small habitat patch increase the competitions, hence supports fewer species). Study [2] shows that even a dominant species eventually get extinction due to its habitat destruction. New infrastructure construction fragments the previously continuous habitat and reduces both the quantity and quality of the habitat [3]. Populations have the extinction risk and a lesser chance of recolonization in the small and isolated habitats [4, 5]. Destroying dispersal links that required to connect unstable local populations is certainly intimidating, motivates the study of searching for ecological sustainable spatial cuts (partitioning) of the metapopulations networks. In other words, we are interested in the set of dispersal connections among local populations (habitat patches), whose removal separate the metapopulations network into two or more subnetworks with a minimal negative effect on populations.

We define such desirable spatial cuts by those cuts which preserve the linear stability in the obtained metapopulations subnetworks. Since linear stability of a metapopulations dynamical system around its fixed point solution tells that if the populations disturbed slightly around the fixed point then that disturbance will not grow as time evolves. Stability of the metapopulations system is interest to many mathematical ecologists, a few studies by them are [6, 7, 8].

Finally, therefore the problem is mathematically modelled as that of determining mathematical conditions for a suitable cut (deletion of a set of edges) of the graph induced by the metapopulations network, where nodes and weighted edges represent the habitat patches and dispersal links (with dispersal rates) between habitat patches respectively. Determining optimal conditions for such desired cuts is not an easy thing. Thus, the focus of this paper will be on providing some necessary and sufficient conditions that can validate or discard a given graph cut.

Paper is organized as follows: in next section we shall analyze the linear stability of metapopulations model and determine the role of Fiedler value in it. Next, we shall provide some necessary and sufficient mathematical conditions for a viable partitioning of metapopulations networks that preserve the linear stability in the partitioned subnetworks.

2 Fiedler Value and Metapopulations Stability

We consider a spatial system of \( m \) patches, where \( n \) species interact in each individual patch and the patches are linked by species' dispersal movement. Let the local dynamics of the \( i \)-th species at the \( j \)-th patch is governed by,

\[
\dot{x}_{i,j} = f_{i,j}(x_{1,j}, \ldots, x_{n,j}), \quad i = 1, \ldots, n, \quad j = 1, \ldots, m,
\]

where \( x_{i,j} \) is the \( i \)-th species in \( j \)-th patch and the real valued function \( f_{i,j} \in C^1([0, \infty)^n) \) represents the dynamics of it.

If an individual has the same dispersal rates in both the directions between any two patches of the network and if there is a dispersal loss, then the system (1) becomes
\[ \dot{x}_{i,j} = f_{i,j}(x_{1,j}, \ldots, x_{n,j}) - \sum_{j \sim k} d_{jk}^i (x_{i,j} - x_{i,k}) - l_i x_{i,j}, \quad i = 1, \ldots, n, \quad j = 1, \ldots, m, \]  

(2)

where \( d_{jk}^i \) is the dispersal rate of the \( i \)-th species between patches \( j \) and \( k \). The parameter \( l_i \) represents the dispersal loss of the \( i \)-th species while dispersing from a patch.

Now writing the \( i \)-th species’ dynamics in the whole patch network together by combining the local dynamics and dispersal, we get

\[ \dot{x}_i = f_i(x_1, \ldots, x_n) - L_i x_i - E x, \quad i = 1, \ldots, n, \]  

(3)

where \( x_i = (x_{i,1}, \ldots, x_{i,m})^T \in \mathbb{R}^m \), \( f_i = (f_{i,1}, \ldots, f_{i,m})^T : R^{m \times n} \to \mathbb{R}^m \) and \( L_i \in M_{mn}(\mathbb{R}) \) is the Laplacian matrix of the network, which represents the dispersal communication of the \( i \)-th species among patches. \( I_m \) denotes the identity matrix of order \( m \).

More compactly and completely, with \( x = (x_1, \ldots, x_n)^T \in \mathbb{R}^{m \times n} \), \( f = (f_1, \ldots, f_n)^T : R^{m \times n} \to \mathbb{R}^{m \times n} \), \( L = L_1 \oplus \cdots \oplus L_n \in M_{mn}(\mathbb{R}) \) and \( E = l_1 I_m \oplus \cdots \oplus l_n I_m \in M_{mn}(\mathbb{R}) \) the dynamics of all species populations in whole patch network can be defined as follows,

\[ \dot{x} = f(x) - L x - E x. \]  

(4)

Here, \( x \) represents all the species populations combinedly in the metapopulations network, and \( f(x) \), \( L \) and \( E \) represent its internal patch dynamics, among-patch dispersal and dispersal loss respectively.

We are interested here in the local behavior of this system at its co-existential equilibrium solution, that is, if the size of species populations perturbed slightly from its co-existential equilibrium solution then whether this perturbation will die out eventually or not. If the perturbation does not grow (either die out or remain constant or decrease) w.r.t. time, then we say the species populations in spatial patch system are locally stable around the co-existential equilibrium point otherwise unstable.

Let \( \bar{x}(t) = \bar{x} \in \mathbb{R}^{m \times n} \), \( t \in [0, \infty) \) is a non-trivial (each component is positive) equilibrium solution of the system (4). Ecologically, it means that all \( n \) species population co-exist with the size \( \bar{x} \) and the size will remain as it is as time passes.

Let \( \varepsilon(t) \) is the perturbation to the equilibrium solution \( \bar{x} \) at time \( t \), that is, \( x(t) = \bar{x} + \varepsilon(t) \), and putting this into the system (4), we get

\[ \dot{\varepsilon} = f(\bar{x} + \varepsilon) - L(\bar{x} + \varepsilon) - E(\bar{x} + \varepsilon). \]  

(5)

Now by using Taylor expansion around \( \bar{x} \) and ignoring the higher order terms, the above system can be written as

\[ \dot{\varepsilon} = (Df(\bar{x}) - L - E)\varepsilon, \]  

(6)
To simplify the system (6), let $\varepsilon = Py$ (change of variables), where $P = P_1 \oplus \cdots \oplus P_n \in M_{nm}(\mathbb{R})$ conformally partitioned with $L$ and columns of each $P_i$ consist of eigenvectors of the Laplacian $L_i$. Since Laplacian matrix is a symmetric matrix, so construction of such matrix $P$ is always possible. Thus system (6) becomes

$$P\dot{y} = Df(\bar{x})Py - LPy - Ey,$$

that is,

$$\dot{y} = (P^{-1}Df(\bar{x})P - \Lambda - E)y,$$  (7)

Since the matrix $L$ is diagonalizable, hence $\Lambda$ is the block diagonal matrix conformal with $L$ whose each block diagonal entries are the eigenvalues of the corresponding block of the matrix $L$. There are total $mn$ equations in the system (7) ($m$ equations for each population or $n$ equations for each patch), out of which $n$ equations corresponds to 0 eigenvalue of $L$ and others are corresponding to positive eigenvalues of $L$.

If the real part of eigenvalues of the coefficient matrix $P^{-1}Df(\bar{x})P - \Lambda - E$ in above system (7) either negative or zero, then certainly the perturbation $\varepsilon$ to the equilibrium solution $\bar{x}$ will not grow over time, hence, in that case, the non-trivial equilibrium solution $\bar{x}$ of the dispersal system will be stable.

One of the necessary conditions for eigenvalues of the matrix $(P^{-1}Df(\bar{x})P - \Lambda - E)$ to have non-positive real part is the condition $\text{tr}(P^{-1}Df(\bar{x})P - \Lambda - E) \leq 0$, which is ensured by having

$$\lambda_2 \geq \frac{1}{n(m-1)} \sum_q (P^{-1}Df(\bar{x})P - \Lambda)_{qq},$$

where $\lambda_2 = \min_i \lambda_i$ : $\lambda_i$ is the second smallest eigenvalue of matrix $L_i$ and it corresponds to the species which have minimum Fiedler value (second smallest eigenvalue) of its Laplacian matrix.

By the Gershgorin disc theorem if following conditions hold true,

1. $l_q - (P^{-1}Df(\bar{x})P)_{qq} \geq \sum_{r \neq q} |(P^{-1}Df(\bar{x})P)_{qr}|$ (where $q$-th row of the coefficient matrix corresponds to zero eigenvalue of $L$) and

2. $\lambda_2 + l_s - (P^{-1}Df(\bar{x})P)_{ss} \geq \sum_{t \neq s} |(P^{-1}Df(\bar{x})P)_{st}|$ (where $s$-th row of the coefficient matrix corresponds to a positive eigenvalue of $L$)

then the system (7) is certainly locally stable around the non-trivial equilibrium solution $\bar{x}$.

Since the Fiedler value $\lambda_2$ signifies the connectivity of a graph network. It is greater than zero if and only if the graph is connected (a path between any two graph nodes exists). More the Fiedler value of a graph is, better connected
the graph is. Interestingly, dispersal connections in the metapopulations structure are also important for the metapopulations stability, for instance, see the example in the appendix, their absence leads to instability.

Thus, in the above analysis, it makes sense that both the necessary and sufficient conditions for linear stability of the metapopulations require the Fiedler value greater than or equal to some threshold level $\tau$ (say). That means, for the metapopulations stability we require the metapopulations network sufficiently connected.

If $\tau = \max \left\{ \max_{s \neq s'} |(P^{-1}Df(\bar{x})P)_{st}| + (P^{-1}Df(\bar{x})P)_{ss} - l_s, 0 \right\}$ and the local populations dynamics remain not altered after the network partitioning, then ensuring the Fiedler value threshold level (i.e., $\lambda_2 \geq \tau$) in the partitioned components is enough for our purpose.

3 Necessary and Sufficient Conditions for Stable Graph Partitioning

We define a simple (no self-loops), undirected and connected graph, denoted by $G(V, E)$ (or simply $G$), to be called stable if its Fiedler value, denoted by $\lambda_2(\mathcal{L}(G))$ (or simply $\lambda_2(G)$), is at least $\tau$. A partition of the graph is stable if it gives rise to components (connected subgraph), and all of them are stable. In this section, we shall provide the necessary and sufficient conditions for the stable components of a graph or stable graph partitioning.

To every graph cut, there are associated costs, namely, internal and external costs. If a graph $G$ is separated into two disjoint subgraphs $G_1$ and $G_2$ by some cut. Then, the external and internal costs of a node $x$ of the sub-graph $G_1$ (or $G_2$) are defined as follows

**External cost of the node** $x$: sum of the weights of edges that links node $x$ and the nodes of $G_2$ (or $G_1$). That is,

$$E(x) = \sum_{y \sim x} w_{xy}, \text{ where } y \in G_2(\text{or } G_1).$$

**Internal cost of the node** $x$: sum of the weights of edges that links node $x$ and the nodes of $G_1$ (or $G_2$). That is,

$$I(x) = \sum_{y \sim x} w_{xy}, \text{ where } y \in G_1(\text{or } G_2).$$

**Theorem 3.1.** Let $G(V, E)$ be a stable graph with size $n(\geq 4)$ and it partitioned into $k$ stable components $G_1, \ldots, G_k$ of size $n_1, \ldots, n_k$ such that $\sum_i n_i = n$, $n_i \geq 2$, $i = 1, \ldots, n$. Then $I_1^i + I_2^i \geq \tau$, $\forall i$, where $I_1^i$ is the $j$-th smallest internal cost of nodes in $G_i$. 

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Proof. Let $L$ be the Laplacian of the graph $G$ and $d_i$, $(i = 1, \ldots, n)$ are the diagonal entries of $L$ in non-increasing order. Let $Lx_i = \lambda_ix_i$, where $\lambda_i$ $(i = 1, \ldots, n)$ are in non-decreasing order and $x\_s$ are orthonormal vectors. Note that $L$ is symmetric, thus the standard unit vector $e_j = \sum_{i=1}^{n}a_{ij}x_i$, $(j = 1, \ldots, n - 2)$. We have,

$$
\sum_{j=1}^{n-2}d_j = \sum_{j=1}^{n-2}e_j^TLe_j = \sum_{j=1}^{n-2}\sum_{i=1}^{n}a_{ij}^2\lambda_i = \sum_{i=1}^{n}\sum_{j=1}^{n-2}a_{ij}^2\lambda_i \leq \sum_{i=3}^{n}\lambda_i \quad (8)
$$

The last inequality arises due to following facts: (1) $\sum_{j=1}^{n-2}a_{ij}^2$ is the $i$-th diagonal entry of the matrix $AA^T$, $A = (a_{ij})$, and (2) $AA^T = \begin{bmatrix} I_{n-2} & 0 \\ 0 & 0 \end{bmatrix}$, since $I_{n-2} = E^TE = (XA)^T(XA)$, where $E = [e_1, \ldots, e_{n-2}]$ and $X = [x_1, \ldots, x_n]$. It infers that $n - 2$ values of $\sum_{j=1}^{n-2}a_{ij}^2$, $(i = 1, \ldots, n)$ are one and other two values of it are zero.

From the equation (8), we have $\lambda_1 + \lambda_2 \leq d_{n-1} + d_n$ for any graph Laplacian $L$. Since $\lambda_1(G_i) = 0$, $\lambda_2(G_i) \geq \tau$ and diagonal entries of $L(G_i)$ represent the internal costs of nodes of the partitioned component $G_i$. Thus $I_1^i + I_2^i \geq \lambda_2(G_i) \geq \tau$. 

\[ \square \]

**Theorem 3.2.** Let $G(V, E)$ be a stable graph with size $n(\geq 4)$ and it partitioned into $k$ components $G_1, \ldots, G_k$ of size $n_1, \ldots, n_k$ such that $\sum n_i = n$, $n_i \geq 2$. Let $E^*_i$ is the largest external cost of a node in $G_i$. Then the components $G_1, \ldots, G_k$ are stable if $E^*_i \leq \lambda_2(G) - \tau$, $\forall \ i$.

**Proof.** Let $L$ is the Laplacian of the graph $G$ and $L_1, \ldots, L_k$ are principal submatrices of $L$ correspond to $G_1, \ldots, G_k$ respectively. By Cauchy interlacing theorem [4], we get the following relation in second-smallest eigenvalues of $L$ and its principal submatrix $L_i$ corresponding to $G_i$,

$$
\lambda_2(L(G)) \leq \lambda_2(L_i)
$$

Now writing $L_i = L(G_i) + D_i$, where $L(G_i)$ is the Laplacian matrix of $G_i$ and $D_i$ is the diagonal matrix whose diagonal entries are consisting of external costs of nodes in partitioned component $G_i$. Applying the Weyl’s inequality [3], we get

$$
\lambda_2(L(G)) \leq \lambda_2(L_i) = \lambda_2(L(G_i) + D_i) \leq \lambda_2(L(G_i)) + \lambda_{\text{max}}(D_i)
$$

Since $\lambda_{\text{max}}(D_i)$ is the maximum external cost $E^*_i$, and $E^*_i \leq \lambda_2(G) - \tau$ (by hypothesis). Thus, from the above inequality, we get $\lambda_2(L(G_i)) \geq \tau$ and which implies $G_i$ is stable partitioned component. 

\[ \square \]
Example: Consider the graph $G(5,6)$ as shown in Figure 1(a) with the Fiedler value $\lambda_2 = 3.625$. Graph cut $C_1$ separates the graph into two components $G_1 = \{v_1, v_2\}$ and $G_2 = \{v_3, v_4, v_5\}$. Both the components having a node with maximum external cost 3. If we assume that the graph is stable, that is, $\tau \leq 3.625$, then the sufficient condition in Theorem 3.2 holds true as long as $\tau \leq 0.625$. Thus both $G_1$ and $G_2$ must be stable subgraphs, in fact they are, as their Fiedler values are 6 and 4.26 respectively. Also, in this case, one can see the necessary condition given by Theorem 3.1 is essentially satisfied. The sum of two smallest internal costs of nodes in $G_1$ and $G_2$ are 6 and 8 respectively, and both are greater than $\tau$ ($\leq 3.625$).

For $\tau > 0.625$, partitioned components with the maximum external cost 3 may or may not be stable. Corresponds to the graph cut $C_1$, both the components are stable for all values of $\tau$. Whereas the component $\{v_1, v_2, v_3\}$ corresponds to the cut $C_2$ is unstable for $\tau > 2.35$, as it has the Fiedler value 2.35.

Now considering the graph $G(4,4)$ shown in Figure 1(b) with the Fiedler value $\lambda_2 = 0.9529$. The sum of two smallest internal costs of the component $\{v_1, v_4\}$ (produces by the cut $C$) is 0.2, thus the component $\{v_1, v_4\}$ is unstable if $\tau > 0.2$ (as the necessary condition given by Theorem 3.1 fails) and stable if $\tau \leq 0.2$ (as the Fiedler value of the component is 0.2).

![Graph (a)](image-a.png)

![Graph (b)](image-b.png)

Figure 1: Figure (a) $\lambda_2(G(5,6)) = 3.625$ (b) $\lambda_2(G(4,4)) = 0.9529$

Note that the condition on maximum external cost in Theorem 3.2 is also sufficient to get the stable subgraph if we remove some nodes and edges associated with them. Ecologically, that corresponds to complete destruction of some habitat patches in the metapopulations structure. An alternative approach to this, is presented in the proof of next theorem while deleting some specific type of nodes.

**Theorem 3.3.** Let $G(V,E)$ be a stable graph with size $n(\geq 3)$ and let $Y$ be a Fiedler vector of the graph Laplacian $L$. Let $W$ be set of all vertices for which valuation of Fiedler vector is zero, that is, $W = \{v \in V : Y(v) = 0\}$. If
\[ E^* \leq \lambda_2(G) - \tau, \] where \( E^* \) is the largest external cost of a node of a component of subgraph \( G - W \) (induced by deleting the set \( W \) of vertices and edges incident on them), then the component is stable.

**Proof.** Let \( L_1, \ldots, L_k \) are the principal submatrices of \( \mathcal{L} \) correspond to graph components of \( G - W \) and \( L_W \) is the principal submatrix corresponds to \( W \). Then the Laplacian \( \mathcal{L} \) can be written as the following way, by using permutation similarity operation, if necessary.

\[
\begin{bmatrix}
L_1 & 0 & \cdots & 0 \\
0 & L_2 & \cdots & 0 \\
\vdots & \vdots & \ddots & \vdots \\
0 & 0 & \cdots & L_k \\
C^T & L_W
\end{bmatrix}
\]

Let \([Y_1^T \ Y_2^T \ Y_2^T]^T\) is the conformal partition of the Fiedler vector \( Y \), where \( Y_2 \) is corresponding to \( W \), hence it is the zero vector. Now using the fact that \( \lambda_2 \) is the Fiedler value of \( \mathcal{L} \), we have \( L_i Y_i^T = \lambda_2 Y_i^T, \ (i = 1, \ldots, k) \). That is, \( \lambda_2 \) is also an eigenvalue of the principal submatrix \( L_i \) corresponds to \( i \)-th component of \( G - W \).

We claim that either it is the smallest or second smallest eigenvalue of \( L_i \). Suppose contrary to it, say, it is the \( r(>2) \)-th smallest eigenvalue of \( L_i \). Then by Cauchy interlacing theorem we know that \( r \)-th eigenvalue of \( \mathcal{L} \) is less than or equal to \( r \)-th eigenvalue of \( L_i \) which is \( \lambda_2 \), a contradiction.

Thus, \( \lambda_2 \) is less than or equal to second smallest eigenvalue of \( L_i \), which is equal to sum of Laplacian matrix of \( i \)-th component of \( G - W \) and some diagonal matrix \( D \). Again like in the proof of the previous theorem, using Weyl’s inequality and \( E^* \leq \lambda_2(G) - \tau \), the Fiedler value of \( i \)-th component of \( G - W \) is at least have the value \( \tau \).

Our last result is about an optimal (necessary and sufficient) condition for the graph stability. It requires the Fiedler vector, which is, in general, hard to determine without the knowledge of the Fiedler value. But for some cases (for example, regular graphs) it is easy to guess, and whenever we have it, the following theorem can be helpful in determining a valid cut.

**Theorem 3.4.** Let \( G(V, E) \) be a graph with size \( n(\geq 2) \) and let it partitioned into two components \( G_1 \) and \( G_2 \) of size \( n_1 \) and \( n_2 \) respectively, such that \( n_1 + n_2 = n, \ n_i \geq 1, \ i = 1, 2 \). Let \( Y \) be the Fiedler vector of the Laplacian \( \mathcal{L} \) of \( G \) corresponding to the Fiedler value \( \lambda_2(G) \). Then the graph \( G \) is stable if and only if one of the following conditions

1. \( \sum_{s \in G_i} Y(s) > 0 \) and \( \sum_{s \in G_i} (E_s - \tau)Y(s) \geq \sum_{s \in G_i \setminus G_i} E_s Y(s) \)

2. \( \sum_{s \in G_i} Y(s) < 0 \) and \( \sum_{s \in G_i} (E_s - \tau)Y(s) \leq \sum_{s \in G_i \setminus G_i} E_s Y(s) \)
is satisfied. Here $E_s$ is the external cost of node $s$ and $Y(s)$ is the valuation of the Fiedler vector at the $s$-th node.

Proof. Decomposing the Laplacian matrix of the graph $G$ as follows:

$$ L = \begin{bmatrix} L_1 & -B \\ -B^T & L_2 \end{bmatrix} = \begin{bmatrix} L_1 + D_1 & -B \\ -B^T & L_2 + D_2 \end{bmatrix}, $$

here $L_1$ and $L_2$ are the principal submatrices of the Laplacian $L$ corresponding to the components $G_1$ and $G_2$ respectively, and $L_1$ and $L_2$ are the respective Laplacian matrices of $G_1$ and $G_2$. $D_1$ (or $D_2$) is the diagonal matrix whose $ii$-th entry is the external cost of $i$-th labelled node in the subgraph $G_1$ (or $G_2$). $B$ is the non-negative matrix whose $ij$-th entry is the weight of the edge $[i,j]$ if $i$-th node of $G_1$ connected with the $j$-th node of the $G_2$ otherwise 0. Thus column sums of the matrix $B$ are the external costs of the respective nodes of subgraph $G_2$.

Now considering and evaluating the term $1^T G_1 L Y$, where $1_{G_1}$ is the column vector of size $n$ whose first $n_1$ entries are one and rest are zero.

$$ 1_{G_1}^T (L Y) = \lambda_2 1^T_{G_1} Y = \lambda_2 (G) \sum_{s \in G_1} Y(s). \quad (9) $$

$$ (1^T_{G_1} L) Y = (1^T L_1 + 1^T D_1 - 1^T B) Y_{G_1}. \quad (10) $$

Here column vector 1 is the vector of size $n_1$ whose all entries are one and it is eigenvector corresponding to eigenvalue zero of the matrix $L_1$, and $Y_{G_1}$ is conformal with $G_1$. Thus from equation (10) we have the following

$$ (1^T_{G_1} L) Y = 1^T D_1 Y_{G_1} - 1^T BY_{G_1} = \sum_{s \in G_1} E_s Y(s) - \sum_{s \in G_2} E_s Y(s) \quad (11) $$

Now by equations (9) and (11), and the fact $\lambda_2 (G) \geq \tau$, we get the desired inequality for the component $G_1$. Similarly, by choosing an appropriate column vector 1 the inequality can be obtained for $G_2$. \qed

Remark. If we need to check the stability of a partitioned component of a graph by using Theorem 3.4, then we have to proceed by further considering a partition (it can be any) tentatively within the component.

4 Conclusion & Discussion

This paper concerns about the preservation of the linear stability of metapopulations after partitioning the metapopulations network. Our study finds that if the internal patch (local populations) dynamics and among-patch dispersal
are appropriately parametric conditioned, then the metapopulations dynamical system will be linear stable around its co-existent equilibrium solution. In other words, the Fiedler value of a metapopulations network that satisfies the threshold criterion is enough for the metapopulations stability, if the local populations dynamics assumed to satisfy some given conditions.

If the internal patch dynamics of species remain the same after a partition, then the partition corresponds to ‘Fiedler value threshold criterion satisfied partitioned components’ does not produce any growing disturbance or threat to existing species. Hence, such partitions are harmless for the existing species in the network and may be population and conservation biologist find them useful to consider in their strategy (against any human-induced habitat destruction) for protecting and maintaining the species in metapopulations structure. Graph-partitioning computer algorithms (such as [10] and min-cut algorithms) can be used in detecting such ecologically sustainable partitions, though they do not provide any optimal partition (unless the network size is small) but approximations.

This work is dedicated to provide some necessary and sufficient conditions to obtain ecologically desirable partitions of the metapopulations networks. These conditions are easy to implement to validate or discard a given partition and can be appreciated for their simplicity (require knowledge of external and internal costs only), as determining optimal graph partition is an NP-hard problem[11].

With the considered model, the linear stability criterion also underpins all the studies that confer the population dispersal among patches matters in persisting or stabilizing the metapopulations. Since, for metapopulation stability, as discussed above, it is sufficient to have $\lambda_2 \geq \tau$, where the Fiedler value $\lambda_2$ signifies the connectivity of the patched network and $\tau$ is unknown but fixed threshold level decided by the local populations dynamics. Also, from the Weyl’s Monotonicity Theorem [9], which establishes the relationship between edges’ weight and the Fiedler value $\lambda_2$ of the same graph network, i.e., any increment in edges’ weight increases the graph Laplacian eigenvalues, in particular, increases the Fiedler value. These two observations certain; low dispersal rates (corresponds to small $\lambda_2$) among patches induce equilibrium instability, whereas high dispersal rates (corresponds to large $\lambda_2$) induce stability.

Appendix

The following illustrative example is provided to show the importance of dispersal connections in the metapopulations stability of a prey and predator species.

**Example:** In a spatially homogeneous environment, consider the Rosenzweig-MacArthur predator-prey system [12] at each patch in a 3-patch spatial network (as Figure 2) and assume that at every patch, the dynamics of this system at its unique non-trivial equilibrium solution is unstable in nature. The Rosezweig-
MacArthur system is defined as follows:

\[
\dot{x}_{1,j}(t) = x_{1,j}(t) \left( 1 - \frac{x_{1,j}(t)}{\gamma} \right) - \frac{x_{1,j}(t)x_{2,j}(t)}{1 + x_{1,j}(t)},
\]

\[
\dot{x}_{2,j}(t) = \beta \left( \frac{x_{1,j}(t)}{1 + x_{1,j}(t)} - \alpha \right) x_{2,j}(t), \quad j = 1, 2, 3,
\]

(12)

here \( x_{1,j}(t) \) and \( x_{2,j}(t) \) are the prey and predator density respectively at the \( j \)-th patch and at a time \( t \). In absence of the predation, prey species follows the logistic dynamics with the carrying capacity \( \gamma \). Parameters \( \beta \) and \( \alpha \) signifies the conversion rate and the mortality rate of predators respectively. The unique nontrivial equilibrium solution of (12) is given by

\[
(x^*_1, j, x^*_2, j) = \left( \frac{\alpha}{1 - \alpha}, (1 + x^*_1, j)(1 - \frac{x^*_1, j}{\gamma}) \right).
\]

At this equilibrium, the Jacobian of the vector field of the system (12) is given as follows

\[
\begin{bmatrix}
\alpha \left( 1 + \frac{1}{\gamma} - \frac{2}{\gamma(1-\alpha)} \right) & -\alpha \\
\beta(1 - \alpha - \frac{\alpha}{\gamma}) & 0
\end{bmatrix}.
\]

Figure 2: Figure shows the 3-patch spatial system with the dispersal connections. Dispersal rates between patches denoted by \( d_{ij}^1 \) and \( d_{ij}^2 \) are of prey and predator species respectively.

Choosing the parameters’ value: \( \gamma = 2, \beta = 0.2, \alpha = 0.3 \), the equilibrium solution \((x^*_1, j, x^*_2, j) = (3/7, 55/49)\) of the system (12) is feasible and nontrivial, and the corresponding Jacobian has the eigenvalues \( 0.0107 \pm 0.1813 \). Clearly, these eigenvalues have positive real part, thus, the dynamics at each patch is unstable around the equilibrium solution with the above choice of parameters’ value.

Now considering together the Rosenzweig-MacArthur predator-prey system at each habitat patch and the species’ dispersal movement among patches, the
dynamics then is

\[
\begin{align*}
\dot{x}_{1,1}(t) &= x_{1,1}(t) \left(1 - \frac{x_{1,1}(t)}{\gamma} \right) - \frac{x_{1,1}(t)x_{2,1}(t)}{1 + x_{1,1}(t)} - d_{12}^1(x_{1,1}(t) - x_{1,2}(t)) - d_{13}^1(x_{1,1}(t) - x_{1,3}(t)) - l_1 x_{1,1}(t), \\
\dot{x}_{1,2}(t) &= x_{1,2}(t) \left(1 - \frac{x_{1,2}(t)}{\gamma} \right) - \frac{x_{1,2}(t)x_{2,2}(t)}{1 + x_{1,2}(t)} - d_{12}^2(x_{1,2}(t) - x_{1,1}(t)) - d_{23}^2(x_{1,2}(t) - x_{1,3}(t)) - l_1 x_{1,2}(t), \\
\dot{x}_{1,3}(t) &= x_{1,3}(t) \left(1 - \frac{x_{1,3}(t)}{\gamma} \right) - \frac{x_{1,3}(t)x_{2,3}(t)}{1 + x_{1,3}(t)} - d_{13}^1(x_{1,3}(t) - x_{1,1}(t)) - d_{23}^2(x_{1,3}(t) - x_{1,2}(t)) - l_1 x_{1,3}(t), \\
\dot{x}_{2,1}(t) &= \beta \left(\frac{x_{1,1}(t)}{1 + x_{1,1}(t)} - \alpha \right) x_{2,1}(t) - d_{12}^1(x_{2,1}(t) - x_{2,2}(t)) - d_{13}^2(x_{2,1}(t) - x_{2,3}(t)) - l_2 x_{2,1}(t), \\
\dot{x}_{2,2}(t) &= \beta \left(\frac{x_{1,2}(t)}{1 + x_{1,2}(t)} - \alpha \right) x_{2,2}(t) - d_{12}^2(x_{2,2}(t) - x_{2,1}(t)) - d_{23}^2(x_{2,2}(t) - x_{2,3}(t)) - l_2 x_{2,2}(t), \\
\dot{x}_{2,3}(t) &= \beta \left(\frac{x_{1,3}(t)}{1 + x_{1,3}(t)} - \alpha \right) x_{2,3}(t) - d_{13}^1(x_{2,3}(t) - x_{2,1}(t)) - d_{23}^2(x_{2,3}(t) - x_{2,2}(t)) - l_2 x_{2,3}(t).
\end{align*}
\]

Rewriting the above system in vector form, we have

\[(\begin{array}{c}
x_{1,1} \\
x_{1,2} \\
x_{1,3} \\
x_{2,1} \\
x_{2,2} \\
x_{2,3}
\end{array}) = \left(\begin{array}{c}
\frac{1}{1 - \frac{x_{1,1}(t)}{\gamma}} - \frac{x_{1,1}(t)}{1 + x_{1,1}(t)} \\
\frac{1}{1 - \frac{x_{1,2}(t)}{\gamma}} - \frac{x_{1,2}(t)}{1 + x_{1,2}(t)} \\
\frac{1}{1 - \frac{x_{1,3}(t)}{\gamma}} - \frac{x_{1,3}(t)}{1 + x_{1,3}(t)} \\
\beta \left(\frac{x_{1,1}(t)}{1 + x_{1,1}(t)} - \alpha \right) \\
\beta \left(\frac{x_{1,2}(t)}{1 + x_{1,2}(t)} - \alpha \right) \\
\beta \left(\frac{x_{1,3}(t)}{1 + x_{1,3}(t)} - \alpha \right)
\end{array}\right) \cdot \left(\begin{array}{c}
\frac{d_{12}^1 + d_{13}^1}{\gamma} \\
-\frac{d_{12}^1}{\gamma} \\
-\frac{d_{12}^2}{\gamma} \\
0 \\
0 \\
0
\end{array}\right) \cdot \left(\begin{array}{c}
x_{1,1} \beta \left(\frac{x_{1,1}(t)}{1 + x_{1,1}(t)} - \alpha \right) \\
x_{1,2} \beta \left(\frac{x_{1,2}(t)}{1 + x_{1,2}(t)} - \alpha \right) \\
x_{1,3} \beta \left(\frac{x_{1,3}(t)}{1 + x_{1,3}(t)} - \alpha \right) \\
x_{2,1} \beta \left(\frac{x_{1,1}(t)}{1 + x_{1,1}(t)} - \alpha \right) \\
x_{2,2} \beta \left(\frac{x_{1,2}(t)}{1 + x_{1,2}(t)} - \alpha \right) \\
x_{2,3} \beta \left(\frac{x_{1,3}(t)}{1 + x_{1,3}(t)} - \alpha \right)
\end{array}\right).
\]

The non-trivial equilibrium solution of this system is \((\bar{x}_{1,1}, \bar{x}_{1,2}, \bar{x}_{1,3}, \bar{x}_{2,1}, \bar{x}_{2,2}, \bar{x}_{2,3})\), where \(\bar{x}_{1,1} = \bar{x}_{1,2} = \bar{x}_{1,3} = \frac{\alpha + l_2}{1 - (\alpha + l_2)}\) and \(\bar{x}_{2,1} = \bar{x}_{2,2} = \bar{x}_{2,3} = \left(1 + \frac{\alpha + l_2}{1 - (\alpha + l_2)}\right) \left(1 - \frac{l_1}{\gamma(1 - (\alpha + l_2))}\right)\).

At this non-trivial equilibrium point, the Jacobian of the system \[\text{J}\] is given by

\[
\begin{bmatrix}
(\alpha + l_2) \left(1 - l_1 + \frac{1}{\gamma} - \frac{2}{\gamma(1 - (\alpha + l_2))}\right) & -L_1 & -L_2 \\
\beta \left(1 - l_1\right) \left(1 - (\alpha + l_2)\right) & -\frac{4}{\gamma} & 0 \\
\end{bmatrix}
\]

where \(L_1\) and \(L_2\) are the Laplacian matrices for prey species \(x_1\) and predator species \(x_2\). Taking the parameter values \(d_{12}^1 = 1 = d_{13}^1, d_{23}^1 = 2, d_{12}^2 = 2, d_{23}^2 = 1 = d_{23}^3\) and \(l_1 = 0.4 = 2l_2\), and other parameters value same as before, the eigenvalues of Jacobian of the dispersal system \[\text{J}\] are: \(-0.0114, -0.4386, -3.0043, -03.4496, -5.0004\) and \(-5.4457\) (all have negative real part). Hence, the coexistential equilibrium solution of the system with among-patch dispersal is asymptotically stable.
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References

[1] ANDREW D TAYLOR. Studying metapopulation effects in predator-prey systems. *Biological Journal of the Linnean Society*, 42(1-2):305–323, 1991.

[2] David Tilman, Robert M May, Clarence L Lehman, and Martin A Nowak. Habitat destruction and the extinction debt. *Nature*, 371(6492):65, 1994.

[3] R Reijnen, EA van der Grift, M Van der Veen, M Pelk, A Lüchtenborg, and D Bal. De weg mét de minste weerstand; opgave ontsnippering. Technical report, Alterra, 2000.

[4] Paul Opdam. Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. *Landscape ecology*, 5(2):93–106, 1991.

[5] I Hanski. *Metapopulation Ecology*. Oxford University Press, 1999.

[6] Vincent AA Jansen and Alun L Lloyd. Local stability analysis of spatially homogeneous solutions of multi-patch systems. *Journal of mathematical biology*, 41(3):232–252, 2000.

[7] Eric Tromeur, Lars Rudolf, and Thilo Gross. Impact of dispersal on the stability of metapopulations. *Journal of theoretical biology*, 392:1–11, 2016.

[8] Toshiyuki Namba, Asako Umemoto, and Eriko Minami. The effects of habitat fragmentation on persistence of source–sink metapopulations in systems with predators and prey or apparent competitors. *Theoretical Population Biology*, 56(1):123–137, 1999.

[9] Rajendra Bhatia. *Matrix analysis*. Springer Science & Business Media, 2013.

[10] Dinesh Kumar, Jatin Gupta, and Soumyendu Raha. Partitioning a reaction–diffusion ecological network for dynamic stability. *Proceedings of the Royal Society A*, 475(2223):20180524, 2019.

[11] Michael R Garey and David S Johnson. *Computers and intractability*. WH Freeman, 2002.

[12] Mark Kot. *Elements of mathematical ecology*. Cambridge University Press, 2001.