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FORUM

Complex questions require complex answers – rejoinder to F. Jordán

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We greatly appreciate the comments on our proposal (Ricotta et al. 2000) to characterize landscape connectivity with topological indices (*TI*s). In our paper, following the geometrical approach of Cantwell and Forman (1993), we proposed to reduce the complexity of landscape patterns into a connected landscape graph. Based on this approach, summary statistics quantifying the spatial relationships among landscape patches may be obtained by mapping graph topology with scalars.

In a recent Forum paper, F. Jordán (2001) emphasized that adding functional considerations to our purely structural approach may limit the conditions of applicability and ultimately the results of the proposed method. In this rejoinder, we would like to stress that, although adding 'function' to 'structure' necessarily requires more refined tools for summarizing landscape connectivity, nonetheless graph-theoretical approaches remain a key for understanding the ecological functions of heterogeneous landscapes.

If, based on the preference of a given organism for certain habitat types, only a subset of habitat patches is analyzed, a 'functional landscape (sub)graph' out of the whole 'structural landscape graph' is obtained. Analyzing the spatial configurations of such subgraphs can be helpful for conservation studies as suggested by Jordán (2001). Nonetheless, unlike structural landscape graphs, functional landscape graphs may be disconnected thus limiting the applicability of traditional measures for quantifying their topology because of the presence of $d_{ij} = \infty$ in the distance matrix **D**. In addition, increasing the level of generality, directed connections between vertices of functional landscape graphs reflecting asymmetric constraints on the underlying landscape structure can also be introduced, for example to model spatially explicit source-sink effects (Harrison 1991, Kunin 1995).

In such cases, to understand more fully the connectivity of functional digraphs, besides the adjacency matrix **A** and the distance matrix **D**, an additional matrix termed 'reachability matrix', **R,** may be introduced by slightly modifying the original definition of Harary (1969) in order to render **R** ecologically more reasonable. In the reachability matrix **R**, $r_{ij} = 1$ if vertex v_i is reachable from vertex v_j and $r_{ij} = 0$ otherwise. In addition, the diagonal elements, r_{ii} are zero unless we deal with loop graphs where a vertex may be bonded with itself. In this latter case, $r_{ii} = 1$. For an artificial example of a functional disconnected digraph along with its reachability matrix, see Figure 1. As usual for undirected graphs, local vertex invariants x_i (i.e., topological indices associated to single graph vertices) can be obtained from **R** by adding all r_{ij} elements along row i or column i of the matrix, whereas, starting from the local vertex invariants x_i, a number of *TI*s can be derived by means of the following operations (Filip et al. 1987):

$$TI_1 = \sum_{i=1}^{N} x_i \quad (1)$$

$$TI_2 = \sum_{i=1}^{N} x_i^2 \quad (2)$$

$$TI_3 = \sum_{i=1}^{N} x_i^{1/2} \quad (3)$$

$$TI_4 = N\left(\prod_{i=1}^{N} x_i\right)^{1/N} \quad (4)$$

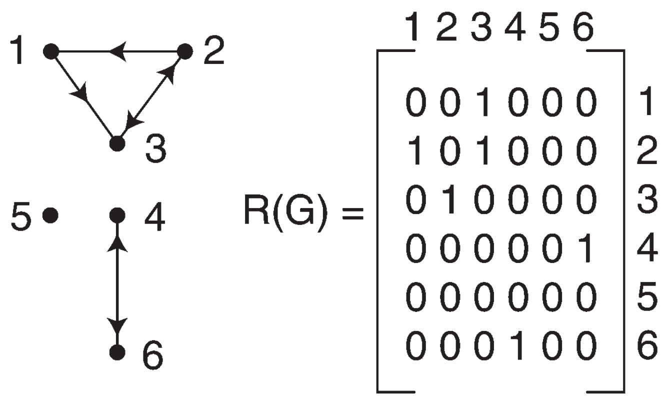

Figure 1. Example calculation of the reachability matrix R(G) for an artificial disconnected digraph without loops. Modified from Ricotta et al. (2000).

$$TI_5 = \sum_{v_i - v_j \in G} (x_i, x_j)^{1/2} \qquad (5)$$

Operations in Equations (1-4) refer to the N vertices v_i of graph G, whilst the summation in Equation 5 is computed over all edges v_i-v_j of G. Alternatively, a different approach for summarizing graph topology consists in the application of information-theoretical formalism to the set of local vertex invariants x_i. For mathematical details, see Bonchev (1983).

Besides its potential applicability for summarizing landscape connectivity with *TI*s, the reachability matrix has some interesting properties within the context of percolation theory and random graph evolution (Stauffer and Aharony 1992). In its original definition (Erdős and Rényi 1960), the evolution of random graphs refers to the changes in structural properties, which a fully disconnected graph composed of N vertices undergoes as successive undirected edges are randomly added. At first (Seeley 2000), there are only isolated edges connecting single pairs of vertices. After more edges are added, multiple branches and small trees with several edges occur until the initial growth of cycles. Cycles start to appear when a tree has an edge added to it, which connects two of the already existing vertices in the tree. When the number of edges has grown to almost exactly 1/2 N, the graph 'percolates' and a giant component of order $N^{2/3}$ suddenly appears for almost all graphs. Hence the connectivity of the overall graph (i.e., the proportion of possible pairs of vertices for which a path exists), measured as,

$$\sum_{i,j} r_{ij} / N(N-1) \qquad (6)$$

suddenly and very rapidly increases from significantly below 1/2 to significantly above 1/2. In other words, a transition in the structure of the random graph from a macroscopically disconnected structure to a connected one occurs.

Within the context of a recovery plan for threatened bird species in the southwestern United States, Keitt et al. (1997) used an extension of random graph evolution to quantify the connectivity of suitable nesting habitats for the Mexican Spotted Owl and to examine the sensitivity of habitat connectivity to changes in landscape configuration, whereas Seeley (2000) studied the evolution of random digraphs, albeit from a more theoretical viewpoint.

These results show that, although the potential applications of topological methods in ecological work remain largely unexplored, graph theory represents a promising tool to create a universal framework for modeling landscape functions at any scale of observation. Green (1994) pointed out that the pattern of dependencies in matrix models, dynamical systems and cellular automata are all isomorphic to directed graphs. In this view, since the range of these models spans almost all mathematical modeling whether it is of physical or biological systems, "there is strong evidence to suggest that directed graphs can be considered as an essential or fundamental model. That is, within any model which purports to describe the dynamics of some aspect of the world there resides a core, directed graph model" (Seeley 2000).

Finally, we conclude with a cautionary remark: as stressed by Hill (1973) in a similar context, there is almost unlimited scope for mathematical generality in relation to topological measures of landscape functions. Ecologically well-understood indices should be used.

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