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Throughflow centrality is a global indicator of the functional importance of species in ecosystems

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ABSTRACT

To better understand and manage complex systems like ecosystems it is critical to know the relative contribution of the system components to the system function. Ecologists and social scientists have described a diversity of ways that individuals can be important; This paper makes two key contributions to this research area. First, it shows that throughflow (T_j), the total energy or matter entering or exiting a system component, is a global indicator of the relative contribution of the component to the whole system activity. It is global because it includes the direct and indirect exchanges among community members. Further, throughflow is a special case of Hubbell status or centrality as defined in social science. This recognition effectively joins the concepts, enabling ecologists to use and build on the broader centrality research in network science. Second, I characterize the distribution of throughflow in 45 empirically-based trophic ecosystem models. Consistent with theoretical expectations, this analysis shows that a small fraction of the system components are responsible for the majority of the system activity. In 73% of the ecosystem models, 20% or less of the nodes generate 80% or more of the total system throughflow. Four or fewer nodes are required to account for 50% of the total system activity and are thus defined as community dominants. 121 of the 130 dominant nodes in the 45 ecosystem models could be classified as primary producers, dead organic matter, or bacteria. Thus, throughflow centrality indicates the rank power of the ecosystems components and shows the concentration of power in the primary production and decomposition cycle. Although these results are specific to ecosystems, these techniques build on flow analysis based on economic input–output analysis. Therefore these results should be useful for ecosystem ecology, industrial ecology, the study of urban metabolism, as well as other domains using input–output analysis.

1. Introduction

Identifying functionally important actors is a critical step in understanding and managing complex systems, whether it is a fortune 500 company or an ecosystem. For example, Ibarra (1993) showed that an employee's power to affect administrative innovation within an advertising agency was in part determined by their positional importance within the organization. In ecological systems, knowing the relative functional importance of species or groups of species is essential for conservation biology, ecosystem management, and understanding the consequences of biodiversity loss (Hooper et al., 2005; Jordán et al., 2006; Lawton, 1994; Saavedra et al., 2011; Walker, 1992). Ecologists have several ways of classifying the relative importance of community members. Whittaker (1965) introduced rank–abundance curves to describe the community richness and indicate the relative importance of the species, assuming that community importance was proportional to abundance. He also presented an alternative rank–productivity curve that indicated the species importance based on their net productivity. Subsequent ecological concepts have built on this. Keystone species (Paine, 1966; Power et al., 1996) are species whose importance to the community are disproportionate to their biomass, like the sea otter in Pacific kelp forests. Ecological engineers (Jones et al., 1994; Lawton, 1994) are species whose actions create whole new habitats, such as beavers that transform terrestrial environments into slow moving aquatic environments. Dayton (1972) introduced the more general term foundational species for fundamentally important species of many types (Ellison et al., 2005). Part of the challenge and the reason for multiple concepts is that there are a diversity of ways in which a species may be important and contribute to a community or ecosystem.

Faced with the analogous problem of identifying important members of human communities, social scientists developed the *centrality* concept (see Wasserman and Faust, 1994). Centrality

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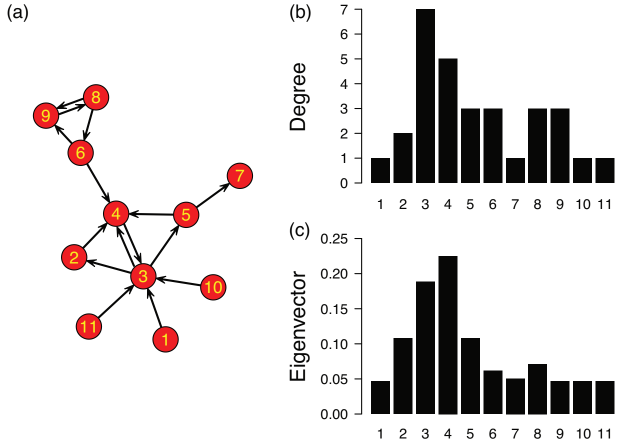

Fig. 1. Hypothetical network model (a) with its associated (b) degree and (c) eigenvector centrality. Degree centrality is a local measure while eigenvector centrality is a global indicator of node importance.

embodies the intuition that some community members are more important, have more power, or are more central to community function. Centrality was developed in the context of network models of communities in which individuals are represented as nodes of a graph and the graph edges signify a specific relationship between two individuals such as friendship or co-authorship (Fig. 1a). The relationship may or may not be directed. Degree centrality is the number of immediately adjacent neighbors on the graph, and it assumes that more connected nodes are more central. It is quantified as the number of edges incident to the node. In the example graph, node 3 has a degree of 7. Fig. 1b shows the distribution of node degrees in the community, which indicates that node 3 is the most central from this local neighborhood perspective.

Scientists have suggested that for some applications (e.g., exchange networks) the local neighborhood is insufficient to determine the node's centrality (Bonacich, 1972; Estrada, 2010; Hubbell, 1965). Instead, a node's importance may be increased because one or more of its neighbors are important. Network models can capture this increased neighborhood size by defining a *walk* as a sequence of edges traveled from one node to another, and walk length (m) is the number of edges crossed. In the example network, there is a walk from 6 to 2 of length $m = 3$ by following $6 \to 4 \to 3 \to 2$. This enables us to consider the neighborhood m steps aways (Estrada, 2010). Fig. 1c shows the eigenvector centrality (Bonacich, 1972, 1987) for the example network which identifies the equilibrium number of paths passing through each node as $m \to \infty$. In this sense it is a global centrality measure because it is a "summary of a node's participation in the walk structure of the network" (Borgatti, 2005) and captures the importance of indirect as well as direct interactions (Borgatti, 2005; Scotti et al., 2007).

Degree and eigenvector are only two examples of centrality indicators. Many centrality measures have been developed and applied in the literature for complex systems modeled as networks (Wasserman and Faust, 1994; Koschützki et al., 2005). Centrality measures tend to be correlated (Jordán et al., 2007; Newman, 2006; Valente et al., 2008), but the differences can be informative (Baranyi et al., 2011; Estrada and Bodin, 2008). Borgatti and Everett (2006) provide a classification of centrality indices and shows how and why different measures are useful for different applications.

Ecologists have applied the centrality concept in several ways. For example, landscape ecologists have used centrality to assess the connectivity of habitat patches, how this connectivity effects organism movement, and how habitat loss changes the connectivity (Baranyi et al., 2011; Bodin and Saura, 2010; Estrada and Bodin, 2008). Community and ecosystem ecologists have developed and used centrality measures to study how organisms influence each other in transaction networks (Allesina and Pascual, 2009; Fann and Borrett, 2012; Jordán et al., 2003). Jordán et al. (2006) argue that mesoscale measures, between local and global centralities, are most useful for ecosystem studies because the impact of indirect effects tend to decay rapidly as they radiate through the system. Recent work used centrality indicators to determine important species in communities of mutualists (Martín González et al., 2010; Sazima et al., 2010). Collectively, this work shows how a range of centrality indicators can be useful for addressing ecological questions.

Here, I identify a new centrality indicator for ecology, termed throughflow centrality. I first recognize that the throughflow measure ecosystem ecologists have long calculated (Finn, 1976; Patten et al., 1976; Ulanowicz, 1986) is a global measure of node importance in generating the total system activity. Further, I show that this is a special case of Hubbell's status index centrality (Hubbell, 1965). I then apply this measure to 45 trophic ecosystem models drawn from the literature to test two hypotheses regarding ecosystem organization. The first hypothesis suggested by both Whittaker (1965) and Mills et al. (1993) is that communities are composed of a relatively few dominant species and larger group that are less central. The second hypothesis is that in ecosystems the dominant species or groups are expected to be comprised of primary producers, decomposers like bacteria, and non-living groups included in ecosystem models like dead organic matter. This hypothesis stems from trophodynamic theory and energetic constraints of food chains (Jorgensen et al., 1999; Lindeman, 1942; Wilkinson, 2006)

2. Theory – throughflow is a centrality indicator

A core claim of this paper is that the amount of energy–matter flowing through each node j in an ecosystem network – termed node throughflow (T_j) – is a global centrality indicator of the node's functional importance. In fact, this centrality measure is a special case of Hubbell's (1965) status score. Further, this centrality indicator is more useful for ecologists and environmental scientists than the classic eigenvector centrality or the recently introduced environ centrality (Fann and Borrett, 2012) because (1) it is more intuitive to calculate, (2) it integrates the transient and equilibrium effects as flow crosses increasingly longer pathways, and (3) it captures the effects of environmental inputs (outputs) on the system flows. This section provides evidence to support these claims.

2.1. Flow analysis

Flow analysis is a major branch of ecological network analysis (ENA) (Borrett et al., 2012; Fath and Patten, 1999; Finn, 1976; Ulanowicz, 1986). It is an environmental application and development of Leontief's (1966) macroeconomic input–output analysis first imported to ecology by Hannon (1973). It traces the movement of energy or matter through the network of transactions in an ecosystem to characterize the organization and development of the system.

2.1.1. Model definition

Flow analysis is applied to a network model of energy or matter exchanges. The system is modeled as a set of n compartments or nodes that represent species, species-complexes (i.e., trophic guilds or functional groups), or non-living components of the system in which energy–matter is stored. Nodes are connected by L observed fluxes, termed directed edges or links. This analysis requires an estimate of the energy–matter flowing from node j to i over a given period, $\mathbf{F}_{n\times n} = [f_{ij}]$, $i, j = 1, 2, \ldots, n$ (note the column to row orientation). This flux can be generated by any process such as feeding