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INTRODUCTORY ARTICLE

Complex networks in ecology

Gili Greenbaum [a,b]*, Oren Hoffman[c], Omri Shalev[b] and Yuval R. Zelnik[a]

[a]*Department of Solar Energy and Environmental Physics, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel;* [b]*Mitrani Department of Desert Ecology, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel;* [c]*The Wyler Department of Dryland Agriculture, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel*

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One of the major goals of ecology as a discipline is to study, model and understand interactions between different entities in nature – biological organisms and their environments. As such, ecology is more about the properties of the sum of interacting units, the "gestalt", than about the specific characteristics of any particular organism or environment. Ecological models are attempts to describe and explain the consequences of such interactions. "Everything should be made as simple as possible, but not simpler" goes the famous saying, attributed to Albert Einstein, and on this fine line treads the complicated task of ecological research. However, the complex nature of many ecosystems has forced ecologists, in most cases, to design simplistic models, ignoring many aspects of the complexity inherent in ecological systems. The fear that such models fail to capture important aspects of ecological systems has, and still does, trouble many ecologists.

By the same time that modern ecological thinkers began confronting these difficult questions regarding ecological systems, the famous German mathematician Leonhard Euler was presenting his work on the solution to the "Seven bridges of Königsberg" problem. Euler showed that it was impossible to traverse the city's seven bridges without crossing any bridge twice. This he did by ignoring the characteristics of the objects – the city's islands and bridges – and by focusing on the way these object relate to one another, their topology. This initiated the mathematical field of graph theory. In the last several decades, researchers from various disciplines have applied graph theory to a variety of real-world systems, in order to understand real-world phenomenon that may arise as a consequence of complex arrays of interactions between discrete elements. This revised mathematical field is termed "network science" (Newman 2010), and its focus is mathematical constructs called networks, or graphs, that comprise of discrete entities termed "*nodes*" (or "*vertices*"), and interactions between the nodes termed "*edges*". Seminal works in the late 1990s, such as the work on "small-world" networks (Watts & Strogatz 1998) and scale-free networks (Barabási & Albert 1999), showed that new insights into complex phenomenon can be attained through the use of networks. They also showed that many unrelated real-world networks, such as the Internet, social networks, power grids or airline flight networks, share unexpected universal properties. This has led to a surge of studies applying network theory to various fields and the use of networks to represent and model many systems.

The application of network science to ecology is therefore more than natural, as both sciences focus on the nature of interactions rather than the nature of objects or units. The number of ecological studies using network theory has been rising in the last three decades (Heleno et al. 2014), as the framework of network science now allows ecologists to model non-trivial interactions between ecosystem components, and to understand how universal properties of networks affect the behavior of such ecosystems (Bascompte 2007). In community ecology, interactions between different species are being modeled using networks called food webs or ecological networks. In ecological epidemiology, the spread of pathogens between individuals is modeled using networks. Networks have been extensively used to describe gene interactions in genetic regulatory networks, and consequently are now being applied to ecological genomics. The genetic structure of populations is also being studied using networks, both to describe genetic interactions between populations via gene flow and the genetic similarities between individuals. Patch networks describe movement of individuals between non-trivially connected habitat patches to study demographic and genetic questions in structured populations. Social networks are used in behavioral ecology to understand social structures and study the evolutionary dynamics that lead to different types of sociality.

However, this synthesis between ecology and network science is only at its infancy, and much more could be gained in terms of understanding complex ecological systems. From a theoretical perspective, network theory has been quite extensively applied to ecological epidemiology, ecological genomics, community ecology, and habitat patch networks and less so to population genetics and animal social networks. Nevertheless, actual ecological datasets describing network structure are scarce, and few experimental ecological studied are designed with the application of network analysis in mind. This special

*Corresponding author. Email: gilgreen@post.bgu.ac.il

issue, dedicated to complex networks in ecology, contains a collection of studies that approach ecological problems, theoretic and empirical, from a network theory perspective. They contribute to our understanding both of the ecological systems themselves and to the manner in which network science can be applied to model and understand ecosystems.

The articles in this issue address problems in varied branches of ecology. The “food chain” in classical ecology has been extended to “food webs”, describing complex community interactions between taxa as networks. Guill and Paulau (2016, this issue) address a theoretical problem with existing food-web models: models constrain the network in a way that cannibalistic interactions of species are prohibited. The authors use simulated and empirical data to show that, when cannibalistic species do occur in the ecosystem, these constraints affect the ecological interpretation, thus suggesting the extension of existing models to include network motifs describing cannibalism. Scotti and Jordán (2016, this issue) discuss the relationship between species abundance and their structural position in the food web. They explore networks describing species interaction in the Prince William Sound ecosystem, and find that there is a positive correlation between species abundance and centrality in the network. Thus, less abundant species are found in the periphery of the food web, and have lower functional importance for the ecosystem as a whole. This work highlights the potential of using network theory to set biodiversity conservation priorities based on functional importance, and not just rarity.

Nitzan et al. (2016, this issue) review the recent advancements in the study of the human microbiome community using metabolic interaction networks. By connecting different bacterial populations through their metabolically mediated interactions, including competition and facilitation, and analyses of the resulting networks, researchers can learn of community–environment relations. In this review, they describe how network science, and specifically the new application of metabolic interaction networks, shines a new light on microbial community ecology. Fonio et al. (2016, this issue) study the interaction of sniffing and whisking behavior in mice in an environment allowing free exploration. The authors find an intricate interplay between the exploratory mode of the mice and both the patterns and the coordination of their active sensing. These results shed light on the underlying neural networks of mice, which appear to process information in distinct time scales, related to the different exploratory modes of the mice. Bouskila et al. (2016, this issue) investigate the factors that influence the structure of a social network of horses. They test the hypothesis that affiliations in the network are affected by relatedness, similar age, and being of the same sex. Of these, the results show that sex homophily is indeed a major factor, while relatedness and age have no significant contribution.

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ORCID

Gili Greenbaum http://orcid.org/0000-0002-1631-8203

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