Editorial

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Ecological networks: assembly and consequences

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One of the central problems in ecology is to understand how patterns observed in ecological systems are linked to ecological and evolutionary processes (Levin 1992). Ecological systems – as biological systems in general – are examples of what Warren Weaver called, almost 70 years ago, "problems of organized complexity", in which systems are characterized by a sizable number of interrelated elements (Weaver 1948). In the last decades, the problems of organized complexity in different scientific fields have been tackled by depicting systems as networks (Amaral and Ottino 2004). In this approach, ecological systems are characterized as networks composed of co-occurring or interacting elements, and the ecological patterns quantified in terms of network structures. Subsequently a suite of approaches is used to infer the underlying processes shaping network structures and/or to explore the consequences of network structures for the way ecological systems respond to different external factors. The characterization of ecological systems as networks is not new, as illustrated by the seminal work by Cohen, Margalef, May, Odum, Paine and others. However, in the last years the use of networks in ecology has rapidly expanded from more traditional descriptions of food webs to the characterization of a wide range of ecological systems as illustrated by this Oikos special issue. These studies collectively explore the workings of processes that shape networks and the functional consequences of network organization of ecological systems.

The notion that network structures in ecological systems inform about the ecological and evolutionary processes is rooted in the intuition that "complex systems must display some organizing principles, which should be at some level encoded in their topology" (Albert and Barabási 2002). In ecological systems, interactions always occur at individual level and, therefore, processes shaping ecological networks are ultimately processes affecting how individuals of different species interact with each other. The most basic aspects affecting interactions among individuals are time and space. For example, Valverde et al. 2016 studied the overlap in the pollinator assemblages of the animal-pollinated plant *Erysimum mediohispanicum* (Brassicaceae), showing that variation in the phenology of individuals of *E. mediohispanicum* partially explain the strong temporal variation in the patterns of pollinator overlap among individuals. Other ecological interactions occur in very localized spatial scales. For example, Encinas-Viso et al. (2016) show that a combination of spatial organization and stochasticity is sufficient to reproduce much of the organization of co-occurrence networks formed by plants and their associated mycorrhizal fungi. On the other hand, the motif analysis performed by Baiser et al. (2016) supports the notion that the organization of more localized food webs in space reflects, to a great extent, the organization of food webs at larger spatial scales.

In addition to temporal and spatial scales, intrinsic preferences of individuals for particular resources may affect network organization of ecological systems. Lemos-Costa et al. 2016 combined empirical data on five animal populations and optimal diet theory to show that the structure of networks describing patterns of resource use by individuals within populations is affected by variation in prey preferences among individuals. In a broader context, network organization can be viewed as a complex interplay between the effects of traits, stochasticity and sampling. The study of Fründ et al. 2016 combines food web models with simulated sampling procedures to provide pathways for tackling the challenge that is to quantify patterns of interaction in ecological networks that are unbiased by sampling effort. Finally, Dalla Riva and Stouffer (2016) use random dot-product graph models to explore the role of functional traits in shaping food webs. The approach used allowed them to detect the effects of evolutionary processes on the food webs backbones – the coarse description of food web organization.

The network organization of ecological systems may also shape ecological and evolutionary processes. For example, Amarasekare (2016) investigated how environmental variability, resource productivity and natural enemies may affect the evolution of dispersal in a given species in different ways, from promoting dispersal to maintaining polymorphism for dispersal properties within species. Among the processes that may be shaped by network organization is how ecological systems respond to perturbations. For example, Santamaría et al. 2016 explored the insidious consequences of the extinction of ecological interactions (Janzen 1974). Their results illustrate how the apparent robustness of mutualistic networks against the extinction of component species may conceal their fragility to the disassembly of species interactions. Accordingly, the attributes of the network in which interactions are embedded may affect the persistence of pairwise interactions to perturbations. This idea is supported by the work of Takimoto and Suzuki (2016) in which small network models are used to show that facultative partners may enhance the likelihood of persistence of pairwise obligate mutualisms. The use of network structure analysis for deriving functionality in mutualistic networks is further illustrated by Ruggera et al. (2016) who show for many plant species that the majority of effective seed dispersal is governed by a small core group of frugivores in the network, irrespective of plant growth form or fruit characteristics. Together these results illustrate the importance of central components in networks for the functional stability of ecosystems.

Network analyses are also well suited to explore impacts of multi-trophic interactions and niche dimensions on ecological and evolutionary processes. Woodland et al. (2016) show how niche-dependent foraging alters the structure of the distributions of consumer trophic position. The work suggests that among higher order consumers vertical trophic niche declines, and illustrates the importance of analysis of trophic position distributions. Network structures summarized as the bottom–up and top–down components of ecological communities can help to understand the emergence of trophic level properties. As shown in the empirical study of Souza et al. (2016) bottom–up effects of nutrient availability primarily act to stimulate primary productivity, whereas top–down effects generated by herbivores alter plant community diversity and composition. Moreover the temporal dynamics of the emergence of these effects appear to differ significantly, suggesting their role in shaping network structures is temporal dependent too. Similarly to aboveground herbivores belowground root mutualist mycorrhizal fungi alter the properties of the primary producer community, as shown by Yang et al. (2016). These authors show that the functioning of the interaction between plant and mycorrhizal communities are dependent on resource quantity and notably the stoichiometry of the available nutrients such that the mycorrhiza enable stoichiometric homoeostasis of the plant community.

The assembly processes shaping networks and the functional consequences of these networks are in some cases the two sides of the same coin. The very same processes that organize network structures may be affected by the network structures. For example, one of the long-lasting problems in the study of ecological networks is how ecological networks shape the flow of energy in ecosystems. There are thermodynamical limits that constrain some basic structural aspects of ecological networks, such as the number of trophic levels. On the other hand, Bellingeri and Bodini (2016) use tools based in spanning trees – trees formed by the links that keep food webs connected – to show that energy may primarily flow through short links in food webs, albeit not via the shortest link. We are just starting to understand the dynamics of these “adaptive networks” in which dynamics and structure change together (sensu Gross and Sayama 2009). One of the first empirical studies along those lines is provided by Gauzens et al. (2016) who experimentally test how gradients in top–down (herbivory) and bottom–up (nutrient availability) effects restructure patterns of interaction of food webs. Their work illustrates how multiple ecological interactions, such as predation, competition and indirect facilitation may change their relative importance as resource availability and the presence of top predators changes.

The study of ecological systems as web-like structures is now facing a rapid development and we applaud the exploration of novel questions and hypotheses and of novel theoretical and empirical approaches, and their application in different ecological systems from aquatic to terrestrial and spanning aboveground and belowground networks. We believe that the challenges ahead for the study of ecological networks include to understand how processes operating in different levels of organization affect patterns and processes of ecological networks, how spatial and temporal scales affect the network organization of ecological systems, how consistent are network patterns in disparate ecological interactions and how ecology, evolution and coevolution affect and are affected by the network organization of species interactions. There is a long way ahead, yet we are convinced that this thematic issue represent a set of papers that collectively contribute to these exciting new directions.

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