

The architecture of Multifunctional Ecological Networks

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The importance of species and their interactions has been the focus of analysis due to their role in maintaining biodiversity and ecosystem functioning. Ecosystem interactions are inherently multidimensional and quantifying such multifunctionality is a major challenge nowadays [1]. However, the identification and quantification of keystone species from a holistic multifunctional perspective remain unknown [2]. To our knowledge, only one study has estimated the weight of edges between layers by quantifying the role of the same individual in two ecological processes [3].

Here, we bridge this gap by developing a framework for data standardization and post-processing analysis via mathematical modeling, inspired by the resource (plant species)-consumer (animal/fungi species) paradigm. We apply such framework by focusing on six ecological functions and capitalize on an unprecedented sampling effort based on direct observations on the islet Na Redona in the Balearic Islands, in Mediterranean Sea, that encompasses 1537 weighted interactions between 695 plant, animal/fungal species. Incorporating the functional dimension, the complete relational dataset is formalized in terms of a rank-3 tensor that we call the Resource-Consumer-Function tensor (RCF).

We interpret the architecture of this tensor as a weighted, multipartite, multilayer network and visualise it as a multipartite edge-colored weighted network (Figure 1). The network displays two types of nodes: resources and consumers, with interactions (links) taking place between groups but no direct intragroup links. Each layer of the network represents a specific function and the strength of each interaction is represented by a link weight that measures the fraction of plants of the species that has been observed participating in the function. Consumers (animals, fungi) are often centered around a single plant species and thus form clusters.

A first question worth addressing is to quantify the relationship between the resources of the ecosystem and the functions the system embodies. This is achieved by integrating out the consumer index and thereby building a Resource-Function Matrix (RFM), which is the adjacency matrix of our Multifunctional Ecological Network. The nested pattern observed suggests the existence of both multifunctional species and multispecies function keystone, a new concept we coined here. Just as keystone species encode, among other properties, robustness and resilience of entire communities the response of the ecosystem to disturbances may also occur in the functional dimension.

To further understand the multifunctional species keystone and the role of plant species as ecosystem assemblers, we project the RFM into the function class and extract a Function-Function Interaction Network (FFIN). We quantify the ecosystem robustness against perturbations (extinctions) of plant species by sequentially pruning edges in FFIN. Additionally, we rank plant species, based on their

multifunctional keystone, by conditioning the FFIN to each single plant species and rank based on the specific role of resources as brokers of functions.

The dual concept of function keystone can be addressed by following a similar mathematical manipulation: initially starting again from RFM we project now on the plant class and thus construct a Resource-Resource interaction network. We address two complementary questions: (i) how robust is the ecosystem against perturbations of functions? And (ii) how to quantify the heterogeneous roles and impacts of each function in the ecosystem?

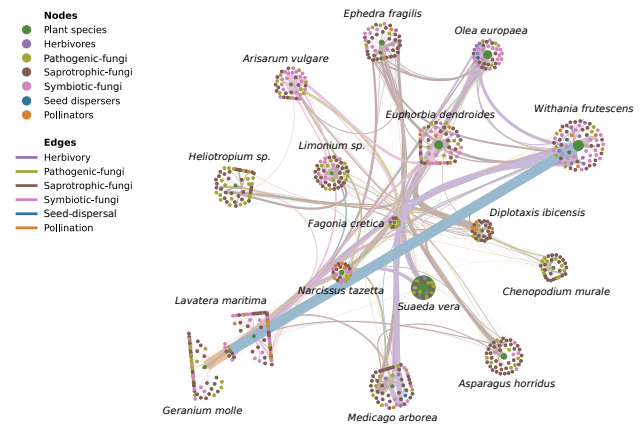


Fig. 1. Network visualization of the Resource-Consumer-Function tensor from the Na Redona dataset. The RCF is composed of two groups of nodes: (resource) plant species (labeled) and (consumers) animal/fungi species. Node and edges colors account for plant species (green) and animal/fungus species according to the functional interaction type. The sizes of plant-nodes represent their observed abundance. Edges represent function connections and their widths quantify the weight of interaction. Species are clustered via Infomaps community detection algorithm.

[1] Bianconi, G., Multilayer networks: structure and function, Oxford university press (2018).

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[3] Hervas-Parejo, S., Tur, C., Heleno, R., Nogales, M., Timteo, S., and Traveset, A., Species functional traits and abundance as drivers of multiplex ecological networks: first empirical quantification of inter-layer edge weights. Proceedings of the Royal Society B, 287(1939), 20202127 (2020).

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