

MARBEFES Project

Title: Assessing Food Web Structure and Function Using Ecological Interaction Network Approaches and Bioenergetic Modelling
Project General Coordinator: Jan Marcin Węśławski Project Scientific Manager: Julie Bremner Project Manager: Joanna Potrykus
Task Leader(s) Marie C. Nordström, University of Helsinki
Author(s) Marie C. Nordström, Tiina Salo, and Iara Diamela Rodriguez, University of Helsinki
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Table of contents

TABLE OF CONTENTS.....	2
1. INTRODUCTION.....	3
1.1. Aims and structure	3
1.2. What are Ecological Interaction Networks?	3
2. STEP-BY-STEP GUIDANCE	4
2.1. Determining Ecological Interaction Network structure and function.....	4
2.2. Defining the study system (spatial-temporal boundaries and network components).....	5
2.3. Assembling the metaweb and extracting local networks	5
2.4. Quantifying structure and function	8
2.5. Limitations and challenges with the approach.....	10
References.....	11

1. INTRODUCTION

1.1. Aims and structure

The primary aim of the document is to offer guidance for the analysis of key aspects of structure and function, focusing on ecological interaction networks as a main approach. These instructions describe the approach, and the associated data needs, to support planning of data collation, sampling and collection. The guidelines offer suggestions for assessments of trophic structure and function and give advice on how to conduct these across the seascape. These guidelines focus on interaction networks describing food webs but can be complemented with other examples of network approaches assessing connectivity and spatial relationships between structure and function in marine seascapes.

This document is structured in three parts: 1) a primer on network ecology, focusing on marine food webs in the assessment of linking biodiversity to ecosystem functions. The suggested approach is described in 2) a step-by-step manner in the main section of the document.

1.2. What are Ecological Interaction Networks?

Networks consist of nodes (or vertices) connected by links (or edges). Networks can describe a wide array of structures, from social interactions among people to computers connected by the internet, to transportation systems with passengers moving between airports, or the density of connections linking regions of the human brain (Bellingeri et al., 2019). **Ecological interaction networks** showcase interactions among nodes that represent taxa, species, or different life stages of species, depending on the focus of the work. The pairwise links can represent different types of interactions among the organisms, e.g., antagonistic, mutualistic, or competitive relationships (Ings et al., 2009; Delmas et al., 2019). In the case of food webs, the nodes represent species, taxa, or functional groups, and the links are directed, showing feeding interactions among the species and the direction of energy flow through the community. As such, the structure of the feeding network is inextricably linked to its functioning (Thébault and Loreau, 2003). During the past decades, the field of network ecology has expanded greatly, with food web ecology at the centre of advancement. Landmark research topics include (i) the non-random structures found in networks, (ii) the consequences of these non-random structures for the stability of the network, as well as (iii) the processes or mechanisms underlying the observed structures (Brose et al., 2017; Delmas et al., 2019; Brose et al., 2019).

Assessments of Ecological Interaction Networks provide insight into the relationship between structure and function in ecological communities. More specifically, network approaches allow us to quantify both interaction structure (topology) and functioning (energy fluxes) of food webs across the seascape (Antunes et al. 2024).

The structure of the network (or topology) can be quantified using information on the presence and absence of nodes and links in the food web. For example, by calculating different metrics describing species-level properties (e.g., generalism) or network-level properties (e.g., connectance) and

assessing how they change over space or time. Many metrics, or food web properties, have been linked to the stability of food webs. For example, modularity is thought to increase the robustness of the network to secondary extinctions by restricting the effects of the disturbances to certain parts, or modules, of the network (Stouffer and Bascompte, 2011). By assessing the topology of networks, one can study the effects of a changing biodiversity and responses to environmental shifts and anthropogenic pressures (e.g., eutrophication, climate change, fishing pressure, non-indigenous species) on food web structure.

Using bioenergetic modelling, based on metabolic theory and allometric scaling, it is possible to quantify the flows of energy, that is, the functioning of the food web (Barnes et al., 2018; Gauzens et al., 2019). This allows us to assess how functioning (energy fluxes) varies between habitats or across a seascape, or how anthropogenic factors influence energy flows within the food web, e.g., through changing biodiversity.

It should be noted that, apart from the definition of the spatial boundaries of the studied community, the network approaches described here are not tools for spatial assessment purposes only. In fact, there is great flexibility in the ecological context the approach can be applied to, and this includes the definition of the spatial aims and considerations. Consequently, network approaches, such as ones focusing on trophic interactions and the flow of energy through the community, are well-suited tools for assessments of seascape structure, function, stability, and dynamics for better understanding the connections between biological entities and the importance of spatial arrangement and composition of habitats in the seascape.

The operationalisation of the Ecological Interaction Network process is given in Section 2.

2. STEP-BY-STEP GUIDANCE

2.1. Determining Ecological Interaction Network structure and function

The process can be separated into three main steps:

STEP 1: Defining the study system

This first step includes defining the spatial-temporal boundaries for the food web, such as the study area and the assessment units within it, and identifying the relevant food web components, the data available for the assessment, and the time over which the data were acquired.

STEP 2: Assembling the metaweb and extracting local networks

When the focal community is defined, the following step is to assemble the metaweb, i.e., compile a list of all the documented feeding interactions among the food components. Based on e.g., habitat-specific species composition, local food webs can be extracted from the metaweb.

STEP 3: Assessing structure and function

For the available network(s) (the metaweb and all local webs), metrics that describe food web structure and functioning are calculated. The resulting metrics or estimates of food web functioning are mapped across spatial units in the study area.

2.2. Defining the study system (spatial-temporal boundaries and network components)

INPUT 1: The first step is to define the study community, *i.e.*, the temporal and spatial boundaries should be set for the study. Food webs can represent an entire study site, coastal zones (inner, middle, outer archipelago), MPAs or specific habitats (e.g., EUNIS habitats). Food webs can also be assembled for areas of different environmental status, different pressure levels, and of course, also for different time points.

INPUT 2: Species list covering all the nodes (*i.e.*, food web components) included in the BBT food web.

The second step is to decide which food web components to include. Ideally, the composition of the food web is representative for the focal ecosystem and for the study question. A marine trophic network can include the following: detritus, basal species/primary producers such as phytoplankton, microphytobenthos and macroalgae/seagrass, as well as zooplankton, meiofauna, benthic epi- and infaunal invertebrates, fishes, as well as seabirds and mammals. However, a subset of species may be selected if data are lacking. As it is rare to have estimates for all food web compartments simultaneously, the species list is often a composite over time.

There is frequently a discrepancy between the resolution of lower vs. higher trophic levels, where the former is usually not resolved to species level but aggregated into functional groups, such as ‘phytoplankton’. For simplicity, in these guidelines on interaction networks, we use ‘species’ to refer to all taxa and functional groups included in the networks.

2.3. Assembling the metaweb and extracting local networks

A metaweb is a summary of all species encountered in the communities as well as the documented feeding links among the species. Information on the feeding links usually comes from published, peer-reviewed studies, which document realized feeding interactions through gut content analysis, feeding experiments or direct observation, for example.

Published metawebs are available, e.g., for

- The Arctic: Barents Sea: Planque et al. (2014) <https://doi.org/10.1890/13-1062.1>; Kongsfjorden: Farage et al. (2021) <https://doi.org/10.1111/2041-210X.13569>
- the Baltic Sea: Nordström et al. (2015) <https://doi.org/10.1890/ES14-00515.1>; Kortsch et al. (2021) <https://doi.org/10.1111/1365-2656.13447>; Garrison et al. (2022) <https://doi.org/10.1002/ece3.8975>; Olivier et al. (2024) <https://github.com/PierreENolier/traitwebs>
- the Atlantic: North Sea: Frelat et al. (2022) <https://github.com/rfrelat/NorthSeaFoodWeb>
- the Mediterranean Sea: Albuoy et al. (2014) <https://doi.org/10.1111/gcb.12467>

Table 1. Food web components that may be included

Food web components	Trophic group	Taxonomic resolution	Spatial resolution	Data source (example)
Detritus	Detritus	One aggregated node	Assumed (omni)present in food web	Published empirical studies
Phytoplankton	Primary producer	Several options: minimum one aggregated 'phytoplankton' node, alt. split into to 'autotrophs' and 'mixotrophs' nodes, or at higher taxonomic resolution	Following smallest spatial unit or EUNIS habitat	Monitoring programs, published empirical studies, project's own sampling
Microphyto-benthos	Primary producer	One aggregated node	Assumed present in spatial units or EUNIS habitats of suitable environmental characteristics	Published empirical studies
Sympagic algae	Primary producer	One aggregated node	Assumed present in spatial units or EUNIS habitats of suitable environmental characteristics (ice) relevant in the BBT	Published empirical studies, project's own sampling
Macrophytes/ macroalgae	Primary producer	Several options: examples of nodes at species level (<i>Zostera marina</i> , <i>Fucus vesiculosus</i>) or genus or "group" level (Rhodophyta, <i>Ulva</i> spp.)	Following smallest spatial units or EUNIS habitat	Monitoring programs, published empirical studies, project's own sampling

Zooplankton	Primary consumers, secondary consumers	Coarsest level of aggregation: 'zooplankton' as one node. Alt. higher taxonomic resolution if possible.	Following smallest spatial units or EUNIS habitat	Monitoring programs, published empirical studies, project's own sampling
Zoobenthos	Primary consumer, secondary consumers	Resolved to species/genus/family level, high resolution where possible	Following smallest spatial units or EUNIS habitat	Monitoring programs, published empirical studies, project's own sampling
Meiofauna	Primary consumer, secondary consumers	Higher level of aggregation following functional groups of meiofauna. Alt. higher taxonomic resolution if possible.	Following smallest spatial units or EUNIS habitat	Published empirical studies, project's own sampling
Fishes	Primary consumer, secondary consumers, top-level consumers	Resolved to species or genus level	Following the largest spatial units	Monitoring programs, published empirical studies, project's own sampling
Birds	Top-level consumers	Resolved to species level	Following the largest spatial units	Monitoring programs, published empirical studies, project's own sampling
Mammals	Top-level consumers	Resolved to species level	Following the largest spatial units	Monitoring programs, published empirical studies, project's own sampling



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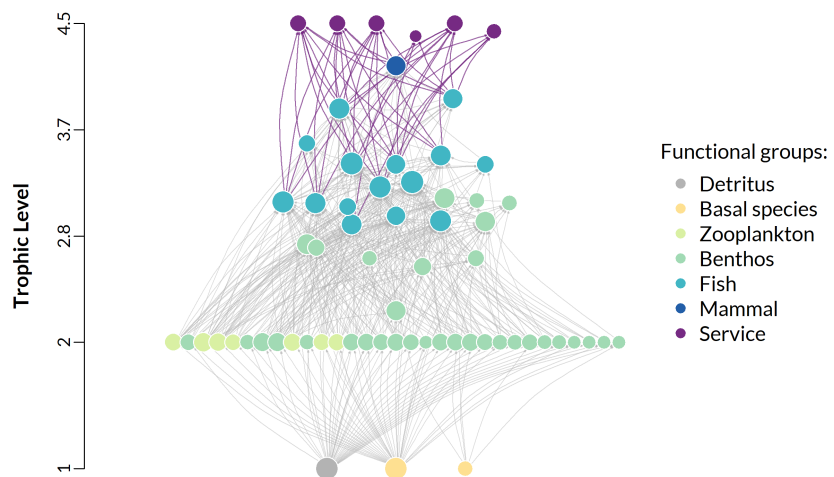


When the metaweb is assembled and ready, spatial information on species occurrences is used to create site/habitat or time-specific food webs.

Ideally, the trophic links are representative for the area and time of interest, but most commonly, the metaweb is a collation of links established over larger temporal and spatial scales. The metaweb thereby represents the *potential* trophic links in the community and does not necessarily show *realized* feeding interactions. If documentation for feeding links is not found in the data from the area, or in the published literature, interactions may be inferred based on expert opinion. It is often practice documenting the differences in certainty by quality coding the links from 1-4, where 1=documented in peer-reviewed literature for the relevant species, and 4=link is inferred and not validated by experts.

As an example from the Finland Archipelago Sea BBT, the metaweb consists of 66 nodes, including detritus, phytoplankton, macrophytes, zoobenthos, zooplankton, fishes, and a mammal, connected by 461 feeding links (Figure 1). For the overall seascape, there are >500 local networks, of which the smallest network contains 27 nodes and 80 feeding interactions. Each network has 3 basal nodes and 6-13 top-level species. In terms of other descriptive food web metrics, connectance ranges between 0.08 and 0.17, mean trophic level between 2.45 and 3.13, and max trophic level ranges between 4.22 to 4.73.

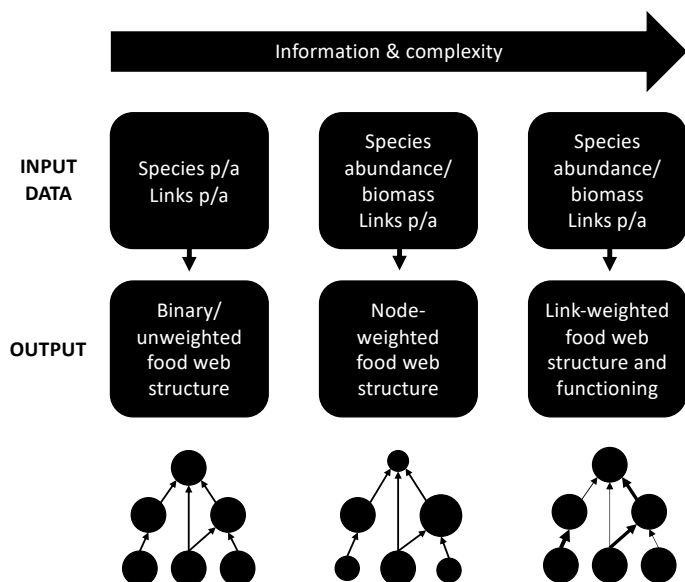
Figure 1. Metaweb for the Finland Archipelago Sea BBT. Nodes represent functional groups and ecosystem services (purple nodes), whereas links denote feeding or service provisioning by mobile vertebrates (purple links). Node size is relative to the number of incoming and outgoing links. The y-axis denotes trophic level.



2.4. Quantifying structure and function

The primary type of data to go into a network for assessing food web topology (i.e., structure) is a record of species occurrences and information on the links among these species (i.e., the metaweb). Combining species occurrence data with the information in the metaweb gives local or snapshot food webs, for which one can calculate metrics to describe food web structure. There are many different metrics available, describing for example node-level or network-level properties (see e.g., Olivier et al., 2019; Kortsch et al., 2021). The choice of metrics should naturally match the study question, and, often, a large suite of metrics is included to provide a broad description of network topologies.

Figure 2. Illustration over the gradient of information and complexity, as well as required input data for (from the left) unweighted, node-weighted and link-weighted metrics describing food web structure.



Networks constructed using information on species presence/absences and link presence/absences represent binary, or unweighted, network structures. In these networks, each species is equally important irrespective of its potential dominance in abundance or biomass (or rarity). Weighted networks and corresponding metrics, on the other hand, consider such differences in relative species abundances, reflecting e.g., node-specific abundances (Olivier et al.

2019). Another approach to weighting networks, is focusing on the relative importance of the different links, e.g., by accounting for the relative in- and out-degree distributions. However, each of these unweighted and weighted approaches describe the topology, or the structure, of the network (Figure 3). Although the structural properties of the network are important, e.g., for the stability of the ecosystem, they do not, as such, provide estimates of the functioning of the food web.

Food web functioning can be assessed e.g., by quantifying the flow of energy, the energy fluxes, in the food web. Energy fluxes function as a universal, common currency for Here, we suggest the bioenergetic approach by Gauzens et al. (2019), which is based on the metabolic theory of ecology and allometric scaling. In brief, the approach is a steady state model that begins with estimating the metabolic losses for the top predators in the network. As no other node feeds on the top predators, i.e., there are no other losses to account for, it is assumed that all these losses are compensated for by influx of energy from the species they feed on. In turn, the prey losses to predators and their metabolic losses are compensated for by feeding. Using this approach requires data on trophic interactions, body masses of the species, biomasses of the populations, and definitions of organism type (i.e., plant, animal, or detritus). The parameters needed for configuring the model can consist of estimates made directly in the field (BBT), or acquired from literature, or assessed from general scaling relationships (e.g., body size) and/or environmental (e.g., temperature) information (Gauzens et al., 2019). Once all fluxes are calculated, they can be summed to represent functions, such as herbivory, zooplanktivory or piscivory, allowing us to study relationships between biodiversity and ecosystem functioning across a complex, natural seascape (Barnes et al., 2018).

The **online tutorial** at <https://github.com/rfrelat/BalticFoodWeb> provides example data from the Baltic Sea and introduces the approach and analyses as used in Kortsch et al. (2021). The tutorial provides examples of unweighted, node-weighted, as well as link-weighted networks, quantified functions (energy fluxes) and metrics associated with each of these approaches.

2.5. Limitations and challenges with the approach

One of the key challenges with using ecological interaction networks to assess changes in the relationship between structure and function under environmental change is the static nature of the links. Most metaweb approaches rely on the assumption that species co-occurrences equate species interactions. However, species interactions are highly dynamic and determined by species abundances, trait distributions and changes in the environment. Consequently, documentation of changes in link presence/absences or interaction strengths would be crucial to estimate the consequences of anthropogenic changes in the environment. Despite being desperately needed, this type of food web knowledge is unfortunately often unavailable.

Another issue relates to the available data. Ideally, high-resolution data (temporal and spatial) of the species in the food web, as well as their links are available. However, there is often a lack of high-resolution data harmonized across the entire food web. For example, monitoring data often focuses on single taxa or a limited taxonomic group. Although food webs are, for example, included as a descriptor (D4) in the EU MSFD, the focus in that assessment is on the balance of abundances within and between trophic guilds and does not include linkages among species or trophic levels, *per se*.



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