

Temporal changes in unweighted and weighted food webs in the Gulf of Riga (1981-2014)



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Master's thesis

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Abstract

Network research offers a framework to investigate how ecological food web structure and function varies over time, which allows addressing and anticipating changes in ecosystems. This understanding is of vital importance for shaping conservation efforts and ecosystem management in light of anthropogenic change. Our current understanding of how resolved food webs vary through time comes primarily from binary (presence/absence) networks. These networks ignore the strength of the trophic interactions. In contrast, weighted networks account for interaction strength (energy fluxes), and hence can reveal more subtle fluctuations in community structure through changes in the biomasses of species, and their fluxes, rather than just through fluctuations in species number and identity.

Using a time series of food webs constructed with long-term biomass data and highly resolved information on species trophic relationships, combined with a bioenergetic modeling approach, allowed the comparison how unweighted (topology-based) and weighted (flux-based) food web approaches differ with regard to modularity through time. The stability of food webs is thought to be enhanced by greater modularity, with respect to the spread of disturbances in a network, as said perturbations may be contained within the modules. Looking at modularity also facilitates the assessment of species functional roles through time by quantifying their position in the network related to modularity.

The analyses revealed that the link-weighted approach resulted in a more refined partitioning of network community structure (modularity) and how it changed over time. The weighted networks also showed more subtle changes in species roles, for example changes in how some species connect modules, giving a better understanding of how the functioning of the network changed over time. For example, the weighted food webs clearly captured a collapse of benthos in the mid-90s through its impact on modularity, which was hardly reflected in the unweighted version.

The results outlined in this thesis further support previous findings that the inclusion of flux-based information and link-weighted food web network analyses is vital to gain a more complete understanding of how ecological networks change through time with regard to their structure and functioning.

Key words: Food webs, link-weighted, modularity, functional roles, ecological network analysis

Table of contents

1. Introduction	1
2. Material and methods	4
2.1 Study area, Gulf of Riga	4
2.2 Biomonitoring data & Time series	5
2.3 Fluxes/weights	6
2.4 Food web metrics	6
2.5 Modularity analysis	7
2.6 Relative topological roles	8
2.7 Null model of time series food web structure.....	9
3. Results	10
3.1 Food web metrics	10
3.2 Structure/modularity	11
3.3 Species roles	15
3.4 Null model	23
4. Discussion.....	23
4.1 Structure/Modularity over time	24
4.2 Species roles	27
4.3 Limitations of the study and considerations for future research	29
5. Conclusions	30
Acknowledgements	31
Summary in Swedish– Svensk sammanfattning Förändringar över tid i Rigabuktens kvalitativa och kvantitativa näringsvävar (1981–2014)	32
References	35
Appendix	40

1. Introduction

Globally, ecosystems are being reshaped, because of anthropogenic pressures including human-induced climate change. Abiotic drivers, such as increasing temperatures, can cause changes in biodiversity through species redistributions, which can result in losses and gains of species (Pimm et al. 2014, Young et al. 2016). These changes in biodiversity are closely linked to how ecosystems functions since ecological and trophic interactions affect the distribution as well as the abundance of species (Bauer et al. 2022). Therefore, an understanding of how changes in species composition and trophic interactions affect the structure and functioning of ecosystems is of vital importance for shaping conservation efforts and ecosystem management in light of anthropogenic change (Cardinale et al. 2012, Thompson et al. 2012).

Food webs describe who eats whom, or the flow of energy, in the ecosystem, where the species are the nodes and the trophic interactions the links (Yletyinen et al. 2016, Olivier et al. 2019). Because these networks can include information on species diversity, interaction structure and energy flow among species, they also provide an opportunity to describe species' ecological roles, in addition to the mechanisms through which species biodiversity influences and maintains ecosystem functioning (Thebault et al. 2003). Although the roles of species have been previously assessed in marine food webs (Cirtwill et al. 2018, Blanchet et al. 2019), it remains elusive how they change over time. This is partly due to the difficulty in monitoring the trophic interactions of species over time.

Studies of highly resolved temporal food webs are relatively rare and many available temporal food webs are limited to smaller networks (such as the Skipwith pond food web, Warren 1989) or to before-and-after comparisons (Kartinen & Roslin 2012, Yletyinen et al. 2016, Bodini et al. 2017). Nonetheless, recently, there has been a growing interest in assessing the temporal and spatial dimensions of food webs to better understand how changes in species composition and trophic interactions affect ecosystems across space and time (Kortsch et al. 2015, Poisot et al. 2015, Kortsch et al. 2018, Olivier et al. 2019, Kortsch et al. 2021, Frelat et al. 2022, Bauer et al. 2022). For example, Kortsch et al. (2015, 2018) investigated the spatial variability of empirical marine food webs, and a similar approach was used to study temporal variability of food webs (Olivier et al. 2019, Kortsch et al. 2021, Frelat et al. 2022). Investigating the spatial and temporal variability of food webs on a network level is important, but species-level information can be somewhat obscured on that scale, leaving a gap between the network

analysis and individual species ecology. Investigating how each species is embedded into the community, or its “role”, offers one way to address this gap (Cirtwill 2016).

Some species can have disproportionately large effects on food web structure, e.g., keystone species (Paine 1966), ecosystem engineers or network hubs (i.e., a node with many links within its own module and across modules) (Kortsch et al. 2018). Network research offers an ideal framework for describing the functional importance of species in the food web (Dunne 2006). Several metrics, for example trophic level or degree distributions, can be used to define different types of role concepts in a network (Cirtwill et al. 2018). Trophic level offers information about the position of a species’ role along the vertical axis from producer to top predator, whereas a species’ degree describes a species’ role in the network in terms of how many other species it interacts with, i.e., its total number of interactions. One way to define a species’ role or functional importance is to quantify its position related to modularity (Guimera & Nunes Amaral 2005). Food webs tend to divide into groups of densely connected nodes called modules (Clauset et al. 2004, Newman 2006). Species of the same module have more trophic links with each other than with species from other modules (Blanchet et al. 2019).

Food webs with greater modularity are thought to be more stable, as any perturbations may be contained within the modules, delaying, or stopping their propagation to other modules and the remaining network (Kortsch et al. 2015). However, in well-connected and less modular food webs it is believed that removal of one species can more easily impact the whole network. With respect to the spread of perturbations, network hubs can be of great importance, since they affect the connectivity and modularity of a food web (Kortsch et al. 2015). Network hubs are usually species that are mobile, use a wide variety of resources and have a broad environmental tolerance (Rezende et al. 2009, Guimera et al. 2010, Borthagaray et al. 2014, Kortsch et al. 2015) and are, therefore, important to the coherence of the whole network as well as in their own module. Hence, a species number of links within its own module, as well as across modules, can be used to identify its topological role within the food web network (Guimera & Nunes Amaral 2005, Olesen et al. 2007, Dupont et al. 2009, Valdovinos et al. 2009)

Ecological communities are not static and binary (i.e., based on presence/absence) as often portrayed in highly-resolution food webs network studies. On the contrary, food web configurations change through time due to fluctuations in the relative biomass and abundances of species. One way to consider the effect of changes in species biomass on food web structure is through weighted networks, for example, node-weighted (Olivier et al., 2019, Frelat et al.

2022) and link-weighted networks (Kortsch et al. 2021). Weighted networks use species abundances or biomasses to assess the importance of their contribution to a network property and can, therefore, be used to assess changes in food web structure caused by a species' relative dominance. By comparing link-weighted metrics and unweighted metrics, Kortsch et al. (2021) found that temporal changes in ecosystem functions could not be predicted using unweighted (binary) food web structure, highlighting the importance of including interactions weights (e.g., trophic fluxes) for assessing ecosystem functioning.

Using a link-weighted approach provides an opportunity to analyze more subtle changes in species' dynamical network roles, and food web importance, through time. A species could, for example, have the same critical network role throughout time, but depending on changes in its biomass, it can have a varying impact in an ecological sense. For example, an abundant top predator is more likely to exert a stronger top-down effect on the ecosystem simply because it interacts more strongly with the ecosystem in comparison to a low-abundance predator species in the same food web. A reduction in the abundance of such a predator could then decrease its top-down regulatory effect, making way for other species to flourish or new species to establish themselves, potentially leading to a cascade effect throughout the network, impacting either network functioning, structure, or both. Even so, abundance on its own does not determine the dynamical importance of a species' interactions. Some species, such as keystone species, may have low abundance compared to other species, but due to its specific set of interactions, and position in the network, it can still have a disproportionately large impact on the ecosystem as a whole (Paine 1995).

In this thesis, standard topological analysis and time series analysis were used on unweighted and link-weighted food web networks to explore changes in species roles over time (1981-2014). Specifically, the goal of this thesis is 1) to compare unweighted and link-weighted networks with regard to modularity over a 34-y period in the Gulf of Riga, 2) to identify species' relative topological roles with respect to unweighted and weighted modularity, and 3) to investigate whether species' relative roles have changed through time in both unweighted and weighted networks. It is expected that species' roles have changed through time in the Gulf of Riga due to changes in community composition and species abundance as a response to large-scale changes in environmental conditions and anthropogenic drivers. For example, decreases in salinity, increasing temperature and high fishing pressure led to a trophic cascade at the end of the 1980s, due to the disappearance of the top predator cod (Casini et al. 2012, Pecuchet et

al. 2020b). Considering that environmental conditions and the ecological communities in the Gulf of Riga have changed considerably, a temporal restructuring of the Gulf of Riga food web following changes in the species richness and abundance is, therefore, expected, as well as a greater change in food web structure and species' topological roles following the 1980s community shift. Specifically, it is expected that the loss of cod will increase the modularity of the network, assuming that cod played a similar role as a network hub as described in Kortsch et al. (2015), foraging across modules, linking them and thus reducing overall modularity. Expectations are also to see differences between the weighted and unweighted food webs with respect to node module affiliation, with the weighted networks revealing module structures that are not solely based on network topology but also the interaction strengths. The number of modules is expected to be greater in the weighted versions of the networks, because inclusion of interaction strength will result in a more refined partitioning of the network with smaller modules but with stronger links. For example, a hypothetical network has 22 nodes, the unweighted version of a network is divided into two modules based on network topology, one with ten nodes and one with twelve nodes. The weighted version of the same web would reveal that five of the species that made up the second unweighted module have very strong links among themselves and relatively weak interactions with the rest of the network. The weighted web would then be divided into three modules, one with ten nodes, one with the five strongly linked nodes and one with seven nodes. As species abundance fluctuates over time, so does the strength of their interactions and, thus, how the species are divided into modules. As a result, the module-based species roles are also expected to differ between the weighted and unweighted versions of the networks reflecting changes in abundance.

2. Material and methods

2.1 Study area, Gulf of Riga

The Gulf of Riga is a relatively shallow and isolated water area that receives freshwater from a large drainage area. The gulf has an area of about 16,330 km² (Kotta et al. 2008) and is a shallow water basin with a mean depth of 27 meters and a maximum depth of 60 meters. Due to being so shallow, the air temperature has a direct influence on both surface and deep-water dynamics in the gulf. The coastal areas of the gulf are heavily impacted by the inflow of rivers and the water of the gulf gradually turns more saline when moving towards open water and the Irbe strait (Kotta et al., 2008). In the offshore area of the gulf, average salinity is about 5.0–6.5psu

with the absence of a permanent halocline (Kotta et al. 2008). The surrounding rivers are also a big part of the nutrient input of the gulf. The gulf turns out to be about twice as eutrophicated as the Baltic Proper, with an outflow of nutrients through the straits that is higher than the inflow (Kotta et al. 2008). Herring (*Sprattus sprattus*) and stickleback (*Gasterosteus aculeatus*) are prevalent in the Gulf of Riga (Kotta et al. 2008) and the Baltic macoma (*Limecola balthica*) is one of the dominating benthic species in most of the soft bottom assemblages (Kotta et al. 2008).

2.2 Biomonitoring data & Time series

The Gulf of Riga food webs represent offshore marine communities in spring. The food web metaweb was collated by using biomonitoring data over a 38-year time-period (1979-2016) and is the same web used in Kortsch et al. 2021. Metawebs are compilations of species and their potential feeding interactions within a specific geographical area and time-period, but are not a representation of an observed realization of a food web in time and space. To build the metaweb, occurrence and biomass of taxa over a 38-year period from 1979 to 2016 was obtained for phytoplankton, zooplankton, benthos and fish, but only the most persistent and abundant taxa were included in the food webs. Persistent taxa were defined as taxa commonly reported over the 38-year study period. In addition to persistence over the time period, taxa with high biomasses were included in the food webs.

To study how food web species roles in the Gulf of Riga varied through time, yearly snapshot food webs were subsampled from the metaweb. For each selected year, a species list was compiled based on the long-term biomonitoring data. This list was used to subsample trophic interactions from the metaweb. Because sampling effort varied among taxonomic groups and between years, sampling was standardized by randomly selecting a fixed number of stations for each taxonomic group within 5-year moving windows. Using the 5-year moving window, a continuous time series with a constant number of samples for each time step was created. This resulted in new time series spanning from 1981 to 2014, where a year in the time series represents the middle of a 5-year window, for example 1981 represents the years 1979-1983 (Kortsch et al. 2021). To study how food web species roles in the Gulf of Riga varied through time, seven food webs (one for each year) were subsampled for the years: 1981, 1986, 1991, 1996, 2001, 2006, and 2011, using the median biomass estimates of the 1000 resampled food webs for each year by Kortsch et al. 2021. Food web snapshots with five years apart were selected to minimize the overlap of species samples because of the 5-year moving windows.

2.3 Fluxes/weights

The link-weighted webs used in this thesis are similar to ones constructed and used by Kortsch et al. (2021). Weights (or the energy fluxes) were assigned to the trophic links using a bioenergetic food web approach (Barnes et al. 2018, Gauzens et al. 2019). This method uses allometric scaling laws between body size and metabolic rates to quantify metabolic losses (Brown et al. 2004). Using the metabolic losses in conjunction with losses to predation and assimilation efficiencies (proportion of ingested food actually available for metabolism and growth) energetic fluxes in and out of each node were calculated (Kortsch et al. 2021). Metabolic losses per gram biomass were multiplied with taxon-specific biomass to calculate metabolic losses at the population-level (Kortsch et al. 2021). Under the assumption that the system is in equilibrium (steady state), it means that each species' losses to predation and metabolism are balanced by its energy gained from incoming fluxes multiplied by the assimilation efficiencies (Barnes et al. 2018, Kortsch et al. 2021). The model calculates energy fluxes in a top-to-bottom manner. In practice, this means that the fluxes at the top of the food web are calculated first, since losses to predation are equal to zero (Kortsch et al. 2021). The fluxes at lower trophic levels are calculated based on the losses to consumption by the higher trophic levels etc. (Kortsch et al. 2021). Consumer dietary preference influences the magnitude of the fluxes (Kortsch et al. 2021). Lacking data of realized dietary preferences for species, the link preferences were based on the assumption that consumers feed on the prey with the highest biomass (Gauzens et al. 2019, Kortsch et al. 2021). As pointed out in Kortsch et al. (2021) this assumption may under- or over-estimate certain energy fluxes among taxa. The assimilation efficiencies were defined depending on prey type to account for differences in resource quality (Kortsch et al. 2021). Body mass estimates for fish, benthos and phytoplankton are specific for Gulf of Riga communities and derived from local biomonitoring data, with the exception of zooplankton estimates which come from other parts within the Baltic Sea (Kortsch et al. 2021). All input parameters including species-specific body masses as well as a description of the equations to calculate the fluxes are described in Kortsch et al. (2021) and supplementary material (Appendix fig. 5S Table S1). To calculate the fluxes, the "fluxweb" packaged in R was used.

2.4 Food web metrics

Seven standard food web metrics will be used to describe the food web: 1) number of species, 2) number of links, 3) mean degree, 4) connectance, 5) modularity, 6) generality (i.e., mean in-

degree), 7) vulnerability (i.e., mean out-degree). For the weighted versions of the networks, weighted modularity and weighted quantitative generality and vulnerability will be calculated.

These metrics were included because they are ecologically important in characterizing the food web. The number of species can be linked to productivity in an ecosystem, increased community level stability and decreased population level stability (Worm & Duffy, 2003). The number of links and connectance (the number of links that are realized out of all the possible links) are linked to the complexity of the food web (Dunne et al. 2002). Modularity describes how closely groups of species interact with each other compared to other groups in the networks (Newman & Girvan 2004). Generality indicates if the system contains more generalist or specialist species. Generality is the number of incoming links, which is the total number of prey items of a species and indicates the degree to which species function as prey. Vulnerability is the number of outgoing links, which is the total number of predators of a species and indicates the degree to which species function as prey (Olivier et al. 2019). Quantitative weighted generality and vulnerability indicate the effective number of outgoing and incoming links a node has, which is the mean number of effective predators or prey a species has (Bersier et al. 2002), and captures that not all links have an equal importance in terms of energy flow in the food web. To calculate the metrics the R-packaged igraph was used.

2.5 Modularity analysis

Modularity was calculated for both the weighted and unweighted versions of the metaweb and the individual time series networks, describing how closely groups of species interact with each other compared to other groups in the networks. Infomap was used to calculate module affiliation of the nodes, and then the overall network modularity was calculated based on this node-module affiliation. Modularity describes how closely groups of species interact with each other compared to other groups in the networks. Modularity is defined as:

$$Q = \frac{1}{(2m)} \sum \left(\left(\frac{A_{ij} - \gamma k_i k_j}{(2m)} \right) \delta(c_i, c_j), i, j \right)$$

where m is the number of edges, A_{ij} is the element of the A adjacency matrix in row i and column j , k_i is the degree of i , k_j is the degree of j , c_i is the type (or component) of i , c_j that of j , the sum goes over all i and j pairs of vertices, and $\delta(x,y)$ is 1 if $x=y$ and 0 otherwise.

Infomap was chosen because it can be used on a myriad of different food web types, including both unweighted and weighted networks, making it ideal for comparing modularity in weighted and unweighted food webs. Infomap captures community structures based on the dynamics of

the network (Farage et al. 2021). Infomap utilizes a function known as the 'map equation' (Rosvall and Bergström, 2008) and optimizes the function using a modified Louvain (Blondel et al. 2008) search algorithm (Farage et al. 2021).

$$L(M) = q \sim H(Q) + \sum_{i=1}^m p_{\cup}^i H(P^i)$$

Infomap has been described thoroughly both mathematically and computationally (Rosvall & Bergstrom, 2008, Rosvall et al. 2010, Rosvall & Bergstrom, 2011, Rosvall et al. 2014). The recent paper by Farage et al. (2021) provides explanations of how Infomap works on ecological networks and provides several examples using empirical food web data. In this study, the R-package called *infomapecology* was used, utilizing version 1.3.0 of Infomap.

2.6 Relative topological roles

Species topological roles are based on their module membership. Species with few links outside of their module and that connect with few species within their module can be defined as network peripheral species. These species are often specialist with a small number of prey items. Species with many links within their own module can be defined as module hubs, and are important for that module's coherence. Species with links evenly distributed among modules can be defined as module connectors. These species play an important role in network coherence as they connect modules together. Species that have links with most of the species within their module as well as many links connecting to species in other modules can be defined as network connectors. These species are important both for their own module but also for the entire network coherence (Guimera & Nunes Amaral 2005, Blanchet et al. 2019).

The module linkage of a species can be addressed using two metrics, the z-score and the participation coefficient (PC). The z-score reflects how well a species is connected to species in its own module relative to the other species within its module. The z-score is relative to the size of the module and the average degree in the module and as well as node degree. The z-score, therefore, works as a relative scale indicating how connected a node is in its module. So, a z-score of 0 indicates a species is as connected as the average node within in its own module. A z-score of >1 means that a species is moderately more connected than the average node in

the module, and a z-score of >2 = very connected, < -1 =moderately unconnected, <-2 = barely any connections, within the species' own module.

$$z = \frac{k_{is} - \bar{k}_s}{SD_{k_s}}$$

k_{is} is the number of links from species i to other species in its own module s and \bar{k}_s and SD_{k_s} are the average and standard deviation of k_{is} over all species in s .

The participation coefficient (PC) score, or among module degree, indicates how well a species is connected to species belonging to other modules (Guimera & Nunes Amaral 2005, Kortsch et al. 2015, Blanchet et al. 2019). PC score values vary continuously between 0 and 1, with 0 meaning a species has no connections to other modules and the closer the score gets to 1 the more evenly the species links are distributed among modules of the food web.

$$PC = 1 - \sum_{t=1}^{N_M} \left(\frac{k_{it}}{k_i} \right)^2$$

k_i is the number of links to or from species i and k_{it} is the number of links from species i to species in module t .

2.7 Null model of time series food web structure

The purpose of the null model is to determine if the temporal food-web structure (e.g., modularity) of the snapshots is ecologically informative or whether it could have emerged by chance. To establish this, the empirical food-webs modularity was compared to those obtained from null model simulations. In the null model, temporal variation in food-web structure results from random distribution of species throughout time under few constraints. The alternative hypothesis is that temporal variation in food-web structure is ecologically driven (i.e., changes in structure reflects changes in the ecosystem), and not a result of random species presence/absence.

The simulated food webs were constrained to preserve four properties of the empirical food web snapshots: 1) the number of species in each temporal snapshot, 2) the frequency of occurrence of species (i.e., if a species is present in e.g., three temporal snapshots, it is also present in three temporal snapshots in the null-model simulations), 3) the connectivity of species (i.e., no species should be disconnected from the rest of the food web), and 4) that non-basal species must have at least one prey.

The simulated food webs were constructed by randomizing the species-by-time matrix using the curveball swap algorithm presented in Strona et al. (2014). The new, randomized list of species for each year was used to generate food webs by subsampling the trophic interactions of the randomized species lists from the metaweb. The simulated food webs that satisfied all of the previously mentioned constraints were retained. This way, 999 randomized food webs for each of the “yearly” snapshots were generated and then modularity was calculated for each of them to acquire the null distribution for the metric. For the weighted versions, the species-by-time biomass matrix was randomized 999 times. The species identities in these new species-by-time biomass matrices corresponded to the unweighted randomized species-by-time networks, so they were comparable, but biomasses were randomly assigned to these. Biomasses were randomly sampled from all the possible empirical biomass estimates of a given species throughout the empirical biomass time series. After creating 999 new species-by-time biomass matrices, flux-based networks were calculated for each of the 999 randomized webs, after which weighted modularity was estimated for the randomized webs. The empirical modularity values of the food webs were considered to differ strongly from the randomized food webs if these were outside the 0.05 to 0.95 quantile range of the null distribution.

3. Results

3.1 Food web metrics

Overall, most of the topology-based (i.e., unweighted) metrics remained relatively stable over time with only minor fluctuations (fig. 1). The number of species ranged from 25 to 31 and the number of links ranged from 118 to 172 (fig. 1a, b). Both the number of species and the number of links showed a positive trend through time. Both metrics showed a drop in 1996. The number of species was reduced by four and the number of links from 167 to 119. After 1996, both metrics showed an upward trend. At the network scale, from 17% to 19% of all the potential links were realized (connectance) (fig. 1c). The average number of connections per species (mean degree) ranged from 9.44 to 11.51 (fig. 1d) and the mean number of prey items per taxon was 5.36 to 6.42 (mean generality) (fig. 1d). The mean number of predators per species ranged from 4.91 to 5.96 (mean vulnerability) (fig. 1f).

Overall, the flux-based (weighted) metrics showed more variation over time, with the exception of weighted generality. Weighted generality (or the mean effective number of prey per species)

ranged from 1.08 to 1.37 (fig. 1h), indicating most species rely on one effective food source through time. Weighted vulnerability (the mean effective number of predators per species) ranged from 2.31 to 5.06, with a positive trend over time (fig. 1i), meaning that the mean strength of the predatory interactions became more even over time. Since weighted vulnerability is higher than weighted generality it points to that important prey taxa in terms of energy outflow are also those with the highest number of consumers.

3.2 Structure/modularity

The Infomap algorithm was used to assess the level of modularity (i.e., community structure) in the food webs to see if and how module partitioning differs between years and between weighted and unweighted food web networks. The food web time series show variability in module detection between unweighted and weighted food webs over the 34-year study period. The Infomap algorithm split the metaweb (fig. 2) and the temporal snapshots into several distinct modules. The results show that both the metaweb and the temporal snapshots of the weighted network were consistently divided into more modules than the unweighted snapshots. In most years, two modules were detected in the unweighted version of the webs and three modules in the link-weighted webs (fig. 1, 2, Appendix fig. 1S-14S). Modularity for the unweighted yearly snapshots ranged from 0.19 to 0.23 (fig. 1g), showing little fluctuations over time. In the unweighted metaweb and network snapshots, nodes were subdivided into a pelagic, plankton-dominated module that also contained some benthos and fish, and a benthopelagic module which was fish-dominated, containing pelagic as well as benthopelagic and demersal fish but also several benthic species (fig. 3, Appendix fig. 16S). Modularity in the weighted versions of the networks showed large fluctuations compared to the unweighted networks, ranging from 0.003 to 0.472 (fig. 1j). The lowest modularity (0.003) was detected in 1996. In the weighted networks the nodes were generally divided into a pelagic plankton-dominated module, a small benthic module as well as a benthopelagic fish-dominated module (fig. 3, Appendix fig. 16S). The benthopelagic module again consisted of pelagic, as well as benthopelagic and demersal fish but also benthic species. One of the weighted temporal food web snapshots (year 1996) was divided into only two modules (fig. 3, Appendix fig. 8S), with the exception of three species, all species that year belonged to one module (Appendix fig. 8S, 16S). The large module consisting of fish and plankton, and a small module consisting of one fish species, one benthic species and detritus (fig. 3, Appendix fig. 16S).

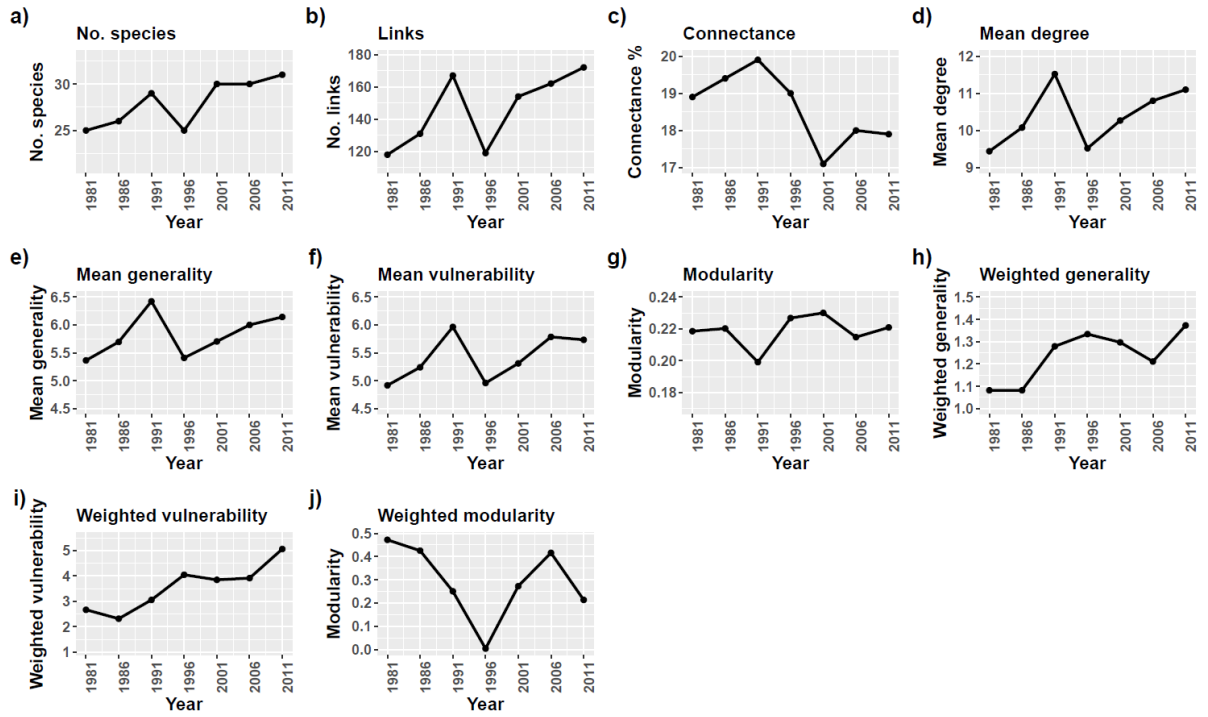


Figure 1. Time series of unweighted and weighted food web metrics, over a 34-year study period (1981–2014) in the Gulf of Riga. Note that the scale on the y-axes is not the same among functions.

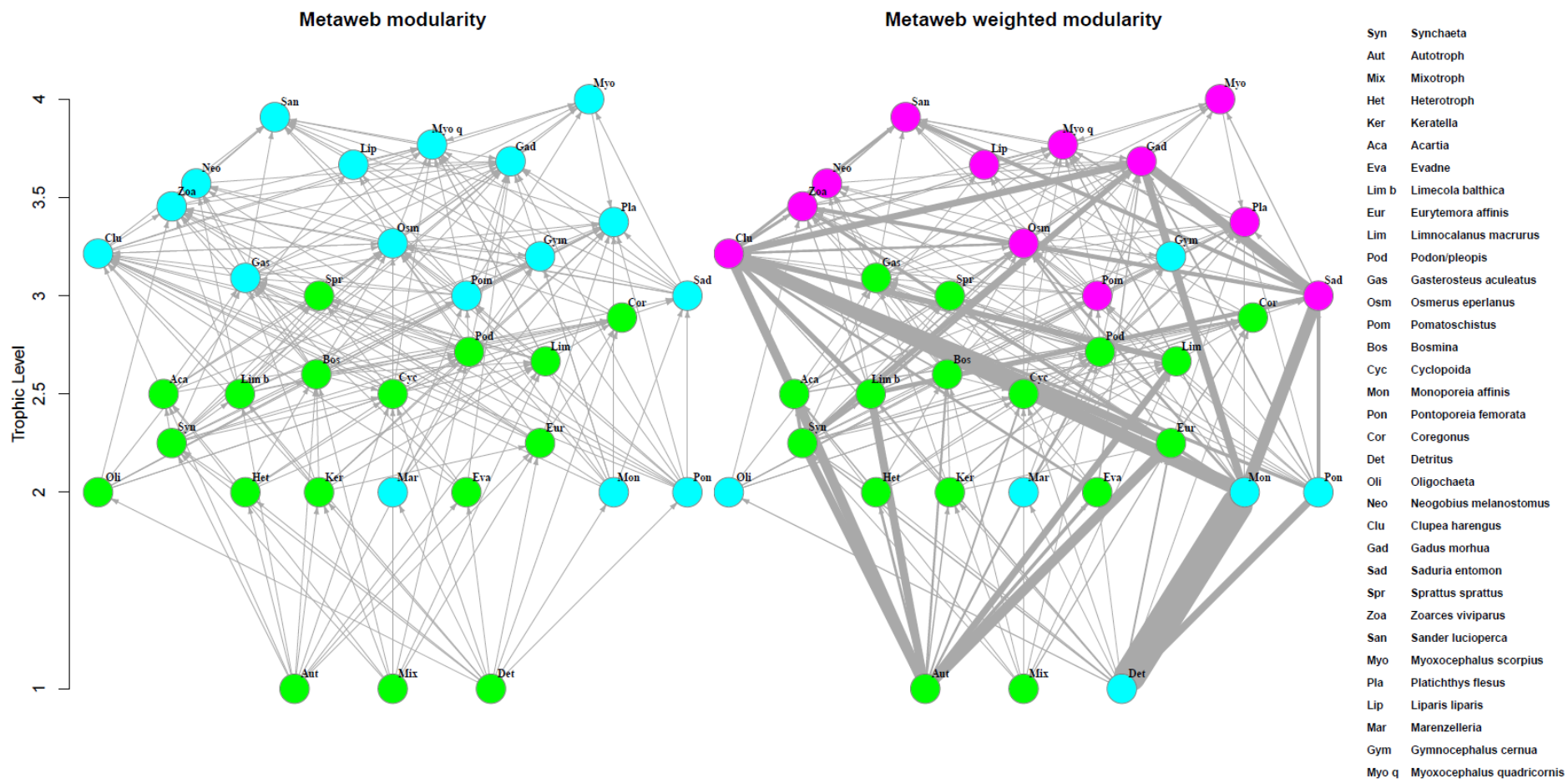
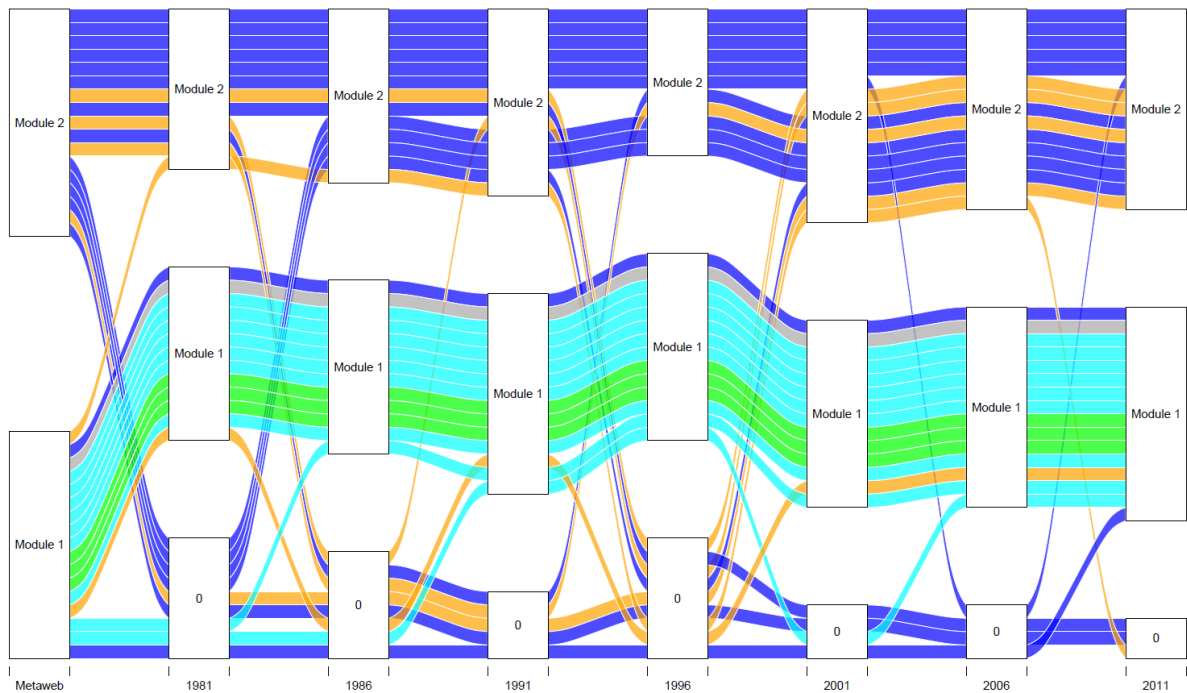


Figure 2. Unweighted (left) and weighted metaweb (right). Color of the nodes indicates module affiliation. Width of links in the weighted metaweb indicates the strength of the interactions between nodes.

In the unweighted networks, species' module membership is fairly consistent over time and changes in module affiliation come from nodes being either present or absent during some years (fig. 3). In the weighted networks, species' module affiliation varies more over time. However, most changes in module affiliation still come from nodes being either present or absent across the years. Yet, some species did change module affiliation due to variation in food web dynamics. For example, *Liparis liparis*, *Osmerus eperlanus* and *Clupea harengus* changed from module 1 to 3 from 2001 to 2006 (Appendix, fig 10S, 12S), and *Pontoporeia femorata* from module 2 to 3 from 1996 to 2006 and back again from module 3 to 2 during 2006 to 2011 (Appendix, fig. 8S, 10S). The largest change occurred in 1996 when the previously distinct plankton and fish-dominated modules merged into one big module. Between 1996 and 2006, the combined plankton-fish module split again and became similar to what was observed pre-1996 with regards to species module affiliation (fig. 3).

Unweighted module membership over time



Weighted module membership over time

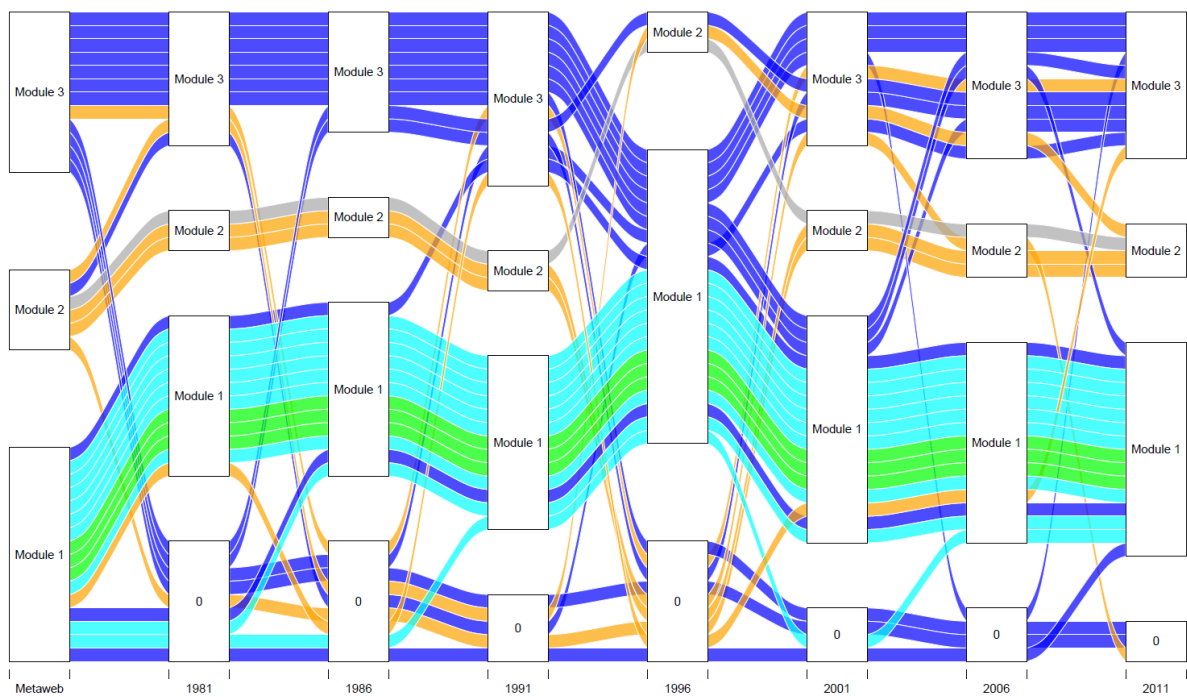


Figure 3. Alluvial diagrams showing module affiliation per species in the metawebs and how module affiliation changed among temporal snapshots. Colors indicate what functional group a species belongs to: blue for fish, yellow for benthos, cyan for zooplankton and green for phytoplankton. The 0 group contains the species that were not present in the web during that snapshot.

3.3 Species roles

The topological role analysis results showed that species' relative z/PC-scores, species relative importance in connecting the web within and outside their own module, varied over time and

differed between the unweighted and weighted temporal snapshots (fig. 4-6). Overall, the within-module degree was more variable over the years in the weighted snapshots (fig. 4-6), although the weighted among-module degree showed the single largest fluctuation for most species during 1996.

In the unweighted networks, plankton within-module degree (i.e., z-score) was relatively stable over time with only minor to moderate fluctuations (fig. 4a). In the weighted time series, species within-module degree fluctuated more and also differed more between species. For example, *Acartia* spp. and *Eurytemora affinis* had completely identical within-module degree between 1986 to 2011 in the unweighted version (fig. 4a), but in the weighted networks they had their own distinct z-score (fig. 4c). *Acartia* had a higher z-core slightly under 0 and *E. affinis* had a z-score closer to -1, but both did fluctuate and showed more variability over time than in the unweighted version. The among-module degree showed greater differences for plankton between the unweighted and weighted versions than the within-module degree. For plankton, the among-module degree varied little in the unweighted timeseries, with only the zooplankton *Synchaeta* spp. and *Keratella* spp. showing larger fluctuations in PC-score. A major difference from the unweighted was that in the weighted versions zooplankton among-module degree showed a lot more variation over time. The phytoplankton aggregate groups (heterotrophs, autotrophs and mixotrophs) all had a PC score of 0 (meaning they had no connections outside their own module) that did not change over time in the unweighted networks. In the weighted version, however, these aggregate groups differed a lot from each other. Heterotrophs among-module degree was consistently a fair amount higher than the other phytoplankton in the weighted version. Mixotrophs still had a PC of 0 (no connections outside its own module) and autotrophs mostly followed suit, but with a spike in among-module degree in 1991 and 2011.

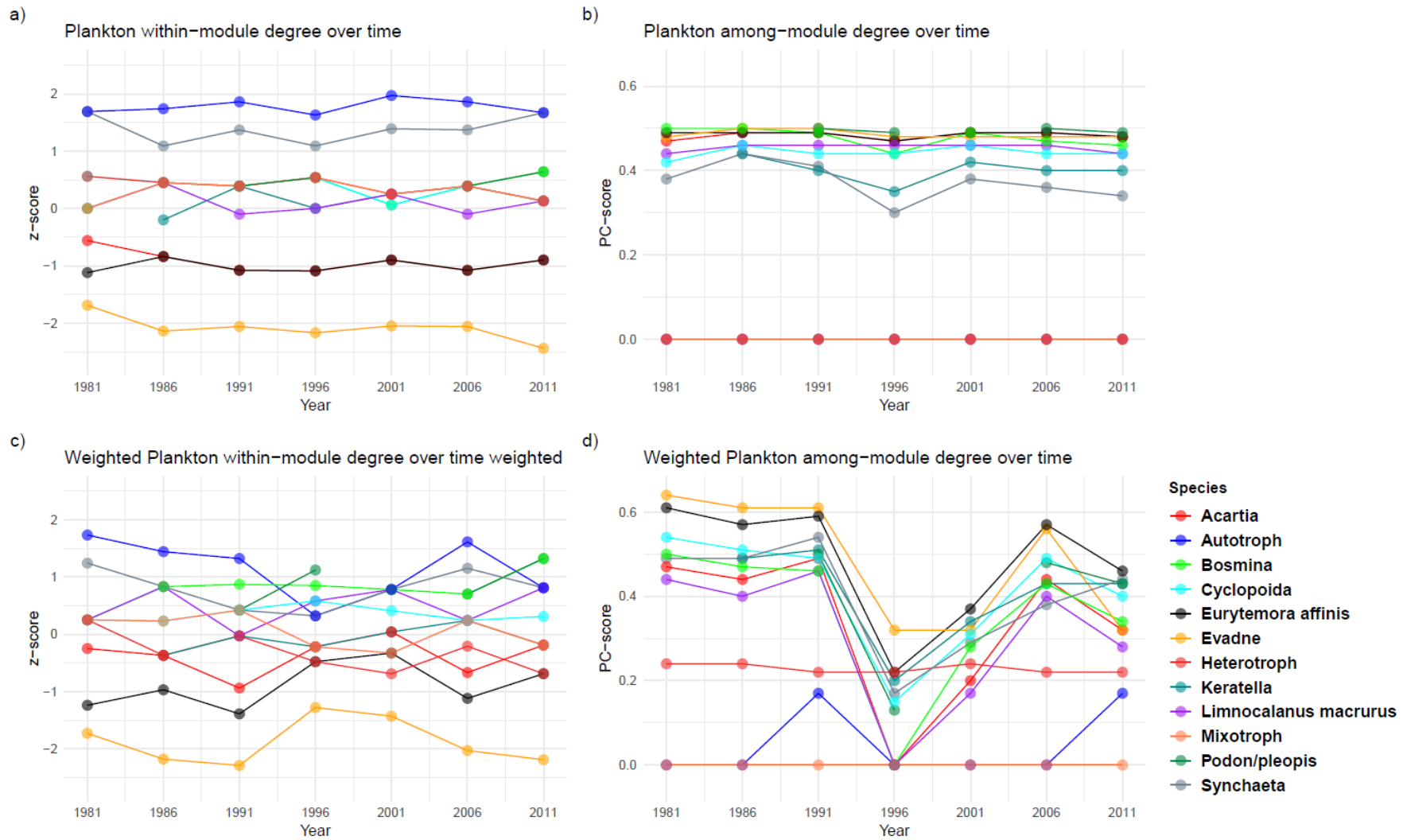


Figure 4. Phyto- and zooplankton within- and among-module degree over time.

For most benthic species, the within-module degree in the unweighted snapshots varied little over time with only minor fluctuations, with the exception of *Saduria entomon* and *Oligochaeta* (fig. 5a). *S. entomon* had an overall downward trend in its within-module degree over time, with the largest decline from 1981 to 1991. *Oligochaeta* within-module degree, on the other hand, steadily increased over time. In the weighted version, the benthos' within-module degree was more dynamic over time. For example, *Limecola balthica* and *Pontoporeia femorata* that had little to no variation in within-module degree in the unweighted version, changed considerably more in the weighted version over time. *P. femorata* was also the only benthic species present during 1996, indicating a collapse of the benthic community during this time. *Monoporeia affinis* had little variation in within-module degree in both unweighted and weighted networks, but went from being averagely connected (with a z-score close to 0) to being mostly unconnected within its own module (close to -2) in the weighted version. The among-module degree for the benthos followed a similar course as the within module degree, in that most of the species in the unweighted version showed only small variation in among module degree. *Oligochaeta* was an exception and did change over time with a consistently negative trend in PC-scores, becoming less and less important in connecting its own module to other modules. In the weighted version, the species among-module degree displayed more variability, with the exception for *Marenzelleria* spp. that did not show any change between the two versions. In the weighted version during 2001, all benthic species had a relatively high among-module degree (fig. 5d).

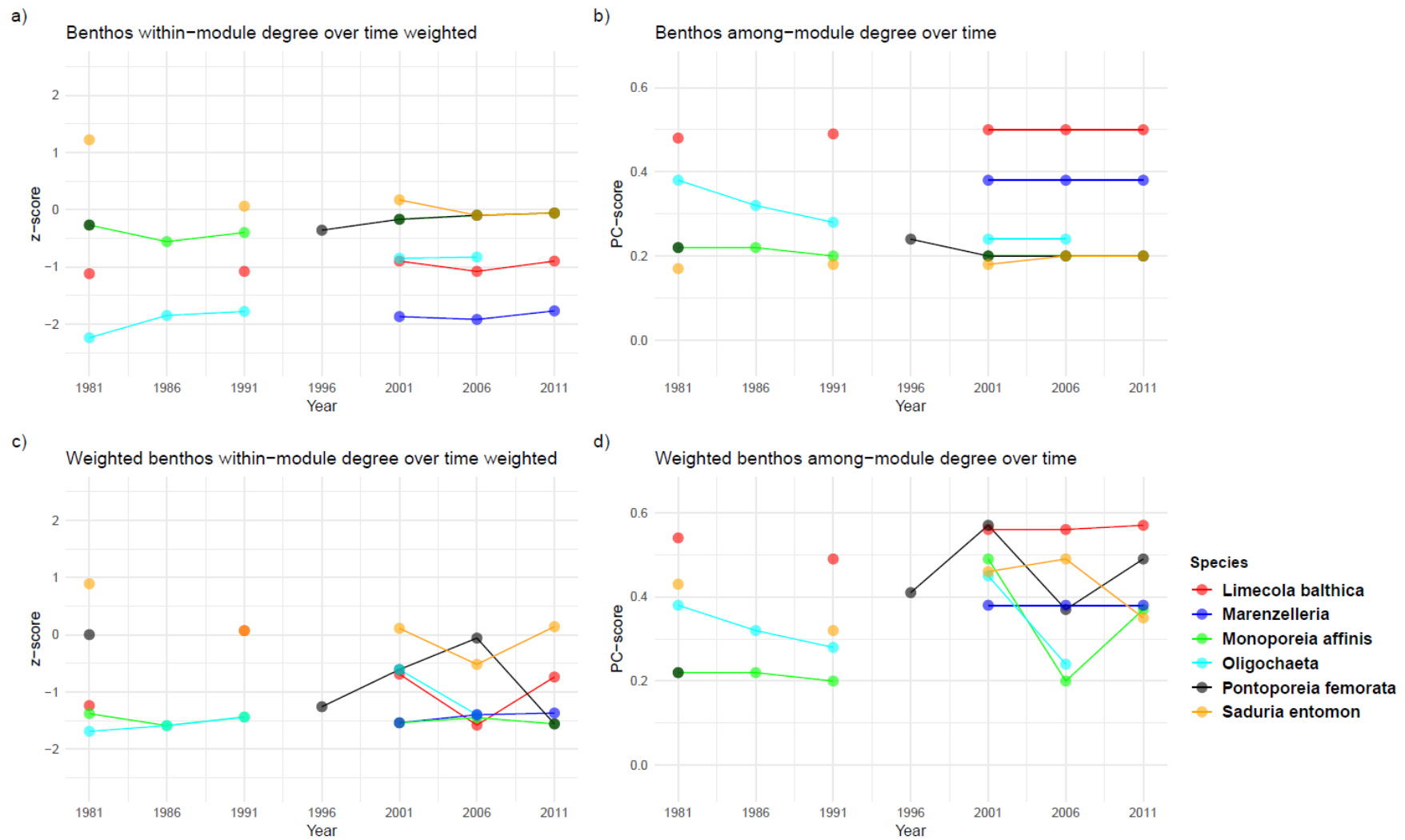
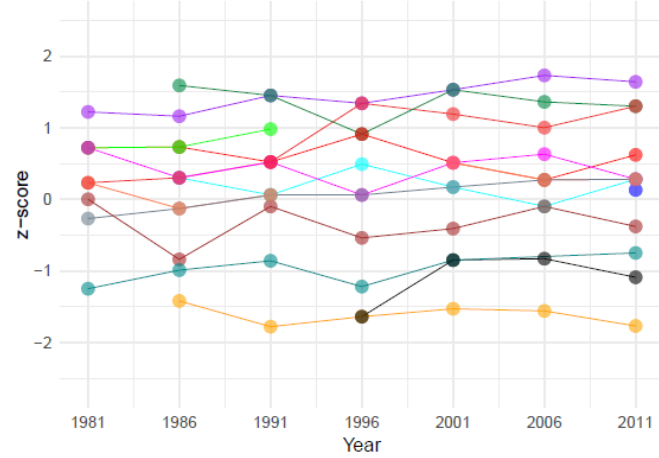


Figure 5. Benthos within- and among-module degree over time.

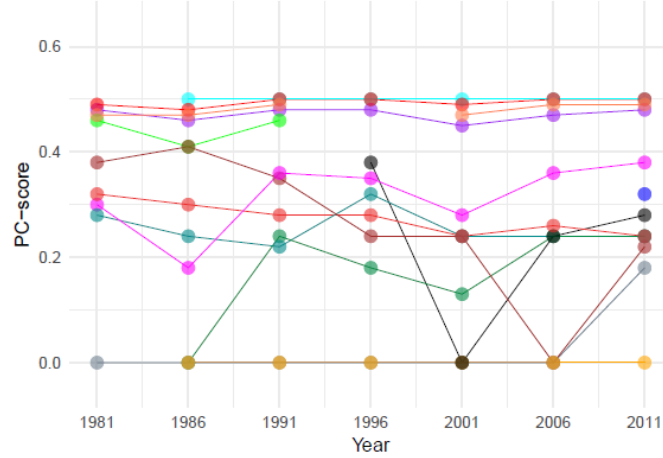
As with plankton and benthos, the unweighted within-module degree for fish showed less variation than the weighted within module degree. In the unweighted version, Cod's (*Gadus morhua*) within-module degree remained unchanged from 1981 to 1986, but showed a slight increase the last year cod was present (1991). The weighted within-module degree for cod showed a very similar z-score, although with slightly more fluctuations. Unlike in the unweighted version, cod's within-module degree in 1986 was lower than in 1981. The increase in z-score was also greater in 1991 compared to the unweighted version. In the unweighted version, sprat (*Sprattus sprattus*) had the largest fluctuations in within-module degree of all fish in 1986. In the weighed version, sprat showed larger changes in within-module degree. From 1981 to 1991, it went from having a z-score of ~0 (mean) to -2 and rose sharply again in 1996. Of note in the weighted version was also *Liparis liparis* in 2001 having the lowest relative z-score (-2.54) out of all species in the food web over time. In the unweighted version, the among-module degree remained relatively stable for most species over time, with the exception of *S. sprattus*, *Zoarces viviparus* and *Gymnocephalus cernua*. *S. sprattus* had an overall downwards trend in among-module degree, reaching a low in 2006 with no connections among modules (fig. 6b), but bouncing back to 2001-levels of among-module degree in 2011. *G. cernua* had a sharp drop in among-module degree from 1996 to 2001 but then changed to an upwards trend from 2001 to 2011. *Z. viviparus* had a slight overall upwards trend in among-module degree in the unweighted version with two larger fluctuations in 1986 and 2006. *Sander lucioperca* had no variation from 1981 to 2006 but showed a spike in among-module degree in 2011. The weighted version's among-module degree again showed more variation, as with plankton and benthos. Almost all fish species showed a large drop in among-module degree in 1996, similar to that seen with plankton. In general, the among-module degree for fish was higher in the weighted version than the unweighted version. Cod's among-module degree was similar in 1981 and 1991, but showed a small decrease in 1986. In contrast, cod's among-module degree in the weighted version was the same in 1981 and 1986, but decreased in 1991. Sprat showed larger fluctuations in among module degree in the weighted version from 1991 to 1996. *Z. viviparus* had a reality stable and slight upward trend in among-module degree, with the exception of 1996 when most fish showed a drop in PC values. *G. cernua* had a low among-module degree in 1996 and spiked after that unlike in the unweighted. In the weighted version, *L. liparis* and *S. lucioperca* differed from unweighted considerably. Both species had higher among-module degree and fluctuated more over time. *L. liparis* was one of few fish that had an increase in among-module degree in 1996 compared to previous years. The among-module

degree of *L. liparis* decreased abruptly from 2006 to 2011. *S. lucioperca*'s among-module degree trend rose constantly over time with only 2006 showing a drop

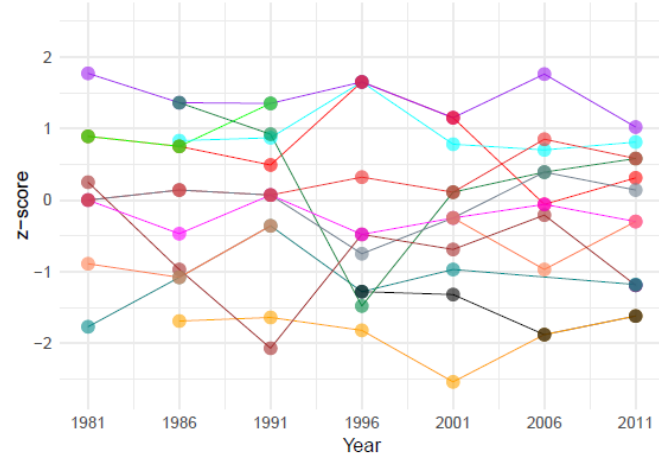
a) Fish within-module degree over time



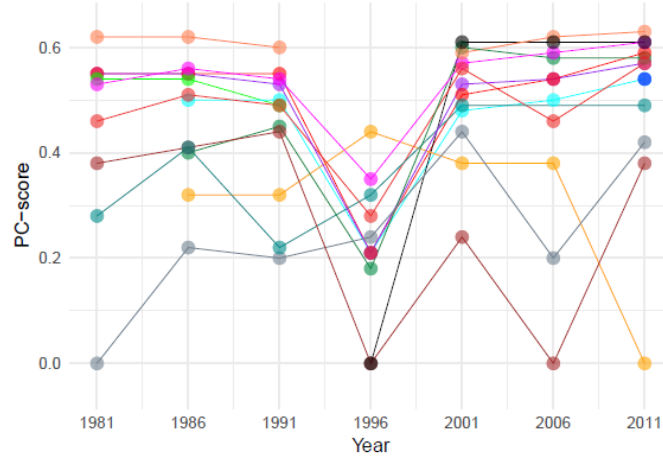
b) Fish among-module degree over time



c) Weighted Fish within-module degree over time



d) Weighted Fish among-module degree over time



- Species**
- *Clupea harengus*
 - *Coregonus*
 - *Gadus morhua*
 - *Gasterosteus aculeatus*
 - *Gymnocephalus cernua*
 - *Liparis liparis*
 - *Myoxocephalus quadricornis*
 - *Myoxocephalus scorpius*
 - *Osmerus eperlanus*
 - *Platichthys flesus*
 - *Pomatoschistus*
 - *Sander lucioperca*
 - *Sprattus sprattus*
 - *Zoarces viviparus*

Figure 6. Fish within- and among-module degree over time.

3.4 Null model

Results from the null model output showed that, of the unweighted yearly snapshots, none of the empirical webs deviated strongly from the randomized networks with regard to modularity (Table. 1). In contrast, the null model showed that four out of seven of the weighted empirical food web snapshots (1981, 1986, 1996 and 2006) (tab. 1) differed strongly from the null model expectation, indicating a stronger structuring component with flux-based links included in the food webs. A few of the unweighted snapshots were relatively close to significance thresholds of 0.05 and 0.95 (1991, 2001, 2011), suggesting that modularity these years differed somewhat compared to random expectations. A summary of the null-model results is also presented in the Appendix, figure S15.

Table 1. Null model p-values. The empirical food-web values for modularity were compared to the null-model distributions. Empirical values were considered to deviate strongly from the randomized food webs if the empirical value was outside the 0.05 to 0.95 quantile range of the null distribution. Significant p-values are marked in bold.

Year	Unweighted	Weighted
1981	0.464	1.000
1986	0.501	0.974
1991	0.178	0.574
1996	0.567	0.003
2001	0.903	0.666
2006	0.620	0.955
2011	0.908	0.302

4. Discussion

A large part of our current understanding of how food webs vary through time comes from binary (i.e., presence/absence-based) networks that ignore the magnitude or strength of the trophic interactions. Weighted networks, unlike their binary counterparts, take into account more subtle fluctuations in community structure through changes in species' biomasses or fluxes rather than through losses or gains of species (Olivier et al. 2019, Kortsch et al. 2021). The aim of this thesis was to study the differences between weighted and unweighted networks with regard to structure and functional species roles, and how both change over time. By applying a module detection algorithm to both unweighted and weighted approaches of a food web time series, it was possible to better assess food web structure as well as how species' relative topological roles vary through time. The analysis of the meta food webs and temporally

resolved food web snapshots revealed that species were consistently divided into more modules, and that functional species roles were temporally more dynamic, in the weighted network versions than in the unweighted ones, revealing a more fine-tuned partitioning of the network community structure and also the roles of the species. The weighted versions also clearly captured a collapse of benthos' in the mid-90s and its impact on the food web structure, as seen by the steep drop in weighted modularity and species' functional roles, which was not as clearly reflected in the unweighted version, other than minor fluctuations.

4.1 Structure/Modularity over time

Using the same data, Kortsch et al. (2021) has previously demonstrated that topology-based metrics are inadequate at capturing processes related to ecosystem functioning and that both a topology and a biomass- or flux-based approach is needed to achieve a more complete picture of temporal ecosystem dynamics. This seems to hold true for modularity and functional species roles as well, as documented in this thesis. Overall, the results were in line with the *a priori* expectations, in that more modules were detected in the weighted networks, and that species module affiliation differed between unweighted and weighted webs, and showed more subtle changes in the weighted networks.

In the time series, the 1996 food web snapshot stands out from the remaining years, especially with regard to modularity for the weighted version, which declines abruptly from 1991 to 1996. The 1996 food web was partitioned into only two modules in both versions. This differs from the overall trend in that the other weighted food webs were all partitioned into three modules. The unweighted version of 1996 had a nearly even split of the species between modules compared to the weighted that had all but three species in one module reflected as a modularity estimate of close to zero. This could be a result of the fact that the 1996 food web is the simplest in terms of species richness and number of links (25 taxa, 119 links), although it is comparable to for example 1981 (25 taxa, 118 links). This indicates that something else explains this deviation from the remaining food webs. The 1996 food web is unique because it contains only one benthic node (*P. femorata*), resulting in a weaker benthic coupling of the network, which probably acted like a bottleneck for the flow of energy through the web. The 1996 food web is also a good example of how the weighted version is more sensitive to changes in species composition. The unweighted 1996 food web did not reflect the reduction of benthic nodes with regard to modularity, unlike in the weighted web, where it led to a complete restructuring of the network's modules. A question with regard to 1996 is why only one benthic species was

present during this year. The question is whether this low benthic diversity is representative for the Gulf of Riga benthic community during that period of time, or it is a result of incomplete sampling. Sampling of benthos was conducted at only one sampling station for the studied area in Gulf of Riga (Kortsch et al. 2021, Appendix:1 Field sampling), and some sampling years were missing during the 1990s, which means that the benthos data could be associated with under-sampling biases and that benthic species composition and biomass is not entirely representative of the actual benthic community at that time.

The steep drop in weighted modularity in 1996 coincides with a drop in the number of species (reduced by four) and a substantial decrease in the number of links (from 167 to 119, which corresponds to a drop of 48 links), which also affects the modular structure of the network (connectivity between modules). Although both the number of species and the number of links increased from 1981 and had a peak during 1991, weighted modularity had already started to decline in 1986. This would indicate that structure and function of the food web was changing due to fluctuations in link-weighted interactions, which were not detectable in the unweighted metrics, and not just by the number of species and the number of links. The fluctuation in weighted modularity does, in fact, coincide with changes in biomasses and, thus, the energy flow throughout the web. Kortsch et al. (2021) identified several distinct periods of change in functional flows in the network. Their study found that the Gulf of Riga had a strong detritivorous flow at the beginning of the 1980s, but that changed during the late 1980s to early 1990s, when zooplanktivorous and phytoplanktivorous flows increased substantially. The 2000s saw an increase in biomasses of several species of zooplankton, planktivorous and benthivorous fish, as well as benthic species (Kortsch et al. 2021), with more even flows in the network. This is further supported by the null model. The null model p-values seem to reflect the functional changes in weighted modularity. The year 1996 has a very low p-value, which means that modularity is significantly lower this year compared to the other years. The modularity that year is low not only because of the number of species per module (3 and 22), but also flows out of the detritus-based modules appears larger than the within-module flow (Appendix, fig. 8S), making the network even less modular. For 1981, 1986 and 2006 the opposite is seen (Appendix fig. 1S, 4S, 10S). These years all have high detritivorous flows, which could mean that the detritus module is stronger and hence the whole network is more modular. Interesting to note is that the energy fluxes at lower trophic levels appear to have the largest impact on the modularity of weighted networks. This makes sense though, since all the energy fluxes in the food web networks originate at the basal nodes (e.g., phytoplankton and

detritus), thus the flows from these modules are also highest, contributing more to the overall modularity of the networks.

Another thing that may be worth noting, is that the food web modules in the weighted versions, in general, seem to be associated with habitats, such as the benthic and pelagic realms, but also the functional groups in them (fig. 3), and partially with trophic level. This finding is logical since habitats form natural boundaries and as such would also limit species' interactions across habitats in nature. That the benthic, detritus-based module persists throughout the entire time series, even during the 1996 benthos collapse, when it seems like the among-module flow is stronger than the within-module flow (Appendix fig. 8S) would support this. This observation is similar to findings in Rezende et al. (2009) and in Kortsch et al. (2015). However, in the unweighted version in the Gulf of Riga food webs, the modules seem to only reflect trophic levels. This is interesting because Kortsch et al. (2015) and Rezende et al. (2009) studied unweighted networks, but in this thesis, it was the weighted networks, and not the unweighted versions, which showed results more in line with their published findings. This could be because different methods were used to detect the compartmentalization of the different food webs, and/or that the size differences between the networks impacted module detection in the different webs. The networks in Kortsch et al. (2015) and in Rezende et al. (2009) were larger, 180 nodes with 1546 links and 249 nodes with 3313 links respectively, compared to the Gulf of Riga web with only 34 nodes and 207 links. There is a known resolution limit in community detection that is related to network size (Fortunato & Barthelemy 2007), making it harder to detect smaller modules. By including weights in the network, this resolution limit may have been mitigated, resulting in a "truer" partitioning of the network, which better reflects the division of species between habitats and functional aspects of the community with respect to energy flow.

The expectation that cod was a network hub like in the Barents Sea food web (Kortsch et al. 2015), and that its removal from the network would lead to an increase in modularity, was not met. Unweighted modularity was lowest in 1991 when cod was still present in the network, and when cod did disappear in 1996, unweighted modularity actually increased slightly. Weighted modularity, however, showed a major drop after cod disappeared, but the decline in weighted modularity had already started in the 1980s. Cod had a high biomass in the early 1980, which started to decline around the middle of the 1980s (Casini et al. 2012), which could indicate that cod's decline had just the opposite effect on modularity than expected. However, due to the rapid decline in cod biomass, the strength of cod's links in the network appears negligible

compared to other species, and as a result, the influence of cod on the weighted modularity may also be negligible. This is further supported by an even lower weighted modularity in 1996 when cod had disappeared, which indicates that other taxa influenced weighted modularity to a greater extent, or simply that cod, specifically, did not influence weighted modularity directly in any substantial way. For example, herring might have had a greater direct impact on modularity than cod. Herring generally had a higher biomass than cod throughout the time series, and thus the strength of herring's connection was also greater. Herring is a major zooplanktivore in the Gulf of Riga ecosystem (Casini et al. 2012), thus its connections between the plankton module and fish module would have decreased the overall modularity. As its biomass increased from the 1980s so would its impact on modularity as its link strength increased. Herring biomass had a peak around the mid-1990s, a slight decline in early 2000s and another peak in the late 2000s (Kortsch et al. 2021, Appendix fig S4). These fluctuations in herring biomass coincides with the fluctuations in the weighted modularity.

4.2 Species roles

As expected, the species role analyses showed that species relative importance in connecting the food webs, both within and outside their own modules, varied over time, and differed between the unweighted and weighted versions. As species biomasses fluctuated over time, so did the strength of their interactions, and thus, how the species roles changed with respect to modularity. As one more module was detected in the weighted versions of the networks (except for 1996), also stronger fluctuations species roles, in both within- and among-module degree, was detected in the weighted networks, indicating that weighted networks are better at capturing changes in the species functional roles.

Compared to other food webs (Blanchet et al. 2019, Kortsch et al. 2015), the Gulf of Riga food webs did not have any network hubs, i.e., species that have a strong within and between module connecting degree. For example, in the Barents Sea food web, cod was a network hub and hence played a network connecting role. Both the within- and among-module degree of cod were at the higher end of the scales in the Gulf of Riga, but several other fish species, and also zooplankton, had similar or even greater within and among module connections. This suggests that cod did not play an especially distinct functional role in the Gulf of Riga food web, for example, compared to the Barents Sea. This further suggests that species' functional roles in food webs may differ between food webs from different marine regions, indicating some level of context-dependency in food webs structure and species roles. Hence, it is important to

account for these regional differences in food web structure and species functional roles. These differences may be related to environmental (e.g., salinity levels) differences among regions and how these may affect individual species traits which in turn affects food web structure. For example, cod body size is significantly smaller in the Baltic Sea compared to the Atlantic or the Barents Sea, and size differences can affect how cod actually interacts in regional food webs, i.e., how broad its diet niche is. The integration of species' functional traits into food web analysis has long been proposed (Thompson et al. 2012) and has the potential to further bridge gaps in our understanding of how ecosystem and function and their interactions.

Fish have the highest among-module degree together with some planktonic species in the Gulf of Riga food webs, showing that they connect the modules in the Gulf of Riga. As modules are associated with habitats in the weighted food webs, this shows that fish species connect habitats in terms of energy flow, which makes sense as fish are mobile and can move between habitats. This is in line with other research finding that food webs in different habitats are coupled by more mobile higher-order consumers (Rooney et al. 2008). The fish species with the highest among-module degree was the European flounder (*P. flesus*). The flounder had an among-module degree of just above 0.6 for most of the time series (fig. 6d). What is interesting it that *Evadne*, a zooplankton genus, also has an among-module degree of around 0.6 during the beginning of the time series (fig. 4d), which would indicate it has an equal or similar overall importance in connecting modules in the network. For example, in 1981 *Evadne* is connected to autotrophs, detritus and is fed on by planktivorous fish like herring and sprat, but also more omnivorous fish like cod. The same year *P. flesus* connects mostly to benthic species but also to plankton and other fish. Since both species have an among-module degree closer to 1 than 0, it means they have their links more evenly distributed among the other modules of the food web. Both species also have a low within-module degree (fig. 4c, 6c), meaning they are not especially well connected within their own module. So, they do seem fill a similar role as connectors in the network, linking the different functional groups across modules. What should be kept in mind is that the total number of connections each species has in the network is not clearly reflected in the among-module degree. For example, *Evadne* has a degree of five in 1981 (Appendix tab. 1S), meaning it has five links that are distributed among the three modules that year. However, that year *P. flesus* has a total of 13 links that are distributed among the modules. Thus *P. flesus* has more connections among modules than *Evadne*. This could have implications for its importance as a connector (since it possibly contributes more the modularity of the network) or at least the stability of its role as a connector. *P. flesus* among-module degree was

similar before and after 1996, which constituted the largest shift in modularity and species within- and among-module degree. However, *Evadne* showed a lower among-module degree after 1996 than before. This is in all likelihood due to the low number of links *Evadne* has throughout the time series. If one just of *Evadne*'s connecting nodes disappears or changes module it probably impacts the among-module degree more than if the total number of links was greater, as is the case with *P. flesus*. A similar pattern was seen with other species. In general, fish had a higher number of links than species in the other functional groups (Appendix tab. 1S). The among-module degree of most fish was also more stable and recovered after the 1996, but several plankton species' among- module degree did not recover to the same extent. This was again something that was not noticeable in the unweighted version of the network because there were fewer modules detected and species module affiliation was less varied over time. As such this thesis presents several examples how the inclusion of link-weights can further enhance our understanding of food web structure and function.

4.3 Limitations of the study and considerations for future research

As with any research, there are limitations that need to be addressed in this study. One main shortcoming of this study has to do with how the yearly food webs were constructed. The drawbacks of the approach have already been noted in Kortsch et al. (2021) but are worth reiterating here. The information on the trophic interactions for each temporal snapshot is not *in situ* field-based information. The yearly snapshots are not representing realized interactions, they are instead subsampled from the metaweb. The strength of using a metaweb approach, however, is that it allows for the construction of temporally or spatially resolved food webs that would otherwise not have been possible. The drawback is that this may lead to false positive interactions, overestimation of interactions and metrics at any given sampling time, as well as reducing the variability in temporal food web structure (Olivier et al. 2019, Kortsch et al. 2021).

Another shortcoming of this study is the lack of data detailing the realized dietary preferences for species in the network. Since consumer dietary preference influences the strength of the links, simply assuming that consumers feed on the prey with the highest biomass may, as pointed out in Kortsch et al. (2021), under- or overestimates certain energy fluxes among taxa. This kind of data may of course not be obtainable for some, or even many, networks, especially for larger ones that include spatial and temporal information. For smaller networks or experimental mesocosm food webs, the information may be obtainable and could offer further valuable additions to ecological network analysis.

A further potential shortcoming is that the networks also made use of aggregated groups for some nodes, for example autotrophs, mixotrophs and heterotrophs. This use of aggregate nodes can lead to over- or underestimates of some network metrics and structure (Olivier & Planque 2017). For microscopic species, aggregate groups may be a sensible approach because of the difficulty in identification and accurate estimates of biomasses. But there were also nodes of macroscopic species in the networks that were only identified at the genus level instead of species level, for example, *Marenzelleria* spp. With advances in technology, genetic identification of species is becoming more and more affordable and available. The combination of phenotype-based and genetic identification of species could be, and is already being used to overcome this issue, allowing for a more accurate construction of food webs.

5. Conclusions

By comparing weighted and unweighted versions of the Gulf of Riga food web, it was found that dynamics in food web modularity differed between approaches over time. Since a link-weighted approach is more adept at capturing fluctuations related to species population dynamics and biomass structure, it was expected that the link-weighted approach made it possible to detect a more refined partitioning of network community structure, and was able to capture major fluctuations in modularity, which was not as clearly reflected in the unweighted version. For example, the weighted versions clearly captured the collapse of benthos in the mid-90s and its impact on structure/modularity, which was not as noticeably reflected in the unweighted version. And how species were partitioned into modules differed between the versions and reflected different ecological aspects. The weighted modules reflected species' habitats (pelagic and benthic) and the unweighted modules reflected the trophic level of the species. Also, the weighted approach made it possible to detect more subtle changes in species roles, for example how some species connect the different modules, giving a better overview of how the functioning of the network changed over time. Comparing the weighted and unweighted approaches, it is evident that some changes could only be observed by using the link-weighted approach. Thus, the results support previous findings that suggests that a flux-based approach is needed in order to capture the subtle fluctuations in species population dynamics and obtain more realistic assessments of structural and functional food web changes.

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Summary in Swedish– Svensk sammanfattning

Förändringar över tid i Rigabuktens kvalitativa och kvantitativa näringsvävar (1981–2014)

Födovävar beskriver energiflödet genom ekosystemet, där arter representeras av noder och de trofiska interaktionerna beskrivs av länkarna i nätverket (Yletyinen et al. 2016, Olivier et al. 2019). Forskning baserad på näringsvävar erbjuder ett bra ramverk för att utforska och beskriva arternas funktionella betydelse i näringsvävar (Dunne 2006). Eftersom näringsvävar innehåller information om arters mångfald, deras samspel och energiflödet mellan arter, ger de en möjlighet att undersöka arternas ekologiska roller, men även de mekanismer genom vilka arternas biologiska mångfald påverkar och upprätthåller ekosystemens funktion (Thebault et al. 2003).

Studier av detaljerade näringsvävar över tid är relativt sällsynta och många tillgängliga tidsserier är begränsade till mindre nätverk (såsom födoväven för Skipwith pond, Warren 1989) eller till före och efter jämförelser (Kaartinen & Roslin 2012, Yletyinen et al. 2016, Bodini et al. 2017). Ändå har det nyligen funnits ett växande intresse för att undersöka de tidsmässiga och rumsliga dimensionerna av näringsvävar för att bättre förstå hur förändringar i artsammansättning och trofiska interaktioner påverkar ekosystem över tid och rum (Kortsch et al. 2015, Poisot et al. 2015, Kortsch et al. 2018, Olivier et al. 2019, Kortsch et al. 2021, Frelat et al. 2022, Bauer et al. 2022).

En stor del av vår nuvarande förståelse av hur näringsvävar förändras med tiden kommer från binära (d.v.s. kvalitativa) nätverk som ignorerar styrkan av de trofiska interaktionerna. Kvantitativa nätverk (eng. "weighted networks"), tar till skillnad från sina binära motsvarigheter, tar hänsyn till mer subtila fluktuationer i nätverksstrukturen genom förändringar i arternas biomassa snarare än bara genom förluster eller ökningar i artantalet (Olivier et al. 2019, Kortsch et al. 2021.) Genom att använda nätverk som innehåller information om länkarnas kvantitativa betydelse, tillsammans med artroller, ges möjligheten att analysera mer raffinerade förändringar i födovävar. Ett sätt att definiera en arts roll eller funktionella betydelse i ett nätverk är att kvantifiera dess position i förhållande till modularitet (Guimera & Nunes Amaral 2005). Födovävar kan bestå av grupper av tätt sammankopplade arter som kallas moduler (Clauset et al. 2004, Newman 2006). Arter i samma modul är mera sammankopplade med varandra än med arter från andra moduler (Blanchet et al. 2019). Beroende på hur en art är kopplad inom sin egen modul och hur den är kopplad till andra

moduler så varierar dess funktionella roll i födoväven (Guimera & Nunes Amaral 2005). Denna kombination av kvantitativa nätverk och art roller skulle kunna göra det lättare att uppskatta artens dynamiska roll och betydelse i ekosystemet. En art kan till exempel ha en kritisk nätverksroll över tid, men beroende på förändringar i dess biomassa kan rollen variera och arten kan ha en varierande inverkan ur en ekologisk synvinkel.

De huvudsakliga målen med denna avhandling är att:

1. jämföra kvalitativa nätverk och kvantitativa nätverk för att se hur de skiljer sig gällande modularitet under en 34 år lång tidsperiod i Rigabukten
2. identifiera arters relativa funktionella roller baserade på modularitet
3. undersöka huruvida arternas roller har förändrats över tiden i både kvalitativa och kvantitativa näringsvävarna.

För att studera förändringar i Rigabuktens näringsväv konstruerades en tidsserie av näringsvävar baserad på långtidsdata från monitoring. Resultatet blev en tidsserie som bestod av sju födovävar (1981, 1986, 1991, 1996, 2001, 2006 och 2011) där åren representerar mitten av ett 5år långt intervall, till exempel representerar 1981 åren 1979–1983 (Kortsch et al. 2021). Sju standardmått användes för att beskriva näringsvävarna: 1) antal arter, 2) antal länkar, 3) medelgrad (eng. "mean degree"), 4) sammanlänkning (eng. "connectance"), 5) modularitet, 6) generalitet (eng. "generality"), 7) sårbarhet. För de kvalitativa versionerna av nätverken räknades även modularitet, samt generalitet och sårbarhet.

För att kvantifiera energiflödena hos interaktionerna i de kvantitativa versionerna av näringsvävarna användes en bioenergetisk metod (Barnes et al. 2018; Gauzens et al. 2019). Denna metod baseras på allometri (eng. "allometric scaling laws") för att räkna ut ämnesomsättningen för arterna (Brown et al. 2004). Genom att beakta ämnesomsättningen samt predation och assimileringseffektivitet (andel av intagen föda som faktiskt är tillgänglig för metabolism och tillväxt) beräknades energiflöden in och ut för varje art på populationsnivå (Kortsch et al. 2021).

För att undersöka hur indelningen av arter i moduler varierade mellan de kvantitativa och kvalitativa näringsvävarna användes Infomap-algoritmen för att räkna ut modulmedlemskapen hos arterna. Infomap använder en funktion som kallas "kartekvationen" (eng. "Map equation") (Rosvall och Bergström, 2008) och optimerar funktionen med en modifierad Louvain-sökalgoritm (Blondel et al. 2008, Farage et al. 2021) för att räkna ut modulmedlemskapen hos

arter i en näringsväv. En s.k. nollmodell (eng. "null model") användes även för att avgöra om näringsvävsstrukturen (modulariteten) för tidsserien är ekologiskt informativ eller om den kunde ha uppstått av en slump. För att fastställa detta jämfördes de empiriska näringsvävarnas modularitet med de som erhöles från simuleringarna.

På det stora hela var de flesta kvalitativa mätvärden stabila över tid och uppvisade endast relativt små fluktuationer (fig.1). Mätvärdena för den kvantitativa näringsväven visade dock mer variation över tid (fig.1), med undantag för generalitet som enbart uppvisade små förändringar(fig.1). Det upptäcktes i allmänhet fler moduler i de kvantitativa födovävarna (fig. 2, 3, Appendix 1S-14S) och arternas roller varierade mera över tid i dessa versioner (fig. 2, Appendix 1S-14S). Med hjälp av information om energiflödet mellan arterna kunde alltså en mer förfinad uppdelning av nätverkens struktur identifieras och hur den förändrades med tiden. De kvantitativa versionerna gjorde det även möjligt att upptäcka mer subtila förändringar i artens roller, vilket gav en bättre insikt i hur nätverkets funktion förändrades över tiden. De visade också tydligt kollapsen av bentos i mitten av 90-talet och dess inverkan på modularitet (fig. 1f), vilket inte återspeglades nämnvärt i födovävarna baserade på binär information (fig. 1f).

Genom användning av samma data, har Kortsch et al. (2021) tidigare visat att mått baserade på binär information är otillräckliga för att få en komplett bild av hur ekologiska nätverk förändras över tid. Detta verkar även gälla för modularitet och modul baserade artroller, vilket framgår i denna avhandling. De huvudsakliga resultaten i denna avhandling stöder alltså ytterligare tidigare forskningsresultat och uppmaningar om att inkludera funktionell information. Denna information är avgörande för att vi ska få en mer fullständig förståelse av ekologiska nätverk med avseende på deras struktur och funktion.

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Appendix

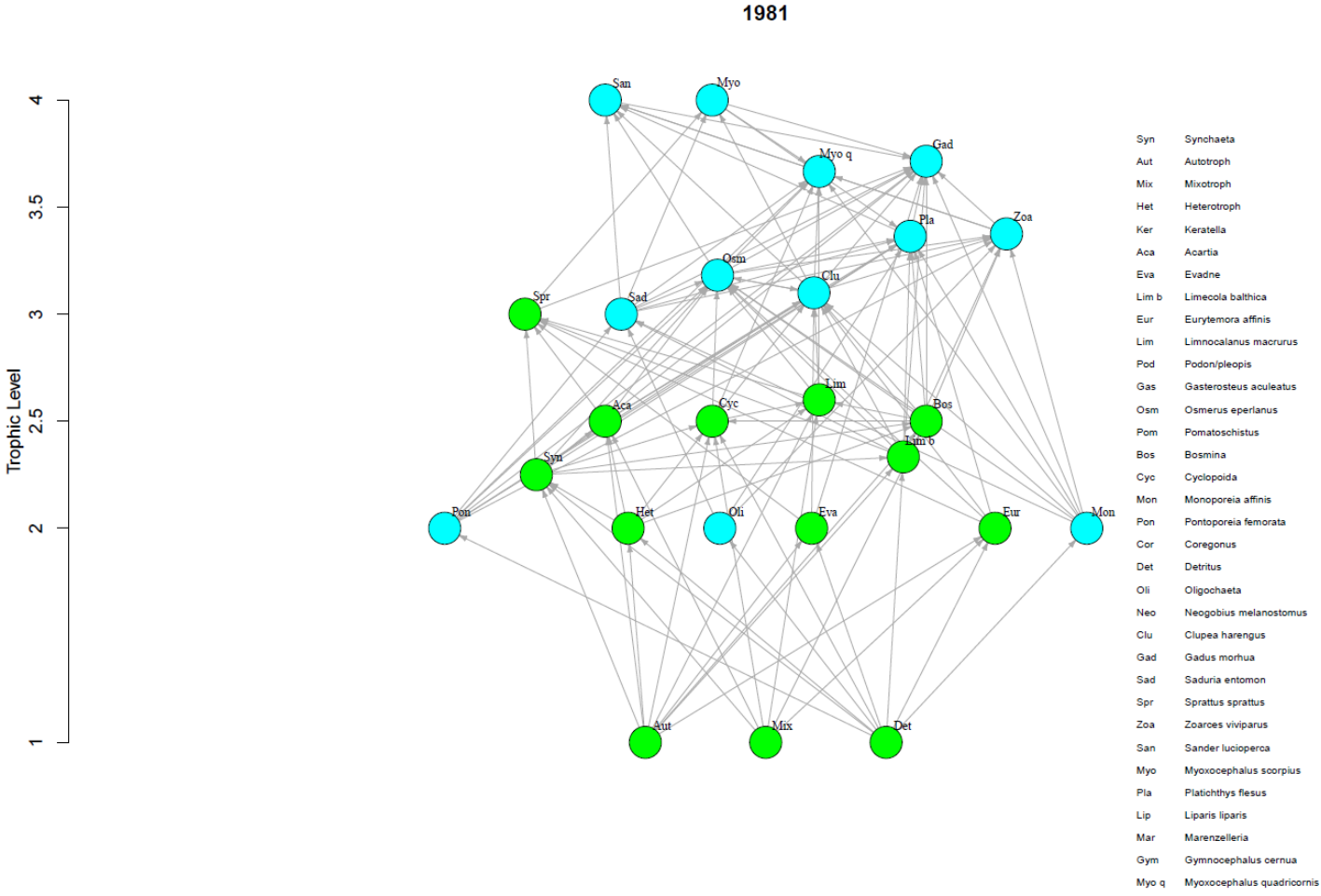


Figure 1S. Node module membership, color of the nodes indicates module affiliation.

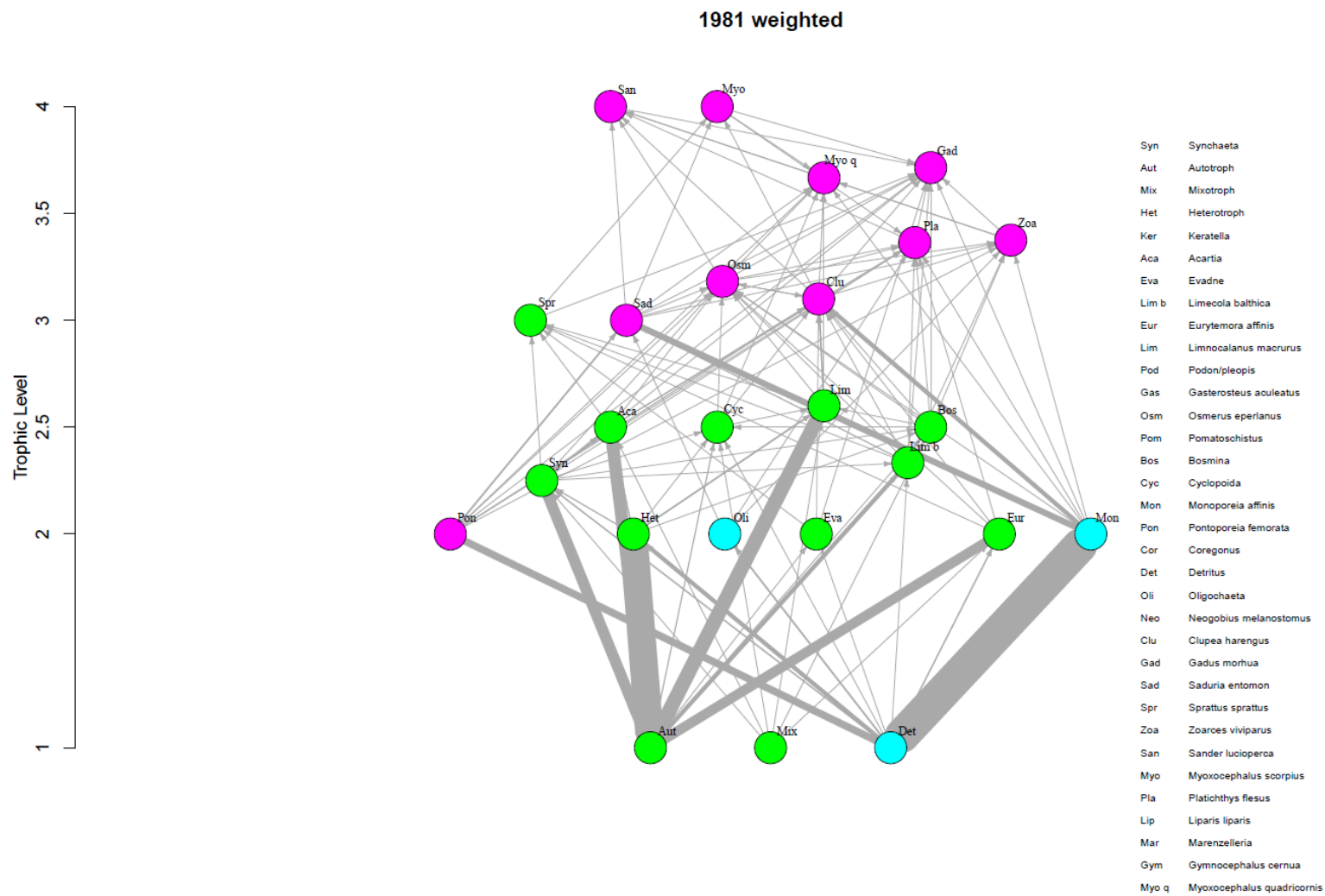


Figure 2S. Node module membership, color of the nodes indicates module affiliation. Width of links in indicates the strength of the interactions between nodes.

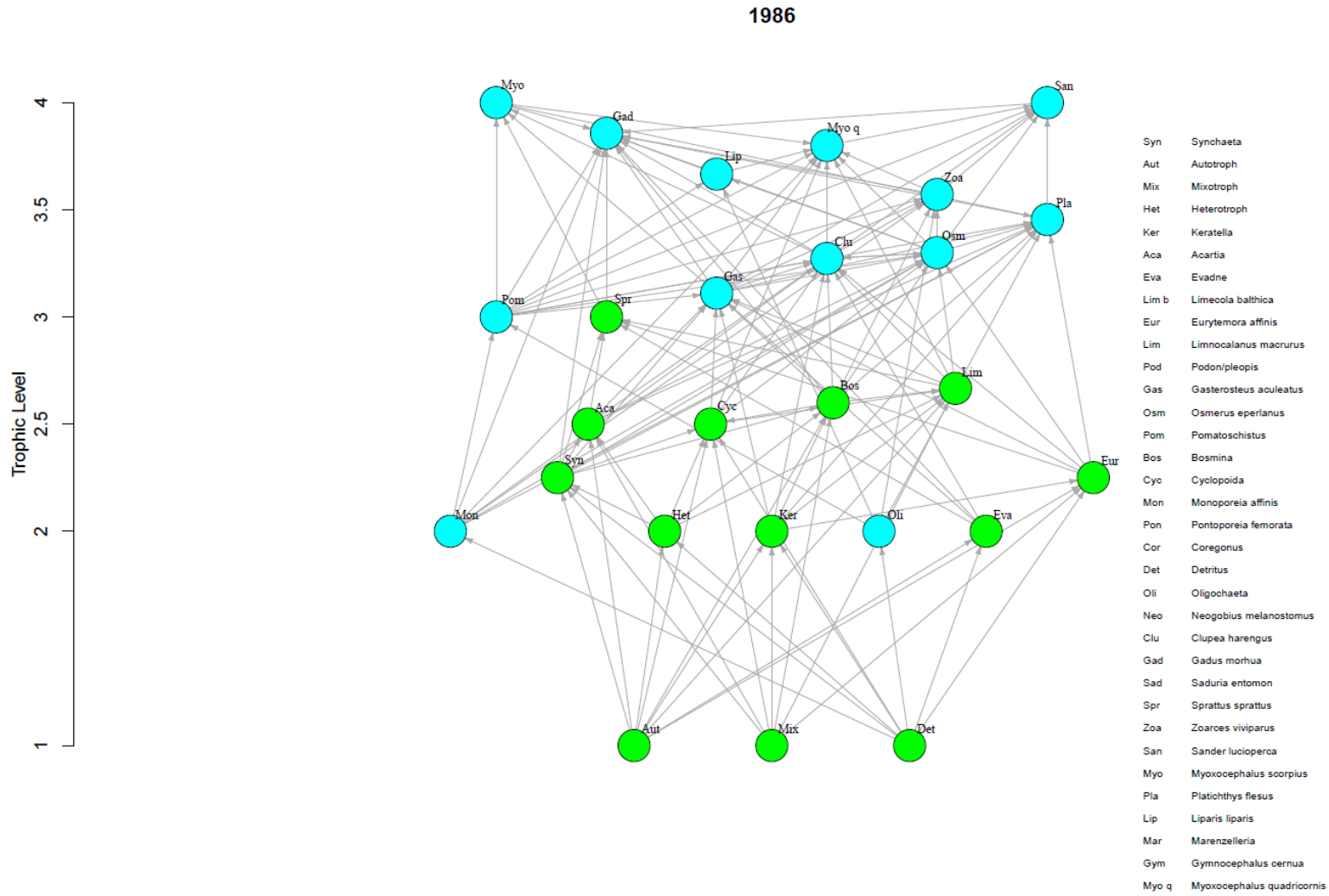


Figure 3S Node module membership, color of the nodes indicates module affiliation.

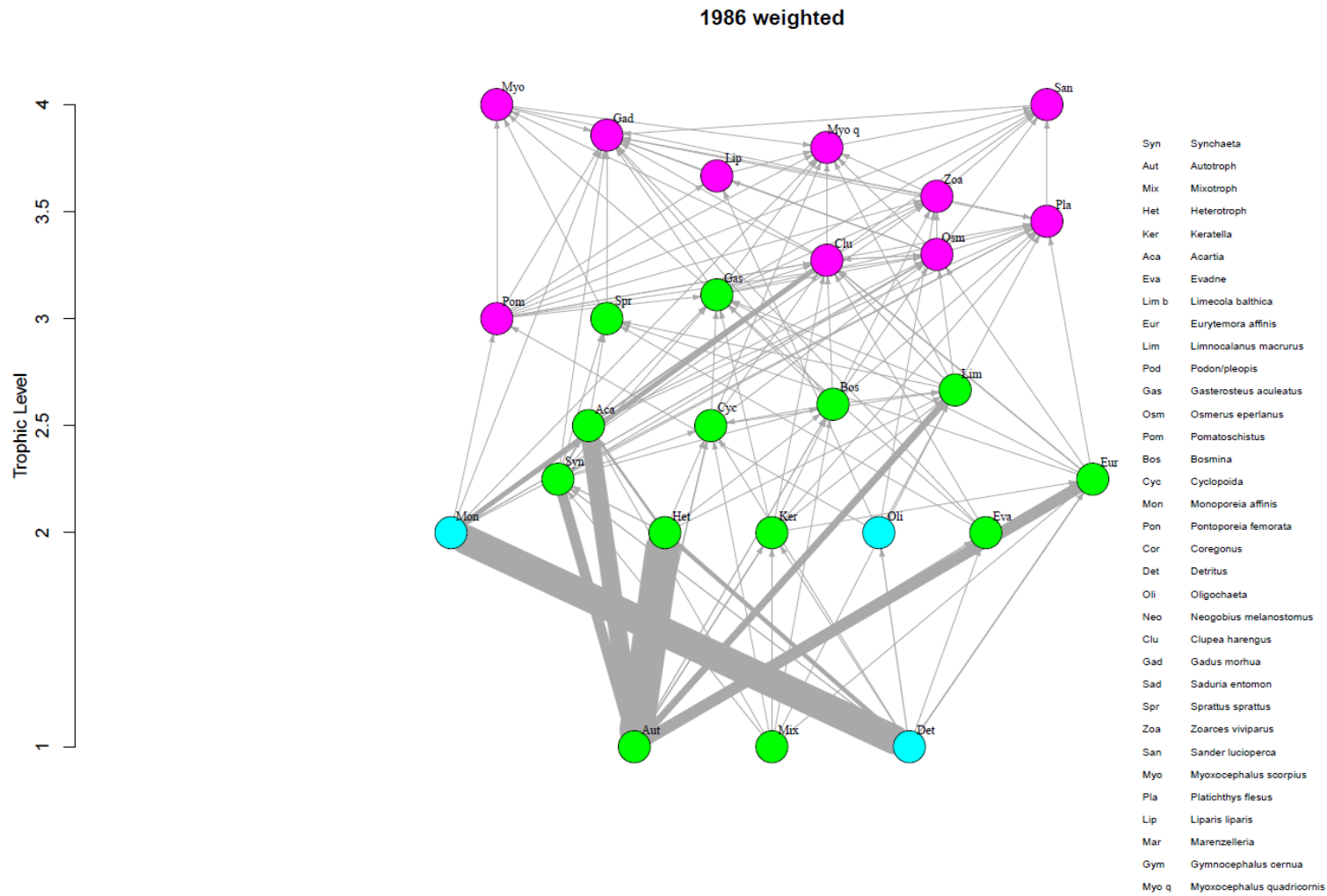


Figure 4S. Node module membership, color of the nodes indicates module affiliation. Width of indicates the strength of the interactions between nodes.

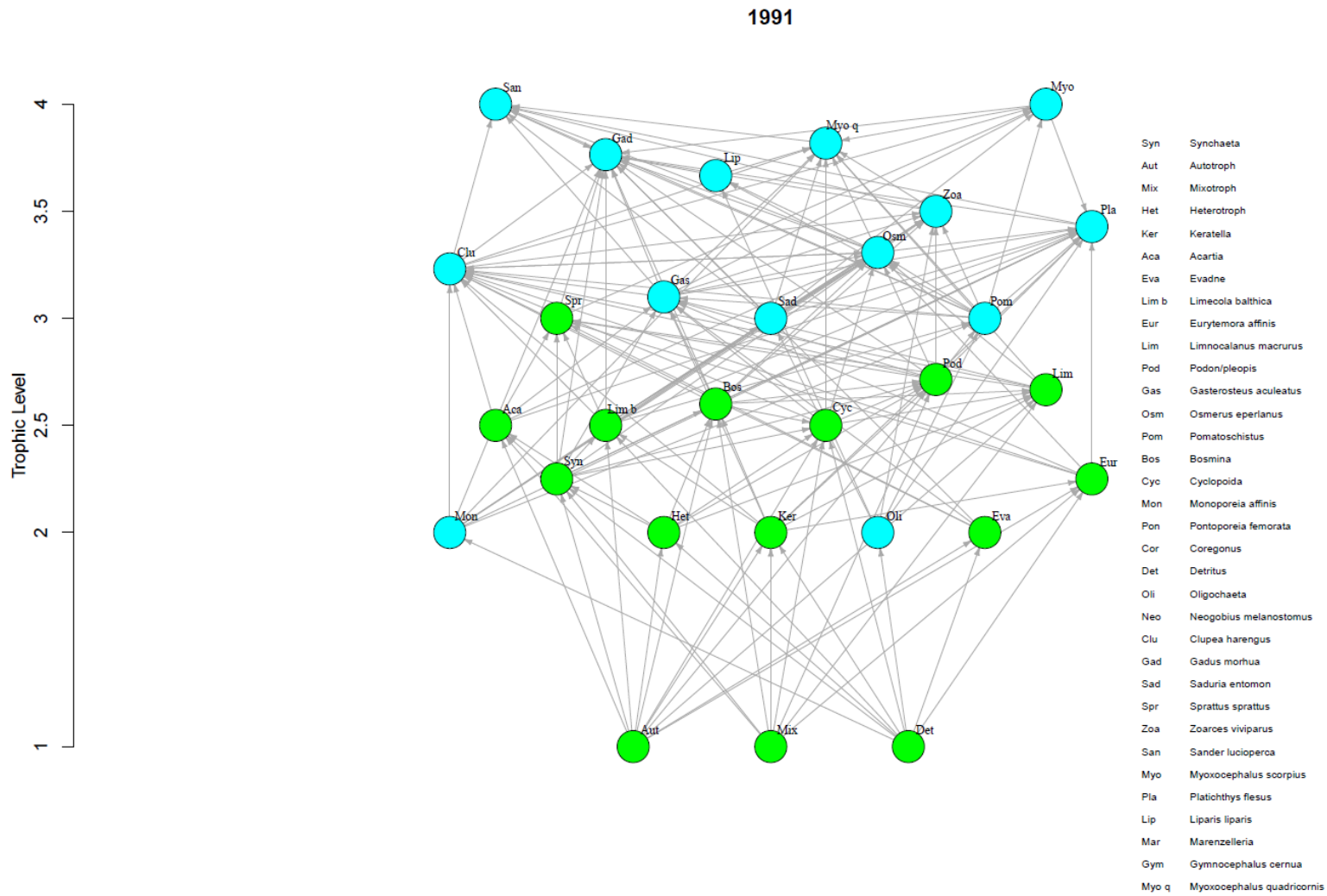


Figure 5S. Node module membership, color of the nodes indicates module affiliation.

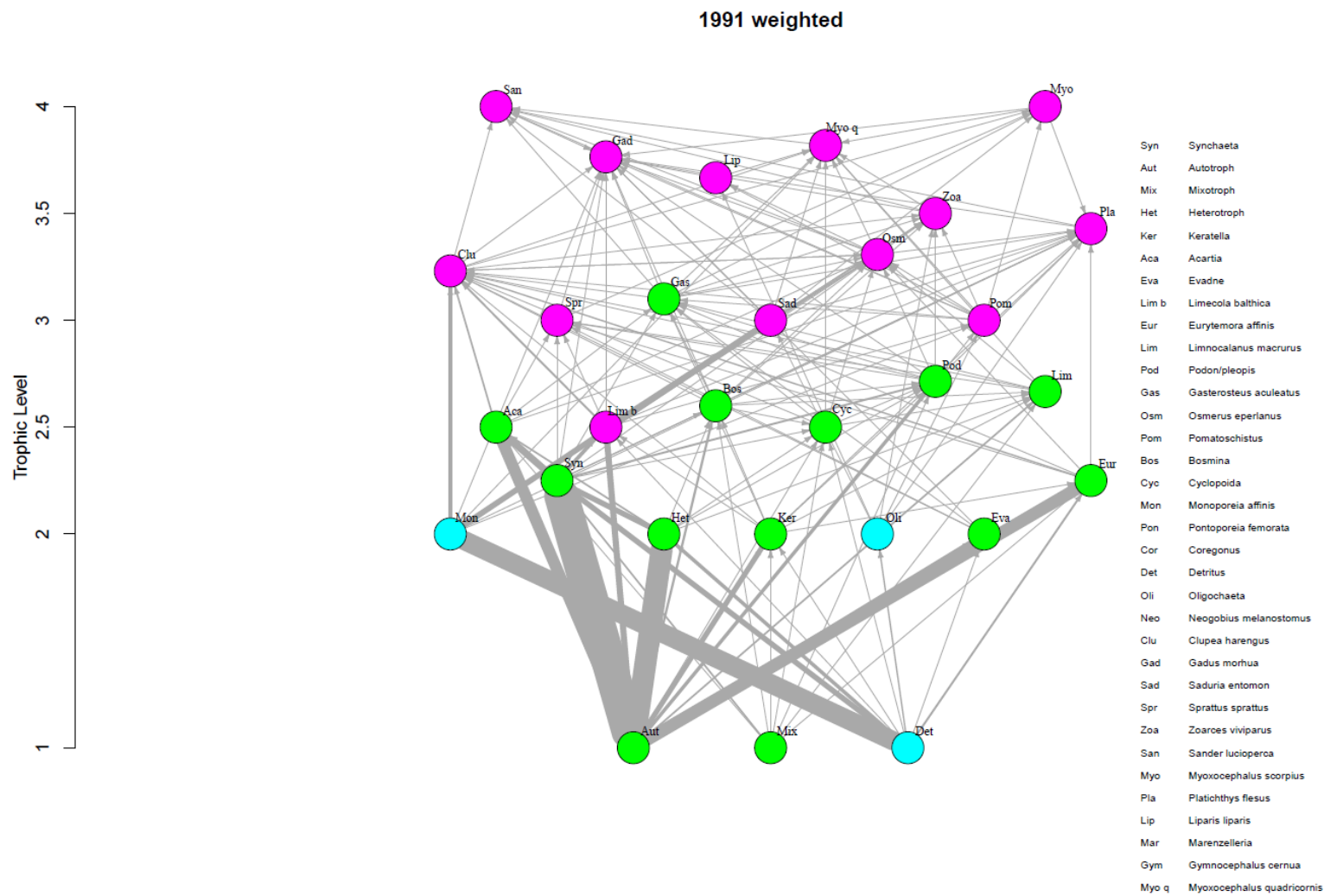


Figure 6S. Node module membership, color of the nodes indicates module affiliation. Width of links indicates the strength of the interactions between nodes.

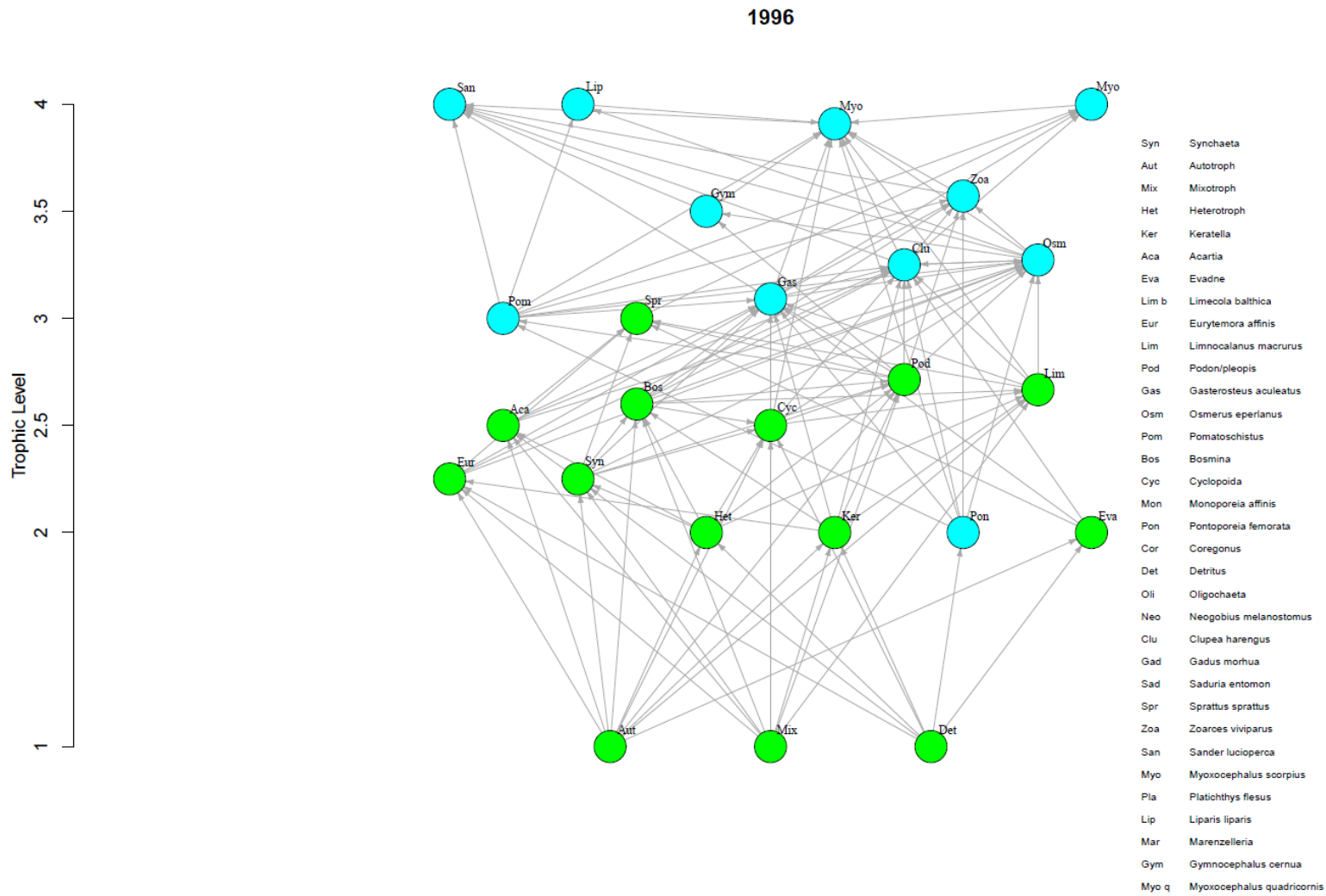


Figure 7S. Node module membership, color of the nodes indicates module affiliation. Width of links indicates the strength of the interactions between nodes.

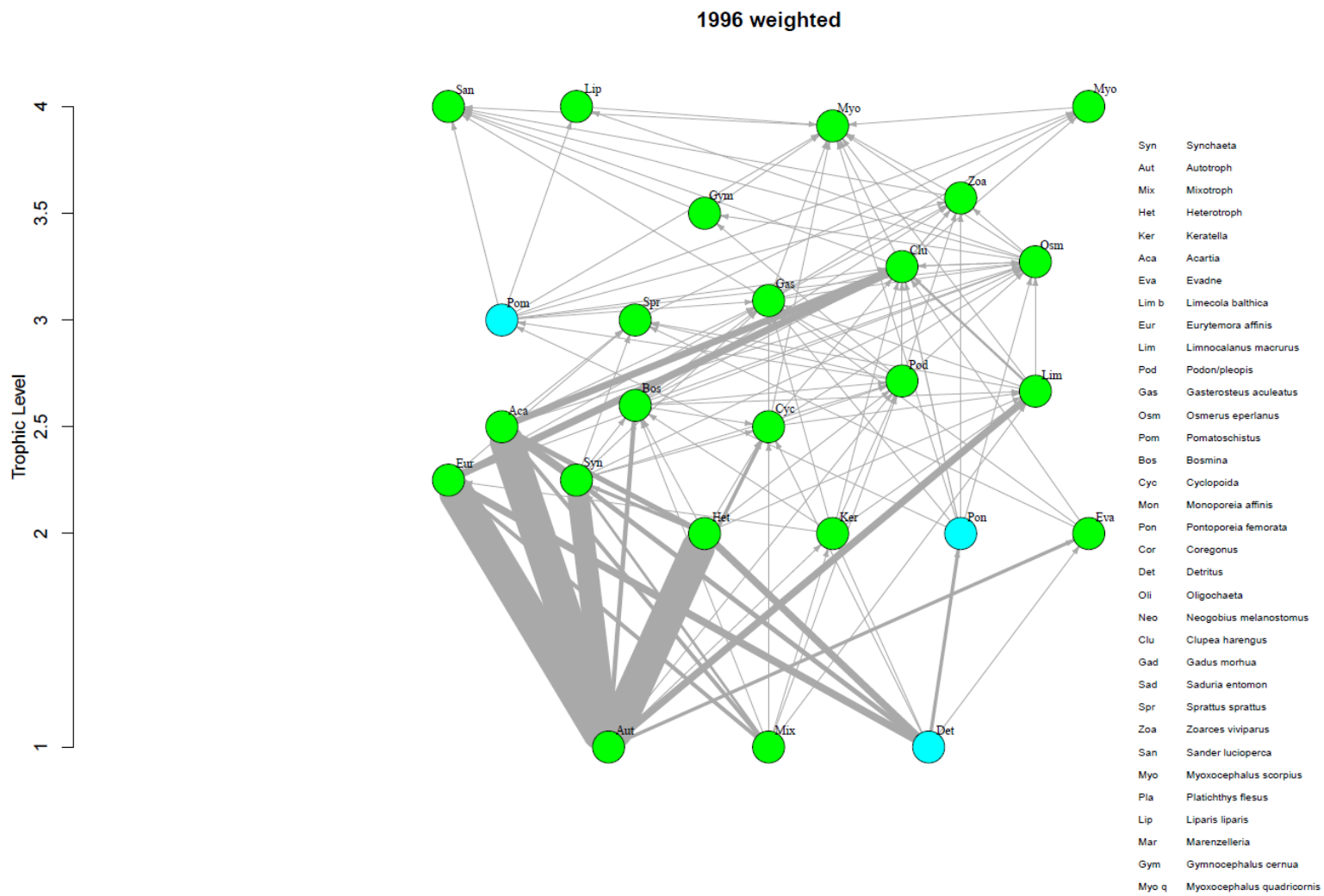


Figure 8S. Node module membership, color of the nodes indicates module affiliation. Width of links indicates the strength of the interactions between nodes.

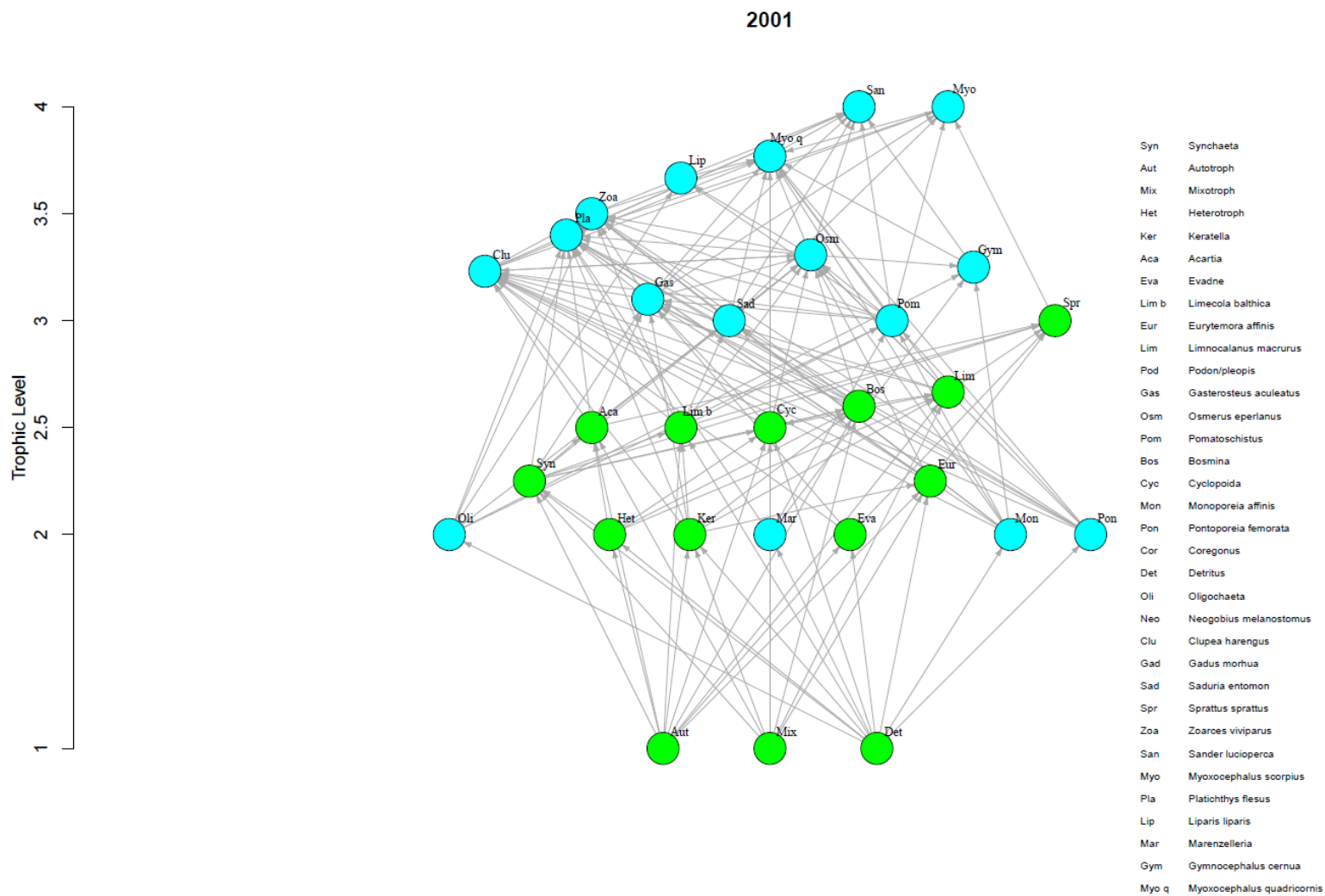


Figure 9S. Node module membership, color of the nodes indicates module affiliation.

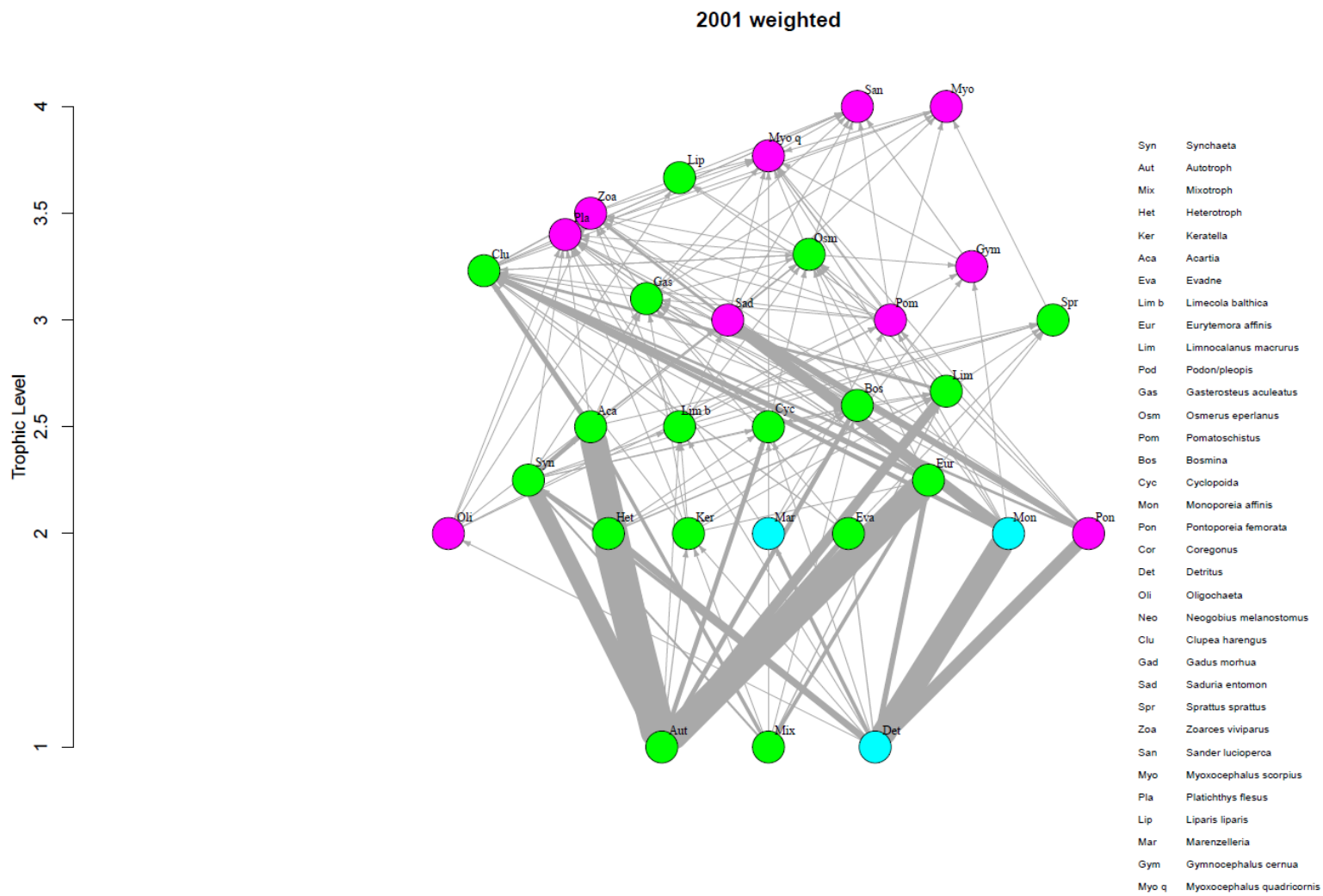


Figure 10S. Node module membership, color of the nodes indicates module affiliation. Width of links indicates the strength of the interactions between nodes.

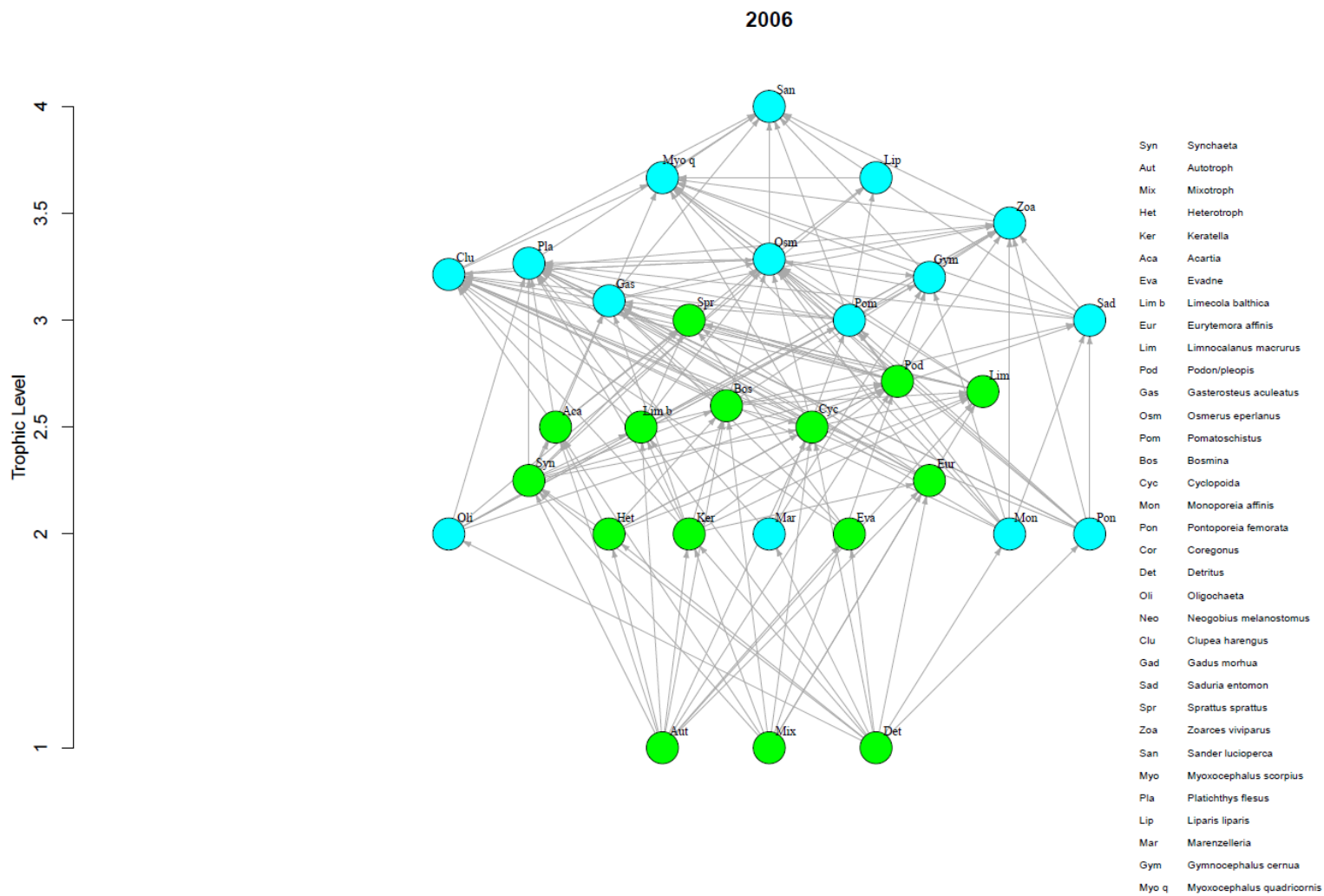


Figure 11S. Node module membership, color of the nodes indicates module affiliation.

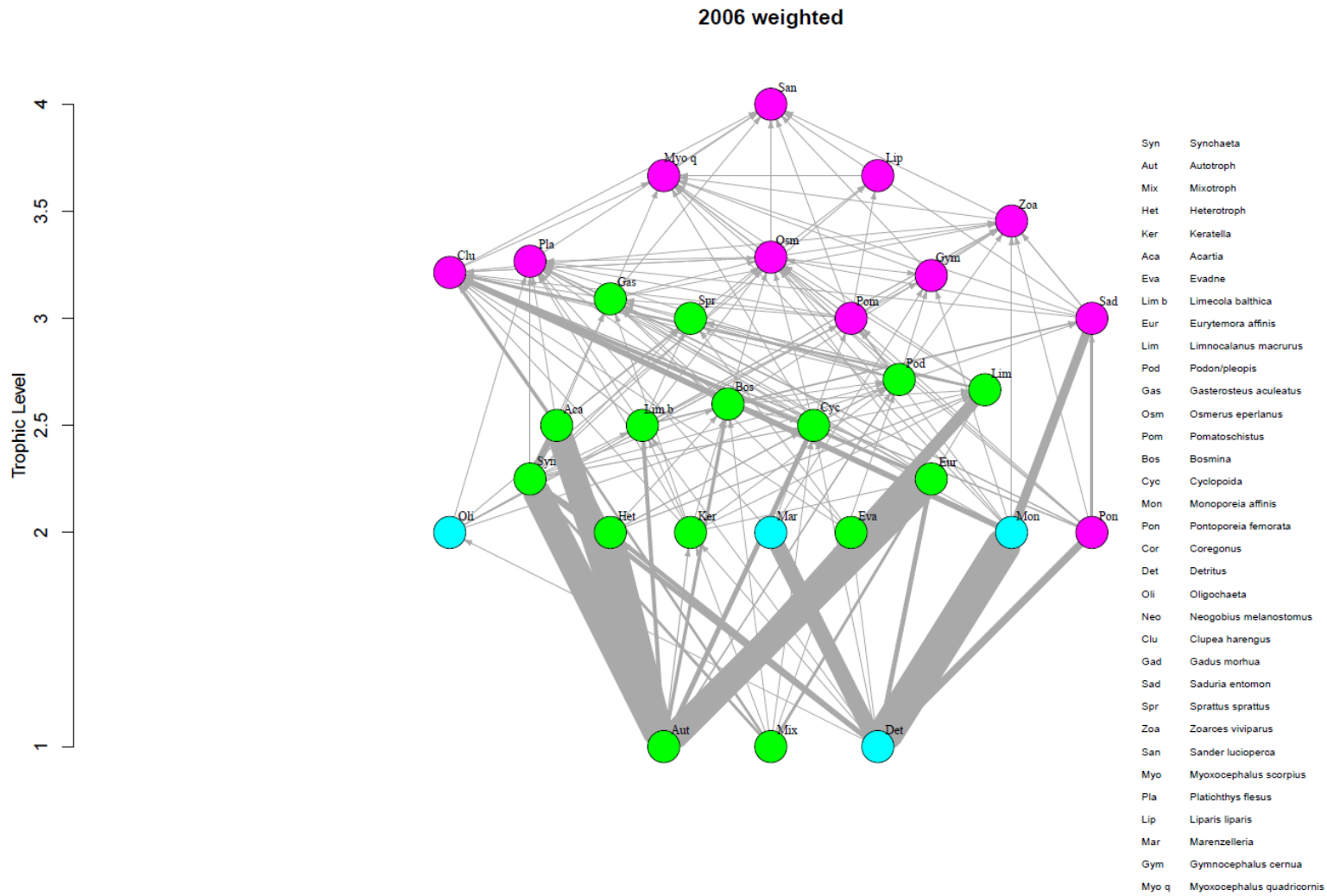


Figure 12S. Node module membership, color of the nodes indicates module affiliation. Width of links indicates the strength of the interactions between nodes.

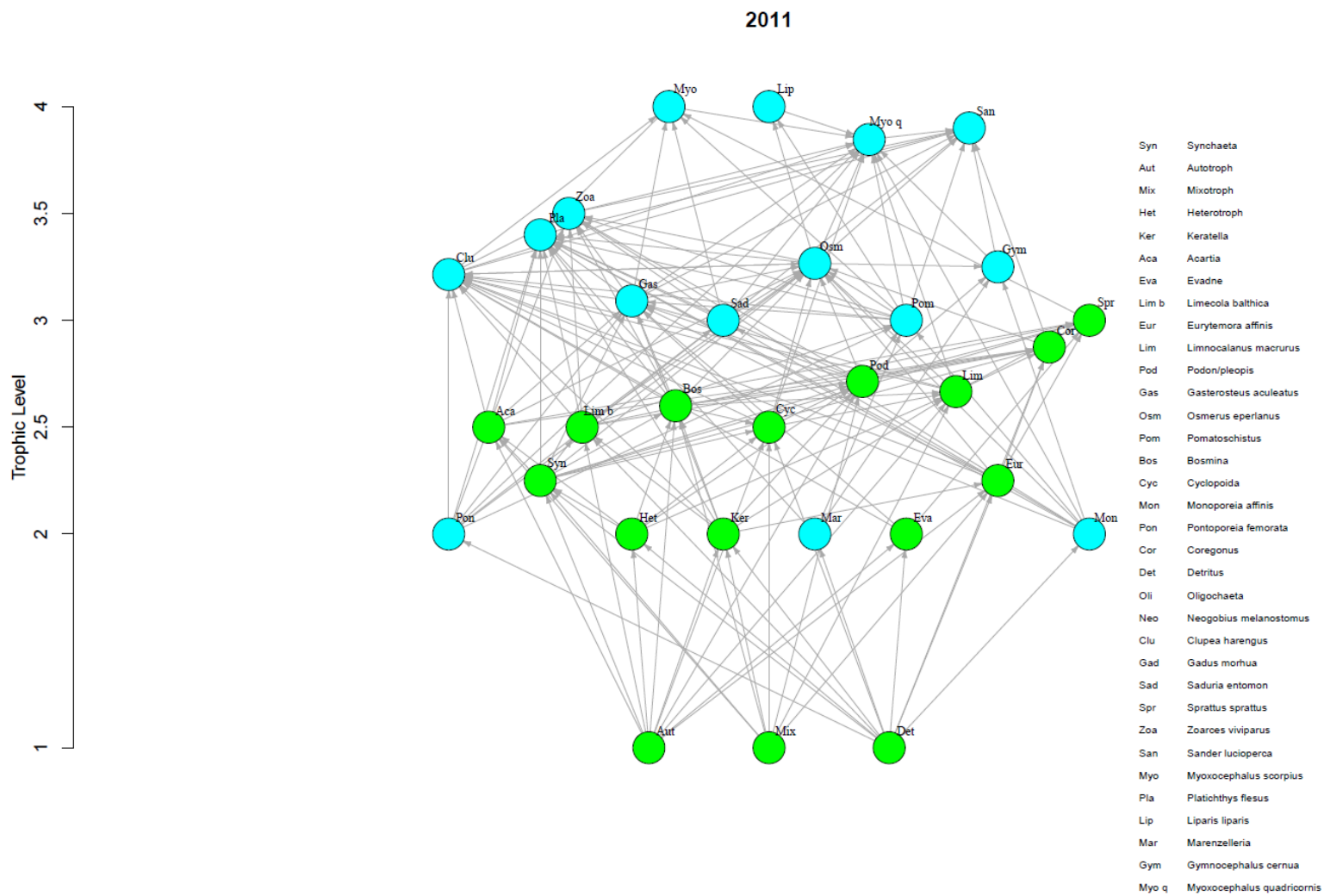


Figure 13S. Node module membership, color of the nodes indicates module affiliation.

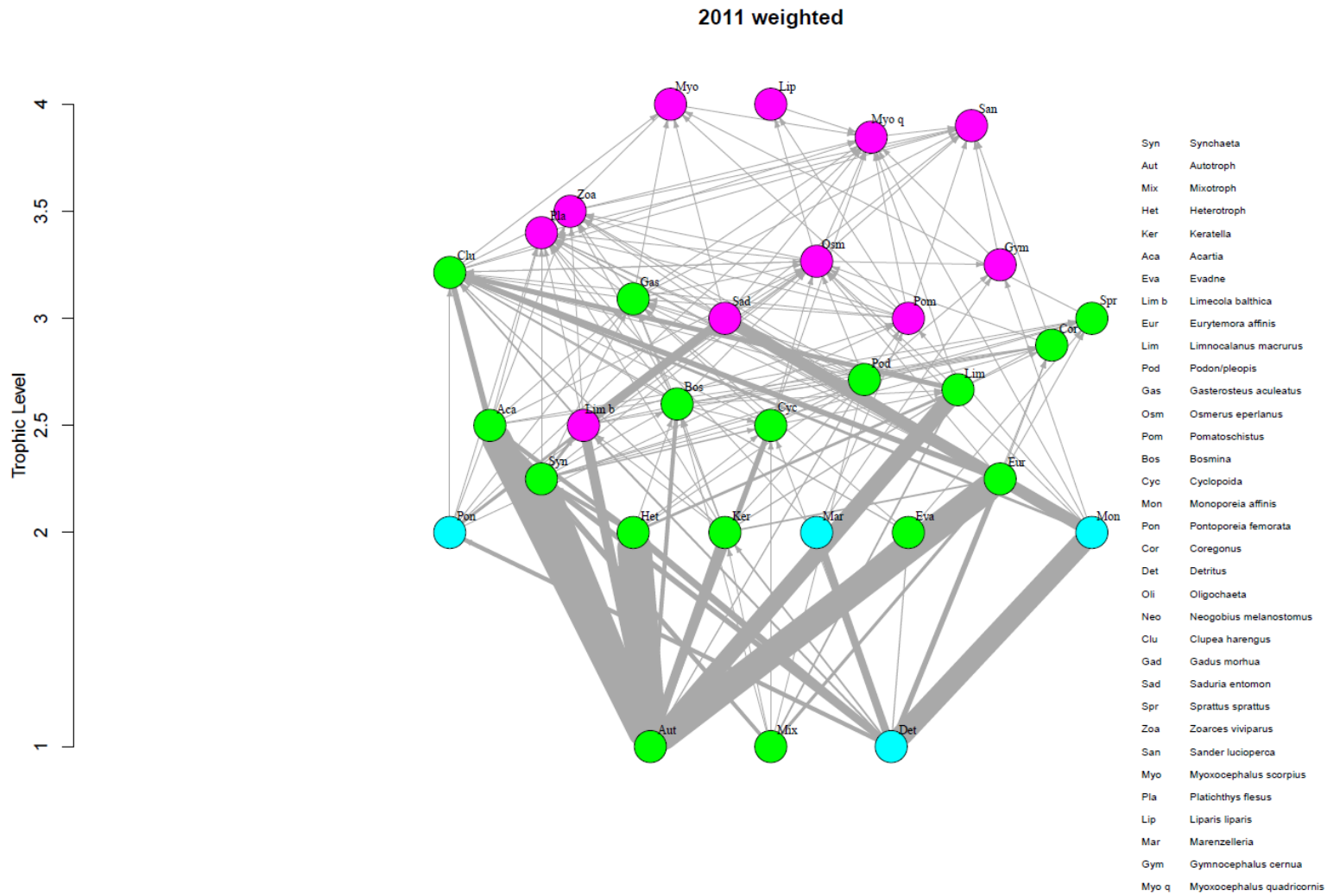


Figure 14S. Node module membership, color of the nodes indicates module affiliation. Width of links in the weighted metaweb indicates the strength of the interactions between nodes.

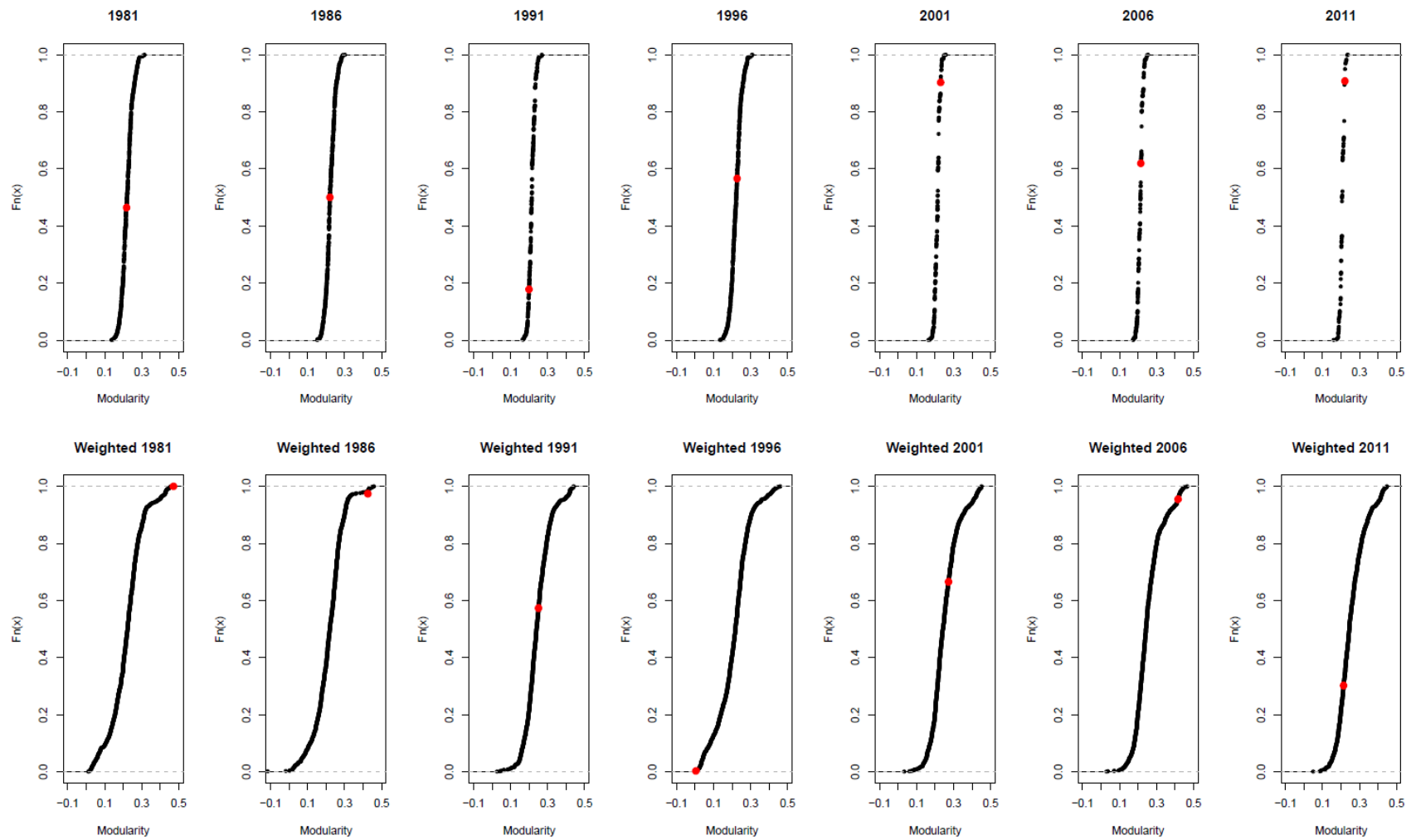


Figure 15S. Cumulative distribution function of the null model. The empirical food-web values were compared to the null-model distributions. Empirical values were considered to deviate strongly from the randomized food webs if the empirical value was outside the 0.05 to 0.95 quantile range of the null distribution. Red dot indicates empirical values.

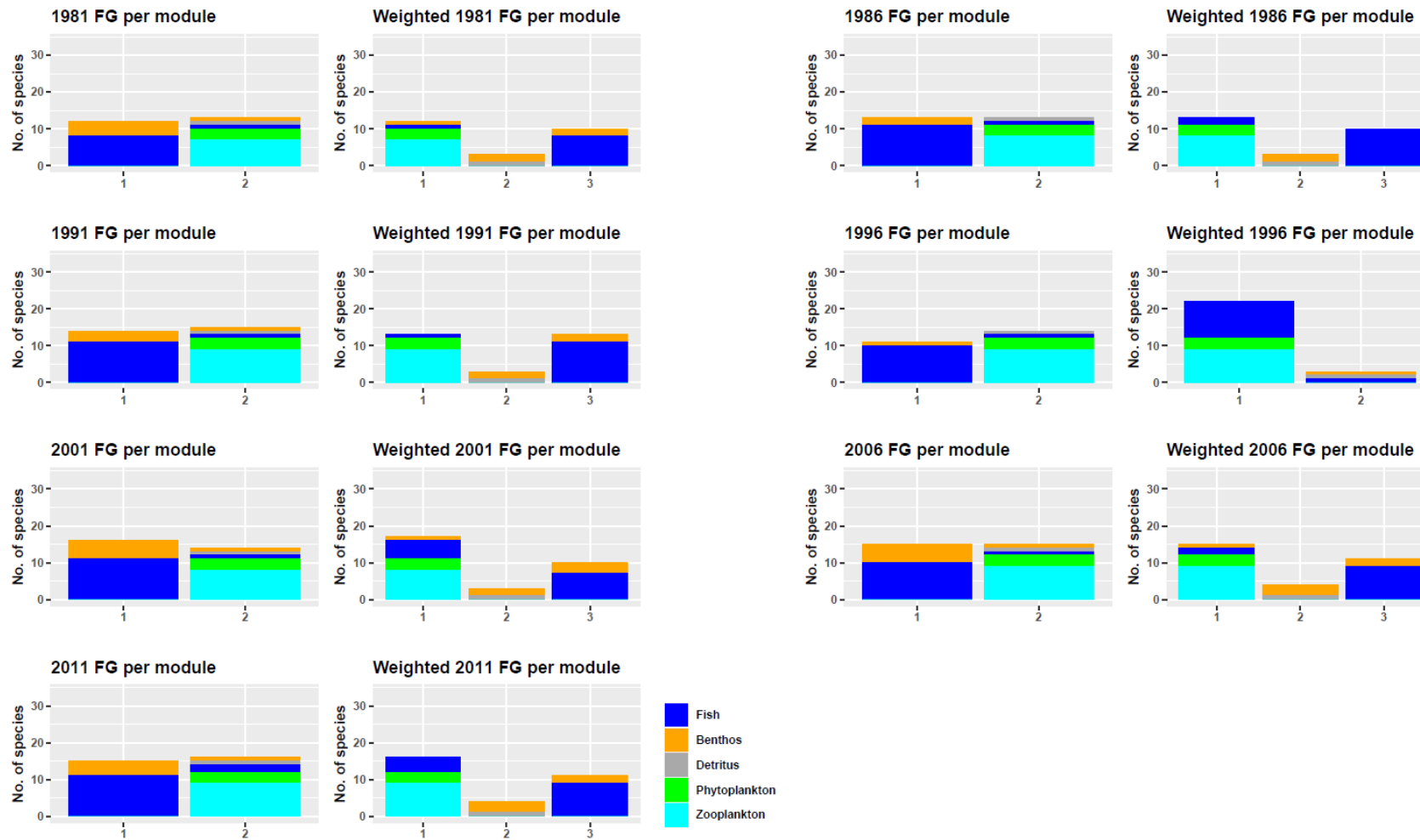


Figure 16S. Number of species from each functional group per module over time, both weighted and unweighted.

Table 1S. Table 1S. Species degree, generality and vulnerability

Functional group	Taxa	Metaweb			1981			1986			1991			1996			2001			2006			2011		
		deg	gen	vun	deg	gen	vun	deg	gen	vun	deg	gen	vun	deg	gen	vun	deg	gen	vun	deg	gen	vun	deg	gen	vun
Benthos	Limecola balthica	14	4	10	10	3	7				12	4	8				11	4	7	11	4	7	12	4	8
Benthos	Marenzelleria	4	1	3													4	1	3	4	1	3	4	1	3
Benthos	Monoporeia affinis	10	1	9	8	1	7	8	1	7	9	1	8				9	1	8	9	1	8	9	1	8
Benthos	Oligochaeta	8	1	7	4	1	3	5	1	4	6	1	5				7	1	6	7	1	6			
Benthos	Pontoporeia femorata	11	1	10	8	1	7							7	1	6	9	1	8	9	1	8	9	1	8
Benthos	Saduria entomon	12	4	8	11	4	7				10	3	7				10	4	6	9	4	5	9	3	6
Benthos	Sander lucioperca	12	11	1	7	6	1	8	7	1	9	8	1	7	7	0	9	9	0	9	9	0	10	10	0
Detritus	Detritus	12	0	12	9	0	9	8	0	8	9	0	9	7	0	7	11	0	11	11	0	11	11	0	11
Fish	Clupea harengus	20	14	6	16	10	6	17	11	6	19	13	6	17	12	5	18	13	5	18	14	4	19	14	5
Fish	Coregonus	11	9	2																			10	8	2
Fish	Gadus morhua	19	19	0	14	14	0	14	14	0	17	17	0												
Fish	Gasterosteus aculeatus	20	11	9				17	9	8	18	10	8	17	11	6	17	10	7	17	11	6	18	11	7
Fish	Gymnocephalus cernua	7	5	2										4	2	2	6	4	2	7	5	2	6	4	2
Fish	Liparis liparis	5	3	2				5	3	2	5	3	2	3	2	1	4	3	1	4	3	1	3	2	1
Fish	Myoxocephalus quadricornis	14	13	1	10	9	1	11	10	1	12	11	1	12	11	1	14	13	1	13	12	1	14	13	1
Fish	Myoxocephalus scorpius	8	5	3	6	3	3	7	4	3	8	5	3	5	4	1	7	5	2				7	5	2
Fish	Osmerus eperlanus	24	15	9	17	11	6	17	10	7	20	13	7	17	11	6	20	13	7	21	14	7	22	15	7
Fish	Platichthys flesus	18	16	2	13	11	2	13	11	2	16	14	2				16	15	1	16	15	1	16	15	1
Fish	Pomatoschistus	16	6	10				12	2	10	14	4	10	10	2	8	14	5	9	14	6	8	14	5	9
Fish	Sprattus sprattus	9	7	2	8	6	2	7	5	2	9	7	2	7	6	1	7	6	1	7	7	0	8	7	1
Fish	Zoarces viviparus	15	11	4	11	8	3	10	7	3	13	10	3	9	7	2	12	10	2	13	11	2	12	10	2
Phytoplankton	Autotroph	11	0	11	9	0	9	9	0	9	11	0	11	10	0	10	10	0	10	11	0	11	11	0	11
Phytoplankton	Heterotroph	8	2	6	7	2	5	7	2	5	8	2	6	8	2	6	7	2	5	8	2	6	8	2	6
Phytoplankton	Mixotroph	8	0	8	6	0	6	7	0	7	8	0	8	8	0	8	7	0	7	8	0	8	8	0	8
Zooplankton	Acartia	10	4	6	8	4	4	9	4	5	9	4	5	8	4	4	9	4	5	9	4	5	10	4	6
Zooplankton	Bosmina	16	5	11	11	4	7	13	5	8	14	5	9	12	5	7	12	5	7	13	5	8	14	5	9
Zooplankton	Cyclopoida	12	6	6	10	6	4	11	6	5	12	6	6	12	6	6	11	6	5	12	6	6	12	6	6
Zooplankton	Eurytemora affinis	10	4	6	7	3	4	9	4	5	9	4	5	8	4	4	9	4	5	9	4	5	10	4	6
Zooplankton	Evadne	6	2	4	5	2	3	6	2	4	6	2	4	5	2	3	5	2	3	5	2	3	5	2	3
Zooplankton	Keratella	11	3	8				9	3	6	11	3	8	9	3	6	10	3	7	11	3	8	11	3	8
Zooplankton	Limnocalanus macrurus	12	6	6	9	5	4	11	6	5	11	6	5	11	6	5	11	6	5	11	6	5	12	6	6
Zooplankton	Podon/pleopis	17	7	10							15	7	8	14	7	7				15	7	8	16	7	9
Zooplankton	Synchaeta	15	4	11	12	4	8	12	4	8	14	4	10	11	4	7	12	4	8	13	4	9	14	4	10