LETTER

Spatial resolution and location impact group structure in a marine food web

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Abstract

Ecological processes in food webs depend on species interactions. By identifying broad-scaled interaction patterns, important information on species' ecological roles may be revealed. Here, we use the group model to examine how spatial resolution and proximity influence group structure. We examine a data set from the Barents Sea, with food webs described for both the whole region and 25 subregions. We test how the group structure in the networks differ comparing (1) the regional metaweb to subregions and (2) subregion to subregion. We find that more than half the species in the metaweb change groups when compared to subregions. Between subregions, networks with similar group structure are spatially related. Interestingly, although species overlap is important for similarity in group structure, there are notable exceptions. Our results highlight that species ecological roles vary depending on fine-scaled differences in the patterns of interactions, and that local network characteristics are important to consider.

Keywords

Communities, ecological networks, food webs, group model, group structure, spatial location, spatial resolution.

INTRODUCTION

A long-standing goal in ecological research is to identify which species, groups of species or other structures are important for delivering and maintaining functionality in an ecosystem. Ecological networks, such as food webs, are commonly used to describe the structural patterns of species and interactions within ecosystems (Newman 2003; Pascual & Dunne 2006). This approach is useful for understanding both broad-scale properties as well as properties of meso-scale structures and individual nodes in these networks (Allesina *et al.* 2008; Ings *et al.* 2009). The distribution of species interactions further affects species extinctions (Dunne *et al.* 2002; Eklöf & Ebenman 2006), stability (Allesina & Tang 2012) and functionality (Schindler 1990; Petchey & Gaston 2002).

In the concept of the Eltonian niche, functional roles of species are defined by their interactions with other species (Elton & Elton 1927; Chase & Leibold 2003). Accordingly, species with different sets of interaction partners are thought to possess different functional roles in the ecosystem, which has indeed been shown in empirical networks (Laigle *et al.* 2018). Based on this view, it is relevant to identify the collections of species that possess certain positions within a network as it can help to understand their ecological role. There are several different approaches to this. Modularity is a commonly used concept for grouping species in ecology (Krause *et al.* 2003; Newman 2006), where one identifies the sets of species which interact more strongly with members of the same set. A different approach is through the concept of trophic species (Yodzis 1982; Cohen & Briand 1984), where species are merged into one trophic species

if they interact with the exact same set of prey and predators. The concept of trophic species has later been modified based on the notion of regular equivalence (White & Reitz 1983). Here, species are less strictly organised into ecologically equivalent groups based on their broader patterns of interactions; species are grouped if they are prone to eat and be eaten by the same groups of species (but not necessarily the exact same species), that in turn are prone to be eaten by the same set of species. Luczkovich *et al.* (2003) pioneered this approach, which was further developed by Allesina & Pascual (2009) in a model known as the group model in ecology. A modified method for detecting trophic groups, but with a strict criterion to avoid species with no interactions in common, was developed by Gauzens *et al.* (2015).

The group model (Allesina & Pascual 2009) is equivalent to the stochastic block model used for community detection in network science (Holland *et al.* 1983). Species have a recursive relationship with each other, meaning that species which are distant from each other in the network still affect each other's group memberships (Allesina & Pascual 2009; Schaub *et al.* 2016). Critically, species with the same group membership have corresponding roles in the ecological network, and are thus also likely to share similar ecological functionality. The group model has indeed been shown to produce groups of species with relevant ecological interpretations, such as trophic guilds and habitat patterns (Baskerville *et al.* 2011; Eklöf *et al.* 2012a; Sander *et al.* 2015; Michalska-Smith *et al.* 2018).

Reliable interpretations of structural patterns in ecological communities are however dependent on how data for ecological networks are obtained. Food web data are often collected over long time periods and large geographical areas to capture the majority of species or trophic interactions (Dunne 2006; Wood *et al.* 2015). The data are often presented as a metaweb, including all interactions observed over the whole area

and time frame. This is certainly a valuable approach when the aim is to get an overview of the diversity of species and interactions in a region. However, if several areas of different types (e.g. coasts and open sea in a marine system) are aggregated, this may give an incorrect picture of the ecological network and its characteristics (Poisot *et al.* 2012). In particular, all species may not be present in all local networks. Also, one may expect that even if a species does exist in both the coastal and open sea habitats, its interactions may differ depending on which other species are present in the respective areas, differences in species traits between areas, etc. (Poisot *et al.* 2012; Bartley *et al.* 2019). These differences can have important implications for both our general understanding of species functional roles in ecological networks, and also for local stability and robustness (McCann *et al.* 2005; Landi *et al.* 2018). When merging such differences into a metaweb, and potentially generating combinations of species and interactions that do not actually co-occur, the utility and reasoning based on such structures may be inaccurate or misleading.

Here, we evaluate whether the partitioning of species into ecologically equivalent groups differs (1) between a meta (regional) network and local networks (subregions) and (2) between different subregions. In particular, we want to understand if certain groups of species and certain species are more variable in their group membership. We use a data set from the Barents Sea (Planque *et al.* 2014; Kortsch *et al.* 2018), consisting of one meta network and several local networks from subregions describing the food webs. We use the group model (Allesina & Pascual 2009) to identify the group structures of the different networks. Differences in group structures are then compared using the Jaccard distance. Further, we analyse if certain species are more or less prone to change their group membership. We show that the group structure in ecological communities is indeed affected by both spatial resolution and spatial location. Additionally, although the grouping of species clearly depends on species composition, our analysis reveals structural characteristics not depending on species composition which contribute to the functioning of ecological communities.

METHODS

Data set

We used a food web data set describing the Barents Sea (Planque *et al.* 2014; Kortsch *et al.* 2018). The Barents Sea is a shelf sea with a heterogeneous environment, bordering the Atlantic Ocean with the dissipating Gulf Steam in the west, and the Arctic Ocean to the north-east (Fossheim *et al.* 2015). The food web data consist of a regional metaweb and 25 subregional local food webs. The subregions used in the Barents Sea data set (Kortsch *et al.* 2018) are delimited by polygons defined by a group of experts in Hansen *et al.* (2016), aiming to make the subregions as homogeneous as possible in regard to hydrography and bathymetry.

The metaweb includes 233 species and 2220 feeding interactions, of which species occurrences are based on catch data, and interactions are based on literature (Planque *et al.* 2014; Kortsch *et al.* 2018). Species range from avian and mammalian predators to primary producers. The subregions

include separate local species occurrences with 115–178 species. We created the subregional food webs by filtering the species of the metaweb to retain only those species present in the respective subregions and all possible interactions based on the species composition. A pairwise feeding interaction between two species in a subregion was assumed to occur if the species had been identified as interacting in the metaweb.

See Figure S1 in Supporting Information for a complete overview of the data process and analyses. Code and data used for the analysis are available at https://git.io/JvMcn.

We made a small modification to the original data set specific to the node *Sebastes spp.*, made up of several species from the genus *Sebastes*. This node lacked prey species in 14 subregions. To ensure that they were not considered primary producers in subsequent analyses, we added to them the complete set of interactions from three species of the same genus, namely *S. marinus*, *S. mentella* and *S. viviparus*. As *Sebastes spp.* is already an aggregate of multiple species, this likely reduced the impact of our modification to a slight over-representation of the genus.

Group model

To evaluate the 'best' partitioning of the species into structurally functional groups, we used the group model (Allesina & Pascual 2009; Sander *et al.* 2015). The model provides a likelihood-based framework to calculate how well a specific partitioning of species into groups fits an empirical network structure. Groupings with high likelihoods have aggregated species which act in a similar way, that is, species with the same group membership tend to eat and be eaten by the same other groups (Allesina & Pascual 2009). We chose the group model due to its strong ecological motivation in addition to its recognised performance (Baskerville *et al.* 2011; Yan *et al.* 2014; Sander *et al.* 2015). A network (food web) *A* has *S* nodes (species) and *L* directed links (feeding interactions) between the nodes. These relationships can be described with an adjacency matrix, where $A_{ij} = 1$ means that resource *i* is eaten by consumer *j*. We can reproduce the empirical web $A(S,L)$ using a directed random graph, where the probability of connecting any two nodes is *p*. Accordingly, the likelihood of obtaining *A* is then given by:

$$P(A(S,L)|p) = p^L(1-p)^{S^2-L}. \tag{1}$$

The group model expands this by looking at the likelihood of randomly generating an empirical network *A* after assigning the nodes into *k* groups. Accordingly, the likelihood of generating network *A* will depend on both the number of groups and the arrangement of the nodes in them according to

$$P(A(S,L)|\vec{p}) = \prod_{i=1}^{k}\prod_{j=1}^{k} p_{ij}^{L_{ij}}(1-p_{ij})^{S_iS_j-L_{ij}}. \tag{2}$$

Here, $\vec{p}$ is a vector of probabilities for links between all combinations of groups. As such, all species in group *j* will have the same probability p_{ij} to connect to any species in group *i*. By testing different partitionings of the species into groups, the aim is to find the partitioning with the highest probability of reproducing the empirical network.

The different combinations of groups differ in their number of parameters, namely the number of groups and the vector $\vec{p}$ of group assignments for each species. Therefore, we cannot directly compare the likelihoods, but have to use some type of model selection to balance the goodness of fit with model complexity. Model selection can here be performed by calculating the Bayes factor (Eklöf *et al.* 2012a, Sander *et al.* 2015), or by choosing the partition with the highest marginal likelihood,

$$P(A(G)|\vec{p}) = \prod_{i=1}^{k}\prod_{j=1}^{k} \frac{L_{ij}!(S_iS_j - L_{ij})!}{(1+L_{ij})(1+S_iS_j)}. \qquad (3)$$

With increasing numbers of species in the networks, the possible combinations of groups quickly become technically overwhelming. Hence, we compared marginal likelihoods while searching for better groupings instead of calculating all possible groupings. Following Sander *et al.* (2015), we searched for the partition of species into groups that maximises the marginal likelihood by using the Metropolis-coupled Markov Chain Monte Carlo (MC^3) algorithm with a Gibbs sampler (see Sander *et al.* 2015 for details and Michalska-Smith *et al.* 2018 for updated version of the code). For both the metaweb and each subregion, the algorithm was executed 10 times, each with a random seed, 300 000 MCMC steps and 20 MCMC chains. For each network, if multiple groupings were produced, the one with the highest marginal likelihood was selected.

Similarity between groups

We were interested in both to what extent and how the partitioning of species into groups changed between different scales and locations. Accordingly, we used two approaches to analyse the group differences, giving us the tools to track both large structural changes, and species-specific roles and influence.

Measuring partition similarity with the Jaccard distance

To track how the overall group structure changed between networks, we used 'best match' comparisons with the Jaccard distance which, for each group in a network, searched for the most similar match in a compared network. The 'best' partition of the species in web A was denoted C^A. We analysed to what extent each species group k in C^A (denoted C_k^A) resembled any group in C^B (the best partition of species in web B). The most similar group was defined as the group l in C^B where the most species from group C_k^A were still grouped together, and we denote that group C_l^B. We then divided the number of species common to both groups k and l by all the species present in both groups k and l. This was done for all groups n in web A, and we calculated the average Jaccard distance (d_J) between partition C^A and partition C^B:

$$d_J(C^A, C^B) = \frac{1}{n}\sum_{k=1}^{n}\min_l\left(1 - \frac{|C_k^A \cap C_l^B|}{|C_k^A \cup C_l^B|}\right) \qquad (4)$$

where the Jaccard distance takes the value of 0 when partition C^A and C^B are identical, and approaches 1 as they become increasingly dissimilar.

The Jaccard distance risks being affected by differences in the number of groups between compared networks, though these effects were limited in our case (Fig. S2). Additionally, the index differs depending on the direction of the comparison ($C^A \rightarrow C^B$ or $C^B \rightarrow C^A$). Related, the group mapping of species can also differ depending on the direction of the comparison, meaning that even if the best match for group C_k^A in network B is C_l^B, the best match for C_l^B in network A is not necessarily C_k^A. To normalise these effects, we measured the Jaccard distance both ways for each network pair and calculated the average distance $\bar{d}_J$:

$$\bar{d}_J(C^A, C^B) = \frac{d_J(C^A, C^B) + d_J(C^B, C^A)}{2}, \qquad (5)$$

which means that $\bar{d}_J(C^A, C^B)$ is equal to $\bar{d}_J(C^B, C^A)$. By doing this, the Jaccard distance was no longer affected by the difference in number of groups between compared networks (Fig. S2b). The methodology is based on Calatayud *et al.* (2019).

Cluster optimisation

To investigate whether some subregions were more similar regarding group structure, we clustered the subregions based on the Jaccard distance as well as based on species overlap. We generated the clusters in two steps. First, we used the Uniform Manifold Approximation and Projection (UMAP, McInnes *et al.* 2018). UMAP is a dimension-reducing algorithm which favours preserving local distances over global ones. In our case, for the Jaccard distances and species overlaps, respectively, UMAP projected the 25 subregions (or 'dimensions') in a two-dimensional space, with more similar subregions being placed closer to each other. We modified the projections by changing the number of neighbours (ranging from two, to the total number of subregions, 25), which varied the focus between local and regional similarities. We also set a low minimum distance, 0.001, which allowed similar subregions to be plotted closer together to better facilitate the clustering algorithm. In the second step, we analysed all generated projections for clusters using the HDBSCAN (Hierarchical density-based spatial clustering of applications with noise) method (Campello *et al.* 2013). We arbitrarily set the minimum cluster size to three subregions, which we deemed a good trade-off between looking at subregion pairs and bigger, potentially more dissimilar, clusters. Since the UMAP projections varied slightly, we repeated this process 10 000 times, from which we selected the best clustering, that is, the one containing the most similarly structured subregions within each cluster.

Species-wise group turnover

For all species, we compared the group relations of all pairs of species to see whether they were in the same group. By then comparing these pairwise relations to the same pairs in other webs, we obtained a measurement of how prone individual species or taxa were to changing their group relations between webs. Accordingly, for each species we identified all possible species pairs in a network A. We checked whether

Table 1 Example of how species-wise group turnover is calculated for species a, using two example networks with same species but with slightly different groupings

Network A		Network B		Same group?			
Species	Group	Species	Group	Pairs	Net A	Net B	Turnover
a	1	a	1	a-b	Yes	No	1
b	1	b	2	a-c	No	Yes	1
c	2	c	1	a-d	No	No	0
d	2	d	3	a-e	No	No	0
e	3	e	2	a-f	No	No	0
f	3	f	3	Species **a** turnover: 2/5			

All possible pairs including species a, excluding self-paired and mirrored, are checked whether they are in the same group in one or both networks. If their relationship changes between the two networks, there has been turnover. The sum of pairs which experienced turnover is then divided with the total number of pairs to obtain the proportional turnover.

each species pair was in the same or different groups in network A. We then compared the status of all pairs in network A to their status in all other networks. If the relationship for a species pair changed (either different groups → same group, or same group → different group) between two webs, there was turnover (Table 1). From this, we calculated the proportion of pairs for each species which experienced turnover to obtain the mean species pairwise group turnover. For comparing the pairs in different networks, we only considered species which co-occurred between the two networks. For a species i, the turnover T between networks A and B is calculated as

$$T_i^{AB} = \frac{1}{S^A \cap S^B - 1} \sum_{j=1}^{S^A \cap S^B} \left(Q_{ij}^A \left(1 - Q_{ij}^B\right) + Q_{ij}^B \left(1 - Q_{ij}^A\right) \right), \quad (6)$$

where $S^A \cap S^B$ is the number of overlapping species between the two networks, and

$$Q_{ij}^A = \left\{ \begin{array}{ll} 1, & \text{if } i \text{ and } j \text{ share group in } A \\ 0, & \text{otherwise} \end{array} \right\}. \quad (7)$$

Note that in eqn 6, at most one of the terms $Q_{ij}^A \left(1 - Q_{ij}^B\right)$ and $Q_{ij}^B \left(1 - Q_{ij}^A\right)$ can take the value 1. From this we calculated the average turnover for species i in network A compared to all other webs.

Species and network metrics

Taxonomic classifications of species were obtained from Kortsch et al. (2018). We calculated the number of interactions and trophic levels for all species in both the metaweb and in each subregion. For species trophic level we used the NetIndices package in R (Kones et al. 2009), which uses the method from Christensen & Pauly (1992). Accordingly, the trophic level of primary producers and detritus is set to one, and subsequent species are set to one plus the sum of their prey trophic levels, multiplied by the constituted diet proportions which we assumed to be spread out equally across all prey. We also calculated species overlap for all networks (metaweb and all subregions); for each pair of networks we calculated the number of species shared between two networks divided by the total number of unique species in both networks.

Importantly, all primary producers in the data set missed spatial data, and were thus assumed to be present in all subregions (Kortsch et al. 2018). Hence, in species-specific analyses involving turnover, we excluded primary producers to avoid biases introduced by missing data.

The group model occasionally places species in the same group that have no interactions in common. We extracted the number and identity of the species this has happened to, evaluating both how common this feature is and also if these species have any specific characteristics.

Correlation with environmental factors

To analyse if the partitioning of the species depends on environmental factors, we obtained environmental and spatial data from Kortsch et al. (2018). The environmental data extracted were mean ocean depth, mean water column temperature and sea ice days, though sea ice was excluded due to its strong correlation with water column temperature. The spatial data extracted were the centres of the subregion polygons. To check for spatial autocorrelation for the group structure, we used the correlog function in the ncf package (Bjornstad 2018) in R. The function looks for autocorrelation using distance classes, which we defined in 50 km increments, which are tested using Moran's I and then visualised as correlograms. Correlation between similarity in group structure and water column temperature as well as ocean depth was tested using a permutation-based multivariate analysis of variance (PERMANOVA) test, conducted using the adonis function from the vegan R package, (Oksanen et al. 2018) with 10 000 permutations and no stratification.

RESULTS

The subregions shared 38–87% of the species between them, with a mean of 62%. Comparing subregions to the complete species composition (metaweb), species overlap ranged from 49% to 76%, with a mean of 63% (Fig. 1a). Species overlap between subregions correlated significantly with distance, where more closely located network pairs had higher proportions of shared species while distant regions differed more (Fig. 1b).

Comparing the group structure of the metaweb to the subregions using the Jaccard distance resulted in differences ranging from 0.34 to 0.67 with a mean of 0.53. Somewhat simplified, the result can be interpreted as 53% of species found in the same group in the metaweb no longer being grouped together in the separate subregions. More specifically, however, the number of species is not directly connected to the Jaccard distance, as the index looks at the proportion of species in each group. Subsequently, small groups have the same weight as large groups. For example, if several small groups tend to break up more than a few large groups, the Jaccard distance will be high regardless the proportion of species the small groups comprise.

Dissimilarity in group structure between subregions varied more than compared to the metaweb, with Jaccard distances ranging from 0.20 to 0.76 (mean 0.57). The Jaccard distance and species overlap correlated significantly using a linear regression ($R^2 = 0.50$, $P < 0.001$). When we clustered the subregions based on their similarity in group structure, we obtained
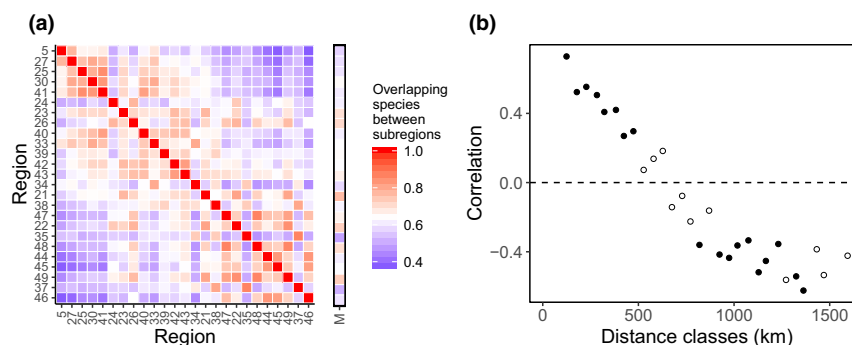
Figure 1 (a) Heat map of the fraction of shared species between the 25 subregions and the metaweb (M) in the Barents Sea. Subregions are ordered in ascending order of distance to subregion 5 as an arbitrary example. Numbers show the subregion ID:s as defined by Hansen et al. (2016) (b) Correlogram of spatial autocorrelation of shared species between networks based on their distance to each other, where autocorrelation is tested in 50 km increments. Filled circles indicate statistically significant autocorrelation according to Moran's I. Points above the line indicate positive autocorrelation, meaning that species compositions are more similar than by chance, and below the line negative autocorrelation, with species compositions more dissimilar than expected.
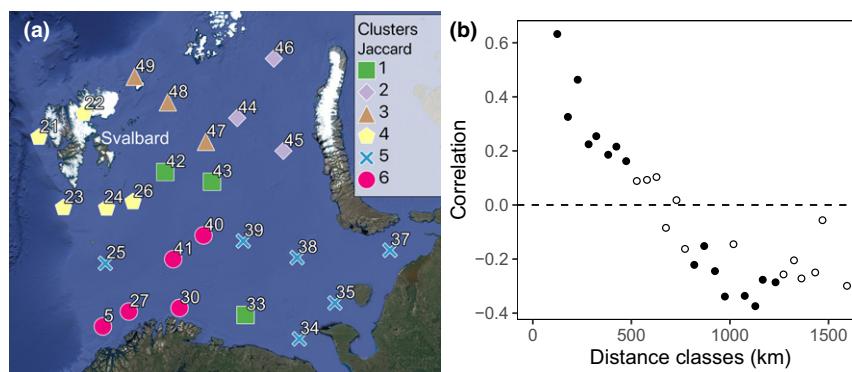
Figure 2 In (a) subregions are clustered based on their similarity in group structures measured by the Jaccard distance. The subregions within each of the clusters, except cluster 5 (blue crosses), showed similar community structures. Numbers show the subregion ID:s as defined by Hansen et al. (2016). Map generated with QGIS 3.2. (b) Shows a correlogram of spatial autocorrelation of the Jaccard distance between the merged subregions, where autocorrelation is tested in 50 km increments. Significant autocorrelation (either positive, above the dashed line, or negative below) was tested with Moran's I and indicated by filled circles.

six clusters (Fig. 2a). We found that one of the clusters had the same mean Jaccard distance as all subregions together (Fig. S2b; cluster 5, mean Jaccard distance: 0.57), while the other five clusters contained considerably more similar subregions (mean Jaccard distance excluding cluster 5: 0.35). Most of the subregions with similar group structure were geographically related, for example subregions 21–26 surrounding Svalbard (Fig. 2a). Indeed, the spatial autocorrelation correlogram showed a clear trend that spatially congregated subregions have more similar group structures than spatially separated subregions (Fig. 2b). While the subregions could be considered somewhat arbitrarily defined, a sensitivity analysis where subregions were merged pairwise retained the overall pattern of group structure similarity (Fig. S3).

While the group structure clearly related to species composition, the result also left room for ambiguity. For comparison, we also generated clusters based on species overlap (Fig. S4). At one extreme, the subregions belonging to clusters 2 and 3 based on group structure (Fig. 2a) also formed clusters based on species overlap. In other cases, the clustering based on species overlap generated clusters which diverged from the group

structure clusters, for example comparing subregions 25 and subregion 41. They belonged to the same species overlap cluster and shared 85% of the species between them and, being among the most similar subregion pairs in the Barents Sea regarding species composition. However, the group structures of subregions 25 and 41 differed substantially, scoring 0.5 in the Jaccard distance (Fig. S5 for compositional changes in the groups).

Environmental variables were tested for correlation to similarity in group structure using PERMANOVA. Indeed, similarity in group structure correlated significantly with water column temperature ($F_{1,22} = 5.08$, $P<0.001$, $R^2 = 0.17$) as well as ocean depth ($F_{1,22} = 2.38$, $P = 0.012$, $R^2 = 0.08$), with regions experiencing similar abiotic conditions having more similar group structures.

Species-wise group turnover

Species-specific group turnover, based on how often pairs of species remained in the same group in different regions, ranged between 0.0024 and 0.57 (median 0.096). Both herbivores
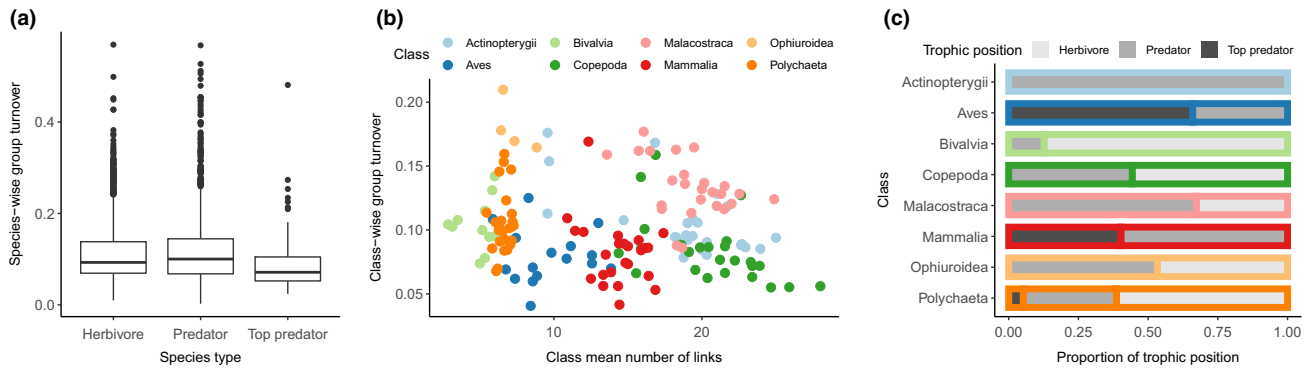
Figure 3 (a) Boxplot of the species-wise group turnover, separated into trophic positions. Data include all species and mean turnover in each network. Boxplots show medians, 1st and 3rd quartiles, whiskers include values up to 1.5 times the interquartile range, and points are outlying values outside these ranges. (b) Shows the average species-wise turnover for the eight most species-rich classes versus their mean number of interactions. Each dot represents the values for a subregion where the total number of species for the respective classes is more than five. (c) Shows the proportions of trophic positions for the species belonging to the classes included in (b).

and predators had relatively high turnover (medians 0.093 and 0.10 respectively), while top predators experienced slightly lower group turnover (median 0.071, Fig. 3a). The logarithmised species-wise group turnover correlated significantly with species number of links ($R^2 = 0.28$, $P<0.01$), where species with more links experienced less turnover. Looking at the group turnover rate for the eight most species-rich taxonomic classes, there was a clear pattern of how class identity held additional importance to the turnover rate (Fig. 3b). Yet, comparing these patterns to the composition of trophic positions for the respective classes (Fig. 3c) discerned little to no further explanation to the observed patterns. At finer scale, we found a very weak but significant correlation between species' trophic level and turnover ($R^2 = 0.018$, $P<0.001$).

An average of 1.5 species per subregion (ranging 1–4) did not share any interactions with other species in the same

group, hence being arguably weakly linked to the group. Indeed, these species experienced higher species-wise group turnover in webs where they did not share interactions with other group members (0.27 mean species-wise group turnover) compared to that in networks where the same species did share interactions (0.19 mean species-wise group turnover). However, due to the rarity of these cases, they will be perceived as outliers rather than change the general trends.

DISCUSSION

Here, we used the group model to analyse discrepancies and similarities in how species interact with each other across spatially divided, but related, ecological networks. Within a group identified by the group model, the species share a
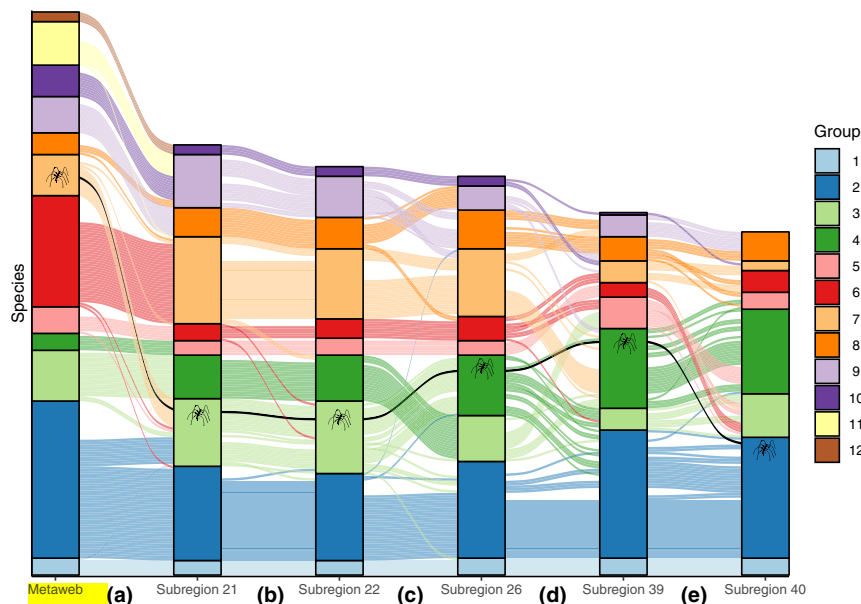
Figure 4 Alluvial plot with the metaweb and five different subregions. Boxes and their colour show species frequencies in the respective group partitions, and flow lines indicate how individual species change group partitions. As an example, the sea spider (*Pycnogonida spp.*) is marked with a black flow line.

similar set of consumers and/or resources. Species within such groups can be assumed to be functionally similar (Laigle 2018). As such identifying how a networks' group structure change between spatial scales and regions can provide important information on species ecological roles. We found that the differently composed and structured subregions (Kortsch *2018*) had group structures which differed substantially, both between each other and compared to the metaweb.

The comparison of the metaweb to its constituent subregions is important, as ecological networks are often compiled over large geographical areas (Dunne 2006). Ecological networks based on such inclusive regions are likely to include local differences in both species composition and patterns of interactions due to varying biotic and abiotic conditions. These differences in interactions can result in species fulfilling different ecological roles in different areas of the network (Laigle *et al.* 2018; Timóteo *et al.* 2018; Bartley *et al.* 2019). Such structural differences can have implications, both for the species direct sensitivity to disturbances (Sellman *et al.* 2016) and the effect of removal of a species on the rest of the community (Dunne 2006), including indirect effects (Eklöf & Ebenman 2006). Our results show that conclusions drawn from the analysis of a metaweb, where various local conditions melded together, should be interpreted with caution.

The group structure between subregions varied more between themselves than compared to the metaweb. This is expected, as while all subregions are subsets of the metaweb, the subregions themselves can be more or less unrelated in regard to both environment and species composition. Further, the subregions are likely influenced by their larger spatial context, for example bordering shorelines or being mainly surrounded by open sea, especially affecting mobile generalists (Bartley *et al.* 2019). This was partly supported by the subregion clusters based on the group structure, for example with a cluster surrounding Svalbard, and the clusters adjacent to the Arctic Ocean in the north.

Similar species compositions naturally relate to similar group structures. However, rather than only a quantitative dependence on overlapping species, the group structure seems further defined by a more fine-grained species composition. Hence, in some subregions with similar species composition, the group structure differed substantially (Fig. S5). The differences in group structures could include both functional changes, such as the forming of a new top predator group, and large compositional changes between groups of pelagic species. These structural differences likely affect various properties of both the network as a whole and on species level, including stability and population dynamics (Thébault & Fontaine 2010).

Importantly, species changing group memberships also suggests that their ecological roles change between subregions (Box 1). There are several empirical examples of species that change their ecological role depending on which environment they inhabit. For example, tiger sharks (*Galeocerdo cuvier*) in Australian waters change diet and thereby trophic position depending on whether feeding occurs in reefs, seagrass beds or pelagic habitats (Ferreira *et al.* 2017). Similarly, loggerhead turtles have different diets in pelagic and neritic areas (Hatase *et al.* 2002). In our analysis, species-wise group turnover

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Box 1. Example of group changes for the Sea Spider.

Here, we exemplify how a taxonomic class of species, in this case the sea spider class (Pycnogonida), changes group membership between different subregions (Fig. 4, the sea spider's group transitions marked black). In the metaweb, sea spiders belong to a group consisting strictly of other benthic species, including Echinodermata, Mollusca and Crustacea species. Tracking the flow of species from the metaweb to subregion 21 (Fig. 4a), we can see that the sea spider and the majority of species moves to group 3, together with an equally large assemblage of species from group 2. As a result, the new group consists of an additional large part of zooplankton species. While most of the species from the sea spider's old group followed, the additional added species from the other group increases the Jaccard distance. In the second comparison (Fig. 4b), the sea spider as well as the majority of species remain in the group, resulting in a low Jaccard distance. Similar to Fig. 4 c, despite most species changing groups, it is mainly an identity change, as the vast majority of species still remain grouped. However, for comparison D, the sea spider's group scatters substantially, resulting in a high Jaccard distance and the sea spider joining a group consisting mainly of fish species. A closer examination of the interactions of the sea spider reveals that in subregion 39, the sea spider is preyed upon by only generalist consumers. In subregion 26, in contrast, the sea spider has two additional predators, namely two more specialised species not present in subregion 39, creating a clear change in its set of interaction partners. For the last comparison (Fig. 4e), despite the two subregions being spatially adjacent, they belong to different clusters and there is considerable turnover of species. In this instance, the sea spider changes group membership from the group consisting mainly of fish species to a group with a mix of both zooplankton and benthic species.

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varied largely between subregions for individual species. This further suggests that while species retain their functional roles in some subregions, others have different conditions where the species change their ecological roles. For example, the common ling (*Molva molva*) is strictly piscivorous in subregion 5, but changes to a more mixed diet in subregion 25, while also experiencing high group turnover.

Species with more links generally had lower group turnover rates. Generalist species, here for example cod, are also habitat generalists in this system (Kortsch *et al.* 2015). Such species have both broader diets and a wide distribution in the region, which could explain the tendency to change groups less often. However, there was also a strong trend of relating species taxonomic identities to their group turnover rate (Fig. 3). For example, species in the classes Copepoda and Malacostraca had similar distributions of number of interactions, but clearly differed in their average species-wise group turnover; despite rather large variation in group turnover for the respective classes in different subregions, the classes rarely overlap in their distributions of species-wise group turnover.

Species taxonomic classifications are strongly coupled to species traits and have been shown to provide important information on how ecological networks are structured (Bersier & Kehrli 2008; Rossberg *et al.* 2010; Eklöf *et al.* 2012b). In fact, taxonomic information can be seen as a summary of several traits shared by closely related species. Certain species traits, such as body size and motility, have an intrinsic connection to network structure (Eklöf *et al.* 2013; Bartomeus *et al.* 2016), hence likely contribute to the observed class differences. Indeed, traits can act as taxonomic proxies, separating different components in (marine) ecosystems (Beauchard *et al.* 2017). In our analysis, highly mobile classes, such as Mammalia and Aves, always had relatively low group turnover rates, whereas more sessile classes, such as Ophiuroidea, had higher group turnover rates. Thereby, motility seems to play a key role, indicating that traits can be relevant indicators of species group turnover. Interestingly, species functionality in ecological networks is dependent on positioning in both trait space (physiological as well as behavioural) and trophic space (Coux *et al.* 2016), indicating that also species group membership is relevant for their ecological functioning.

A limitation in our study is that in the data set used, species interactions are not specific to the subregions, but literature based. Structural discrepancies between two empirical ecological networks can stem from two mechanisms; differences in species composition and differences in interactions (Poisot *et al.* 2012), both of which can lead to changes in group structure. Species interactions can depend on environmental settings (Schleuning *et al.* 2011; Ferreira *et al.* 2017), potentially enabling or disabling interactions in different subregions (Poisot *et al.* 2012; Chamberlain *et al.* 2014). Hence, in our case, some interactions which are considered present may actually be false positives (Cirtwill *et al.* 2019). Effects of such interactions risk propagating to additional species due to the recursive nature of the group model, assigning species into false groups that lack coherent ecological basis. Inferred from this, additional changes in interactions due to local variation will likely further influence the subregions' group structures.

CONCLUSIONS

Data collected as metawebs can provide a general overview of the diversity of species and interactions in geographical areas with homogeneous environmental conditions and habitats. However, local conditions in various regions of the same metaweb can have vastly different network structures, where small changes in species composition may lead to substantial changes in species' ecological and functional roles. In turn, these changes risk propagating into large structural changes, potentially changing network properties such as robustness, functionality and stability.

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AUTHORSHIP

Both the authors contributed to the ideas and writing. MO performed the analyses.

DATA ACCESSIBILITY STATEMENT

No new data were used in this study.

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