

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

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# Abstract

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

## 13 Introduction

14 A long-standing goal in ecological research is to identify which species, groups of species,  
15 or other structures are important for delivering and maintaining functionality in an  
16 ecosystem. Ecological networks such as food webs are commonly used to describe the  
17 structural patterns of species and their interactions within ecosystems (Newman 2003,  
18 Pascual & Dunne 2006). This approach is useful for understanding both broad-scale  
19 properties as well as properties of meso-scale structures and individual nodes in these  
20 networks (Allesina *et al.* 2008, Ings *et al.* 2009). The distribution of species interactions  
21 further affects species extinctions (Dunne *et al.* 2002, Eklöf & Ebenman 2006), stability  
22 (Allesina & Tang 2012), and functionality (Schindler 1990, Petchey & Gaston 2002).  
23 In the concept of the Eltonian niche, functional roles of species are defined by their  
24 interactions with other species (Elton & Elton 1927, Chase & Leibold 2003).

25 Accordingly, species with different sets of interaction partners possess different  
26 functional roles in the ecosystem. This view is closely related to the concept of trophic  
27 species used in early food web analyses (Dunne 2006), where species are merged into one  
28 trophic species if they share the same sets of prey and predators. The group model  
29 (Allesina & Pascual 2009) uses a relaxed version of the trophic species concept by  
30 organizing species into ecologically equivalent groups based on their patterns of  
31 interactions; species are grouped if they are prone to eat and be eaten by the same  
32 groups of species that in turn are prone to be eaten by the same set of species. The  
33 group model is equivalent to the stochastic block model used for community detection in  
34 network science. This recursive relationship implies that species which are distant from  
35 each other in the network still affect each other's group memberships (Krause *et al.*  
36 2003, Allesina & Pascual 2009, Schaub *et al.* 2016). Critically, species belonging to the  
37 same group have corresponding roles in the ecological network, and are thus also likely  
38 to share similar ecological functionality. The group model has indeed shown to produce  
39 groups of species with relevant ecological interpretations, such as trophic guilds and  
40 habitat patterns (Baskerville *et al.* 2011, Eklöf *et al.* 2012, Sander *et al.* 2015).

41 Reliable interpretations of structural patterns in ecological communities are however  
42 dependent on how data for ecological networks is obtained. Food web data is often  
43 collected over long time periods and large geographical areas in order to capture the  
44 majority of species or trophic interactions (Dunne 2006, Wood *et al.* 2015). The data is  
45 often presented as a metaweb, including all interactions observed over the whole area  
46 and time frame. This is certainly a valuable approach when the aim is to get an  
47 overview of the diversity of species and interactions in a region. However, if several areas  
48 of different types (e.g. coasts and open sea in a marine system) are aggregated, this may  
49 give an incorrect picture of the ecological network and its characteristics (Poisot *et al.*  
50 2012). In particular, all species may not be present in all local networks. Also, one may  
51 expect that even if a species does exist in both the coastal and open sea habitats, its  
52 interactions may differ depending on what other species are present in the respective

53 areas, differences in species traits between areas, etc. (Poisot *et al.* 2012, Bartley *et al.*  
54 2019). These differences can have important implications for both our general  
55 understanding of species functional roles in ecological networks, and also for local  
56 stability and robustness (McCann *et al.* 2005, Landi *et al.* 2018). When merging such  
57 differences into a metaweb, and potentially generating combinations of species and  
58 interactions that do not actually co-occur, the utility and reasoning based on such  
59 structures may be inaccurate or misleading.

60 Here, we evaluate whether the partitioning of species into ecologically equivalent groups  
61 differs i) between a meta (regional) network and local networks (subregions), and ii)  
62 between different subregions. In particular, we want to understand if certain groups of  
63 species and certain species are more variable in their group membership. We use a  
64 dataset from Barents Sea (Planque *et al.* 2014, Kortsch *et al.* 2018b), consisting of one  
65 meta network and several local networks from subregions describing the species present  
66 and their feeding interactions. The group model (Allesina & Pascual 2009) is used to  
67 identify the group structures of the different networks. The differences of the group  
68 structures are then compared using the Jaccard index of dissimilarity. Further, we  
69 analyse if certain species are more or less prone to change group membership. We show  
70 that the group structure in ecological communities is indeed affected by both spatial  
71 resolution and spatial location. Additionally, although the grouping of species clearly  
72 depends on the species composition, the group model reveals additional structural  
73 patterns which likely have implications for the functioning of ecological communities.

## 74 **Methods**

### 75 **Dataset**

76 We used a food web dataset describing the Barents Sea (Planque *et al.* 2014, Kortsch  
77 *et al.* 2018a). The Barents Sea a shelf sea with a heterogeneous environment bordering

78 the Atlantic Ocean, with the dissipating Gulf Stream in the west and the Arctic Ocean to  
79 the north-east (Fossheim *et al.* 2015). The food web data consists of a regional metaweb  
80 and 25 local food webs in subregions. The subregions are delimited by polygons whose  
81 boundaries are defined by the topography, and enclose areas which are relatively  
82 homogeneous with respect to hydrography and bathymetry (Hansen *et al.* 2016, Kortsch  
83 *et al.* 2018b). The metaweb includes 233 species and 2220 feeding interaction, with  
84 species ranging from avian and mammalian predators to primary producers (Planque  
85 *et al.* 2014, Kortsch *et al.* 2018b). The subregions include separate species occurrences  
86 with 115–178 species and 679–1771 interactions. We created the subregion food webs by  
87 filtering the metaweb to retain only those species present in the respective subregions  
88 and all interactions between them. A pairwise feeding interaction between two species in  
89 a subregion was assumed to occur if the species had been identified as interacting in the  
90 metaweb.

91 We made small modifications to the original dataset to ensure that all species that were  
92 not primary producers were still connected to food resources; the fish genus *Sebastes*  
93 *spp.* lacked prey species in 14 of the subregions. To address this problem, we added the  
94 complete set of interactions from three specific species from the same genus, namely *S.*  
95 *marinus*, *S. mentella* and *S. viviparus*. As *Sebastes spp.* is already an aggregate of  
96 multiple species, this likely reduced the impact of our modification to a slight  
97 over-representation of the genus.

## 98 **Group model**

99 In order to evaluate the “best” partitioning of the species into structurally functional  
100 groups, we used the group model (Allesina & Pascual 2009, Sander *et al.* 2015). The  
101 model provides a likelihood-based framework to calculate how well a specific  
102 partitioning of species into groups fits an empirical network structure. Groupings with a  
103 high likelihood have groups of species which acts in a similar way, that is, species within

104 a group tend to eat and be eaten by the same other groups (Allesina & Pascual 2009).  
 105 We chose the group model due to its strong ecological reasoning in addition to its  
 106 recognized performance (Baskerville *et al.* 2011, Yan *et al.* 2014, Sander *et al.* 2015).  
 107 The group model uses a likelihood-based approach to find an optimal grouping. A  
 108 network (food web)  $A$  has  $S$  nodes (species) and  $L$  directed links (feeding interactions)  
 109 between the nodes. These relationships can be described with an adjacency matrix,  
 110 where  $A_{ij} = 1$  means that  $i$  resource is eaten by consumer  $j$ . Based on the knowledge  
 111 from the empirical web, there is a probability  $P$  to randomly create the same network  
 112 when using the same number of nodes and probability  $p$  of links between the nodes:

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

113 The group model expands this by instead looking the probability of randomly creating a  
 114 network  $A$ , where the nodes in group  $i$  have the same probabilities  $p_{ij}$  to connect to  
 115 nodes affiliated to the different groups  $j$ , for  $k$  number of groups.

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

116 where  $\vec{p}$  is a vector of probabilities for links between all combinations of groups. By  
 117 testing different sets of groups, the aim is to find the partitioning with the highest  
 118 probability of reproducing an empirical network.

119 The different combinations of groups differ in their number of parameters. Therefore, we  
 120 cannot directly compare the likelihoods, but have to use some type of model selection to  
 121 balance the goodness of fit with model complexity. Model selection can here be  
 122 performed by calculating the Bayes factor (Eklöf *et al.* 2012, Sander *et al.* 2015), or by  
 123 choosing the partition with the highest marginal likelihood.

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

124 With increasing numbers of species in the networks, the possible combinations of groups  
125 quickly become technically overwhelming. Hence, we compared marginal likelihoods  
126 while searching for better groupings instead of calculating all possible groupings.  
127 Following Sander *et al.* (2015), we searched for the partition of species into groups that  
128 maximizes the marginal likelihood by using Metropolis-Coupled Markov Chain Monte  
129 Carlo ( $MC^3$ ) with a Gibbs sampler. For both the metaweb and each subregion, the  
130 algorithm was executed 10 times, each with a random seed, 300,000 MCMC steps and  
131 20 MCMC chains. For each network, if multiple different groupings were produced, the  
132 grouping with the highest marginal likelihood was selected.

### 133 **Similarity between groups**

134 We were interested in how the partitioning of the species into groups changed between  
135 the metaweb and the subregions, and between the subregions. This would give an  
136 insight in whether, and how, groups of species as well as specific species changed roles  
137 depending on resolution and location. To track both how the overall group structures  
138 changed and also whether certain species or taxa were more prone to changing groups,  
139 we used two approaches.

### 140 **Jaccard index of dissimilarity for comparison of partition similarity**

141 To track how the overall group structure changed between networks, we used “best  
142 match” comparisons with the Jaccard index of dissimilarity which, for each group in a  
143 network, searched for the most similar match in a compared network. The “best”  
144 grouping, or community, in web  $A$  was defined as  $C^A$ . We analysed to what extent each  
145 group  $k$  in  $C^A$  resembled any group  $l$  in  $C^B$ . The most similar group was defined as the  
146 group in  $C^B$  where the most species from group  $C_k^A$  were still grouped together. We then  
147 divided the number of species in the most similar group by the total number of unique  
148 species in groups  $k$  and  $l$  from both webs. After doing this for all groups  $n$  in web  $A$ , we

149 then calculated the mean dissimilarity:

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

150 The dissimilarity index takes the value of 0 when communities  $A$  and  $B$  are identical,  
151 and approaches 1 as they become increasingly dissimilar. The Jaccard index risks being  
152 affected by differences in the number of groups between compared networks, though  
153 these effects were limited in our case (see Fig. S1 in Supporting Information).

154 Additionally, the index differs depending on the direction of the comparison (network  
155  $A \rightarrow B$  or network  $B \rightarrow A$ ). To normalise these effects, we measured the dissimilarity  
156 both way for each network pair and calculated their average:

$$J(C^A, C^B) = \frac{J(C^A, C^B) + J(C^B, C^A)}{2} \quad (5)$$

157 The methodology is based on Calatayud *et al.*, 2019, arXiv:1905.11230.

## 158 **Cluster optimization**

159 To investigate whether some subregions were more similar regarding group structure, we  
160 clustered the subregions based on the Jaccard index of dissimilarity as well as based on  
161 species overlap. We generated the clusters in two steps; first, we used the Uniform  
162 Manifold Approximation and Projection (UMAP, McInnes *et al.* 2018). UMAP is a  
163 dimension reducing algorithm which favours preserving local distances over global. In  
164 our case, this meant that the results from the UMAP were more focused on grouping  
165 similar webs together than accurately describing how dissimilar very different webs were.

166 By changing the number of neighbours (ranging from two, to the total number of  
167 subregions, 25), the projection additionally varied in its focus on local versus regional  
168 similarities. In the second step, we analysed all projections with different neighbour  
169 settings for clusters using the HDBSCAN (Hierarchical density-based spatial clustering

170 of applications with noise) method (Campello *et al.* 2013). We arbitrarily set the  
171 minimum cluster size to three subregions. From the results we selected the best network  
172 clustering, that is, the one with the lowest mean dissimilarity within the clusters. Since  
173 the UMAP projections varied slightly, we repeated this process 10 000 times, from which  
174 we chose the best clustering.

### 175 **Species-wise group turnover**

176 For all species, we compared the group-relations of all pairs of species to see whether  
177 they were in the same group. By then comparing these pairwise relations to the same  
178 pairs in other webs, we obtained a measurement of how prone individual species or taxa  
179 were to changing their group-relations between webs. Accordingly, for each species we  
180 identified all possible species pairs (excluding mirrored and self-paired) in a network *A*.  
181 We checked whether each species pair was in the same or different groups in network *A*.  
182 We then compared the status of all pairs in network *A* to their status in all other  
183 networks. If the relationship for a species pair changed (either different groups  $\rightarrow$  same  
184 group, or same group  $\rightarrow$  different group) between two webs, there was turnover (Table  
185 1). From this, we calculated the proportion of pairs for each species which experienced  
186 turnover to obtain the mean species pairwise group turnover. For comparing the pairs in  
187 different networks, we only considered species which co-occurred between the two  
188 networks.

### 189 **Species and network metrics**

190 Taxonomic classifications of species were obtained from Kortsch *et al.* (2018b). We  
191 calculated the number of interactions and trophic levels for all species in both the  
192 metaweb and in each subregion. For species trophic level we used the NetIndices package  
193 in R (Kones *et al.* 2009), which uses the method from Christensen & Pauly (1992).  
194 Accordingly, the trophic level of primary producers and detritus is set to one, and

195 subsequent species are set to one plus the sum of their prey trophic levels, multiplied by  
196 the constituted diet proportions. We also calculated species overlap for all networks  
197 (metaweb and all subregions); for each pair of networks we calculated the number of  
198 species shared between two networks divided by the total number of unique species in  
199 both networks.

## 200 **Correlation with environmental factors**

201 To check for spatial autocorrelation for the group structure, we used the *correlog*  
202 function in the *nfc* package (Bjornstad 2018) in R. The function looks for autocorrelation  
203 using distance classes, which are tested using Moran’s I and then visualised as  
204 correlograms. Correlation between similarity in group structure and water column  
205 temperature as well as ocean depth was tested using a permutation-based multivariate  
206 analysis of variance (PERMANOVA) test, conducted using the *adonis* function from the  
207 *vegan* R package, (Oksanen *et al.* 2018) with 10 000 permutations and no stratification.

## 208 **Results**

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

215 Comparing the group structure of the metaweb to the subregions using the Jaccard  
216 index of dissimilarity resulted in differences ranging from 0.34–0.67 with a mean of 0.53.  
217 Somewhat simplified, the result can be interpreted as on average, 53% of the species  
218 found in the same group in the metaweb were no longer grouped in the separate

219 subregions. More specifically however, the number of species is not directly connected to  
220 the Jaccard index, as the index looks at the proportion of species in each group.

221 Subsequently, small groups have same weight as large groups. For example, if several  
222 small groups tend to break up more than a few large groups, the dissimilarity index will  
223 be high regardless of how big proportion of the amount of species the small groups  
224 comprise.

225 Comparing the subregions to each other, the dissimilarity in group structure had a  
226 bigger variability than when compared to the metaweb, ranging from 0.20–0.76 with a  
227 mean of 0.57. When we clustered the subregions based on their similarity in group  
228 structure, we obtained six clusters (Fig. 2A). We found that one of the clusters had the  
229 same mean dissimilarity as all subregions together (Fig. S2B; cluster 5, mean Jaccard  
230 dissimilarity: 0.57), while the other five clusters contained considerably more similar  
231 subregions (mean Jaccard dissimilarity excluding cluster 5: 0.35). Most of the subregions  
232 that were similar in their group structure were located in the same region, e.g.  
233 subregions 21–26 surrounding Svalbard (Fig. 2A). Indeed, the spatial autocorrelation  
234 correlogram showed a clear trend that spatially congregated subregions have more  
235 similar group structures than spatially separated subregions (Fig. 2B). Additionally, the  
236 Jaccard index and species overlap correlated significantly using a linear regression  
237 ( $R^2=0.50$ ,  $p<0.001$ ). Similarity in group structure also correlated significantly with  
238 water column temperature ( $F_{1,22}=5.08$ ,  $p<0.001$ ,  $R^2=0.17$ ) as well as depth ( $F_{1,22}=2.38$ ,  
239  $p=0.012$ ,  $R^2=0.08$ ), with regions experiencing similar abiotic conditions having more  
240 similar group structure.

## 241 **Species-wise group turnover**

242 Species-specific group turnover, which was based on how often pairs of species remained  
243 in the same group in different regions, ranged from 0.0024–0.57 with a median of 0.094.  
244 In general, primary producers had a very low turnover (0.015 median), meaning that

245 they generally stayed grouped independent of subregion (Fig. 3A). Both herbivores and  
246 predators had relatively high turnover (medians 0.093 and 0.10, respectively), while top  
247 predators experienced slightly lower group turnover (median 0.071). Species-wise group  
248 turnover correlated significantly with species number of links ( $R^2=0.29$ ,  $p<0.01$ ), where  
249 species with more links experienced less turnover. Looking at the group turnover rate for  
250 the eight most species rich classes, there was a clear pattern of how class identity held  
251 additional importance to the turnover rate (Fig. 3B). Yet, comparing these patterns to  
252 the composition of trophic positions for the respective classes (Fig. 3C) discerned little  
253 to no further explanation to the observed patterns.

## 254 Discussion

255 Ecological communities are complex with numerous interacting species. Grouping these  
256 species in different ways is common practice in order to simplify the community  
257 structures and potentially reveal underlying factors which are important for community  
258 functionality. Here, we used the group model to analyse discrepancies and similarities in  
259 how species interact with each other across spatially divided, but related, ecological  
260 networks. The trophic roles defined by the group model can be thought of as functional  
261 groups, since the species within a group are defined based on their direct and indirect  
262 relationships to other groups of species. Accordingly, species within a group tend to  
263 interact with other species in the network in a similar way. We looked at how these  
264 groupings changed from two perspectives; (i) from a metaweb perspective with  
265 comparisons to the constituent subregions, and (ii) from a subregion perspective with  
266 comparisons between different subregions. Both perspectives showed substantial  
267 differences in group structures, with different species being varyingly prone to changes  
268 group memberships.

269 The comparison of the metaweb to its constituent subregions is important because  
270 interaction networks are often compiled over large geographical areas (Dunne 2006).

271 Ecological networks based on such inclusive regions are likely to include local differences  
272 in both species composition and patterns of interactions due to varying biotic and  
273 abiotic conditions. Indeed, we found substantial differences in the group structure  
274 between the metaweb of the Barents Sea and its subregions, indicating that species were  
275 organised differently depending on data resolution and region considered. Consequently,  
276 identification of species' ecological roles inferred from the general interaction patterns of  
277 a metaweb can result in erroneous conclusions on network structure and functioning.

278 Structural discrepancies between a metaweb and its subregions can stem from two  
279 mechanisms – i) differences in species composition or ii) differences in interactions –  
280 both of which can lead to changes in group structure. The dataset used here is based on  
281 the metaweb concept, which assumes that a pair of species interacting in one location  
282 will do so whenever present together. Therefore, structural changes can only come from  
283 changes in link structure directly dependent on the species composition (i.e., if an  
284 interaction partner  $j$  of species  $i$  is present in location  $A$  but not in location  $B$  the  
285 interaction will only be realized in location  $A$ , and accordingly  $i$  will have a changed set  
286 of interactions). Inferred from the previous reasoning, using local food webs where  
287 interactions have been directly sampled will likely give a more accurate identification of  
288 group structure. Nevertheless, at the very least we here present a picture of species  
289 composition and its variation between areas, and most importantly how these factors  
290 affect group structure. Indeed, species inhabiting different habitats can have different  
291 preys and predators reflecting the local species composition, and thus play different  
292 ecological roles (Timóteo *et al.* 2018, Bartley *et al.* 2019). Such structural changes can  
293 have implications both for the species direct sensitivity to disturbances (Sellman *et al.*  
294 2016) and the effect of removal of a species on the rest of the community (Dunne 2006)  
295 including indirect effects (Eklöf & Ebenman 2006).

296 However, it is not necessarily true that a pair of species will always interact if present  
297 together, as the presence of an interaction can be dependent on different environmental  
298 settings (Schleuning *et al.* 2011, Ferreira *et al.* 2017), which will enable or disable

299 specific interactions (Poisot *et al.* 2012, Chamberlain *et al.* 2014). Changes in  
300 interactions due to this mechanism are not accounted for in the dataset analysed here,  
301 as the metaweb from where the interactions are inferred merges all different habitats  
302 and potentially different trophic roles, from which the groups are then defined.  
303 Subsequently, interactions which are considered present in a subregion may actually be  
304 false positives (Cirtwill *et al.* 2019). Given the recursive nature of the group  
305 identification, the effect of these merged roles risks propagating to more species,  
306 assigning them into “false” groups that may lack coherent ecological basis. Inferred from  
307 this, our results can be considered as representing the maximum possible similarity  
308 between groups, with species’ roles likely being more variable in reality.

309 When comparing subregions to each other, we found that their group structures varied  
310 more between themselves than when compared to the metaweb. In this dataset, the  
311 subregions were originally defined from their distinct environmental features (Hansen  
312 *et al.* 2016). Accordingly, the subregions vary in how similar they are to each other,  
313 including environmental factors such as average temperature and days of ice cover, but  
314 also variation in habitat types such as coastal and open water. This contributes to  
315 differences in species compositions, and subsequently group structure. Accordingly,  
316 species can potentially change its realized ecological role between the various subregions  
317 more than compared to the “averaged” roles obtained from the metaweb. The large  
318 variability in group structure between subregions motivated our clustering analyses of  
319 the subregions. Based on the Jaccard index results, aside from six subregions which did  
320 not have more in common than the overall mean, the subregions formed spatially related  
321 clusters based on group structure similarity. However, while the subregions were  
322 generally adjacent, spatial context often differed between clusters; for example  
323 depending on whether they included a shore line (e.g., cluster 4, Fig. 2A) or included  
324 mostly open sea (e.g., cluster 2, Fig. 2A). The relationship between spatial context and  
325 group structure was further supported by the positive correlation between group  
326 structure similarity and both ocean depth and sea temperature.

327 There was a clear relationship between species composition and group structure, but the  
328 result also left room for ambiguity. For comparison, we also generated clusters based on  
329 species overlap (see Fig. S2). At one extreme, the subregions belonging to clusters 2 and  
330 3 based group structure (Fig. 2A) also formed clusters based on species overlap. In other  
331 cases, the clustering based on species overlap generated clusters which diverged from the  
332 group structure clusters, e.g., comparing subregions 25 and subregion 41. They belonged  
333 to the same species overlap cluster and shared 85% of the species between them and, as  
334 such, were among the most similar subregion pairs in the Barents Sea regarding species  
335 composition. However, the group structures of subregions 25 and 41 differed  
336 substantially, scoring 0.5 in the Jaccard dissimilarity index. Hence, rather than only a  
337 quantitative dependence on overlapping species, the group structure was further defined  
338 by a more fine-grained species composition (see Fig. S3). The group changes included  
339 both clear functional changes, such as the forming of a top predator group and a  
340 *Copepoda* group, but also big compositional changes in the pelagic and surface species  
341 groups. As the groups were based on similarities in trophic interactions, the example of  
342 the forming of a top predator group in subregion 41 suggested that some predatory  
343 species were no longer present, and thus some of the species in subregion 25 branched off  
344 to form a new solely predatory group. Group differences such as these likely affect  
345 various ecological properties, including stability and population dynamics (Thébault &  
346 Fontaine 2010).

347 There are several empirical examples of species that change their ecological role  
348 depending on which environment they are present in. For example, tiger sharks in  
349 Australian waters change diets and trophic position depending on if feeding occur in  
350 reefs, seagrass based or pelagic habitats where food web composition differ (Ferreira  
351 *et al.* 2017), and loggerhead turtles change diet depending on if feeding occur in pelagic  
352 or neritic areas (Hatase *et al.* 2002).

353 From a species perspective, there was large variability in how frequently-grouped species  
354 pairs changed relationships. Primary producers such as algae or phytoplankton

355 experienced the least pairwise turnover. Yet, there was no further relationship with  
356 trophic level. Instead we found a slight, but statistically significant, correlation with  
357 number of interactions of species, where species with more links had lower turnover  
358 rates. However, this trend was seemingly outweighed by the species taxonomic identities  
359 (Fig. 3). For example, species in the classes Copepoda and Malacostraca had similar  
360 distributions of number of interactions, but clearly differed in their average species-wise  
361 turnover. Despite rather large differences in turnover between subregions, the two  
362 example classes rarely overlap in their distribution of species-wise turnover.  
363 Additionally, there was large variation in the turnover rates for the different taxa  
364 between different subregions; that is, between some subregions, the majority of group  
365 members stayed intact, while in others, species split into completely different groups  
366 (example in Box 1). This further strengthens the idea that the roles of a relatively large  
367 proportion of species are dynamic and dependent on local conditions.

## 368 **Conclusions**

369 Species interactions drive many ecological processes in food webs. Therefore, finding  
370 groups of species that are structurally similar is essential for our understanding of the  
371 functioning of ecological networks. Although all groups identified by the group model  
372 are not by necessity relevant for ecosystem functionality, species within a group do  
373 possess a unique ecological role different from species in other groups. Despite the often  
374 large overlap in species composition between the subregions in the Barents Sea dataset,  
375 we here show that there are still large differences their group structures, both when we  
376 compare the metaweb to more geographically limited subregions and when we compare  
377 subregions to each other. Hence, the ecological roles of the species often differ  
378 substantially depending on their spatial context. Species functionality in ecological  
379 networks is dependent on positioning in both trait space (physiological as well as  
380 behavioural) and trophic space (Coux *et al.* 2016). When a species' trophic position

381 changes, this recursively changes other species positions, potentially affecting the whole  
382 network. Consequently, even relatively small differences in species composition risks  
383 propagating into substantial differences in group structures. We conclude that data from  
384 metawebs can provide a general overview of the diversity of species and interactions in  
385 geographical areas with homogeneous environmental conditions and habitats.  
386 Nevertheless, in order to understand the role of a specific species in a network, we must  
387 consider that local conditions can have a large effect on the community composition and  
388 interaction pattern, subsequently changing species functional roles, with possible  
389 implications for network robustness, functionality and stability.

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## 507 **Supporting information**

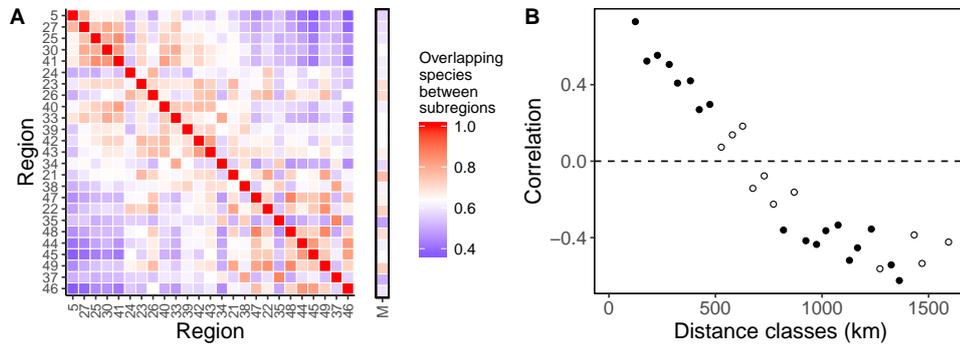
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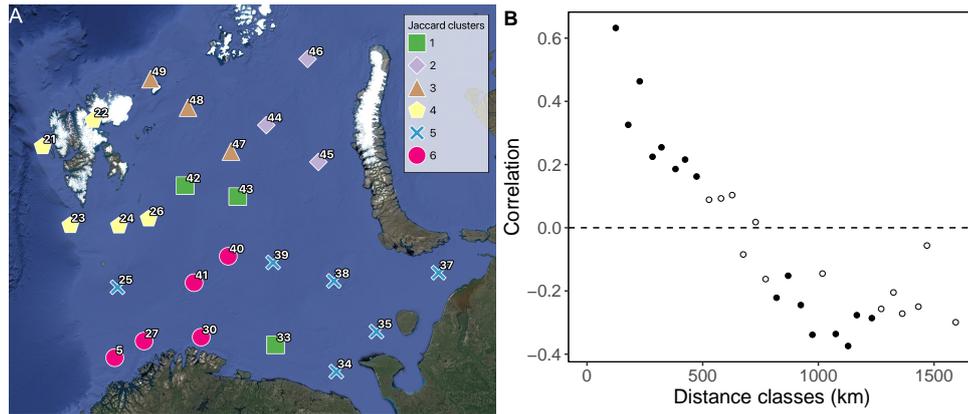
## Tables

**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. 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.*

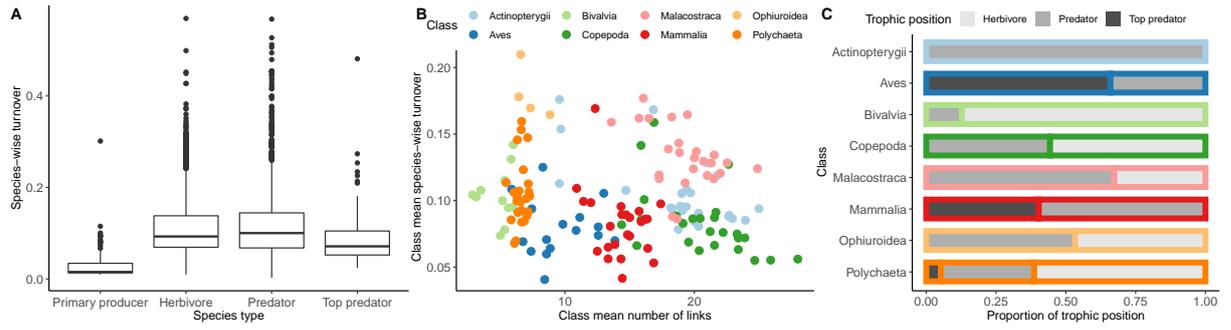
Network A		Network B		Same group?			
Species	Group	Species	Group	Pairs	Net A	Net B	Turnover
a	1	a	1	a-b	yes	no	1
b	1	b	2	a-c	no	yes	1
c	2	c	1	a-d	no	no	0
d	2	d	3	a-e	no	no	0
e	3	e	2	a-f	no	no	0
f	3	f	3	Species <b>a</b> turnover: 2/5			



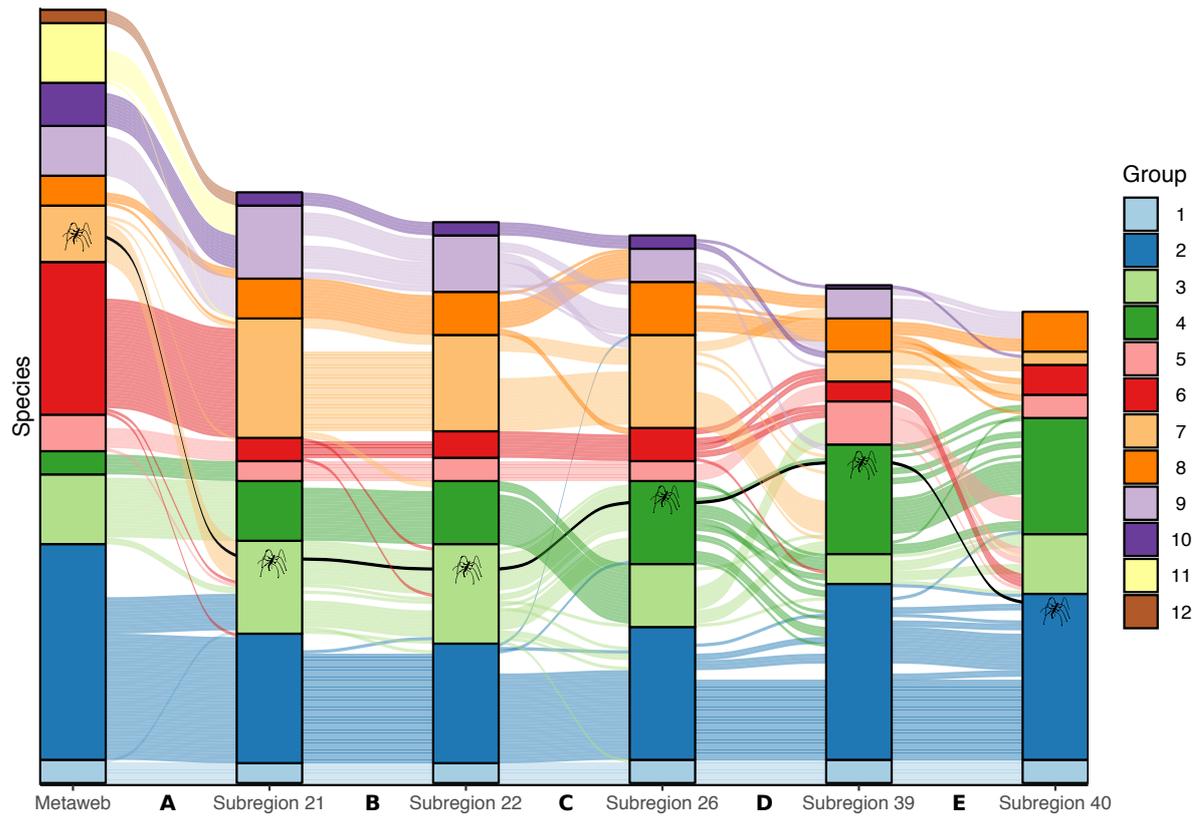
**Figure 1:** **A:** Heat map of the fraction of shared species between the 25 subregions and the metaweb ( $M$ ) in the Barents Sea. Subregions are ordered in ascending order of distance to subregion 5 as an arbitrary example. **B:** Correlogram of spatial autocorrelation of shared species between networks based on their distance to each other. 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 index of dissimilarity. 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). **B** shows a correlogram of spatial autocorrelation for the Jaccard index of dissimilarity. Significant autocorrelation (either positive, above the dashed line, or negative below) was tested with Moran's I and indicated by filled circles.



**Figure 3:** *A:* Boxplot of the species-wise turnover, separated into trophic positions. Data includes 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*.



**Figure 4:** Alluvial plot with the metaweb and five different subregions. Boxes and their color 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.

**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 dissimilarity index. In the second comparison (Fig. 4B), the sea spider as well as the majority of species remain remain in the group, resulting in a low Jaccard index. Similarly to Fig. 4C, 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 index and the sea spider joining a group consisting mainly of fish species. 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 groups from the group consisting mainly of fish species to a group with a mix of both zooplankton and benthic species.