

Food-web aggregation, methodological and functional issues

Benoît Gauzens, Stéphane Legendre, Xavier Lazzaro and Gérard Lacroix

B. Gauzens (gauzens@biologie.ens.fr) and G. Lacroix, UMR 7618-Bioemco (CNRS, ENS, INRA, UPMC), École Normale Supérieure, 46, rue d'Ulm, FR-75230 Paris cedex 05, France. GL also at: UMS 3194 CEREEP – Ecotron IDF (CNRS, ENS), 78 rue du Château, FR-77140 Saint-Pierre-Lès-Nemours, France. – S. Legendre, UMR 7625-Ecologie et Evolution (CNRS, ENS, UPMC), École Normale Supérieure, 46, rue d'Ulm, FR-75230 Paris cedex 05, France. – X. Lazzaro, UMR BOREA IRD 207/CNRS 7208/MNHNI/UPMC, Unidad de Limnología y Recursos Acuáticos (ULRA), Univ. Mayor de San Simón (UMSS), CP 2352, Cochabamba, Bolivia.

Trophic species in food webs are often aggregated into fewer groups, using theoretical and empirical approaches, either for modelling tractability or because of the lack of data resolution. Heterogeneities in the resolution of food webs used in the literature have led to question their use to establish general topological rules. Despite an increasing number of studies relating topology to ecosystem functioning, we still have no idea on how species' aggregation affects our perception of network functionalities. Therefore, we re-examined the conclusions drawn from an experimental manipulation relating top-predator foraging behaviour and biomass to food-web topology (Lazzaro et al. 2009) by aggregating a 74-species network according to different criteria (taxonomy, trophic similarity, size, expertise). We found that initial significant effects and functional properties were preserved over a large portion of the aggregation gradient (2/3) despite strong variations in the topological descriptor values along the gradient. Aggregation tended to produce more type II errors (false positive) than type I errors, advocating that most effects in aggregated networks are not methodological artefacts. Aggregation by taxonomy, trophic similarity and expertise better preserved functional properties (down to 38, 30 and 17 nodes, respectively) than aggregation by size (down to 40 nodes). Our results suggest that it is possible to relate the structure of aggregated networks to ecosystem properties provided that the methodological approaches are standardized and the level of lumping does not exceed a reasonable threshold.

Understanding how trophic interactions affect community dynamics and ecosystem functioning is a major goal in ecology. Mechanisms involved in trophic relationships have been studied in highly distinct aquatic and terrestrial communities, using both theoretical and empirical approaches. In order to focus on system functionalities, or to reduce the complexity of trophic interactions in ecosystems, researchers have often aggregated complex trophic networks into more simple ones. For instance, by comparing theoretical models of intermediate complexity and experimental approaches, Hulot et al. (2000) showed that models integrating key information on prey edibility, size refuges to predation and omnivory successfully predict the responses of aquatic food webs to environmental perturbations.

However, the aggregation of food webs into fewer components brings several questions: what is lost when simplifying food webs? To which extent can we reduce food-web complexity without losing essential information about functionality? For example, it is necessary to consider all species in a site to analyse indirect interactions like the impact of omnivory on trophic cascades, or the effect of species loss within food webs (Petchey et al. 2004).

A food web is conveniently represented by a directed graph where arcs represent the trophic interactions and

nodes represent the actors of these interactions. The actors of trophic interactions are usually thought of as 'species' or 'trophic species'. But, are these actors precisely defined? In the construction of food webs, the term 'species' is in fact ambiguous. For example, in Bacteria, the notion of species is not well defined, and bacteria are usually represented as a single node in trophic networks, though they could be further divided into several nodes according to various criteria. Also, in some taxa, different ontogenetic stages (e.g. larval, juvenile and adult) ought to be represented by different nodes because these stages do not consume the same resources. Moreover, some taxa are not resolved at the species' level because the expertise is rare and not always available (e.g. identification criteria are frequently less precise on the larval or juvenile stage than on the adult stage). In the sequel, we shall still call 'species' the nodes of a well-resolved food web, keeping in mind that these nodes do not always correspond to species in the taxonomic sense.

Representing the food web as a directed graph provides several informative descriptors, generic to networks (e.g. connectance) or specific to food webs (e.g. trophic height). To understand the relationships between network descriptors, community dynamics, and ecosystem functioning

(Jordán and Scheuring 2004), one can explore global patterns, as May (1972), who determined constraints on connectance values and interaction strengths to ensure food-web stability. In a more descriptive approach, general rules based on meta-analyses, have been proposed for the relationships between topological descriptors and factors constraining their values, e.g. the relationship between the number of links and the number of species (Cohen et al. 1993, Ings et al. 2009), and the constancy of the ratio of the number of predators to the number of prey (Closs et al. 1993). Unfortunately, these approaches were limited by heterogeneities in the resolution of food webs used in the literature, which ranged from the species or infraspecific level to large functional groups. Such discrepancies have led to question the use of differently resolved food webs to establish general topological rules (Paine 1988).

These points raise the question of 1) the quantity of biological information needed to understand the relationship between food-web architecture and ecosystem functioning, and 2) the relationship between food-web resolution and the pertinence of topological descriptor values. The problem has led to contrasted results across studies (Abarca-Arenas 2002, Angelini and Agostinho 2005 for functionality; Sugihara et al. 1989, 1997, Martinez 1991, 1993, Baird et al. 2009 for topological incidence). For example, Sugihara et al. (1989, 1997) found that most descriptors were insensitive to aggregation, whereas Martinez (1991, 1993) concluded that most of them were affected. Results may also depend upon the aggregation method: (a) taxonomy (lumping species to the genus or family level), (b) trophic similarity (e.g. lumping species with the highest percentage of common links, Martinez 1991), (c) body size (Optiz 1993), or (d) 'groups of convenience' to mimic the unevenness of taxonomic resolution in most food-web studies (Thompson and Townsend 2000, Angelini and Agostinho 2005). Other types of aggregation have been considered: temporal and spatial aggregation (Jordán and Osváth 2009, Poisot et al. 2012). This is not the topic of this study.

Food-web organisation is a central issue in ecology (Woodward and Hildrew 2001, Tylíanakis et al. 2007, Layer et al. 2010). Beyond the potential effect of network resolution on topological descriptor values, exploring how food-web resolution affects the perception of its organisation is essential (Jordán 2003). How the simplification of food webs modifies the nature, magnitude, and significance of the relationships between functional properties and food-web architecture has not been explored. The topic is challenging when the goal is to study food-web dynamics using networks that have a low number of nodes but keep the functional properties of more detailed ones. First, one should wonder whether actual topological responses to community changes are true regardless of network resolution. Second, potential discrepancies in response to different aggregation methods might also bring additional information on the effects of environmental factors on community components, and thus on community structure.

Herein, we explored both the responses of topological descriptors and the robustness of relationships between ecosystem functioning and food-web topology to different

aggregation methods. To this end, we reconsidered the results of an experimental study based on a well-resolved aquatic food-web. This experimental study focused on the impact of the fish foraging type and biomass on food-web topology (Lazzaro et al. 2009).

Our results indicate that 1) the comparison of aggregated food webs properties remains informative provided that the food webs are constructed with similar rules and at similar resolution levels, and 2) the relationships between topology and ecosystem functioning remain valid over a rather large aggregation gradient provided that food webs are aggregated using biologically relevant methods, applied consistently within the same study. We find that even if topological descriptor values are modified by the aggregation process, biologically relevant aggregation methods (size, trophic similarity, taxonomy, biological expertise) lead to a surprisingly low number of misinterpretations when compared to the results obtained with the fully resolved food web.

Material and methods

Experimental study

Using different aggregation levels and methods, we reanalysed the data of Lazzaro et al. (2009) exploring the link between fish feeding behaviour and network topology. This study was based on a four-week mesocosm experiment involving four fish biomass levels (10, 30, 50 and 75 g m⁻³), each associated with two planktivorous fish species representative of contrasted foraging behaviours on plankton. Each treatment was duplicated and weekly sampled (more details in Lazzaro et al. 1992). The top-predators were the filter-feeding gizzard shad *Dorosoma cepedianum* and the visually feeding bluegill *Lepomis macrochirus*. The study showed that food-web topology (described using a large set of topological descriptors) is significantly impacted by the predator foraging type. Compared with food webs comprising a visually feeding fish, food webs with a filter-feeding fish displayed a higher specific richness, and shared more edible basal species. They were also less pyramidal (higher percentage of top predators), more connected, and had a higher number of chains, which were shorter. In presence of the filter feeder, consumers were also more generalist and omnivorous. Fish biomass affected only marginally the topological descriptors.

Cumulated versus instantaneous food webs

In a first step, we constructed a cumulated binary food web comprising 74 species, taking into account all taxa observed in the whole experiment. All taxa were identified to the species level, with the exception of copepod nauplii, benthic invertebrates (chironomids) and bacteria. As mentioned in the introduction, within Copepods, two ontogenic stages (nauplii copepodids and adults) were considered as different trophic species. Feeding links in the cumulated network were attributed mainly using detailed knowledge of the literature, and personal expertise. In a few instances, when information was not available in the literature,

well-known allometric relationships between filter feeders and their prey (Burns 1968) were used. To assess fish effects on food-web architecture, we constructed an ‘instantaneous’ food web as a subsample of the 74-species network, for each tank on each sampling date, by including only the observed taxa. Note that Lazzaro et al. (2009) focused on the comparison of the topological effects of the two fish species, and used a 58-species cumulated food web (fish treatments only). Our more complete network was based on a larger set of treatments (including fishless tanks and tanks containing the two fish species), which were combined to the data used by Lazzaro et al. (2009) in order to estimate the correlation between the percentage of inedible basal species and the chlorophyll-*a* concentration.

Food-web descriptors

We used 15 classical topological descriptors, most of them used in Lazzaro et al. (2009). They can be split into four categories.

Species properties

Species were classified as basal (primary producers, i.e. having no prey), intermediate consumers (having both prey and predators), and top consumers (having no predators and at least one prey), and their numbers were computed for each food web. Basal species were either edible (initiating at least one food chain) or inedible (having no consumer). We used the percentages of basal, edible or inedible, intermediate and top species as descriptors.

Link properties

The link density (L/S) is the ratio of the number of trophic links (L) to the number of species (S). Connectance ($C = L/S^2$) is the number of realized links over the number of possible links.

Trophic position

The trophic height of a species is the mean value of the lengths of all chains from basal species to this focal species. The trophic height of basal species is zero. Chain length is the number of links joining a basal species to a top species. We computed the number of chains of each food web. We used the trophic height of each species to compute the mean height and the maximal height of all species in the food web.

Generalism and omnivory

The generalism index of a non-basal species is the number of taxa that it consumes. The generalism index of the food web is the mean value of the generalism indices of all non-basal species. The omnivory index of a non-basal species is the standard deviation of the trophic heights of its prey. The food-web omnivory index is the mean value of the omnivory indices of all non-basal species.

Aggregation methods

We aggregated the 74-species cumulated food web according to four different criteria.

Trophic similarity

Species sharing the highest percentage of common prey and predators were lumped together (Martinez 1991).

Size similarity

Species with the closest log-transformed body sizes were lumped together.

Taxonomic similarity

Taxa belonging to a similar higher taxonomic level were lumped together. We considered five taxonomic levels: species, genus, family, order and class.

Expertise

We combined taxonomy, functionality and body size in order to mimic functional groups as usually identified. Functional groups obtained were: gizzard shad, bluegill, chironomids, small (rotifers, nauplii, copepodites) and large herbivorous zooplankton (cladocerans, adult calanoid copepods), carnivorous invertebrates (adult cyclopoid copepods, *Asplanchna*), detritus, bacteria, and five main algal divisions (Cryptophyta, Euglenophyta, Chrysophyta, Pyrrophyta and Chlorophyta) that were split into particles with greatest axial linear dimension (GALD) smaller and larger than 20 μm .

Apart from aggregation by trophic similarity, which is an algorithmic approach, we considered aggregation by taxonomy or body size because these criteria are frequently used by ecologists to construct food webs. For taxonomy, Bersier and Kehrlí (2008) have shown a significant coupling between phylogeny and trophic structure. It is also known that body size is a major determinant of trophic interactions (Brose et al. 2006, Petchey et al. 2008).

In the aggregation process, we constructed a link between two groups A and B only if at least one link existed before the aggregation between the species (nodes) of group A and the species (nodes) of group B (maximum linkage criterion sensu Martinez 1991).

Because some species had the same body size or were characterized by the same similarity index, there were potentially several alternative combinations to lump nodes at any level of the aggregation process. To avoid a sampling bias, the aggregation procedure was replicated 50 times, with the species to be lumped randomly selected. Statistical analyses were made independently on these 50 aggregation trajectories.

The impact of aggregation on topological descriptor values according to size, trophic similarity, taxonomy and expertise is presented in the Supplementary material Appendix A1 Fig. A1.

Analysis of aggregation effects on experimental results

We tested the robustness of the results of Lazzaro et al. (2009) to food-web aggregation. At each step of the aggregation processes (trophic similarity, size similarity, taxonomic similarity, expertise), and for each aggregation trajectory, we analysed the responses of the descriptors using two-way repeated measure ANOVAs, with fish foraging type and biomass as independent factors, and time as random effect. Significance was inferred at $p = 0.05$ for all analyses.

To determine how species aggregation affected our experimental results on the 15 descriptors, we analysed our data separately for each aggregation method and level. These statistical analyses on aggregated systems were compared to the analyses performed on the non-aggregated well-resolved food webs. We assumed that the statistical effects obtained without aggregation were closer to the true effects than the responses obtained when lumping species. Indeed, in order to analyse topological features, the best information comes from the best-resolved food web, the one that has the most precise information on feeding links. Thus, we considered that aggregation led to an error when either a significant effect before aggregation was no more significant after aggregation, remained significant but with an opposite sign, or when a non-significant effect became significant after aggregation. At high aggregation levels, treatment variance was sometimes null, and statistical tests were no more feasible. Such cases were also considered as errors due to aggregation. We considered that aggregation led to a type I error (false positive) when an effect was not significant before aggregation but significant after (the null hypothesis, initially not rejected, was erroneously rejected when lumping species). We considered that aggregation led to a type II error (false negative) when an effect was significant before aggregation and no more significant thereafter (the null hypothesis, initially rejected, was erroneously not rejected when lumping species).

We did not correct statistical significance using a Bonferroni adjustment. Our objective was only to test whether statistical analyses would let to similar conclusions regardless of the lumping level.

To assess more deeply what occurred during the aggregation process, we considered the variation along the aggregation gradient of the fish effect strength for each descriptor i (ES_i). ES_i was estimated as the normalised difference of mean values of each descriptor i in mesocosms with gizzard shad (GS_i) and bluegill (BG_i):

$$ES_i = \frac{GS_i - BG_i}{\frac{1}{2}(GS_i + BG_i)}$$

Analysis of aggregation effects on a functional relationship

We further examined whether a functional relationship – the correlation between the percentage of inedible basal species and the chlorophyll-a concentration – was affected by aggregation. This relationship was obtained by associating the data of Lazzaro et al. (2009) with other treatments not considered in this publication (no fish, co-occurrence of gizzard shad and bluegill). When using the complete network (74 nodes), the relationship could be described by a non-linear saturation function depending on two parameters a and b , relating the mean chlorophyll-a concentration in tanks on dates 14, 21 and 28 (y) to the percentage of inedible basal species (x) in the experimental food webs:

$$y = a(1 - e^{-bx}) \quad (1)$$

We tested whether aggregation affected the values and significance levels of the parameters a (the asymptotic chlorophyll-a value) and b (the natural logarithm of the rate constant) of this functional relationship (SSasymptOrig procedure of the statistical R software, ver. 2.15.1).

Parameters were estimated along the aggregation gradient for all aggregation methods (size, trophic similarity, taxonomy and functional groups).

Results

The impact of aggregation on experimental results

The strength of the fish type effect (visual feeder vs filter feeder) remained roughly constant along a large part of the aggregation gradient for both trophic similarity and taxonomic aggregation (Fig. 1), despite a clear impact of aggregation on some descriptor values (Supplementary material Appendix A1 Fig. A1). Most of the discrepancies appeared when food webs were aggregated into less than 25 nodes. When aggregation was performed according to size similarity, trajectories were more impacted, with a first shift of several descriptors (top species mean height, number of chains, mean omnivory and percentages of top and intermediate species) around 40 nodes. The observed shift in the size-aggregation trajectory occurs when zooplanktonic taxa with similar sizes but with different feeding behaviours (e.g. Cyclopid, Calanoid and *Simocephalus*) are lumped together (Fig. 2).

The pattern observed for the strength of the fish effect on the number of inedible basal species was quite different from other descriptors patterns, with an effect more impacted by taxonomy than by size aggregation. This underlies the major role of size in the determination of algae edibility (Burns 1968).

Globally, results found for the well-resolved food webs were preserved when considering aggregated networks (an example is given in the Supplementary material Appendix A1 Fig. A2). The number of errors remained low whatever the aggregation criterion over a large range of the gradient (Fig. 3). Aggregation using trophic similarity only led to wrong interpretations of fish type effects below 30 nodes and the number of errors stayed really low (less than 2 errors for 15 possible ones down to an aggregation level of 15 nodes). Errors appeared earlier when using size aggregation, with three errors coming at the 40-nodes level. As previously underlined, these two thresholds (30 and about 40) occur when the two aggregation methods start to group species from different trophic levels (Fig. 2). The number of errors under taxonomy and trophic similarity aggregation was close, without any error over a large part of the gradient (the first error only appeared at the order level, when only 38 nodes remained). When species were aggregated according to expertise into 17 functional groups only two errors were detected.

Errors for the fish biomass effect started to appear earlier in the aggregation process, and stayed roughly constant along the aggregation gradient, with a number of errors around four (Fig. 3). However, this number of errors should be considered relatively to the low number of significant

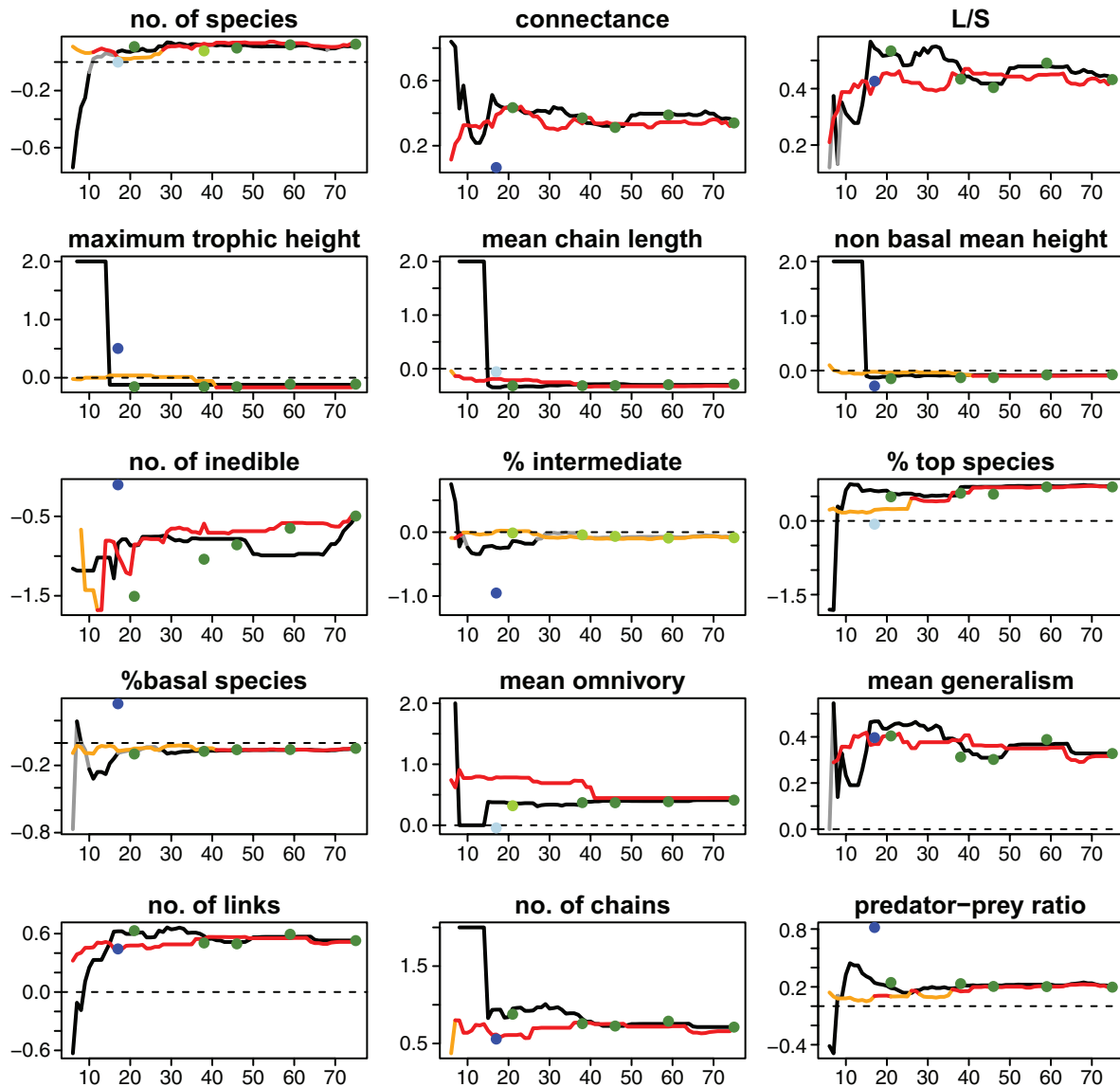


Figure 1. Strength of the fish type effect on descriptors along the aggregation gradient (from 74 nodes on the right to 1 node on the left) according to different aggregation criteria: black for trophic similarity (grey when non significant), red for size (yellow when non significant), green dots for taxonomy, blue dot for expertise (light green and light blue for non significant effects).

effects found on the non-aggregated network (5 significant effects for 15 topological descriptors analysed). This indicates that most of the previously significant biomass effects, which were less marked than fish effects (Lazzaro et al. 2009), rapidly became non significant (Fig. 4). Whatever the independent variable (fish type or fish biomass), we are more likely to observe a significant effect to become non significant when aggregating species (type II error or false negative) than the opposite (type I error or false positive) (Fig. 1, 4).

The impact of aggregation on a functional relationship

The two-parameter relationship between the mean percentage of inedible basal species and the mean concentration of chlorophyll-a in the mesocosms could be described by a

non-linear saturation function (Eq. 1). When the resolution of the food web was above 15–20 nodes, the relationship remained significant and was explained by the same function, although residual errors tended to increase with aggregation intensity (Fig. 5): the curves were more slanted, with slightly lower asymptotic values. Under 15–20 nodes, the non-linear regression model did not converge, and the data were better explained by a linear model.

Discussion

Simplifying trophic networks by aggregating species into groups is a common practice in food-web studies. It is a consequence of their complexity, but also has the potential to help elucidate ecosystem functioning. To examine the preservation of food-web functionalities under different

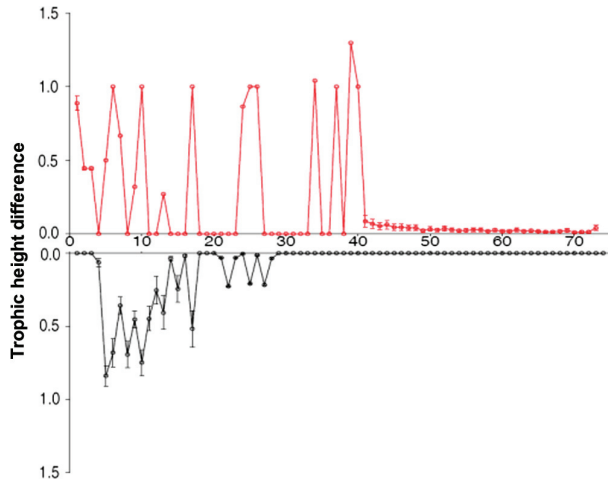


Figure 2. Difference of trophic heights for species lumped at each step of the aggregation process for size and trophic similarity criteria. Same color and symbol conventions as in Fig. 1.

aggregation methods, we used experimental results on a well-resolved food web comprising 74 species, and studied how these results were affected when the food web was aggregated from 74 nodes to one node. Several conclusions arise from our study:

- 1) The level of significance of statistical effects on food-web topology was preserved by aggregation over a large portion (2/3) of the aggregation gradient. This preservation of effects included functional properties, as indicated by the conservation of a functional relationship.
- 2) The preservation of experimental effects under aggregation took place despite strong variations in descriptor values along the aggregation gradient (Supplementary material Appendix A1 Fig. A1; results vary across descriptors but are coherent across aggregation criteria).
- 3) Some aggregation methods (trophic similarity, taxonomy) performed better than others (size).
- 4) Aggregation produced more type II errors (false positives) than type I errors (false negatives), suggesting that most effects found on aggregated networks were not methodological artefacts.

The preservation of experimental results under aggregation is good news to ecologists. However, this was only true for very significant effects: the observed proportion of type II errors was much higher when analysing the impact of fish

biomass, which was less marked than the impact of the fish foraging type (Lazzaro et al. 2009). This suggests that network aggregation could lead to a strong underestimation of subtle effects of environmental variations on food-web topology.

Methodological issues

Despite an increasing number of studies focusing on the response of food-web topology to perturbations (Woodward and Hildrew 2001, Laver et al. 2010, Hogsden and Harding 2012), we do not know whether biological conclusions are robust to the various approximations made when elaborating trophic networks. This is especially true when networks are built using gut contents, which make prey taxonomical identifications to a specific level sometimes difficult, in particular for the relationships between small species, such as zooplankton–phytoplankton trophic links. Our study demonstrates that the topological structure of aggregated food webs is altered by the lack of resolution, but also suggests that the observed differences between fully detailed food webs may be preserved under biologically relevant aggregation criteria (size, trophic similarity, taxonomy and functional groups), provided that the effects found on the fully detailed webs are sufficiently strong. Indeed, it seems that aggregation tends to increase the second order risk, and thus decreases the power of the test.

Relevant aggregation methods probably underlie implicitly most studies on trophic networks. However, taxonomical groups are often differently aggregated, with a large reduction in the number of basal species (due to a lack of taxonomical identification), whereas top predators are usually fully determined. Thompson and Townsend (2000) showed that this kind of unbalanced aggregation induces several biases in topological analyses. Even if the functional properties of food webs may be preserved by aggregation, the observed aggregation effects on most descriptor values indicate that only trophic networks aggregated at the same level should be compared. In the light of our results, differences in resolution between food webs could bias relationships between topological descriptors (e.g. number of species and number of links, Ings et al. 2009) or bias the observed range constraints on quantities such as the predator–prey ratio (Cohen 1977, Closs et al. 1993). Using similarly constructed webs would allow to determine more accurately these relationships. As fully detailed food webs are difficult to achieve, aggregating

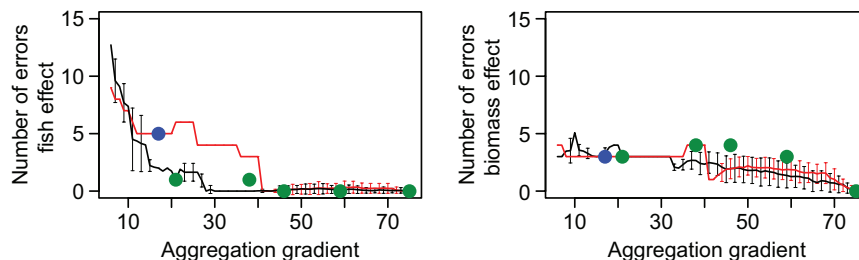


Figure 3. Mean number of errors (\pm SE) made for 50 replicates along the aggregation gradient for fish (left) and biomass (right) effects. Same color and symbol conventions as in Fig. 1.

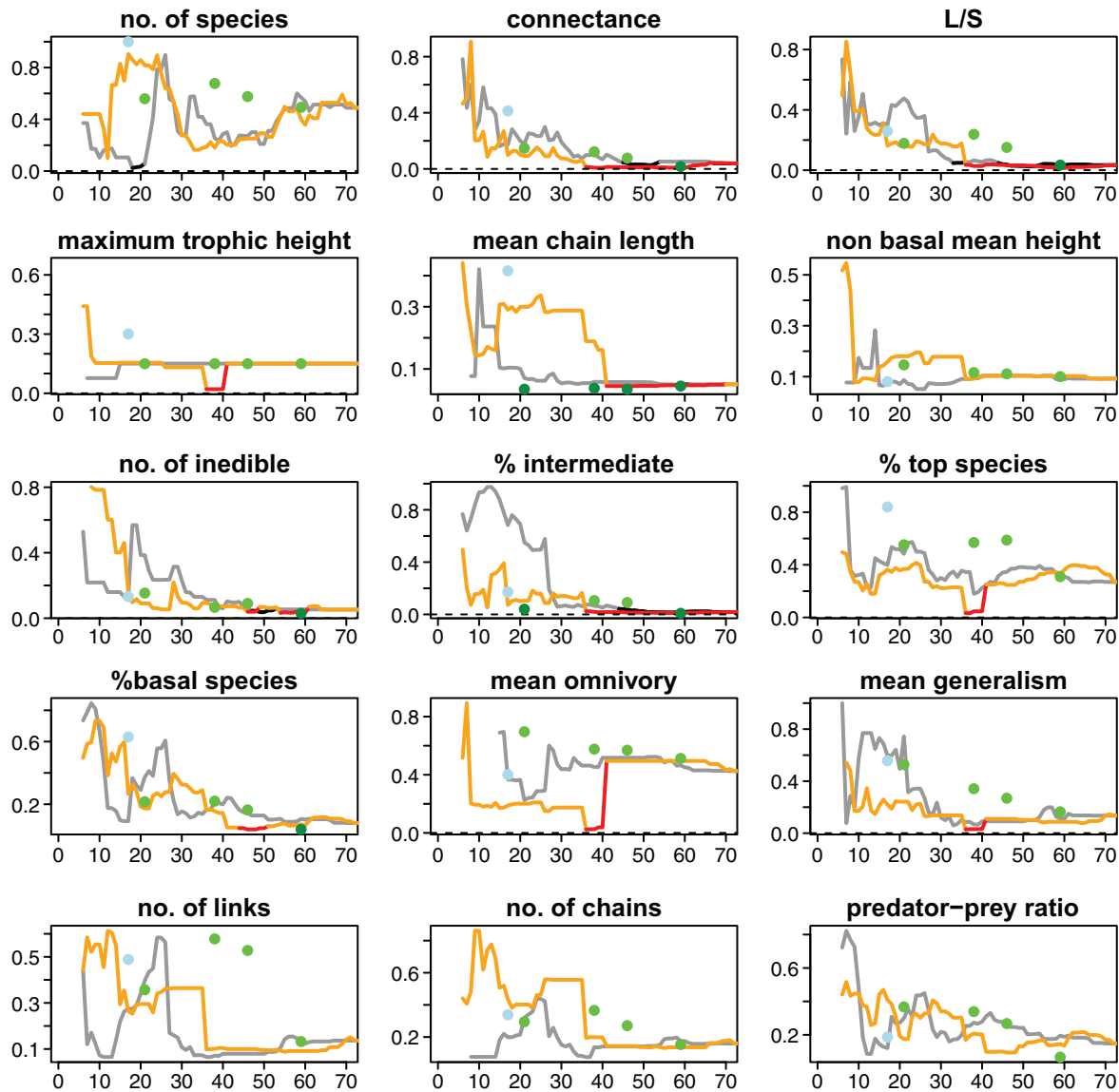


Figure 4. p-values of the biomass effect on descriptor values along the aggregation gradient according to different aggregation criteria. Same color and symbol conventions as in Fig. 1.

species at a similar and biological relevant level might represent a good compromise between sampling effort and system precision. Note that trophic similarity requires the knowledge of the complete network. In most cases this information is not available, and proxies must be used. Taxonomy appears as a good alternative, and presents an interesting tradeoff between quality of description and sampling effort. The good results obtained with this method are coherent with recent papers assessing the importance of phylogeny on the shape of food webs (Eklöf et al. 2011, Naisbit et al. 2011). Even if size is an important factor in food-web organization (Woodward et al. 2005), especially in aquatic communities, considering groups determined only according to this parameter does not seem to be the best choice. Consistently with previous studies (Petchey et al. 2008, Rohr et al. 2010), size alone is insufficient to determine trophic links precisely. For example, at similar sizes, visually-feeding fish feed on larger prey

than filter-feeding fish (Lazzaro et al. 2009). It is worth noting that the trophic similarity criterion (the maximum percentage of common links between two species) is a simple algorithmic rule that constitutes a good tool for assessing the importance of biological criteria such as size, taxonomy, and functionality.

From topological networks to functional webs

The fact that lumping species maintained the effects of top predators on food-web structure and the observed relationship between chlorophyll-a concentration and the percentage of inedible basal species means that functional properties were preserved for highly aggregated networks. This preservation of effects with aggregation means that top predators feed on prey from rather similar taxonomical groups (Naisbit et al. 2011) that share a high percentage of predators and prey (Pimm et al. 1991, Persson et al. 1996).

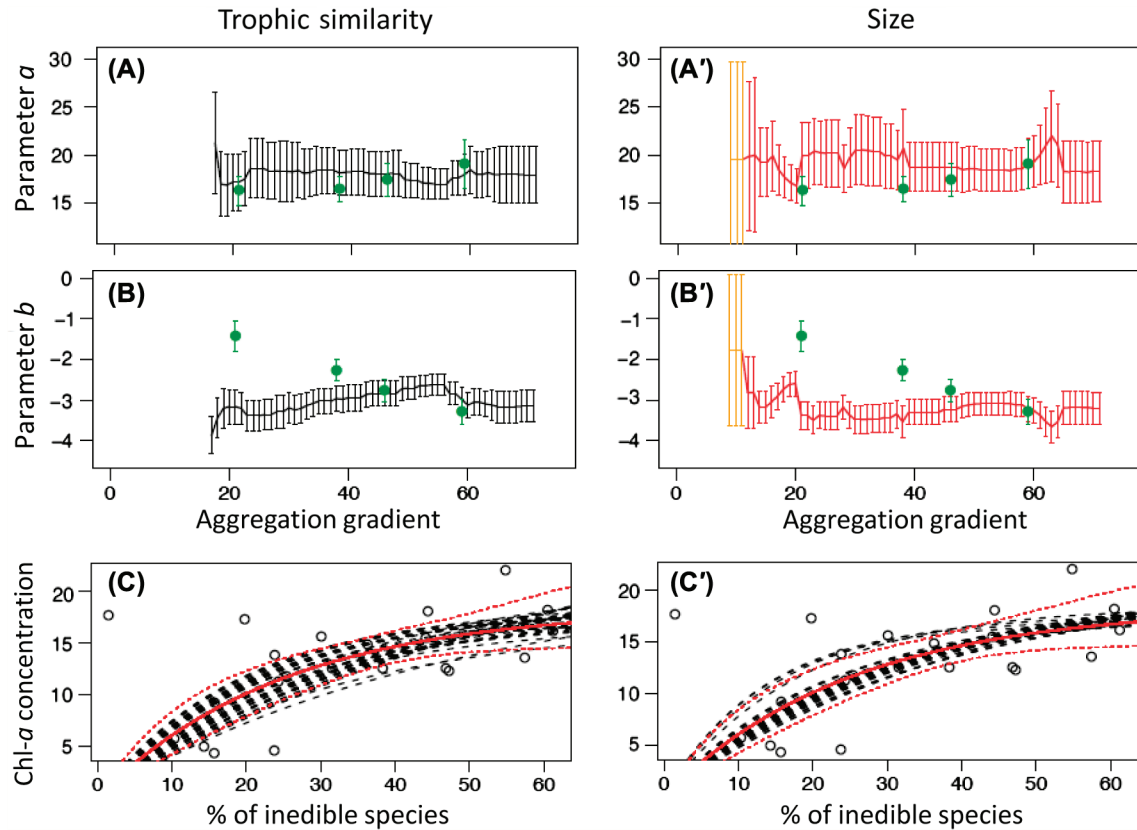


Figure 5. Two-parameter relationship between chlorophyll-a concentration and the percentage of inedible basal species. Aggregation according to trophic similarity (A, B, C) and size (A', B', C'). Variations of parameter a (A, A'), and parameter b (B, B') along the aggregation gradient. Predicted curves under aggregation with percentage of inedible species in abscissa and chlorophyll-a concentration in ordinate (red for non aggregated data, dotted lines indicate the 95% confidence interval; dashed black lines indicate aggregated data) (C, C'). In (A, A', B, B'), same color and symbol conventions as in Fig. 1.

This confirms that aquatic trophic networks are structured into trophic guilds (Allesina and Pascual 2009, Baskerville et al. 2011), and validates the functional approaches based on simplified groups of species. The preservation of food-web functional properties when lumping species according to trophic similarity suggests that this aggregation method provides a good compromise between food-web simplicity – allowing the ecological modelling of food webs of intermediate complexity (Thrush et al. 2008, Boit et al. 2012), and preservation of ecosystem properties.

While our results on species lumping strongly reflect the importance of top-down effects on the functional organization of networks, no clear pattern exists on how a bottom-up manipulation would have influenced this organization. It would be interesting to perform similar analyses on experiments manipulating nutrient load or ratio, where species aggregation could reveal different functional criteria, based on stoichiometric characteristics (Woodward et al. 2005) or on the ability of some species to acquire limiting nutrients (e.g. nitrogen fixation by Cyanobacteria). Moreover, the phylogenetic proximity among species is positively related to their ecological similarity, and community structure is the complex outcome of the action of environmental filtering forces, which tend to favour the coexistence of closely related species (phylogenetic attraction), and competition, which tends to induce

phylogenetic repulsion (Webb et al. 2002). One could expect that bottom-up perturbations might primarily affect the coexistence of taxonomically close species. In such a case, aggregation of these species would greatly increase the risk of type II errors (false positives) on network topology in bottom-up experiments, in comparison with our observations for top-down manipulations. Studying the persistence or disappearance of ecological effects under aggregation might help understand at which scale the considered effects apply within trophic networks.

Network construction and aggregation criteria

As for many food webs, our network was constructed according to different sources of knowledge. Most links were determined using information from the literature (Chesapeake bay, Baird and Ulanowicz 1989; Caribbean Reef, Optiz 1996; Little Rock Lake, Martinez 1991), observations in microcosms (Skipwith, Warren 1989; Ythan estuary, Hall and Raffaelli 1991), personal expertise (Little Rock Lake, Martinez 1991), or size (Skipwith, Warren 1989; Tuesday Lake, Jonsson et al. 2005). This might have led to a risk of circular reasoning. For example, we interpreted our results on aggregation effects according to size, although some links had been determined using size-based relationships. However, we do not feel that our

methodological choices have strongly affected our conclusions. First, size relationships were mainly used to determine links between zooplanktonic filter feeders and their phytoplanktonic prey, and this only when direct information on taxa was not available. This strategy seems reasonable as size effectively appears to be a major driver of the diet of these zooplanktonic grazers (Burns 1968). Second, we concluded that size was the less efficient aggregation criterion among those chosen in our study. Thus, supposing that our approach had led us to overestimate the correspondences between size criteria and trophic similarity trajectories, analysing trophic networks determined without any use of size would have reinforced the conclusion that size is the worst criterion used among those chosen for this study.

Conclusion

Studies on food-web aggregation not only lead to a better understanding of the relationships between species and ecosystem structure and functioning, but also help to specify methodological rules. The dependency of descriptor values upon aggregation could be problematic in studies relating topological structure and functional properties based on food webs heterogeneously aggregated (Thompson and Townsend 2000). In view of our results, it seems possible to relate topological descriptor values and ecosystem properties if the methodological approaches are strongly standardized. In ecological studies, the need to minimize the potential sources of variations reinforces the proposition of Lazzaro et al. (2009) to use experiments conducted on food webs to analyse the effects of ecological variables on network topology while maintaining network comparability. Such experimental approaches would guarantee similar aggregation criteria and levels, and direct hypotheses testing on factors influencing network topology.

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Supplementary material (available online as Appendix oik-00266 at <www.oikosoffice.lu.se/appendix>). Appendix A1: Fig. A1–A2. Appendix A2: Network: adjacency matrix of the network (Excel-file).