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Short Note

The strength of simulated indirect interaction modules in a real food web

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A B S T R A C T

There is an increasing body of literature on the topological analysis of modules (motifs, building blocks) in different networks. Most of these results are of descriptive, comparative and statistical nature, while dynamical simulations of their behaviour are missing. We present a stochastic food web simulation and study the relative strength of different simple food web modules. We found that (1) the effects of prey groups on predators are significantly stronger than other effects, (2) indirect loops have strong effects only on mean population sizes, not on their variabilty, and (3) some short indirect interactions are not stronger than some longer ones. We believe that these findings may contribute to systems-based conservation practice in the future.

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1. Introduction

Network modules (or motifs) are increasingly studied in various systems ranging from food webs to gene regulation networks. The key questions are (1) how to define modules, (2) how frequent they are, (3) how strong their functional effects are and (4) how do they differ among different biological (and non-biological) systems? The last, comparative problem is already quite heavily studied (Milo et al., 2002), even if we still do not really know the answers to the previous, more basic questions. Studying network modules can be a key to better understanding complex biological networks, e.g., food webs (Fig. 1).

In ecological research, network modules have already been richly analysed, both experimentally (Menge, 1995) and theoretically (Brose et al., 2005; Mullon et al., 2009). In this paper, by "network modules" we refer to a particular set of small food web subgraphs shown in Fig. 2: these are richly described experimentally and seem to have solid ecological relevance. Although the nomenclature differed, the interest in indirect effects (especially interaction chain effects, Wootton, 1994) is very old (Elton, 1927) and experimentally inspired (Ohgushi, 2005). Moreover, indirect effects between two groups can be stronger than a direct interaction (Patten, 1982; Higashi and Patten, 1989; Palomares et al., 1995), giving a strong justification for studying small network modules as the building blocks of food webs. In a broader

sense, studies on dense subgraphs also belong to this problematics (Melián and Bascompte, 2004).

One of the key problems of food web research is over-emphasizing structural (topological) properties. It is the same in studying modules: counting them, determining their frequency distribution and checking whether it is significantly non-random, although excellent first steps, do not help enough to better understand their functioning. Dynamical approaches are basically lacking (but see Melián et al., 2005). It is a major task, thus, to study the behaviour of modules in suitable dynamical modelling frameworks. However, these modelling approaches should probably be motivated by experimental findings (relative strength and frequency distribution; see Menge, 1995; Abrams et al., 1996).

Here we dynamically simulate a food web and compare the relative strength of some kinds of modules. Computing module strength is based on sensitivity analysis in a stochastic simulation model. Our results may contribute to better understand the behaviour of indirect interaction modules.

2. Data

We study the Prince William Sound food web (Okey and Pauly, 1999; Okey, 2004; Okey and Wright, 2004; Fig. 1). It is composed of 51 trophic components but we only analyze the subgraph of the 48 living ones ($S = 48$), containing $L = 355$ trophic links (directed connectance, $C = L/S^2 = 0.154$), including 12 cannibalistic ones. The reason is that living-living interactions refer to ingestion/assimilative events, with a different dynamics in comparison to transfers involving non-living nodes (Whipple, 1998). Here we focus more on community dynamics than ecosystems nutrient

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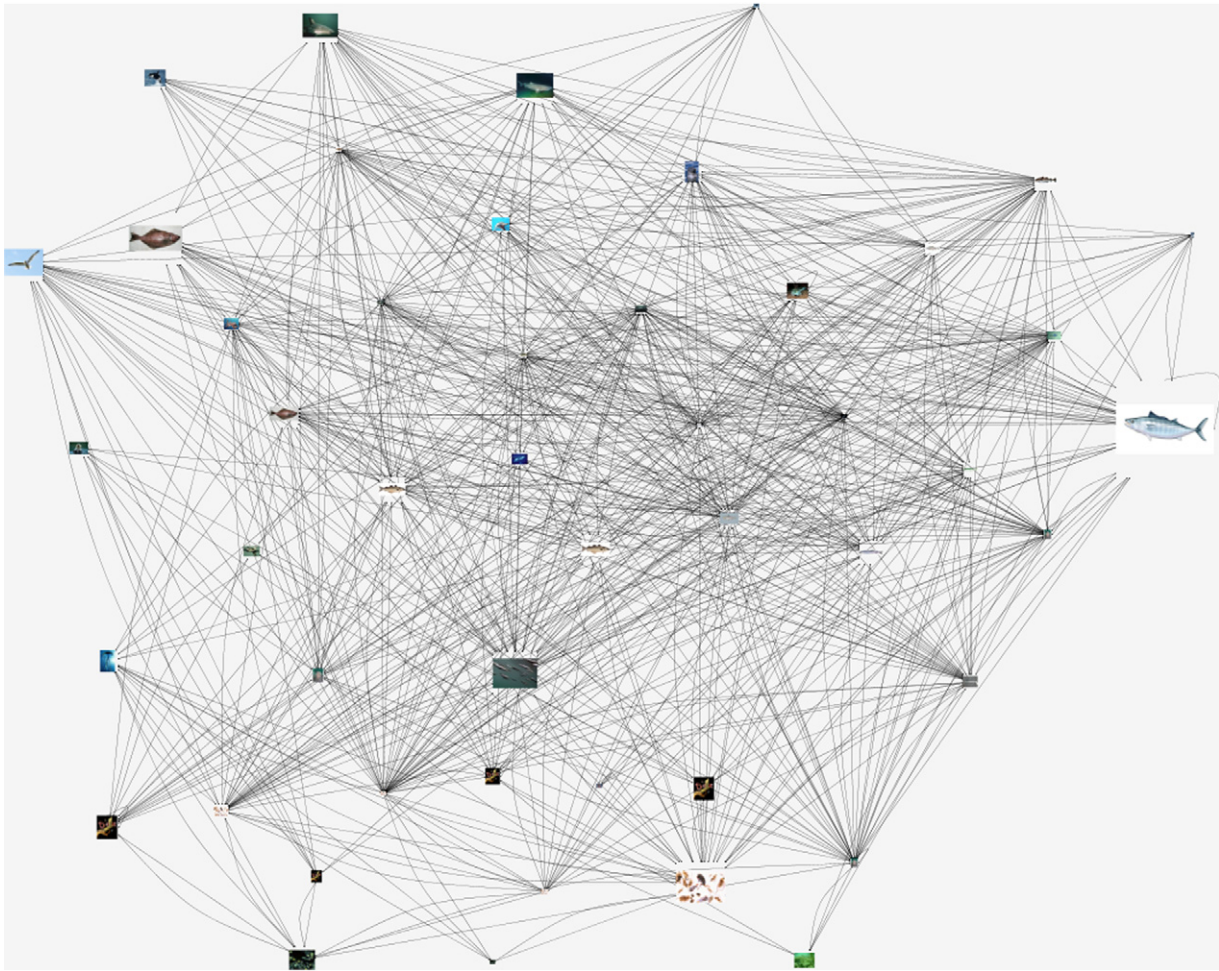E-mail address: jordan.ferenc@gmail.com (F. Jordán).

Fig. 1. The food web of the Prince William Sound ecosystem (data from Okey, 2004). The size of the pictures is proportional to the community importance of trophic groups based on our stochastic dynamical simulations (global effects of local perturbations). Drawn by COSBILAB Graph (Valentini and Jordán, 2010). Direction of links is not shown, for simplicity.

dynamics (however it is clear that the two are intimately linked and this is a simplification). Although non-living groups are clearly important for the original, EwE modelling framework (Christensen and Walters, 2004), we excluded egestive transfers for performing stochastic simulations (e.g., flows from biotic compartments to non-living nodes or flows between non-living compartments). The list of the living trophic components is given in Table 1.

3. Methods

3.1. Structure

For simplicity, we focus only on trophic interactions and the indirect interaction modules they compose (e.g., "trophic cascade" containing only "predation" links; Abrams et al., 1996). This also means that we cannot study indirect interaction modules containing non-trophic effects (e.g., no "apparent predation" containing "enhancement of recruitment" link; Abrams et al., 1996).

We were interested in comparing modules of different size and indirect interaction pathways of different length (see also Jordán et al., 2003). We have quantified cannibalistic loops (one group, one step), longer feedback loops (several groups, n steps), prey–predator interaction (2 groups, one step), predator–prey interaction (2 groups, one step), mutual consumption (2 groups, 2 steps), trophic cascade (3 groups, 2 steps) and keystone predation (4 groups, 3 steps). These effects are schematically presented in Fig. 2.

We note that keystone predation is defined here in a somewhat unconventional way: since we have no data on non-trophic effects, we consider exploitative (indirect) instead of direct competition in the module. We have constructed an algorithm for finding all possible modules in the network.

The S × S matrix of the 48 groups contains 2304 cells, including the main diagonal. Effects of group i on group j were categorized according to the above categories and we found 12 cannibalisms, 36 longer feedback loops (all non-cannibalistic groups influence itself through pathways of at least 2 steps), 4 mutual consumptions (two pairs), 343 prey–predator and 343 predator–prey interactions as well as 396 trophic cascades and 588 keystone predation interactions (see Fig. 3).

Clearly, several types of direct and indirect effects may act in parallel between a particular pair of group i and j, so no classification can be perfect. In order to minimize these overlaps, we have not examined two very frequent and well-known interaction modules, exploitative and apparent competition. Doing so, we have found only very few (<10) ij effects that are mixtures of the above interactions. When categorizing, we have always given priority to the shorter interaction type. For example, if i consumes j and k, and also j consumes k, we have considered this relationship as a predator–prey interaction (from i to k), however there exists also a trophic cascade from i to k (through j). Without additional information or experimental evidence, this may be an intuitively correct simplification.
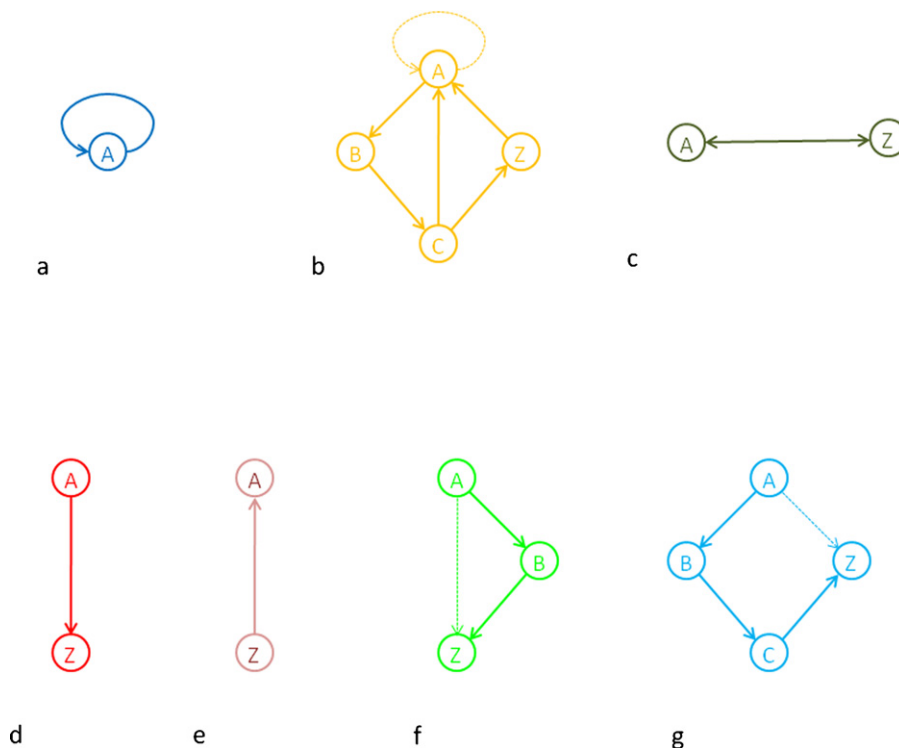
Fig. 2. The food web modules analyzed: cannibalism (a), indirect self-loop (b), mutual consumption (c), predator–prey (d), prey–predator (e), trophic cascade (f) and keystone predation (g). Dotted arrows show indirect effects: for example, A → B (A eats B) and B → Z (B eats Z) are direct, while the effect of A on Z is indirect in module (f). Color code is the same as in Fig. 3.
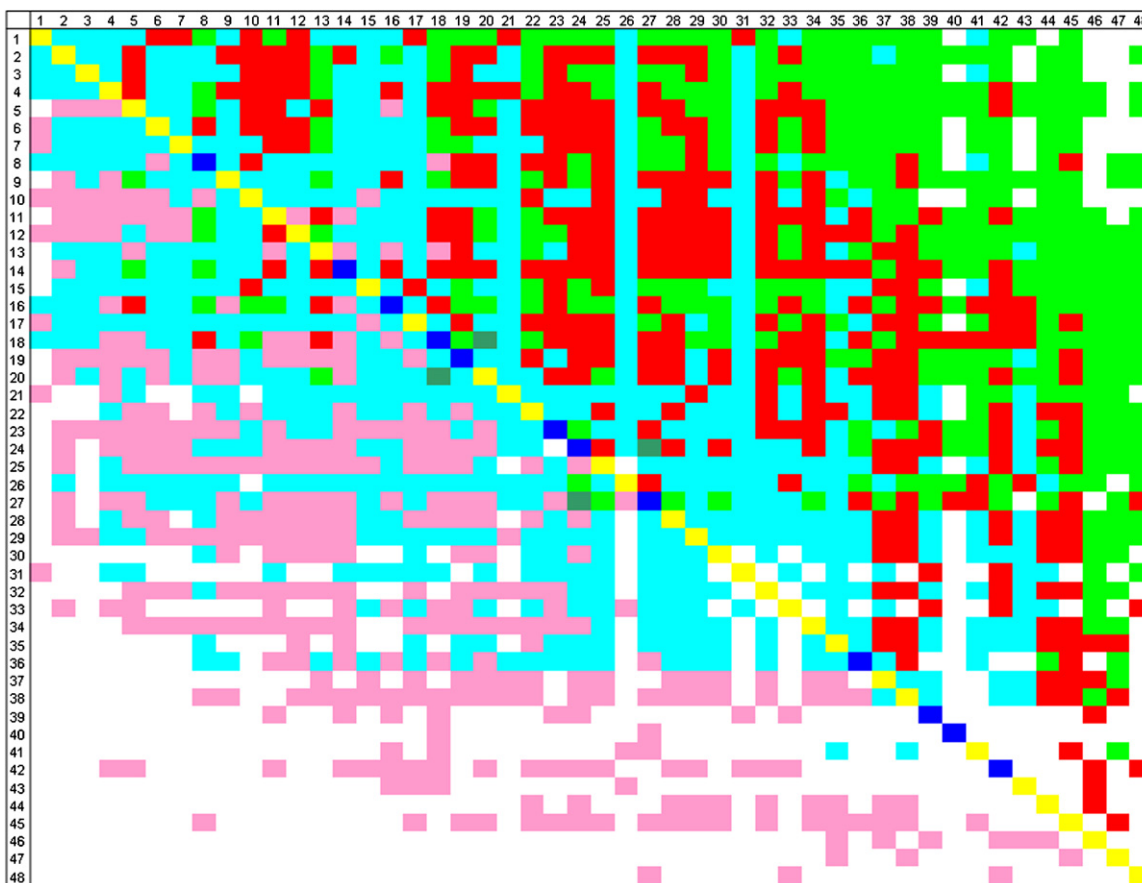

Fig. 3. The interaction profile of the Prince William Sound food web. Colors showing the interactions from species in the ith row to species in the jth column (cannibalism in dark blue, indirect self-loop in yellow, mutual consumption in greenish, predator–prey in red, prey–predator in pink, trophic cascade in light green, keystone predation in light blue, none of these in white). Color code is the same as in Fig. 2.

Table 1
The 48 living components of the Prince William Sound food web (Okey, 2004).

1	Transient orca
2	Salmon sharks
3	Resident orca
4	Sleeper sharks
5	Halibut
6	Pinnipeds
7	Porpoise
8	Lingcod
9	Adult arrowtooth
10	Adult salmon
11	Pacific cod
12	Sablefish
13	Juvenile arrowtooth
14	Spiny dogfish
15	Avian predators
16	Octopods
17	Seabirds
18	Deep demersals
19	Pollock 1+
20	Rockfish
21	Baleen whales
22	Salmon fry 0-12
23	Nearshore demersals
24	Squid
25	Eulachon
26	Sea otters
27	Deep epibenthos
28	Capelin
29	Adult herring
30	Pollock 0
31	Invertebrate-eating birds
32	Sandlance
33	Shallow large epibenthos
34	Juvenile herring
35	Jellies
36	Deep small infauna
37	Nearshore omniorous zooplankton
38	Omnivorous zooplankton
39	Shallow small infauna
40	Meiofauna
41	Deep large infauna
42	Shallow small epibenthos
43	Shallow large infauna
44	Nearshore herbivorous zooplankton
45	Herbivorous zooplankton
46	Nearshore phytoplankton
47	Offshore phytoplankton
48	Macroalgae

3.2. Dynamics

3.2.1. Simulation model

Having identified the type of interactions between group i and j, it is of interest how strong is their effect on each other (a_{ij} and a_{ji}). We have used a stochastic simulation model written in BlenX, a process algebra-based language (Dematté et al., 2007, 2008). This makes it possible to simulate parameter-rich models of parallel ecological processes in a truly stochastic way, using the Gillespie algorithm (Gillespie, 1977). During the last years, the number of applications based on individual-based stochastic dynamics for the study of food web models is increasing (Powell and Boland, 2009; Okuyama, 2009; Livi et al., 2011). Trophic flows and compartment biomasses have been translated to interaction rates and number of individuals, respectively. For the trophic compartments, the average individual body weight values of the dominant species were determined (based on literature data and www.fishbase.org) and dividing the biomass of the compartment by average body weight provided some approximation of the number of individuals.

In order to be able to perform sensitivity analysis, the original model (parameterized by real data) was set to quasi-balance by an evolutionary algorithm searching for quasi-equilibrium parameter combinations. We used an evolutionary approach based on Particle Swarm Optimization (PSO, Kennedy and Eberhart, 1995; Forlin, 2010). By using this evolved parameter set, simulation outcomes are much more consistent than before and ready for meaningful sensitivity analysis.

3.2.2. Sensitivity analysis

The balanced model was run $R = 20$ times and the population size for each compartment was recorded after time $t = 40,000$ (equivalent to roughly 30 years). We have calculated mean and variation (in a stochastic modelling framework, the latter provides novel information, compared to deterministic models). This first step was to characterize the undisturbed scenario (providing reference values of population size for each group). Then, the number of individuals was halved for each compartment, one by one, and for each case 20 simulations were run. After time t, population sizes were recorded and the mean and standard deviation were calculated. In this second step, we quantified the community-wide effects of local perturbations.

The dynamical effect of group i on group j is measured for both the mean and the variation, similarly. For calculating the effect of group i on the mean population size of group j, we first define the reference value of group j as

$$A_j = \frac{\sum_{k=1}^{R} a_{k,j}(t)}{R} \tag{1}$$

where R simulations are run and population size is recorded at time t ($a_{k,j}(t)$). The normalized value of group j after disturbing group i is

$$A_{ij} = \frac{\sum_{k=1}^{R} a_{ij}(t)}{R} \tag{2}$$

with $a_{ij}(t)$ standing for the populations size of group j at time t, once the group i is disturbed. The relative response of group j to disturbing group i is

$$RR_{ij} = \frac{|A_j - A_{ij}|}{A_j} \tag{3}$$

The normalized relative response, defined as

$$NRR_{ij} = \frac{RR}{\sum_{i=1}^{S} RR_{ij}} \tag{4}$$

gives the relative contribution of group i to influencing group j, and this measure is comparable among different pairs of groups, across the whole food web (of S groups).

The effects on variability are calculated similarly, but using the standard deviation instead of the mean in (1) and (2). Finally, we obtain the NRR_{ij} (M) and NRR_{ij} (V) measurements. We believe that this response measure is suitable for our purposes, however there are many alternative ways how to calculate community impor-tance and the response of individual groups to disturbance (see Hurlbert, 1997).

3.3. Statistical analysis

We performed Kruskal–Wallis test in order to determine whether different interaction types are of different strength. We had eight categories: the seven above mentioned effects plus the rest of i and j pairs with none of these effects between them (since group sizes differed we could not use the otherwise useful Goodman–Kruskal lambda or Kendall tau statistics).

Then, we compared the groups, one by one, against all of the other interactions (since interaction strength data are clearly not independent values in a network simulation, we could not use the F-test).

4. Results

The Kruskal–Wallis rank sum test says that, for the mean values, there is significant difference between the eight groups ($\chi^2 = 15.484$; df = 7; $p = 0.030$). For the variation, there is quite strong but just non-significant difference between the groups ($\chi^2 = 12.496$; df = 7; $p = 0.085$).

Based on the further statistics, for the mean, prey–predator interactions and indirect feedbacks are significantly stronger than other interactions (cannibalistic $\chi^2 = 0.839$; df = 1; $p = 0.360$, indirect self loop $\chi^2 = 5.853$; df = 1; $p = 0.016$, mutual $\chi^2 = 0.367$; df = 1; $p = 0.545$, predator–prey $\chi^2 = 0.000$; df = 1; $p = 0.999$, prey–predator $\chi^2 = 5.876$; df = 1; $p = 0.015$, trophic cascade $\chi^2 = 1.358$; df = 1; $p = 0.244$, keystone predation $\chi^2 = 3.178$; df = 1; $p = 0.075$, neutral $\chi^2 = 0.000$; df = 1; $p = 0.997$). For the variation, only prey–predator interactions are significantly stronger than other interactions (cannibalistic $\chi^2 = 0.000$; df = 1; $p = 0.997$, indirect self loop $\chi^2 = 1.350$; df = 1; $p = 0.245$, mutual $\chi^2 = 3.519$; df = 1; $p = 0.061$, predator–prey $\chi^2 = 0.761$; df = 1; $p = 0.383$, prey–predator $\chi^2 = 6.400$; df = 1; $p = 0.011$, trophic cascade $\chi^2 = 1.772$; df = 1; $p = 0.183$, keystone predation $\chi^2 = 0.035$; df = 1; $p = 0.851$, neutral $\chi^2 = 0.038$; df = 1; $p = 0.845$).

5. Conclusions

Better understanding the behaviour (e.g., strength) of food web modules may contribute to unveiling the functionality of complex ecological networks and clarifying the structure to function relationship, an old problem in community ecology (Jordán et al., 2008).

In our simulation study, the effects of prey on predators was significantly stronger than other interactions. A possible conclusion drawn from this result could be that bottom-up mechanisms are stronger in this system than top-down ones. We note here that this kind of finding is clearly sensitive to the details of the actual model. For instance, if the resolution of the food web is different (e.g., phytoplankton aggregated into more, smaller groups), systems dynamics will surely change, beyond topology. All conclusions are valid only for the presented network and its presented dynamical model. The above finding applies for both the mean population size and its variability, however the effects of indirect loops are significantly stronger only on the mean, and not on standard deviation. This raises the issue that stochastic models, explicitly studying variability, might usefully complement deterministic approaches focusing on the mean. Variability is a key component of biological systems as a proxy for adaptability (being relevant to management in case of higher levels of fluctuations) and its significance is being recognized in conservation science (Feest et al., 2010; see also Livi et al., 2011).

In concert with earlier field results (Palomares et al., 1995), we found that indirect effects are not necessarily weaker than direct ones: the effects of predators on their prey are not statistically weaker than the trophic cascades they exert on groups feeding at lower levels in the trophic chain.

The relevance of all results we provided is a function of the relevance of the model we built. Beyond choosing an appropriate model structure (e.g., mechanistic rules, topology), parametrization of the model is also critical, even if we start from available, realistic field data. The results of sensitivity analysis may strongly depend on parameter estimation techniques, for example. Future studies should also involve more food webs, considering also interaction sign (positive vs. negative effects) and extending the analysis towards other interaction types (e.g., comparing exploitative to apparent competition). Despite all limitations, the importance of our contribution is that it seems to be the first dynamical analysis of the strength of interaction modules in complex models with real parameters.

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