

Ecosystem functioning: simple predictors in complex food webs

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WORKING PAPER

1 Introduction

The complexity of natural ecological communities was qualified of '*baroque*' [7], on account of the multiplicity of ways in which two or more species can embed themselves in a web of interactions. This prompted a series of studies of "community modules", i.e. the pattern of interactions between three species, which were thought to be the right scale of observation to capture mechanisms underlying the organization of more complex communities. Most of the recent research on species interaction networks in general, and food webs in particular, aimed at making sense of this complexity at a large scale, and render it manageable. Berlow et al. [2] showed that perturbations of one species rarely spread farther than one or two of its closest neighbors, meaning that even in highly complex networks, community modules are an appropriate scale of observation.

Establishing links between the structure and the dynamics of food webs is a firmly

established research agenda [9], and one which have been taking prominence over the last few years so as to understand how trophic downgrading will affect the maintenance of ecosystem services [4]. Yet, our understanding of this relationship is scarce: most research focused on the variations in biomass of species as a function of their position in the food web [15, 2], which is still a very species-centric view. Most of our knowledge about the fact that food web structure does affects the functioning of ecosystem comes from analyses of networks of low complexity (i.e. discrete, well identified trophic levels), and focused on extreme cases of connectance [e.g. 14, 13] **Our PNAS MS**. These studies emphasized that functioning is driven by food web structure when this structure allows to regulate the impact of apparent *vs.* exploitative competition. Building on our newly found ability to make sense of complex structures by looking at smaller modules, there is an opportunity to revisit this relationship by investigating how the functioning of realistic networks is affected by their structure.

Milo et al. [8] proposed that complex networks are built up from simple blocks, termed “motifs”. Motifs represent all the possible ways under which n nodes can be connected by directed edges. For the three species case, there are thus 13 different motifs. Most empirical networks display a non-random distribution of these motifs [1, 11], indicating that they emerge through a resource/prey selection process. More importantly, for some of the simplest motifs (which also happen to be the most abundant), it is easy to understand how they contribute to the flow of energy across trophic levels (Fig. 1). Because these motifs can be enumerated in any food web, regardless of its complexity, and because each of them represent a

different mechanism of biomass transfer across trophic levels, they are most likely a key to understand how food web structure translates into functioning. Furthermore, the position occupied by species in different motifs (i.e. at the top of a linear food chain, or as the arbiter of apparent competition) shows strong evolutionary conservatism [12], or in other words, species tend to be involved more in some motifs than in others. This implies that species functional role within the food web can be studied through its contribution to different motifs, making them a tool to both compare functioning between food webs with different structures, and understand differences in biomass between species of a food web.

In this paper, by using a well-documented, calibrated, and widely used model of food web dynamics [3], we seek to explain (i) the functioning of complex communities and (ii) the productivities of species within a food web, through an investigation of motif composition. We show that functioning is strongly impacted by the presence of exploitative competition (which decreases functioning), linear food chains (having the same effect), and apparent competition (which increases functioning). We show that biomass production can be predicted using a competition-type ratio, *i.e.* the frequency of exploitative over apparent competition motifs, which requires only topological information to be calculated.

These results are discussed in the light of previous literature building on similar models to find predictors of food web stability.

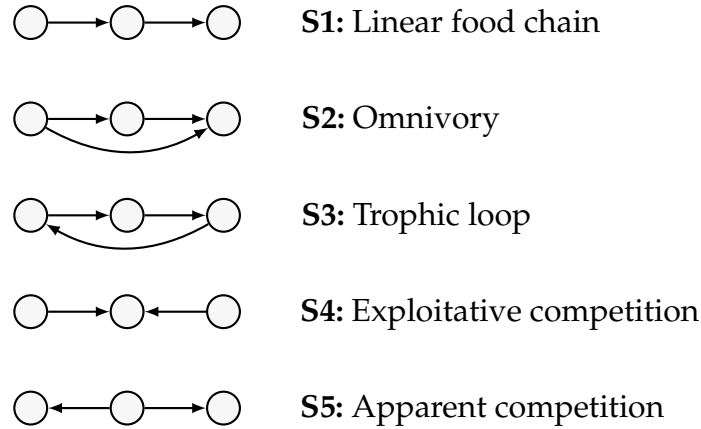


Figure 1: The 5 simple-link motifs encompass important scenarios for the flow of biomass across trophic level. Arrows indicates a *feeding* link. Next to each motif is the ecological reality it implies.

2 Methods

2.1 Data

We use a collection of 178 community food webs, represented by their adjacency matrix. These food webs were previously published and analyzed by DUNNE, COHEN, and Havens [6]. The data were collected by Gravel et al. [5].

2.2 A model of biomass dynamics in food webs

We apply a dynamical model to these food webs. We use an expansion of the classical Yodzis and Innes [16] model to food webs, such as proposed by Brose, Williams, and Martinez [3].

$$\frac{dB_i}{dt} = B_i \times r \left(1 - \frac{B_i}{K}\right) - \sum_{j \in \text{consumers}} \frac{x_j y_j B_j F_{ji}}{e_{ji}} \quad (1)$$

$$\frac{dB_i}{dt} = -x_i B_i + \sum_{j \in \text{resources}} x_i y_i B_i F_{ij} - \sum_{j \in \text{consumers}} \frac{x_j y_j B_j F_{ji}}{e_{ji}} \quad (2)$$

In this model, the extent to which allometric scaling exists in the interaction strength is regulated by a single parameter Z , which represents the body mass ratio of consumers and their resources. For $Z = 0$, there is no allometric scaling, and for other values of Z , we can explore situations in which consumers are heavier or lighter than their resources. As in the original model, we used a value of unity for r and K , so that all biomasses are expressed relatively to the biomass of primary producers. In the formulation of the original model, we assume that our food webs are made of ectotherm vertebrates and most of the interactions are carnivory, meaning that the parameter values are as follows: e_{ij} , the assimilation efficiency, is 0.85; x_i , the maximum metabolic rate, is equal to $(a_x/a_r) \times (M_C/M_P)^{-0.25}$; y_i , the maximal consumption rate, is equal to a_y/a_x ; $M = Z^T$, $a_r = 1$, $a_x = 0.88$, and $y_i = 4$.

The functional responses are assumed to be of the predator interference type (hill exponent $h = 1$, competition coefficient $c = 1$), so that

$$F_{ij} = \frac{\omega_{ij} B_j^h}{B_0^h + c B_i B_0^h + \sum_{k \in \text{preys}} \omega_{ik} B_i^h}, \quad (3)$$

with B_0 fixed to $1/2$, and ω_{ij} fixed to $1/n$ wherein n is the number of preys, to

reflect uniform relative consumption rate over consumers, and no prey preference. For more informations about this model, readers are encouraged to refer to the original publications [3, 15].

In each of the 178 food webs, we simulate this model using 100 replicates of the following procedure. First, species with a out degree of 0 are primary producers. Then, we use this information to measure the trophic rank, as the minimal distance between one species and a primary producer. While other measures have been used [10], this definition makes sense in an ecosystem functioning perspective, as most of the biodiversity-functioning relationship appears driven by complementarity in resource use (in addition, using either the mean or the maximum distance to primary producers yielded qualitatively similar results). We use the trophic rank information to calculate the species-specific parameters. At the beginning of each simulation, each species of the network is assigned a starting population density, drawn uniformly from $[0.05, 1]$. We let the system run for 10^4 time steps, and record the individual biomass of each species over the last 10^3 time steps.

2.3 Analyses

Network structure For each network, we count the number of motifs using the following procedure. We took all possible groups of three species, and look at the linkage pattern between them. Motifs are attributed and named as in Stouffer et al. [11]. The total number N_m of motifs is counted, and, so as to normalize motif

counts by the network size and connectance, we use the frequency of each motif in the analyzes, so that for any motif n found N_n times,

$$f(n) = \frac{N_n}{N_m}. \quad (4)$$

This procedure is also done at the level of the species, *i.e.* each time a species i is found in motif n , N_n^i increases by 1. As for networks, the motif count of each species is transformed in a frequency, so that if species i is found in a total of N_m^i motifs,

$$f^i(n) = \frac{N_n^i}{N_m^i}. \quad (5)$$

Because of the strong negative linear correlation between the frequency of motifs S4 and S5 (resp. exploitative and apparent competition), we define a competition-type ratio, such that

$$C_R = \frac{f(S_4)}{f(S_5)}. \quad (6)$$

For values of this ratio larger than unity, there are more exploitative than apparent competition motifs.

Functioning We record the biomass of the whole food web, which we divide by the number of species S , so that

$$\bar{B} = \sum_{i=1}^S \frac{B_i}{S}. \quad (7)$$

In addition, the raw biomass of each species is also recorded.

3 Results

The 178 networks from our dataset show a large variation in their composition in the different motifs (Fig. 2). Most of the double-link motifs are really rare, and because their relevance to energy flow is difficult to establish, we focus our analysis on the single-link motifs. We present results at two scales of organization: biomass production for the whole network, and biomass production for each species within a set of representative networks.

Biomass production between food webs We report patterns of biomass as a function of the composition of each network in the five single-linked (S1 to S5) motifs (Tab. 1). Switching from scaling ($K = 2$) to no scaling ($K = 0$) has only quantitative differences on the patterns, with simulations with scaling resulting in a higher mean biomass. Unless explicitly stated, the figures depict the results of the simulations with no scaling. Out of the 5 motifs we study, only S5 (apparent competition) favored biomass production (Fig. 3). The most important effect on biomass production is the frequency of motif S_4 , either by itself or when examined as part of the competition type ratio C_R . Note that using C_R or the additive effect

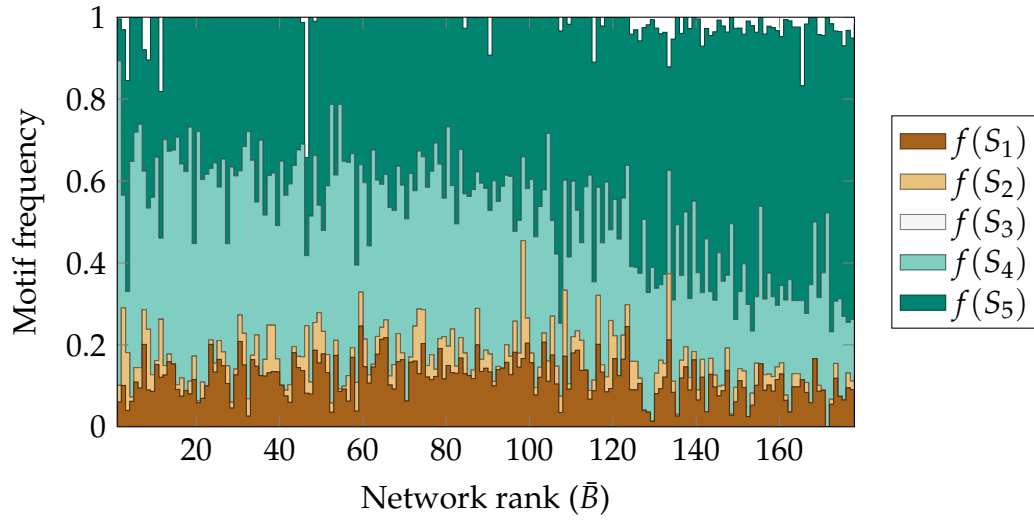


Figure 2: Variation in motif composition across the 178 food webs studied. Networks are ranked on the x-axis as a function of their mean biomass per species at equilibrium. Motif S_4 and S_5 are the most abundant, and motif S_3 is the least abundant. Some double-link motifs are found in the food webs from our dataset, accounting for the small white space atop some bars.

Table 1: F-values in the ANOVA explaining mean biomass of all species in the food web, only producers, and only consumers, by the frequency of each motif. All F-values which are not significant ($P \geq 0.05$) are noted as —. The adjusted R^2 are given in the last row. **First rows:** $\bar{B} \propto f(S_1) + f(S_2) + f(S_3) + f(S_4) + f(S_5)$; **last rows:** $\bar{B} \propto f(S_1) + f(S_2) + f(S_3) + \log_{10} C_R$.

	No scaling			Scaling		
	Whole web	Producers	Consumers	Whole web	Producers	Consumers
S1	3219	1352	3547	2286	482	3018
S2	540	37	674	685	166	795
S3	57	8	57	63	—	54
S4	12×10^3	5655	10×10^3	12×10^3	5637	10×10^3
S5	29	72	119	31	63	125
R^2	0.64	0.44	0.61	0.63	0.41	0.62
S1	3176	1317	3452	2254	469	2945
S2	532	36	655	676	162	776
S3	56	8	56	62	—	53
C_R	11×10^3	5348	9629	12×10^3	5297	10×10^3
R^2	0.63	0.43	0.60	0.62	0.40	0.61

of $S_4 + S_5$ yields the same R^2 . As C_R represents the relative importance of two competition mechanisms, we will focus on discussing it rather than S_4 and S_5 separately.

Biomass production within food webs

4 Discussion

FOOD WEB LEVEL

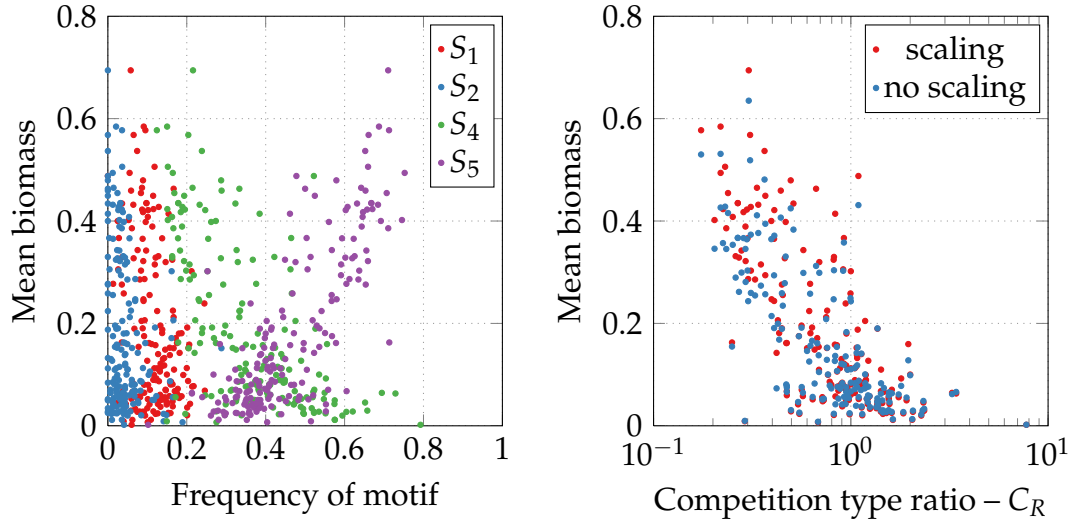


Figure 3: Mean biomass produced by each species within the 178 food webs. **Left:** mean biomass expressed as a function of the frequency of the four most important motifs: S1, S2, S4 and S5. Of all the motifs considered here, only the one indicating apparent competition (S5) results in an increase in biomass production. **Right:** mean biomass expressed as a function of C_R , with values above unity indicating more exploitative than apparent competition. Simulations with and without allometric scaling yield the same pattern.

- The frequency of two types of competitions is the most significant effect – this confirms our result from the PNAS MS than complementarity is the most important mechanism
- The frequency of S1 (linear food chains) has a strong impact on consumers, but not producers, biomass – not sure what it means
- Results are not affected by scaling: most of the functioning depends on topology – good thing, because it means we need much less information to predict functioning than if allometry is important (also worth noting, the patterns here are exactly the same as with my previous extremely simple Lotka-Volterra model)

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