

# Maximum entropy modelling of food-web structure

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**Abstract:** The principle of maximum entropy is a rigorous mathematical method of finding constrained probability distributions that has been proven useful in many ecological modelling problems. However, despite its broad application in graph and network theory, it has seldom been used to model ecological networks. Here we show how the (joint) degree distribution of maximum entropy can be directly derived using the number of species and the number of links in terrestrial and aquatic food webs. We also present a heuristic and flexible approach of finding the network of maximum entropy based on simulating annealing and SVD entropy. We built two of these network-level models using constraints given by the connectance and the joint degree sequence, respectively. All maximum entropy models were compared against open access food-web data and null and neutral models commonly used in network ecology. We found that the maximum entropy network model constrained by the joint degree sequence was a good predictor of food-web structure, including nestedness and motifs distribution. Overall, our results suggest that many properties of ecological networks are mainly driven by the joint degree distribution and statistical phenomena.

## **1 Introduction**

2 Statistical and mathematical models can help fill many gaps in our knowledge about species  
3 interactions. Two complementary types of models have been developed in network ecology for  
4 this purpose. On one hand, predictive models can partially alleviate the Eltonian shortfall, which  
5 describes our current lack of knowledge on food webs and other ecological networks (Hortal et  
6 al. 2015). A variety of such models have recently been developed using machine learning and  
7 other statistical tools, most of which are presented in Strydom et al. (2021). On the other hand,  
8 null models help us identify potential ecological mechanisms that drive species interactions.  
9 They do so by comparing empirical data with an unbiased distribution of measures generated  
10 using a set of rules that exclude the mechanism of interest (M. A. Fortuna and Bascompte 2006;  
11 Delmas et al. 2019). Both types of models are frequently topological, i.e. they often predict the  
12 adjacency matrix or specific measures of network structure without taking into account species'  
13 identity. According to Strydom et al. (2021), these topological models could be used to make  
14 better predictions of pairwise species interactions by constraining the space of feasible networks.  
15 The principle of maximum entropy (MaxEnt) is a statistical and topological model that can be  
16 used for both of these purposes, i.e. to make predictions of network structure and to better un-  
17 derstand processes shaping ecological networks. This mathematical method, briefly presented  
18 in Box 1, has been used in a wide range of disciplines, from thermodynamics to chemistry and  
19 biology (Martyushev and Seleznev 2006). It has also been proven useful in ecology, e.g. in  
20 species distribution models (Phillips, Anderson, and Schapire 2006) and macroecological mod-  
21 els (J. Harte et al. 2008; John Harte and Newman 2014). As discussed in Box 1, maximizing a  
22 measure of entropy ensures that the derived probability distributions are unique and least biased  
23 under the set of constraints used. These constraints are built using state variables, i.e. variables  
24 that represent the macrostate of the system. The challenge is to find the set of state variables  
25 that best represent natural systems and to translate them into appropriate statistical constraints.  
26 Having a validated maximum entropy model for the system at hand allows us to make rigorous  
27 predictions using a minimal amount of data, as well as helping us describe the most important  
28 factors driving that system.

29 Despite its extensive use in graph and network theories (e.g., Park and Newman 2004; van der  
30 Hoorn, Lippner, and Krioukov 2018), MaxEnt has in comparison been little used in network  
31 ecology. The very nature of ecological networks (directed simple graphs frequently having self-  
32 loops) makes the mathematical optimization of maximum entropy graph models more com-  
33 plicated than with many other types of (non-ecological) networks. MaxEnt has nevertheless  
34 been used to predict the degree distribution of bipartite ecological networks from the number  
35 of species and the number of interactions (Williams 2011) and to predict interaction strengths  
36 between species pairs using their relative abundances within an optimal transportation theory  
37 regularized with information entropy (Stock, Poisot, and De Baets 2021). However, to the best of  
38 our knowledge, MaxEnt has never been used to predict food-web structure directly, even though  
39 food webs are among the most documented and widespread ecological networks.

40 In this contribution, we used two complementary approaches to predict the structure of food  
41 webs using the principle of maximum entropy. We then compared our predictions against em-  
42 pirical data and null and neutral models commonly used in network ecology. The first approach  
43 consists in deriving constrained probability distributions of given network properties directly.  
44 We derived the joint degree distribution (a probability distribution) of maximum entropy using  
45 only the number of species  $S$  and the number of interactions  $L$  as state variables. Then, we pre-  
46 dicted the degree distribution of maximum entropy directly from the joint degree distribution  
47 since the first is the sum of the marginal distributions of the second (a species' degree is the  
48 sum of its in and out-degrees). Because of the scarcity of empirical data on the number of links  
49 in ecological networks, in Box 2 we present a method to predict  $L$  from  $S$ , thus allowing the  
50 prediction of the joint degree distribution from  $S$  solely. In turn, the second approach consists  
51 in finding, using different constraints, the adjacency matrix of maximum entropy from which  
52 network properties can be measured. To do so, we used a flexible and heuristic approach based  
53 on simulating annealing to find networks *close* to maximum entropy. As discussed above, our  
54 choice of algorithm stands from the very nature of food webs (i.e., simple directed networks  
55 allowing self-loops) that makes the analytical derivation of a maximum entropy graph model  
56 difficult. We first built our type I MaxEnt network model constrained by the connectance of  
57 the network (i.e., the ratio  $L/S^2$ ). A comparison of this model against empirical data indicated

58 that connectance alone was not sufficient to predict many aspects of network structure. For this  
59 reason, we built our type II MaxEnt network model, which instead uses the whole joint degree  
60 sequence as a constraint. Overall, we found that this second model was much better at predicting  
61 food-web structure than the one based on connectance.

## 62 **Box 1 - The principle of maximum entropy: A primer for ecologists**

63 The principle of maximum entropy is a mathematical method of finding probability distribu-  
64 tions, strongly rooted in statistical mechanics and information theory (Jaynes 1957a, 1957b;  
65 Harremoës and Topsøe 2001). Starting from a set of constraints given by prior knowledge of  
66 a system (i.e., what we call state variables), this method helps us find least-biased probabil-  
67 ity distributions subject to the constraints. These probability distributions are guaranteed to be  
68 unique given our prior knowledge and represent the most we can say about a system without  
69 making more assumptions. For example, if the only thing we know about a biological commu-  
70 nity is its average number of individuals per species, the least-biased inference we could make on  
71 its species abundance distribution is the exponential distribution (Frank and Smith 2011; John  
72 Harte and Newman 2014). However, this does not imply that this distribution will be the best fit  
73 to empirical data. The challenge is to find the right set of constraints that would best reproduce  
74 distributions found in nature.

75 Entropy measures the amount of information given by the outcome of a random variable. Many  
76 measures of entropy have been developed in physics (Beck 2009), but only a fraction of them  
77 could be used as an optimization measure with the principle of maximum entropy. According  
78 to Beck (2009) and Khinchin (2013), a measure of entropy  $H$  should satisfy four properties  
79 in the discrete case: (1) it should be a function of a probability distribution  $p(n)$  only; (2) it  
80 should be maximized when  $p(n)$  is uniform; (3) it should not be influenced by outcomes with a  
81 null probability; and (4) it should be independent of the order of information acquisition. The  
82 Shannon's entropy (Shannon 1948)

$$H = - \sum_n p(n) \log p(n) \quad (1)$$

83 satisfies all of these properties. Finding the probability distribution  $p(n)$  that maximizes  $H$  under  
 84 a set of  $m$  constraints  $g$  can be done using the method of Lagrange multipliers. These constraints  
 85 could include one or many properties of the probability distribution (e.g., its mean, variance, and  
 86 range). However, the normalization constraint always need to be included in  $g$  in order to make  
 87 sure that  $p(n)$  sums to 1. The objective is then to find the values of the Lagrange multipliers  $\lambda_i$   
 88 that optimize a function  $F$ :

$$F = H - \sum_{i=1}^m \lambda_i(g_i - c_i), \quad (2)$$

89 where  $g_i$  is the mathematical formulation of the constraint  $i$  and  $c_i$ , its value. Note that  $F$  is just  
 90 Shannon's entropy to which we added terms that each sums to zero ( $g_i = c_i$ ).  $F$  is maximized by  
 91 setting to 0 its partial derivative with respect to  $p(n)$ . We will show how this can be done when  
 92 we derive the joint degree distribution analytically from the number of species and the number  
 93 of links in food webs.

94 In this contribution, we also use the SVD entropy as a measure of entropy, which is an applica-  
 95 tion of Shannon's entropy to the relative non-zero singular values of a truncated singular value  
 96 decomposition (t-SVD; Strydom, Dalla Riva, and Poisot 2021) of a food web's Boolean ad-  
 97 jacency matrix. This measure also satisfies all four properties above-mentioned, while being a  
 98 proper measure of the internal complexity of food webs (Strydom, Dalla Riva, and Poisot 2021).

99 We measured SVD entropy as follows:

$$J = - \sum_{i=1}^R s_i \log s_i, \quad (3)$$

100 where  $s_i$  are the relative singular values ( $s_i = \sigma_i / \sum_{i=1}^R \sigma_i$ , where  $\sigma_i$  are the singular values).  
 101 Following Strydom, Dalla Riva, and Poisot (2021), we standardized this measure with the rank  
 102  $R$  of the matrix (i.e.,  $J / \ln(R)$ ) to account for the difference in dimensions between networks  
 103 (Pielou's evenness; Pielou 1975). In a following section, we will show how SVD entropy can  
 104 be used to predict a network of maximum entropy (i.e., of maximum complexity) heuristically.

105 **Testing MaxEnt models**

106 **Data**

107 We tested our MaxEnt models (both approaches) against open food-web data queried from three  
108 different sources and integrated into what we call our *complete dataset*. First, all food webs  
109 archived on `mangal.io` were directly queried from the database ( $n = 235$ ). Most ecological  
110 networks archived on Mangal are multilayer networks, i.e. networks that describe different types  
111 of interactions. We kept all networks whose interactions were mainly of predation and herbivory  
112 types, and removed the largest network ( $S = 714$ ) for computational efficiency reasons. Then,  
113 to this set we added food webs from two different sources: the New-Zealand dataset ( $n = 21$ ;  
114 Pomeranz et al. 2018) and the Tuesday lake dataset ( $n = 2$ ; Cohen, Jonsson, and Carpenter  
115 2003). Of these two datasets, 19 networks had data on species' relative abundances that were  
116 used in the neutral model presented in a following subsection. These networks are part of what  
117 we call our *abundance dataset*, which is a subset of our complete dataset.

118 All code and data to reproduce this article are available at the Open Science Framework. Data  
119 cleaning, simulations and analyses were conducted in Julia v1.5.4.

120 **Null models (types I and II)**

121 Our maximum entropy network models (second approach only) were compared with two topo-  
122 logical null models. The first is the type I null model of M. A. Fortuna and Bascompte (2006),  
123 in which the probability that a species  $i$  predares on another species  $j$  is given by

$$p(i \rightarrow j) = \frac{L}{S^2}. \quad (4)$$

124 The second is the type II null model of Bascompte et al. (2003), in which the probability of  
125 interaction is instead given by

$$p(i \rightarrow j) = \frac{1}{2} \left( \frac{k_{in}(j)}{S} + \frac{k_{out}(i)}{S} \right), \quad (5)$$

126 where  $k_{in}$  and  $k_{out}$  are the in and out-degrees, respectively. The type I null model is based on  
127 connectance, whereas the type II null model is based on the joint degree sequence. Therefore,  
128 the type I and II topological null models correspond with our type I and II MaxEnt network  
129 models, respectively, since they use similar constraints.

130 We predicted both types of null networks for all empirical networks in our complete dataset  
131 ( $n = 257$ ). We converted all probabilistic networks to Boolean networks by generating 100  
132 random Boolean networks for each of these probabilistic webs. Then, we counted the number  
133 of times each interaction was sampled, and kept the  $L$  entries that were drawn the most amount  
134 of time, with  $L$  given by the number of links in each food web. This ensured that the resulting  
135 null networks had the same number of interactions as their empirical counterparts.

## 136 Neutral model

137 We also compared our MaxEnt network models with a neutral model of relative abundances, in  
138 which the probabilities of interaction are given by

$$p(i \rightarrow j) \propto \frac{n_i}{N} \times \frac{n_j}{N}, \quad (6)$$

139 where  $n_i$  and  $n_j$  are the abundances (or biomass) of both species, and  $N$  is the total abundance  
140 (or biomass) of all species in the network. We predicted neutral abundance matrices for all  
141 empirical networks in our abundance dataset ( $n = 19$ ), and converted these weighted matrices  
142 to Boolean networks using an approach analogue to the one we used for our null models.

## 143 Analytical models: Measures of maximum entropy

### 144 Joint degree distribution

145 The joint degree distribution  $p(k_{in}, k_{out})$  is a joint discrete probability distribution describing  
146 the probability that a species has  $k_{in}$  predators and  $k_{out}$  preys, with  $k_{in}$  and  $k_{out} \in [0, S]$ . Basal  
147 species (e.g., plants) have a  $k_{out}$  of 0, whereas top predators have a  $k_{in}$  of 0. In contrast, the

148 maximum number of preys and predators a species can have is set by the number of species  $S$   
 149 in the food web. Here we show how the joint degree distribution of maximum entropy can be  
 150 obtained given knowledge of  $S$  and  $L$ .

151 We want to maximize Shannon's entropy

$$H = - \sum_{k_{in}=0}^S \sum_{k_{out}=0}^S p(k_{in}, k_{out}) \log p(k_{in}, k_{out}) \quad (7)$$

152 subject to the following constraints:

$$g_1 = \sum_{k_{in}=0}^S \sum_{k_{out}=0}^S p(k_{in}, k_{out}) = 1; \quad (8)$$

$$g_2 = \sum_{k_{in}=0}^S \sum_{k_{out}=0}^S k_{in} p(k_{in}, k_{out}) = \langle k_{in} \rangle = \frac{L}{S}; \quad (9)$$

$$g_3 = \sum_{k_{in}=0}^S \sum_{k_{out}=0}^S k_{out} p(k_{in}, k_{out}) = \langle k_{out} \rangle = \frac{L}{S}. \quad (10)$$

153 The first constraint  $g_1$  is our normalizing constraint, whereas the other two ( $g_2$  and  $g_3$ ) fix the  
 154 average of the marginal distributions of  $k_{in}$  and  $k_{out}$  to the linkage density  $L/S$ . It is important  
 155 to notice that  $\langle k_{in} \rangle = \langle k_{out} \rangle$  because every edge is associated to a predator and a prey. Therefore,  
 156 without any further constraints, we expect the joint degree distribution of maximum entropy to  
 157 be a symmetric probability distribution with regards to  $k_{in}$  and  $k_{out}$ . However, this does not mean  
 158 that the joint degree *sequence* will be symmetric, since the joint degree sequence is essentially  
 159 a random realization of its probabilistic counterpart.

160 The joint probability distribution of maximum entropy given these constraints is found using the  
 161 method of Lagrange multipliers. To do so, we seek to maximize the following expression:

$$F = H - \lambda_1(g_1 - 1) - \lambda_2 \left( g_2 - \frac{L}{S} \right) - \lambda_3 \left( g_3 - \frac{L}{S} \right), \quad (11)$$

162 where  $\lambda_1$ ,  $\lambda_2$ , and  $\lambda_3$  are the Lagrange multipliers. The probability distribution that maximizes

<sup>163</sup> entropy is obtained by finding these values. As pointed out in Box 1,  $F$  is just Shannon's entropy  
<sup>164</sup> to which we added terms that each sums to zero (our constraints).  $F$  is maximized by setting to  
<sup>165</sup> 0 its partial derivative with respect to  $p(k_{in}, k_{out})$ . Because the derivative of a constant is zero,  
<sup>166</sup> this gives us:

$$\frac{\partial H}{\partial p(k_{in}, k_{out})} = \lambda_1 \frac{\partial g_1}{\partial p(k_{in}, k_{out})} + \lambda_2 \frac{\partial g_2}{\partial p(k_{in}, k_{out})} + \lambda_3 \frac{\partial g_3}{\partial p(k_{in}, k_{out})}. \quad (12)$$

<sup>167</sup> Evaluating the partial derivatives with respect to  $p(k_{in}, k_{out})$ , we obtain:

$$-\log p(k_{in}, k_{out}) - 1 = \lambda_1 + \lambda_2 k_{in} + \lambda_3 k_{out}. \quad (13)$$

<sup>168</sup> Then, solving eq. 13 for  $p(k_{in}, k_{out})$ , we obtain:

$$p(k_{in}, k_{out}) = \frac{e^{-\lambda_2 k_{in} - \lambda_3 k_{out}}}{Z}, \quad (14)$$

<sup>169</sup> where  $Z = e^{1+\lambda_1}$  is called the partition function. The partition function ensures that probabilities  
<sup>170</sup> sum to 1 (our normalization constraint). It can be expressed in terms of  $\lambda_2$  and  $\lambda_3$  as follows:

$$Z = \sum_{k_{in}=0}^S \sum_{k_{out}=0}^S e^{-\lambda_2 k_{in} - \lambda_3 k_{out}}. \quad (15)$$

<sup>171</sup> After substituting  $p(k_{in}, k_{out})$  in eq. 9 and eq. 10, we get a nonlinear system of two equations and  
<sup>172</sup> two unknowns:

$$\frac{1}{Z} \sum_{k_{in}=0}^S \sum_{k_{out}=0}^S k_{in} e^{-\lambda_2 k_{in} - \lambda_3 k_{out}} = \frac{L}{S}; \quad (16)$$

$$\frac{1}{Z} \sum_{k_{in}=0}^S \sum_{k_{out}=0}^S k_{out} e^{-\lambda_2 k_{in} - \lambda_3 k_{out}} = \frac{L}{S}. \quad (17)$$

<sup>173</sup> We solved eq. 16 and eq. 17 numerically using the Julia library JuMP.jl v0.21.8 (Dunning,  
<sup>174</sup> Huchette, and Lubin 2017). JuMP.jl supports nonlinear optimization problems by providing

175 exact second derivatives that increase the accuracy and performance of its solvers. The estimated  
176 values of  $\lambda_2$  and  $\lambda_3$  can be substituted in eq. 14 to have a more workable expression for the joint  
177 degree distribution.

178 We predicted the joint degree distribution of maximum entropy for each food web in our com-  
179 plete dataset, i.e. using their numbers of species and numbers of links as state variables. We then  
180 sampled one realization of the degree sequence for each network using the probabilities given  
181 by the joint degree distribution. In fig. 1 (left panels), we show the relationship between  $k_{out}$  and  
182  $k_{in}$  standardized by the number of species in their networks, for empirical and maximum entropy  
183 joint degree distributions. We see that our model predicts a greater number of generalist species  
184 than empirical food webs (i.e., relative values of  $k_{out}$  and  $k_{in}$  closer to 1). However, plotting the  
185 difference between predicted and empirical values for each species gives a different perspective.  
186 The right panel of fig. 1 presents these differences when species are ordered by their total degree  
187 in their network (i.e., by the sum of their in and out-degrees). Indeed, our predicted joint degree  
188 sequences have the same number of species as their empirical counterparts, but they are species  
189 agnostic; in other words, instead of predicting a value for each species directly, we predicted  
190 the entire joint degree sequence without taking into account species' identity. When we asso-  
191 ciate predictions and empirical data according to their rank in total degrees, we see that species  
192 predicted to be have a higher generality (number of preys) generally have a lower vulnerability  
193 (number of preys) than what is observed (and conversely). In fig. S1, we show how these differ-  
194 ences change when species are instead ordered by their out-degrees (left panel) and in-degrees  
195 (right panel), respectively.

196 [Figure 1 about here.]

197 We plotted the Kullback–Leibler divergence between in and out-degree distributions to compare  
198 the symmetry of empirical and maximum entropy joint degree sequences fig. 2. As we expected,  
199 our model predicted more similar in-degree and out-degree distributions than empirical data.  
200 However, this difference decreased with connectance right panel of 2. Overall, this suggests that  
201 other ecological constraints might be needed to account for the asymmetry of the joint degree  
202 distribution, especially for networks with a lower connectance.

203

[Figure 2 about here.]

204 **Degree distribution**

205 The degree distribution  $p(k)$  represents the probability that a species has  $k$  links in a food web,  
 206 with  $k = k_{in} + k_{out}$ . It can thus be directly obtained from the joint degree distribution:

$$p(k) = \sum_{i=0}^k p(k_{in} = k - i, k_{out} = i).$$

207 In fig. S2, we show that the degree distribution of maximum entropy, given  $S$  and  $L$ , predicts  
 208 very low probabilities that a species will be isolated in its food web (*i.e.*, having  $k = 0$ ). As  
 209 MacDonald, Banville, and Poisot (2020) pointed out, the size of food webs should at least be of  
 210  $S - 1$  links, since a lower number would yield isolated species, *i.e.* species without any predators  
 211 or preys. Our results show that, under our purely information-theoretic model, the probability  
 212 that a species is isolated is quite high below this threshold. The expected proportion of isolated  
 213 species rapidly declines by orders of magnitude with increasing numbers of species and links.

214 The degree distribution could also have been obtained directly using the principle of maximum  
 215 entropy, as discussed in Williams (2011). This gives the following distribution:

$$p(k) = \frac{e^{-\lambda_2 k}}{Z}, \quad (18)$$

216 with  $Z = \sum_{k=0}^S e^{-\lambda_2 k}$ .

217 This can be solved numerically using the constraint of the average degree  $\langle k \rangle = \frac{2L}{S}$  of a species.  
 218 Note that the mean degree is twice the value of the linkage density, because every link must be  
 219 counted twice when we add in and out-degrees together.

$$\frac{1}{Z} \sum_{k=0}^S k e^{-\lambda_2 k} = \frac{2L}{S} \quad (19)$$

220 The numerical solution is identical to the one we obtained using the joint degree distribution  
 221 as an intermediate. Ecologists wanting to model a system without considering isolated species

222 could simply change the lower limit of  $k$  to 1 and solve the resulting equation numerically.

223 In this section, we showed how important measures of food-web structure, namely the degree  
224 distribution and the joint degree distribution, could be derived with the principle of maximum  
225 entropy using minimal knowledge on a biological community. This type of models, although  
226 useful to make least-biased predictions on many network properties, can be hard to apply for  
227 other measures. Indeed, there are dozens of measures of network structure (Delmas et al. 2019)  
228 and many are not calculated with mathematical equations, but with algorithms. Moreover, the  
229 applicability of this method to empirical systems is limited by the state variables we can actu-  
230 ally measure and use. In the next section, we propose a more flexible method to predict many  
231 measures of network structure simultaneously, i.e. by finding networks of maximum entropy  
232 heuristically.

## 233 Box 2 - Working with predicted numbers of links

234 Our models need information on the number of species and the number of links. However,  
235 since the later is rarely estimated empirically, ecologists might need to use predictive methods  
236 to estimate the total number of links in a food web.

237 We used the flexible links model of MacDonald, Banville, and Poisot (2020) to predict the  
238 number of interactions from the number of species. The flexible links model, in contrast to  
239 other predictive models of the number of links, incorporates meaningful ecological constraints  
240 into the prediction of  $L$ , namely the minimum  $S - 1$  and maximum  $S^2$  numbers of interactions  
241 in food webs. It estimates the proportion of the  $S^2 - (S - 1)$  *flexible links* that are realized.  
242 More precisely, this model states that the number of *realized* flexible links  $L_{FL}$  in a food web  
243 represents the number of realized interactions above the minimum (i.e.,  $L = L_{FL} + S - 1$ ) and  
244 is obtained from a beta-binomial distribution with  $S^2 - (S - 1)$  trials and parameters  $\alpha = \mu e^\phi$   
245 and  $\beta = (1 - \mu)e^\phi$ :

$$L_{FL} \sim \text{BB}(S^2 - (S - 1), \mu e^\phi, (1 - \mu)e^\phi), \quad (20)$$

246 where  $\mu$  is the average probability across food webs that a flexible link is realized, and  $\phi$  is the  
247 concentration parameter around  $\mu$ .

248 We fitted the flexible links model on all food webs in our complete dataset, and estimated the  
249 parameters of eq. 20 using a Hamiltonian Monte Carlo sampler with static trajectory (1 chain  
250 and 3000 iterations):

$$[\mu, \phi | \mathbf{L}, \mathbf{S}] \propto \prod_{i=1}^m \text{BB}(L_i - (S_i - 1) | S_i^2 - (S_i - 1)), \mu e^\phi, (1 - \mu) e^\phi \times \text{B}(\mu | 3, 7) \times \mathcal{N}(\phi | 3, 0.5), \quad (21)$$

251 where  $m$  is the number of food webs ( $m = 257$ ) and  $\mathbf{L}$  and  $\mathbf{S}$  are respectively the vectors of their  
252 numbers of interactions and numbers of species. Our weakly-informative prior distributions  
253 were chosen following MacDonald, Banville, and Poisot (2020), i.e. a beta distribution for  $\mu$   
254 and a normal distribution for  $\phi$ . The Monte Carlo sampling of the posterior distribution was  
255 conducted using the Julia library Turing v0.15.12.

256 The flexible links model is a generative model, i.e. it can generate plausible values of the pre-  
257 dicted variable. We thus simulated 1000 values of  $L$  for different values of  $S$  using the joint  
258 posterior distribution of our model parameters, and calculated the mean degree for each simu-  
259 lated values. The resulting distributions are shown in the left panel of fig. 3 for three different  
260 values of species richness. In the right panel of fig. 3, we show how the probability distribution  
261 for the mean degree constraints can be used to generate a distribution of maximum entropy de-  
262 gree distributions, since each simulated value of mean degree generates a different maximum  
263 entropy degree distribution.

264 [Figure 3 about here.]

265 **Heuristical models: Networks of maximum entropy**

266 **MaxEnt network models (types I and II)**

267 We define networks of maximum entropy as the configuration of the adjacency matrix with the  
268 highest SVD entropy under a set of constraints. As mentioned in Box 1, we used the SVD  
269 entropy as our measure of entropy since it has been shown to be a reliable measure of food-web  
270 complexity (Strydom, Dalla Riva, and Poisot 2021), in addition to having the required properties  
271 of a proper measure of information entropy. We thus seek to find the network with the highest  
272 complexity, or randomness, that exactly reproduces specified constraints on its structure. Our  
273 method is in contrast with maximum entropy graph models that predict a probability distribution  
274 on networks under soft or hard constraints Cimini et al. (2019). We believe our approach to be  
275 more flexible, easier to compute, while allowing direct comparisons of empirical food webs with  
276 more complex networks with similar structure.

277 We built two types of MaxEnt network models: one based on connectance (type I MaxEnt net-  
278 work model) and the other based on the joint degree sequence (type II MaxEnt network model).  
279 They are based on the same constraints as the types I and II null models presented above. For  
280 both models, we used a simulating annealing algorithm with 4 chains, 2000 steps and an initial  
281 temperature of 0.2. For each chain, we first generated one random Boolean matrix with the same  
282 order (number of species) as empirical webs, while maintaining the total number of interactions  
283 (type I MaxEnt network model) or rows and columns sums (type II MaxEnt network model).  
284 These are our initial configurations. Then, we swapped interactions sequentially while main-  
285 taining the original connectance or the joint degree sequence for types I and II MaxEnt network  
286 model, respectively. Configurations with a higher SVD entropy than the previous one in the  
287 chain were always accepted, whereas they were accepted with a probability conditional to a de-  
288 creasing temperature when lower. The final configuration with the highest SVD entropy among  
289 the four chains constitute our estimated MaxEnt network. Even though we decided to work with  
290 point estimates, it is possible to have a (non MaxEnt) probability distribution of networks when  
291 working with the entire chains after burn-in. For each network in our complete and abundance  
292 datasets, we estimated their configuration with maximum entropy using both types of MaxEnt

293 network models.

294 **Structure of MaxEnt networks**

295 We compared different measures of the structure of empirical food webs with the ones of null,  
296 neutral, and MaxEnt networks [tbl. 1](#), and [2](#). For instance, we measured the nestedness  $\rho$  accord-  
297 ing to Staniczenko, Kopp, and Allesina (2013), i.e. using the spectral radius of the adjacency  
298 matrix. Nestedness indicates how much the diet of specialist species is a subset of the one of  
299 generalists, and is strongly associated with network modularity (Miguel A. Fortuna et al. 2010).  
300 We also measured the maximum trophic level *maxtl*, network diameter *diam* (i.e., the longest of  
301 the shortest paths between all species pairs; Albert and Barabasi 2002), the average maximum  
302 similarity between species pairs *MxSim*, the proportion of cannibal species *Cannib* (i.e., the  
303 proportion of self loops), and the proportion of omnivorous species *Omniv* (i.e., species whose  
304 preys are of different trophic levels). *MxSim*, *Cannib*, and *Omniv* are more deeply defined in  
305 Williams and Martinez (2000).

306 Overall, we found that models based on the joint degree sequence (type II null and MaxEnt  
307 network models) reproduced the structure of empirical networks much better than the ones based  
308 on connectance and the neutral model of relative abundances. On average, the type II MaxEnt  
309 network model was better at predicting nestedness ( $0.62 \pm 0.08$ ) than its corresponding null model  
310 ( $0.73 \pm 0.05$ ; empirical networks:  $0.63 \pm 0.09$ ), as well as the proportion of cannibal species.  
311 However, the type II null model was better at predicting network diameter and average maximum  
312 similarity between species pairs. Predictions were similar between both type II models for the  
313 maximum trophic level and the proportion of omnivorous species.

Table 1: Standardized mean differences of predicted network measures with empirical data for all networks ( $n = 257$ ). Positive (negative) values indicate that the measure is overestimated (underestimated) on average. Empirical networks are all food webs archived on Mangal, as well as the New Zealand and Tuesday lake food webs (our complete dataset). Null 1: Type I null model based on connectance. MaxEnt 1: Type I MaxEnt network model based on connectance. Null 2: Type II null model based on the joint degree sequence. MaxEnt 2: Type II MaxEnt network model based on the joint degree sequence.  $\rho$ : nestedness measured by the spectral radius of the adjacency matrix. *maxtl*: maximum trophic level. *diam*: network diameter. *MxSim*: average maximum similarity between species pairs. *Cannib*: proportion of cannibal species (self loops). *Omniv*: proportion of omnivorous species. *entropy*: SVD entropy.

model	rho	maxtl	diam	MxSim	Cannib	Omniv	entropy
null 1	-0.167	0.980	1.428	-0.502	2.007	1.493	0.056
MaxEnt 1	-0.226	0.831	1.274	-0.524	1.982	1.863	0.106
null 2	0.160	-0.125	0.016	0.007	1.078	0.559	-0.023
MaxEnt 2	-0.015	0.178	0.565	-0.282	0.698	0.589	0.058

Table 2: Standardized mean differences of predicted network measures with empirical data for networks having abundance data ( $n = 19$ ). Positive (negative) values indicate that the measure is overestimated (underestimated) on average. Empirical networks are all New Zealand and Tuesday lake food webs with abundance data (our abundance dataset). Null 1: Type I null model based on connectance. MaxEnt 1: Type I MaxEnt network model based on connectance. Null 2: Type II null model based on the joint degree sequence. MaxEnt 2: Type II MaxEnt network model based on the joint degree sequence.  $\rho$ : nestedness measured by the spectral radius of the adjacency matrix. *maxtl*: maximum trophic level. *diam*: network diameter. *MxSim*: average maximum similarity between species pairs. *Cannib*: proportion of cannibal species (self loops). *Omniv*: proportion of omnivorous species. *entropy*: SVD entropy.

model	rho	maxtl	diam	MxSim	Cannib	Omniv	entropy
neutral	0.367	-0.090	0.027	0.266	6.870	0.576	-0.083
null 1	-0.134	0.950	1.919	-0.369	2.077	0.614	0.068
MaxEnt 1	-0.229	1.020	1.946	-0.355	2.215	0.801	0.121
null 2	0.128	-0.115	-0.135	0.157	1.444	0.029	-0.021
MaxEnt 2	-0.010	0.054	0.243	-0.062	-0.038	0.083	0.038

<sup>314</sup> The picture slightly changes when we consider another important property of ecological net-

<sup>315</sup> works, i.e. their motifs profile. We measured the proportion of three-species motifs, which can

316 be considered as simple building blocks of ecological networks (Milo et al. 2002; Stouffer et al.  
317 2007). Motifs are the backbone of complex ecological networks from which network structure  
318 is built upon and play a crucial role in community dynamics and assembly (Bastolla et al. 2009;  
319 Stouffer and Bascompte 2011). In fig. 4, we show that the motifs profile of networks generated  
320 using the type II MaxEnt network model was very close to the one of empirical data, and that  
321 they made better predictions than the type II null model. This is also shown in fig. 5, where we  
322 see that relationships between motifs pairs of empirical food webs are very similar to the ones  
323 of the type II MaxEnt networks. Overall, these results suggest that the type II MaxEnt network  
324 model can reproduce many aspects of network structure. This highlights the importance of the  
325 joint degree sequence in shaping ecological networks.

326 [Figure 4 about here.]

327 [Figure 5 about here.]

328 Moreover, we found that empirical networks are close to their maximum entropy considering a  
329 fixed joint degree sequence (fig. S3). Empirical networks had an SVD entropy of  $0.89 \pm 0.04$ ,  
330 compared to type II MaxEnt networks which had values of  $0.94 \pm 0.03$ . The relationship between  
331 the SVD entropy of empirical food webs and their maximum entropy configuration is plotted in  
332 the last panel of fig. 6. We also found no relationship between the difference in SVD entropy  
333 between empirical and type II MaxEnt networks and species richness, the number of links, or  
334 connectance (fig. S4). Similarly, we found no correlation between the difference in SVD entropy  
335 and the Jaccard distance of empirical and type II MaxEnt networks.

336 Finally, in fig. 6 we also show how well empirical measures are predicted using the type II  
337 MaxEnt network model. In accordance with our previous results, we found that nestedness was  
338 very well predicted by our model. However, the type II MaxEnt network model overestimated  
339 the maximum trophic level and network diameter, especially for networks with high empirical  
340 values. In fig. S5, we show that the pairwise relationships between these four measures and  
341 species richness in empirical food webs are similar (in magnitude and sign) to the ones in type  
342 II MaxEnt networks.

344 **Conclusion**

345 The principle of maximum entropy is a robust mathematical method of finding least-biased  
 346 probability distributions that have some desired properties given by prior knowledge on a sys-  
 347 tem. We first used MaxEnt to predict the joint degree distribution and the degree distribution  
 348 of maximum entropy given known numbers of species and of interactions. We found that the  
 349 resulting joint degree distributions were more symmetric than the ones of empirical food webs,  
 350 which suggests that other constraints might be needed to improve those predictions. We also  
 351 used MaxEnt to predict networks of maximum entropy with a specified structure. These net-  
 352 works are the most complex, or random, given the constraints used. Likewise, we found that  
 353 knowledge of species richness and of the number of links were not sufficient to reproduce many  
 354 aspects of network structure found in nature. However, a model based on the entire joint degree  
 355 sequence, i.e. on the number of preys and predators for each species, gave more convincing re-  
 356 sults. Our type II MaxEnt network model yielded better or similar predictions than the type II  
 357 null model, also based on the joint degree sequence, for most measures considered including  
 358 the motifs profile. This suggests that the joint degree sequence drives many aspects of network  
 359 structure. Indeed, considering our findings that empirical networks are close to maximum en-  
 360 tropy for a given joint degree sequence, our results suggest that food-web topology is configured  
 361 almost entirely randomly around these marginal numbers of predators and preys.

362 Our method and results could be used for different purposes. First, they could be used as first-  
 363 order approximations of network structure when only state variables are known. This could  
 364 prove useful when predicting network structure at large spatial scales, where few ecological in-  
 365 formation is known at that scale. Second, they could be used as informative priors in Bayesian  
 366 analyses of the structure of ecological networks. Third, they could be used to make better predic-  
 367 tions of pairwise species interactions by constraining the space of feasible networks, as discussed  
 368 in Strydom et al. (2021). Finally, they could be used as alternative null models of ecological net-  
 369 works to better understand ecological mechanisms driving food-web structure. In that case, our

370 model might need to be slightly adapted to give a probability distribution of Boolean networks  
371 (in contrast with point estimates of maximum entropy networks).

372 One of the biggest challenges in using the principle of maximum entropy is to identify the set  
373 of state variables that best reproduce empirical data. We found that the numbers of preys and  
374 predators for each species are important state variables for the prediction of maximum entropy  
375 networks. However, our predictions overestimated some measures of network structure, espe-  
376 cially the maximum trophic level and network diameter. Therefore, we should continue playing  
377 the ecological detective to find these other topological constraints that would improve the pre-  
378 dictions of our MaxEnt network models.

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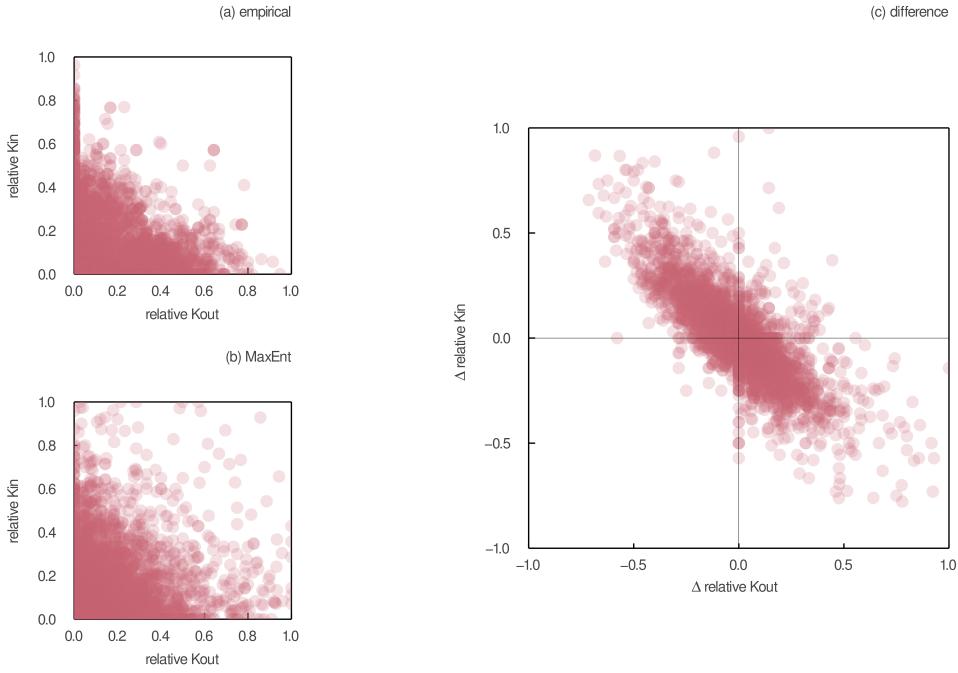


Figure 1: Relative number of predators ( $k_{in}$ ) as a function of the relative number of preys ( $k_{out}$ ) for each species in (a) empirical and (b) maximum entropy joint degree sequences. Empirical networks include all food webs archived on Mangal, as well as the New-Zealand and Tuesday lake datasets (our complete dataset). The predicted joint degree sequences were obtained after sampling one realization of the joint degree distribution of maximum entropy for each network. (c) Difference between predicted and empirical values when species are ordered according to their total degrees. In all panels, each dot corresponds to a single species in one of the network of our complete dataset.

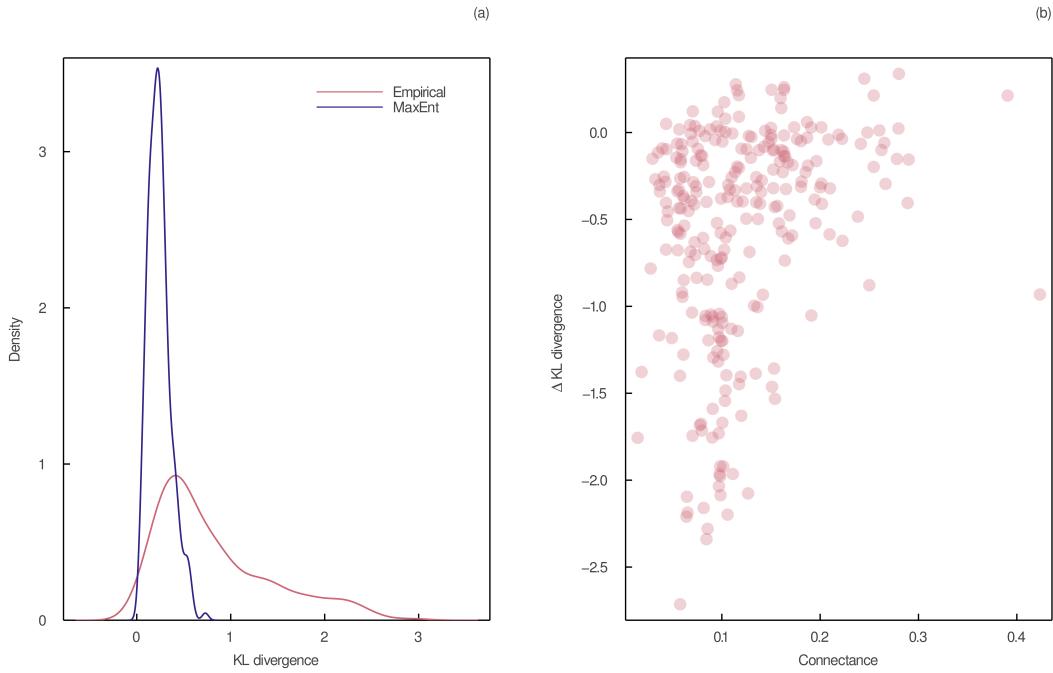


Figure 2: (a) Probability density of KL divergence between in and out-degree sequences of empirical and maximum entropy joint degree sequences. (b) Difference between the KL divergence of empirical and predicted networks as a function of connectance. In both panels, empirical networks include all food webs archived on Mangal, as well as the New-Zealand and Tuesday lake datasets (our complete dataset). The joint degree sequence of simulated networks was obtained after sampling one realization of the joint degree distribution of maximum entropy for each network.

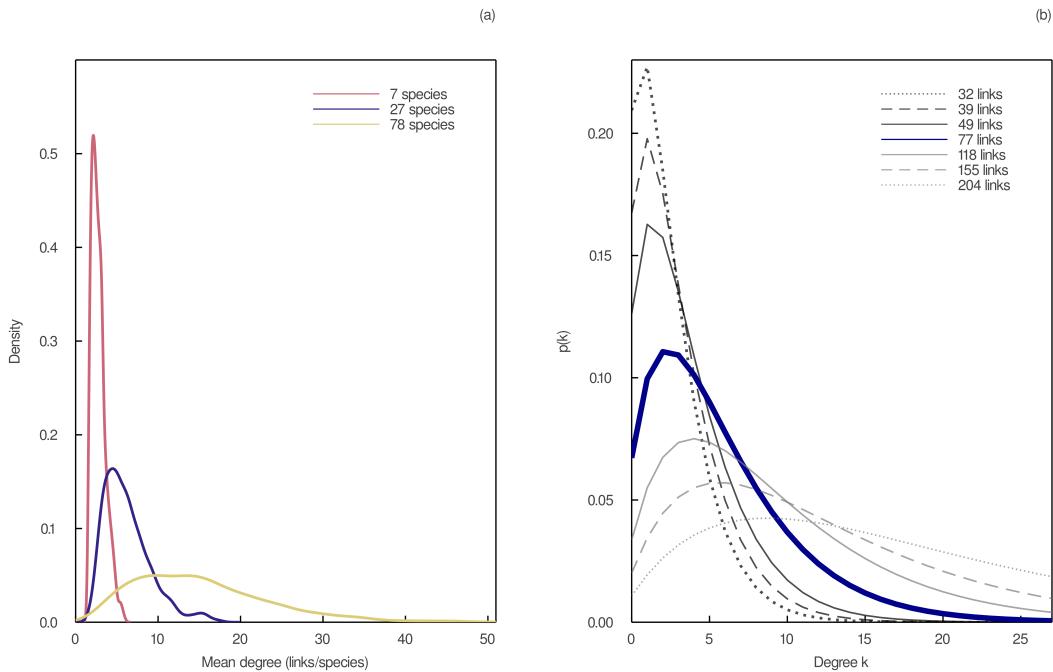


Figure 3: (a) Probability density of the predicted mean degree for different values of species richness. The number of links was predicted using the flexible links model fitted to all empirical networks in our complete dataset. (b) Degree distributions of maximum entropy for a network of 27 species and different numbers of links. The numbers of links correspond to the lower and upper bounds of the 67, 89, and 97 percentile intervals (PI), as well as the median, of the counterfactuals of the flexible links model.

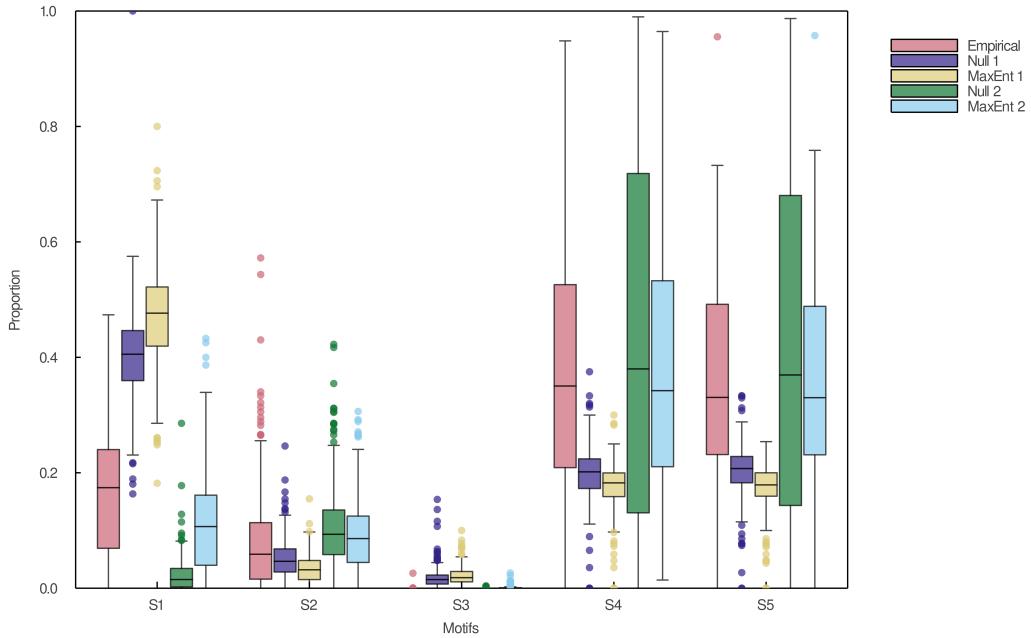


Figure 4: Motifs profile of empirical, maximum entropy, and null food webs. Empirical networks include all food webs archived on Mangal, as well as the New-Zealand and Tuesday lake datasets (our complete dataset). Maximum entropy networks were estimated using a simulating annealing algorithm to find the network of maximum SVD entropy while maintaining the connectance (type I MaxEnt network model) or the joint degree sequence (type II MaxEnt network model). The predictions of the types I and II null models are also plotted. Boxplots display the median proportions of each motif (middle horizontal lines), as well as the first (bottom horizontal lines) and third (top horizontal lines) quartiles. Vertical lines encompass all data points that fall within 1.5 times the interquartile range from both quartiles, and dots are data points that fall outside this range. Motifs names are from Stouffer et al. (2007).

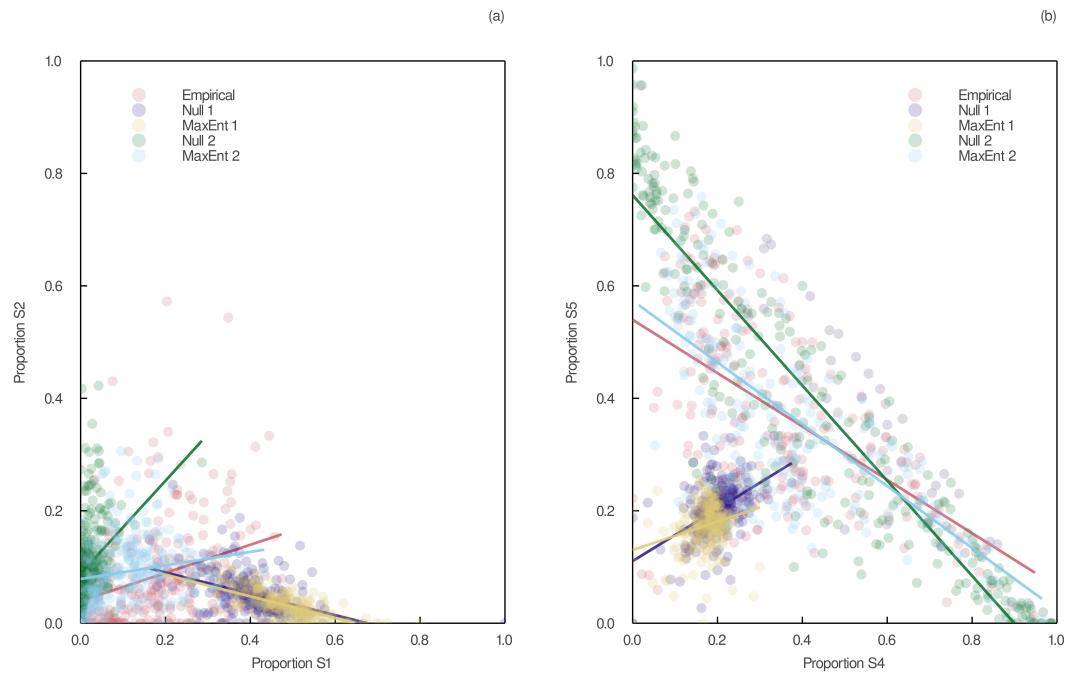


Figure 5: Relationship between motifs proportions of empirical, maximum entropy, and null food webs. Empirical networks include all food webs archived on Mangal, as well as the New-Zealand and Tuesday lake datasets (our complete dataset). Maximum entropy networks were estimated using a simulating annealing algorithm to find the network of maximum SVD entropy while maintaining the connectance (type I MaxEnt network model) or the joint degree sequence (type II MaxEnt network model). The predictions of the types I and II null models are also plotted. Regression lines are plotted in each panel. Motifs names are from Stouffer et al. (2007).

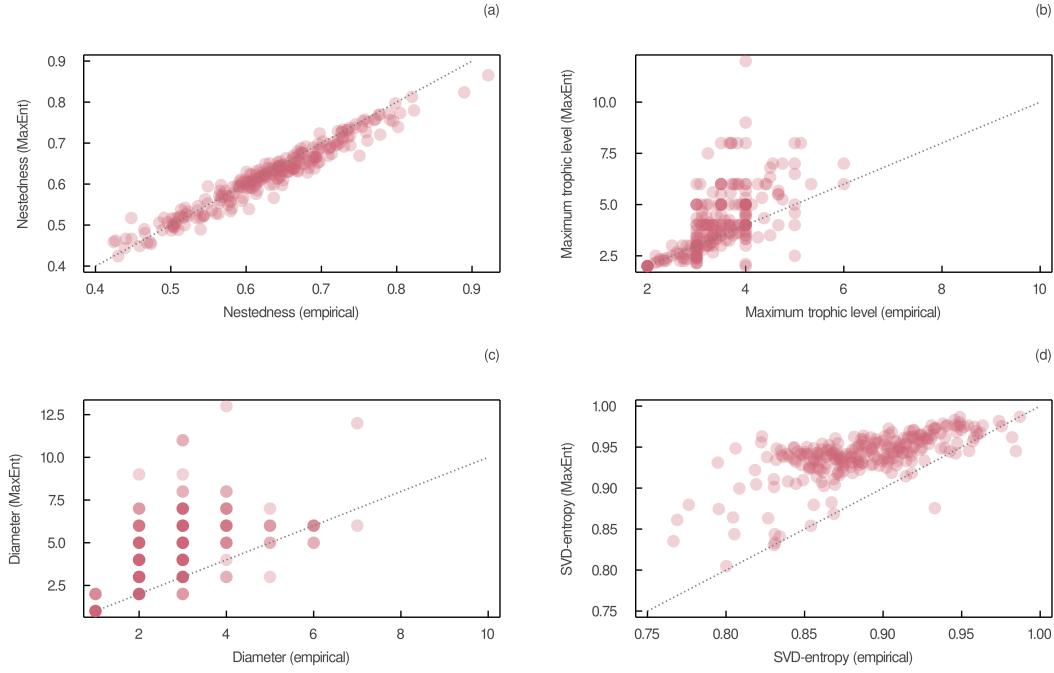


Figure 6: Relationship between the structure of empirical and maximum entropy food webs. Empirical networks include all food webs archived on Mangal, as well as the New-Zealand and Tuesday lake datasets (our complete dataset). Maximum entropy networks were estimated using a simulating annealing algorithm to find the network of maximum SVD entropy while maintaining the joint degree sequence (type II MaxEnt network model). (a) Nestedness (estimated using the spectral radius of the adjacency matrix), (b) the maximum trophic level, (c) the network diameter, and (d) the SVD entropy were measured on these empirical and maximum entropy food webs. The identity line is plotted in each panel.