Predicting trophic relations in ecological networks: a test of the Allometric Diet Breadth Model

Stefano Allesina
Dept. of Ecology & Evolution,
Computation Institute,
The University of Chicago
sallesina@uchicago.edu

November 10, 2009

Abstract

Few of food web theory hypotheses/predictions can be readily tested using empirical data. An exception is represented by simple probabilistic models for food web structure, for which the likelihood has been derived. Here I test the performance of a more complex model for food web structure that is grounded in the allometric scaling of interactions with body size and the theory of optimal foraging (Allometric Diet Breadth Model - ADBM). This deterministic model has been evaluated measuring the fraction of trophic relations correctly predicted. I contrast this value with that produced by simpler models based on body sizes and find that the data does not favor the more complex model: the information on allometric scaling and optimal foraging does not significantly increase the fit to the data. Also, I take a different approach and compute the p-value for the fraction of trophic interactions correctly predicted by ADBM with respect to three probabilistic null models. I find that the ADBM is clearly better at predicting links than random graphs, but other models can do even better. Although optimal foraging and allometric scaling could improve our understanding of food webs, the models need to be ameliorated to find support in the data.
Introduction

Understanding the main forces shaping the topology of food webs (networks depicting who eats whom in an ecosystem) is a central problem in ecology that has received a lot of attention (Cohen et al. 1990, Williams and Martinez 2000, Cattin et al. 2004, Allesina et al. 2008, Allesina and Pascual 2009). This problem has been typically investigated using simple probabilistic models, but recently models that incorporate explicitly relevant biological quantities in their assumptions have started appearing in the literature (Loeuille and Loreau 2005, Rossberg et al. 2006, Petchey et al. 2008).

In a work that investigated the role of body size and optimal foraging theory in shaping food web structure, Petchey et al. (2008) assessed the goodness of variants of their main model, measuring the proportion of empirical connections a model is able to predict. If a model proposes $K$ connections among species of which $M$ are present in the empirical data set, then the proportion of correct links (overlap) is $\Omega = M/K$. They measured this overlap for their Allometric Diet Breadth Model (ADBM), and they showed that the best version of the ADBM is able to correctly predict, depending on the empirical network examined, between 5% and 65% of the proposed links (Petchey et al. 2008). The ADBM is based on two main ideas: optimal foraging theory and allometric scaling of relevant quantities with body size (Beckerman et al. 2006, Petchey et al. 2008). The ADBM is different from most previous models also because it is not probabilistic: given an empirical
network, body sizes for all the species and number of links in the network, 4 further parameters dealing with the foraging are optimized numerically and a single network is produced deterministically. Here I compare the ADBM with simpler deterministic models that include information on body size but do not make use of allometric scaling and optimal foraging, and I find that the data does not support the use of the more complex model.

Also, I derive a p-value for the Ω produced by the ADBM using as a reference a random digraph \( \text{[Erdös and Rényi 1960]} \), a variation of the cascade model \( \text{[Cohen et al. 1990]} \) and a recently proposed group-based random digraph \( \text{[Allesina and Pascual 2009]} \). The derivation of the probability mass function for these simple models is a step forward in the analysis of more complex models for food web structure, for which the derivation of a likelihood can be almost impossible. The derivation presented here can help associating statistical significance to the results of highly complex models, such as those based on evolving networks or systems of differential equations \( \text{[Caldarelli et al. 1998]} \).

Results show that the ADBM performs significantly better than the random graph in terms of overlap. It also performs better than the cascade model analyzed here in most of the cases. The performance is significantly worse than that of the group-based random digraph.

In summary, even though allometric scaling and optimal foraging have the potential to illuminate the topology of food webs, the present models do not provide enough evidence to support this claim.
Methods

The Allometric Diet Breadth Model

Here I briefly describe the ADBM in its “Ratio” incarnation, that is the one that produces the best fit to the empirical data. A more detailed description of the model and its variations can be found in the original articles [Beckerman et al. 2006, Petchey et al. 2008].

The model takes as an input a vector $\vec{B}$ describes the species body sizes. The model requires the number of links ($L$) for the empirical food web one wants to replicate that will be used in the numerical optimization routine. Then, the model uses four other parameters $a$, $a_1$, $a_2$ and $b$ that determine the foraging behavior of the species in the food web. The model consists of two steps: a) compute, for each predator, the profitability of each possible prey; b) compute a diet breadth (i.e. number of prey) for each predator: this number is chosen to maximize the rate of energy intake. Repeating the two steps for all the consumers produces a food web.

Here is a detailed description of the two steps outlined above:

1. Profitability. The profitability $P_{ij}$ of prey $i$ for consumer $j$ is defined as:

$$P_{ij} = \frac{B_i(bB_j - B_i)}{B_j}$$  \hspace{1cm} (1)

where $B_i$ is the body size of species $i$ and $b$ is a positive parameter.

2. Diet Breadth. A predator $j$ will prey upon $z$ species, where $z$ is the
value in $0, 1, \ldots, S$ that maximizes the function:

$$f(z, j) = \frac{a \sum_{i=\sigma_1}^{\sigma_{z}} B_i^{\left(\frac{1}{4} + a_1\right)} B_j^{a_2}}{1 + a \sum_{i=\sigma_1}^{\sigma_{z}} B_i^{\left(\frac{3}{4} + a_1\right)} B_j^{a_2}}$$

(2)

where the permutation $\sigma$ is the permutation that orders the prey according to decreasing profitability: if $z = 1$ is the value that maximizes $f(z, j)$, then consumer $j$ will choose only the most profitable prey, if $z = 2$ then it will choose the two most profitable prey and so on. This apparently complicated function is easily justifiable in terms of optimal foraging. The three parameters $a$, $a_1$ and $a_2$ are needed for computing the attack rate, and the parameter $b$ is involved in the computation of the handling time.

Repeating the two steps for all consumers generates a food web that will be compared with the empirical data. The performance of the model is measured as the fraction of links that correctly match the ones in the empirical food web. If an instance of the ADBM for a given network produces $K$ links of which $M$ are present in the empirical food web, then the proportion of links correctly predicted, or overlap is $\Omega = M/K$. The parameters $a$, $a_1$, $a_2$ and $b$ are optimized numerically so that the model a) correctly predicts the total number of links in the network ($K \approx L$) and b) $\Omega$ is maximized.

Running the ADBM for the 9 published food webs examined here yields $\Omega \in [0.08, 0.65]$ (Table 1).
Four simple models based on body size

One of the characteristics of the ADBM is that it produces interval networks: when species are ordered according to body size all the prey of a given predator are adjacent. Food webs are known to be quasi-interval\cite{Williams2000, Cattin2004, Stouffer2006, Allesina2008}, and this could be a main driver of the performance of the ADBM. It makes sense therefore to compare its performance with that of models that retain the intervality but do not contain extra information regarding optimal foraging and allometric scaling. Of all possible models, I analyze here four that have the virtue of being very simple and sharing the same structure. For each possible predator-prey couple, one computes a value that depends on body sizes of predator and prey: $z_{ij} = f(B_i, B_j)$. If $a \leq z_{ij} < b$, where $a$ and $b$ are food web-dependent parameter estimates, one draws a connection. If $z_{ij}$ is not included in the interval $(a,b]$, no connection is drawn. In what follows, I analyze four different $f(B_i, B_j)$:

1. “Diff”: $f(B_i, B_j) = B_i - B_j$. The difference between predator ($i$) and prey ($j$) sizes must fall in $(a,b]$ to draw a connection.

2. “Ratio”: $f(B_i, B_j) = B_i / B_j$. The ratio between the body sizes is what drives the structure of the food web.

3. “LogRatio”: $f(B_i, B_j) = ln(B_i + 1) / ln(B_j + 1)$. Where 1 is added so that the function is positive for all possible body sizes.
4. “DiffRatio”: \( f(B_i, B_j) = (B_j - B_i)(B_i/B_j) \). This model combines the first two models. Note that the function is very similar to Eq. 1 (profitability).

All the four models produce interval networks, are deterministic in nature (as the ADBM), and require the optimization of two parameters \((a, b)\) that can be easily accomplished by trying all relevant combinations.

For each model/food web, I optimize \(a, b\) so that a) the number of links produced is similar to the one measured empirically: if the ADBM proposes \(K\) links and \(|K - L| = t\), I accept as possible solutions only those whose number of connections is in \([L - t, L + t]\) (this is to ensure that the comparison is fair). b) Among all solutions satisfying the previous requirement, I choose the one that maximizes \(\Omega\). Contrasting these values with those produced by the ADBM can help us determine whether optimal foraging and allometric scaling do play a crucial role in predicting the links in the food web.

**p-value: a random digraph**

Another way to assess the goodness of a given \(\Omega\) is to associate a p-value to it. This quantity expresses the probability of obtaining a result that is equally good or better using a null model. In the remainder of the section I derive analytically such a p-value when the null model is a random digraph, while in the Appendix I derive the p-value when the null model is a cascade model or a group-based random digraph. I chose these models because they share the same derivation, and are in a continuum of complexity that makes
the comparison easier.

A random digraph (Erdős and Rényi [1960]) is the simplest possible way to produce networks: it takes just two parameters ($S$, the number of nodes in the network - standing for species, and $p$, the probability that two species are connected by feeding relations) and produces a network connecting any two species with a directed link with probability $p$. We want to know the probability $P(M, K | S, p, N(S, L))$ that a random graph using parameters $S$ and $p$ produces a network with $K$ links, of which $M$ are matching those of an empirical network $N$ that contains $S$ species and $L$ links. We can start by writing the probability that the random graph produces exactly $K$ links. This is a binomial probability mass function (pmf):

$$P(K | S, p, N(S, L)) = \binom{S}{K} p^K (1 - p)^{(S^2 - K)} \quad (3)$$

If we set $p = L/S^2$ we maximize the probability of obtaining $L$ links in the generated network (this is also the maximum likelihood estimate for the parameter). Once we know that the graph has produced $K$ links, we can compute the probability that of these $M$ are matching those of the empirical network $N(S, L)$ using a hypergeometric distribution:

$$P(M | S, p, N(S, L), K) = \binom{L}{M} \binom{S^2 - L}{K - M} \binom{S}{K} \quad (4)$$

The joint bivariate pmf becomes:
\[ \mathcal{P}(M, K|S, p, N(S, L)) = p^K(1 - p)^{(S^2 - K)} \binom{L}{M} \binom{S^2 - L}{K - M} \] (5)

This pmf assumes values for \( K \in [0, \ldots, S^2] \) and, for each \( K \), \( M \in [0, \ldots, \min(K, L)] \). We can therefore describe the pmf in a table with \((S^2 + 1)(L + 1) - L(L + 1)/2\) values associated with all the possible combinations of \( K \) and \( M \). An example of such a table is reported in Figure 1 for a small network. The table expressing the bivariate probability mass function shows the probability of obtaining any combination of \( K \) and \( M \). Because we are interested in the pmf for \( \Omega = M/K \) we can map the results from the bivariate pmf into a univariate distribution by summing the probabilities for all the combinations of \( K \) and \( M \) leading to the same \( \Omega \). For example, in Figure 1 I report the first few rows of such a table. From this, one can draw the complete pmf for \( \Omega \).

Deriving the probability of reproducing exactly the data shows the relation between \( \Omega \) and the likelihood. In fact, the likelihood can be seen as the probability of having \( \Omega = 1 \) when \( M = K = L \). By substituting in Eq. 5 we obtain:

\[ \mathcal{P}(L, L|S, p, N(S, L)) = p^L(1 - p)^{(S^2 - L)} = \mathcal{L}(S, p|N(S, L)) \] (6)

We can readily write also the expression for the AIC, whose values will be used in the Discussion. The number of parameters of the model is \( \theta = 2 \). The Akaike’s Information Criterion (Akaike 1974) becomes:

9
\[ AIC = 2\theta - 2\log L = 4 - 2(L\log(p) + (S^2 - L)\log(1 - p)) \] (7)

Results

I replicated the results obtained by Petchey et al. (Petchey et al. 2008) for nine food webs: Benguela Pelagic (Yodzis 1998), Broadstone Stream (Woodward and Hildrew 2001), Scotch Broom (Memmott et al. 2000), Carpinteria Salt Marsh (Lafferty et al. 2006), Coachella Valley (Polis 1991), Sierra Lakes (Harper-Smith et al. 2005), Skipwith Pond (Warren 1989), Tuesday Lake (Jonsson et al. 2005) and Ythan Estuary (Hall and Raffaelli 1991). The optimized parameters for the ADBM were taken from the original article (Petchey et al. 2008) so that for the produced network the number of connections match that of the corresponding empirical network and the overlap is maximized. I then analyzed the same networks using the four simple models based on body sizes presented above. I am reporting in Table 1 all the overlap values. In three cases the ADBM is the best performing model (including 2 ties). In the other cases one or more models have higher \( \Omega \) than the ADBM. Each of the four models produces the highest \( \Omega \) in three cases (including ties). For the “Broom” system all the four models have better overlap than the ADBM. The “Diff” model shows higher or equal \( \Omega \) values for 5 networks. The “LogRatio” in 4 cases. The other two models yield higher or equal values in 3 cases.

In all cases the results are quite similar to those produced by the ADBM,
as confirmed when the exact location of predicted and non-predicted links is examined (Figures 2 and 3): the models tend to correctly predict the same links and fail in the same regions of the matrix. The similarity with the ADBM is particularly pronounced for the “Ratio”, and “LogRatio”, while the “Diff” model tends to select a different set of links compared to the other models. In no case any of the models predicted exactly the same links.

Note however that the four simpler models optimize 2 parameters, while the ADBM requires 4 parameters. The ADBM is therefore more flexible and this should lead to better performance. How can we then fairly compare the models? If these were probabilistic models, then we could use for example AIC (or BIC, or any other selection criteria) to balance model performance and complexity. No simple solution however exists for deterministic models. One possibility is therefore to make the models probabilistic. This can be done in a straightforward way. Every time a deterministic model would draw a link, we can instead draw it with probability $q_1$. If the deterministic model does not predict a link, we can still draw it in the probabilistic counterpart with probability $q_2$. Deriving the likelihood for such a process is a simple extension of that of the models presented above, and we can see that the maximum likelihood estimates for $q_1$ and $q_2$ are $\Omega = M/K$ and $(L-M)/(S^2-K)$ respectively. While this modification makes all the models general (i.e. they can produce any network), it also negatively affect the expected $\Omega$ value. For a deterministic model $X$ that proposes $K$ links of which $M$ are present in the empirical network, the expected $\Omega$ for its probabilistic version $X'$ is:
\[
E\left[\frac{\Omega}{X'}\right] = \frac{Mq_1 + (L - M)q_2}{Kq_1 + (S^2 - K)q_2} = \frac{M^2S^2 + L^2K - 2LMK}{LK(S^2 - K)}
\] (8)

For example, if the ADBM yields \(\Omega_{ADBM} = 0.57143\) for the Benguela food web in the deterministic case, the probabilistic version yields \(E[\Omega_{ADBM'}] = 0.37843\), a decrease of 1/3 in performance. Nevertheless, this allows a fair comparison among the models by means, for example, of AIC. The values are reported in Table 2. When we account for model complexity, the probabilistic version of the ADBM never yields the best AIC, the “Diff” has the best value in 4 cases and the remaining 5 cases are split among the remaining models. The use of AIC allows also the use of “Akaike weights” (Burnham and Anderson 2002). These quantities provide a measure of strength of the evidence for each model. The results are reported in Table 2 and show that we can say with confidence that the ADBM is not the best among the models in all cases but three (Benguela, Skipwith and Tuesday, A.W. \(\geq 0.05\)). In no case we find strong evidence for the ADBM (A.W. \(\geq 0.95\)).

I also computed the probability of obtaining an \(\Omega\) that is greater or equal than that of the ADBM using the random graph, cascade model and group based model (Methods, Appendix). In all these cases, I chose parameters that a) made the expected number of links \(E[K] = L\) and b) minimized the AIC. Note that this optimization does not target the overlap directly. For the random graph the optimization is simply done by setting \(p = L/S^2\). For the cascade model, I searched using a genetic algorithm the best hierarchy that maximized the likelihood. The two parameters were set to \(p_U = 2L_U/(S(S-\)
1)) and \( p_L = 2L_L/(S(S + 1)) \) to maximize the likelihood and obtain on average \( L \) links. The same type of search can be performed for the group-based random graph. Also here, I tried to find the configuration with the minimum AIC. While in the cascade model the number of parameters is fixed (and therefore maximizing the likelihood minimizes AIC), in this model the number of parameters varies according to the number of groups \( \gamma \). I therefore searched, following Allesina and Pascual (2009), for the balance between the number of parameters and goodness of fit using Akaike’s AIC (Akaike 1974). The results in terms of likelihoods, number of parameters and AIC values are reported in Table 3.

For each model, I computed the expected overlap with the data \( (E[\Omega]) \) and the probability that a model \( x \) produces an overlap value equal or greater than that of the ADBM \( (P(\Omega_x \geq \Omega_{ADBM})) \) (Table 1). I computed these quantities analytically for the random graph (RND) and cascade (CASC) models. Because listing all combinations for the group-based case (GROUP) is not computationally feasible, I constructed \( 10^5 \) networks for each data set using this model, and I measured the overlap in this set of generated networks.

**Discussion**

I contrasted the ADBM with four deterministic models that retain intervality (predators prey upon consecutive species) and information on body sizes, but do not include optimal foraging and allometric scaling. I found that
these models perform as well as or even better than the ADBM. This is true regardless the specific analysis performed (i.e. Ω values, AIC of the probabilistic counterpart of each model, Akaike weights, direct inspection of the predicted links). The results indicate that including allometry and optimal foraging, although biologically realistic, does not improve the fit to the data. This can be happening either because these features do not leave a strong signature in food web structure or because they have not been correctly included in the models. Also, the similarity among the results of the simpler models (especially “Ratio” and “LogRatio”) and the ADBM is so strong that one may suspect that the results of the ADBM are totally driven by simpler mechanisms. In particular, intervality accounts for most of the successes and failures of these simple models in predicting links. Note however that possibly using body size is not the way of ordering the species that maximizes intervality: if we were to find the best species’ trait that maximizes diet intervality, we could build models such as the ones illustrated above that would yield a better fit to the empirical data.

By examining $p$–values I found that the ADBM performs, in terms of overlap, significantly better than the random digraph in all cases $\left( P \left( \Omega_{RND} \geq \Omega_{ADBM} \right) < < 0.05 \right)$. With respect to the cascade model presented in the Appendix, the ADBM performs significantly better in 7 cases, and yields non-significant results in two cases (Broom, $P > 0.06$ and Skipwith $P > 0.45$). The group-based model performs significantly better than the ADBM ($P \approx 1.0$ in all cases). These results are exactly reflected also in
the expected values for the overlap of the three models: the random graph on average presents much lower overlap than the ADBM (mean difference between models = −0.232), the cascade is better than the random (mean difference with the ADBM = −0.13) and the group-based model does much better than the ADBM (mean difference = 0.292). These results are hardly surprising, given that they mirror perfectly the complexity of the models: the random and cascade have less parameters than the ADBM, while the group-based has many more. AIC (or BIC, or other criteria) for probabilistic models can deal with the assessment of the goodness of fit of a model accounting for both its performance and its complexity: a model has to do much better in terms of performance to justify a greater number of parameters. AIC is well rooted in the information theory, being a measure of information loss when the model is used instead of the data. Of the three probabilistic models presented here, the group-based has better overlap, likelihood and AIC in all cases (Table 4). Note that the AIC for the probabilistic version of the ADBM presented above is worse than that of the random case in 5 cases, and worse than the cascade in all cases. This means that the straightforward way of making the model probabilistic greatly hampers its performance. Producing a better model grounded in optimal foraging theory that is probabilistic in nature is definitely possible, and should be pursued to test whether these mechanisms could contribute to our understanding of network structure.

The results of this exercise also show that measuring overlaps without a quantitative comparison with other models is far from being satisfactory.
Accepting these numbers at face value without including the probability of obtaining them using simpler models or even at random can lead us to finding patterns and results that vanish once we scrutinize the models in detail. In order to test whether and how optimal foraging, allometric scaling or any other mechanism do influence food web structure, a rigorous statistical analysis such as the one presented here is required. Based on the data, one can conclude that in order to prove that optimal foraging and allometric scaling are important for food web structure, they need to be embedded in better models than the current ones. In the meantime, for lack of a better alternative we cannot reject the null hypothesis that these forces play no role in shaping food webs.

**Acknowledgments**

I wish to thank O.L. Petchey for providing the data necessary to replicate the ADBM results and for interesting discussion. Two anonymous referees provided useful comments. Part of this work was carried out when S.A. was a postdoctoral associate at the National Center for Ecological Analysis and Synthesis, a center funded by National Science Foundation grant DEB-0072909, and the University of California, Santa Barbara. This work was supported by NSF grant EF-0827493.
References

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723.

Allesina, S., D. Alonso, and M. Pascual. 2008. A General Model for Food Web Structure. Science 320:658–661.

Allesina, S., and M. Pascual. 2009. Food web models: a plea for groups. Ecol. Lett. 12:652–662.

Beckerman, A., O. Petchey, and P. Warren. 2006. Foraging biology predicts food web complexity. Proceedings of the National Academy of Sciences 103:13745–13749.

Burnham, K., and D. Anderson. 2002. Model selection and multimodel inference: a practical-theoretic approach. Springer, New York.

Caldarelli, G., P. G. Higgs, and A. J. Mckane. 1998. Modelling Coevolution in Multispecies Communities. Journal of Theoretical Biology 193:345–358.

Cattin, M. F., L. F. Bersier, C. Banasek-Richter, R. Baltensperger, and J. P. Gabriel. 2004. Phylogenetic constraints and adaptation explain food-web structure. Nature 427:835–839.

Cohen, J., F. Briand, and C. Newman. 1990. Community food webs: data and theory. Springer-Verlag, Berlin, Germany.
Erdős, P., and A. Rényi. 1960. On the evolution of random graphs. Publications of the Mathematical Institute of the Hungarian Academy of Sciences 5:17–61.

Hall, S., and D. Raffaelli. 1991. Food-Web Patterns: Lessons from a species rich web. J. Anim. Ecol. 60:823–842.

Harper-Smith, S., E. L. Berlow, R. Knapp, R. J. Williams, and N. Martinez, 2005. Dynamic Food Webs. Multispecies Assemblages, Ecosystem Development and Environmental Change, Chapter communicating ecology through food webs: Visualizing and quantifying the effects of stocking alpine lakes with trout, pages 407–423. Academic Press, Burlington.

Jonsson, T., J. Cohen, and S. Carpenter, 2005. Food Webs: from Connectivity to Energetics, volume 36 of Advances in Ecological Research, Chapter food webs, body size, and species abundance in ecological community description, pages 1–84. Elsevier Academic Press.

Lafferty, K., A. Dobson, and A. Kuris. 2006. Parasites dominate food web links. Proc. Nat. Acad. Sci. USA 30:11211–11216.

Loeuille, N., and M. Loreau. 2005. Evolutionary emergence of size-structured food webs. Proc Natl Acad Sci U S A 102:5761–5766.

Memmott, J., N. D. Martinez, and J. E. Cohen. 2000. Predators, Parasitoids and Pathogens: Species Richness, Trophic Generality and Body Sizes in a Natural Food Web. J. Anim. Ecol. 69:1–15.
Petchey, O. L., A. P. Beckerman, J. O. Riede, and P. H. Warren. 2008. Size, foraging, and food web structure. Proceedings of the National Academy of Sciences 105:4191–4196.

Polis, G. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. Am. Nat. 138:123–155.

Rossberg, A. G., H. Matsuda, T. Amemiya, and K. Itoh. 2006. Food webs: Experts consuming families of experts. Journal of Theoretical Biology 241:552–563.

Stouffer, D. B., J. Camacho, and L. A. Amaral. 2006. A robust measure of food web intervality. PNAS 103:19015–19020.

Warren, P. 1989. Spatial and temporal variation in the structure of a freshwater food web. Oikos 55:299–311.

Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. Nature 404:180–183.

Woodward, G., and A. Hildrew. 2001. Invasion of a stream food web by a new top predator. Journal of Animal Ecology 70:273–288.

Yodzis, P. 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. J. Anim. Ecol. 67:635–658.
Figure 1: Building the exact probability mass distribution for the overlap of links using a random digraph. First, evaluate relevant parameters (left). Then, build a table for all the possible combinations of $K$ and $M$ (center, just 10 of the 87 rows presented). Finally, condense the table according to $\Omega$, creating a univariate pmf (right).

Appendix

p-value: a cascade model

Here I repeat the analysis above for a version of the cascade model. The cascade model was the first probabilistic model for food web structure to be proposed (Cohen et al. 1990). I examine here a simple variation on the original model. To produce a network, a vector $\vec{H}$ representing a hierarchy (an order) of the species is required. If we order the empirical network according to $\vec{H}$, we can divide the links in the network into two classes: a) connections from lower ranked species to higher ranked species (forward connections) and b) connections from higher to lower or equal ranked species (backward connections). In the adjacency matrix associated with the ordered network, the forward connections are contained in the upper triangular part of the matrix, while the backward connections lie either on the lower triangular
Figure 2: Benguela Pelagic food web. For each model, I report the links correctly predicted (black), those incorrectly predicted (red) and those not predicted by the model but present in the empirical web (blue).
Figure 3: Ythan Estuary food web. For each model, I report the links correctly predicted (black), those incorrectly predicted (red) and those not predicted by the model but present in the empirical web (blue).
| Food Web | S | L | Ω_{ADBM} | Ω_{Diff} | Ω_{Ratio} | Ω_{LogRatio} | Ω_{DiffRatio} |
|----------|---|---|----------|----------|-----------|--------------|---------------|
| Benguela | 29 | 191 | 0.57143 | 0.48705 | 0.56771 | 0.557895 | 0.54497 |
| Broadstone | 29 | 156 | 0.40385 | 0.42308 | 0.38461 | 0.384615 | 0.40385 |
| Broom | 68 | 101 | 0.07767 | 0.1 | 0.13592 | 0.137255 | 0.09804 |
| Carpinteria | 72 | 238 | 0.16456 | 0.21429 | 0.16318 | 0.172996 | 0.15900 |
| Coachella | 26 | 228 | 0.65065 | 0.52863 | 0.63877 | 0.656388 | 0.57205 |
| Sierra | 33 | 175 | 0.60366 | 0.61047 | 0.50610 | 0.487805 | 0.55758 |
| Skipwith | 71 | 347 | 0.13833 | 0.12680 | 0.13256 | 0.132565 | 0.13833 |
| Tuesday | 73 | 410 | 0.46472 | 0.40146 | 0.46472 | 0.462287 | 0.43796 |
| Ythan | 88 | 425 | 0.18824 | 0.21177 | 0.20235 | 0.202353 | 0.17412 |

Table 1: Overlap values for the ADBM and the four simpler models based on body size described in the text.

| Food Web | \( \text{AIC}_{ADBM} \) | \( \text{AIC}_{Diff} \) | \( \text{AIC}_{Ratio} \) | \( \text{AIC}_{LogRatio} \) | \( \text{AIC}_{DiffRatio} \) | A.W. |
|----------|----------------|----------------|----------------|----------------|----------------|------|
| Benguela | 825.25 | 880.56 | 821.08 | 831.32 | 842.5 | 1.100E-01 |
| Broadstone | 824.63 | 811.5 | 829.04 | 829.04 | 820.63 | 1.400E-03 |
| Broom | 1110.72 | 1100.12 | 1085.6 | 1085.34 | 1100.45 | 1.640E-06 |
| Carpinteria | 2036.7 | 1991.09 | 2033.25 | 2026.37 | 2036.29 | 1.250E-10 |
| Coachella | 777.31 | 869.37 | 786.82 | 769.85 | 840.33 | 2.340E-02 |
| Sierra | 823.69 | 798.66 | 900.53 | 913.57 | 858.9 | 3.670E-06 |
| Skipwith | 2658.12 | 2660.53 | 2657.49 | 2657.44 | 2654.12 | 8.700E-02 |
| Tuesday | 2516.69 | 2654.99 | 2512.69 | 2518.53 | 2575.28 | 1.140E-01 |
| Ythan | 3380.31 | 3343.62 | 3357.12 | 3357.12 | 3394.18 | 1.070E-08 |

Table 2: AIC values for the probabilistic extensions of the ADBM and the other four simpler models described in the text. The AIC accounts for the number of parameters as well as the goodness of fit. Akaike weights (A.W.) measure the confidence that the ADBM is the best among the examined models.
| Food Web | $\Omega_{ADBM}$ | $P(\Omega_{RND} \geq \Omega_{ADBM})$ | $E(\Omega_{RND})$ | $P(\Omega_{CASC} \geq \Omega_{ADBM})$ | $E(\Omega_{CASC})$ | $P^*(\Omega_{GROUP} \geq \Omega_{ADBM})$ | $E^*(\Omega_{GROUP})$ |
|----------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Benguela | 0.571           | 2.289E-27       | 0.227           | 6.123E-09       | 0.411           | 1.000E+00       | 0.727           |
| Broadstone | 0.404          | 3.965E-12       | 0.185           | 8.152E-04       | 0.306           | 1.000E+00       | 0.858           |
| Broom    | 0.078           | 1.145E-03       | 0.022           | 6.038E-02       | 0.044           | 1.000E+00       | 0.386           |
| Carpinteria | 0.165       | 1.714E-12       | 0.046           | 1.246E-04       | 0.093           | 1.000E+00       | 0.396           |
| Coachella | 0.651          | 4.645E-28       | 0.337           | 2.070E-07       | 0.531           | 1.000E+00       | 0.834           |
| Sierra   | 0.604           | 6.327E-37       | 0.161           | 3.992E-19       | 0.317           | 1.000E+00       | 0.855           |
| Skipwith | 0.138           | 1.155E-06       | 0.069           | 4.515E-01       | 0.136           | 1.000E+00       | 0.559           |
| Tuesday  | 0.465           | 1.213E-83       | 0.077           | 1.045E-53       | 0.149           | 1.000E+00       | 0.833           |
| Ythan    | 0.188           | 1.010E-22       | 0.055           | 1.474E-07       | 0.109           | 1.000E+00       | 0.447           |

Table 3: Size ($S$) and number of connections ($L$) in nine empirical networks. For each of the probabilistic models, I report both the probability that they produce an overlap greater than that of the ADBM and their expected overlap. The last two values (marked with *) have been obtained through simulations, because the exact computation is not feasible.
Table 4: Likelihood and AIC values for all the networks using the three probabilistic models described in the main text. The AIC takes into account the number of parameters that is 2 for the random digraph (RND), 2+S for the cascade model (CASC) and 2+S+γ² in the group-based random digraph. Because γ varies among networks, its value is reported as well.

| Food Web | log $\mathcal{L}_{RND}$ | AIC $\mathcal{L}_{RND}$ | log $\mathcal{L}_{CASC}$ | AIC $\mathcal{L}_{CASC}$ | log $\mathcal{L}_{GROUP}$ | AIC $\mathcal{L}_{GROUP}$ | γ |
|----------|------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|---|
| Coachella | -431.11                | 866.22          | -350.4535       | 704.907         | -141.637        | 411.274         | 8 |
| Benguela  | -449.575               | 903.15          | -364.77         | 733.54          | -189.4495       | 476.899         | 7 |
| Broadstone| -402.36                | 808.72          | -363.1855       | 730.371         | -99.9415        | 271.883         | 6 |
| Sierra    | -479.06                | 962.12          | -388.266        | 780.532         | -107.6645       | 313.329         | 7 |
| Broom     | -485.1                 | 974.2           | -480.4365       | 964.873         | -279.8005       | 657.601         | 7 |
| Skipwith  | -1262.36               | 2528.72         | -1097.235       | 2198.47         | -559            | 1360            | 11|
| Carpinteria| -964.745              | 1933.49         | -862.555        | 1729.11         | -536.475        | 1272.95         | 10|
| Tuesday   | -1444.36               | 2892.72         | -1254.93        | 2513.86         | -295.6795       | 833.359         | 11|
| Ythan     | -1645.715              | 3295.43         | -1444.84        | 2893.68         | -828.445        | 1898.89         | 11|

part or on the diagonal. Having set the number of species and the hierarchy among them, we connect species in the following way: we draw forward connections with probability $p_U$ and backward connections with probability $p_L$. We define $L_U$ as the number of links in the upper triangular part of the empirical network, $L_L$ as the number of links in the lower part, $K_U$ and $K_L$ as the number of links proposed by the model in the upper and lower part and $M_U$ and $M_L$ as the matched links. It is trivial, given the derivation for the random graph, to write the probability mass function for this case:

\[
P(M_U, M_L, K_U, K_L | S, p_U, p_L, \bar{H}, N(S, L_U, L_L)) =
P_U^{K_U} (1 - p_U)^{\left(\frac{S(S-1)}{2} - K_U\right)} \left(\frac{L_U}{M_U}\right)^{\left(\frac{S(S-1)}{2} - L_U\right)} \left(\frac{L_U}{M_U}\right)^{K_U - M_U}
\]

\[
P_L^{K_L} (1 - p_L)^{\left(\frac{S(S+1)}{2} - K_L\right)} \left(\frac{L_L}{M_L}\right)^{\left(\frac{S(S+1)}{2} - L_L\right)} \left(\frac{L_L}{M_L}\right)^{K_L - M_L}
\]

25
Where $K_U \in [0, \ldots, \frac{S(S-1)}{2}]$, for each $K_U M_U \in [0, \ldots, \min(K_U, L_U)]$, while $K_L \in [0, \ldots, \frac{S(S+1)}{2}]$ and $M_L \in [0, \ldots, \min(K_L, L_L)]$. The total number of combinations for the four values of interest therefore can be quite large:

$$\text{Num. cases} = \left( \left( \frac{S(S-1)}{2} + 1 \right) (L_U + 1) - \frac{L_U(L_U+1)}{2} \right) \cdot \left( \left( \frac{S(S+1)}{2} + 1 \right) (L_L + 1) - \frac{L_L(L_L+1)}{2} \right).$$

(10)

For example, for the Ythan estuary food web we have $L_U = 421$, $L_L = 4$, $S = 88$ leading to more than $2.989 \cdot 10^{10}$ possible combinations. Although the number of combinations is very high, it is still possible to compute the univariate distribution for $\Omega$ in the same exact way as for the random graph by condensing the multivariate distribution.

Also for this model one can easily derive the likelihood by setting $K_U = M_U = L_U$ and $K_L = M_L = L_L$:

$$\mathcal{L}(S, p_U, p_L, \vec{H} | N(S, L_U, L_L)) = p_U^{L_U} p_L^{L_L} (1 - p_U)^{\frac{S(S-1)}{2}-L_U} (1 - p_L)^{\frac{S(S+1)}{2}-L_L}$$

(11)

And the AIC:

$$AIC = 6 + 2S - 2 \left( L_U \log(p_U) + \left( \frac{S(S-1)}{2} - L_U \right) \log(1 - p_U) \right)$$

$$-2 \left( L_L \log(p_L) + \left( \frac{S(S+1)}{2} - L_L \right) \log(1 - p_L) \right)$$

(12)
p-value: a group-based random digraph

Finally, I derive here the probability of obtaining any Ω for a model that is a collection of random digraphs in which species interact according to the “group” they belong to (Allesina and Pascual 2009). For example, if we divide the nodes of a network into two groups (“red” and “green”), we will use four probabilities for deciding whether to connect a red node to a red node ($p_{rr}$), a red node to a green node ($p_{rg}$), a green to a green ($p_{gg}$) and a green to a red ($p_{gr}$). The number of probabilities required will therefore be $\gamma^2$ where $\gamma$ is the number of groups. This model is simply a collection of random subgraphs. We first define a vector $\vec{G}$ containing, for each species, the group the species is assigned to. We further define $L_{ij}$ as the number of links in the empirical network connecting resources belonging to the $i^{th}$ group to consumers belonging to the $j^{th}$ group, $K_{ij}$ as the number of links proposed by the model for the interaction between these groups and $M_{ij}$ the matched links. Finally, we write $<i>$ for the size of the $i^{th}$ group. We can now write the multivariate pmf for all combinations of $K_{ij}$ and $M_{ij}$:

$$P(\vec{K}_{ij}, \vec{M}_{ij}|S, \vec{p}_{ij}, \vec{G}, N(S, \vec{L}_{ij})) = \prod_{i}^{\gamma} \prod_{j}^{\gamma} \left[p_{ij}^{K_{ij}}(1-p_{ij})^{<i><j>-K_{ij}} \binom{L_{ij}}{M_{ij}} \binom{<i><j>-L_{ij}}{K_{ij}-M_{ij}}\right]$$ (13)

Note that the model is conceptually very simple: in the case $\gamma = 1$ the model reduces to the random digraph described above. Although listing all the possible cases is theoretically feasible, their number can be immense:
Num. cases = $\prod_{i}^{\gamma} \prod_{j}^{\gamma} \left[ (<i> <j> + 1)(L_{ij} + 1) - \left( \frac{L_{ij}(L_{ij} + 1)}{2} \right) \right]$ \hspace{1cm} (14)

For example, for the Coachella Valley food web examined below, I found more than $10^{43}$ possible combinations, so that obtaining the exact distribution is not computationally feasible. Nevertheless, as for the other cases, the likelihood and the AIC are readily derived and easy to compute:

$$\mathcal{L}(S, \vec{p}_{ij}, \vec{G} | N(S, \vec{L}_{ij})) = \prod_{i}^{\gamma} \prod_{j}^{\gamma} \left[ p_{L_{ij}}^L (1 - p_{ij})^{<i> <j> - L_{ij}} \right]$$ \hspace{1cm} (15)

$$AIC = 2 + 2S + 2\gamma^2 - 2 \sum_{i}^{\gamma} \sum_{j}^{\gamma} \left[ L_{ij} \log(p_{ij}) + (<i> <j> - L_{ij}) \log(1 - p_{ij}) \right]$$ \hspace{1cm} (16)