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

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ABSTRACT

Few food web theory hypotheses/predictions can be readily tested using likelihoods of reproducing the data. Simple probabilistic models for food web structure, however, are an exception as their likelihoods were recently 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 by measuring the fraction of trophic relations it correctly predicts. I contrasted this value with that produced by simpler models based on body sizes and found that the quantitative information on allometric scaling and optimal foraging does not significantly increase model fit. Also, I present a method to compute the *p*-value for the fraction of trophic interactions correctly predicted by the ADBM, or any other model, with respect to three probabilistic models. I find that the ADBM predicts significantly more links than random graphs, but other models can outperform it. Although optimal foraging and allometric scaling may improve our understanding of food webs, the ADBM needs to be modified or replaced to find support in the data.

1. 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 (Dunne, 2006; Bersier, 2009). This problem has been typically investigated using simple probabilistic models (Cohen et al., 1990; Williams and Martinez, 2000; Cattin et al., 2004; Allesina et al., 2008; Allesina and Pascual, 2009), 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).

To investigate the role of body size and optimal foraging theory in shaping food web structure, Petchey et al. (2008) developed the “Allometric Diet Breadth Model” (ADBM). This model 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 differs from most previous models (Cohen et al., 1990; Williams and Martinez, 2000; Cattin et al., 2004; Allesina et al., 2008; Allesina and Pascual, 2009) because it is deterministic, rather than probabilistic. Given an empirical network, body sizes for all the species, and number of links in the network, four further parameters regulating the foraging are optimized numerically and a single network is produced deterministically.

Petchey et al. (2008) assessed the goodness of fit of the ADBM and its variants 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 found 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).

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 more complex ADBM model is not favored by model selection.

Also, I report a different method that can be used to derive a p-value for the Ω produced by the ADBM using as a reference: a random digraph (Erdös and Rényi, 1960), a variation of the cascade model (Cohen et al., 1990), and a recently proposed group-based random digraph (Allesina and Pascual, 2009). The derivation of the probability mass function for these simple models provides the means for analyzing more complex models for food web structure, where the derivation of a likelihood can be almost impossible. The derivation presented here can help associate statistical significance to the results of highly complex models, such as those based on evolving networks or systems of differential equations or probabilistic models that are difficult to analyze (Caldarelli et al., 1998; Loeuille and Loreau, 2005; Rossberg et al., 2006). In fact, for each model, however, complex,

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it is easy to compute a value for Ω (e.g. averaging across several simulations). A p-value can then be associated with the Ω, providing a coarse comparison among models.

In terms of overlap, results show that the ADBM performs: (a) significantly better than the random digraph in all cases; (b) better than the cascade model in most cases; (c) significantly worse than the group-based random digraph in all cases.

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

2. Methods

2.1. The allometric diet breadth model

Here I briefly describe the ADBM in its "Ratio" incarnation, which produces the best fit among the ADBM variants to the empirical data. Therefore, I am assuming as a starting point for this model selection exercise a model that has already been chosen among other similar formulations based exactly on the data analyzed here. As such, there is a risk of starting with an over-fitted model. A more detailed description of the model, its variations, and the model selection can be found in the original articles (Beckerman et al., 2006; Petchey et al., 2008).

The ADBM takes an input vector $\vec{B}$ that describes the species body sizes. The number of links L for the empirical food web one wants to replicate is used in the numerical optimization routine. Four other parameters a, a_1, a_2 and b determine the foraging behavior of the species in the food web. Generating the network consists of two steps: (a) for each predator, compute the profitability of each possible prey; (b) for each predator, compute a diet breadth (i.e. number of prey) that maximizes the rate of energy intake. Connecting all the prey within a diet breadth to their predators produces the food web.

The values are computed as follows:

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

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

   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,…,S that maximizes the function:

   $$f(z,j)=\frac{a\sum_{i=\sigma_1}^{\sigma_z} B_i^{(1/4+a_1)}B_j^{a_2}}{1+a\sum_{i=\sigma_1}^{\sigma_z}\dfrac{B_i^{(-3/4+a_1)}B_j^{a_2}}{b-\dfrac{B_i}{B_j}}} \tag{2}$$

   where the permutation σ 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 (Beckerman et al., 2006; Petchey et al., 2008). The three parameters a, a_1 and a_2 are needed to compute the attack rate, and the parameter b is involved in the computation of the handling time.

The generated food webs are compared to the empirical data. The model performance is measured as the fraction of links that correctly match those 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 numerically optimized so that (a) the model correctly predicts the total number of links in the network ($K\approx L$) and (b) Ω is maximized.

Running the ADBM for the 14 published food webs examined here yielded $\Omega\in[0.08,0.65]$ (Petchey et al., 2008) (Table 1).

Note that determining whether two species interact can be seen as a classification problem. It would be interesting to investigate whether machine-learning techniques could be applied to the problem using empirical food web as training sets. Also, this would provide a wealth of methods for statistically testing the precision of the classification.

2.2. Three simple models based on body size

One characteristic 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 (Williams and Martinez, 2000; Cattin et al., 2004; Stouffer et al., 2006; Allesina et al., 2008), and this could be the main driver of the performance of the ADBM. Thus, it makes sense to compare its performance with that of models that retain intervality but do not contain extra information regarding optimal foraging or allometric scaling. Of all possible models, I analyze three that are very simple and share 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 $a\le z_{ij}<b$, 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. I analyze three different $f(B_i,B_j)$:

1. "Diff": $f(B_i,B_j)=B_j-B_i$. The difference between predator (j) and prey (i) 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 drives the structure of the food web.
3. "DiffRatio": $f(B_i,B_j)=(Bj-Bi)(B_i/B_j)$. This model combines the other two models. Note that the function is very similar to the profitability in the ADBM.

All three 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. Note also that all of the models retain some notion of optimal foraging: consumers eat all the species whose sizes are included in an "optimal" range. Unlike the ADBM, however,

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

Food web	S	L	Ω_{ADBM}	Ω_{Diff}	Ω_{Ratio}	$\Omega_{DiffRatio}$
Benguela	29	191	0.5714	0.4870	0.5677	0.5450
Broadstone	29	156	0.4038	0.4231	0.3846	0.4038
Broom	68	101	0.0777	0.1000	0.1359	0.0980
Carpinteria	72	238	0.1646	0.2143	0.1632	0.1597
Caricaie	158	1349	0.1320	0.1625	0.1187	0.1358
Coachella	26	228	0.6507	0.5286	0.6388	0.5721
EcoWEB41	19	51	0.3922	0.4118	0.3922	0.4510
EcoWEB60	33	68	0.2239	0.2239	0.2090	0.2388
Mill	80	367	0.3665	0.2507	0.3672	0.3481
Sierra	33	175	0.6037	0.6105	0.5061	0.5576
Skipwith	71	347	0.1383	0.1268	0.1326	0.1383
Small Reef	50	556	0.4036	0.3982	0.4093	0.3975
Tuesday	73	410	0.4647	0.4015	0.4647	0.4380
Ythan	88	425	0.1882	0.2118	0.2024	0.1741