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Fit, efficiency, and biology: some thoughts on judging food web models

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Attempts to explain patterns in food web structure go back at least to Elton's (1927) discussion about the importance of organism size. Subsequent explanations have drawn on energetics, population stability, evolution, stoichiometry, natural history, statistical constraints, and observational artefacts (de Ruiter et al., 1995; Dunne et al., 2005; e.g., Lawton, 1989; Pimm, 1991; Polis, 1991). Few of these explanations address all aspects of food web structure and, necessarily, the way they have been developed and tested differs. The complexity of food webs, the difficulties of simultaneously investigating all processes in them, and the diversity of questions we want to ask of them result in explanations of food web structure that are numerous and diverse in form, function, and motivation. In our opinion, this diversity can make judgements about the 'best' explanations of food web structure quite difficult. Here we consider a recent evaluation of different food web models (Allesina in this issue), which includes a model recently proposed by us, in this wider context of the diversity of possible approaches and motivations.

Joel Cohen and Charles Newman's cascade model (Cohen and Newman, 1985) initiated interest in what are sometimes termed 'static food web models'. The cascade model was one of the first topological explanations for food web structure (Lawton and Warren, 1988). The original goal of the cascade model was to explain the scaling among food webs of the number of basal, intermediate, and top species. Various refinements and extensions of the cascade model have subsequently been developed (Allesina and Pascual, 2009; Allesina et al., 2008; Cattin et al., 2004; Cohen et al., 1990; Rohr et al., 2010; Stouffer et al., 2005; Warren, 1996; Williams and Martinez, 2000). Their capacity to predict a variety of food web patterns has been thoroughly explored.

One major driver of this development and refinement has been the quantitative assessment of how well models reproduce the structure of real food webs (Allesina et al., 2008; Cattin et al., 2004; Stouffer et al., 2005; Williams and Martinez, 2000; Williams and Martinez, 2008). Such quantitative comparisons usually involved measuring how accurately a set of structural properties are predicted, for example proportions of basal, intermediate, and top species. The model with the smallest error is deemed the most plausible explanation (Williams and Martinez, 2008). Recent developments include the formulation of static models of food webs for which likelihood-based methods

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of comparison can be performed (Rossberg et al, 2006; Allesina et al., 2008). The goal has been to find the simplest and simultaneously best model for the observed food web data. Models, based on remarkably few and simple rules of assembly, provide very good matches between modelled and real food webs (though see Fox, 2006).

All of these models require as a parameter connectance, the density of links in a food web, which contributes to complexity. None of these models, therefore, explain connectance, which itself is thought to determine many features of food web dynamics (e.g., Cohen et al., 1990; MacArthur, 1955; May, 1972). The initial development of our recently proposed DBM model (Beckerman et al., 2006) was to examine whether an explanation of connectance could plausibly be derived from optimal foraging theory – a theory which identifies specific consumer and resource traits as determinants of diet choice and breadth. We found that such a model, when parameterised with empirical data, did indeed make reasonably accurate predictions of observed connectance. An extension of this work related these foraging traits through their links with body size (i.e., allometric scaling) (Petchey et al., 2008) and had quite variable success in explaining the structure (distribution of trophic links among species) of 15 food webs, with the percentage of links correctly predicted ranging from about 5 to 65%. The fit of this model (the allometric diet breadth model – ADBM) varied with characteristics of the food webs being modelled and also with the type of interspecific interaction within the food webs. For example, interactions that are thought to be less well predicted by optimal foraging (diet) theory, such as parasitism, were not well predicted. This finding is broadly in line with Sih and Christensen's (2001) report about how optimal diet theory generally works well for foragers feeding on immobile prey, and not so well for those that attack mobile prey. We emphasise that employing a different foraging models for different types of prey and predator might improve our ability to predict food web structure.

The quantitative successes (and failures) of these models are, in our opinion, intriguing. However, perhaps more interesting were the qualitative features of the work (Berlow et al., 2008). Specifically, it (i) focused on determinants of connectance; (ii) linked biologically testable mechanisms of individual foraging behaviour to food web structure; and (iii) provided a model that could, in theory, be parameterised independently of the data it aimed to

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predict. Recently, Petchey *et al.* (2010) have shown how a model founded in the foraging behaviour of individual organisms can be extended to make predictions about the effects of temperature change on aspects of food web structure. These predictions were greatly facilitated by the level of mechanism that was included in the ADBM.

Allesina (this issue) presents comparisons of the ADBM with two types of model. First, the ADBM was compared to three models that included a phenomenological foraging rule (e.g., consumers can forage on resources within a particular size range), but did not make explicit use of optimal foraging, or any other particular, theory to derive those rules. Broadly speaking, the three models predicted as successfully (or badly) as the ADBM, but had somewhat fewer parameters. Therefore, a comparison that cared only for explanatory power and model complexity favoured these less complex models (i.e., not the ADBM). We note, in passing, that we did examine the effect of ADBM complexity (i.e., number and combination of parameters) on predictive power. In the online Supporting Information for Petchey *et al.* (2008) we report the effect on explanatory power of removing parameters from the model. The results indicate that some parameters are more important than others, for example the scaling of attack rate with prey size appears to have little influence on explanatory power. This could be due to more complex forms of scaling of attack rate with prey (and predator) mass (Aljetlawi et al., 2004; Vucic-Pestic et al., 2010).

Second, the ADBM was compared with three other static food web models: a random model, the cascade model (Cohen and Newman, 1985), and a group model (Allesina and Pascual, 2009). These three models share the common feature of lacking an explicit biological mechanism for assigning links. In this comparison, the results indicated that the ADBM predicted more successfully than the random and cascade model, but not as well as the group model. Attempting to account for difference among the complexity of the competing models was not straightforward and although conclusions appeared not to favour the ADBM, they were heavily driven by differences in model complexity. Again, comparisons that cared only for the probability of obtaining the observed data tended to suggest that the ADBM was not the best model.

These results provide a useful perspective, and we applaud the

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development of appropriate techniques (e.g., calculation of AIC) to facilitate comparison among comparable models. However, we are concerned that wholly statistical comparisons, for example by comparing AIC, cannot account for important qualitative differences among models, such as the level at which mechanism is represented. In the DBM and ADBM the 'mechanism' of prey selection is based on energy maximisation. Other models – such as the niche model (Williams and Martinez, 2000) for example – set diet breadths according to some statistical rule. In the case of the niche model, in essence, each consumer exploits a random fraction of the niche axis 'below' it. This rule mimics, stochastically, the sort of pattern of diet breadths that might emerge from constraints generated by a more complex mechanistically based understanding of foraging biology. In other words, the simpler model is a statistical approximation to the more complex mechanistic one. Were the two to make equally good predictions, the fact remains that the simpler model, while a 'better' explanation in the sense of efficiency in the use of parameters, is the poorer in terms of biological understanding. In more general terms, one might develop a biologically grounded mechanistic model that predicts a particular relationship between two variables, and then find that a regression model (i.e., a statistical description) with fewer parameters predicts equally well. Can analysis of the efficiency of the regression model be considered a 'test' of the more mechanistic model? Reviewers of our original article seemed to think not, and advised us against the types of comparison performed by Allesina. Thus, we believe that the analysis in Allesina's article is interesting, but places the emphasis, in our view too exclusively, on statistical model comparison, and too little on the knowledge of the biology and behaviour of organisms. The approach itself is not at fault, but we are not convinced that it should be the only arbiters in judging the value of the models. We believe both types of model (and different methods of testing them) have important, but different, parts to play in developing our understanding of food webs, but simple comparison of the two is not the best way to take this forward. The remainder of this ms describes what we consider are stronger tests of the ADBM.

Ours and other models might be getting the right answers (sometimes) for (sometimes) the wrong reasons. The difficulty this presents is compounded by features of the food web data that the models are trying to

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predict, such as sampling, scale and resolution. It is always possible a model is capturing some fundamentally correct processes, but fails to correctly account for particular characteristics in the data, which may reflect limitations of the data, rather than fundamental features of the system being described. The following illustrative tests could provide information about if and when this is the case. 1) Comparisons of predicted with observed food web structure when the ADBM is parameterised independently of food web data. This will require quantifying the allometries of foraging behaviour that feed into our model (e.g., Brose 2010). Insufficient, appropriate information of this kind at the time of publication meant that we had to estimate the allometries that best fit the food web data (Petchey et al., 2008). Assessments using independent data about allometries will be able to test if the model can simultaneously predict connectance and structure.

2) Assessment of the model's ability to explain comparative data about food web structure, for example variation in food web structure along an environmental gradient, or among different environments. This type of test would require quantified variation in foraging allometries along the gradient, which would be fed into the model to give predictions of food web structure as a function of environmental conditions (e.g., Petchey et al., 2010). This could be compared to observed variation in food web structure caused by environmental variation.

Common to these two types of test is manipulation of the assumptions or variables of the model. Measurements of deviation between predicted and observed patterns of complexity or structure illuminate when and why the model is wrong. These deviations then lead to developments, refinements, and possibly even to rejection of the idea that foraging allometries and or optimal foraging are influential drivers of food web structure (note that this is not necessarily the same as rejecting foraging allometries and or optimal foraging themselves). Useful developments might include the addition of stochastic processes, such as sampling, which could produce models that are 'probabilistic in nature' (Allesina this issue), and account for the diversity of foraging modes and habits among consumer.

We have identified a number of tests we feel would be appropriate for evaluating our model(s). These tests are the result of defining philosophically that our model was formulated by considering the biological processes that

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generate links in a food web – i.e., that optimal foraging behaviour underpins the complexity and structure of the food web. We believe that much could be revealed about the usefulness, appropriateness and effectiveness of food web models by natural or manipulative experiments. Nevertheless, it is clear that there are many complementary approaches to building a food web model, with different motivations, different formulations, and different types of biological detail specified (and these features may be confounded among models). As a result, there are a wide variety of methods for testing the models against data – not all of which are appropriate in all cases. Whether we choose to start from the biology end of the spectrum (build from the ground up), or from the more abstract modelling end (reverse engineering), so long as we can meet in the middle there might be little problem with taking both approaches at once.

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Model comparisons should take these differences into consideration.

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