

## FLEXIBLE FORAGERS IN FOOD WEBS

# Scaling from individuals to networks in food webs

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### Summary

1. Food webs, the set of predator–prey interactions in an ecosystem, are a prototypical complex system. Much research to date has concentrated on the use of models to identify and explain the key structural features which characterize food webs.
2. These models often fall into two general categories: (i) phenomenological models which are built upon a set of heuristic rules in order to explain some empirical observation and (ii) population-level models in which interactions between individuals result in emergent properties for the food web. Both types of models have helped to uncover how food-web structure is a product of factors such as foraging behaviour, prey selection and species' body sizes.
3. Historically, the two types of models have followed rather different approaches to the problem. Despite the apparent differences, the overlap between the two styles of models is substantial. Examples are highlighted here.
4. By paying greater attention to both the similarities and differences between the two, we will be better able to demonstrate the ecological insights offered by phenomenological models. This will help us, for example, design experiments which could validate or refute underlying assumptions of the models. By linking models to data, scaling from individuals to networks, we will be closer to understanding the true origins of food-web structure.

**Key-words:** food webs, phenomenological models, population-level models, theoretical ecology, network theory

Food webs are the network of who eats whom in an ecosystem and the study of food webs focuses upon understanding the holistic properties of the entire community (Cohen, Briand & Newman 1990; Pimm 2002; Pascual & Dunne 2006). Ecologists have studied aspects of food-web structure – such as food-web intervality (Cohen 1978; MacDonald 1979; Sugihara 1982, 1984; Cattin *et al.* 2004; Stouffer, Camacho & Amaral 2006) – for at least the past 30 years because understanding food-web structure provides important insights into, for example, the stability of ecosystems to perturbations (Allesina & Pascual 2008).

Recent increases in the availability of computational tools have facilitated. Our ability to explore numerous properties of food webs. (Each of the contributions by Abrams 2009; Brose 2009; Loeuille 2009 in this issue is an excellent example on this theme.) In particular, several models have been proposed that aim to describe the structure of food webs (Cohen & Newman 1985; Williams & Martinez 2000; Cattin *et al.* 2004; Loeuille & Loreau 2005; Rossberg *et al.* 2005, 2006a;

Beckerman, Petchey & Warren 2006; Petchey *et al.* 2008). Such models tend to fall into two broad categories: (i) phenomenological models and (ii) population-level models. Phenomenological models generally rely upon heuristic 'rules', for example how species might select their prey (Williams & Martinez 2000), to generate the food web. Typically, population-level models consider the behaviours and implications of an ecologically relevant process, such as the evolution of species' body size (Loeuille & Loreau 2005), and the interactions between individual species produce the food-web structure.

In this paper, I will first discuss recent research which uses phenomenological models to attempt to explain the hows and whys of food-web structure. I pay particular emphasis on whether and how we can extract the ecological implications of the mechanisms or rules employed and how they relate to foraging behaviour. I will next provide examples of what I refer to as population-level models. The reader will see that the general theme of population-level models is that the interactions between individuals produce emergent properties for the food-web network. In providing the dual perspectives, I hope to impress upon the reader that though the approaches

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appear and are often expected to follow independent paths, they are remarkably complementary. Excitingly, the conclusions reached from both perspectives converge upon the critical elements which explain empirically observed food-web structure. I conclude by discussing how we can better unify and make use of the advances in this field.

### Phenomenological food-web models

Throughout the study of empirical food webs, a number of statistical patterns or regularities have been identified (Cohen, Briand & Newman 1990; Pimm 2002; Pascual & Dunne 2006). Phenomenological, rule-based models have often been proposed as attempts to explain the source of these patterns (Cohen & Newman 1985; Williams & Martinez 2000; Cattin *et al.* 2004; Stouffer *et al.* 2005; Stouffer, Camacho & Amaral 2006; Allesina, Alonso & Pascual 2008). As the objective is to understand the network of predator–prey interactions, these models describe foraging behaviour with rules which describe the manner in which predators select their prey.

The ‘cascade model’ of Cohen & Newman (1985) was proposed in order to capture ‘the phenomenology of observed food web structure, using a minimum of hypotheses’. It was likely the very first phenomenological food-web model. In the cascade model, each species has a niche-value which determines its position in the hierarchy and prey are chosen randomly from those species whose ranking is less than that of the predator. In the cascade model, an interaction between a forager and a resource exists almost exclusively by chance. Even so, the cascade model compared quite favourably to a large set of empirical food webs in that it was able to explain many secondary structural properties given only the number of species  $S$  and number of interactions  $L$  (Cohen & Newman 1985). To validate phenomenological models, such as the cascade model, authors generally create a large ensemble of model-generated food webs and compare how well the ensemble’s average properties match those of empirical food webs (Cohen & Newman 1985; Williams & Martinez 2000; Cattin *et al.* 2004; Williams & Martinez 2008); these properties tend to include things such as the number of basal, intermediate and top species, the average food chain length and number of omnivores, to name just a few (Vermaat, Dunne & Gilbert 2009).

In the cascade model, the niche-value concept is an excellent example of its phenomenological nature. Mathematically, the existence of an empirical proxy to the niche-value is unimportant; the model would continue to generate food webs whose properties compared well to those of empirical food webs. This means that the model’s rules may or may not end up pointing us towards the ecological mechanisms which actually drive observed food-web structure. Intriguingly, and despite these reservations, the cascade model’s niche-value has provided a fundamental ingredient – and assumption – underlying nearly all phenomenological food-web models proposed in the last 20–30 years. Later research has helped to validate the idea by showing that a single factor – species’ mass – does indeed provide a suitable proxy for this

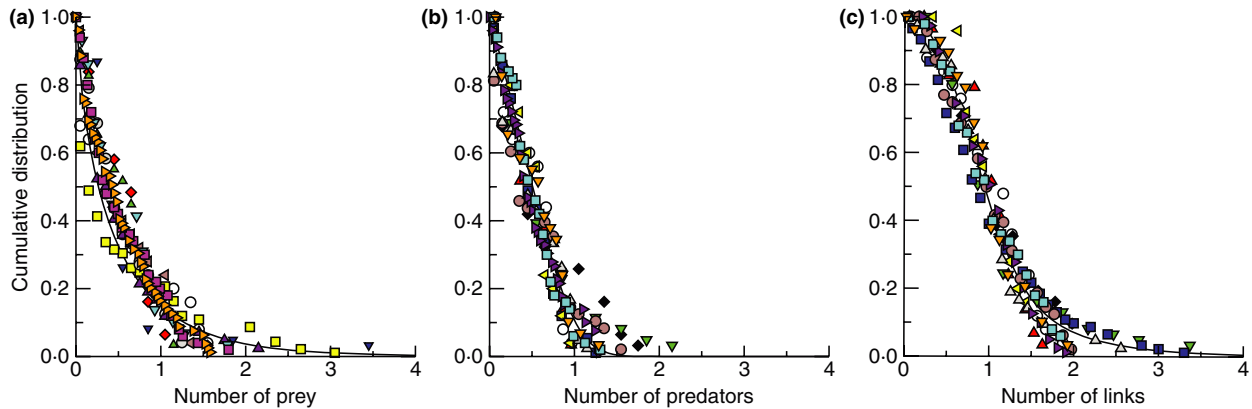
dimension as predators are larger than their prey in a majority of empirical predator–prey interactions (Cohen & Newman 1985; Warren & Lawton 1987; Cohen 1989; Lawton 1989; Cohen *et al.* 1993; Neubert *et al.* 2000; Cohen, Jonsson & Carpenter 2003; Petchey *et al.* 2008).

As the amount of empirical food-web data increased, particularly in the size of the webs and the resolution of the data collected, the cascade model was less and less able to explain empirical observations. Another model – the ‘niche model’ (Williams & Martinez 2000) – was proposed as an alternative to the cascade model. In the niche model, species again are ordered according to some niche-value; however, predators in the niche model instead select their prey as a contiguous range along the niche axis. The niche model was demonstrated to explain properties of empirical food-web data to a far greater extent than the cascade model (Williams & Martinez 2000). Shortly thereafter, Cattin *et al.* (2004) proposed the ‘nested-hierarchy model’ in which species selected their prey in a manner intended to simulate phylogenetic constraints and adaptation. The nested-hierarchy model was demonstrated to compare equally as well to empirical food webs as the niche model. Interestingly, these two models had very different heuristic rules, yet appeared to have equivalent explanatory power.

Stouffer *et al.* (2005) performed a detailed analytical and numerical study of the models in an attempt to reconcile why the two models appeared to explain empirical food webs equally well and why the cascade model did not. The authors concluded that there exist two conditions which a food-web model must satisfy in order to successfully predict the commonly tested properties of empirical food webs (Stouffer *et al.* 2005): (i) the niche-values to which species are assigned form a totally ordered set and (ii) each species has a specific, exponentially decaying probability  $P(x)$  of preying on a fraction  $x$  of the species with lower niche-values. Despite their apparent differences, the authors demonstrated that the heuristic rules of the niche and nested-hierarchy models both adhered nearly perfectly to these constraints; the cascade model did not.

In satisfying these two constraints, the niche and nested-hierarchy models reproduced the empirically observed functional forms for the distributions of numbers of prey, predators and links per species (Camacho, Guimerà & Amaral 2002b; Dunne, Williams & Martinez 2002; Stouffer *et al.* 2005) (fig. 1). This enabled the models to also explain a large number of ecologically relevant properties. Each of the distributions has a characteristic scale, the ecological implication of which is that there is a typical or expected degree of specialization for all predators in the food web (Stouffer *et al.* 2005). From the functional forms of these distributions, one can see that species on average have more prey than predators because of the faster decay of the distribution of number of predators (Fig. 1). It is therefore more common to observe highly generalist predators than a highly generalist prey.

The fundamental similarities between the two models presented a significant ecological problem: two distinct hypotheses and foraging strategies which appear equally valid



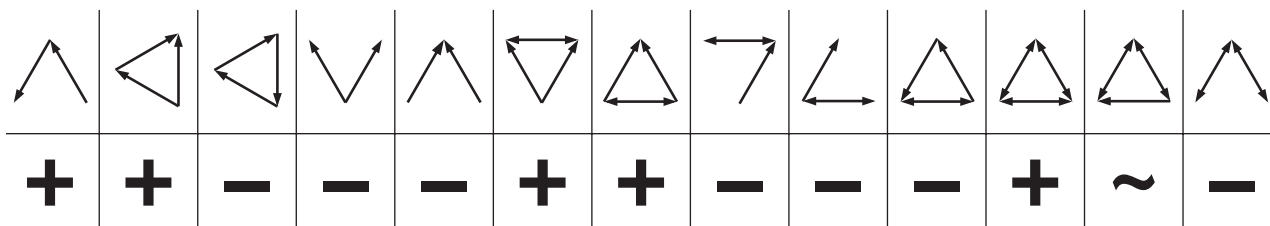
**Fig. 1.** Food web degree distributions. Cumulative distributions of numbers of (a) prey, (b) predators and (c) links for empirical food webs examined by Stouffer *et al.* (2005). It is visually apparent that the different food webs appear to obey the same functional form. The solid lines are the analytical prediction of the niche model (Camacho, Guimerà & Amaral 2002a) (modified from Stouffer *et al.* 2005).

but which carry significant implications regarding foraging behaviour. In the niche model (Williams & Martinez 2000), predators consume prey falling within a contiguous range of niche-values. In the nested-hierarchy model (Cattin *et al.* 2004), predators select their prey similar to the random predation of the cascade model (Stouffer *et al.* 2005). This means that the nested-hierarchy model assumes negligible specialization of predators whereas the niche model implicitly assumes that selection pressures force predators to specialize upon prey with a typical niche-value.

Later investigations into food-web structure at a more intricate scale have helped to determine which foraging mechanism is most consistent with the empirical observations. These studies examined community modules (Holt 1997; Holt & Hochberg 2001) and food-web motifs (Milo *et al.* 2002; Arim & Marquet 2004; Bascompte & Melián 2005; Camacho, Stouffer & Amaral 2007; Stouffer *et al.* 2007). Specifically, Camacho, Stouffer & Amaral (2007) and Stouffer *et al.* (2007) examined the over- and under-representation profiles of unique three-species subgraphs in model-generated and empirical food webs (fig. 2). By examining these patterns of interactions, one moves up the organizational scale from

understanding structure based on the diets of individual predators to understanding interactions between the diets of multiple predators and prey. The analyses unveiled the subgraphs which appear more frequently than expected at random – true structural motifs which form the backbone of food-web structure – and those which appear less frequently than expected at random. They concluded that the subgraphs found in empirical food webs are consistent with the niche model and its contiguous prey selection mechanism and not that of the nested-hierarchy model (Stouffer *et al.* 2007).

By looking deeper at the structure of empirical food webs, the authors were able to demonstrate the validity of the phenomenological rule behind the niche model, without having to conduct additional, and potentially difficult, empirical studies. Their results imply that foragers indeed appear to specialize about some attribute, in agreement with the intuition behind the proposal of the niche model (Williams & Martinez 2000). Similarly, the results imply that the intuition behind the nested-hierarchy model was not actually representative of empirical observations. Only through further research was it possible to link these phenomenological models to empirical reality and distinguish between the two.



**Fig. 2.** Food-web motifs. In the top row, I show the 13 unique food-web motifs composed of three species (Milo *et al.* 2002; Stouffer *et al.* 2007). Each motif represents the predator–prey interactions between a triplet of species with vertices representing species and arrows pointing in the direction of biomass and energy transfer, from prey to predator. The left-most motif, therefore, represents a tri-trophic food chain. Stouffer *et al.* (2007) examined the over- and under-representation of each of these motifs in empirical food webs. They observed a conserved pattern in the majority of food webs investigated. Furthermore, this pattern could be explained by a contiguous prey selection mechanism as found in the niche model (Williams & Martinez 2000). In the bottom row, I show the direction of the over- and under-representation in this conserved pattern. A plus sign signifies that a subgraph appears more frequently than expected by chance, a negative sign signifies that a subgraph appears less frequently than expected by chance, and the symbol ~ signifies that there is no conserved pattern or prediction.

There is a flaw, however, in the niche model which was both a justification for the nested-hierarchy model and a direct consequence of the contiguity of diets. Diet contiguity implies that niche-model food webs are strictly interval (Sugihara 1984; Williams & Martinez 2000), whereas real food webs are generally non-interval (Cohen 1977, 1978) and thus, strictly speaking, incompatible with the niche model (fig. 3). One obstacle in resolving this paradox is the concept of intervality itself. Historically, food webs were classified as ‘interval’ or ‘non-interval’, in a binary fashion (Cohen 1977, 1978; Sugihara 1982, 1984). Even a single interaction can change a food web from one category to another, as Williams & Martinez (2000) noted in their initial proposal of the niche model.

Instead of utilizing the binary measure, Stouffer, Camacho & Amaral (2006) proposed a continuous metric to gauge the intervality of food webs; their index is a direct estimation of the degree of diet contiguity found in a food web. According to their results, empirical food webs exhibit a tendency towards diet contiguity – intervality – and are therefore consistent with the niche model (Stouffer, Camacho & Amaral 2006) (Fig. 3). This conclusion has also been reached by other analyses of food-web structure (Allesina, Alonso & Pascual 2008; Williams & Martinez 2008), and intriguingly appears to hold well for other types of ecological networks such as host–parasite networks (Mouillot, Krasnov & Poulin 2008).

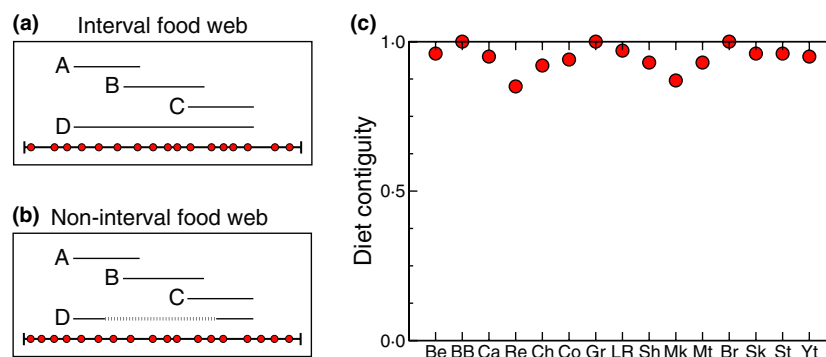
### Population-level food-web models

Because a phenomenological model may not direct us to the correct empirical mechanism, as we saw in the case of the nested-hierarchy model (Cattin *et al.* 2004; Stouffer *et al.* 2005), some scientists have chosen instead to develop models based on ecologically accurate individual behaviour. These population-level models rely upon emergent phenomena – the generation of complex global behaviours by a small or tractable set of local individuals’ decisions (Johnson 2001) –

to generate the eventual food-web structure. Often, the model is framed to be conducive to straightforward verification from empirical data. Population-level models can thus be thought of as an attempt to explicitly consider ecological realism, in contrast to the phenomenological models discussed previously. In the following, I describe a set [albeit incomplete; see Caldarelli, Higgs & McKane (1998) and Yoshida (2003), among others] of recent population-level models below while paying close attention to the similar features between them and the phenomenological models discussed earlier.

A recent population-level model, developed by Loeuille & Loreau (2005), attempts to explain the structure of empirical food webs by considering ‘lower-level’ processes, such as adaptation. In their model, adaptation acts on body size because ‘[its] impact on the metabolism and interactions of organisms is well established’. The model’s principle parameters are species’ consumption niche width and the intensity of competition. It is important to note, as the authors do, that the model is structured with two parameters that can hopefully be measured or verified empirically. Species in the model were set up to be most effective predators when their size and that of their prey are separated by a fixed value shared by all predators. This implies that competition is strongest between similarly sized predators (Loeuille & Loreau 2005). Using their model, Loeuille & Loreau (2005) were able to generate food webs which emerged from a single ancestral species and the structural properties of which compare well with empirical food webs. In addition to generating the structure, this model and other similar models often provide additional information such as species abundance and interaction strengths. This provides abundant opportunities for additional comparisons to empirical data.

Operating under similar intentions, Rossberg *et al.* (2005) recently proposed the speciation model – a model of evolutionary dynamics of food webs – as a similar dynamic attempt to explain food-web structure. In the speciation model, three macro-evolutionary processes are considered: speciation,



**Fig. 3.** Food-web intervality. (a, b) Species (red circles) are placed along a single dimension which we denote the resource axis. For each predator A, B, C and D the solid line is placed above the prey (resources) it consumes. A food web is interval if there exists a permutation of the species along the resource axis such that for each predator the diet is contiguous. In contrast, a food web is non-interval if no permutation exists for which all diets can be represented as contiguous segments. This is because of the gap in the diet of species D, represented by the dashed segment. (c) I plot the degree of diet contiguity for 15 empirical food webs, as measured by Stouffer, Camacho & Amaral (2006), where a value of 1 represents the limit of perfectly contiguous diets. That empirical food webs exhibit a significant tendency to contiguous diets, a feature similarly observed in subsequent studies (Allesina, Alonso & Pascual 2008; Petchey *et al.* 2008; Williams & Martinez 2008), validates an important assumption of the niche model (Williams & Martinez 2000).

extinction and the adaptation of new species to the habitat (Rossberg *et al.* 2005). Importantly, interactions in the speciation model are largely size structured, a feature which we have already seen is common among recent phenomenological models.

The speciation model is dependent upon a very important assumption, the scaling of evolution rates with adult body mass, which has ambiguous empirical support (Rossberg *et al.* 2005, 2006a). To overcome this drawback, Rossberg *et al.* (2006a) proposed a related model, the matching model, to provide an alternative to explain food-web structure in an evolutionary context. In the matching model, the dynamics are again driven by the same set of macro-evolutionary processes, but the species now are characterized by sets of vulnerability and foraging traits, the overlap of which decides the interactions between predators and prey (Rossberg *et al.* 2006a). The evolution of these traits, and the avoidance of direct competition between related species, creates a dynamic model which compares as well with empirical food-web data as any such model (Rossberg *et al.* 2006a). A drawback of the speciation and matching models is the inherent difficulty in empirical estimation or verification of model parameters, such as rate of speciation.

Because of some of the difficulty in empirically verifying the evolutionary models discussed above, other scientists have been working to incorporate optimal foraging theory in explaining aspects of food-web structure (Beckerman, Petchey & Warren 2006; Petchey *et al.* 2008). A common complaint regarding phenomenological models is that they often rely upon 'emergent' properties, such as linkage density, as their input parameters. This means that while the models are able to explain many complex aspects of food-web structure, they are unable to provide an explanation for more basic and fundamental features. To this end, Beckerman, Petchey & Warren (2006) demonstrated that diet breadth provides an explanation for food-web connectance based upon individual foraging behaviour. Their model was based upon the straightforward assumption that a species' diet breadth should maximize the rate of energy uptake.

Building upon this result, Petchey *et al.* (2008) adapted the diet-breadth model to include species allometries to predict the network of interactions in real food webs. They constrained upon the set of allowable interactions with the relationship between body size and ecological variables such as handling times (Petchey *et al.* 2008). By coupling empirical food-web data with information about species' masses, they demonstrated that their 'allometric diet-breadth model' predicted a significant fraction of the empirically observed interactions. As opposed to the evolutionary models discussed earlier, the authors' model is built largely upon directly measurable species traits, such as mass. This makes the model not only more intuitive but quite accessible for future empirical validation. Importantly, as the authors describe, their results lend credence to 'the hypothesis that individual behaviour, subject to natural selection, determines individual diets and that food web structure is the sum of these individual decisions'.

There is at least one very important distinction about the model of Petchey *et al.* (2008) in contrast to each of the previous models I have discussed. The authors developed a model which attempts to explain the very interactions observed between the exact species which are found within the food web. Most models instead attempt to produce model-generated food webs with similar secondary properties but where the identities of the species are unimportant. The work by Petchey *et al.* (2008) then provides a platform to identify the trophic links which are explained by a particular hypothesis and those which remain unexplained. The ability to directly map each of the other models to empirical data would provide us substantially greater power and ecological insight into the processes at work.

Despite this difference, one observes that the allometric diet-breadth model of Petchey *et al.* (2008) makes a number of predictions that mirror those of the phenomenological niche model (Williams & Martinez 2000), where species are ordered by their masses and niche-value respectively. This includes that the bulk of consumers' prey are smaller and that species diet breadths increase as one moves up the ordering (Williams & Martinez 2000; Petchey *et al.* 2008). Notably, consumers in both models select their prey from a contiguous range; the same is true for the model of Loeuille & Loreau (2005). The speciation model, in contrast, generates non-interval webs but to a degree consistent with empirical observation (Rossberg *et al.* 2006b). Phenomenologically, diet contiguity has been shown to be important in explaining empirical food-web structure (Williams & Martinez 2000, 2008; Stouffer, Camacho & Amaral 2006; Stouffer *et al.* 2007) and one wonders what role it plays for the population-level models and their own explanatory power. It would be similarly interesting to see if the assumptions underlying these, and other, population-level models satisfy the two phenomenological conditions outlined by Stouffer *et al.* (2005) for model success.

## Discussion

Recent growth in both the development and validation of phenomenological food-web models can be traced to the field of network theory (Newman 2003). Network concepts and tools have proved integral as the investigations proceeded to levels of greater detail. In addition to properties such as the numbers of basal, intermediate and top species, scientists began to examine degree distributions (Camacho, Guimerà & Amaral 2002b; Dunne, Williams & Martinez 2002; Stouffer *et al.* 2005), compartmentalization (Krause *et al.* 2003; Allesina & Pascual 2009; Rezende *et al.* 2009) and motifs (Milo *et al.* 2002; Arim & Marquet 2004; Bascompte & Melián 2005; Camacho, Stouffer & Amaral 2007; Stouffer *et al.* 2007; Bascompte & Stouffer 2009) directly following studies of complex networks in other disciplines. While such models and such studies have helped us to better characterize food webs, there is no guarantee of inherent ecological relevance, as we have seen. It is only by uncovering the intricate relationship between the patterns and the mechanisms which

reproduce them that allows us to make ecologically relevant conclusions. For this reason, many ecologists have turned to population-level models as a means to explain empirical food-web structure.

While the ultimate goal tends to be the same – an improved understanding of the processes which shape food-web structure – the two types of models can often seem both opposing and orthogonal. The complication arises because it is often not directly possible to bridge the gap between the heuristics underlying phenomenological models and the implied empirical behaviour. This means that future empirical validation of the models' assumptions may be many steps away, in stark contrast to population-level models which attempt to incorporate well-established ecological theories, such as optimal foraging (MacArthur & Pianka 1966). Unfortunately, this also implies that it can be more difficult to understand exactly why a phenomenological model behaves as it does, how its behaviour may be sensitive to the parameters chosen and what represents the next step in the line of research.

It is important to point out that while both phenomenological and population-level models are developed to explain food-web structure, it is often quite complicated to perform direct comparisons between any two. A specific example is the difficulty in comparing, for example, the niche model to the allometric diet-breadth model. The niche model was designed to statistically reproduce empirical food webs and food-web structure over a large number of stochastic realizations (Williams & Martinez 2000). For the allometric diet-breadth model, in contrast, the objective is to understand why precise interactions exist between the specific species present (Petchey *et al.* 2008).

One facet of the difference between these two models can be viewed as alternate hypotheses or perspectives on the processes that give rise to the observed food-web structure. On the one hand, the observed structure exists because real species have optimized their behaviour through, for example, optimal foraging (Beckerman, Petchey & Warren 2006; Petchey *et al.* 2008). On the other hand, an empirical food web is just a single realization of a fundamentally stochastic process. This implies that the observed food-web structure could indeed be different if history were repeated, even for the same set of species and their sizes.

Another matter which complicates comparisons between models is the question of how best to compare dynamic population-based models with static counterparts. The model proposed by Loeuille & Loreau (2005) overcomes this obstacle because its dynamics appear to converge to a steady state. In the speciation and matching models (Rossberg *et al.* 2005, 2006a), in contrast, the number of species fluctuates significantly and the models frequently do not appear to reach a steady state. Although this can be accounted for via complicated statistical methods (Rossberg *et al.* 2006a), they are not as straightforward as direct comparisons between phenomenological models. Even comparisons between phenomenological models, however, are often based upon secondary structural properties. This is why the niche and nested-hierarchy models appeared to explain some aspects of

food-web structure equally well (Cattin *et al.* 2004; Stouffer *et al.* 2005). Detailed analytical or numerical approaches have proved instrumental in moving past secondary comparisons to unify apparent mechanistic differences (Stouffer *et al.* 2005) or uncover their roots (Allesina, Alonso & Pascual 2008).

Despite the differences between the phenomenological and population-level approaches, there is substantial overlap. An important similarity among each of the models discussed is the direct or indirect role of species mass as a, if not *the*, critical species trait. This was manifested, for example, in terms of the evolution of species masses (Loeuille & Loreau 2005), the scaling of evolutionary rates (Rossberg *et al.* 2005) or the elusive niche-value (Cohen & Newman 1985). It has recently been questioned whether or not ecologists utilize mass because of convenience as opposed to outright ecological relevance (Berlow, Brose & Martinez 2008). To determine if this is indeed the case, it will be necessary to identify complete chains of causality. Imagine the situation where phylogenetics (Cattin *et al.* 2004; Bersier & Kehrlí 2008; Rezende *et al.* 2009) and species masses (Petchey *et al.* 2008; Rezende *et al.* 2009) both appear to explain some aspect of food-web structure. It would then be critical to determine the relationship or independence between the two and which can best explain the other.

The work that I have discussed is largely focused on static properties and static comparisons between the food-web models and empirical data. Because of the complexity of empirical food webs, most dynamic studies have concentrated on the smaller scale of trophic modules (Holt 1997; McCann, Hastings & Huxel 1998; Emmerson & Yearsley 2004; Bascompte, Melián & Sala 2005; Otto, Rall & Brose 2007). (See the contribution of Abrams 2009 in this issue as an example on this theme.) Nevertheless, a number of exciting results into food-web dynamics have emerged at the level of community modules or food-web motifs. These include the role of omnivory (McCann & Hastings 1997; Emmerson & Yearsley 2004; Tanabe & Namba 2005; Vandermeer 2006; Namba, Tanabe & Maeda 2008) and the stabilizing effects of weak links (McCann, Hastings & Huxel 1998; Bascompte, Melián & Sala 2005). Otto, Rall & Brose (2007) demonstrated that tri-trophic food chains are most persistent if the species' predator-prey body-mass ratios fall within a specific range. At the scale of an entire community, it has been observed that predator-prey body-mass ratios play a similar role in augmenting community persistence (Brose, Williams & Martinez 2006). Similarly, Kondoh (2008) recently demonstrated that a Caribbean food web is largely made up of modules which are stable in isolation and that the less stable modules benefit from being embedded within the larger community. Intriguingly, no study to date has examined the relationship between module composition and the parameters of a population-level model; such investigations should provide a direct link between ecological behaviours and a finely detailed food-web characteristic.

The models themselves can also play a very important role in motivating new empirical data collection. Sometimes, as in

the case of dietary contiguity (Stouffer, Camacho & Amaral 2006), models' assumptions can be validated using existing empirical data. More often, this is not the case. The scientists who propose and develop models could help advance the field both empirically and theoretically by plainly identifying data which could prove or disprove critical assumptions underlying their models. In this aspect, it seems phenomenological models are best suited. Population-level models strive to demonstrate exactly why we observe what we observe. Phenomenological models achieve the same but often without the need for detailed parametrization or fine-tuning; such models, for example, generally only rely upon the empirical number of species and number of interactions. These models then provide an excellent platform to push ecological research, on food webs or otherwise, to places where empirical studies have not or simply cannot reach. Examples include exploring scenarios where data collection or experimentation is difficult, impossible, or unwise such as cascading extinctions (Srinivasan *et al.* 2007) or the introduction of invasive species (Ng *et al.* 2008). The models I have discussed tend to be validated with comparison to food webs from pristine environments and their constituent species. The question remains whether invasive species, for example, exhibit the same foraging behaviours as native species; we will only be able to answer this question through empirical investigations.

In future, we must make greater efforts not just to directly compare models of the different types, but link them across the different scales and take full advantage of the problems for which they are best suited. Because of their focus on the whole community, phenomenological models are well positioned to the development of general ecological theory. These general theories in turn are best fine-tuned, and the implications expanded upon, with a combination of empirical data and work at the scale of anywhere from one or a few species to a population-level model. Upon validation with detailed empirical data, from the field or laboratory, we can confidently posit potential evolutionary mechanisms in order to understand the true origins of the ecological phenomena of interest. If we can construct such an organized strategy, we can guarantee that all of these computational tools will continue to lead ecology forward at an exhilarating pace.

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