8.2 | POPULATION DYNAMICS AND FOOD WEB STRUCTURE—PREDICTING MEASURABLE FOOD WEB PROPERTIES WITH MINIMAL DETAIL AND RESOLUTION

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Real food webs exhibit both exquisite detail and exhaustive resolution (Paine, 1980; Schoener, 1989; Winemiller, 1990; Polis, 1991). This observation presents a considerable challenge for food web theory because both detail (e.g., parameters describing feeding relationships) and resolution (e.g., the number of state variables representing species) increase model complexity thereby reducing the analytical tractability of model systems and the clarity of their prediction. Traditionally, the field has carefully avoided this problem by building models that capture *either* detail *or* resolution. The divide between detail and resolution has in turn led to the formation of two very distinct schools of food web theory. The first school, which we call the "detail school," focuses on *population*

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dynamics and relies strongly on reductionism. This school simplifies food webs to a system of two to four focal interactions and examines the effects of variation at the level of the individual on the stability of population dynamics over time (Lotka, 1925; Volterra, 1926; Gause, 1934; Rosenzweig and MacArthur, 1963; Schoener, 1973; Holt, 1977; Yodzis and Innes, 1992; McCann et al., 1998). Here, details such as spatial refugia, size structure, diet specialization, predator satiation, and many other individual properties determine patterns of coexistence, the location of stable equilibria or the nature of variability in abundance patterns over time. The quintessential features of population dynamics models (i.e., the "detail school") are detailed mechanism at the individual or behavioral level and measurements in units of time.

The second school, which we call the "resolution school," focuses on regularities in the *food web structure* and the stability of non-random structures in more resolved, speciose food webs (Gardner and Ashby, 1970; May, 1972; DeAngelis, 1975; Cohen, 1977a; Yodzis, 1981a, 1982; Cohen and Newman, 1988; Cohen et al., 1990a; Martinez, 1991, 1992, 1993b; Moore et al., 1993; de Ruiter et al., 1995; Williams and Martinez, 2000). For example, numerous studies over the last three decades show how "regularities" in the structure of food webs determine their capacity to return to equilibrium following small perturbations (i.e., system resilience).

These regularities can be divided into two categories—macroscopic and microscopic. Classical examples of macroscopic descriptors are global connectance (Gardner and Ashby, 1970; May, 1972), the ratio predator to prey species (Cohen, 1977b; Cohen et al., 1990a) and the degree of omnivory (Pimm and Lawton, 1978; Williams and Martinez, 2000). By contrast, microscopic descriptors of food web structure include guilds (Root, 1967), blocks and modules (May, 1972), cliques and dominant cliques (Cohen, 1977a; Yodzis, 1982), compartments (Pimm, 1979), subwebs (Paine, 1980), block submatrices (Critchlow and Stearns, 1982), and complexes (Sugihara et al., 1989). In contrast to models of population dynamics advocated by the detail school, the resolution school focuses on the structure of feeding links between consumers and resources and the stability of this structure within more complete sets of species comprising a food web (but see Polis, 1991). Further, these maps occur in one place and at one time or in one place over different stages, representing cumulative data.

Clearly there are strengths and weaknesses to both approaches. The trade-off between detail at the level of the individual and resolution at the level of the whole system best exemplifies the compromises made by each. Models of *population dynamics* (hereafter, synonymous with the

"detail school") typically focus only on a few (two to four) species but capture copious mechanistic detail when describing the interactions among these select few species. Conclusions from these models are then inferred to apply to more complex systems with higher numbers of species. However, few studies have identified empirical or formal rules for distilling a complex system to a smaller, more analytically tractable subset of interactions (Murdoch et al., 2002). By contrast, models of *food web structure* (hereafter, synonymous with the "resolution school") describe the binary relationships of qualitative feeding among a more complete set of species in a community. Resolution at the system level often comes at the cost of mechanistic detail at the level of the individual. Only recently have studies begun to integrate detail, temporal dynamics and topological resolution into a more cohesive theory of food webs (Neutel et al., 2002; Cohen et al., 2003; Kondoh, 2003a; Emmerson and Raffaelli, 2004b).

Empirical studies of food webs can also be distinguished along gradients of detail and resolution. For example, experimental studies of food chains (Estes et al., 1978; Oksanen et al., 1981; Carpenter and Kitchell, 1988; Power, 1990) simplify communities to a subset of strongly interacting species that presumably determine the dynamics of the larger system. These studies draw heavily from theories of population dynamics (Rosenzweig and MacArthur, 1963; Rosenzweig, 1969, 1971, 1973). By contrast, comparative studies of food web energetics characterize patterns of biomass and energy flow through more complete food webs (Lindeman, 1942; Margalef, 1963; Winemiller, 1990; Polis, 1991; Polis and Strong, 1996; Hall et al., 2000; Neutel et al., 2002). These studies find a more natural foundation in theories of food web structure (May, 1972; Cohen, 1977a; Pimm et al., 1991; de Ruiter et al., 1995; Williams and Martinez, 2000) though this foundation is not always upheld by empirical observation (Paine, 1980; Winemiller, 1989b; Polis, 1991).

Finally, despite the diversity of food web theory, only rarely do predictions from models map to the temporal or spatial scales of either type of empirical investigation (Berlow et al., 2004). Population dynamic models typically evaluate the effects of detail on *asymptotic behavior* (Hastings, 2004) occurring often over very long periods of time. Predictions at time scales of longer than a few years are out of reach of experimental food web studies executed on seasonal or short, multi-annual time scales. This is especially true for studies that include long-lived or slow growing species. More importantly, transient dynamics may play a stronger role in empirical systems than assumed by most theoretical studies (Higgins et al., 1997; Hastings, 2004). Similarly, more resolved models of food webs evaluate the effects of

subsets of non-randomly interacting species on the resilience of the whole system in the face of small perturbations in the abundance of one or at most a small number of species. Often the return times predicted by models of food web structure are much longer than the typical empirical studies of food webs, grant cycles, or even lifetimes of investigators. Moreover, most empirical data used to test models of food web structure is static—a snap shot of the structure at one time in one place. Thus, empirically measured topologies may offer only a glimpse of transient rather than stable structure in time and space. In either case, current theory rarely provides predictions at time scales relevant to real webs observed over measurable time intervals.

In this chapter we argue that two major deficiencies of food web theory to date are (1) the almost mutually exclusive treatment of *detail* and *resolution* in food web models and (2) the lack of tangible timescales in mapping theory to empirical research on food webs. We highlight some recent advances in food web theory that represent the first steps towards integrating detail at the individual and population level with resolution at the whole system level and suggest that future progress depends on continued integration of these historically separate lines of investigation. Finally, we suggest a working conceptual model for integrating detail and resolution to make predictions about the links between population and whole system persistence. We argue that models of real food webs will only be valuable for more general empirical prediction if they include the *minimum* amount of detail *and* resolution necessary for capturing *measurable* properties of real food webs.

OSCILLATING THEORETICAL PERSPECTIVES—
ROADBLOCKS OR GRIST FOR INTEGRATION?

Over the past century, interests have oscillated between "detail" (theories of population dynamics: Lotka, 1925; Volterra, 1926; Gause, 1934; Holling, 1959a; Hairston et al., 1960; Rosenzweig and MacArthur, 1963; Paine, 1966; Murdoch, 1969; Rosenzweig, 1969, 1973; Holt, 1977; Paine, 1980; Oksanen et al., 1981) and "resolution" (theories of food web structure: Lindeman, 1942; Odum, 1957; Patten, 1959; Gardner and Ashby, 1970; May, 1972, 1973; Cohen, 1977b; Pimm and Lawton, 1977; Lawton and Pimm, 1978; Rejmánek and Stary, 1979; Pimm, 1980a, b; Briand and Cohen, 1984; Briand and Cohen, 1987, 1989). This scientific divide has continued over the past 30 years. For example, studies of the structure of more resolved food webs inspired by classic studies of diversity and complexity (Maynard Smith, 1974) were in vogue from the late seventies

through the late eighties (May, 1972; DeAngelis, 1975; Cohen, 1977a, b; Pimm and Lawton, 1977; DeAngelis et al., 1978; Pimm and Lawton, 1978; Pimm, 1979; Rejmánek and Stary, 1979; Pimm, 1980a, b; Pimm and Lawton, 1980; Yodzis, 1980, 1981a, b, 1982, 1984; Briand and Cohen, 1987, 1989; Yodzis, 1989). Interest in this approach waned in the late eighties as the field experienced a shift towards empirical research on population dynamics in simple food chains (Carpenter et al., 1985; Carpenter and Kitchell, 1988; Power, 1990, 1992), indirect effects (Schmitt, 1987; Wootton, 1994a; Wootton, 1994b, c) and interaction strength (Paine, 1992; Wootton, 1997). Most recently, ecology has seen a revitalized interest in more holistic studies of food web structure, cat-alyzed in large part by theory on self-organized networks imported from studies in physics and informatics (Albert et al., 2000; Dunne et al., 2002a, b; Neutel et al., 2002; Williams et al., 2002; Cohen et al., 2003). Many of the newer structural models have built on the empirical criti-cisms levied against older structural models.

Several of these studies provide evidence that the gap between detail and resolution in food web theory may be narrowing. First, mounting empirical evidence upholds a positive relationship between omnivory and stability (Polis, 1991; Diehl, 1992, 1995; Fagan, 1997). As a result, there has been increasing interest in understanding the role of weak interactions in conferring whole system stability (McCann et al., 1998; Berlow, 1999; Neutel et al., 2002). Empirical studies of microcosm communities suggest that population dynamics and non-random extinctions constrain feasible food web structures to those with constant connectance (Fox and McGrady-Steed, 2002). Finally, dynamic models of food webs now include more species (Yodzis, 2000) and focus specifically on how the prevalence of strong and weak interactions may increase the stability of small modules of three to four species by striking a balance between strongly oscillatory and more stable subsystems within these small modules (McCann et al., 1998). Taken together, these results may have implications for under-standing the stability of more resolved food webs. For example, whole system stability may be influenced by the *arrangement* of stable and unstable groups of interacting species, the structural organization of weak and strong links, and the correlation structure of interaction coefficients within a community (de Ruiter et al., 1995; McCann et al., 1998; Kokkoris et al., 2002; Neutel et al., 2002). These studies suggest that a more synthetic theory of community organization will arise from further explorations of how population dynamics and link struc-ture interact because all links, not just the strong ones, may regulate community-level dynamics.

BRIDGING THE DIVIDES BETWEEN DETAIL AND RESOLUTION

Despite recent advances in the integration of structural and dynamic approaches to food webs, few theoretical approaches satisfactorily combine detail and resolution to identify links between population dynamics and the stability of system structure. For example, does the strength of interactions between two to three interacting species depend on their location within a trophic network? Or conversely, do the details of population dynamics in one or a few modules change the structure of whole systems over time? We suggest that progress will come only by identifying strong empirical links between the details of population dynamics and the resolution of food web structure. Later we outline how the population and whole system persistence are linked through properties at the individual, internal system or external system level (Figure 1).

Persistence of Populations and Systems

Models of population dynamics and food web structure both attempt to understand *persistence* (see Figure 1A). Population models analyze population persistence as a function of individual properties, while models of larger food webs evaluate the resilience of whole systems of interacting species as a function of observed structural properties of entire food webs. The analysis of persistence is achieved in both cases via the same methods—by evaluating the sign and magnitude of the real components
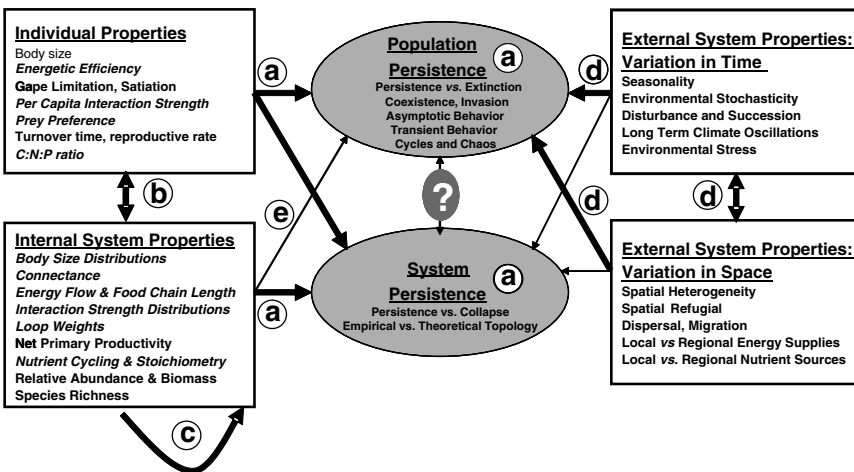

FIGURE 1 | Conceptual model linking population dynamics to food web structure.

of eigen values from the determinant of an *n x n* community matrix, where *n* is the number of species included in the model (May, 1973).

Scaling between Individual and System Properties

There is a great deal of *empirical* interest in understanding system properties by scaling up from individual properties (see Figure 1B). Ecological efficiencies (Lindeman, 1942) for example, are at the heart of most arguments about food chain length (Schoener, 1989; Post et al., 2000b; Post, 2002a). Similarly, consumers can determine the body size distribution of resources (Brooks and Dodson, 1965), and gape limitation can determine the relative strength of top down control of resource biomass by consumers (Hairston and N.G. Hairston, 1993). Diet generality and prey preference patterns in concert with species diversity (a systems property) determine connectance (Williams and Martinez, 2000). Recent work suggests that body size, through its influence on metabolism and prey choice, may be one critical determinant of consumer-prey interaction strengths, biomass flows, and link structure (Cohen et al., 2003; Emmerson and Raffaelli, 2004b).

Control Pathways among system Properties

There has been a great deal of attention devoted to causal links between various system properties (see Figure 1C). For example, studies of exploitation ecosystems (Oksanen et al., 1981; Oksanen, 1988; Persson et al., 1992; Schmitz, 1993; Wootton and Power, 1993; Power et al., 1996a) examine the effects of net primary productivity and food chain length on the relative biomass at individual trophic levels. Similarly, the numerous cause and effect relationships between ecosystem functions (e.g., net primary productivity) and species diversity are reviewed in this volume.

External Effects on Structure

External system processes such as climate forcing, environmental stochasticity, spatial heterogeneity, and source sink dynamics all have well-known effects on population persistence (see Figure 1D; Pulliam, 1988; Pulliam and Danielson, 1991; Ives, 1995; Tilman and Kareiva, 1997; Ives and Jansen, 1998; Ripa et al., 1998; Cuddington and Yodzis, 1999; Anderies and Beisner, 2000; Turchin et al., 2000; Ives et al., 2003; Kilpatrick and Ives, 2003). In some cases, the effects of both spatial and temporal variability are well understood (Kendall et al., 2000; Bjornstad and Grenfell, 2001). The effects of these external system

properties are almost completely ignored by models of more resolved food webs (Winemiller, 1990).

System Effects on Dynamics

Very little theory in population dynamics relates system properties directly to population persistence (see Figure 1E). By contrast, since most system properties (e.g., interaction strength distributions or loop weights) derive from individual properties (e.g., prey choice and feeding rates), structural studies at least indirectly rely on properties at multiple scales to understand structural persistence.

EXAMPLES OF INTEGRATING DETAIL AND RESOLUTION

As we have previously outlined, food web theory has oscillated between diparate schools promoting population-level detail or system-level resolution, and these oscillations were largely fueled by important empirical observations (Lindeman, 1942; Paine, 1980; Power, 1990; Polis, 1991; Paine, 1992; Hairston and N.G. Hairston, 1993; Polis and Strong, 1996). Yet population and system persistence are clearly linked in many ways through the relationships between individual and system properties (see Figure 1). Integration of these two types of empirical observations and theoretical approaches depends on combining the strengths of the two approaches—the scaling of the details of individual properties to whole system structure and understanding the constraints set by structure on the dynamics of smaller groups (modules) of species. We provide a few examples of how these two paradigms may be merged to construct productive and testable hypotheses.

Oscillatory Subsystems Scaled up?

McCann et al. (1998) showed that the stability of small modules of species depends on a balance struck by oscillatory and stable "subsystems" within these modules. Here subsystems are really individual populations. From a network perspective, this result suggests that understanding the mean, variance, and relative location of stable modules (groups of three to four interacting species) within a food web network may provide insights into the stability of the network as a whole. Post et al. (2000b) examined at how food chain couplings influenced stability. Their work, motivated by the observation that mobile predators

frequently link littoral and pelagic pathways in lake food webs, suggests that such coupling could be a potent stabilizing factor. Other systems show similar structure. For example, soil food web ecologists have argued that higher order, more mobile, generalist consumers couple the bacterial and fungal channels (see McCann et al., Chapter 2.4, for other examples), and this coupling has important implications for food web stability (Moore et al., 2003). Teng and McCann (2004) extended the Post et al. (2000b) analysis to consider an array of modules coupled by higher order consumers. The results suggest that oscillatory modules (three to seven species) coupled to stable modules (three to seven species) can act to dampen the dynamics of the potentially oscillatory system. These results argue that the weak interaction effect can be scaled up to the weak module or compartment effect.

Interaction Strength: Detail vs. Resolution

Interaction strengths among species, are both individual and system level properties (see Figure 1). As such they may be a unifying bridge between the "detail vs. resolution divide." A clear problem is the lack of consensus on how interaction strengths are defined and measured. One root of this problem is the difference between population and system level approaches (Berlow et al., 2004). Some interaction strengths specify individual or population-level traits (e.g., the Jacobian matrix element, maximum feeding rate, biomass flow along one link); while other interaction strengths are system-level traits (e.g., the impact of a change in one link or all links to and from a given species on the dynamics of other species). The second category includes the majority of field and microcosm perturbation experiments. Thus, in the first category individual interaction strengths are independent of the network, in the second category they are in theory inseparable from their network context. Empiricists and theoreticians with a population dynamics focus often argue that if one wishes to characterize the dynamic linkages among species, very few methods will be as accurate as direct manipulations of species. However, even when these studies focus on a single interaction, the outcome of press perturbations will always be a whole system response (Bender et al., 1984; Yodzis, 1988).

Ironically, empiricists and theoreticians with a system-level focus actually tend to use interaction strength measures that are more specifically an individual or population-level, rather than system-level, trait. These measures may have more easily quantified empirical proxies than those extracted from a laborious species perturbation experiment. For example, when characterizing interaction strengths for a large assemblage

of species, it is possible to translate the partial derivatives of the inverse community matrices into measurable units in empirical settings (de Ruiter et al., 1995; Neutel et al., 2002). Other promising approaches for rapidly assessing feeding rates to parameterize dynamic food web models include the use of biomass abundance patterns, predator and prey body size ratios, and metabolic theory to estimate relevant parameter values (Yodzis and Innes, 1992; Neutel et al., 2002; Cohen et al., 2003; Emmerson and Raffaelli, 2004b; Williams and Martinez, 2004a).

Interaction strengths that are easily measured or estimated properties of individuals or populations, such as maximum feeding rates, may translate easily into model parameters, but they do not necessarily predict the strengths of dynamic linkages among populations (Paine, 1980; de Ruiter et al., 1995). Given these constraints and trade-offs, species manipulation experiments are unlikely candidates for directly parameterizing community models. Instead they may be better used as independent tests of models that were parameterized with more empirically accessible data. Thus, some critical ingredients for integrating detail and resolution concerning population dynamics in food webs include: (1) Translating individual or population-level interaction strength parameters of both detailed and resolved community models into units that are easily measured or estimated; (2) Using both detailed and resolved models to target specific species manipulations that would serve as critical system-level empirical tests of individual/population-level interaction strengths parameterized with other data; and (3) Using experimental manipulations to test both detailed and resolved models in order to determine the minimum level of detail and/or resolution necessary to capture key population dynamics within a whole-system context.

Switching, Omnivory, and Connectance

One of the most difficult details to integrate into more resolved models of food webs is the empirical reality of predator–prey behavior. Many behaviors have been routinely shown to have strong dynamic effects on the stability of more detailed models of population dynamics. These behaviors include, non-linearities in the response of consumers to prey (functional responses, Holling, 1959a; Murdoch, 1973; Oaten and Murdoch, 1975b; Oaten and Murdoch, 1975a) predator interference and ratio dependence (DeAngelis et al., 1975; Free et al., 1977; Getz, 1984; Arditi and Ginzburg, 1989; Berryman, 1992) and seasonal, density- or frequency-dependent and ontogenetic shifts in diet (Murdoch, 1973; de Roos and Persson, 2002). For example, saturating (Type II) functional responses make even moderately sized structural webs unstable and thus from the standpoint of

theory, less likely to exist empirically. Sigmoidal functional responses alleviate this problem to a certain extent (Williams and Martinez, 2004a). The sigmoidal functional response is a potentially common emergent property of a variety of plausible ecological mechanisms including switching, prey refuges, predator learning and weak links (Murdoch, 1973; McCann, 2000; van Baalen et al., 2001). On the surface, this would seem to suggest that a potentially rich set of details could be simplified into a functional response that produces stable food web topologies.

Asymptotic functional responses suggest that predator per capita effects (i.e., interaction strength) and population effects (i.e., energy flow between prey and predator populations) may depend on prey density. Similarly, switching among alternate prey species by predators (seasonally or spatially) implies variability in patterns of food web structure or connectance. Thus, both switching and saturation imply that patterns of energy flow, interaction strength and link structure, all central to structural food web approaches, are not constant over time—a common assumption made when applying point estimates of these properties in more resolved models of food webs. Kondoh (2003a) showed that switching by adaptive foragers stabilized large and complex food webs similar in structure to those observed in nature. Though switching, ontogenetic diet shifts and even individual variability in diet preferences are well known behavioral attributes of a variety of predators, empirical measures of temporal variation in connectance, interaction strength or energy flow at the system level are rare. Taken together, these results suggest that empirical "snap-shots" of food web structure may not be adequate benchmarks for testing models of large, more resolved food webs.

Clearly, multiple point estimates of the membership and feeding links within a single food web is not a trivial empirical endeavor. At a coarse scale, stable isotopes may prove useful in alleviating this problem by identifying time-integrated measures of energy flow from various source pools at either different trophic levels, from different habitats or from different energy channels (Post, 2002b). At a finer scale, diet information from multiple individuals (e.g., of different age classes and from different spatial locations) could be used to calculate the probabilities of consumption of different prey types and thus, a less binary roadmap of feeding links within a food web.

Temporal Variability

Cycles, chaos, and stability are all deterministic concepts—measurements of the signal or "process" underlying population dynamics. In the field, we often see more noise than signal. Some of this noise is

measurement error, while a good deal of it is stochastic environmental variability in recruitment or survival ("process error") unrelated to the underlying process of interest. Stochasticity is one of the most difficult divides between theory and data in food web science. Many models of population dynamics evaluate the effect of stochastic variation in abundance on the persistence of interacting species (Ives and Jansen, 1998; Ripa et al., 1998; Kilpatrick and Ives, 2003; Sabo, in press); however, very few of these insights have been integrated into a systems perspective. New work suggests that species interactions (process) can attenuate (Kilpatrick and Ives, 2003) or amplify (Sabo, in press) stochastic variation in abundance (process error) of key species in simple food webs. This new work suggests that empiricists may find more fruitful tests of theory by measuring second rather than first moments of abundance in (longer term) experiments.

Numerous new approaches provide rigorous statistical tools for quantifying process (e.g., interaction strength) in the face of process and measurement error (De Valpine and Hastings 2002; De Valpine, 2003; Ives et al., 2003; De Valpine 2004). For example, multivariate autoregressive models, or MARs, (Ives et al., 2003) use time series of abundance data from a set of interacting species to estimate interaction strength and the stability of the entire species assemblage. Stability can also be assessed under different environmental regimes or in response to a perturbation thus providing a tool for predicting the effects of environmental stress and disturbance on both population dynamics and food web structure.

Timescale Mismatch

Useful models should yield predictions that are tractable for testing by either field experiments or observational data. Models of population dynamics provide qualitative answers to two types of questions: (1) do the species described by the model coexist? (i.e., population persistence, see Figure 1), and if so, (2) how stable (or variable) are their abundances in time as a result of their species interaction? Predictions from the first of these questions are frequently tested by short-term experiments, most during the active season of a single year (Nisbet et al. 1997). Predictions of the latter type have rarely been tested in field settings, but have been more the realm of lab studies of cultured populations (Costantino et al., 1997; Cushing et al., 2001; Dennis et al., 2001). In both cases, predictions may be based on long term (i.e., asymptotic) model behavior that ignores transient behavior and stochastic variation—both prevalent in real ecosystems.

By contrast, models of food web structure provide a qualitative answer to questions about the stability and thus the "persistence" (see Figure 1) of theoretical food webs of varying size (number of species), complexity (number of feeding links), and dynamics (relative distribution of weak and strong feeding links). One then asks if empirical webs (assumed to be stable by virtue of being observed) have similar properties to feasible theoretical webs. Large empirical food webs are rarely constructed in multiple sequential seasons or years (see previous discussion). In some of our best food webs, time may even be ignored (e.g., diets sampled in multiple seasons of the same year). As is the case with predictions from population dynamics, structural models also focus on asymptotic behavior (resilience) ignoring transient dynamics and stochastic variation.

Given the mismatch between the timescales of theory (asymptotic behavior) and data (seasonal collections or experiments), future models of food webs must either be refocused to make predictions at smaller timescales, or empiricists must learn to measure variability in the effects of their experiments or the membership of larger food webs across larger time scales. We acknowledge that neither is a trivial task; however several recent approaches suggest some promise. For example, Nisbet et al. (1997) modeled *single season* interactions among three trophic levels in open ecosystems by substituting dispersal (immigration) for reproduction for higher trophic levels. Predictions from models on such short timescales are more appropriate for evaluation with data from short-term experiments. At higher levels of food web resolution, Multivariate Autoregressive Models (Ives et al. 2003) provide a promising tool for evaluating whole system stability, once more comprehensive time series data on larger sets of species are available.

DISCUSSION AND CONCLUSIONS

Approaches to food web theory have historically oscillated been the perspective of population-level detail or system-level resolution. Details include predator–prey behavior, temporal variability, spatial habitat structure, and links among food webs supported by alternate energy sources (detritus or primary production) or disparate habitats. Resolution includes the architecture of large ecological networks, including system-level patterns of biomass flow, interaction coefficients, and species' body sizes and abundances. Each viewpoint has strengths and weaknesses. Neither viewpoint will ever provide an accurate caricature of a real food web without acknowledging the strengths of the countervailing view. We suggest that progress will come only by identifying

strong empirical links between the details of population dynamics and the resolution of food web structure. Population and whole system persistence are linked through properties at individual, internal system, and external system levels (see Figure 1). We argue that models of real food webs will only be valuable for more general empirical prediction if they include the minimum amount of detail and resolution necessary for capturing measurable properties of real food webs. Model predictions should be testable with logistically feasible experiments (e.g., at seasonal timescales) or creative uses of non-experimental empirical data (e.g., longer-term properties of whole systems).