



8.1 | HOW DO COMPLEX FOOD WEBS PERSIST IN NATURE?

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THE COMPLEXITY–STABILITY RELATIONSHIP

Natural ecological communities are composed of a large and often indeterminate number of taxonomic species that trophically interact in myriad ways. Food webs describe the networks of these relations. While the population dynamics of individual species are often highly variable (Bjornstad and Grenfell, 2001), the overall structure of the trophic relations of the community, its food web, is comparatively more stable as they exhibit remarkably consistent patterns (Martinez, 1993b, 1994; Warren, 1994; Camacho et al., 2002a; Garlaschelli et al., 2003) and follow surprisingly consistent rules (Williams and Martinez, 2000; Camacho et al., 2002b; Cattin et al., 2004). This consistency combined with population variability makes natural food webs both rather dynamically and structurally complex and also somewhat stable over ecological time. For the most part theory has been unable to explain these high levels of complexity in terms of diversity and number of trophic relations because these elements are traditionally thought to decrease stability (May, 1973) and population persistence (Brose et al., 2003; Williams and Martinez, 2004c) in modeled communities. This disparity between real patterns and those predicted by theory has been one of most pressing issues facing ecologists for the past few decades. If the mechanisms

driving the trophic dynamics of natural communities are to be understood, this paradox needs to be resolved and a robust theoretical framework needs to be developed that adequately explains the persistence of complex food webs in a way that is consistent with high quality empirical data. Identification of the mechanisms or “devious strategies” (May, 1973) that permit the persistence of complex food webs would be a valuable discovery for community ecology and would resolve a major paradigm within the complexity–stability debate (Brose et al., 2003). This chapter broadly outlines the current state of the complexity–stability relationship in food webs, the different approaches used to examine this issue, our current understanding of the mechanisms that appear to stabilize complex natural food webs and highlights some of the most promising research directions for future focus.

FOOD WEBS, STABILITY AND COMPLEXITY

A food web is a simplified model of the trophic structure and dynamics of a community that is used to derive and test food web theory. Therefore, empirical and conceptual limitations of food webs can limit our understanding of the trophic dynamics of natural communities. A prime example is the failure of the food web community to adopt a universal convention that defines a food web and details precisely how one should be constructed—problems that stem from this are well recognized (Winemiller, 1990; Martinez, 1991; Polis, 1991; Cohen et al., 1993b; Martinez, 1993a; Deb, 1997; Goldwasser and Roughgarden, 1997; Martinez et al., 1999; Borer et al., 2002). Proponents of food web theory argue that while such problems are important, they can be rigorously addressed so that general robust conclusions can still be made about the underlying mechanisms that structure ecological communities. Until general conventions are better developed and adopted, researchers need to describe in detail the precise way in which each food web was constructed to avoid confounding food web research—this involves describing in detail aspects of web construction and the use of a well-defined and tractable vocabulary to both avoid confusion and facilitate research. We therefore briefly introduce the concepts of complexity and stability.

Understanding Complexity and Stability

The complexity–stability paradigm was formalized by MacArthur (1955) who expressed stability as the effect of a species with ‘abnormal’ abundance on the abundance of other species (the community was

stable if the effect was small). Citing Odum (1953), MacArthur considered the 'amount of choice which the energy has in following the paths up through the food web' as a direct measure of stability. This 'amount of choice,' a static feature of web topology, is more synonymous with what is now called complexity (its past usage as a measure of stability illustrates how both concepts are closely entwined). Because complexity refers to a static description of food webs while stability is a characteristic of their dynamical behavior, we describe both concepts separately.

By defining complexity as the amount of choice energy has when flowing through a food web it is clear that complexity is a function of both the number of species S and the number of trophic links L . Complex food webs contain many species and many interactions. A classic measure of complexity is connectance and while many different expressions have been used for the number of possible interactions (Warren, 1994) the most commonly accepted is L/S^2 which counts all possible inter- and intra-specific interactions (Martinez, 1992). Importantly, though, connectance reflects a proportion of links and therefore does not fully account for the number of species in a web. A measure incorporating both the proportion of links C and species richness S is simply their product SC , which simplifies to L/S (a quantity called 'link density'). Link density is perhaps the measure that best corresponds to the essence of MacArthur's 'amount of choice.'

While a conceptual appreciation of stability in the context of complex food webs appears straightforward, measurement of stability in dynamic systems is more difficult, not least because it is often ill-defined (Pimm, 1982; McCann, 2000). McCann (2000), in an excellent review on this topic, grouped definitions of stability into two broad categories—those based on a system's ability to defy change and those based on the system's dynamic stability. MacArthur's (1955) definition of stability centers on the ability of the system to withstand 'abnormal' abundance of one of its species (and would therefore fall into the first category) whereas the influential efforts of May (1972), who used local stability analysis to examine the dynamics of randomly constructed food webs with randomly assigned interaction strengths in the vicinity of its equilibrium, refers to the stability of the system as a whole (the second category). Recently, the problem of species loss in a food web has been examined through the study of secondary extinctions; that is, the cascade of extinctions caused by the removal of a species (Dunne et al., 2002a). Such a measure of the robustness of food webs is intriguing because it does not rely on dynamical models, but only on the architecture of the system. This methodology, interestingly enough, is in close agreement with MacArthur's (1955) original concept of stability.

APPROACHES FOR EXPLORING THE COMPLEXITY–STABILITY RELATIONSHIP

It is somewhat paradoxical that the recent escalation in diversity of approaches used to explore the stability–complexity relationship is on one hand the cause of much contention within the food web community and on the other appears directly responsible for generating so much recent advancement on this issue. Evidence to date indicates the significant role of multiple mechanisms in allowing the persistence of complex food webs (see later discussion), suggesting that a synthetic approach employing an array of investigatory techniques is most likely to provide the intellectual breakthrough ecologists are hoping for. Empirical descriptions of real food webs are likely to always be open to improvement, but theory is invaluable in revealing new and unsuspected behaviors (Raffaelli, 2002) and subsequently confirming and further elucidating those mechanisms observed in real systems.

Topological Analysis of Complex Empirical Webs

The topological analysis of empirical webs has historically been a productive way to search for mechanisms that might stabilize real webs (MacArthur, 1955; Pimm, 1979; Schoenly and Cohen, 1991) and recent advances in the study of complex networks has renewed interest in this approach (Williams and Martinez, 2000; Solé and Montoya, 2001; Camacho et al., 2002a, b; Dunne et al., 2002a, b; Montoya and Solé, 2002; Allesina and Bodini, 2004). Topological studies assess food web properties using the number and distribution of connections among nodes in the food web (Borer et al., 2002). Understanding the topology of complex food webs is a key requirement in understanding their stability because a web's structure can directly affect its ability to tolerate extinction of species (Arii and Parrott, 2004). The past decade has seen considerable growth in the number of properties that describe food web topology (Bersier et al., 2002; Dunne et al., 2004) many of which directly describe aspects of web complexity and stability. Increasing the taxonomic resolution of empirical webs remains a major empirical focus with current well-resolved webs containing well over 100 trophic species (Dunne et al., 2002b). While it is clear that the number of species and trophic interactions recorded in these webs are still below that in nature, determining the mechanisms that stabilize them will be a major step towards isolating those mechanisms that act in real communities.

Theoretical Analysis of Complex Webs

Since the seminal work of May (1973), much theoretical work has been devoted to the search for mechanisms that might allow complex model webs to persist. Lotka-Volterra type equations have long been used in the exploration of the complexity–stability relationship. Although historically productive, the use such linear approaches has been criticized as unrealistic by many authors. For example, linear shaped functional responses imply that a predator’s capability is not restrained when prey is abundant (Armstrong and McGehee, 1976), which certainly cannot be true in real systems. The recent integration of non-linear dynamics into food web models has resulted in a substantial increase in the levels of complexity at which stable communities can be maintained (Drossel et al., 2004). The success of this approach, together with significant advances in computing technology that are a requirement of such techniques, has seen significantly advancement on this front. The works by Vandermeer et al. (2002), Huisman and Weissing (2000, 2001), Williams and Martinez (2004c), and Kondoh (2003a; see Chapter 3.3) are great examples of the power of non-linear dynamic approaches.

WHAT MECHANISMS MIGHT ALLOW COMPLEX FOOD WEBS TO PERSIST IN NATURE?

Real community food webs are complex and, at least at some level, persistent. Whilst a variety of mechanisms have been proposed, ecologists still lack a clear understanding of what processes maintain the trophic structure of natural communities. Still, much progress has been made on this front. It would be surprising if one mechanism was solely responsible for these patterns and evidence to date suggests a central role of the following mechanisms:

Food Web Topology Is Not Random

It is now universally accepted that food web structure is not random, but the precise nature of these patterns remains contentious (Havens, 1992; Martinez, 1993a). In general, non-random patterns in food web structure appear to be an emergent property of dynamical constraints on species interactions (Fox and McGrady-Steed, 2002; Montoya and Solé, 2002). Comparative studies of food webs from a wide variety of ecosystems have isolated several topological patterns that appear to apply to a wide range of webs from different ecosystems (Pimm, 1982; Pimm et al., 1991; Williams

and Martinez, 2000). Four well-established patterns that appear to be critical to the stability of complex webs are that (i) connectance is scale-invariant, (ii) webs are characterized by short average path lengths between species, (iii) webs are short and fat, and (iv) omnivory is common.

Connectance Is Scale-Invariant

Early work suggested that connectance was scale-dependent (Schoenly et al., 1991; Havens, 1992), but re-analyses of these data (Martinez, 1993b; Murtaugh and Kollath, 1997) and of more complex empirical webs (Williams and Martinez, 2000) indicates that connectance is a scale-invariant property of food webs (i.e., it does not change systematically with the number of species). Connectance varies considerably in empirical food webs from about 3 to 32 percent (Dunne et al., 2002a, b), but on average is around 10 percent. Connectance is generally highest in empirical webs that have high proportions of intermediate and omnivorous species, two features that have been invoked as factors that increase the stability of natural food webs (Dunne et al., 2002a, b). However, theoretical studies often suggest a destabilizing effect of connectance on stability (May, 1973, Williams and Martinez, 2004b, c), but this is not always true (Dunne et al., 2002b; Fussmann and Heber, 2002; Kondoh, 2003a). While considerable attention is still required to determine how connectance affects food web stability, there is no doubt that the stability of natural food webs is, to some extent, influenced by the diversity of ways in which energy flows throughout it.

Short Average Path Lengths Between Species

As connectance increases, the mean distance between all nodes in a web also decreases. A recent analysis of seven highly resolved empirical webs (Williams et al., 2002) shows that species are, on average, only two links apart, with >95% of species typically within three links of each other. This suggests that real food webs could be sensitive to external forcing because local effects could permeate both rapidly and widely. Counter to this is the observation that real food webs are highly connected, have short path lengths, and are stable. Williams et al. (2002) suggest short path lengths may be a function of mechanisms associated with population dynamics and in particular the effects of weak interactions which can increase web stability and species coexistence (Warren, 1994; Berlow, 1999; McCann, 2000). For example, McCann et al. (1998) show that strong links are embedded in weak links and Neutel et al. (2002) show that strong links should not occur in the same interaction loop.

Webs Are Short and Fat

Numerous mechanisms have been invoked as to why food chain lengths are apparently quite short (Pimm, 1982), including organismal design or size constraints (Elton, 1927), available energy (Elton, 1927), disturbance (Power et al., 1996a), and ecosystem size (Post et al., 2000b). While a single mechanism does not appear to limit food chain length across ecosystems, the number of trophic transfers is ultimately limited by dissipation of energy both within and between trophic levels. One hypothesis that may account for the shortness of food chains relates to dynamical constraints associated with longer food chains—constraints that appear related to the productivity of the system (Moore et al., 1993). Pimm and Lawton (1977) showed that in a two to four trophic level system longer food chains had longer return times, suggesting they were less stable than chains of shorter length. Similar results have been observed in more complex models (DeAngelis et al., 1983; Carpenter et al., 1992; Moore et al., 1993) and in some simple real webs (Pimm and Kitching, 1987; Lawler and Morin, 1993) but these results are not universal (Sterner et al., 1997).

Omnivory Is Common

The prevalence of omnivory and its role in stabilizing or destabilizing food web dynamics has been a recurring focus of both empirical and theoretical research. Omnivory is usually defined as feeding at more than one trophic level, and is quantified by various ways of characterizing means and standard deviations of the length and sometimes strength of food chains leading from a consumer species to one or more basal taxa (Williams and Martinez, 2004b). Early food web stability modeling work, following May's (1973) equilibrium Lotka-Volterra community matrix approach, predicted that omnivory was likely to be uncommon in natural food webs, based on studies of 4-species modules (Pimm and Lawton, 1977, 1978). In particular, local food web stability depended on there being few omnivorous species, with any omnivores feeding on prey separated by only one trophic level. Initial surveys of empirical food web structure appeared to uphold this dynamical prediction (Pimm, 1982).

A prominent review of early food web research (Pimm et al., 1991) began to backpedal on earlier empirical claims by suggesting that omnivory is rare in "some webs" with "many exceptions." That same period of time saw the emergence of detailed empirical studies of complex food webs displaying high degrees of omnivory (Polis, 1991; see Polis and Strong, 1996 for review), with many researchers now suggesting that

earlier data was severely flawed due to poor species resolution. Recent analyses of 18 relatively high quality terrestrial and aquatic community food webs (Dunne et al., 2004) show that percentages of omnivorous taxa range from 8% to 86%, with 13 of the webs displaying omnivory levels of 50% or greater.

Not surprisingly, modeling work also eventually shifted its tone, aided by a diversification of its approaches and definitions. Recent simple food web models (generally less than 10 taxa) suggest a stabilizing role of omnivory. Using a Lotka-Volterra approach, but exploring a different aspect of stability (the resistance of food webs to further extinction following species loss), Borvall et al. (2000) reported that omnivory appears to augment resistance when a herbivore is lost. Non-equilibrium approaches also suggest that omnivory stabilizes simple food webs by eliminating locally chaotic dynamics or positively bounding such dynamics further from zero (McCann and Hastings, 1997). Metacommunity structure analysis provides evidence that in food webs with high levels of omnivory, top species may persist at higher levels of habitat destruction (Melian and Bascompte, 2002). A purely structural analysis of “reliability flows” in small empirical food webs, an engineering stability concept which refers to the probability that sources are connected to sinks, showed that high levels of omnivory are favorable for reliable network flows (Jordan and Molnar, 1999).

Nonetheless, modeling in more specious systems has uncovered less evidence for either a positive or negative relationship between omnivory and aspects of stability. Dunne et al. (2002a), focusing on the network structure of 16 empirical food webs, examined rates of potential secondary extinctions due to primary species loss. Their simulations suggested that food web robustness to species loss (i.e., lower levels of secondary extinctions) increases with connectance but is unrelated to species richness and omnivory. In a modeling framework that integrates realistic food web structure and diversity with plausible non-linear, non-equilibrium dynamics, Williams and Martinez (2004c) found that omnivores that prefer prey at higher trophic levels lead to lower persistence of species. However, this behavior is unusual in empirical food webs (Williams and Martinez, 2004b). When omnivores prefer lower trophic level prey, there is little effect on food web persistence (Williams and Martinez, 2004c). In general, omnivory tends to be correlated with connectance (Dunne et al., 2004), and thus the teasing apart of a connectance versus omnivory effects, if indeed there is any difference, needs to be carefully considered.

The Importance of Weak Links

Variations in the strength of species interactions within food webs may also contribute to the stability of food webs over ecological time. In 1972, May bridged the gap between two, up to that point, largely separate approaches to food web analysis. By combining parameters pertaining to food web topology and derived from binary information on feeding interactions (S and C) with a measure of the strength of these interactions (average interaction strength) he was able to formulate stability criteria for model communities. His considerations are based on randomly assembled food webs as well as randomly distributed interaction strengths and predict increases in average interaction strength and/or complexity (i.e., S and/or C) to yield a decrease in stability for the given system. These results suggest that average interaction strength should be weak in species-rich, highly connected systems (May, 1973). In May's models, measures of interaction strength are the elements in a Jacobian matrix at equilibrium, which represent the direct effect of an individual of one species on the total population of another species at equilibrium (Wootton, 1997; Laska and Wootton, 1998). However, this is just one of several possible definitions of "interaction strength" within an ecological context (Wootton, 1997; Laska and Wootton, 1998).

Indeed, it is worth noting that the way in which empiricists deal with interaction strengths (with a focus predominantly on ecosystem response to disturbance) is very different from the per capita effects used in models. Depending on the concept adopted, the analysis of a food web can reveal differing of interaction strength, which may involve different interpretations of the same data set (Laska and Wootton, 1998; Berlow et al., 2004). Empirical work on real systems shows interaction strengths to be highly skewed towards many weak and a few strong interactions (Paine, 1992; Goldwasser and Roughgarden, 1993; Fagan and Hurd, 1994; Raffaelli and Hall, 1996; Wootton, 1997). This pattern is especially noteworthy because it contradicts the practice of drawing estimates of interaction strength from a uniform distribution to feed dynamic models for lack of better approximations, or of understanding the focus of many ecologists on putative "important" interactions to mean that most interactions in nature are strong.

But is the configuration of interaction strength important for questions of community stability? De Ruiter et al. (1995) linked the differing approaches by deriving values of the Jacobian matrices from empirical observations. Their results indicate that the patterning of interaction strengths is indeed essential to maintaining system stability (see also Yodzis, 1981a; Haydon, 2000) even though the strength of an interaction

is not directly correlated with its impact on stability. What appears decisive is that “weak” interactions may be “strong” in reference to their stabilizing effects for the community as a whole (Paine, 1980; Hall and Raffaelli, 1993; Polis, 1994; Laska and Wootton, 1998; Kokkoris et al., 1999). More detailed work on the distribution of interaction strengths within food webs has shown that trophic loops are organized in such a way that long loops contain relatively many weak links and suggests that this patterning enhances food web stability because it reduces maximum ‘loop weight’ and thus reduces the amount of intraspecific interaction needed for matrix stability (Neutel et al., 2002). The results of a laboratory-based mesocosm study in turn imply that the patterning of interaction strengths in an ecosystem is determined by the body size distributions of its predators and prey (Emmerson and Raffaelli, 2004b).

In recent models that relate interaction strength to food-web dynamics, weak links appear to dampen strong and potentially oscillatory consumer-resource interactions (McCann et al., 1998) thus increasing food web persistence. The mechanisms responsible rely on a reduction in resource growth rates and consumer attack rates to stabilize consumer-resource interactions (Rosenzweig and MacArthur, 1963; McCann et al., 1998). Apparent competition occurs when a consumer species involved in a potentially oscillatory consumer-resource interaction trades off resource preference, thus mitigating the potentially critical interaction. The same effect is achieved by exploitative competition if a further consumer competing for the same resource is able to inhibit the growth rate of the shared resource. Lastly, food-chain predation describes the situation of top-down control when a top predator feeds on an intermediate species and thus indirectly restrains the interaction between the intermediate species and its resource (Hairston et al., 1960).

An additional effect of weak interactions is advocated by Berlow (1999) who experimentally assessed variability in the strength of these links. By magnifying spatio-temporal variation in natural communities “weak” interactions may be essential for the maintenance of diversity (or complexity), which in turn is expected to give rise to stability (McCann, 2000). A possible explanation for this relationship is that a system’s stability depends on its capability to respond differentially to fluctuating conditions, which can increase as the system becomes more diverse (Naeem and Li, 1997; Naeem, 1998). Random distributions of interaction strength—as employed in May’s models—cannot produce such structures (McCann, 2000).

The Dynamic Nature of Food Web Topology

Organisms may temporally change their diet and feeding activity through ontogenetic niche shift (Werner and Gilliam, 1984), behavioral flexibility (Stephens and Krebs, 1986), and evolutionary diet shift (MacArthur and Levins, 1964; Pimentel, 1971). Similarly, prey behavior such as anti-predation defense may influence a trophic interaction with the predator (Lima and Dill, 1996). Intra-population synchronization of such foraging-related behavior would activate or inactivate a trophic link at the population level. Furthermore, fluctuation in abiotic environmental conditions, which determine the possibility of prey-predator encounter, also leads to a temporal variation in food web architecture (Schoenly and Cohen, 1991; Tavares-Cromar and Williams, 1996). On top of this, trophic links can fluctuate at multiple time scales driven by different factors operating at different time scales. The time scale of the fluctuation would range from hours (Dell, unpublished data) to multiple years depending on the species that are linked and the precise mechanism involved. Such patterns hint towards a food web topology that is dynamic.

But is such temporal variation in food web architecture likely to affect population dynamics and the complexity–stability relationship in real ecological systems? Theory suggests a key factor is the relative time-scale of the linkage dynamics to that of population dynamics: if the linkage dynamics occurs at a time scale much longer than the population dynamics then food web topology can be considered, in effect, “constant” while the population level fluctuates. If true, then flexibility is less likely to have a major effect on complexity–stability relationship as it only defines the “static” food web architecture, which constrains the population dynamics (Pimm, 1991). In contrast, if the time scale of the focal linkage dynamics is comparable to that of population dynamics, the change in population level should be continuously influenced by the changing link strength (Abrams, 1982, 1984). In this situation there emerges the possibility that fluctuations qualitatively alter the complexity–stability relationship.

Among a number of factors that drive linkage dynamics, adaptation (population-level evolution, individual-level behavioral flexibility) has been intensively studied as a major factor that could alter the relationship between food-web architecture and population stability (Holling, 1959a; Abrams, 1982, 1984; Matsuda and Namba, 1991; Matsuda et al., 1993; Kondoh, 2003a; Takimoto, 2003). An important property of such an adaptation effect is that it creates a reciprocal interaction between population dynamics and linkage dynamics through the selection of links to

be dependent on the relative population levels of interacting species. Predators tend to consume more abundant prey (foraging switch, Stephens and Krebs, 1986) and prey tends to avoid more abundant consumers (defense switch, Sih et al., 1998). It follows then that in the presence of adaptation an increase in trophic links can have very different effects on population stability. Competitive exclusion usually results in the sole persistence of the superior competitor when two or more predators share resources (Tilman, 1982) so the addition of more predators simply leads to more extinctions. However, in the presence of defence switch, a predator, whose (adaptive) prey has additional predators, is more likely to be “ignored” by the prey when its population level is low. An increase in predator species can therefore enhance the persistence of more predators (Tansky, 1978; Teramoto et al., 1979). A similar argument holds for a multiple-prey-one-predator system (Matsuda et al., 1993; Abrams and Matsuda, 1996; Matsuda et al., 1996). In the absence of adaptation such a system is unstable as all prey species other than the prey that is most tolerant to the predator become extinct due to the negative indirect effect between the prey species (apparent competition, Holt, 1977). A population of a prey species whose (adaptive) predator has other prey can be more stable when its population level is low as it is more likely to be “ignored” by the predator. Kondoh (2003a) directly showed that foraging adaptation reverses a classically negative complexity–stability relationship into a positive one in some cases (Brose et al., 2003).

A central unresolved topic here is the relationship between the relative time scale of population dynamics to that of linkage dynamics in model and real food webs. In considering how such processes affect the persistence of complex food webs, it seems essential to account for interspecific heterogeneity within each web. Because the time scale at which populations or trophic links fluctuate is likely to vary between species, so too will the time scale of linkage dynamics that are most influential to the population dynamics of each species. This suggests varying effects of linkage dynamics to the population dynamics of each species. It would be interesting to explore if this heterogeneity has any consistent effects on the relationship between topological flexibility and population dynamics or community maintenance.