

Stabilization of chaotic and non-permanent food-web dynamics

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Abstract. Several decades of dynamical analyses of food-web networks [1–6] have led to important insights into the effects of complexity, omnivory and interaction strength on food-web stability [6–8]. Several recent insights [7,8] are based on nonlinear bioenergetic consumer-resource models [9] that display chaotic behavior in three species food chains [10,11] which can be stabilized by omnivory [7] and weak interaction of a fourth species [8]. We slightly relax feeding on low-density prey in these models by modifying standard food-web interactions known as “type II” functional responses [12]. This change drastically alters the dynamics of realistic systems containing up to ten species. Our modification stabilizes chaotic dynamics in three species systems and reduces or eliminates extinctions and non-persistent chaos [11] in ten species systems. This increased stability allows analysis of systems with greater biodiversity than in earlier work and suggests that dynamic stability is not as severe a constraint on the structure of large food webs as previously thought. The sensitivity of dynamical models to small changes in the predator-prey functional response well within the range of what is empirically observed suggests that functional response is a crucial aspect of species interactions that must be more precisely addressed in empirical studies.

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1 Introduction

Studying large networks that combine dynamical and structural complexity is severely limited by the lack of mathematical tools for analysis [13]. One of the clearer examples of such limitations includes ecological food webs [14,15]. For example, realistic modeling of the effect of reducing seal populations on populations of the fishes they eat is prevented by the current mathematical intractability of large networks involving the many species within marine ecosystems [14]. Similarly, recent insights [7,8] based on nonlinear bioenergetic consumer-resource models [9] into the effects of complexity, omnivory and interaction strength on food-web stability [6–8] are largely limited to unrealistically small networks containing less than five species. Here, we show that slight and empirically reasonable modification of standard “type II” food-web interactions, which very slightly reduces organisms’ consumption at low resources levels, escapes these limitations by stabilizing chaotic and non-permanent population dynamics of species embedded in food webs of 10 or more species. This new mathematical tool allows more sophisticated applications to larger networks and basic scientific insights [7,8] based on nonlinear bioenergetic consumer-resource models [9] to be examined in networks

that more accurately represent the complexity found in nature.

Most recent work on complex food webs has focused on their network structure or “topology”. Such food webs or networks are simply characterized as nodes representing species and links representing binary directed feeding interactions between species. A rich history of topological food-web analysis began in the 1970’s [16] and has accelerated recently with interdisciplinary interest in networks [17–19]. Food webs are thought to share certain statistical properties including constant connectance, scale dependence, heavy-tailed degree distributions and short characteristic path lengths of approximately two. Constant connectance asserts that directed connectance (C), or the fraction of all possible links (L) among species (S) that are realized within food webs ($C = L/S^2$), does not systematically vary with species number [20–23]. This hypothesis is equivalent to asserting a power law where links scale with the square of species number. Scale dependence asserts that the fractions of top and basal species and links between them decrease with increasing species number while the fractions of intermediate species and links between them increase [21,22,24]. Top species have resource species (e.g., prey, hosts, etc.) but no consumers (e.g., predators, parasites, etc.) while basal species have consumers but no resource species and intermediate species have both consumers and resources.

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In contrast to these patterns among food webs, more recent analyses stimulated by network theory has focused on patterns within food webs. Food-web degree distributions representing the probability of species having at least a certain number of links attached to them have been found to be “heavy-tailed”, meaning that there are fewer highly connected species than expected in the well-known “scale-free” networks [25]. Also, while food webs have short minimum undirected distances or “characteristic path lengths” between species, their clustering coefficient appears too low for food webs to be considered small world networks [17,25]. Most recently, food webs have been found to have a nearly constant power-law exponent representing a remarkably robust balance between a star-shaped pattern where all species are basal species deriving energy directly from the environment and all species existing in a single long food chain with one plant, one herbivore, one primary carnivore, one secondary carnivore and so on [18]. Finally, the historical disparity between the theoretically stabilizing effects of compartments in food webs and their empirical absence has been reduced by improved data and analyses that illustrate the presence of such compartments in nature [19].

While these statistical patterns form much of the analytical foundation for complex food webs, we focus here on models of mechanisms that may explain food-web structure rather than more phenomenological aspects of their structure discussed above. One such model [17,26] that we employ here successfully explains much of the structure of the most complex food webs in the primary literature (Fig. 1). Another well-known model that we focus most upon here is a bioenergetic model of the nonlinear dynamics or evolution of species’ biomass over time [9–11]. By altering the details of this model, we show how subtle ecological nonlinearities can stabilize large ecological networks and permit more of the interaction between their structure and dynamics to be explored.

2 Methods

We base our approach on a bioenergetic consumer-resource model of the time evolution of species biomass that follows previous work [7–9,11] that is generalized to n species and arbitrary functional responses. Extending the earlier notation [9] to n -species systems, the variation of B_i , the biomass of species i , is given by

$$B'_i(t) = G_i(B) - x_i B_i(t) + \sum_{j=1}^n (x_i y_{ij} \alpha_{ij} F_{ij}(B) B_j(t) - x_j y_{ji} \alpha_{ji} F_{ji}(B) B_j(t) / e_{ij}), \quad (1)$$

where t is time; $G_i(B)$ is the growth rate of species i , and is potentially a function of the biomass of all species; x_i is the mass-specific metabolic rate; e_{ij} is the energy conversion efficiency of species i for biomass from species j ; y_{ij} is a measure of the maximum rate at which species i ingests species j per unit metabolic rate of species i ; and α_{ij}

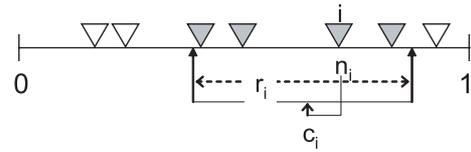


Fig. 1. Niche model diagram. The niche model [17,26,43–45,47] hypothesizes that food-web structure is a result of a particular arrangement of a one-dimensional community niche space where all species and their diets are located. S (trophic species richness, here $S = 7$, each shown by inverted triangles) and C (connectance) are set at the observed values for the empirical web being modeled. The niche model assigns each of S species a uniformly random “niche value” $0 \geq n_i \geq 1$ that establishes each species’ location in the community niche. Each species is then assigned a beta distributed feeding range $0 \geq r_i \geq 1$ with a mean equal to connectance ($C = L/S^2$). Each i th species consumes all species within their r_i which is placed completely on the niche by choosing a uniformly random center (c_i) of the range between $r_i/2$ and $\min[n_i, 1 - (r_i/2)]$. The species with the lowest n_i is assigned $r_i = 0$ so that each “niche web” has at least one basal species. All other species that happen to eat no other species are also basal species.

is the relative preference of species i for species j , normalized so that $\sum_j \alpha_{ij} = 1$ for consumer species and is zero for producer species. $F_{ij}(B)$, the non-dimensional functional response, gives the fraction of the maximum ingestion rate of predator species i consuming prey species j and is a function of the biomass of the various species. The many parameters in these equations have been estimated from empirical measurements [9] and there are wide ranges of biologically plausible values.

The growth rate is

$$G_i(B) = r_i B_i(t) (1 - B_i(t)/K_i), \quad (2)$$

where r_i is the intrinsic growth rate and K_i is the carrying capacity. There is no competitive exclusion among basal species in systems with more than one producer species.

The functional response of predator i and prey j is

$$F_{ij}(B) = \frac{B_j(t)^{1+q_{ij}}}{\sum_{k=1}^n \alpha_{ik} B_k(t)^{1+q_{ik}} + B_{0ji}^{1+q_{ij}}} \quad (3)$$

where B_{0ji} is the half saturation density of species j when consumed by species i and the parameter q_{ij} controls the form of the functional response (Fig. 2). When $q_{ij} = 0$, the response is the standard Holling type II response [12] used in many earlier studies [7–11] and is a linear response when the prey density B_j is small that saturates to a constant when B_j is large. Increasing q_{ij} alters the type II response [27,28] to become the sigmoidal type III response [9,29,30] when $q_{ij} = 1$. Type III responses have previously been shown to stabilize two-species systems [9,29,30], but intermediate functional responses with variable q and the role of type III responses in larger systems have not been explored before.

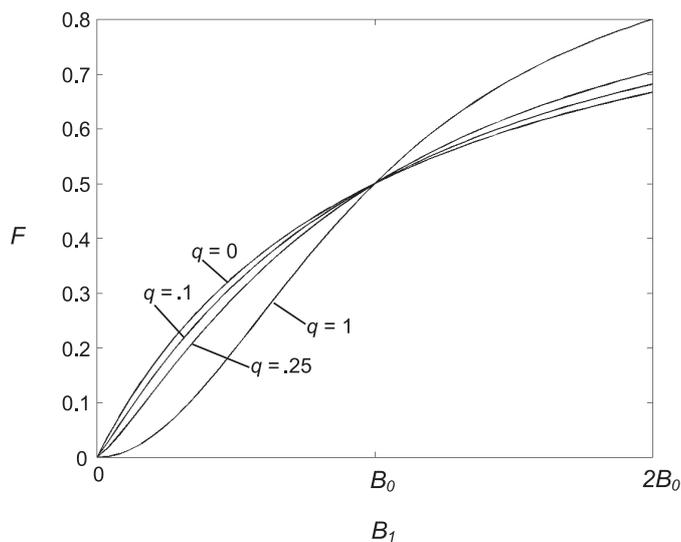


Fig. 2. Single species type II ($q = 0$), modified type II ($q = 0.1, 0.25$) and standard type III ($q = 1$) functional responses.

3 Results and discussion

There is a range of biologically reasonable parameters over which a simple three species food chain with type II functional responses has chaotic dynamics [11]. In order to more clearly build upon the foundations of earlier work, we use the same parameter set used in recent investigations of the effects of omnivory and interaction strength on food web stability [6,7]. In this three species system, increasing q to make both links type “II.2” responses ($q_{21} = q_{32} = 0.2$, Fig. 2) causes a dramatic change in the system’s dynamics (Fig. 3). As q increases, the system quickly stops being chaotic before $q = 0.05$ and then passes through period-doubling reversals and the stabilization of limit cycles, eventually reaching a stable stationary solution when $q \approx 0.2$. Note that the form of the functional response (Fig. 2) changes very little as the system moves from chaotic to stable solutions.

Allowing different links to have different functional responses shows that locating the more stabilizing functional response higher in the food chain leads to more stability than locating it lower in the chain. When only the link from the top species to the intermediate species is the modified type II response ($0 < q_{32} < 0.5$, $q_{21} = 0$, Fig. 4a), overall the behavior of the systems is virtually identical to when both links are modified type II responses (Fig. 3). When only the link from the intermediate species to the producer species is a modified type II response ($0 < q_{21} < 0.5$, $q_{32} = 0$, Fig. 4b), the chaotic system becomes doubly periodic as q initially increases but the system becomes chaotic again at $q > 0.4$.

The system (1-3) has a large number of free parameters, which is convenient for matching the dynamics to a range of biological conditions but is inconvenient when trying to understand the general behavior of systems with a large number of species. For general understanding, it helps to make some simplifying assumptions about the parameter values while maintaining biologically realistic

values. We studied a ten-species system with the growth rate and carrying capacity of all producer species equal to one, and used equal biomass conversion efficiencies for all species and identical responses for all interactions ($r_i = K_i = 1$, $e_{ij} = e$ and $q_{ij} = q$). The topology and diet preferences α_{ij} of this system are shown in Figure 5. This network is constrained by several empirical patterns. Its connectance ($C = L/S^2$) of 0.14 is close to the middle of its commonly observed range [20]. The network topology was generated by the empirically successful niche model (Fig. 1 [26]) and the diet preferences emphasize energy flow along the energetically predominant short chains to basal species [31–33].

The results of running this system over a range of q is shown in Figure 6. As in the three species system, there is a drastic change in the system’s dynamics over a small range of q but q stabilizes the 10-species system at a 50% higher value (0.3) than in the 3 species system (Fig. 3). As q is lowered, the system becomes unstable, passes through a number of bifurcations and eventually becomes chaotic when $q \approx 0.2$. When $q \approx 0.09$ species 6 and 10 go extinct, followed by species 9 at $q \approx 0.06$, so that when $q = 0$, there is no solution, stable or chaotic, in which all ten species are present. The extinctions eliminate the two top species of the original network, eliminate omnivory and lower the maximum trophic level from just over four to three.

As q decreases in the chaotic area of Figure 6, the minimum biomass of most species also drops and eventually becomes very close to zero. These very low minimum populations are thought likely to go extinct and biologically reasonable solutions are thought to be bounded some “healthy” distance away from zero to maintain “persistent chaos” [9,11]. If species in non-persistent chaos go extinct, extinctions would be more prevalent and occur at higher values of q than discussed above for the 10-species system shown in Figure 5.

Ten-species systems with different network topologies and sets of parameter values were tried. It was easy to find parameter values that gave a permanent stationary solution when $q = 0.5$. All of these permanent systems showed similar behavior as q decreased, becoming unstable and passing through limit cycles to chaos that was usually non-persistent for several species. In many cases, as shown in Figure 6, this progression continued to one or more extinctions.

Holling [12] introduced type II models ($q = 0$) as typical of invertebrate behavior and type III ($q = 1$) models as typical of vertebrates, but later empirical studies have shown the situation to be more complex. Type II responses are typical of mammalian herbivores [34,35], and are found in other vertebrate predators [36], while type III responses are found in invertebrates such as arthropod predators and parasitoids [30] and phytoplankton-consuming zooplankton [37,38]. It appears that the responses examined here that are intermediate between type II and III have not been formally examined. However, our informal surveys of data and the literature suggest that our type II.1, II.2, and II.3 responses fit many data as well as standard type II responses. Therefore, we

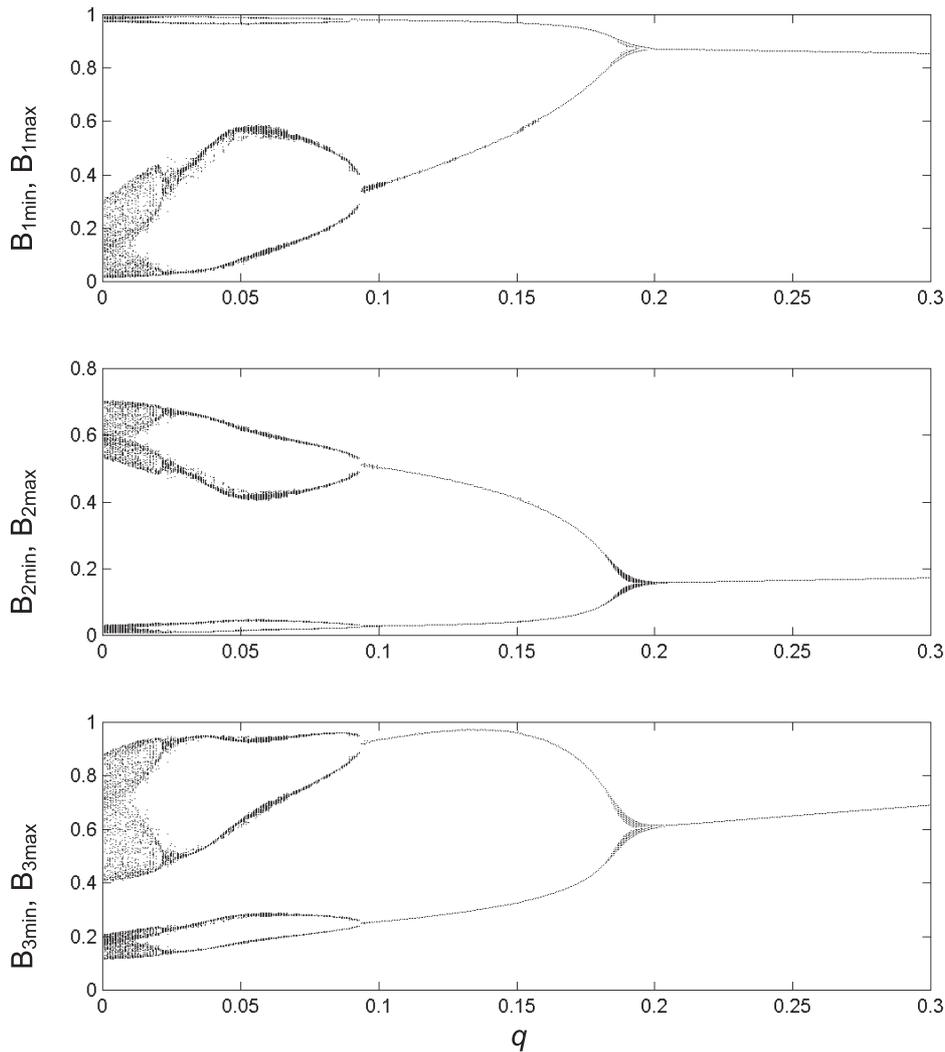


Fig. 3. Local minima and maxima for each species in a simple three-species food chain for a range of values of q . Species 1, 2 and 3 are the basal (producer), intermediate, and top species respectively. The non-zero parameter values are $x_1 = 0.4$, $x_2 = 0.08$, $y_{21} = 2.09$, $y_{32} = 5$, $\alpha_{21} = 1$, $\alpha_{32} = 1$, $e_{ij} = 1$, $r_1 = 1$, $K_1 = 1$, $B_{012} = 0.16129$, $B_{023} = 0.5$.

feel that our intermediate responses have as much empirical support as do standard type II and III responses. A thorough review of existing empirical studies and possibly further empirical work are needed to determine the overall distribution and patterns of functional responses with respect to factors such as organism type (endotherm, ectotherm, vertebrate, invertebrate, etc.), diet type (herbivore, carnivore, specialist, generalist, degree of omnivory, etc.) or trophic level of predator or prey.

This brief overview of some empirical results shows that strong type III interactions have been found at all positions in food chains. Extrapolating from the results of the three species model with mixed functional responses to larger systems suggests that not all the interactions in larger systems need to be modified type II or type III for a chaotic or non-permanent type II system to be stabilized and that stabilization will be more effective if modified type II and type III links are high in the food chains. The

existing empirical data suggest that type III interactions are sufficiently common and widely distributed to play an important role in the stabilization of food webs, though much empirical and theoretical work is necessary to further assess this.

Most empirical studies only discern a fairly strong ($q \approx 1$) type III response, but the models explored here are stabilized at much smaller values of q (typically $q \approx 0.1-0.3$). Also, the dynamics are very sensitive to small changes in q in the transition from stable to chaotic dynamics. The difference between modified type II functional responses and a standard type II response is so slight that it is typically indistinguishable in available empirical data. The main difference occurs when the prey density is small and existing studies are not generally designed to closely examine functional responses in this range. New experimental approaches may be needed to detect these slight but dynamically significant variations in functional response.

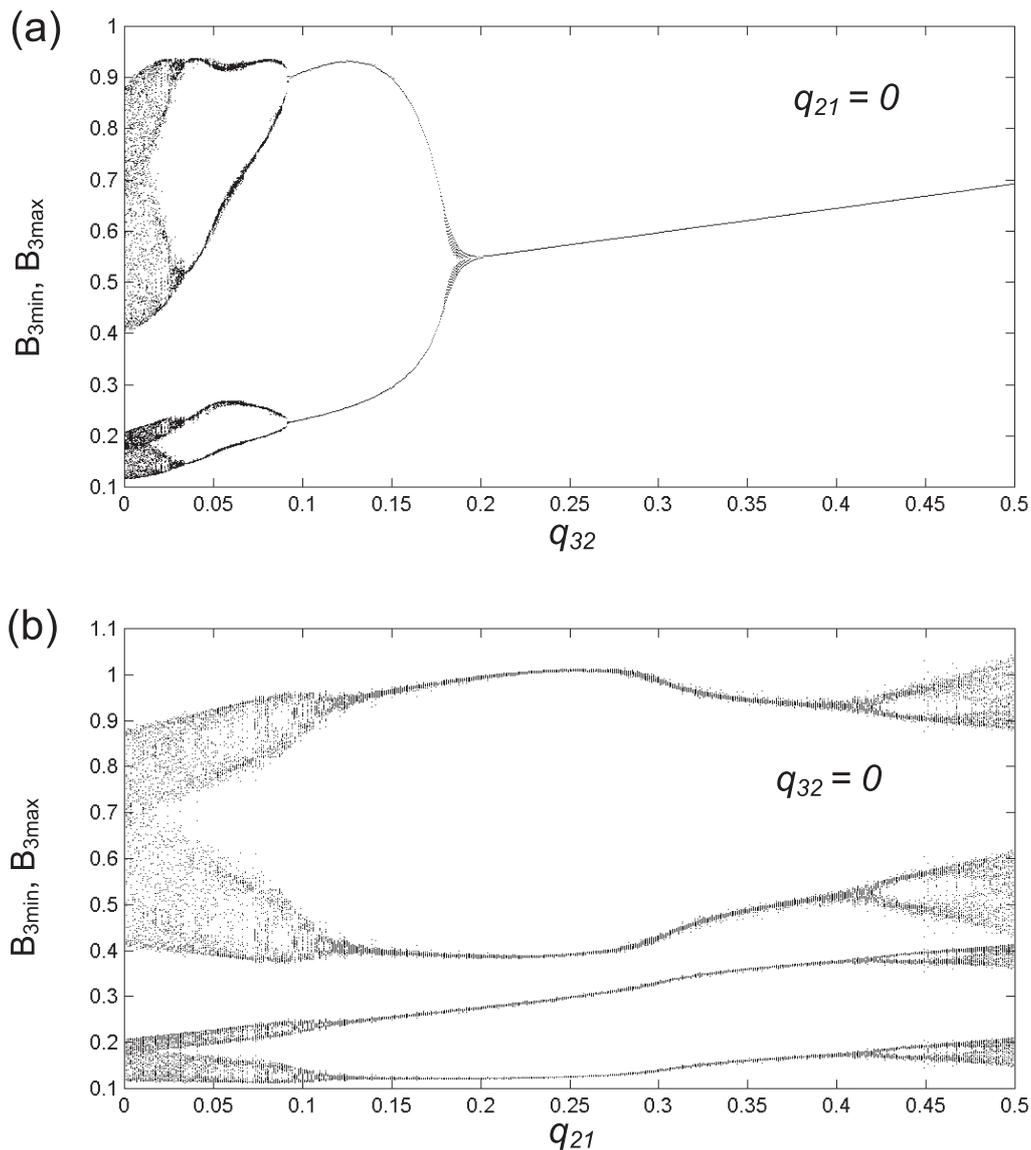


Fig. 4. Local minima and maxima for the top species in a simple three-species food chain with one type II link and one type III link. The non-zero parameter values are as in Figure 3: $x_1 = 0.4$, $x_2 = 0.08$, $y_{21} = 2.09$, $y_{32} = 5$, $\alpha_{21} = 1$, $\alpha_{32} = 1$, $e_{ij} = 1$, $r_1 = 1$, $K_1 = 1$, $B_{012} = 0.16129$, $B_{023} = 0.5$. (a) The link between the top and intermediate species has type III functional response. (b) The link between the intermediate species and the producer species has type III functional response.

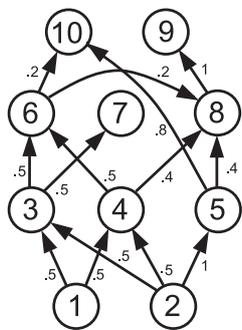


Fig. 5. Ten species network. Primary producers are at the bottom of the diagram (species 1 and 2) and arrows show the flow of biomass from prey to predator. The number by each arrow is α_{ij} where i is the predator and j the prey.

Stabilization of five-species system has previously been demonstrated in a model of two food chains linked by the top predator [39]. The model combines ratio-dependent prey switching and single-species type II functional responses to give an overall functional response with that is similar to a $q = 1$ type III functional response but with some predator-prey ratio dependence. Like the results presented here, this system sometimes has chaotic dynamics that can be stabilized by small changes in a parameter, in this case the prey-preference parameter. These findings imply that large ecological networks may have their stability increased by relatively subtle but specific changes in the direct interactions between network nodes that slightly change the functional response. However, like earlier findings on the role of omnivory [7] and weak

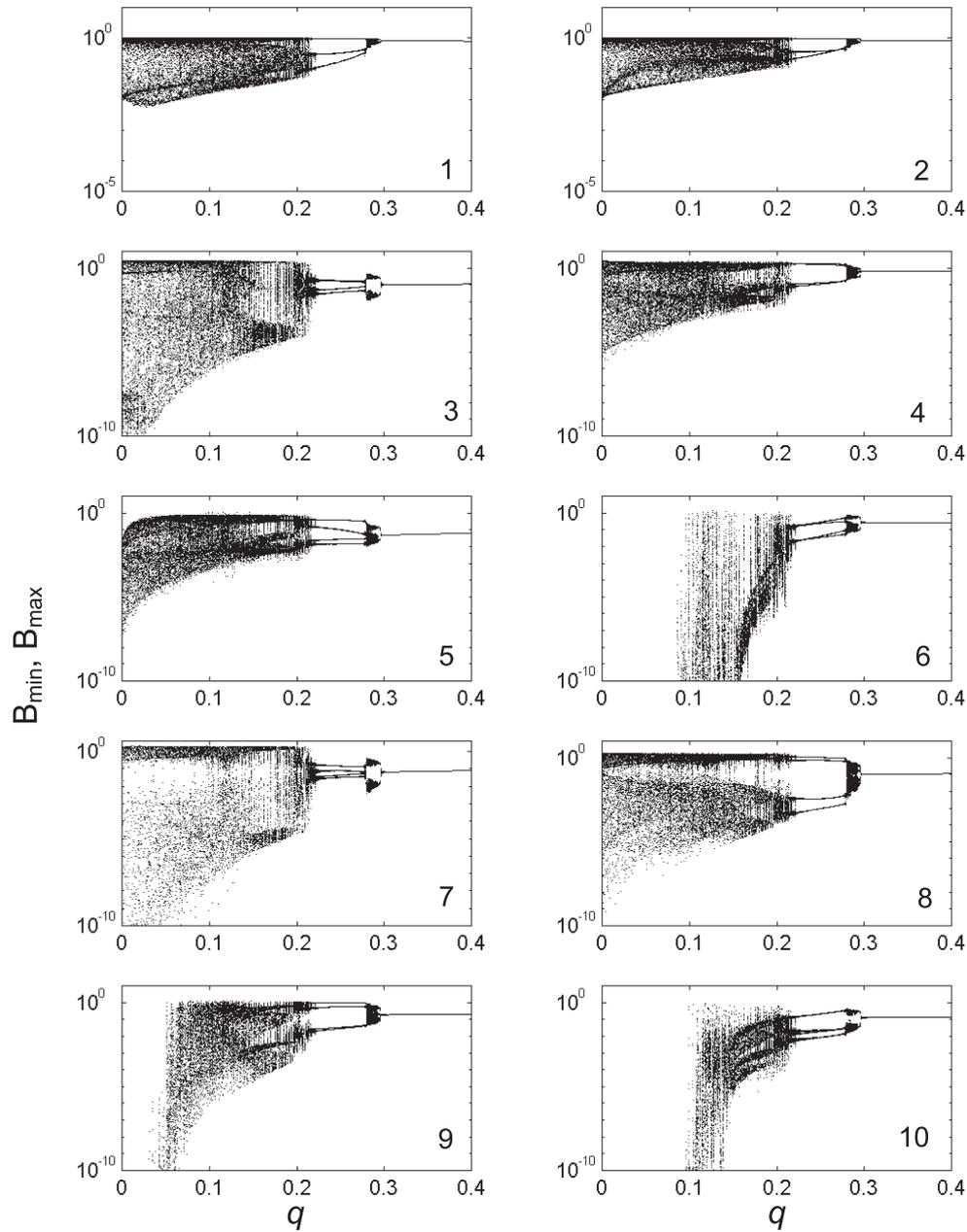


Fig. 6. Local minima and maxima for each species in the ten-species food web shown in Figure 5 for a range of values of q . Each panel is labeled with the species number; species 1 and 2 are the producer species. Note the use of a log axis to show in more detail the behavior of the minima. The non-zero parameter values are $x_{3-10} = 0.2$; $y_{ij} = 2.5$ for $i = 3 - 6$, $y_{ij} = 5$ for $i = 7 - 10$; $\alpha_{31} = \alpha_{32} = \alpha_{41} = \alpha_{42} = 0.5$, $\alpha_{51} = 1$, $\alpha_{63} = \alpha_{64} = 0.5$, $\alpha_{73} = 1$, $\alpha_{84} = \alpha_{85} = 0.4$, $\alpha_{86} = 0.2$, $\alpha_{98} = 1$, $\alpha_{10,5} = 0.8$, $\alpha_{10,6} = 0.2$; $e_{ij} = 1$; $r_1 = r_2 = 1$; $K_1 = K_2 = 1$; $B_{0ji} = 0.3$ for any i, j where $\alpha_{ij} > 0$.

interactions [8], this finding must be treated with caution. The sensitivity of the dynamics to slight changes in the functional responses makes it difficult to ascribe empirically observed patterns, for example in population fluctuations or food web structure, to specific dynamical mechanisms, especially in the face of both stochastic and chaotic variability in many extrinsic environmental factors.

To date, structural and dynamical studies of complex food webs have been very separate although this is beginning to change [40–42]. Structural studies have

tackled systems with large biodiversity, while many dynamical studies, particularly those with biologically based features such as non-linear functional responses, are typically restricted to systems with few species. The results presented here suggest that modified type II interactions stabilize complex food webs and permit the construction of dynamically persistent food webs over a much broader range of species and interaction parameters. This will allow the dynamics of much larger networks to be studied in a more empirically realistic manner, while remaining

dynamical constraints might provide insight into the origins of food web network topology. In particular, such insights should go far in explaining why food webs exhibit such predictably and precisely constrained structure [17, 18, 21, 26, 42–47].

Combining modified type II functional responses with the network topology of the niche model [26] enables dynamical analyses of large, realistically linked networks. The robustness of these models may form an effective foundation for including non-trophic effects such as nutrient dynamics and population migrations in rigorous models of ecological networks. Even without such extensions, the modeling framework described here should allow other important questions, such as the effects of topology, omnivory, interaction strength, indirect interactions, and extinctions [43] on network stability, to be studied in much larger systems than have been investigated so far.

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