

# **Stabilization of chaotic and non-permanent food web dynamics**

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**A long history of dynamical analyses of food-web networks<sup>1-6</sup> has led to important insights into the effects of complexity, omnivory and interaction strength on food-web stability<sup>6-8</sup>. Some recent insights<sup>7,8</sup> are based on nonlinear bioenergetic consumer-resource models<sup>9</sup> that display chaotic behavior in three species food chains<sup>10,11</sup> which can be stabilized by omnivory<sup>7</sup> and weak interaction of a fourth species<sup>8</sup>. By altering these models to slightly relax predation on low-density prey (changing from type II to weak type III functional response<sup>12</sup>), we drastically alter the dynamics of systems containing up to ten species. Our model stabilizes chaotic dynamics in three species systems and reduces or eliminates extinctions and non-persistent chaos<sup>11</sup> 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 suggests that this response is a crucial aspect of species interactions that must be more precisely addressed in empirical studies.**

We use a bioenergetic consumer-resource model of the time evolution of species biomass that follows previous work<sup>7-9,11</sup> but is generalized to  $n$  species and arbitrary functional responses. Extending the earlier notation<sup>9</sup> to  $n$ -species systems, the variation of  $B_i$ , the biomass of species  $i$ , is given by

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

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 assimilation efficiency of species  $i$  for 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  $\alpha_{ij}$  is the relative preference of species  $i$  for species  $j$ , normalized so that  $\sum_j \alpha_{ij} = 1$  for predator 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<sup>9</sup> 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 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. When  $q_{ij} = 0$ , the response is the Holling type II response<sup>12</sup> used in many earlier studies<sup>7-11</sup> and is a linear response when the prey density  $B_j$  is small that saturates to a constant when  $B_j$  is large. Positive  $q_{ij}$  gives a generalization<sup>13,14</sup> of the usual ( $q_{ij} = 1$ ) sigmoidal type III response<sup>9,15,16</sup>. Type III responses with  $q = 1$  have previously been shown to stabilize two-species systems<sup>9,15,16</sup>, but type III functional responses with variable  $q$  and their role in larger systems have not been explored before.

There is a range of biologically reasonable parameters over which a simple three species food chain with type II functional responses has chaotic dynamics<sup>11</sup>, and from this range, we use the same parameter set used in recent investigations of the effects of omnivory and interaction strength on food web stability<sup>6,7</sup>. In this three species system, making both links weakly type III ( $q_{21} = q_{32} = q > 0$ , figure 3) causes a dramatic change in the system's dynamics. As  $q$  increases, the system quickly stops being chaotic and then passes through period-doubling reversals and the stabilization of limit cycles, eventually reaching a stable stationary solution when  $q \approx .2$ . 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 either type II or III functional responses shows that locating the type III interaction 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 type III ( $q_{32} > 0$ ,  $q_{21} = 0$ , figure 3a), the period doubling bifurcations actually occur at very slightly lower  $q_{32}$  than when both links are type III (figure 1), but overall the behavior of the system is virtually identical. When only the link from the intermediate species to the producer species is type III ( $q_{21} > 0$ ,  $q_{32} = 0$ , figure 3b), as  $q$  increases, the chaotic system becomes doubly periodic for a range of  $q$  but as  $q$  increases further the system becomes chaotic again.

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 use equal assimilation efficiencies for all species and equal type III responses for all interactions ( $r_i = K_i = 1$ ,  $e_{ij} = e$  and  $q_{ij} = q$ ).

The topology and diet preferences  $\alpha_{ij}$  of this system are shown in figure 4. This network is constrained with a number of features supported by empirical observations. The system has a connectance ( $C = L/S^2$ , where  $L$  is the number of links and  $S$  the number of species) of .14<sup>17</sup>, the network topology conforms to the constraints of the niche model<sup>18</sup> and the diet preferences emphasize energy flow along short chains to basal species<sup>19,20</sup>.

The results of running this system over a range of  $q$  is shown in figure 5. As in the three species system, there is a drastic change in the system's dynamics over a small range of  $q$ . When  $q > .3$ , the system has a stable solution. As  $q$  is lowered, the system becomes unstable, passes through a number of bifurcations and eventually becomes chaotic when  $q \approx .2$ . When  $q \approx .09$  species 6 and 10 go extinct, followed by species 9 at  $q \approx .06$ , 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 to three.

As  $q$  drops in the chaotic regime 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"<sup>9,11</sup>. If species in non-persistent chaos go extinct, extinctions would be more prevalent and occur at high values of  $q$  than discussed above for the 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  $q = .5$ . All of these permanent systems had similar behavior as  $q$  decreases, becoming unstable and

passing through limit cycles to chaos that was usually non-persistent for several species. In many cases, as shown here, this progression continued to one or more extinctions.

Holling<sup>12</sup> introduced type II models 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<sup>21,22</sup>, and are found in other vertebrate predators<sup>23</sup>, while type III responses are found in invertebrates such as arthropod predators and parasitoids<sup>16</sup> and phytoplankton-consuming copepods<sup>24</sup>. A thorough review of existing empirical studies and possibly further empirical work is needed to determine the overall rate of type III interactions and to look for patterns in functional response with factors such as diet type (herbivore vs. carnivore, specialist vs. generalist, degree of omnivory) 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 type III for a chaotic or non-permanent type II system to be stabilized and that stabilization will be more effective if the 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 a role in the stabilization of food webs, though much empirical and theoretical work is necessary to further assess this.

Most empirical studies can 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  $q \approx .1 - .3$ ). Also, the dynamics are very sensitive to small changes in  $q$  in the transition from stable to chaotic dynamics. The difference between this weakly type III functional response and a 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.

Stabilization of five-species system has previously been demonstrated in a model of two food chains linked by the top predator<sup>25</sup>. 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, this time 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<sup>7</sup> and weak interactions<sup>8</sup>, this 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 food web studies have been very separate. Structural studies have tackled systems with large biodiversity, while many dynamical studies, particularly those with biologically based features such as non-linear functional responses, have been restricted to systems with few species. The results presented here suggest that type III 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, while remaining dynamical constraints might provide insight into the origins of food web network topology. Combining weak type III functional response with the network topology of the niche model<sup>18</sup> enables dynamical analyses of large, realistically linked networks. This will allow other important questions, such as the effects of omnivory, interaction strength and indirect interactions on network stability, to be studied in much larger systems than have so far been investigated.

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### Figure Captions

Figure 1. Local minima and maxima for each species in a three-species food chain for a range of values of  $q$ . Species 1 is the producer. The non-zero parameter values are  $x_1 = .4$ ,  $x_2 = .08$ ,  $y_{21} = 2.09$ ,  $y_{32} = 5$ ,  $\alpha_{21} = 1$ ,  $\alpha_{32} = 1$ ,  $e_{ij} = 1$ ,  $r_1 = 1$ ,  $K_1 = 1$ ,  $B_{012} = .16129$ ,  $B_{023} = .5$ .

Figure 2. Single species type II ( $q = 0$ ), weak type III ( $q = .25$ ) and standard type III ( $q = 1$ ) functional responses.

Figure 3. Local minima and maxima for the top species in a three-species food chain with one type II link and one type III link. The non-zero parameter values are as in figure 3:  $x_1 = .4$ ,  $x_2 = .08$ ,  $y_{21} = 2.09$ ,  $y_{32} = 5$ ,  $\alpha_{21} = 1$ ,  $\alpha_{32} = 1$ ,  $e_{ij} = 1$ ,  $r_1 = 1$ ,  $K_1 = 1$ ,  $B_{012} = .16129$ ,  $B_{023} = .5$ . (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.

Figure 4. 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  $\alpha_{ij}$  where  $i$  is the predator and  $j$  the prey.

Figure 5. Local minima and maxima for each species in the ten-species food web shown in figure 4 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  $x_{3-10} = .2$ ;  $y_{ij} = 2.5$  for  $i = 3-6$ ,  $y_{ij} = 5$  for  $i = 7-10$ ;  $\alpha_{31} = \alpha_{32} = \alpha_{41} = \alpha_{42} = .5$ ,  $\alpha_{51} = 1$ ,  $\alpha_{63} = \alpha_{64} = .5$ ,  $\alpha_{73} = 1$ ,  $\alpha_{84} = \alpha_{85} = .4$ ,  $\alpha_{86} = .2$ ,  $\alpha_{98} = 1$ ,  $\alpha_{10,5} = .8$ ,  $\alpha_{10,6} = .2$ ;  $e_{ij} = 1$ ;  $r_1 = r_2 = 1$ ;  $K_1 = K_2 = 1$ ;  $B_{0ji} = .3$  for any  $i,j$  where  $\alpha_{ij} > 0$ .

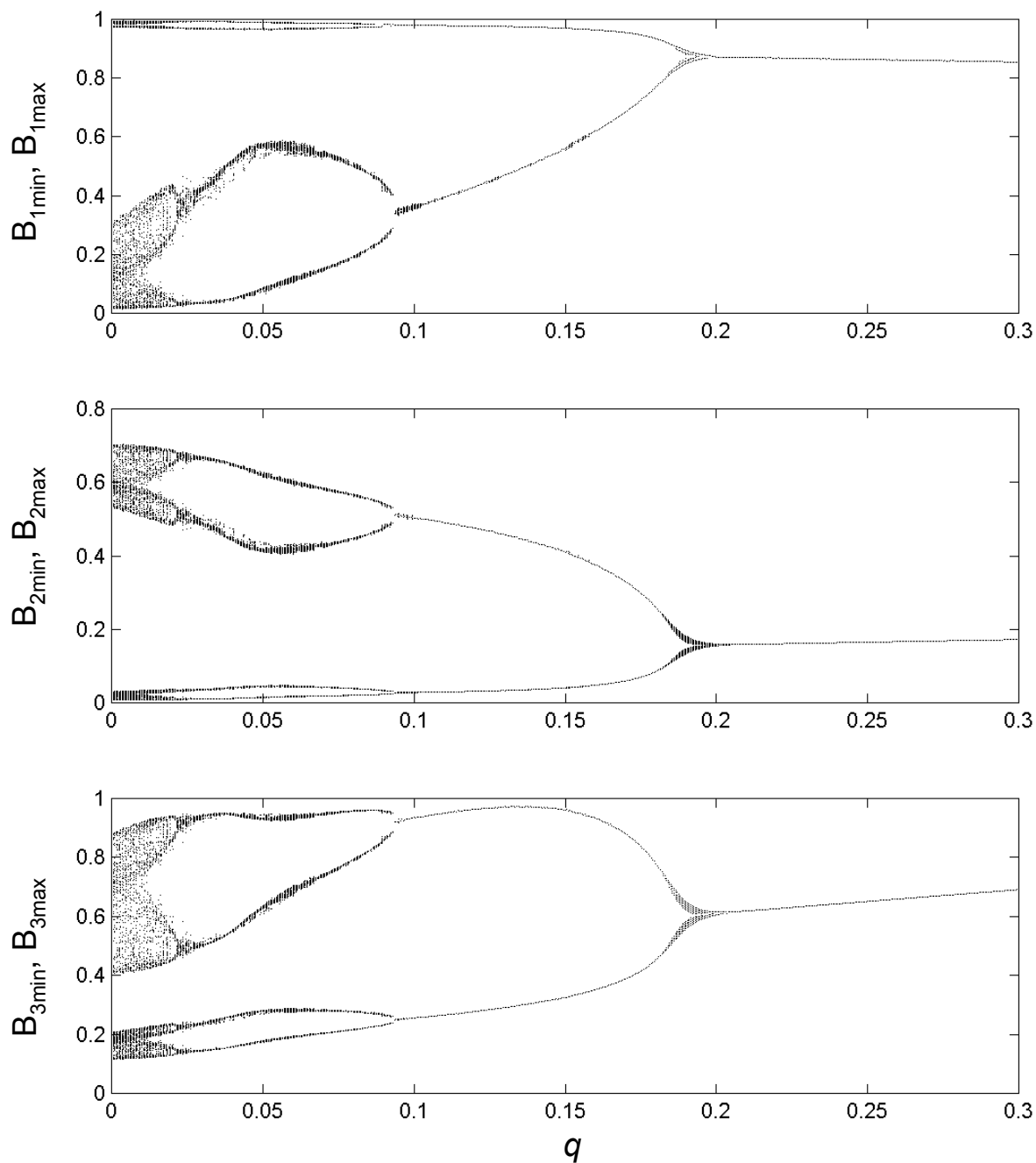


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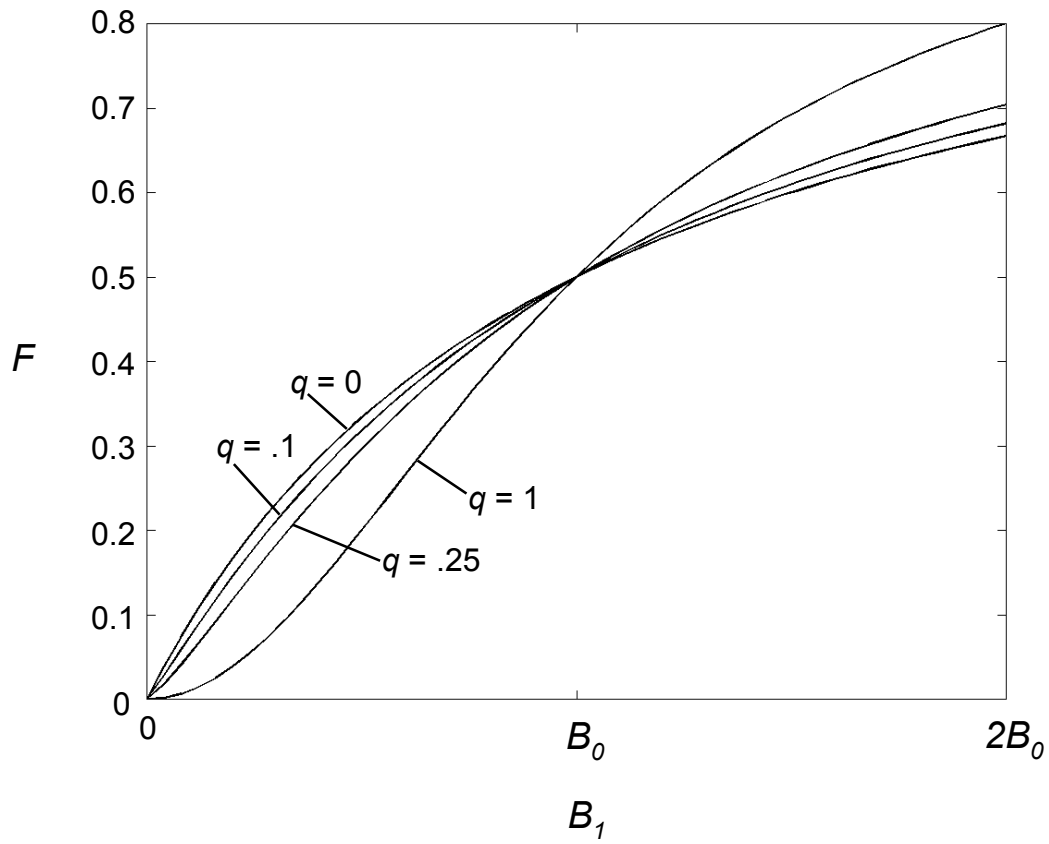


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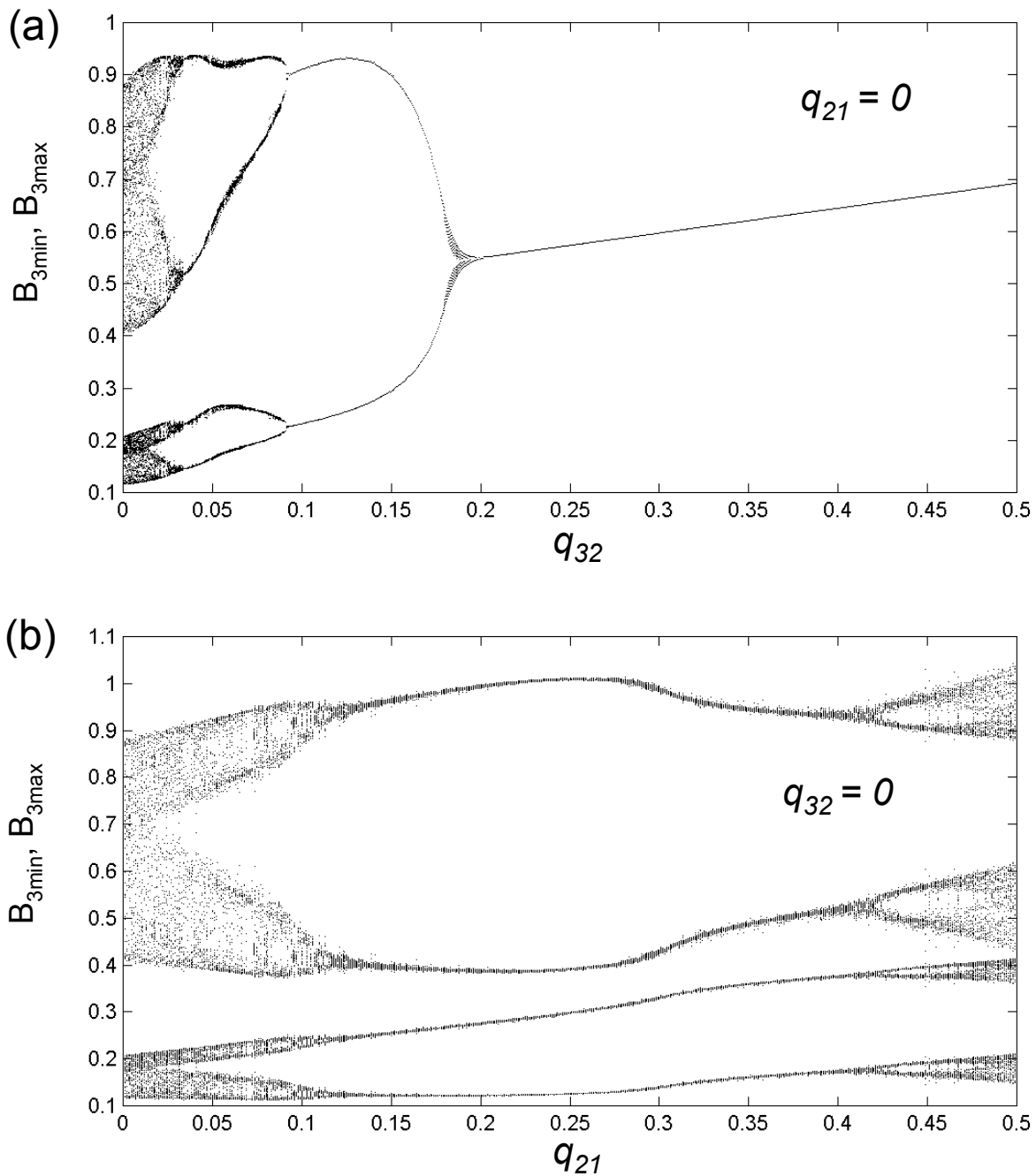


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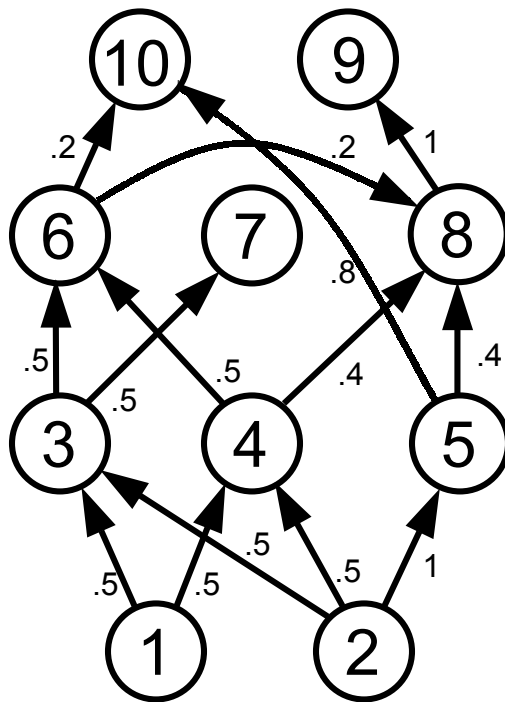


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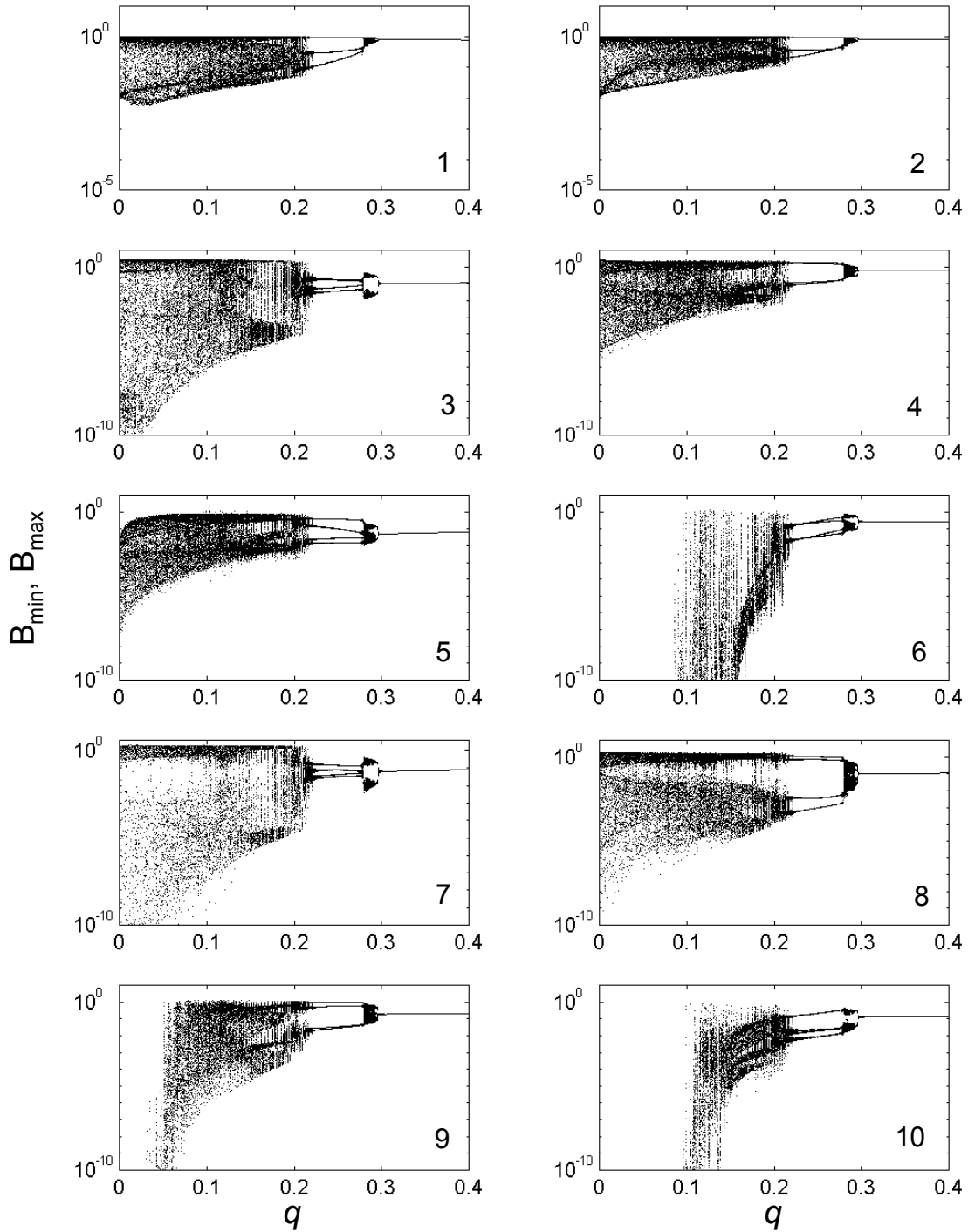


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