

Chapter 1

Chaotic dynamics in food web systems

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It is a long-standing debate among ecologists whether chaotic dynamics are likely to occur in food web systems. Simple mathematical models predict frequent chaotic dynamics for food webs of relatively low complexity suggesting that the long-term dynamics of natural populations could be essentially unpredictable. This result is at odds with observations from the field where chaos appears to be rare. In this contribution I review the evidence for chaotic dynamics from mathematical food web models of varying complexity. I argue that mathematical models which allow for the specific structural properties of natural food webs are more likely to predict realistic patterns of chaos and stability in field and experimental food webs.

1.1. Introduction

Food webs are networks that reflect the feeding relationships among ecological populations. Food webs are a biological reality because many populations of species coexist as a community in a confined space - the ecosystem - and predator-prey relationships are an important type of interaction among them. Trophic (= feeding) interactions in food webs directly determine the populations' vital rates, i.e. their growth rates (when they consume prey) and their mortality (when they are being consumed). "Food web" is also an expression for a type of conceptual model that ecologists use to describe real food webs, usually in the form of topological graphs in which the nodes represent the populations and the edges the feeding relationships. Such food webs are always simplifying, incomplete representations of the real world because (1) it is virtually impossible to determine all the feeding relationships in a complex ecological network and because (2) they disre-

gard non-trophic properties of populations and non-trophic interactions¹ that exist among populations. Such properties and interactions include animal behavior, plant dispersal,² direct competition, and chemical or social interactions. Nonetheless, food web models serve an important purpose in ecology in that they are a structured attempt to analyze the topological and dynamical properties of ecological communities and can, in principle, be extended to account for non-trophic properties.

Topological food web models have been traditionally used to predict patterns of species abundance, biomass distribution and energy flow in real food webs. Indeed, some ecological key concepts are direct logical derivations from conceptual food chain models (food chains are special food webs in which predators cannot have more than one prey). One example is the response to enrichment across a food chain that consists of multiple trophic levels. The prediction here is that, as biomass production increases at the basal trophic level (enhanced primary productivity in ecological terms), this biomass will eventually end up at the top trophic level and every second level down.^{3,4} This follows intuitively from the fact that the top level is not controlled by predation but controls the next level down. This effect percolates down the food chain as a “trophic cascade”, decreasing even-numbered levels down from the top but benefiting odd-ones. This view of the “enrichment response” continues to be a popular concept in ecology although no convincing examples from the field exist.⁵ The two major reasons for this lack of evidence are probably: (1) Real food webs encompass several trophic levels but hardly ever exist as true chains. In more complex networks, however, prediction of the biomass distribution is non-trivial because it involves balancing direct and indirect effects across trophic levels and different branches of the food web. (2) Dynamical versions of food chain models show that the described patterns of biomass distribution can only be expected for food chain communities that coexist at stable equilibria (Fig. 1.1), an assumption that can hardly be upheld, as I will show in this chapter.

Fig. 1.1 also demonstrates that the community dynamics in food webs can be highly nonlinear and that an analysis which is restricted to equilibrium states necessarily delivers an incomplete picture of the dynamical patterns in multi-species assemblages. Therefore, ecological modelers are challenged to expand the dynamical analysis of coupled populations beyond the classical two-species analyses of Lotka and Volterra⁶ and their refinements in the 1960s (notably by Rosenzweig and MacArthur⁷) and, at the same time, to allow for the full range of dynamical behavior present

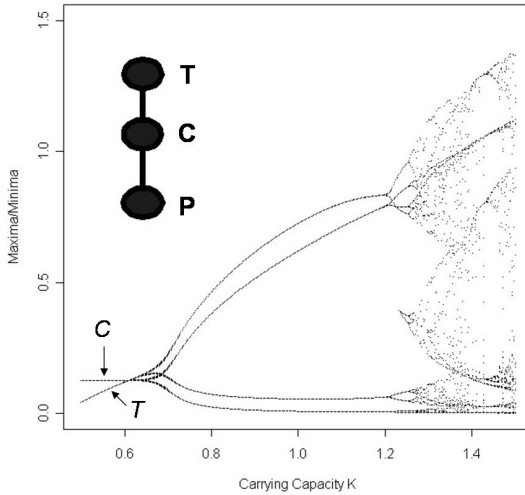


Fig. 1.1. Bifurcation diagram of a tri-trophic food chain with enrichment (increasing carrying capacity K). Plotted are the minima and maxima of computer simulated time series in the interval $[750, 1000]$ of the top-predator (T) and consumer (C) populations, respectively. For $0.5 \leq K \leq 0.7$ the model predicts equilibrium dynamics and T increases linearly with K while C remains unchanged, as predicted by classical food chain theory. With enrichment beyond $K \approx 0.7$ the model predicts complex (limit cycle and chaotic) dynamics and no monotonous relationships exist between the population extrema or averages (not shown) and the value of enrichment. The inset shows the topological graph of a tri-trophic chain. Parameterization of ODE system Eqs. (1.1 and 1.2): $r = 2.5$; $a_C = 7.5$; $b_C = 5.0$; $a_P = 1.0$; $b_P = 2.0$; $e_C = e_P = 1$; $m_C = 1.0$; $m_P = 0.1$.

in these more extensive models. Most of these analyses need to be performed in the form of computer simulations since general three- or higher dimensional systems of differential equations defy graphical or analytical methods. Not surprisingly, two three-species structures were historically the first model food networks for which theoretical ecologists undertook such a dynamical analysis: a predator population coupled to two different prey populations^{8,9} and the tri-trophic food chain which couples two predator-prey systems vertically^{10,11} (Fig. 1.1).

Both of these trophic structures display a rich inventory of dynamical behavior: equilibria and stable limit cycle oscillations (which occur also in lower-dimensional system) but also quasi-periodicity and deterministic chaos (see Fig. 1.1, $K \geq 1.3$). Chaotic oscillatory dynamics, characterized

by sensitivity to initial conditions, are a constant source of concern to the ecologist whose aim it is to understand and predict the change of species abundances over time. Ever since Robert May demonstrated the possibility of chaos in a single-population discrete-time model system¹² ecologists must accept that the long-term forecast of population densities may be, in principle, an unachievable task.

Whether chaotic dynamics are detrimental to the long-term persistence of ecological communities is an unresolved problem. It would seem that the unpredictable population fluctuations that go along with chaotic dynamics should be maladaptive because they make populations more likely to become extinct.¹³ However, in spatially extended model communities, coupled through dispersal, chaotic dynamics have been shown to promote global persistence of the system by desynchronizing the dynamics among local communities.^{14,15} Thus, ecological scenarios are conceivable under which evolution would favor chaotic food webs.

With chaos also occurring in the simplest continuous-time models (the Poincaré-Bendixson theorem forbids its occurrence below dimension three¹⁶) we now need to study how prevalent chaotic dynamics are in food webs and whether their frequency is related to any properties of the whole food web or its components. This chapter attempts to give an overview over recent developments and results in the analysis of chaos in dynamic food web models and finishes with a brief excursion into laboratory studies that use real organisms to explore nonlinear population dynamics.

1.2. Food web model formulation

The first step in the analysis of food web models is to find a mathematical formulation that adequately represents nodes and edges of the food web graph and is, at the same time, a realistic description of the interaction that occurs between predator and prey populations. Second, parameter values used in such a model should be realistic when compared to those of natural communities. Third, the predictions of the model should be, in general, interpretable as time-series produced by living organisms. For instance, excessively rapid population increases of non-microbial organisms or recovery from infinitesimally small population sizes are biologically questionable results. Finally, if the modeler attempts to simulate a concrete example of natural community dynamics, the fit of the observed to the simulated data is an obvious criterion for the quality of the model.¹⁷⁻¹⁹

Systems of coupled ordinary differential equations (ODEs) with one

state variable per population appear to be the most popular choice for food web models although coupled difference equations have been used to describe the dynamics resulting from the interaction among the different stages of an insect population.^{20,21} ODEs are probably preferable in food webs because, in general, it will be impossible to define a discrete time step that is common to all populations in the network. One should, however, keep in mind that the assumption of continuous and immediate consumption, reproduction and interaction implicit in these models is an idealization hardly ever met by real food webs (some plankton communities in lakes and oceans are the closest equivalents).

The bottom level of the food web usually consists of one or several resource populations, i.e. primary producers that require no food populations in order to grow. Because the lowest level in the food web lacks control through food availability, population regulation is achieved by assuming density-dependent logistic growth. (An alternative is to explicitly model limitation by a mineral resource, as it happens in some ecosystem models²² or simulations of real laboratory microbial systems^{23,24}).

Populations at the next trophic level up (herbivores) consume populations at the bottom level and reproduce according to a linear function of food uptake. It is also customary to assume density-independent mortality (which, for the bottom level, is already incorporated in the logistic growth term). Higher trophic levels are modeled in analogy to the herbivore level. For the tri-trophic food chain we formulate:

$$\begin{aligned}\frac{dR}{dt} &= rR \left(1 - \frac{R}{K}\right) - CF(R) \\ \frac{dC}{dt} &= e_C CF(R) - PF(C) - m_C C \\ \frac{dP}{dt} &= e_P PF(C) - m_P P,\end{aligned}\tag{1.1}$$

where R , C , P are the abundance or biomass of the resource, primary consumer, and secondary consumer populations; r is the intrinsic growth rate and K the carrying capacity of the resource; e_C and e_P are the conversion efficiencies across trophic levels; m_C and m_P are the density-independent mortalities. $F(R)$ and $F(C)$ are the functional responses of the consumers that describe the uptake of prey by the predator as a function of prey density. More recent analyses use a ‘‘Holling type-2’’ functional response²⁵ which increases monotonously but saturates with increasing prey density:

$$F(R) = \frac{a_R R}{1 + b_R R}; \quad F(C) = \frac{a_C C}{1 + b_C C}.\tag{1.2}$$

Here, a and b are parameters that are specific for each predator-prey system and determine the saturation level and the steepness of the response. Alternative mathematical formulations exist for type-2 responses and in some studies type-2 responses are replaced by type-1 (piecewise linear) or type-3 (sigmoid) responses. Theoretical ecologists are only beginning to understand how some of these different functional responses affect the dynamics of simple²⁶ and complex²⁷ food web architectures.

By using the introduced building block method food chain ODE systems of any length can be constructed. For the formulation of food webs, however, we need to specify how the nonlinear (type-2 or type-3) response is to be distributed if one predator feeds on more than one prey population. Simply summing up the functional response terms is not a solution because this leads to inconsistent equations when the prey populations are assumed identical.²⁸ The following n -species functional response is most widely used because it retains the concept of satiating predator uptake and collapses to the one-prey equation for the two cases $R_1 = R_2 = \dots = R_n$ and $R_1 > 0 \wedge R_2 = R_3 = \dots = R_n = 0$:

$$F(R_1, \dots, R_n) = \frac{\sum_{i=1}^n a_{R_i} R_i}{1 + \sum_{i=1}^n b_{R_i} R_i}. \quad (1.3)$$

Parameters are defined as above. Fig. 1.2 shows the multi-species functional response for the case $n = 2$.

This modeling framework enables us to formulate, simulate and analyze food web models of any desired degree of complexity. The framework can also easily be extended to accommodate additional properties of natural food webs. The most important extension is probably the introduction of omnivory, the capability of a predator to feed on more than one trophic level. This is simply accomplished by allowing the prey species R_i in Eq. (1.3) to belong to any trophic level (and even to be the predator species itself, in the case of cannibalism). Model realizations of the following specific food web properties can be found by consulting the cited references: omnivory,^{29–32} type-3 functional responses,²⁷ allochthonous input of biomass,³³ nutrient recycling,^{22,34} density-dependence of not just the primary producer level,³⁵ inducible defensive structures in the prey,³⁶ mixotrophy³⁷ (the same species may be an autotrophic primary producer or a heterotrophic predator), availability of alternative prey,¹⁷ prey preference^{38,39} and adaptive foraging of the predator.⁴⁰

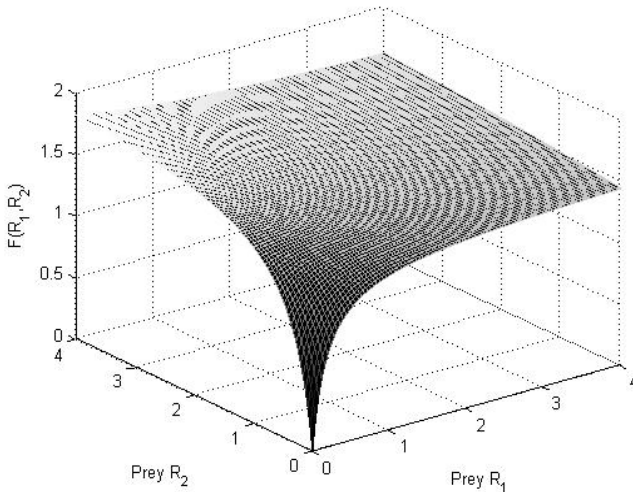


Fig. 1.2. Multi-species Holling type-2 functional response for two prey species R_1 and R_2 . $F(R_1, R_2)$ denotes the uptake of prey by a predator feeding simultaneously on both prey populations. Note that for $R_1 = 0$ and for $R_2 = 0$, respectively, the single-species Holling type-2 response emerges, while the function interpolates elsewhere. $a_{R_1} = 7.5$; $b_{R_1} = 5.0$; $a_{R_2} = 5.0$; $b_{R_2} = 2.5$.

1.3. Detecting and quantifying chaotic dynamics in model food webs

Mathematical ecologists interested in assessing the degree to which complex food web topologies are chaotic face two particular challenges. First, they need to find a representative sample of parameter combinations for the numerical analysis and, second, an efficient method is required for assessing whether any given parameter combination leads to chaotic dynamics.

With increasing complexity food web models are subject to an inflationary increase of parameters since the number of possible links increases with the square of the number of species (= state variables). It is usually impossible to perform a simultaneous numerical analysis for more than a few parameters whose values vary over wide ranges; all other parameters need to assume fixed values. Another problem encountered is the enormous separation of timescales that exists among the demographic parameters of species found in natural food webs, which can lead to stiff systems of differential equations. This being said, in the majority of studies only one parameter value is continuously changed and the dynamics are represented

graphically in the form of a bifurcation diagram (e.g. Fig. 1.1). This method allows rapid analysis of a target parameter but there is normally no a priori assumption that no other parameters can be subject to change at the same time, which would have unknown consequences for the dynamical patterns driven by the target parameter. There is no satisfying solution to this problem (unless a complete analysis can be performed) but, interestingly, Rinaldi et al.⁴¹ found qualitatively very similar bifurcation patterns for six population parameters which they analyzed separately in a predator-prey model with seasonal perturbation. If there is no particular parameter of interest it is advisable to concentrate on parameters with finite ranges set by the model assumptions. Fussmann & Heber,³⁰ for instance, restricted their food web analysis to the mortalities m_i . All m_i are non-negative by definition and any m_i exceeding the maximum growth rate of species i (as defined by the functional response) will necessarily lead to the extinction of this species. Thus the range to be analyzed for non-trivial dynamical behavior is confined between these boundaries.

Computation of the dominant Lyapunov exponent^{16,19} is the safest method to decide whether time series generated through numerical simulation are chaotic or not. A positive Lyapunov exponent indicates exponential divergence of nearby trajectories and thus directly quantifies sensitivity to initial conditions, the hallmark of chaotic dynamics. Advanced methods are available for the computation of Lyapunov exponents from time series,⁴²⁻⁴⁴ as generated by numerical simulation, laboratory experimentation, or field data collection (see Becks et al.⁴⁵ for an applied example). Chaotic dynamics can also be inferred from bifurcation diagrams (Fig. 1) or Poincaré maps.¹⁰ Although these methods have been widely used for the analysis of ecological model systems they can only serve as diagnostic tools for the detection of chaotic dynamics (chaotic and quasi-periodic dynamics, for instance, are not readily distinguished by these methods). Since these are graphical methods they also do not lend themselves to the quantification, comparison, and statistical analysis of large numbers of different food web model parameterizations.

Numerical computation of the Lyapunov exponents from time series can be time-consuming, especially because frequently thousands of parameter combinations need to be evaluated to obtain a highly resolved representation of the dynamical domains present in a particular food web model. In order to determine the relative frequency of the four general types of dynamics in food webs (trivial equilibrium with one or more populations equal to zero; stable equilibrium of all populations coexisting; stable limit

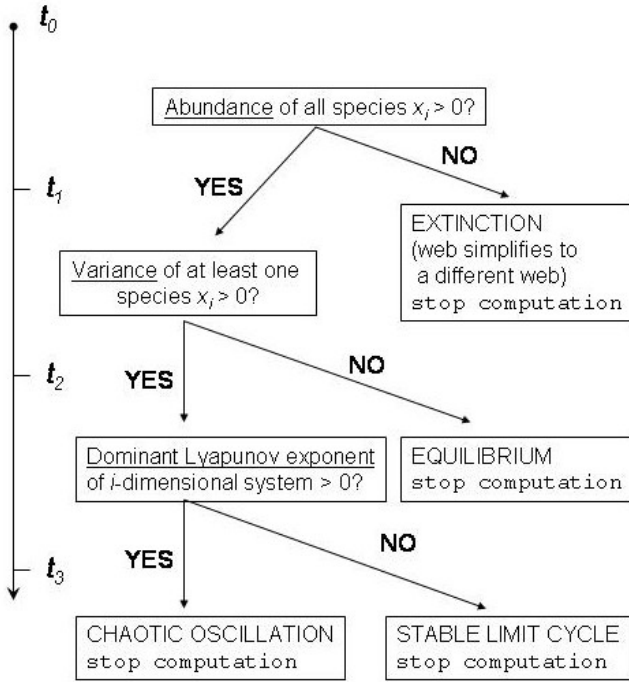


Fig. 1.3. Decision tree for classifying time series generated by numerical simulations of dynamic food web models with i species x_i . The axis indicates the flow of time during the numerical integration and decisions are made at pre-determined time intervals defined by the number of integration steps (t_1, \dots, t_3). The time interval $[t_0, t_1]$ should be sufficiently long to allow for transient dynamics to subside (typically several thousand time steps). The computation routine will automatically identify the dynamical categories “extinction”, “equilibrium”, “stable limit cycle”, and “chaos”. Because of numerical fluctuations it is advisable to use in practice a decision criterion less stringent than “ > 0 ”, e.g. “ $> 10^{-4}$ ”. Extinction can also occur “non-deterministically” through extreme oscillations that lead to unrealistically low abundances; the computation routine can be adjusted to score oscillations below a defined threshold as “extinction”.

oscillations; chaotic oscillations) it is, however, not necessary to compute the Lyapunov exponent for each parameterization. It is preferable to follow a computation routine that restricts the computation of Lyapunov exponents to the non-extinct and non-equilibrium cases, as outlined in Fig. 1.3. Although this method has been effectively used to determine the dynamical state of an extended set of food web models,³⁰ some cautionary remarks are necessary. In high-dimensional models, the dynamical state may not just

depend on the parameter values but also on the initial values chosen for the state variables (sensitivity to initial conditions). Fussmann and Heber³⁰ checked several sets of initial conditions for the tri-trophic chain and a highly connected food web consisting of five species but found only little variability for the relative frequency of chaotic and other dynamics. However, food webs that include competitive dynamics for limiting resources have been shown to be extremely sensitive to initial conditions.⁴⁶ An exhaustive numerical food web analysis may be impossible in such food webs because the number of food web realizations to be screened is magnified by a nearly limitless set of initial conditions. It must also be noted that the algorithm presented in Fig. 1.3 is designed to detect “truly” chaotic dynamics but does not distinguish between periodic limit cycle and quasi-periodic dynamics. Finally, on a positive note, the dynamical evaluation of multiple food web structures and parameterizations lends itself to parallel computation, which will considerably increase the number of parameter combinations that can be evaluated during a given time interval.

Numerical simulation is a method that probes the dynamical behavior predicted by food web models. As such, results derived from this method never reach the status of generality although they may approach it when a sufficiently large number of cases are analyzed. For simple systems of differential equations, which describe trophic structures, analytical stability analyses can be performed⁴⁷ but it is impossible to determine analytically the nature of the unstable dynamics (regular vs. chaotic oscillations). Recently, Gross et al.⁴⁸ proposed a novel method to analytically prove the potential for chaotic dynamics in generic food chain models of variable length. It would be exciting if this approach, based on bifurcations of higher codimension as indicators of chaos, could be extended to food web architectures.⁴⁹

1.4. Dynamical patterns in food webs

The relationship between structural properties of food webs and their stability is an old problem in ecology.⁵⁰ Traditionally, ecologists believed that large and reticulate food webs should be dynamically more stable than small webs and food chains (i.e they tend to display equilibrium dynamics rather than community oscillations).^{51,52} This view had been challenged by May⁵³ who derived a negative relationship between complexity and dynamical stability for randomly constructed, simple food web models. However, similar community models, based on non-random, more realistic food web

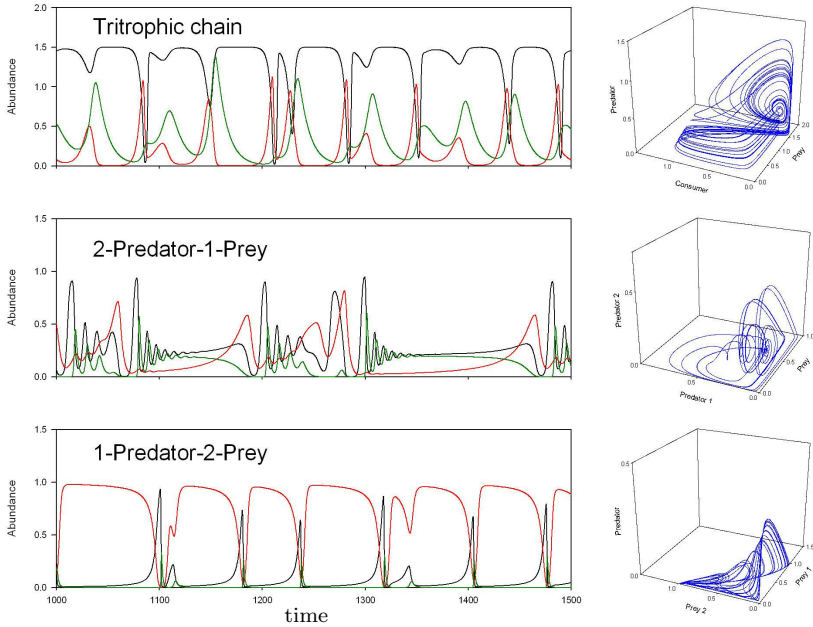


Fig. 1.4. Chaotic dynamics in three different three-species food webs. Left: time series; right: chaotic attractors in three dimensions. Black line: prey, prey, prey1; red line: consumer, predator1, prey2; green line: predator, predator2, predator (in tritrophic chain, 2-predator-1-prey, and 1-predator-2-prey webs, respectively). Parameterization: Tritrophic - $K = 1.5$, otherwise as in Fig. 1.1; 2-Predator-1-Prey - $r = K = 1.0$, $a_{R1} = 5.0$, $b_{R1} = 10.0$, $a_{R2} = 4.0$, $b_{R2} = 2.0$, $m_{C1} = 0.327273$, $m_{C2} = 0.78$ (this parameterization follows closely Abrams et al.,⁵⁷ except that both consumers have a Holling type-2 functional response here); 1-Predator-2-Prey - $r_1 = r_2 = K_1 = K_2 = 1.0$, $a_{R1} = 15.0$, $b_{R1} = 0.0$, $a_{R2} = 1.0$, $b_{R2} = 0.0$, $m_C = 1.0$, $e_C = 0.5$; this food web requires direct competition between the two prey species (here competition factors are $\alpha = 1.0$ and $\beta = 2.5$); see Takeuchi and Adachi⁵⁸ for details of the model.

structures, have repeatedly been shown to generate more stable dynamics with increasing structural complexity.⁵⁴⁻⁵⁶ Here, I review the relationship between food web structure and stability with regard to chaotic dynamics, a special type of unstable dynamics.

Chaotic dynamics are impossible in a two-species predator-prey system, where stable limit cycles are the most complex dynamics. But chaos has been shown to occur in all three possible three-species combinations (Fig. 1.4): the three-species food chain,^{10,11} the two-prey one-predator system,^{9,58} and the one-prey two-predator system⁵⁷ (for which coexistence of all three species is only possible if the dynamics are oscillatory⁵⁹ un-

less specific life history differences exist among the competitors⁶⁰). This is not to say that chaos is the prevalent dynamical type in these systems, or that the chaotic dynamics are persistent and biologically feasible. The tri-trophic food chain is probably the dynamically best investigated three-species structure. McCann and Yodzis¹¹ have shown that chaotic dynamics in this food chain can occur at biologically plausible parameterizations and that the oscillations are frequently well bounded away from extremely low population abundances (and therefore likely to be persistent). It appears that chaos occurs less frequently in the other two food webs³⁰ and Takeuchi and Adachi⁵⁸ noted that, in the two-prey one-predator system, stable coexistence on a chaotic attractor “is nonsense from the biological point of view since the population densities of three species become nearly equal to zero in the evolution of the system.”

The results from two- and three-species “webs” suggest that an increase in structural complexity is accompanied by increased dynamical complexity if one is ready to accept that chaotic dynamics are more complex than stable limit cycles. The question is whether this trend holds for larger food webs, supporting the negative relationship between food web complexity and dynamical stability that May⁵³ proposed.

There appears to be good evidence that food chains (not webs) become increasingly chaotic with increasing trophic length. Fussmann and Heber³⁰ analyzed a set of 28 structurally different model food webs and quantified the frequency of chaotic dynamics in them (using the procedures outlined in sections 1.2 and 1.3). In these food chains, chaotic dynamics became steadily more likely with an increasing number of trophic levels (Fig. 1.5). These results are corroborated by a recent theoretical study by Gross et al.⁴⁸ who found analytically that long food chains are “in general chaotic”.

The trend toward more chaotic dynamics with increasing number of trophic levels is much less pronounced in reticulate food web structures (Fig. 1.5, 1.6). McCann et al.^{29,61} were the first to observe this effect in food web models allowing for chaotic dynamics and to propose a mechanism for how complexity may lead to stabilization. In the tri-trophic food chain chaotic dynamics result from the coupling of two consumer-resource modules (the prey-consumer and the consumer-predator pairs) that oscillate at incommensurate frequencies. Adding alternative, weak trophic pathways (i.e. alternative prey) has a dampening effect on the dynamic behavior of the food web because the rigid coupling of oscillatory subsystems is destroyed. The probability of observing equilibria or stable limit cycle dynamics increases with the number of alternative, potentially stabilizing

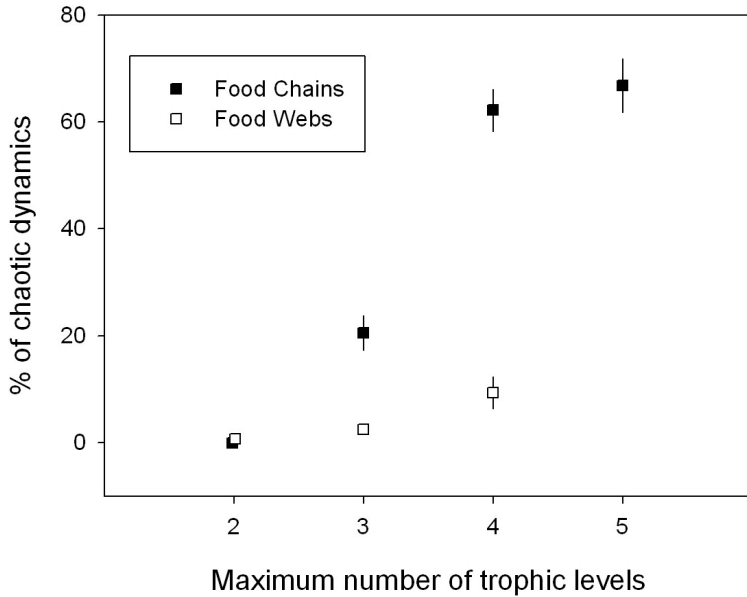


Fig. 1.5. Frequency of chaotic dynamics in mathematical models of food chains vs. reticulate food webs. 12 parameterizations of 4 different chains and 45 parameterization of 23 structurally different webs were evaluated. Percentages are averages of all chain/web structures with a given maximum number of trophic levels; error bars denote ± 1 standard error (only shown if larger than symbol). Note that no food webs with more than four trophic levels were analyzed. Data from Fussmann and Heber.³⁰

trophic links. In line with this theory, long food chains are more likely to be chaotic because they contain multiple subsystems that potentially oscillate at incommensurate frequencies. The same trend occurs in food webs, which destabilize with increasing number of trophic levels, but reticulateness of the webs may invert this trend and lead to re-stabilization in complex model structures (Fig. 1.5, 1.6).³⁰

Several variations exist on the theme of the stabilizing effect of alternative pathways in food webs. First, adding potentially stabilizing interactions to a trophic structure does not necessarily imply adding new species. New interactions may also arise by establishing feeding relationships among existing species that had previously not been connected. Ecologists speak of “omnivory” when a single species feeds on multiple trophic levels. Omnivory is very common in natural food webs⁶² and omnivorous feeding relationships have been shown to stabilize model food chains and webs by elim-

inating chaotic dynamics.^{29–31,38} The existence of multiple trophic links facilitates the dampening of oscillations at incommensurate frequencies which leads to stabilization. Fussmann and Heber³⁰ found that reticulateness and omnivory act additively to stabilize food web models although the effect of omnivory tended to be not quite as strong. Two recent studies^{32,63} suggest that omnivory may be either stabilizing or destabilizing in food webs, depending on structural properties of the food web³² or the relative strengths of the omnivorous links.⁶³

As dynamic food web model studies have accumulated over the last decade, ecologists and modelers can observe a consistent trend: the more natural attributes food web models contain, the less likely they are to display chaotic dynamics. Reticulateness and omnivory are such realistic alterations, and the spatial organization of food webs is another example. In ecosystems, multiple food webs are often linked with one another; in lakes, for instance, food webs based on benthic (lake bottom) and on planktonic (open water) production are connected by predatory fish with the ability to feed on both subsystems. Modeling studies have shown that such adaptive foraging by a consumer has a stabilizing effect in food webs in general.^{40,64} More specifically, linking two tritrophic food chains³⁹ or spatially extended food webs³⁸ by a common consumer may eliminate chaotic dynamics from model systems (however, whether coupling is stabilizing or destabilizing depends, in the latter case, on the expanse of the coupled webs³⁸). The mechanism that stabilizes these systems is the same that effects the stabilization of the tri-trophic food chain, with the difference that not a single alternative prey but a whole alternative sub-web is added to the system.^{38,65}

In essence, preferential consumption by a predator effectively transforms the multi-species Holling type-2 response into individual Holling type-3 responses²⁵ (characterized by a decrease in prey uptake at low prey densities) because the predator preferentially feeds on the most abundant prey species.^{50,65} The stabilizing effect of type-3 responses on chaotic dynamics has also been demonstrated in food web models using this type of functional response explicitly.²⁷ It is surprising, however, that even the slightest deviation from a true Holling type-2 response may stabilize chaotic dynamics.

In conclusion, model food webs of any complexity are able to generate the full range of dynamical behavior: equilibria, stable limit cycles, chaotic oscillations. There is a clear trend, however, that chaotic dynamics become less frequent in favor of more stable dynamics when food webs contain an increasing number of characteristics found in natural ecological communities.

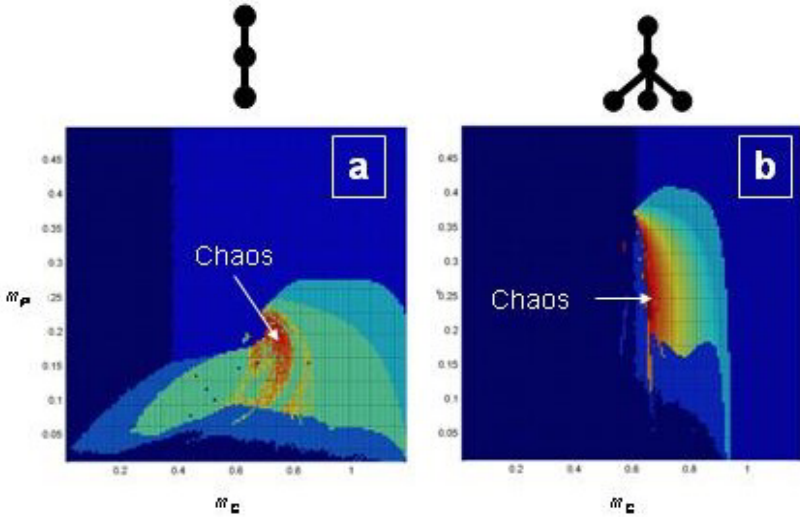


Fig. 1.6. Different frequencies of occurrence of stable and unstable dynamics in two food webs. **a)** Tritrophic food chain (parameterization: $K = 1.0$, otherwise as in Fig. 1.1). **b)** Tritrophic food web with three basal species (parameterization: $K_1 = K_2 = K_3 = 1.0$, $r_1 = r_2 = r_3 = 2.5$, $a_{R1} = 7.5$, $a_{R2} = 5.0$, $a_{R3} = 2.5$, $b_{R1} = b_{R2} = b_{R3} = 5.0$, $a_C = 1.0$, $b_C = 2.0$). Results of numerical simulations on a 200×200 lattice in the plane unfolded by consumer and top-predator mortalities m_C and m_P . Colors indicate the dynamics for each parameter combination. Dark blue: deterministic extinction; middle blue: extinction through extreme oscillations with values $< 10^{-4}$; light blue: equilibrium; turquoise: stable limit oscillations; yellow to red: chaotic oscillations with increasing positive Lyapunov exponents. Chaos is more frequent in **a)** (16.3% of all persisting parameter combinations) than in **b)** (7.2%). Data after Fussmann and Heber.³⁰

1.5. Chaos in real food webs and conclusion

A full review of the evidence for and against chaotic dynamics in natural food web systems is beyond the scope of this article. The prevailing opinion is that the vast majority of ecological communities persist at non-chaotic dynamics although some examples of chaotic dynamics have been reported.^{42,66,67} These findings are in agreement with the evidence gathered from food web models that incorporate increasing levels of real-world features such as omnivory, spatial structure, and variability of feeding relationships. It is possible, then, that chaotic dynamics are only common in long food chains, idealized structures that hardly exist in the wild.

To test this hypothesis a live model system is required that displays chaotic dynamics and can be adequately described by a mathematical

model. This system could then be manipulated in a controlled fashion so that ecologists could test whether the stabilization of chaotic dynamics occurs when the model predicts it. One potential laboratory system is the *Tribolium* (flour beetle) system, for which chaotic dynamics have been demonstrated.^{68,69} However, this system consists only of a single species and complex dynamics arise through the interaction of different life history stages (larvae, pupae, adults). With respect to food web theory a recently proposed microbial laboratory system seems more promising. Becks et al.⁴⁵ showed that their one-predator-two-prey food web could persist at equilibrium, stable limit cycle, or chaotic dynamics. The dynamical state depended on a single parameter, the flow-rate of culturing medium through the chemostat (the experimental vessel that contains the microbial food web). If this food web could be parameterized for a mathematical model that predicts its behavior correctly ecologists would possess a magnificent system to test dynamical food web theory, including questions related to the occurrence and prevalence of chaotic dynamics.

References

1. E. Meron and E. Gilad, Dynamics of plant communities in drylands: a pattern formation approach. *World Scientific Lecture Notes in Complex Systems*, 49–75, (2007).
2. K. Parvinen and M. Gyllenberg, Metapopulation dynamics and the evolution of dispersal. *World Scientific Lecture Notes in Complex Systems*, 77–107, (2007).
3. S. D. Fretwell, Regulation of plant communities by food-chains exploiting them, *Perspectives in Biology and Medicine*. **20**, 169–185, (1977).
4. L. Oksanen, S. D. Fretwell, J. Arruda and P. Niemela, Exploitation ecosystems in gradients of primary productivity, *American Naturalist*. **118**, 240–261, (1981).
5. C. X. J. Jensen and L. R. Ginzburg, Paradoxes or theoretical failures? The jury is still out, *Ecological Modelling*. **188**, 3–14, (2005).
6. V. Volterra, Fluctuations in the abundance of a species considered mathematically, *Nature*. **118**, 558–560, (1926).
7. M. L. Rosenzweig and R. H. MacArthur, Graphical representation and stability conditions of predator-prey interactions, *American Naturalist*. **97**, 209, (1963).
8. M. E. Gilpin, Spiral chaos in a predator-prey model, *American Naturalist*. **113**, 306, (1979).
9. R. R. Vance. Predation and resource partitioning in one predator-two prey model communities, *American Naturalist*. **112**, 797–813, (1978).
10. A. Hastings and T. Powell, Chaos in a three-species food chain, *Ecology*.

- 72**, 896, (1991).
11. K. McCann and P. Yodzis, Biological conditions for chaos in a three-species food chain, *Ecology*. **75**, 561–564, (1994).
 12. R. M. May, Simple mathematical models with very complicated dynamics, *Nature*. **261**, 459–467, (1976).
 13. A. A. Berryman and J. A. Millstein, Are ecological systems chaotic - and if not, why not?, *Trends in Ecology & Evolution*. **4**, 26–28, (1989).
 14. J. C. Allen, W. M. Schaffer and D. Rosko, Chaos reduces species extinction by amplifying local population noise, *Nature*. **364**, 229–232, (1993).
 15. R. V. Solé and J. G. P. Gamarra, Chaos, dispersal and extinction in coupled ecosystems, *Journal of Theoretical Biology*. **193**, 539–541, (1998).
 16. S. H. Strogatz, *Nonlinear dynamics and chaos*. (Perseus, Reading, 1994).
 17. B. Blasius, A. Huppert and L. Stone, Complex dynamics and phase synchronization in spatially extended ecological systems, *Nature*. **399**, 354–359, (1999).
 18. B. E. Kendall, C. J. Briggs, W. W. Murdoch, P. Turchin, S. P. Ellner, E. McCauley, R. M. Nisbet and S. N. Wood, Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches, *Ecology*. **80**, 1789–1805, (1999).
 19. P. Turchin, *Complex population dynamics*. (Princeton University Press, Princeton, 2003).
 20. R. F. Costantino, J. M. Cushing, B. Dennis and R. A. Desharnais, Experimentally induced transitions in the dynamic behaviour of insect populations, *Nature*. **375**, 227–230, (1995).
 21. S. M. Henson, R. F. Costantino, J. M. Cushing, R. A. Desharnais, B. Dennis and A. A. King, Lattice effects observed in chaotic dynamics of experimental populations, *Science*. **294**, 602–605, (2001).
 22. F. D. Hulot, G. Lacroix, F. O. Lescher-Moutoué and M. Loreau, Functional diversity governs ecosystem response to nutrient enrichment, *Nature*. **405**, 340–344. (2000).
 23. G. F. Fussmann, S. P. Ellner, K. W. Shertzer and N. G. Hairston, Crossing the Hopf bifurcation in a live predator-prey system, *Science*. **290**, 1358–1360, (2000).
 24. S. Clodong and B. Blasius, Chaos in a periodically forced chemostat with algal mortality, *Proc. R. Soc. Lond. B*. **271**, 1617–1624, (2004).
 25. C. S. Holling. The components of predation as revealed by a study of small-mammal predation of the European Pine Sawfly, *The Canadian Entomologist*. **91**, 293–320, (1959).
 26. G. F. Fussmann and B. Blasius, Community response to enrichment is highly sensitive to model structure, *Biology Letters*. **1**, 9–12, (2005).
 27. R. J. Williams and N. D. Martinez, Stabilization of chaotic and non-permanent food-web dynamics, *European Physical Journal B*. **38**, 297–303, (2004).
 28. P. A. Abrams, Dynamics and interactions in food webs with adaptive foragers. In eds. G. Polis and K. Winemiller, *Food Webs: Integration of patterns and dynamics*, pp. 113–121, (Chapman and Hall, 1996).

29. K. McCann and A. Hastings, Re-evaluating the omnivory-stability relationship in food webs, *Proc. R. Soc. Lond. B.* **264**, 1249–1254, (1997).
30. G. F. Fussmann and G. Heber, Food web complexity and chaotic population dynamics, *Ecology Letters.* **5**, 394–401, (2002).
31. L. D. J. Kuijper, B. W. Kooi, C. Zonneveld and S. Kooijman, Omnivory and food web dynamics, *Ecological Modelling.* **163**, 19–32, (2003).
32. J. Vandermeer, Omnivory and the stability of food webs, *J. Theor. Biol.* **238**, 497–504, (2006).
33. G. R. Huxel and K. McCann, Food web stability: The influence of trophic flows across habitats, *American Naturalist.* **152**, 460–469, (1998).
34. S. Diehl, S. Berger and R. Wohrl, Flexible nutrient stoichiometry mediates environmental influences, on phytoplankton and its resources, *Ecology.* **86**, 2931–2945, (2005).
35. R. W. Sterner, A. Bajpai and T. Adams, The enigma of food chain length: Absence of theoretical evidence for dynamic constraints, *Ecology.* **78**, 2258–2262, (1997).
36. M. Vos, B. W. Kooi, D. L. DeAngelis and W. M. Mooij, Inducible defences and the paradox of enrichment, *Oikos.* **105**, 471–480, (2004).
37. T. F. Thingstad, H. Havskum, K. Garde and B. Riemann, On the strategy of “eating your competitor”: A mathematical analysis of algal mixotrophy, *Ecology.* **77**, 2108–2118, (1996).
38. K. S. McCann, J. B. Rasmussen and J. Umbanhowar, The dynamics of spatially coupled food webs, *Ecology Letters.* **8**, 513–523, (2005).
39. D. M. Post, M. E. Connors and D. S. Goldberg, Prey preference by a top predator and the stability of linked food chains, *Ecology.* **81**, 8–14, (2000).
40. M. Kondoh, Foraging adaptation and the relationship between food-web complexity and stability, *Science.* **299**, 1388–1391, (2003).
41. S. Rinaldi, S. Muratori and Y. Kuznetsov, Multiple attractors, catastrophes and chaos in seasonally perturbed predator-prey communities, *Bulletin of Mathematical Biology.* **55**, 15–35, (1993).
42. S. P. Ellner and P. Turchin, Chaos in a noisy world: New methods and evidence from time-series analysis, *American Naturalist.* **145**, 343, (1995).
43. M. T. Rosenstein, J. J. Collins and C. J. Deluca, A practical method for calculating largest Lyapunov exponents from small data sets, *Physica D.* **65**, 117–134, (1993).
44. A. Wolf, J. B. Swift, H. L. Swinney and J. A. Vastano, Determining Lyapunov exponents from a time series, *Physica D.* **16**, 285–317, (1985).
45. L. Becks, F. M. Hilker, H. Malchow, K. Jürgens and H. Arndt, Experimental demonstration of chaos in a microbial food web, *Nature.* **435**, 1226–1229, (2005).
46. J. Huisman and F. J. Weissing, Fundamental unpredictability in multi-species competition, *American Naturalist.* **157**, 488–494, (2001).
47. K. McCann and P. Yodzis, Bifurcation structure of a three-species food chain model, *Theoretical Population Biology.* **48**, 93–125, (1995).
48. T. Gross, W. Ebenhöf and U. Feudel, Long food chains are in general chaotic, *Oikos.* **109**, 135–144, (2005).

49. T. Gross, M. Baurmann, U. Feudel and B. Blasius, Generalized models - a new tool for the investigation of ecological systems. *World Scientific Lecture Notes in Complex Systems*, 21–48, (2007).
50. K. S. McCann, The diversity-stability debate, *Nature*. **405**, 228–233, (2000).
51. C. S. Elton, *The ecology of invasions by animals and plants*. (University of Chicago Press, Chicago, 1958).
52. R. MacArthur, Fluctuations of animal populations, and a measure of community stability, *Ecology*. **36**, 533–536, (1955).
53. R. M. May, *Stability and complexity in model ecosystems*. (Princeton University Press, Princeton, 1973).
54. D. T. Haydon, Maximally stable model ecosystems can be highly connected, *Ecology*. **81**, 2631–2636, (2000).
55. S. L. Pimm and J. H. Lawton, Number of trophic levels in ecological communities, *Nature*. **268**, 329–331, (1977).
56. I. D. Rozdilsky and L. Stone, Complexity can enhance stability in competitive systems, *Ecology Letters*. **4**, 397–400, (2001).
57. P. A. Abrams, C. E. Brassil and R. D. Holt, Dynamics and responses to mortality rates of competing predators undergoing predator-prey cycles, *Theoretical Population Biology*. **64**, 163–176, (2003).
58. Y. Takeuchi and N. Adachi, Existence and bifurcation of stable equilibrium in two-prey, one-predator communities, *Bulletin of Mathematical Biology*. **45**, 877–900, (1983).
59. R. A. Armstrong and R. McGehee, Competitive exclusion, *American Naturalist*. **115**, 151–170, (1980).
60. K. McCann, Density-dependent coexistence in fish communities, *Ecology*. **79**, 2957–2967, (1998).
61. K. McCann, A. Hastings and G. R. Huxel, Weak trophic interactions and the balance of nature, *Nature*. **395**, 794–798, (1998).
62. G. A. Polis and D. R. Strong, Food web complexity and community dynamics, *American Naturalist*. **147**, 813–846, (1996).
63. K. Tanabe and T. Namba, Omnivory creates chaos in simple food web models, *Ecology*. **86**, 3411–3414, (2005).
64. J. Teng and K. S. McCann, Dynamics of compartmented and reticulate food webs in relation to energetic flows, *American Naturalist*. **164**, 85–100, (2004).
65. K. McCann, J. Rasmussen, J. Umbanhowar and M. Humphries, The role of space, time, and variability in food web dynamics. In eds. P. C. de Ruiter, V. Wolters and J. C. Moore, *Dynamic food webs*, pp. 56–70, (Elsevier, Amsterdam, 2005).
66. I. Hanski, P. Turchin, E. Korpimäki and H. Henttonen, Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos, *Nature*. **364**, 232–235, (1993).
67. P. Turchin and S. P. Ellner, Living on the edge of chaos: Population dynamics of Fennoscandian voles, *Ecology*. **81**, 3099–3116, (2000).
68. R. F. Costantino, R. A. Desharnais, J. M. Cushing and B. Dennis, Chaotic dynamics in an insect population, *Science*. **275**, 389–391, (1997).

69. R. F. Costantino, R. A. Desharnais, J. M. Cushing, B. Dennis, S. M. Henson and A. A. King, Nonlinear stochastic population dynamics: The Flour Beetle *Tribolium* as an effective tool of discovery. In *Advances In Ecological Research*, vol. 37, *Population Dynamics And Laboratory Ecology*, pp. 101–141, (2005).