Food web complexity and chaotic population dynamics

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Abstract
In mathematical models, very simple communities consisting of three or more species frequently display chaotic dynamics which implies that long-term predictions of the population trajectories in time are impossible. Communities in the wild tend to be more complex, but evidence for chaotic dynamics from such communities is scarce. We used supercomputing power to test the hypothesis that chaotic dynamics become less frequent in model ecosystems when their complexity increases. We determined the dynamical stability of a universe of mathematical, nonlinear food web models with varying degrees of organizational complexity. We found that the frequency of unpredictable, chaotic dynamics increases with the number of trophic levels in a food web but decreases with the degree of complexity. Our results suggest that natural food webs possess architectural properties that may intrinsically lower the likelihood of chaotic community dynamics.

Keywords
Chaos, ecosystem stability, food web, population dynamics.

INTRODUCTION
Chaotic oscillations, stable equilibria and regular, stable limit oscillations are the principal dynamical states that mathematical models of multispecies communities generate (Hastings & Powell 1991; McCann & Hastings 1997; McCann et al. 1998; Post et al. 2000). Examples of chaotic dynamics in field (Hanski et al. 1993) or laboratory populations (Costantino et al. 1997) have attracted much attention, but do not appear to be the dominant type of dynamics in nature (Ellner & Turchin 1995). Here we are concerned with how frequently chaotic and non-chaotic dynamics occur in realistic community models and whether a correlation exists between community structure and the prevalent type of dynamics generated. The answer matters for a number of reasons related to the unpredictability of chaotic systems. First, organisms that coexist in a community with unpredictable internal dynamics may face similar ecological and evolutionary constraints to organisms living in an unpredictable environment. If the dynamics are chaotic, traits and strategies that typically are associated with changing environments (e.g. dormancy; Hairston et al. 1996) may be adaptive even when the extrinsic environment is spatially and temporally homogeneous. Second, our current understanding of ecosystem function relies on the predictability of ecosystem dynamics and the prevalence of cause–effect relationships. Some of the major ideas in community ecology, such as the trophic cascade (Carpenter et al. 1985) or the keystone predator concept (Paine 1966), are built on this assumption. Chaotic dynamics, though deterministic, are not easily reconciled with these concepts. Finally, interventions in ecosystems for the purpose of conservation, pest management, or control of invasive species are more likely to succeed if the dynamics of the system are predictable.

Because of the web-like structure of natural species assemblages, ecologists have searched for a relationship between the complexity and stability of communities. Historically, the prevailing opinion has swayed between a positive (e.g. MacArthur 1955) or a negative (e.g. May 1973) relationship, but various methods and definitions of stability (Pimm 1984; reviewed by McCann 2000) have been mingled in the discussion. In Lotka–Volterra type models of food webs, return times of populations to stable equilibria decrease (indicating greater stability), when food chain lengths are shortened or when omnivorous links are added (Pimm & Lawton 1977). More recently, model food webs have been shown to be potentially more stable when their complexity increases (Haydon 2000; Rozdilsky & Stone 2002).
Non-linear models have been used to demonstrate that adding complexity to food chains (McCann & Hastings 1997; McCann et al. 1998) or linking two food chains together (Post et al. 2000) can move the systems away from chaotic dynamics towards stable limit cycles and equilibria. It is this kind of stability we are concerned with here.

We designed food web models that differ in complexity (Fig. 1) and in the number of trophic levels and omnivorous links they contain, ran simulations on parallel computers, and determined the frequency of chaotic and non-chaotic dynamics. For each model, the species’ mortality rates were “free” parameters and, numerically, we performed a complete stability analysis by evaluating the stability of the food webs for all possible mortality combinations. We allowed a maximum of five trophic levels in our models, with one to three primary producers at the bottom, one or two consumers, and one primary, secondary, and tertiary predator. We incorporated different degrees of omnivory into the model by letting the primary predator either feed exclusively on the consumer(s) or, additionally, on one to three species of primary producers.

THE FOOD WEB MODEL

The food web in Fig. 1(b) can be described by a system of eight ordinary differential equations:

\[
\frac{dP_i}{dt} = P_i \left[ r_i (1 - \frac{P_i}{K_i}) - \frac{a_{Pi} C_i}{1 + b_{Pi} P_i + b_{Pi} P_2 + b_{Pi} P_3} \right] - \frac{a_{Pi} C_i}{1 + b_{Pi} P_i + b_{Pi} P_2 + b_{Pi} P_3}
\]

\[
\frac{dY}{dt} = Y \left[ \frac{a_{YX} X}{1 + b_{Y} Y} - d_Y \right] - \frac{a_{YZ} Z}{1 + b_{Y} Y} - d_Y
\]

\[
\frac{dZ}{dt} = Z \left[ \frac{a_{ZX} X}{1 + b_{Z} Z} - d_Z \right]
\]

\[
\frac{dC_i}{dt} = C_i \left[ \frac{a_{Ci} P_i + a_{Ci} P_2 + a_{Ci} P_3}{1 + b_{Ci} P_i + b_{Ci} P_2 + b_{Ci} P_3} \right] - d_C
\]

\[
\frac{dX}{dt} = X \left[ \frac{a_{X} X}{1 + b_{X} X} - d_X \right]
\]

\[
\frac{dP_1}{dt} = P_1 \left[ r_1 (1 - \frac{P_1}{K_1}) - \frac{a_{P1} C_1}{1 + b_{P1} P_1 + b_{P1} P_2 + b_{P1} P_3} \right] - \frac{a_{P1} C_1}{1 + b_{P1} P_1 + b_{P1} P_2 + b_{P1} P_3}
\]

\[
\frac{dP_2}{dt} = P_2 \left[ r_2 (1 - \frac{P_2}{K_2}) - \frac{a_{P2} C_2}{1 + b_{P2} P_1 + b_{P2} P_2 + b_{P2} P_3} \right] - \frac{a_{P2} C_2}{1 + b_{P2} P_1 + b_{P2} P_2 + b_{P2} P_3}
\]

\[
\frac{dP_3}{dt} = P_3 \left[ r_3 (1 - \frac{P_3}{K_3}) - \frac{a_{P3} C_3}{1 + b_{P3} P_1 + b_{P3} P_2 + b_{P3} P_3} \right] - \frac{a_{P3} C_3}{1 + b_{P3} P_1 + b_{P3} P_2 + b_{P3} P_3}
\]

\[
\frac{dP_4}{dt} = P_4 \left[ r_4 (1 - \frac{P_4}{K_4}) - \frac{a_{P4} C_4}{1 + b_{P4} P_1 + b_{P4} P_2 + b_{P4} P_3} \right] - \frac{a_{P4} C_4}{1 + b_{P4} P_1 + b_{P4} P_2 + b_{P4} P_3}
\]

\[
\frac{dP_5}{dt} = P_5 \left[ r_5 (1 - \frac{P_5}{K_5}) - \frac{a_{P5} C_5}{1 + b_{P5} P_1 + b_{P5} P_2 + b_{P5} P_3} \right] - \frac{a_{P5} C_5}{1 + b_{P5} P_1 + b_{P5} P_2 + b_{P5} P_3}
\]

Figure 1 (a) Architecture of food web models with two (row 1), three (rows 2–4), and four to five trophic levels (row 5). (b) Food web of maximum complexity. All webs in (a) can be generated as substructures of this web. \(P_i, P_2, P_3\): primary producers; \(C_1, C_2\): consumers; \(X, Y, Z\): primary, secondary, tertiary predators. Thickness of lines is proportional to intensity of predator–prey relationship and numbers on lines are the values of parameters \(a = \text{the product of } b \text{ and the maximum birth rate for the predator [day}^{-1}]\) and \(b \text{inverse of the half-saturation constant}\) for this trophic link. Omnivorous links between \(P_1, \ldots, P_3\) and \(X\) may or may not be present in model. Dynamic stability was determined for all possible combinations of mortality rates that the heterotrophs \(C_1, C_2, X, Y, Z\) experience.

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where \( P_1, P_2, P_3 \) are the population sizes of the primary producers and \( C_1, C_2 \) are the population sizes of the (herbivorous) consumers. \( X, Y, \) and \( Z \) are the population sizes of the primary, secondary, and tertiary predators, respectively. Primary producers are modelled to grow logistically with growth rate \( r \) (we parameterized: \( r_1 = r_2 = r_3 = 2.5 \text{ day}^{-1} \)) and carrying capacity \( K_1 \) which we set to unity. Therefore, all population sizes in our models are relative to the primary producers’ carrying capacity. We assumed no density dependence for heterotrophic species.

Predation is the only type of direct interaction between species, i.e. only indirect – exploitative or apparent – competition occurs. Predator birth rates equal the uptake of prey and follow nonlinear, saturating Holling type II response curves. In a food web, a predator can prey on more than one species. We modelled this relationship as a multispecies type II response:

\[
B(P_1, \ldots, P_n) = \frac{\sum_{i=1}^{n} d_{C_i} P_i}{1 + \sum_{j=1}^{n} b_{C_j} P_j}
\]

where \( B \) is the instantaneous birth rate of the predator \( C_i \) preying on \( n \) prey species \( P_1, \ldots, P_n \) \( d_{C_i} \) is the inverse of the half-saturation constant for \( C_i \) preying on \( P_j \) \( d_{C_i} = \frac{K_{C_i}}{b_{C_i}} \) is the product of \( K_{C_i} \) and the maximum birth rate for \( C_i \) preying on \( P_j \) (see Fig. 1 for parameterization). For example, if \( P_1 \) is the only prey and \( C_1 \) the only predator, \( C_1 \) reaches a maximum birth rate of \( d_{C_1} / b_{C_1} = 1.5 \text{ day}^{-1} \); \( C_1 \)'s birth rate is half the maximum (0.75 day\(^{-1} \)) at \( 1/b_{C_1} = 0.2 \) (times the capacity of the primary producers). The parameter pairs \( d_{C_i}, b_{C_i} \) characterize saturation level and steepness of the multispecies type II response for the predator–prey relationship between species \( n \) and \( m \). The heterotrophic species \( C_1, X, Y, Z \) experience mortality rates \( d_{C_1}, d_X, d_Y, d_Z \). Equation systems for less complex food webs (Fig. 1a) can be produced by omitting equations and interaction terms that pertain to absent species.

Our parameterization is consistent with growth rates and predation intensities typically found in planktonic food webs. We presume that the homogeneous environment and the ubiquity of asexual reproduction that characterize plankton communities are the most realistic framework for our continuous-time approach to modelling food webs.

**METHODS**

Model simulation

We built our simulation environment around A. Hindmarsh’s cvode solver (http://www.netlib.org/ode/index.html) and ran the codes on parallel computers of the AC3 Velocity complex of the Cornell Theory Center. We modelled the 28 structurally different food webs shown in Fig. 1(a), among them all 24 possible bi- and tritrophic food webs (Fig. 1a, rows 1–4). Interaction strengths between primary producers and consumers vary for most of the structurally identical webs (Fig. 1b). For example, the tritrophic chain (Fig. 1a, 2a) has three different parameter realizations with either \( P_1 \) or \( P_2 \) or \( P_3 \) as the basal species. For the bi- and tritrophic webs, we included all possible variations of this sort, which resulted in a total number of 60 webs. Whenever several realizations of a web exist, percentages given in Table 1 reflect the mean of all percentages found for this web structure, and standard deviations of the mean are given.

For a particular food web we chose the mortality rates \( (n = 1, \ldots, 4) \) of all heterotrophic species to be parameters subject to change. Using a fine grid of mortality values we found for each web the \( n \)-dimensional space of mortality combinations that led to coexistence of all species and determined the relative frequency of equilibrium, stable limit cycle, and chaotic dynamics in this space. For each parameter combination we preiterated the simulation for 50 000 time steps. We omitted parameter combinations from the analysis for which at least one species trajectory fell below an extinction threshold \( \varepsilon \) (results for \( \varepsilon = 10^{-3} \) are presented but results were consistent over the range \( 10^{-20} \leq \varepsilon \leq 10^{-2} \)). We considered these species to go extinct and, consequently, the food web to simplify to a different web of lower complexity. Over another 1000 time steps we computed the variance \( \hat{\varepsilon} \) of all species trajectories separately. If we found \( \hat{\varepsilon} < 10^{-4} \) for each trajectory, we assigned equilibrium dynamics to this parameter combination. If \( \hat{\varepsilon} \geq 10^{-4} \), we computed the dominant Lyapunov exponent \( \lambda \) (Wolf et al. 1982) over the next 10 000 time steps. A positive dominant Lyapunov exponent marks exponential divergence of nearby trajectories, a signature of chaotic dynamics. Conservatively, we rated the dynamics as chaotic oscillations if \( \lambda \geq 10^{-3} \), otherwise as stable limit oscillations. Only one mortality rate was subject to change in the simplest webs (Fig. 1a, 1A–C). Because parallel computing was unwarranted in these instances we used standard software (MATLAB) to determine the dynamical stability.

For our simulations we set the initial values of all state variables to 0.5. However, the existence of multiple basins of attraction can lead to different dynamical states of a system, depending on the initial conditions. To estimate the potential variability of our results within a single web parameterization due to this effect we performed the computation routine for two of our webs (Fig. 1a, 2A and 3F) with eight different sets of initial conditions (combinations of initial values 0.1, 0.5, and 0.9) and compared the results for the “percentage of chaotic dynamics” of these webs. We found standard deviations of the mean of 0.31 and 0.71 for these eight simulations, respectively, which was lower than the SD of each of 65 000 combinations of
eight webs chosen randomly from our 60 food web models. Although not a formal analysis of variance, this exercise suggests that the variance within food webs (due to multiple basins of attraction) is small compared with the variance among webs. We assume that multiple basins of attraction were a minor source of variation in this study and are unlikely to have interfered with our general conclusions.

Quantifying food web structure

We use two compound parameters to quantify structural properties of our model food webs. Let \( N_{\text{spec}} \) be the number of species in a particular web and let \( \bar{z}_i \) be the average chain length of all food chains linking species \( i = 1, \ldots, N_{\text{spec}} \) to basal species. Then we define \( 1 + \bar{z}_i \) as the “trophic level” of species \( i \) in a food web. The “Average Trophic Level” (ATL) is the mean of the trophic levels of all \( N_{\text{spec}} \) species present in a food web:

\[
\text{ATL} := \frac{\sum_{i=1}^{N_{\text{spec}}} (1 + \bar{z}_i)}{N_{\text{spec}}}
\]

ATL increases with the number of trophic levels in a web but decreases when species predominate in the lower trophic levels or with the addition of omnivorous links.

To measure the bias of the distribution of species towards the bottom or top of a food web we defined the “Centre of Gravity”:

\[
\text{CG} := \frac{\sum_{i=1}^{N_{\text{spec}}} H_i}{N_{\text{spec}} \max\{\mu_i\}}, \quad 0 < CG < 1
\]


<table>
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<tr>
<th>Web</th>
<th>TL</th>
<th>ATL</th>
<th>CG</th>
<th>Omni</th>
<th>Equilibrium (%) ± SD</th>
<th>Oscillation (%) ± SD</th>
<th>Chaos (%) ± SD</th>
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<td>17.9 ± 2.5</td>
<td>15.4 ± 6.4</td>
<td>66.7 ± 8.7</td>
</tr>
</tbody>
</table>

TL, no. of trophic levels that the web encompasses.

ATL, Average Trophic Level.

CG, “Centre of Gravity” of web.

Omni, no. of omnivorous links in web.

*Percentages are computed from the combinations of mortality rates that led to coexistence of all species in a web. Codes for webs from Fig. 1(a). See Methods for details and definitions.
with \( l_i = \) maximum chain length linking species \( i \) to basal species. \( CG = 0.5 \) marks an unbiased distribution of species (as in all food chains), a \( CG \) greater (smaller) than 0.5 marks a concentration of species at the upper (lower) trophic levels of the web. Note that the value of ATL depends on the number of omnivorous links, whereas the value of CG does not.

**RESULTS**

For all but one of the structural types of food webs we found parameter combinations that led to the coexistence of all the species involved (Table 1). The only exception was web 1D (Fig. 1a) where competitive exclusion always resulted in extinction of one consumer species. The simplest web structures 1A–1C (Fig. 1a) displayed only equilibrium and limit cycle dynamics. Chaotic dynamics occurred in all other food webs. When we compared the community dynamics among different food webs we found the frequency with which chaotic dynamics occurred to be related to the structure of the webs. The incidence of chaotic dynamics increased with the number of trophic levels a particular web encompassed (averages from Table 1 are: 0.6% chaos for webs with two trophic levels (TL); 9.1% for three TL; 26.9% for four TL; 66.7% for five TL). However, at a fixed chain length web-like structures tended to display fewer instances of chaotic dynamics than their chain-like counterparts (Fig. 2). Increasing the number of trophic links by introducing omnivory was another structural trait that lowered the occurrence of chaotic dynamics (Table 2).

We used linear regression analyses to test whether structure and dynamic stability of our model food webs were correlated. We found a positive relationship between the ATL of a food web and the percentage of chaotic dynamics that occurred in this web (Fig. 3a). We also found a weak relationship between ATL and the percentage of equilibria (Fig. 3b). We conclude that the general trend towards more stable dynamics with decreasing ATL is largely due to shifts from chaotic dynamics to stable limit cycles rather than to shifts from limit cycles to equilibria.

We performed a multiple linear regression with the percentage of chaotic dynamics in a food web as dependent

![Figure 2](image_url)  
*Figure 2* Chaotic dynamics disappear from model food webs along a gradient of increasing complexity (bottom left to top right). Results from simulations of nine tritrophic food webs representing different combinations of the numbers of basal species and omnivorous links. For each web are plotted the results of numerical simulations on a 200 \( \times \) 200 grid in the \((d_C, d_X)\) parameter plane, with \( d_C = \) mortality of consumer, \( d_X = \) mortality of predator. For each parameter combination a coloured dot was placed at its co-ordinates that represents the type of dynamics found: blue = extinction, green = equilibrium, yellow = stable limit oscillation, red = chaotic oscillation. In each panel \( d_C \) and \( d_X \) are scaled linearly between \([0, 1.2 \text{ day}^{-1}]\) and \([0, 0.45 \text{ day}^{-1}]\), respectively. Inset gives percentage of chaotic dynamics amongst parameter combinations that did not lead to extinction. Average Trophic Level is indicated for each web on top of panel.

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variable and three independent variables (Table 2) to investigate the relative significance of structural food web properties for the dynamic stability of these webs. We found that “maximum trophic level” correlates positively with the likelihood of chaotic dynamics, whereas chaos occurs less frequently in complex architectures with a high concentration of species near the base of the food web (low “centre of gravity”) or an increasing number of omnivorous links. Among other parameters commonly used to characterize food webs (e.g. Morin 1999), “connectance” was about as good a predictor as “omnivory” to be included as a third parameter into a stepwise regression procedure ($P$-value for increment of determination $= 0.001$; $R^2 = 0.82$), whereas other third parameters were worse predictors of model behaviour (“number of links”, $P = 0.03$; “linkage density”, $P = 0.06$; “number of species”, $P = 0.20$). ATL alone accounted for a greater proportion of the variability in “percentage of chaotic dynamics” (Fig. 3) than any combination of the common measures of food web complexity.

In our food webs, primary production available for consumption increases with the number of primary producers the web contains. To separate the effects of greater web complexity from those of higher primary production we recalculated two tritrophic web architectures with two and three primary producers (Fig. 1a, 2B and 2C). We used capacities $K = 0.50$ and $K = 0.33$, respectively, in order to standardize total primary production among these webs and the straight tritrophic chain (Fig. 1a, 2a). Chaotic dynamics occurred less frequently when complexity increased (20.5% ± 5.6 for 2A, 9.6% ± 5.5 for 2B, 7.0% for 2C), just as in the non-standardized webs (Table 1).

**DISCUSSION**

Using computer simulations of food web models we have shown that the dynamical stability of a web depends critically on its architecture. The likelihood of chaotic dynamics tends to increase with the number of trophic levels a web contains; however, structural properties that increase the complexity of a web in particular ways may counterbalance this effect and reduce the probability of chaos. Natural communities possess structural properties similar to those that led to non-chaotic dynamics in our simulations. They typically contain many taxa at a relatively low number of trophic levels (Briand & Cohen 1987), the number of taxa tends to decrease towards the top of the web (Havens 1992) – a relationship that can be obscured by inadequate taxonomic resolution (Pimm 1982) – and omnivory is common (Polis & Strong 1996). We suggest that these characteristics may be responsible for the scarcity of chaos observed in communities in the wild (Ellner & Turchin 1995).

We have identified the “average trophic level” of a food web as a measure that correlated very well with the dynamic stability of that web. The ATL integrates over the food web properties we suspect to be important in connection with dynamic stability. It increases with maximum chain length and decreases both with the addition of omnivorous links and with an over-proportionally high concentration of species in the lower levels of a web. To our knowledge, ecologists have not proposed ATL yet as a relevant way to quantify aspects of food web complexity that matter to the dynamics; nor is ATL closely connected to any of the measures used to quantify graph or network complexity. Unlike these generic measures, ATL accounts for an important feature of food webs: their directionality. In that it differentiates between topologically identical webs depending on their orientation (top to bottom or bottom to top, e.g. the difference between web 1B and 1D.

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**Table 2 Linear multiple regression**

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Multiple $R^2$</th>
<th>P-value for increment of determination</th>
</tr>
</thead>
<tbody>
<tr>
<td>X1: Maximum trophic level</td>
<td>0.62</td>
<td>$&lt; 10^{-13}$</td>
</tr>
<tr>
<td>X2: “Centre of gravity”</td>
<td>0.78</td>
<td>$&lt; 10^{-7}$</td>
</tr>
<tr>
<td>X3: No. of omnivorous links</td>
<td>0.81</td>
<td>0.003</td>
</tr>
</tbody>
</table>

Dependent variable $Y =$ “relative frequency of chaotic dynamics (%) in a food web”

Regression equation: $Y = 20.2 X_1 + 72.5 X_2 - 4.3 X_3 - 72.9$, $n = 60$ food webs

**Figure 3** Regression of Average Trophic Level (see Methods) of model food webs with the relative frequency of (a) chaotic and (b) equilibrium dynamics in these webs.
in Fig. 1a) ATL appears to be especially suitable to characterizing food webs.

An increase in primary production is usually considered to have a destabilizing effect on the community dynamics (e.g. Rosenzweig 1971). We were surprised that making the webs more complex can have a stabilizing effect even though the system becomes enriched at the same time. When we standardized primary production in some of our webs (with 1, 2, 3 basal species) the frequency of chaotic dynamics remained virtually unchanged compared with the non-standardized webs. It appears that the amount of primary production had almost no impact on which dynamics prevailed in these webs, but that the existence of alternative prey species provides a very potent mechanism for reducing unstable dynamics.

Almost all experimental evidence for a relationship between dynamical stability and community structure stems from studies restricted to the primary producer level (Tilman 1996; McCann 2000), and studies that categorized dynamics as equilibria, limit cycle or chaotic oscillations have been restricted to systems of one (Costantino et al. 1997) and two (Fussmann et al. 2000) species. Other measures of stability (variability of population size and persistence of the community over time) have been used in experimental food web manipulations and, interestingly, the results agree with our findings (Fig. 2) that communities as a whole are less likely to coexist when complexity increases (Hairston et al. 1968; Lawler 1993), whereas the variability of populations in persisting communities tends to decrease with complexity (Fagan 1997; McGrady-Steed et al. 1997).

Theoretical ecologists are only beginning to sort out the mechanisms that may cause tamer, non-chaotic dynamics in complex food web architectures. It has been suggested that chaos develops in multispecies models from the coupling of incommensurate frequencies of oscillation (McCann et al. 1998; McCann 2000; Post et al. 2000). In straight food chains predator–prey modules are the oscillators and interact with one another vertically. Their frequencies depend rigidly on the parameterization that will, in certain cases, lead to incommensurate frequencies and chaotic oscillations. The longer the food chains, the more oscillators are coupled together, which increases the potential for incommensurate frequencies. In food webs predators choose among multiple prey species and, again, each of these interactions supplies a new oscillator to the system. The frequencies of these oscillations, however, are not rigidly determined by a fixed interaction between the predator and each of its prey species separately. Rather, the predator and all prey species together co-determine the oscillation frequencies, which is mathematically reflected by the multispecies type II response. We suspect that adding alternative prey species to a food web creates elasticity as to what frequencies oscillators in the system take and makes the system more likely to settle on stable attractors. We propose this as a hypothesis that is open to elaboration, but our results strongly suggest that adding predator–multiple prey interaction may be instrumental in removing chaotic dynamics from our webs.

Parallel computing power has enabled us to explore previously uncharted degrees of complexity in community models that capture some of the essential structural elements of food webs, i.e. the existence of alternative prey species and omnivory. Although computationally demanding, our web architectures feature rather a restricted number of species when compared with natural communities. We do not know whether our findings may be extrapolated to larger food webs, but given the strong directionality of the trends within our two-to-eight-species universe this ought to be a viable hypothesis. Barring this restriction, our models suggest that natural communities, in spite of their complexity, are more likely to coexist on predictable trajectories rather than on strange attractors which would make them a “fuzzy” object of study.

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