Food-web complexity emerging from ecological dynamics on adaptive networks

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Abstract

Food webs are complex networks describing trophic interactions in ecological communities. Since Robert May’s seminal work on random structured food webs, the complexity–stability debate is a central issue in ecology: does network complexity increase or decrease food-web persistence? A multi-species predator–prey model incorporating adaptive predation shows that the action of ecological dynamics on the topology of a food web (whose initial configuration is generated either by the cascade model or by the niche model) render, when a significant fraction of adaptive predators is present, similar hyperbolic complexity–persistence relationships as those observed in empirical food webs. It is also shown that the apparent positive relation between complexity and persistence in food webs generated under the cascade model, which has been pointed out in previous papers, disappears when the final connectance is used instead of the initial one to explain species persistence.  

Keywords: Food webs; Foraging adaptation; Complexity; Scaling laws

1. Introduction

The importance of the pattern of ecological interactions for the community stability has been a long discussed topic in ecology. While in food-web theory most of the analytical approaches have been based on stochastic models derived to capture the main features of observed food-web topologies (species richness, number of trophic levels, linkage density—mean number of trophic interactions per species, etc.), less effort has been allocated to analyzing the interplay between structure and dynamics in food webs (see Pascual and Dunne, 2006 for the state-of-the-art). The influential work of Robert May in the 1970s (May, 1972, 1974) was a cornerstone of this approach and a breaking point with the former belief of ecologists that higher food-web complexity promotes a higher stability in the dynamics of the network. More recently, it was shown that the presence of weak trophic links in food chains tends to stabilize the dynamics of the latter by dumping down population fluctuations and preventing the loss of species (McCann et al., 1998). Therefore, the cohesive role of complexity overtook again the ecological understanding of complex webs (Polis, 1998). Lately, the role of weak links in the stability of trophic chains has been extended in terms of fast and slow energy channels in food webs, where the former are composed mainly by strong links, which are characterized by high biomass turnover rates, whereas slow channels are richer in weak links. Such an asymmetry in the energy pathways inside a food web has been claimed to confer stability to it (Rooney et al., 2006).

Weak links can be considered in model food webs by means of the so-called adaptive foraging theory. Under this assumption, consumer species maximize the energy gain per unit of foraging effort by changing behaviorally their food preferences. This feature introduces flexibility in the strength of trophic interactions and, hence, in the food-web configuration. However, while in most of the models the update of such a maximization is taken to be instantaneous (Drossel et al., 2001; Křivan and Schmitz, 2003; Křivan and Diehl, 2005), only few works consider dynamical equations for the evolution of foraging efforts (Brose et al.,

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These latter works present innovative models that provide a better understanding of the interplay between dynamics and complexity in food webs, which is one of the main concerns in ecology.

Another goal in the comprehension of complex ecological systems is to achieve a general description of food-web structure by means of simple (statistical) laws. The existence of a constant mean number of trophic links per species across different network sizes was an empirical prediction supported by the first food-web descriptions in the 1980s and was termed link-species scaling law. However, during the 1990s, from the analysis of improved food-web datasets, it seemed that real food webs are better described by the so-called constant connectance law. Denoting by \( L \) the number of links in the food web, by \( S \) the species richness, and by \( C \) the network connectance (i.e., \( C = L/S^2 \)), both situations can be described by the relation \( C = aS^b \), with \( b \approx -1 \) in the link-species scaling law (MacDonald, 1979; Rejmánek and Stárny, 1979; Briand, 1983; Briand and Cohen, 1984; Sugihara et al., 1989) and \( b \approx 0 \) in the constant connectance law (Warren, 1990; Martinez, 1992, 1993). Recent field observations of food webs with high level of resolution show that, indeed, the exponent \( b \) takes values between these two extreme cases (\( b = -0.6, -0.7, -0.5 \) in Havens, 1992; Schmid-Araya et al., 2002; Dunne et al., 2004, respectively). Moreover, food-web connectance seems to be constrained to the interval \([0.03, 0.3]\), with a central tendency in \([0.1, 0.15]\) (Pascual and Dunne, 2006, Chapter 2; Dunne et al., 2002).

Following the dynamical approach introduced by Kon dokh (2003) for both populations and diet choice, we will consider a multi-species bioenergetic model (Yodzis and Innes, 1992; Brose et al., 2003) with a fixed fraction of adaptive predators investing different foraging efforts on different prey species according to the aforementioned basic rule of the foraging theory. Under this modeling framework we see that, when a significant degree of adaptive predation is present and regardless the stochastic model used to generate the initial configuration of a food web (the cascade or the niche model), the more connected a final food web is, the less species it has. This fact is nicely reflected by a hyperbolic law between the final connectivity of a food web and its number of survival species. Moreover, we also show that the analysis of the fraction of survival species in terms of the initial connectance, instead of the final connectance, is the reason for the apparent positive complexity–stability relationship in food webs where initial configurations are obtained from the cascade model. Altogether, our results overturn some existing ideas about the role of the initial food-web configuration (cascade or niche) and contribute to clarify the complexity–stability relationship in dynamic food-web models.

2. The food-web model

The evolution in time of the abundance of each species in the food web is modeled as a dynamical system on an underlying graph (nodes and links) that defines the network configuration. We use a bioenergetic model for trophic interactions (Yodzis and Innes, 1992) with the assumption of dynamic foraging efforts (Brose et al., 2003; Kon dokh, 2006). Precisely, denoting by \( x_i = x_i(t) \) the density (or biomass) of species \( i \) of a total number of \( S \), its dynamics is governed by

\[
\frac{dx_i}{dt} = r_i \left( 1 - \frac{x_i}{k_i} \right) x_i - \sum_{j=1}^{S} l_{m_{ij}}F_{ij}(X)a_{ij}x_i - \sum_{j=1}^{S} l_{m_{ij}}F_{ij}(X)a_{ij}x_j,
\]

(1)

where \( r_i \) is the growth rate which is non-zero only for basal species, \( m_{ij} \) is the maximum assimilation rate (per unit metabolic rate) of \( i \) in consuming \( j \), \( l_i \) is the mass-specific metabolic rate, \( k_i \) is the carrying capacity, \( a_{ij} \) is the rate of foraging effort that predator \( i \) spends on prey \( j \), and \( F_{ij}(X) = f_{ij}x_j/(B_{ij} + \sum_{k=1}^{S} a_{ik}x_k) \) is the Holling’s type II functional response with \( f_{ij} \) being the foraging efficiency of \( i \) in consuming \( j \), and \( B_{ij} \) being the half-saturation rate of \( i \) in consuming \( j \). Basal species are those prey species that have no prey.

The dynamics of the foraging effort \( a_{ij} \) is driven by a differential equation of the replicator type that compares the energetic gain that predator \( i \) would obtain in consuming only prey \( j \) with its actual energetic gain, that is,

\[
\frac{da_{ij}}{dt} = g_{ij} \left( l_{m_{ij}}F_{ij}(X) - \sum_{k=1}^{S} l_{m_{ik}}a_{ik}F_{ik}(X) \right),
\]

(2)

where \( g_{ij} \) is the adaptation rate of \( i \). The efforts of every predator \( i \) satisfy the trade-off condition

\[
\sum_{j=1}^{S} a_{ij}(t) = 1 \quad \forall t > 0.
\]

(3)

This is guaranteed by the fact that, according to (2), \( \sum_{j=1}^{S} da_{ij}/dt = 0 \), and by the choice of initial conditions \( a_{ij}(0) \) satisfying (3). The \( a_{ij}(t) \) functions give the structure of the underlying graph of the food web as a function of time. Note that \( a_{ij}(T) = a_{ij}(T) = 0 \) for some \( T > 0 \) (and hence for all \( t \geq T \)) means that the graph at time \( T \) does not have a link between \( i \) and \( j \) (and nevermore). That \( a_{ij}(t) > 0 \) indicates that \( i \) is a predator of \( j \) at time \( t \), and thus the graph has a (directed) link from \( j \) to \( i \) at this time.

The parameter values used in the simulations are \( k_i = 1, m_{ij} = 6, B_{ij} = 1, f_{ij} = 1, l_i = 0.5 \). These values are inherited from Brose et al. (2003) and Kon dokh (2006), and, therefore, allow us to compare our simulation results and conclusions with those previously published by those authors. Note that, under this choice of parameter values, it is assumed that all non-basal species are metabolically equivalent in the sense that all of them have the same foraging efficiencies \( f_{ij} \) and the same maximum assimilation rates \( m_{ij} \), regardless of the trophic level of the \( j \)-species and the \( j \)-species. The only differences among species are
the set of predators preying upon them, and their set of prey. Other parameter values give rise to similar qualitative results as long as this mean field assumption holds. Finally, growth rates are set equal to 1 (\(r_i = 1\)) for all basal species.

The initial configuration of the trophic relationships among species is given by those efforts \(a_{ij}(0) > 0\) and is established by means of a randomly generated community matrix with a given connectance \(C = L/S^2\). Two different stochastic models are considered to generate the community configuration: the cascade model (Cohen and Newman, 1985) and the niche model (Williams and Martinez, 2000). In the niche model, the existence of at least one basal species is guaranteed by assigning the species with lowest niche value to this trophic group, while such an existence is guaranteed in the cascade model because the species with the lowest rank in the cascade hierarchy is, by definition of the model, a basal species.

To assign the ability of being an adaptive predator, we take into account the following rule: the larger the set of prey of a predator is, the more capable of adaptation it is. So, it will be important to order the predators in terms of the number of prey species they have and assign foraging adaptation ability to the \(Q\) fixed fraction that have more prey. As expected, a simple rank correlation reveals that the strong hierarchy of food webs furnished by the cascade model gives us the desired order (Spearman’s correlation coefficient \(\rho \approx 0.95\) for network sizes \(S = 20, 30\), and \(C = 0.3\)). On the contrary, we find a lower rank correlation for the niche model because predators with a high niche value have few prey and vice versa (Spearman’s correlation coefficient \(\rho \approx 0.64\) for \(S = 20, 30\), and \(C = 0.3\)). In preceding models (Kondoh 2003, 2006; Brose et al., 2003) foraging adaptation was randomly assigned with probability \(Q\) among predator species. Therefore, in our model, \(Q\) is the fraction of potential adaptive predators that effectively become adaptive since, for those predators preying only on one species, adaptation is meaningless.

The adaptation rate of species \(g_i\) is taken to be equal to 1 for all adaptive predators, and 0 otherwise. This choice implies that adaptation and population dynamics take place at the same time scale, and thus that adaptation is due to behavioral changes. Therefore, values of \(g_i\) of the same order will render the same qualitative results. It is worth noticing that this assumption does not imply an instantaneous optimal adaptation (Drossel et al., 2001; Křivan and Schmitz, 2003) because, in this case, predators continuously would adopt the optimal foraging efforts and, hence, it is required that the behavioral time scale to be faster than the populational one. Conversely, when changes in diet choice are assumed to be an evolutionary process, adaptation dynamics takes place at a much lower time scale than the populational one and, hence, adaptation rates are close to 0. In this latter case, previous works have shown that the presence of adaptive predators plays no role in the food-web dynamics (see Kondoh, 2003, 2006; Brose et al., 2003).

In the numerical simulations of the model, for every choice of initial number of species \(S(0) = 10, 20, 30\), of initial connectance \(C(0) = 0.2, 0.3, 0.4\), starting food-web pattern (niche or cascade), and fraction of adaptive predators \(Q = 0, 0.25, 0.75\), we generate 100 random matrices. For each matrix, the initial value for the foraging effort that species \(i\) invests on prey \(j\) \((a_{ij}(0))\) is set equal to 1/(initial number of preys of \(i\)). The initial values for the abundance densities of species \(i\) \((x_i(0))\) are randomly taken between 0 and 1.

We let the system given by Eqs. (1) and (2) evolve in time until \(T = 500\) (for which the dynamics is sufficiently close to an equilibrium point). At this time, we remove species and links for which abundance and foraging effort fall below \(10^{-10}\), respectively. If species \(i\) is removed, so are all links emanating from/arriving at \(i\). After that, we register the final number of species \(S(T)\) in the resulting food web and its final connectance \(C(T)\).

3. Results

After the network evolution in time according to Eqs. (1) and (2), food webs with a fraction of adaptive predators in their initial configuration show a functional relationship between connectance and number of surviving species of the form \(C(T) \propto S(T)^b\) with \(b \in (-1, 0)\) (Fig. 1). This fact does not depend on the stochastic model used to generate the initial food-web configuration (cascade or niche), although the value of the exponent \(b\) is slightly different in each case (Table 1). In both cases, the range of persistent species increases significantly with the fraction \(Q\) of adaptive predators, which leads to a better goodness of fit for \(Q = 0.75\). In particular, for this value of \(Q\), the size of this range is doubled in networks generated with the cascade model with respect to that in networks generated with the same model but with \(Q = 0.25\) (Fig. 1B, C).

A summary of the results of the potential regressions according to different stochastic models and different values of \(Q\) is shown in Table 1. The best fit of the data to a potential function is achieved by food webs initially constructed using the niche model with \(S(0) = 30\) and \(C(0) = 0.4\).

Comparing Fig. 1B, C with Fig. 1E, F it follows that, with the cascade model, the deviations of \(C(T)\) from its expected value according to a potential law are smaller than those with the niche model. This is due to the fact that, under the cascade model, the range of potential food-web configurations is smaller than under the niche model (Williams and Martinez, 2000). In order to reduce the initial food-web variability, we have compared final configurations of food webs initially generated by the niche model and by the cascade model with similar realized initial connectances (between 0.3 and 0.35), and having one or two basal species. These final configurations, described in terms of connectance, \(C(T)\), and species richness, \(S(T)\), are shown in Fig. 2A, B, respectively, whereas the aggregate data of these figures are shown in Fig. 2C.
Fig. 1. Scatter plots of connectance and species persistence after time evolution until \( T = 500 \), segmented by stochastic model: cascade model (A–C) and niche model (D–I), and fraction of adaptive predators \( Q = 0 \) (A, D, and G), \( Q = 0.25 \) (B, E, and H) and \( Q = 0.75 \) (C, F, and I). Curves are potential regressions (see Table 1 for statistic values for \( Q = 0.25, 0.75 \)). Circles in A–F represent the output of 100 realizations of numerical simulations of the model for every choice of an initial connectance \( C(0) = 0.2, 0.3, \) and 0.4, and an initial number of species \( S(0) = 10, 20, \) and 30. Circles in G, H, and I are the output of 100 realizations of numerical simulations for food webs initially generated with the niche model with \( C(0) = 0.4 \) and \( S(0) = 30 \). Note that for \( Q = 0 \) the number of coincident results is larger than for \( Q = 0.75 \), and also that there are more coincident results with the cascade model than with the niche model.

Table 1
Potential type regressions for connectance–persistence relationships in Fig. 1B, C, E, F, H, and I, with \( Q = 0.25, 0.75 \), and mean and standard deviation (\( \bar{C}, \sigma \)) of the connectance distributions

<table>
<thead>
<tr>
<th>Case</th>
<th>Model</th>
<th>( Q )</th>
<th>Data</th>
<th>( C = a S^b )</th>
<th>( R^2 )</th>
<th>( \bar{C} )</th>
<th>( \sigma )</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>Cascade</td>
<td>0.25</td>
<td>Aggregated data</td>
<td>( a = 0.403, b = -0.569 )</td>
<td>0.669</td>
<td>0.149</td>
<td>0.039</td>
</tr>
<tr>
<td>C</td>
<td>Cascade</td>
<td>0.75</td>
<td>Aggregated data</td>
<td>( a = 0.495, b = -0.704 )</td>
<td>0.773</td>
<td>0.091</td>
<td>0.035</td>
</tr>
<tr>
<td>E</td>
<td>Niche</td>
<td>0.25</td>
<td>Aggregated data</td>
<td>( a = 0.393, b = -0.567 )</td>
<td>0.575</td>
<td>0.161</td>
<td>0.090</td>
</tr>
<tr>
<td>F</td>
<td>Niche</td>
<td>0.75</td>
<td>Aggregated data</td>
<td>( a = 0.406, b = -0.595 )</td>
<td>0.719</td>
<td>0.123</td>
<td>0.067</td>
</tr>
<tr>
<td>H</td>
<td>Niche</td>
<td>0.25</td>
<td>( S(0) = 30, C(0) = 0.4 )</td>
<td>( a = 0.459, b = -0.624 )</td>
<td>0.663</td>
<td>0.205</td>
<td>0.115</td>
</tr>
<tr>
<td>I</td>
<td>Niche</td>
<td>0.75</td>
<td>( S(0) = 30, C(0) = 0.4 )</td>
<td>( a = 0.447, b = -0.657 )</td>
<td>0.860</td>
<td>0.126</td>
<td>0.076</td>
</tr>
</tbody>
</table>
Remarkably, in this figure, both datasets fit in a complementary manner to a hyperbolic relationship due to the different dependence of $C(T)$ on the initial connectance under each stochastic model (see the next paragraph). In the particular case of final configurations of food webs with one basal species (filled circles), this hyperbolic relationship between $C(T)$ and $S(T)$ becomes clearly noticeable (see Discussions for details).

For a high degree of adaptive predation in the food web ($Q = 0.75$), plotting the mean percentage of persistent species ($Robustness$) and the mean final connectance ($Mean\ C(T)$) as functions of the realized initial connectance ($Realized\ C(0)$) (Fig. 3C, F), it follows that the more connected a final food web is, the less species it has, but the dependency of this fact with realized $C(0)$ under the cascade model: $Mean\ C(T)$ increases with realized $C(0)$ under the cascade model while it decreases with realized $C(0)$ under the niche model. On the contrary, with no adaptive predation at all ($Q = 0$) or with a low degree of it ($Q = 0.25$), networks initially generated by both stochastic models share the same behavior as functions of realized $C(0)$ (Fig. 3A, B, D, and E). In all cases, food-web robustness increases monotonously with the fraction $Q$ of adaptive predators, whereas the mean final connectance decreases monotonously. Note that, only for $Q = 0$, the mean fraction of survival species in food webs generated under the cascade model is always lower than that of food webs generated under the niche model regardless the value of the realized $C(0)$, whereas the mean final connectance under the cascade model is always higher than under the niche model.

4. Discussions

Two important conclusions follow from the results showed in Fig. 1. First, comparing the evolution of networks generated with both stochastic models without adaptive predation ($Q = 0$) and with it ($Q = 0.25, 0.75$), it follows that adaptive predation acts as a catalyzer that drives the network dynamics toward optimal configurations where connectance and number of surviving species are balanced. This is particularly clear for high values of initial connectance and initial species in food webs whose initial configuration is provided by the niche model. These values and the higher variability of the niche model give chance to explore a larger number of network configurations with a low number of basal species (Kondoh, 2006). Hence, a sharp convergence to an optimal configuration emerges from such a degree of freedom in the network (see Fig. 1I). This convergence becomes manifest under both stochastic models in food webs with a large fraction of adaptive predators and with one or two basal species. This low number of basal species clearly restricts the number of feasible food-web architectures under both stochastic models increases as well, and the food-web...
evolution leads to a greater variability in the final configurations (see Fig. 2).

Secondly, when a fraction of adaptive predators is initially present, the model predicts a power-law connectivity–persistence relationship for aggregated data whose parameters are close to the empirical data of recent papers (Dunne et al., 2004; Havens, 1992; Schmid-Araya et al., 2002). Moreover, there is no remarkable difference between food webs whose initial structure is given by the niche or the cascade model, from which we derive that the initial food-web configuration does not have a great influence on the balance, which seems to be a final feature depending mostly on the dynamics itself. In fact, the main role of adaptive predation, under both stochastic models, is to increase species persistence which depends crucially on the initial fraction of adaptive predators.

Kondoh (2003) studied the influence of foraging adaptation on species survival in food webs that were generated according to the cascade model. The conclusion of his numerical results was that the presence of a significant fraction of adaptive predators can stabilize complex food webs and, hence, there was a positive correlation between connectivity and species persistence in food webs. These results were argued by Brose et al. (2003) using a different model for the population dynamics. While for the cascade model the same behavior was observed, for the niche model this correlation became negative. To be precise, and using our notation, what was proved in the cascade case was the positive correlation

Fig. 3. Plots for the niche model and the cascade model representing the mean percentage of persistent species (Robustness) (A, B, and C) and final connectivity $C(T)$ (D, E, and F) as a function of the realized initial connectivity (Realized $C(0)$), with a fraction of adaptive predators $Q = 0.0, 0.25, and 0.75$. Theoretical initial connectances of $0.2, 0.3$, and $0.4$ are considered for each stochastic model. For every realization, the initial connectivity is computed and the resulting range of values of Realized $C(0)$ is split in four intervals from 0.1 to 0.5. Lines connect the mean value of Realized $C(0)$ for each interval (circle) considering the aggregated data for $S(0) = 10, 20, and 30.$
between initial connectance $C(0)$ and the fraction of persistent species, while for the niche model this correlation becomes negative, always under the adaptive foraging assumption. But this is only one half of the story.

Our numerical investigations agree with both results as it is shown in Fig. 3C, where the fraction $Q$ of adaptive predators is set equal to 0.75. But, in a complementary and revealing way, Fig. 3F shows that, in both cases, the correlation between initial and final connectances is the other way round: negative for the cascade model and positive for the niche model. Clearly, this has to be the case when a large fraction of predators are adaptive since, then, the more connected a final food web is, the less species it has (see Fig. 1C, F, and I). An explanation for such a different behavior under each stochastic model (when a large fraction of adaptive predators is present) lies in the higher degree of complexity inherent to the niche model, under which cannibalism and mutual predation are present in the initial food web. For high initial connectances, this greater complexity implies a significative number of direct and indirect effects on the dynamics of the population densities, which diminish the whole persistence in the food web as time goes on but, in turn, the remaining species exhibit a higher connectance than those whose initial configuration is generated by the cascade model. Interestingly enough, the behavior of Robustness as a function of realized $C(0)$ for $Q = 0$ is similar to the one obtained by Martinez et al. (2006) (see Pascual and Dunne, 2006, p. 171, Fig. 1d) for the same stochastic models under a non-adaptive mechanism for assigning foraging efforts to omnivore species.

Therefore, the influence of the adaptive predation hypothesis on the explanation of the complexity–stability relationship remained unclear after the works by Kondoh (2003) and Brose et al. (2003), and the more recent by Kondoh (2006) where the role of basal species in enhancing the food-web complexity is emphasized. However, it is important to note that foraging adaptation implies that the dynamics relies not only on the species density (nodes in the network) but also on the species interactions (links in the network), and consequently the action of dynamics on the network can make links or/and nodes disappear, thus obtaining a rich spectrum of topologies that cannot be achieved without this hypothesis. This means that the number of surviving species in a food web and its connectance must be viewed as functions depending on time, $S(t)$ and $C(t)$, respectively. So, results in Brose et al. (2003) and Kondoh (2003), although incorporating adaptive predation, share the same methodological lack, namely, the complexity–stability relation in food webs cannot be explained in terms of the initial connectance $C(0)$ since food-web evolution introduces changes in their connectance.

A correct reading of the numerical simulations reveals that, after the action of dynamics and when a significant fraction of adaptive predators is present, the resulting food-web configuration shares the same qualitative topological features, independently of the initial configuration (niche or cascade). In other words, the complexity–stability relationship in both cases turns out to be negative. Remarkably, the relationship between $C(T)$ and $S(T)$ is clearly hyperbolic, reminding May’s criterion for the (linear) stability of Lotka–Volterra systems defined on randomly constructed networks (May, 1972), and reflecting simple food-web topologies. However, it is also noteworthy that the way to attain these final configurations by dynamic model food webs depends on the stochastic model used to generate their initial configurations. While under high enough initial connectances, the cascade model renders richer food webs with lower final connectances than those provided by the niche model, under low initial connectances the situation is the opposite, namely, poorer food webs with (slightly) higher final connectances are provided by the cascade model.

Foraging adaptation, although permitting of weak trophic links among species and enhancing species persistence, is not sufficient to create a positive complexity–stability relationship in food-web models. Other mechanisms related to the appearance of new species not considered in the present approach, like species co-evolution (Quince et al., 2005) or migratory flows among populations, could be responsible of an additional number of weak links in food webs and might allow this relationship to be positive.

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References
