

Evolutionary emergence of size-structured food webs

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Explaining the structure of terrestrial and aquatic food webs remains one of the most important challenges of ecological theory. Most existing models use emergent properties of food webs, such as diversity and connectance as parameters, to determine other food-web descriptors. Lower-level processes, in particular adaptation (whether by behavioral, developmental, or evolutionary mechanisms), are usually not considered. Here, we show that complex, realistic food webs may emerge by evolution from a single ancestor based on very simple ecological and evolutionary rules. In our model, adaptation acts on body size, whose impact on the metabolism and interactions of organisms is well established. Based on parameters defined at the organism scale, the model predicts emergent properties at the food-web scale. Variations of two key parameters (width of consumption niche and competition intensity) allow very different food-web structures and functionalities to emerge, which are similar to those observed in some of the best-documented food webs.

complex adaptive system | evolutionary assembly | macroevolution | food-web structure

Although prevailing food-web models, such as the cascade model (1, 2), the niche model (3), and the more recent nested-hierarchy model (4), are able to describe food-web structure satisfactorily, they fail to provide clear mechanisms explaining how this structure emerges. There are two reasons for this shortcoming. First, these models are parameterized by using some emergent properties of observed food webs (usually diversity and connectance), although these properties result from lower-level processes. Second, they consider only binary food webs in which species and trophic links are either present or absent, but are not quantified. The dynamical aspects of food webs, linked to population dynamics and adaptation processes, although ubiquitous in ecosystems (5), are absent from these theoretical studies.

Consideration of adaptive processes may provide new approaches to understand the structure and functioning of food webs. A few recent pioneering studies (6–8) have suggested that complex food webs may emerge from evolutionary assembly processes. These models consider variations of a large set of traits that determine the strength of predator–prey interactions. Considering a large number of traits is appealing because many characteristics are likely to have a role in trophic interactions. However, because these traits are numerous and are not explicitly identified, it is not possible to understand the evolutionary dynamics in terms of selective pressure or to test model predictions by using empirical data. Here, we propose a simpler approach in which body size is the single biological trait subject to evolution. This simple approach allows us to make testable predictions on how evolution shapes ecosystem structure and functioning.

Model and Methods

The reasons for using body size as a key trait are numerous. The trophic cascade model (1, 2) is based on a hierarchy among species, and body size is a good candidate to explain this hierarchy (9, 10). Body mass, M , is also tightly linked to individual metabolism, B , by the allometric relation $B \cong M^a$. The exponent a in this relation is usually 0.75 (11–13), or -0.25 if

metabolism is measured per unit mass (mass-specific metabolic rate) (13). Because of this allometric relation, it is possible to correlate body size and a number of life-history traits of organisms, thereby making a link between organismic and community scales (13, 14). We modeled the population dynamics of species i with biomass N_i and body size x_i by

$$\frac{dN_i}{dt} = N_i \left(f(x_i) \sum_{j=0}^{i-1} \gamma(x_i - x_j) N_j - m(x_i) - \sum_{j=1}^n \alpha(|x_i - x_j|) N_j - \sum_{j=i+1}^n \gamma(x_j - x_i) N_j \right), \quad [1]$$

where the x_i are ranked by increasing values, $f(x_i)$ is the production efficiency of species i , and $m(x_i)$ is its mass-specific mortality rate. Because these two parameters are related directly to mass-specific metabolic rate, they are assumed to depend on body size (13): $f(x_i) = f_0 x_i^{-0.25}$ and $m(x_i) = m_0 x_i^{-0.25}$.

The function $\gamma(x_i - x_j)$ describes the consumption rate exerted by predator i on prey j . It is assumed to be a Gaussian function with standard deviation s and a maximum value when the body sizes of the predator and the prey are separated by a distance d as follows:

$$\gamma(x_i - x_j) = \frac{\gamma_0}{s \sqrt{2\pi}} \exp \left[\frac{-(x_i - x_j - d)^2}{s^2} \right],$$

with $x_i > x_j$ (Fig. 1). The choice of this type of function is based on the idea that, for a predator of a given size, energy gains should increase with its prey body size, whereas the probability of such successful attacks should decrease with the prey body size. As a result, body size should then be optimum at an intermediate value. This type of relationship between interaction strength and body size is supported by empirical data (13, 15, 16).

Exploitation competition among individuals of similar size is implicit in the γ function because they consume the same kind of resources. Also, these individuals of similar body size may also hamper, interfere physically, or even harm each other while competing for the resource. This interaction is called “interference competition.” The function $\alpha(|x_i - x_j|)$ corresponds to the interference-competition rate and is defined as follows:

$$\alpha(|x_i - x_j|) = \begin{cases} \alpha_0 & \text{if } |x_i - x_j| \leq \beta \\ 0 & \text{if } |x_i - x_j| > \beta. \end{cases}$$

The value of β was chosen to be small (0.25), which means that competition is assumed to occur mainly within species or with closely related types. Interference competition among species with similar body sizes has been shown in some groups (17); the mechanisms involved may be interference (18, 19). Habitat partitioning leads to similar effects (20). Our qualitative results

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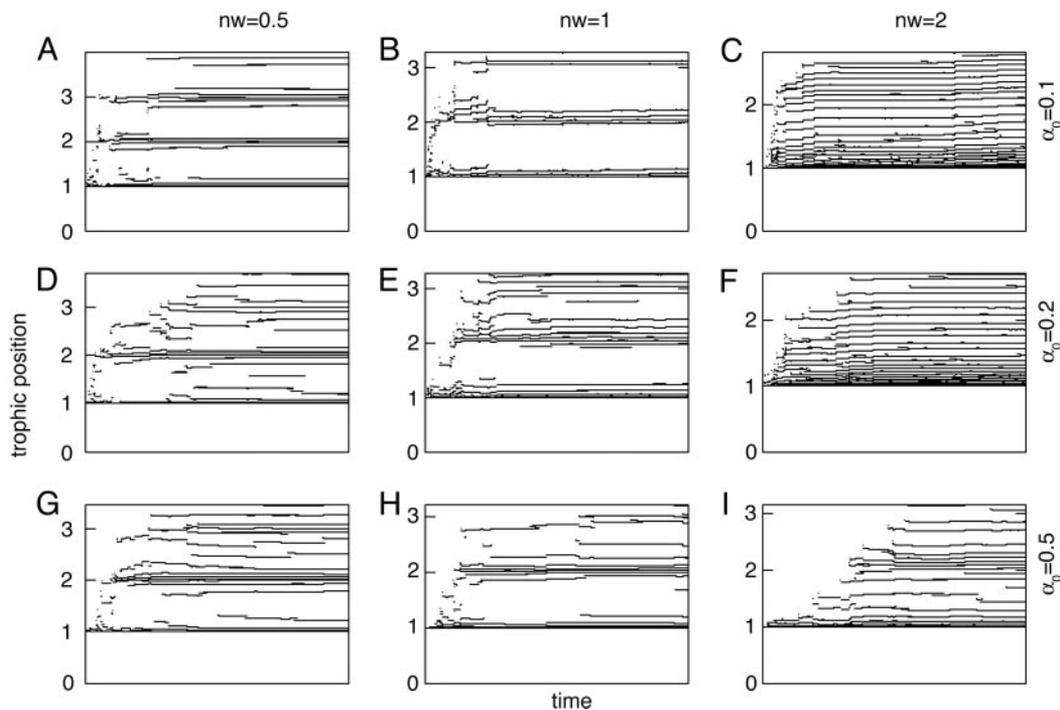


Fig. 2. Food-web structure. The evolution of simulated food webs during 10^8 time steps for three values of niche width (nw) and competition intensity (α_0) is shown. Trophic position is computed as explained in *Model and Methods*. Because this measure is strongly correlated with body size, similar patterns would be obtained by using body size. The following parameter values were used in these simulations: $l = 10$, $e = 0.1$, $v = 0.5$, $\gamma_0 = 1$, $d = 2$, $f_0 = 0.3$, $m_0 = 0.1$, and $\beta = 0.25$.

chain length, and the distribution among bottom, intermediate, and top species. This variability underlines the limits of the binary approach to describing food webs because the threshold value depends on the reliability of the determination of trophic interactions in the field. Although the threshold value may have an impact on the absolute value of the aggregated food-web parameters measured, it is unlikely to have an impact on their qualitative variations with niche width and competition intensity.

The structure of the resulting binary food webs was described by using classical parameters. Quantitative changes in the emergent properties of our model food webs with niche width and competition intensity are displayed in Fig. 3. Connectance is measured as $2L/S(S-1)$, where L is the total number of links and S is the number of species. Chain length corresponds to the mean chain length in the food web. Omnivory is measured by the proportion of species that are able to eat species positioned at different levels in the food chain. “Bottom” corresponds to the

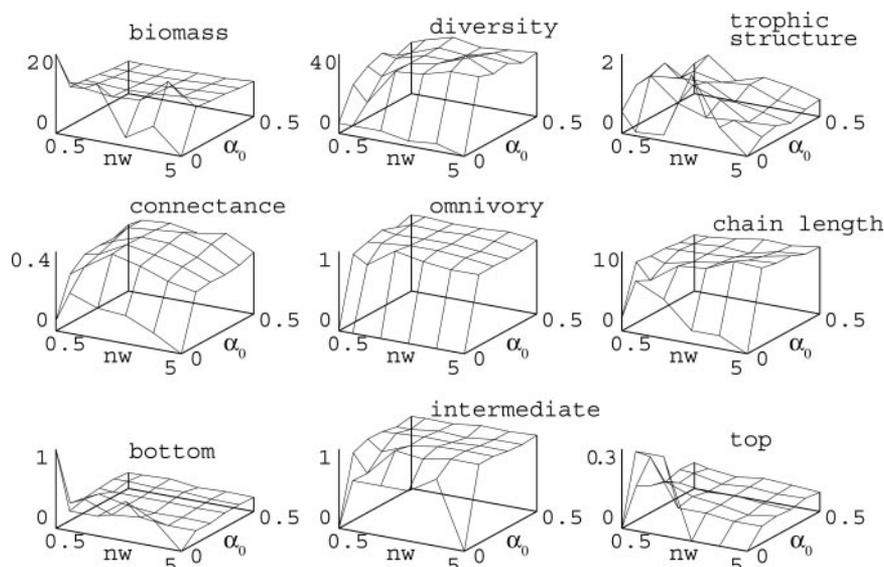


Fig. 3. Emergent properties of simulated food webs as functions of niche width (nw) and competition intensity (α_0). Properties were measured at the end of simulations (i.e., after 10^8 time steps). See *Model and Methods* for computation of the various properties. Parameter values are as in Fig. 2.

proportion of species feeding on the inorganic nutrient, “top” corresponds to the proportion of species that are not consumed by any other species, and “intermediate” corresponds to the remaining species in the food web. Fig. 3 also shows variations of a trophic structure index. It corresponds to the ratio between the variance of the difference between two adjacent body sizes and the expected variance of this variance for a random distribution of these traits (26). This index is expected to be high if species are packed in distinct trophic levels and low if species are homogeneously distributed along the body-size axis.

However, for many food-web properties, competition intensity appears to be more important than niche width (Fig. 3). In particular, substantial variations in these properties occur between the cases in which interference competition is absent ($\alpha_0 = 0$) and present, even at a low level ($\alpha_0 = 0.1$). Webs without interference competition contain very few species (usually three or four). Because evolution of the community is then only driven by consumption, their structure is chain-like (high trophic structure index, low connectance, and low omnivory). Populations then tend also to have unstable dynamics.

Interference competition favors the emergence of diversity (Fig. 3). The trophic structure index confirms the important role of the niche width shown in Fig. 2. As explained above, competition tends to homogenize the body-size distribution and, therefore, to increase the connectance as well as the omnivory. As the connections between species become more numerous, the mean chain length increases. If the competition intensity is fixed, connectance is maximum at intermediate value of the niche width. This intermediate optimum may be explained by the fact that increasing niche width blurs the trophic structure (Fig. 2), making it more connected, but it decreases the interaction strength (the γ function being normalized), thus decreasing the probability of recording this interaction. This decrease in the mean interaction strength as nw increases also explains why the omnivory index decreases. Last, note that variations of the total biomass with the parameters are weak, which means that the evolved communities are similar in their efficiency to exploit the resource.

Based on these results, we selected the niche width and competition intensity giving the best match between the properties of our model ecosystems and those of seven of the best-documented food webs. By using the data shown in Fig. 3, we interpolated the values for connectance, omnivory, chain length, and distribution among bottom, intermediate, and top species in our model food webs. Least-square fitting of the interpolated functions to the observed properties of the seven documented food webs allowed us to determine the niche width and competition intensity that would best match model predictions and observations. Biomass and diversity were not included because these two properties are determined mainly by nutrient input I and production efficiency $f(x_i)$ in our model. Also, we did not consider the trophic structure index in the comparison because this property is not documented in empirical data. Although we are aware that a lot of other properties could have been included, we limited our study to the six properties mentioned above, for two main reasons. First, some properties (such as number of loops) are not relevant given the assumptions of the model. Second, our model cannot be fully predictive because data on niche width and competition intensity are not available for the observed food webs. We performed the comparison between predicted and observed webs to show simply that the variety of structures found in the model is representative of the variety of structures observed in nature. Reliable data on interaction strength in food webs would make the comparison with the results of our model much more interesting.

Observed food webs fall into three groups (Fig. 4). One group includes the food webs of the Ythan Estuary, the Chesapeake Bay, and St. Martin Island. These food webs have very similar

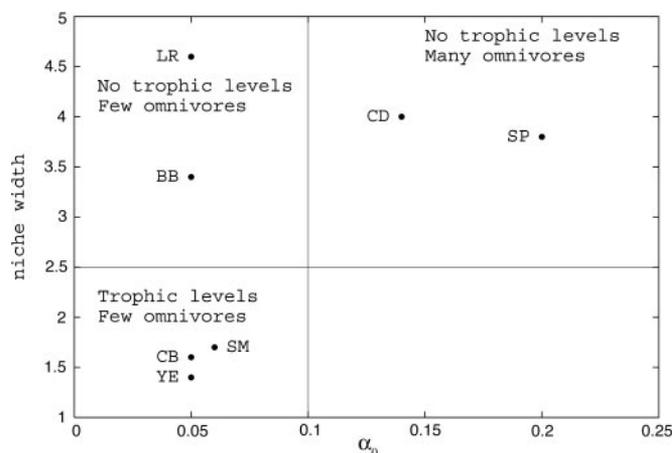


Fig. 4. Comparisons with documented food webs. Niche width and competition intensity that lead to food-web properties that best fit those of seven well documented food webs (BB, Bridge Brook Lake; CB, Chesapeake Bay; CD, Coachella Desert; LR, Little Rock Lake; SM, St. Martin Island; SP, Skipwith Pond; and YE, Ythan Estuary). We use the emergent properties given in Table 1. The main characteristics of the corresponding model food webs (level of omnivory and trophic structure) are indicated to give a better idea of the structure of the evolved communities. Empirical data are from Cattin *et al.* (4). Parameters are the same as in Fig. 2.

properties and are comparable with evolved food webs in which competition is weak and niches are narrow (well differentiated trophic levels and little omnivory). Another group includes Little Rock Lake and Bridge Brook Lake, which have properties that are comparable with evolved food webs in which competition is weak and niches are broad (poorly defined trophic structure). The third group consists of Coachella Desert and Skipwith Pond. Their properties are comparable with evolved food webs in which competition is strong and niches broad (blurred trophic levels and large proportion of omnivores). The characteristics of these empirical food webs and their model counterparts are summarized in Table 1. For comparison, the corresponding predictions from the niche model are also included. The relative errors of the two models show that our evolutionary model is usually better at fitting the emergent properties than the niche model is. Comparison between the niche model and ours is limited by the fact that the niche model has been used to fit more properties and considers connectance as a parameter. However, note that the evolutionary model is unable to reproduce the high proportion of basal species (Skipwith Pond) or the very low connectance (Chesapeake Bay and Ythan Estuary) that are sometimes observed in food webs.

Discussion

The qualitative results presented here are robust to variations in other parameters. In particular, we varied nutrient input I (1, 10, and 100), basal production efficiency f_0 (0.1, 0.3, and 0.5), and the threshold parameter β below which two species compete (0.1, 0.25, and 0.5). Other simulations were performed at very low values of the competition rate α_0 (0.001, 0.01, 0.025, 0.05, and 0.075) because several emergent food-web properties are particularly sensitive to changes in this range (Fig. 3). We also replaced the linear functional response of the predator by a Holling type II function. In total, 201 simulations were made to check the robustness of the results. The production efficiency $f(x_i)$ and inorganic nutrient input I have large, positive effects on phenotypic diversity, total biomass, and maximum trophic position, in agreement with many ecological data and models (23, 27–29). The production efficiency $f(x_i)$ and mortality rate $m(x_i)$ also affect the distribution of biomass within the food web (top

basal species). Our model could give a good description of aquatic or soil food webs, because they seem to be largely size-structured. It is also likely to be applicable to ecosystems that are relatively closed, ensuring that local adaptation is important, or in open systems in which invaders have traits that are not too different from resident populations. In contrast, it should not apply to systems invaded by exotic species introduced by human activities. If it were considered as a macroevolutionary model *sensu stricto*, we expect that the process of the evolutionary assembly would require long periods of time and, hence, take place on large spatial scales. Last, if rules applied here to link size and consumption were reversed, the model might be used to portray parasite–host interactions.

We think that the main strengths of our model lie in the fact that it provides (i) an approach to investigate the links between adaptive dynamics, community ecology, and ecosystem functioning, and (ii) testable predictions on the evolutionary consequences of body size for food-web structure. Although a single trait was considered here, the variety of structures obtained is impressive, and the extension of our evolutionary framework to include a few other well chosen traits should enlighten our understanding of natural food webs.

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