

# Emergence and Analysis of Complex Food Webs in an Individual-based Artificial Ecology

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**Abstract**—Food webs are complex networks of trophic interactions in ecological communities that are crucial in creating and maintaining biodiversity, and are prominent examples of biological complexity themselves. In this paper, we present an individual-based model of an artificial ecology demonstrating the emergence of complex food webs through the evolution of rich phenotypes. Individuals are simple structures that map several traits in a nonlinear fashion. Interaction and evolution of these structures leads to the self-assembly of food webs in complex ecological communities. Ecological and network analysis of the evolved artificial ecologies shows remarkable similarities in various patterns known from natural ecological communities.

## I. INTRODUCTION

**F**OOD WEBS are descriptions of ecological communities that capture feeding relations between the member species. The trophic interactions between species are a fundamental attribute of communities that relate biodiversity to ecological stability. Research on food webs has therefore long been a central topic in ecology. Traditionally, these studies have focused on static topological patterns in food webs [1], [2]. More recently, there is an increasing interest for the dynamic processes by which trophic networks are assembled [3], [4], [5]. As customary in theoretical ecology, food web models typically study interactions between species, using populations as the basic modeling units, without consideration of emergent effects of the interactions between individual organisms.

Here, we propose an artificial life approach to food web studies. Creating individual-based artificial ecologies that evolve and self-assemble in trophic networks can help understanding the fundamental properties underlying ecological communities [6]. Artificial food webs circumvent many constraints of laboratory or field experiments that are severely limited in space and time and sampling efforts. Moreover, artificial ecologies can be manipulated in ways that are impossible for real communities.

We present an individual-based model in which food webs evolve due to phenotypic interactions between individuals. A key element in our model is a rich phenotype that maps to functional traits and interactional properties in a nonlinear fashion. Competition between species drives differentiation, leading to the formation of complex trophic networks. The

evolved artificial ecologies are analyzed using traditional ecological methodologies, revealing species-area relationships (SAR) and species-abundance distributions (SAD) that correspond closely with results of classical theoretical ecology. Moreover, network analysis of the topological features of the evolved trophic networks shows that our model suffices to reproduce patterns known from empirical food webs with striking similarity.

The paper is organized as follows: Section II introduces the details of the model and nonlinear mapping central to it. Simulation results with ecological and network analysis are presented in Section III. We conclude in Section IV with a discussion of our approach to food web research.

## II. MODEL

The model is an individual-based stochastic cellular automaton, consisting of two toroid lattices (of size 300x300) in which each site can be occupied by at most one individual. All sites are updated in a random order, such that they are updated exactly once per every Monte Carlo step. The two lattices are inhabited by artificial organisms of two predefined types: producers and consumers.

Individuals are specified by a "rich phenotype" by which we mean that the type, traits and interaction properties of an individual are specified in an interdependent and nonlinear way. Each individual has four traits (subsection II-A) that are determined by the "morphological" structure (II-B) that also controls the trophic interaction properties of the individual (II-C). This nonlinear mapping results in inherent trade-offs between functional traits, and allows for a rich evolutionary dynamics (II-D).

### A. Individuals and Traits

Each individual has a variable energy value, which decreases by a metabolic cost, and increases through production or consumption. When energy exceeds a certain threshold, the individual reproduces, provided there is an empty site in the adjacent 8-member neighborhood. Upon reproduction the child receives half of the parent's energy. An individual is removed when its energy decreases below zero, or by a small external probability corresponding to natural mortality. The energetical behavior is specified by two traits. One determining the metabolic costs, the other setting the reproduction threshold. The two additional traits depend on the type of the individual (autotroph or heterotroph).

Producers are autotrophic individuals that make up the basal species in the food web. They are modeled as sessile

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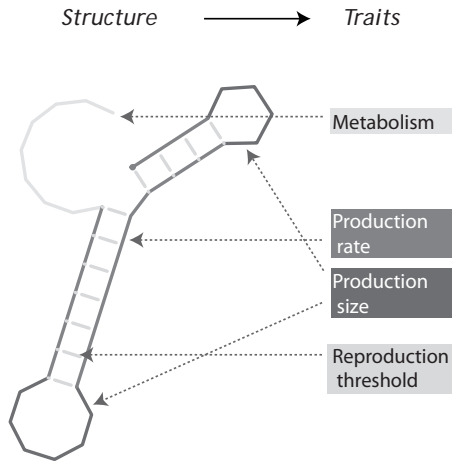


Figure 1. Encapsulation of phenotype properties. The mapping of structural features to traits of an example producer individual. The course-grained structure (structural features) determines the trophic type of the individual, the fine-grained structure (lengths of structural features) maps to traits associated with the given type. The structure as a whole determines the interaction properties of the individual.

(non-mobile) organisms that feed on nutrients from the abiotic environment. The acquisition of resources is limited by two producer traits that determine the production rate and production volume.

Consumers are mobile organisms. Mobility is modeled as (Margolus) diffusion over the lattice. Consumers are heterotrophs that feed on other organisms, either producers or consumers. Upon interaction between two individuals, the probability of consumption is determined by a normalized Gaussian distribution, specified by the two consumption traits. The prey preference trait defines the mean of the distribution, whereas the standard deviation of the distribution is controlled by the consumer’s generalism trait.

### B. Phenotype-Trait Mapping

Each individual is specified by a “morphology” that maps to the individuals’ traits and interactions in a nonlinear way (see Figure 1). This morphology is a simple 2D structure, borrowed from models of molecular folding (to use an arbitrary, but robust and well understood structure)[7]. Such a morphology can be decomposed in various level of detail. A course-grained description of the structures provides information of the presence of various structural features (e.g. hairpins, internal loops, bulges, number of stems), while a fine-grained description lists the sizes of these structural features (e.g. number of elements in the hairpin). Finally, the structure as a whole can be used to compare structures.

Despite the simplicity of the morphology, these multiple levels of description make them suitable to serve as a rich phenotype, by mapping the various structural descriptions to functional characteristics. The course-grained description is used to determine the trophic type of organisms. If a so-called multiloop (i.e. a loop with multiple stems) is present, the individual is a consumer, and it is a producer otherwise. The

fine-grained description determines the specific values for the traits associated with the two organism types (as shown in Figure 1).

### C. Interaction

Apart from the mapping that links distinct structural features to functional traits, the structure is used to compare structures. The distance between two structures controls the probability of consumption, based on the prey preference (for a particular distance) and the degree of specialism. We use the tree edit distance in which the structures are represented as trees and the number of edit operations are counted that are needed to transform one tree into the other [7].

### D. Mutation

The morphological structure is represented in a dot-bracket notation. In this notation, dots represent points and brackets represent points that are joined. Each left bracket is closed by a right hand bracket. Mutation acts directly on the structure by replacing a dot by a bracket, or visa versa, and balancing the brackets after mutation (leaving the length  $l$  fixed).

Each mutation opens or closes a pair of points and, as such, always change the overall structure, and therefore changes interaction properties. Most mutations result in an alteration that affects the fine-grained description. These changes affect the values of traits, and may simultaneously affect multiple traits. Moreover, mutations may also change the course-grained structure which determines the trophic type.

The effect of mutations on the phenotype (i.e. the trophic type, the traits and the interaction properties of an individual) is therefore highly nonlinear. This allows for a large variation of phenotypes, facilitates a rapid exploration of phenotype space and has important consequences for the evolutionary dynamics. Although no trade-offs between traits are predefined, the latter are bound to each other by a nonlinear interdependence. The system has the freedom to evolve those particular trade-offs that are most relevant in the ecological context.

## III. SIMULATION RESULTS

We have run 8 independent simulations with different random seeds of a habitat for a duration for 200,000 Monte Carlo cellular automata steps. Each simulation is initialized with a single homogeneous producer species ( $l = 60$ ) and a mutation rate  $\mu = 1.0 \times 10^{-5}$  per reproduction. Before presenting the quantitative results of the simulations, let us briefly discuss the selection processes and their results that arise in the model.

In the absence of consumers, the producer population shows a slow process of diversification and exclusion. More efficient producer species out-compete others. In contrast to what the well-known competitive exclusion principle (or Gause’s law) [8], [9] predicts, however, this process does not here necessarily lead to the exclusion of all but one optimal species, for at least two reasons. (1) The spatial population structure decreases the force of exclusion, since individuals



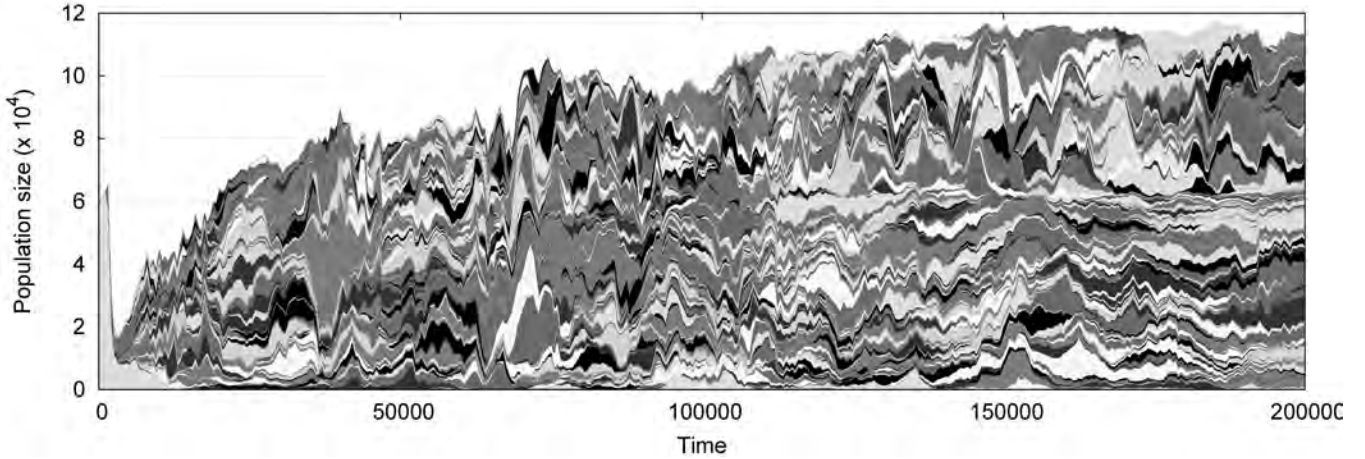


Figure 2. Time plot of population dynamics. Abundances of the various species are depicted in different shades of gray (consumer species are stacked on top of producer species). Invasion of first consumer is followed by differentiation and steep increase in community productivity, measured as total population size. After an long transient period, the population dynamics shows an increased stability after  $\pm 125,000$  MSC.

are not in direct competition with all others, but merely compete with the individuals in their own neighborhood, which primarily consist of individuals from the same or similar (ie. mutant) species<sup>1</sup>. (2) As a consequence of the nonlinear structure-trait mapping, the optimization of producer behavior is essentially a multi-objective optimization process. It is well-known that in such processes, there is no single optimal combination of traits. Rather, a range of optimal combinations exist, together forming a Pareto-optimal front. Therefore, the coexistence of multiple producer species can be expected even if time and other factors permit otherwise.

When, now, through random mutation, a consumer species invades the population, the selection process becomes more complicated. Consumption imposes a new selection pressure on the producer population. In addition to the efficiency of production, adaptations that increase the avoidance of predation, by changing the structural distance to the predator, are favored. This leads to a rapid diversification of the producer population, after which the consumer population follows suit in order to improve their consumption. As consumers themselves become predated by other consumers, a similar predator-avoidance selection starts acting upon them. This results in a co-evolutionary "arms race" [10] involving all species that are coupled in a prey-predator relationship.

This iterative process of differentiation, co-evolution and exclusion leads to the dynamical formation of artificial ecological communities structured in complex trophic networks (such as the one shown in Figure 3). In contrast to traditional assembly models, the community in this stochastic individual-based model does not approach equilibrium before being augmented (see Figure 2). The population dynamics of the assembly phase shows interchanging of chaotic transients and periods of relative stability. The periods of community restructuring lead to increased productivity, measured as

total population size, and finally (after  $\pm 125,000$  MSC) to increased stability, although equilibrium is never attained.

We analyze the ecological complexity of these evolved communities, and the network complexity of the resulting food webs.

#### A. Ecological complexity

The simplest measure of biodiversity in a given habitat is the species richness  $S$ . The average number of species encountered in communities evolved in the simulation clearly depends on the mutation rate and at its current value is  $S = 123$  ( $SD = 19.72$ ). (In order to cancel out the effect of nonviable invaders, we only count those species that have more than 50 members.) Simply quantifying the species richness of the community is of limited use, as this

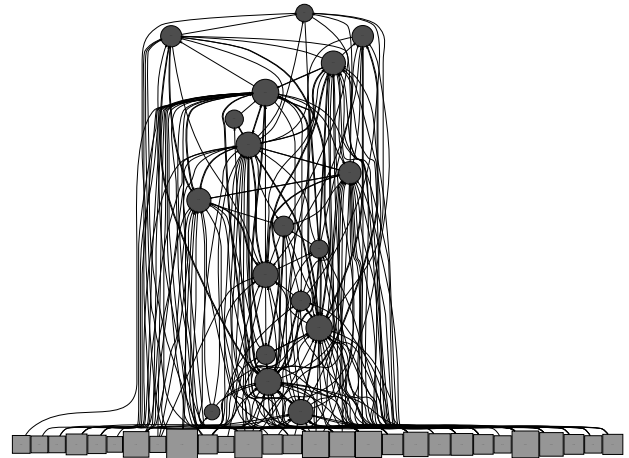


Figure 3. A typical food web (after 25,000 MCS). Producer species are depicted as boxes at the bottom; consumer species are represented as circles. Sizes of boxes and circles indicate the logarithm of the population size. Links indicate trophic interactions between two species.

<sup>1</sup>We will refer to a species as a population with identical structures, and therefore identical traits and interaction properties.

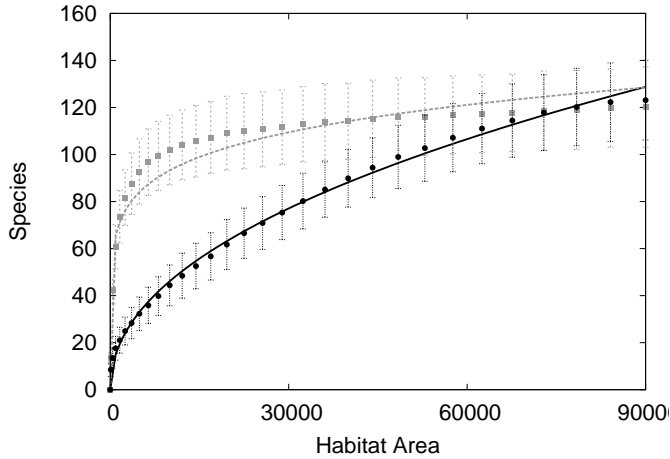


Figure 4. Species-area relationship. Points (squared and circle) show number of species per habitat area, averaged over 80 snapshots (10 per simulation) of the spatial model with bars indicating standard deviation. Grey points are results from sampling in mixed population; black points are results from nested habitat sampling. The lines shows the fit to a power law function (eq. 1) obtaining ( $c = 24.3; z = 0.15$ ) for mixed sampling, ( $c = 0.62; z = 0.47$ ) for nested habitat sampling.

number can be a combined artifact of mutation rate, our stringent definition of species (as individuals with identical phenotypes), and the size of the simulated habitat. More informative, therefore, is to observe statistical regularities using standard ecological methodologies, which allows to compare the simulation results with empirical data.

1) *Species-Area distribution*: One of the most widely observed patterns in ecology is the tendency for species richness to increase with habitat area [11], [12]. The relationship between the number of species  $S$  in an ecological community with the habitat area  $A$  can often be approximated by a power-law scale

$$S = cA^z \quad (1)$$

where  $c$  and  $z$  are positive constants and the quantity  $z$  describes the strength of the scaling of species richness with area, independent of the units used to measure area [12], [13].

We have assessed the species-area relationship (SAR) between richness and habitat size in our model using nested samples to obtain a "type 1" species-area relationship. This method consists of counting the number of different species encountered in a region, while incrementally increasing the size of the region. The results, summarized in Figure 4 (black circles and fitted curve), show that the power law scaling is a good approximation for the species-area relationship in our model.

Two main explanations for this scaling experienced in natural systems have been proposed: sampling and heterogeneity. The former states that, in a nested quadrants approach, small quadrants necessarily contain fewer individuals. At small spatial scales, therefore, an increase in species richness with increasing quadrant size almost surely reflects merely

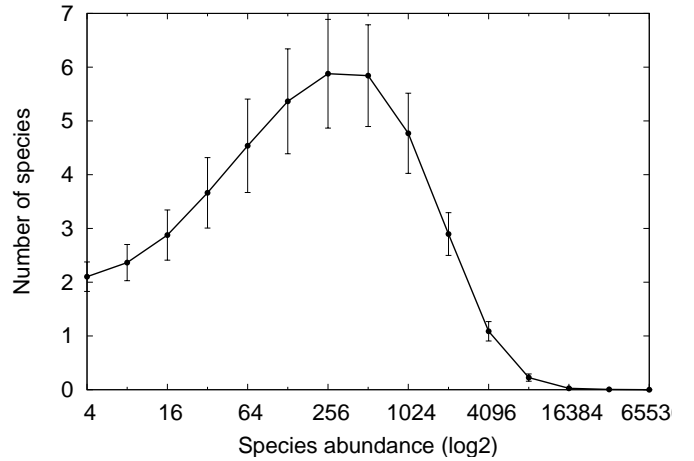


Figure 5. Species abundance distribution (SAD), represented in octaves (log2) (following [14]). Circles represent the average frequency occurrence of species at a certain abundance, averaged over a time series for all 8 simulations; bars indicate the standard deviation. The SAD approaches a log-normal distribution, but an excess of rare species is observed.

an increase in sample size. The latter explanation holds that habitat heterogeneity is likely to increase with area. This can influence species richness, because large areas are likely to include species with specialized and usually less extended habitats.

To be able to distinguish between these two mechanisms, we conducted an additional analysis. If the obtained species-area relationship merely reflects the number of individuals in the nested samples, the scaling must be independent of spatial heterogeneity. A similar relationship would thus be expected for equal-sized samples taken from the environment irrespective of the spatial structure. To test this hypothesis, we have conducted a similar analysis as above, with the difference that the area size is replaced with sample size, such that each sample can be taken from the whole environment (mixed sampling). The results, also shown in Figure 4 (gray squares and fitted curve), demonstrate that an approximate power law scaling is indeed recovered. The strength of this scaling, however, is much lower from the relationship found in the nested area approach ( $z = 0.15$  for mixed sampling against  $z = 0.47$  for nested habitat sampling). Hence, comparison between the two different explanations suggest a strong contribution of habitat heterogeneity in determining the actual species-area relationship in the model.

2) *Species-Abundance distribution*: A very common observation in large natural ecological communities is that some species are exceptionally abundant, whereas most are rare. This pattern of commonness and rarity is so pervasive that it has been called a "law of ecology". Although about 40 different statistical and biological hypotheses have been proposed, there is no general agreement on the mechanisms underlying this observation.

Four different quantitative models are known that account for species abundance patterns: geometric series, log series, log-normal series and the broken stick series [14], [11], [12].

Each of these have been successfully applied to empirical data of various ecologies. The distribution according to an approximate log-normal series is, however, by far the most frequently observed in natural communities, although rare species are often over-represented in large communities.

Analysis of the species abundance distribution (SAD) in our model reveals the same trend, shown in Figure 5. Generally speaking, species abundance follows a log-normal distribution in our model. The presence of rare species is, however, slightly higher than predicted by a log-normal model, consistent with observations in natural communities of large assemblies.

The excess of rare species can be explained by dividing into persistent species, with a long presence in the community, and occasional species, that are present during a brief period only. In our model, occasional species occur as a consequence of mutation, which continually introduces potential invader species, most of which are not rapidly excluded. Whereas persistent species follow a log-normal abundance pattern, occasional species are distributed according to a log-series. Overlaying these two distributions accounts for the log-normal distribution with an excess of rare species [15].

### B. Network complexity

Apart from the ecological analysis above, the artificial ecologies in our model were analyzed in the context of the network properties of the evolved food webs as well. During simulation, the trophic interactions between individuals are recorded in a species interaction matrix. This matrix holds information on the energy transferred between members of the various species present in the community at a given time, and is refreshed after a fixed time interval (250 MSC). We thus obtain dynamically changing weighted networks that describe the structure of the food web over time.

With the rise of network approaches in ecology, a large body of literature is emerging on food web analysis presenting a wealth of methodological tools to analysis food web topologies. Here, we discuss some of the most important analyzes in order to demonstrate the similarity between empirical data and the food webs evolved in our model.

1) *Link-species relation*: One of the basic and frequently cited quantitative food web patterns is the relationship between the number of trophic links and the number of species in the community. Although the number of links clearly increases with the number of species, the rate of this increase is unclear. The two main models for this relationships are the "link-species scaling law" [1], and the "constant connectance hypothesis" [16]. Both have the same generalized functional form:

$$L = bS^u \quad (2)$$

where  $b$  and  $u$  are positive constants [13]. The link-species scaling law basically asserts that consumers have a finite number of resources that is independent of the species richness in the community. Therefore, the number of links increases linearly with the number of species ( $u = 1$ ).

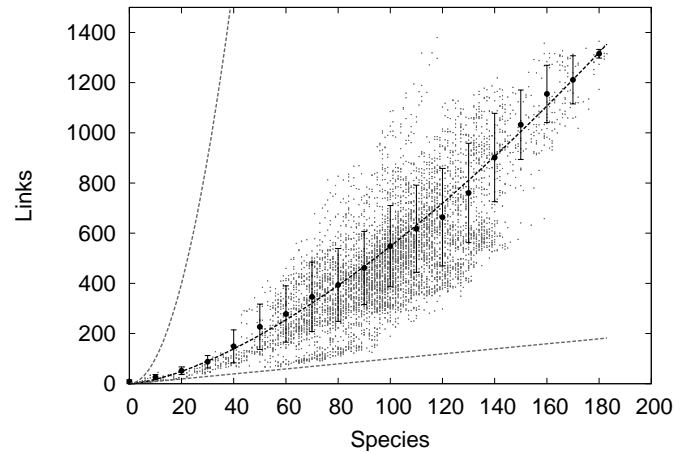


Figure 6. Links species scaling. Grey dots are the data points obtained from 8 independent simulations. Circles represent the mean of the data points, binned in species intervals of 10; bars show standard deviation. Dashed gray lines indicate the theoretical minimal ( $L = S - 1$ ) and maximal ( $L = S^2$ ) connectance. The black line show the fitted function (equation 2; with  $u = 1.50$  and  $b = 0.55$ ).

The constant connectance hypothesis, in contrast, holds that species are linked on average to a fixed fraction of other species and that links therefore scale with the square of the number of species in the web ( $u = 2$ ). Analyzes of empirical food web data have found exponents spanning this range ( $1 \leq u \leq 2$ ).

An empirical study of this relationship would be difficult. Firstly, there is a need for detailed food web descriptions that are specified to the level of species instead of lumped into groups of trophic layers. Secondly, there is a need for a large collection (or time series) of such food web descriptions, since each food web is described by a single point along the dimensions of the species-links plane. Here, the food web data from our artificial ecology offers an important advantage over empirical data. The artificial food web model can be simulated for multiple times and readily provides precise food web descriptions. Moreover, our simulations allows to us to obtain complete data over the whole period of food web assembly.

It is relatively straightforward to assess the connectance in the food webs evolved in our model. We have collected information on the number of species and number of trophic links over the entire duration of the 8 simulations (with an interval of 250 MC steps). The results are depicted in Figure 6. From the fact that the raw data (gray dots) are concentrated in a relatively small region of the permissible area (delimited by gray lines), it is clear that there is a non-random relationship between links and species. In order to distinguish between the hypotheses given above, we have estimated the exponent of equation 2 by data fitting.

The resulting exponent  $u = 1.50$  lies exactly between the two values predicted by the link-species law and the constant connectance hypothesis. As this is consistent with observations in various empirical food webs that differ significantly

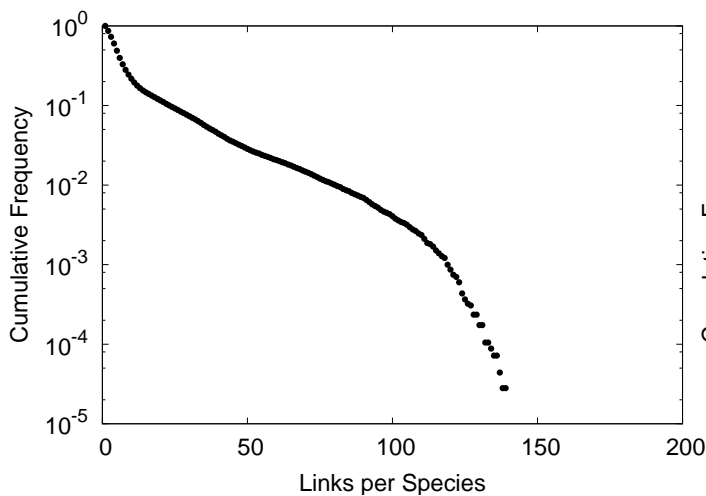


Figure 7. Degree distribution, presented as cumulative frequency distribution (following [18] and [19]). Circles represent the cumulative frequency of a species with a given (in + out) degree, averaged over 500 evolved food webs. In this log-linear plot, exponential distribution appear as a straight line, a uniform distribution as a downward curve, and scale-free distribution would be an upward curve.

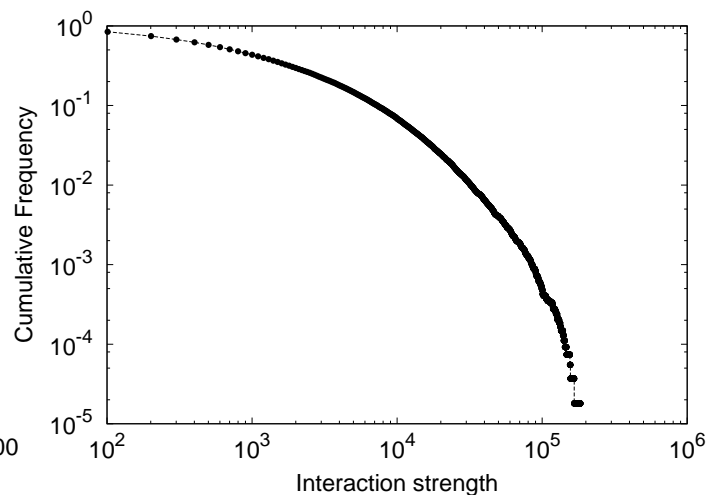


Figure 8. Distribution of interaction strength on double logarithm scales. The interaction strengths are collected over 100 food webs in all 8 simulations with a binsize of 100. Interaction strengths vary over more than 4 orders of magnitude. The distribution is strongly skewed towards weak interactions and approximates an exponential distribution.

from both hypotheses (e.g. [17]), our finding lends support to calls to reconsider the relation between the number of trophic links and species richness in ecological community, whereas fitting our model well into the range of observations that characterize natural ecologies.

2) *Degree distribution*: The recent interest in complex networks have spawned a great deal of interest in social, technological and biological networks, many of which are characterized by “scale-free” degree distribution, which means that the links per node are distributed according to a power-law. Whether this descriptions is valid for food webs as well, remains a topic of active debate [20], [19]. Food webs differ from other networks in several important respects. They are usually much smaller in terms of the number of nodes, nodes are classified into two fundamental classes with different behavior (i.e. basal species and consumer species), also food webs generally have much higher connectance, etc., all of which can have important implications for network topology.

Apart from the fact that degree distributions in food webs differ from the Poisson distribution expected from random networks, there does not seem to be a typical form of degree distribution in natural food webs. In general, they vary from scale-free to exponential to uniform distribution as the number of species and connectance increase [19].

The degree distribution of food webs evolved in simulation is shown in Figure 7. In agreement with common observations, these show that in the evolved food webs there are many species with low degree, and few with high degree. As with empirical data, the distribution is not easily characterized by a simple generalized model. The large middle part, encompassing most species, follows an exponential distribution (appearing as a straight line). At the tail, the distribution drops off in a uniform fashion (downward curve), which means that highly connected species occur less frequently

as would be predicted by an exponential distribution. At the same time, the frequency of poorly connected species is higher than expected by the exponential distribution. This excess of species with low degree can be explained by the presence of small mutant populations, that are likely to be linked to only few other species.

It is clear that the tail drops off much faster than expected for scale-free networks. The lack of power-law degree distributions in food webs may be related to how ecosystems assemble and evolve, as compared with other networks. The general mechanism of ‘preferential attachment’ (a new node is preferentially attached to a node with a high degree) which known to produce scale-free networks [21], may not be applicable to ecological communities. The probability of successful invasion of a mutant in the community decreases with the number of predators that are able to consume the mutant. Therefore, a new node in the network is expected to be linked with few other consumer nodes. Therefore, the augmentation of the typical ecological network does not conform to preferential attachment.

3) *Weak links*: Degree distributions are obtained by simplifying networks by ignoring the direction and weight of links between nodes. For food webs, however, the strengths of trophic interactions between species may be more important than the presence or absence of an interaction. The focus on degree distributions in food web research is at least partly due to the difficulty of gathering precise empirical data on the interactions strengths. This is another point where artificial ecology models can help theoretical food web studies, since it is relatively straightforward to obtain information on the trophic interactions in the artificial food web.

The available data on interaction strengths in natural food webs unequivocally indicate that distributions of interaction strength are strongly skewed towards weak interactions [22].



Although strong interactions are largely responsible for the energy and material flow through the food web, theoretical [23], [24] and experimental studies [25], [26] have shown that weak interactions may be responsible for ecological stability of the network. Weak to intermediate strength links seem to be important in promoting community persistence and stability by acting to dampen oscillations caused by strong resource-consumer pairs [27], [23].

The trophic interaction strengths between species of the artificial community in our model are measured throughout the simulations. The energy transferred in each trophic interaction is recorded in an interaction matrix, according to the species to which the predator and prey interactors belong. We thus obtain weighted networks representing the energy flowing through the food webs.

The (cumulative) frequency distribution of weights of the links in the evolved networks is depicted in Figure 8. It shows that interaction strengths between species vary over more than 4 orders of magnitude, and are, as expected, strongly skewed towards weak interactions with many weak links and few strong interactions. Although accurate empirical data are very scarce, the few existing field studies agree that interaction in natural community roughly follow an exponential distribution [28], [29], [30]. Indeed, our simulation results shows an exponential distribution in interactions between species as well. This both corroborates the early findings, and leads us to expect similar distributions when more detailed empirical food web data will come available.

#### IV. DISCUSSION / CONCLUSIONS

The study of complex ecological systems is driven by the desire to find universal rules that underlie the organization of ecosystems and communities. Even though ecological communities evidently consist of large sets of interacting and evolving individuals, they are typically studied in models that are defined not at the individual but at the population level.

Here, we are interested in the emergence of macroscopic community-level patterns from microscopic individual-level phenotypic interactions. We have shown that the ecological communities that emerge through evolution of rich phenotypes in our model exhibit multiple regularities that closely correspond to expectations from theoretical and empirical ecology and food web studies. Simulation results reproduce species-area relations (SAR), species-abundance distributions (SAD), link-species relations, degree distributions and distributions of interaction strengths with striking similarity to empirical data.

Many of these patterns have been reproduced in earlier studies, using simpler (population-level) models. However, the present study demonstrates various ecological relationships and network patterns that emerge simultaneously from a model that was not designed to reproduce any of them. Moreover, these results were obtained “for free” in a relatively simple model without the need for complex mechanisms as environmental heterogeneity, stoichiometry, or phenotypic plasticity. Rather, the observed regularities in ecological and network statistics arise as natural consequences

or side-effects of local interactions between individuals with rich phenotypes.

Phenotypes are described by a simple structures that encapsulates an organism’s characteristics (i.e. four traits plus interaction properties). The ‘richness’ of this phenotype stems from the fact that the various characteristics are encapsulated in a limited-sized structure, and are thereby coupled in a nonlinear fashion. Under multiple selective pressure due to intra- and inter-specific competition (e.g. increasing production rate while avoiding predation), trade-offs arise that cause niche differentiation by exploiting ecological opportunities. This process leads to assembly of ecological communities that are structured in complex trophic networks.

The artificial life approach to community ecology studies presented in this paper we believe may serve as a helpful tool for future food web studies to explore community-level consequences of individual interactions. At the same time, it may stimulate the use of phenotype-based models in artificial life by presenting an example of the evolution of rich phenotypes resulting in the emergence of complex biological structures.

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