Dynamics and Topology of Species Networks

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Abstract. We study communities formed by a large number of species, which are an example of dynamical *networks* in biology. Interactions between species, such as prey-predator relationships and mutual competition, define the links of these networks. They also govern the dynamics of their population sizes. This dynamics acts as a selection mechanism, which can lead to the extinction of species. Adaptive changes of the interactions or the generation of new species involve random mutations as well as selection. We show how this dynamics determines key topological characteristics of species networks. The results are in agreement with observations.

1 Introduction

Complex networks are ubiquitous in biology. Recent attention has focused on examples at the intra-cellular or inter-cellular level, such as transcription regulatory networks, gene networks, protein networks, or cell signalling. These are regulatory elements transforming genetically encoded information into structure and function or coordinating the actions of several cells. They are often quite complicated, and we are only beginning to understand their important structural elements, let alone their evolutionary genesis.

Two complementary properties of biological networks are often discussed: their *robustness* under short-term environmental fluctuations or deleterious mutations and their *evolvability* in response to longer term selective forces. These response characteristics reflect a fundamental dynamical property: A biological network can have multiple and widely differing characteristic time scales. It remains a challenge for experimentalists and for theorists to quantify the dynamical properties and relate them to observed topological features.

In this article, we discuss a macroscopic type of biological networks, namely communities of many species that interact via predation and competition. A number of field data are available, describing their large-scale dynamics as well as their topological structure. We discuss a simple theoretical model that can be compared to these observations on a quantitative basis. The main conceptual result is the intimate statistical connection between the long-term dynamics and typical network structures: Evolution shapes the network topology.

Due to the relationship between dynamics and structure, these networks are an interesting subject for theoretical physicists. Clearly, a similar link is expected also for their molecular counterparts, and in this aspect the example of species networks may be useful for model building in a more general context. However, topological characteristics are seen to depend quite sensitively on, for example, the level of competition between species. Thus, the reader should be cautioned not to expect one universal theory of biological networks.

Species networks in nature have been studied on quite different scales of space and time. Ecologists' attention has focused on *food webs*, i.e., communities of animal species in a closed environment where food chains can be observed. Fig. 1(a) shows the graph of such a network, each arrow representing a prey-predator relationship. Despite large variations in size and environmental conditions, large ecosystems share a few important topological characteristics: (i) Every species lives at a certain *trophic level*. The level number can be defined as the minimum, the maximum or a suitable average length of its relevant 'downward' food chains; the differences between these definitions turn out not to be significant for the statistical properties of food webs we discuss here. Species at level one feed from external resources. (ii) The number of trophic levels is small, typically between three and seven. (iii) Most species have a small number of relevant prey species (typically around three), mainly from the next lower level. (iv) The number of species at level l increases with l for lower values of l and decreases again sharply for higher l [1,2], see Fig. 1(b). Networks of co-evolving species thus have a characteristic *shape*.

Evolutionary biologists and paleontologists have a different point of view on species communities. They record adaptive changes and extinctions of species and the arrival of new species. More than 99% of the species that have ever existed are extinct. It is only the slight excess of speciations over extinctions in the last 600 million years that has produced our diverse biosphere [3]. The dynamics of species numbers can be quite intermittent. Periods of relative stasis ($\sim 10^{4-6}$ years) alternate with bursts of extinctions and or speciations, leading to large fluctuations in the number of species [4,5]. It has been argued that these temporal patterns are generated by the complex interactions between species [6,7] and the resulting correlations, rather than by external variations alone.

These complementary descriptions refer to different time scales. Over short intervals, the relevant variations in a species network are in the population numbers (this is referred to as population dynamics), while the network structure (i.e., the species and their interaction links) remains fairly robust. The average time between network changes (extinctions, speciations, or adaptive changes) is much longer. However, as shown by recent field observations and theoretical results on sympatric speciation, also structural changes can be rather rapid (see the article by Rost and Lässig in this volume). So a strict separation of the relevant time scales should not always be assumed. Moreover, the network interactions induce large correlations and fluctuations. For example, an extinction may trigger rapid other extinctions and subsequent speciations. A statistical ensemble emerges from averaging over yet longer time intervals containing many speciations and extinctions, and this statistics is the subject of the article.

Classical work in mathematical biology has established stability criteria for networks with random interactions g_{ij} [8]. They are, however, of limited use for real ecosystems where the interactions are not random, but are themselves subject to selection. Only recently, a model for species networks with rather detailed interactions has been formulated and analyzed by numerical simulations [10] (see the article by Quince et. al. in this volume). Another class of recent models focuses directly on the dynamics of extinctions and speciations. These models have no explicit population dynamics and mostly random topology, with the important exception of Ref. [11].

Here we discuss the simplest models of species networks that can be compared to observations on a quantitative basis. These models are introduced in Section 2. The *global* shape of the model networks can be obtained from an approximate analytical calculation (see Section 3). The underlying dynamics and the resulting *local* fluctuations are discussed in Section 4.

2 Modelling species networks

A model for species communities has to specify the type of interactions and the resulting population dynamics, as well as the slower dynamics of the network itself, that is, of its nodes and links.

2.1 Species interactions and population dynamics

Lotka-Volterra equations. The simplest population dynamics for a community of species with population numbers $N_i(t)$ is

$$\frac{1}{N_i}\frac{\mathrm{d}N_i}{\mathrm{d}t} = \sum_{j=1}^{s} g_{ij} N_j + h_i \qquad (i = 1, \dots, s) \ , \tag{1}$$

a set of coupled differential equations for the relative growth rates. The coefficients g_{ij} represent interactions between species, the most important of which are predation and competition. Accordingly, we decompose the interaction matrix into a predation part and a competition part,

$$g_{ij} = \gamma_{ij} - \beta_{ij} \ , \tag{2}$$

which are defined below. The terms h_i denote intrinsic production or decay rates. This type of equations, as well as many generalizations thereof, has been used to model coexistence, invasions, and adaptive change of populations. Of great importance is the conceptual connection to mathematical *game theory* [12]. A set of populations $(N_1, \dots, N_S)$ represents a mixed strategy in a game with payoff matrix g_{ij}. An optimal strategy of this game – called Nash equilibrium – can often be realized as a stable fixed point $(N_1^*, \dots, N_S^*)$ of an associated Lotka-Volterra dynamics. This explains how strategic optimization is reached in biological systems through reproductive success, with no need for rational thinking.

Predation denotes here any interaction between two species i and j that is advantageous for i and disadvantageous for j. It is described by matrix elements

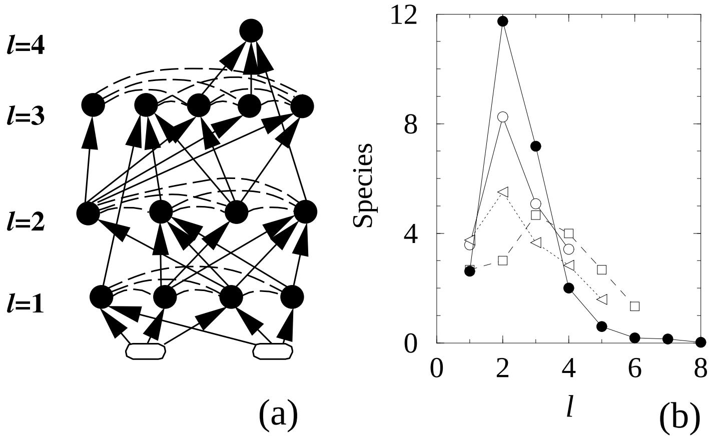

Fig. 1. (a) The Pamlico estuary foodweb in North Carolina, consisting of 14 species (filled circles) at four trophic levels. *Detritus*, *dinolagellates* and *diatoms* are at the bottom level ($l = 1$) and feed from external resources (empty symbols). There is a single trophic group at the highest level ($l = 4$), formed by the predatory fishes *Roccus* and *Cynoscion*. Arrows point from prey to predator; dashed lines connect species pairs with a nonzero link overlap (see text). Data from [1]; the level is defined here by the longest relevant food chain. (b) Average species numbers per level for a set of natural ecosystems, taken from Ref. [1] (empty symbols) and [9] (filled circles). This last case corresponds to an average over 61 food webs, most of which are empty at high levels.

$\gamma_{ij} > 0$ and $\gamma_{ji} < 0$, taken for simplicity to be proportional, $\gamma_{ij} = \Delta|\gamma_{ji}|$. The matrix γ_{ij} is sparse in natural systems. Its nonzero matrix elements define the *predation network*, which is represented by solid lines in Fig. 1(a). The *productivity* of a species i is defined as the net contribution of predation to its growth rate,

$$P_i \equiv \sum_{j \in \pi(i)} \gamma_{ij} N_j - \sum_{j \in \Pi(i)} \gamma_{ji} N_j \, , \tag{3}$$

where $\pi(i)$ is the set of its prey species and $\Pi(i)$ the set of its predators.

Competition is the mutual interference of two species i and j in each other's livelihood. Again for simplicity, it is described by a symmetric matrix, $\beta_{ij} = \beta_{ji} > 0$. Competition takes place for nesting places, mating opportunities, and other resources not explicitly represented in the model. It is strongest between individuals of the same species, but also occurs between different species [13]. This interaction turns out to be the main limiting factor for the coexistence of species in a common network.We set the intra-species competition $\beta_{ii} = 1$; this normalization amounts to an appropriate choice of the time scale in (1). It is then a natural choice to quantify the inter-species competition in terms of the *predation overlap*

$$\rho_{ij} \equiv \sum_{k\in\pi(i)\cap\pi(j)} \gamma_{ik}\gamma_{jk} \Bigg/ \sqrt{\sum_{k\in\pi(i)} \gamma_{ik}^2 \sum_{k\in\pi(j)} \gamma_{jk}^2} \ . \tag{4}$$

We set $\beta_{ij} = \beta\rho_{ij}$ for $i \neq j$ with a coupling constant $\beta < 1$. The nonzero matrix elements ρ_{ij} define the *overlap network*, which is represented by dashed lines in Fig. 1(a). It is typically sparse as well in natural systems. The inter-species competition load of a species i is defined as

$$Q_i \equiv \beta \sum_{j\neq i} \rho_{ij} N_j \ . \tag{5}$$

Fixed points, viability threshold. The population dynamics (1) can now be written as

$$\frac{1}{N_i}\frac{\mathrm{d}N_i}{\mathrm{d}t} = (P_i - Q_i - \alpha_i)N_i - N_i^2 \ . \tag{6}$$

In general, the population numbers will converge to a stable fixed point of the form

$$N_i^* = P_i(N_1^*, \dots, N_s^*) - Q_i(N_1^*, \dots, N_s^*) - \alpha_i \ . \tag{7}$$

Furthermore, we require a minimum population size N_c for viable species, and count all species with $N_i^* < N_c$ as extinct. A uniform death rate $\alpha_i = \alpha$ is an equivalent cutoff for small population sizes.

External resources. The species community is maintained by a number of external resources, which are represented as extra 'populations' N_i with $h_i = \gamma_{i,0}R$ and predators only (i.e., $\gamma_{ij} \leq 0$ and $\beta_{ij} = 0$ for all j). The external resources and the viability threshold play the role of boundary conditions for the population dynamics. The dimensionless parameter $R/N_c \gg 1$ turns out to control the vertical size of the network, i.e., the length of food chains.

2.2 Network dynamics

As explained above, the population dynamics can lead to the extinction of one or more species, i.e., to the loss of nodes in the species network. The other changes in the network structure are adaptive mutations of the links γ_{ij} and speciations, which generate additional nodes.

At the molecular level, most mutations are neutral or deleterious. In this effective model, however, neutral mutations are not taken into account and the effect of deleterious mutations (the so-called mutation load) enters only through the viability threshold N_c and the death rate α. Only rare advantageous mutations leading to viable mutants are represented explicitly.

These mutations are modeled as follows. Consider the bare predation matrix with integer coefficients $x_{ij} = 0, 1, \dots, x_0$. These define the coefficients $\gamma_{ij} > 0$ by

$$\gamma_{ij} = \gamma_0 \frac{x_0 x_{ij}}{x_0 + \sum_{k \in \pi(i)} x_{ik}} \qquad \text{for } j \in \pi(i). \tag{8}$$

Here γ_0 is the overall predation strength, and $x_0 > 0$ is a saturation scale. For well-adapted species (i.e., for $\sum_{k \in \pi(i)} x_{ik} \gg x_0$), increasing predation on one resource implies an equal decrease of predation on the other resources.

We assume the population dynamics has settled at a fixed point with s viable species, $(N_1^*, \dots, N_s^*)$. One species i is chosen randomly as parent species. We denote by c_i the number of its prey species. Now we introduce a mutant of the species i, which is labelled as a new 'species' i' with initial population size $N_{i'}$ of order N_c. It differs from its parent species by a single bare predation coefficient. Either one of the c_i existing links $x_{ij} > 0$ is modified, $x_{i'j} = x_{ij} \pm 1$, or a new link $x_{i'j} = 1$ is created randomly; each of these $c_i + 1$ different cases is chosen with equal probability $1/(c_i + 1)$. The mutant has a different productivity $P_{i'}$ and a different competition load $Q_{i'}$, which includes a contribution $\rho_{ii'} N_i^*$ from the competition with the parent. The viability condition for the mutant reads $P_{i'} - Q_{i'} > \alpha + N_c$; the sign of the link modification is chosen at random.

A viable mutation generates an unstable perturbation of the fixed point $(N_1^*, \dots, N_s^*)$. The mutant population $N_{i'}$ grows, leading to the temporary coexistence of $(s + 1)$ populations. We assume mutations are so rare that the population dynamics reaches a fixed point $(N_1^{*\prime}, \dots, N_{s'}^{*\prime})$ before a new mutation takes place[1]. This population dynamics acts as selection. The new fixed point has $s' \leq s + 1$ species. In most cases, the parent species i is replaced by the mutant i', which is counted as an adaptive mutation of i. In some cases, if the overlap $\rho_{ii'}$ is small enough, the species i and i' coexist at the new fixed point; this is a speciation.

3 The shape of a species network

Here we derive the global shape of a food web in a 'mean-field' approximation, following ref. [14]. Details of the dynamics are not needed at this stage. It is sufficient to assume that the mutation-selection process maintains a broad distribution of productivitities and, hence, of biomasses. This asssumption is well supported by field observations; it reflects the diversity of habitats and ecological niches. In the framework of the network model, it can be verified by the numerical simulations discussed in section 4.

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[1] Of course, any mathematical fixed point of Eq. (1) is reached only after infinite time. However, the time-dependent population numbers $N_i(t)$ get exponentially close to the corresponding fixed point values for large times. In practice, the numerical integration of (1) is carried out until the number of species with $N_i(t) < N_c$ no longer varies.

Throughout this section, we disregard fluctuations of the predation coefficients and set $\gamma_{ij} = \gamma_+$ if j is prey of i and $\gamma_{ij} = -\gamma_- = -\Delta\gamma_+$ if i is prey of j, with $0 < \Delta < 1$.

To illustrate of the relative roles played by predation and competition, we analyse first two types of simple networks, before we turn to species networks of general topology.

3.1 A single food chain

A food chain is a community of L species on L trophic levels where species at level l feed from that at level $l-1$. All the competition loads vanish, and thus the population numbers at each level are given simply by $N_l^* = P_l - \alpha$. Hence, the entire chain is viable if $P_l > P_c$ for all species l, with the productivity threshold

$$P_c = \alpha + N_c \; . \tag{9}$$

The productivity of a species at level l is

$$P_l = \gamma_+ N_{l-1}^* - \gamma_- N_{l+1}^* \qquad (l = 1, \ldots, L) \tag{10}$$

and $P_0 = -\gamma_1 N_1^*$, with the boundary condition $N_{L+1}^* = 0$. These equations can be solved exactly by recursion starting from the top level $l = L$. Asymptotically, we obtain an exponential decrease in the biomasses for increasing level number. In the biologically relevant case $\gamma_+ \ll \gamma_-$, we get

$$N_l^* = \gamma_+ N_{l-1}^* - \frac{\alpha}{1+\gamma_-} \; ; \tag{11}$$

the resulting length of the food chain scales as

$$L \sim \log\left(\frac{R}{N_c + f(\gamma_-)\alpha}\right) \tag{12}$$

with some function $f(\gamma_-)$. The important qualitative conclusion is that food chains are always short, as observed in real systems. The parameters α and N_c are seen to be equivalent viability cutoffs for the length of the chain.

3.2 A single trophic layer

A trophic layer is a group of S species at the same level. These species have a significant overlap in their predation links and a resulting competition load. We assume there is no predation within the layer, that is, the productivities P_i depend only on the interactions with 'external' species. Here we consider the P_i as fixed and concentrate on the effects of the direct competition terms Q_i. In the mean field approximation, we replace the individual link overlaps ρ_{ij} between different species by their expectation value $\bar{\rho}$, which has to be determined self-consistently. Consider, for example, a trophic layer feeding from a set of S' prey species with an average number of $\bar{c}$ prey species per predator species. We use a simple approximation for the link overlap which (i) takes into account that a configuration with zero overlap exists for $S \leq \max(S'/\bar{c}, 1)$ and (ii) assumes random predation for larger values of S. This approximation reads

$$\bar{\rho}(S, S') = \begin{cases} 0 & \text{if } S \leq \max(S'/\bar{c}, 1) \\ \min(\bar{c}/S', 1) & \text{if } S > \max(S'/\bar{c}, 1) \end{cases} . \tag{13}$$

The competition load in eq. (7) can now be evaluated approximately, yielding the fixed point populations

$$N_i^* = \frac{P_i - \beta\bar{\rho}S\bar{N} - \alpha}{1 - \beta\bar{\rho}} . \tag{14}$$

The average $\bar{N} \equiv S^{-1} \sum_{i=1}^{S} N_i^*$ is given by

$$\bar{N} = \frac{\bar{P} - \alpha}{1 + \beta\bar{\rho}(S-1)} . \tag{15}$$

Inserting the viability condition $N_i^* > N_c$ into (14) determines the productivity threshold

$$P_c = \alpha + (1 - \beta\bar{\rho})N_c + \beta\bar{\rho}S\bar{N} . \tag{16}$$

For small values of S, we have $\bar{\rho} = 0$ by (13), and (16) reduces to (9). With increasing S, the threshold increases as well.

The actual productivites P_i are constantly changing as a consequence of the mutations of species i as well as those of the other species. The statistical assumption used here (and verified in the next section) is that the productivities P_i are drawn from a broad probability distribution given by $\Phi(q) \equiv \text{Prob}(P_i/\bar{P} < q)$. This distribution is assumed to be independent of S; that is, the number of species enters only via the average $\bar{P}$. The qualitative results do not depend strongly on the form of $\Phi(q)$; we use the simple approximation

$$\Phi(q) = \frac{q - q_0}{2(1 - q_0)} . \tag{17}$$

The expectation value of the smallest productivity P_{min} in a community of S species can then be estimated from the relation $S\Phi(P_{\text{min}}/\bar{P}) = O(1)$, giving

$$P_{\text{min}} = \left(q_0 + \frac{1 - q_0}{S} \right) \bar{P} . \tag{18}$$

The species community becomes unstable if the least productive species falls below the viability threshold. Equating (16) and (18) therefore gives an implicit relation for S as a function of $\bar{P}/N_c$, α/N_c, the relative productivity spread q_0, and the average pairwise competition load $\beta\bar{\rho}$ given by (13). That is, competition determines the number of 'ecological niches' in a trophic level as a function of the prey diversity and the competition strength β. For sufficiently large β, only non-overlapping species can coexist, i.e., $S = \max(S'/\bar{c}, 1)$. The number of ecological niches increases with decreasing β and increasing productivity spread q_0. This result generalizes the well known theorem of competitive exclusion [15], which states the condition for coexistence of two competing species. Note that this limiting effect on the number of species exists independently of the population numbers. It is indeed crucial for the buildup of high population numbers at the lower trophic levels. For example, a trophic level feeding from resources of size $R \gg \max(\alpha, N_c)$ acquires an extensive population number per species, $\bar{N} \sim R/S$ with S asymptotically independent of R. Without competitive exclusion ($\beta = 0$), speciations would further increase S and eventually lead to an extensive number of marginally viable species, $S \sim R/\bar{N}$ with $\bar{N}$ of order N_c. Such a level could not support sizeable predation from above.

3.3 The full network

We now turn to a full ecological network with L trophic levels. In the mean field approximation, we treat all species at the same level on an equal footing and derive self-consistent equations for the level averages of population and species number, $\bar{N}_l$ and S_l ($l = 1, \ldots, L$). The average productivities $\bar{P}_l$ satisfy the recursion relations

$$\bar{P}_l = \gamma_+ \bar{c} \bar{N}_{l-1} - \gamma_- \bar{c} (S_{l+1}/S_l) \bar{N}_{l+1} \ , \tag{19}$$

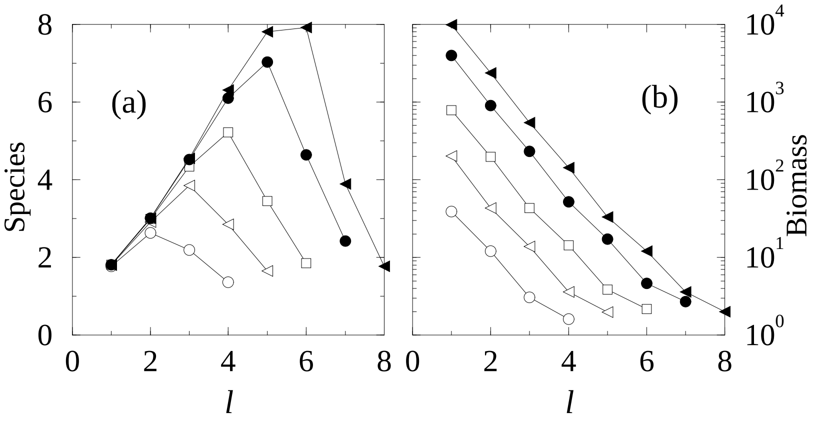

Fig. 2. The shape of ecosystems. (a) The species numbers S_l ($1 \leq l \leq L$) for networks with L trophic levels. The parameters are $\bar{c} = 3$, $\gamma_+ = 0.3$, $\gamma_- = 2.0$, $\lambda = 0.2$, $q_0 = 0.35$, $\alpha/N_c = 1$, and $R/N_c = 2 \times 10^3$, 10^4, 4×10^4, 2×10^5, and 5×10^5 for the cases $L = 4$, 5, 6, 7, and 8, respectively. (b) The average population numbers $\bar{N}_l$ for the same cases as in (a).

where we assume that the species at every level predate only on the species at the next lower level. The average number $\bar{c}$ of predation links per predator is taken to be independent of l; this is indeed suggested by field data. The average number of predators per prey is then simply $\bar{c}S_{l+1}/S_l$. The productivity $\bar{P}_l$ is linked to $\bar{N}_l$ and S_l as in (15), using for $\bar{\rho}(S_l, S_{l-1})$ the approximation (13). Hence, the relations (19) determine the population numbers given the species numbers. The latter are again limited by the stability criteria $S_l\Phi(P_{c,l}/\bar{P}_l) = O(1)$ with the minimum productivities $P_{c,l}$ given as in (16); these relations determine the S_l given the $\bar{N}_l$. The coupled set of equations can be solved iteratively. Finally, the number of levels L follows from the condition $\bar{N}_L \approx N_c$, which is equivalent to $S_L \approx 1$.

Over a wide range of relevant parameters, these networks have the characteristic shape shown in the example of Fig. 2: The species numbers S_l increase with l at low levels due to the increasing prey diversity, which opens up more and more niches. They reach a maximum at an intermediate level and decrease again at higher levels, because more and more species have population numbers too low to support further predation. Hence, these two regimes reflect the two kinds of species interactions. The population numbers show an approximately exponential decrease in both regimes, just like for a single vertical chain. Hence, L is always small, in agreement with observations and with the results of [10,16].

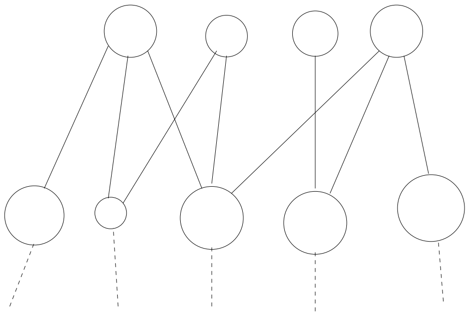

Fig. 3. A trophic bilayer in a stationary environment. The number of species at the lower level and their predation gain (dashed lines) are kept constant in time as appropriate for external resources. We focus on the dynamics of the species at the upper level and of the predation links within the bilayer (solid lines).

4 The local structure and fluctuations

We now discuss the long-term dynamics of species networks, following ref. [17]. In the present model, a single step of this dynamics consists of a mutation and the subsequent selection by population dynamics; see section 2.1 above. The cumulative effect of many such steps is large fluctuations in the size of the networks and in many of its local characteristics. Here we illustrate this for the particularly simple case of a trophic *bilayer* in a stationary environment, as shown in Fig. 3. The number of species at the lower level and their predation gain are kept constant in time as appropriate for external resources. We focus on the dynamics of the species at the upper level (the predators) and of the prey-predation links between the two levels. Links to higher levels are neglected.

Fig. 4 shows the stationary fluctuations in the number of viable species at the upper level. Here the 'time' coordinate T is just the number of mutation-selection steps.

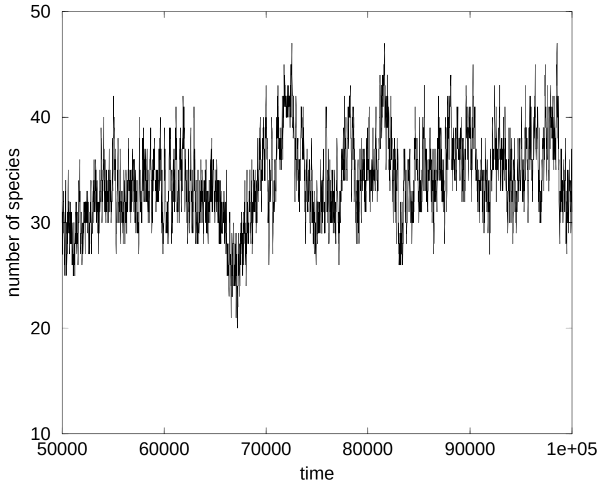

Fig. 4. Fluctuations in the number $s(T)$ of viable species. Each time-step corresponds to an attempted mutation or speciation.

This should be compared to the time series for the population number $N(T)$ of a randomly chosen 'tracer' species i shown in Fig. 5(a). The fluctuations originate from the 'noise' of its own adaptive mutations and speciations and those of the other species. We can think of them as a random walk in N with variable step size. Since large values of $N(T)$ are suppressed, the random walk is essentially constrained to the range $N_c < N(t) < O(\bar{N})$ with an absorbing boundary at $N = N_c$. Hence, every species faces a continuous threat of extinction, which leads to an exponentially decaying survival probability. It will eventually get extinct when the pace of its own adaptations cannot keep up with the changes in its environment. This is the well-known *Red Queen effect* of co-evolutionary systems. Extinct species are replaced by speciations, leading to a long-term balance. The resulting stationary probability distribution of population numbers is shown in Fig. 5(b). It is indeed a broad distribution as anticipated in the previous section.

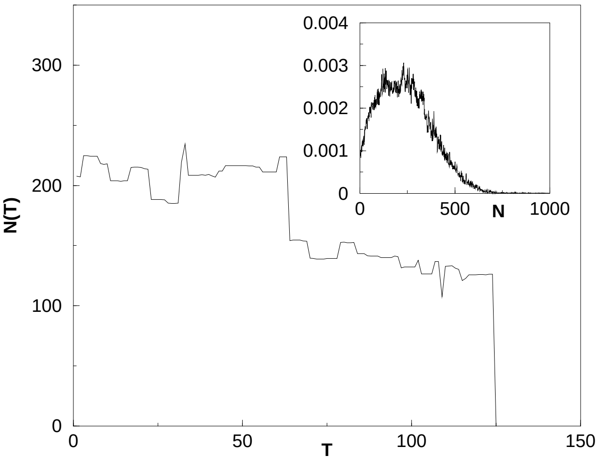

Fig. 5. (a) The fate of a given species. Large fluctuations in the population number or biomass $N(T)$ can be given by the extinction or arrival of a strong competitor. Typically, the sudden decline of a population is caused by the arrival of a daughter that takes its place in the network. (b) The corresponding stationary probability distribution $\mathcal{P}(N)$.

We now return to the effect of interactions on the network structure. Fig. 6(a) shows a typical snapshot of the overlap network at $\beta = 1$. The network is seen to be rather sparse: the species are forced into different ecological niches with little mutual overlap. In this example, there are 10 different resources and 9 predators. A typical predator species feeds on about 3.5 resources. It has nonzero overlap with 2 other predators on average; a random pair of predator species has an average overlap of 0.04 (clearly, these network characteristics depend on the overall size of the network).

If competition is weak (e.g. $\beta = 0.5$), typical overlap networks are much denser, see fig. 6(b). The number of predators strongly increases, while their population numbers decrease. In this example, there are now 300 predators, each having a nonzero overlap to about 40 others. Hence, the system is no longer organized in ecological niches.

5 Conclusion

We have seen that the structure of species networks is shaped by evolutionary forces over long periods of time. Some of the resulting features are far from random: these networks are graded into trophic levels with a characteristic 'shape' defined by the level dependence of the number of species.

Darwinian evolution is a coupled process of mutations and selection. At the level of species communities, selection takes place through the dynamics of population numbers, and this dynamics depends on the interactions between species.

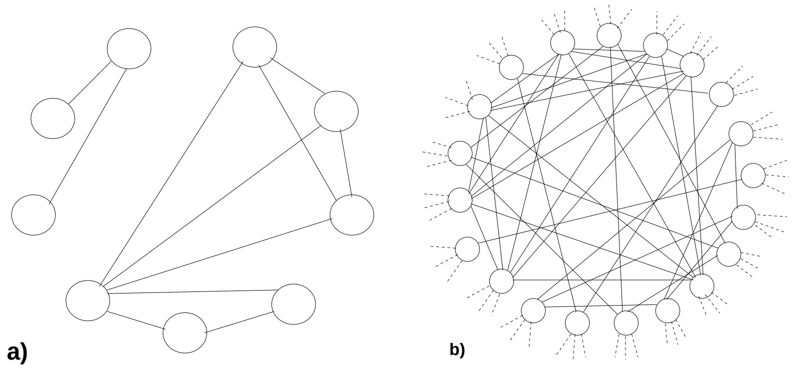

Fig. 6. (a) The overlap network at the upper level of a trophic bilayer for large competition ($\beta = 1$). The network is sparse, the species are organized into ecological niches with little mutual overlap. (b) At smaller competition (here $\beta = 0.5$), the size of the network strongly increases. Only a fraction of the nodes is shown. A species is connected to many other species, the ecological niches have disappeared.

We have identified two universal selective interactions, which are remarkably simple. Predation is the basic transport of energy in the system, competition forces the species into states with little overlap. In physics, mutual avoidance is a well known property of fermions. Competitive exclusion may thus be regarded as the Pauli principle of co-evolution: It generates the complexity of species networks just as its quantum-mechanical counterpart does for atoms and molecules.

Fig. 6 shows an example of the dependence of the local network structure on species interactions. In a more general context of biological networks, such relationships pose an interesting set of what physicists call *inverse problems*. Can we deduce from observed structures the evolutionary forces that have produced them?

Biologists have another important way of looking into the past. Phylogenetic trees can be constructed from phenotypical characteristics or from molecular sequences of today's species; molecular trees are becoming more and more accurate and complex with the rapidly increasing amount of available data. They are a partial record of speciations for those species that have survived to date. Uncovering the connections of their statistical properties with the underlying co-evolutionary dynamics is a challenging problem for the future.

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