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Part–whole relations between food webs and the validity of local food-web descriptions

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ABSTRACT

This work analyzes the relationship between large food webs describing potential feeding relations between species and smaller sub-webs thereof describing relations actually realized in local communities of various sizes. Special attention is given to the relationships between patterns of phylogenetic correlations encountered in large webs and sub-webs. Based on the current theory of food-web topology as implemented in the matching model, it is shown that food webs are scale invariant in the following sense: given a large web described by the model, a smaller, randomly sampled sub-web thereof is described by the model as well. A stochastic analysis of model steady states reveals that such a change in scale goes along with a re-normalization of model parameters. Explicit formulae for the re-normalized parameters are derived. Thus, the topology of food webs at all scales follows the same patterns, and these can be revealed by data and models referring to the local scale alone. As a by-product of the theory, a fast algorithm is derived which yields sample food webs from the exact steady state of the matching model for a high-dimensional trophic niche space in finite time.

1. Introduction

Both empiricists and theorists often depict food webs as closed, local entities, all well aware that this is a simplification which might be misleading (Polis et al., 2004). Populations are spatially dispersed, and the areas of dispersal differ from species to species. It is therefore common to distinguish *potential* consumer–resource relationships from those that are actually *realized* at a particular location simply because both the consumer and the resource are present. In fact, empirical food-web databases have been constructed by first setting up a web of potential feeding links for a large set of species based on general knowledge, and then reducing this set and the set of links to those species actually present at a given habitat (e.g., Havens, 1992). It may be asked if the relationship between potential webs and realized webs is really that simple, and

what consequences this would have for the relationships between sub-webs of different size.

Modelers of complex food webs often ignore spacial effects. Since it helps reducing computation times, this simplification has nearly always been made for models that include a description of the evolution and phylogeny of the member species of a web (e.g., Caldarelli et al., 1998; Drossel et al., 2001; Yoshida, 2002). But this simplification should be questioned. Evolution theory and observation suggest that most speciations are allopatric: new species evolve *because* they are spatially separated from their ancestors. If sympatric speciation is rarely realized in nature, is it justified to invoke it in models?

The most accurate theoretical description of food-web topology currently available is the matching model (Rossberg et al., 2006a). Similar to the models of Caldarelli et al. (1998);

Drossel et al. (2001), or Yoshida (2002), it constructs food-web topologies based on the degree of correspondence between consumer- and resource traits. But, while these models also invoke population dynamics to select topologies, the set of species in the matching model and their traits evolve simply by random, uncorrelated speciations and extinctions and the occasional addition of new random species (see Section 2.1 for details). Characteristic food-web patterns arise from phylogenetic correlations between member species and the resulting correlations in the consumer- and resource sets of related species (Cattin et al., 2004; Rossberg et al., 2006a; Bersier and Kehrli, 2007). That is, the model combines the assumption common in empirical research that trophic (i.e., feeding) links are determined only by the traits of consumer and resources, independent of the remaining food-web structure, with a local model of evolution. A rigorous statistical model validation showed that the accuracy to which with the model reproduces ecological characteristics of empirical prey–predator food webs – based on these assumptions – leaves only little room for improvement (Rossberg et al., 2006a). The habitats from which the analyzed food-web data was sampled ranged in size from small ponds (Warren, 1989) and creeks (Townsend et al., 1998) to the full North East US Shelf, ranging from Cape Hatteras, NC, to the Gulf of Maine (Link, 2002).

These considerations imply the following three conjectures:

1. Links in food webs are, to a large part, determined by the traits of consumer and resource, independent of the remaining topology.
2. Local food-web evolution is a good approximation for the more complex evolutionary processes on large scales.
3. Food-web topology is, in some sense, invariant under changes of spacial scale.

The first two conjectures are incorporated in the food-web theory underlying the matching model. Internal consistency of the third conjecture requires that going over from a whole, large food web to a part of it that is defined by restricting the web to a smaller, local community, will, in some sense, leave essential food-web properties intact. Consistency of the third conjecture with the other two can be tested by testing it within the framework of a particular theory that incorporates the first two assumptions, e.g., the matching model. And to the degree that the theory is consistent with empirical data, this will also answer the question what ''in some sense'' in (3.) really means. This question is not a priori clear, and therefore testing the third hypothesis directly on empirical data could prove difficult and might yield, at best, episodic results.

Since most food-web models do not explicitly describe spacial effects, an additional hypothesis is required for how local communities are assembled from larger species pools. A common view is that local communities are composed following specific assembly rules (Diamond, 1975). Three effects are thought to contribute to these rules: (i) preference of species for particular habitats, (ii) non-trophic, often facilatory interaction, and (iii) competitive exclusion. The first two effects are unrelated to the patterns of trophic interactions of interest here, and can therefore be modeled as random selection from a large-scale food web. The last effect is highly related to trophic interaction. But the number of relevant variables and parameters is so large, and the mechanisms involved are so complex that, as far as only food-web topology is concerned, it should also be modeled well by independent, random selection, uncorrelated with topology.

Thus, what remains to be investigated is if sub-webs assembled at random from large food webs generated by a given model of food-web topology will also be described by this model directly, just with a smaller number of species (see Fig. 1). For the cascade model (Cohen et al., 1990), for example, this is easily seen to be the case, provided the connectance (the fraction of combinatorically possible links realized) is kept fixed. But the cascade model is a rather coarse description, not including the effects of phylogenetic correlations.

The analysis below will reveal that, to a good approximation, the matching model has this scaling property, too. But the picture becomes richer in this case. Scaling of food-web size is accompanied by a re-normalization of model parameters, as expressed by Eqs. (19), (24), (30), and (32). These re-normalization equations describe the relationships between large food webs and their random sub-webs. They predict in what sense food-web topology is scale invariant and how food-web structure and the patterns of phylogenetic correlations change with the fraction of species included. The accuracy to which the scaling property holds is illustrated by Table 2. Only with ''good'' parameters chosen according to the renormalization equations, the scaling property is retained. Another plausible (but ''bad'') parameter set breaks it.
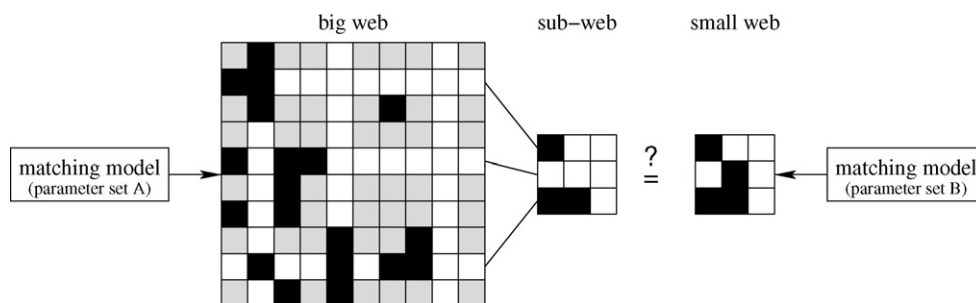

Fig. 1 – Illustration of the problem of scale invariance of food-web topology under random sub-sampling. Food-web topologies are represented by adjacency matrices, with black squares indicating that the consumer corresponding to its column eats the resource corresponding to its row. Gray areas in the big web correspond to species not included in the sub-web.

Unfortunately, the long-standing question how connectance scales with the size of food webs (May, 1973; Yodzis, 1980; Havens, 1992; Martinez, 1993, 1994; Bersier and Sugihara, 1997; Banašek-Richter et al., 2005; Rossberg et al., 2006c) is left open by the theory. Connectance is a freely adjustable parameter of the matching model and thought to depend on the precise criteria by which links are included in empirical data sets (Rossberg et al., 2006a, c). Thus, these two kinds of scale invariance must be considered as independent problems.

The fact that food webs obtained by local evolution are a good approximation for real food webs that evolved by allopatric speciations can be understood by taking the increases in the apparent sizes of mutations with decreasing web size, as described by Eqs. (30) and (32), into account. What appears as a local speciation is actually the result of a complex evolutionary history after which one species A invades a community that contains another species B that is similar to A because it shares a common ancestor. From the local perspective, it appears as if A speciates from B by a large mutation. With respect to the matching model, the analysis of Section 4.2 shows that for a basic characterization of phylogenetic trees – the distribution of the degrees of relation between pairs of species – global evolution is well approximated in terms of local evolution. For degree distributions involving more than two species, however, the situation remains unclear.

In the following, a stochastic theory of food-web topology is developed based on the matching model. First, an exact description of the model steady state is derived. Most results are stated explicitly. Other aspects of the steady state, phylogenetic trees, are described in terms of an algorithm that yields exact steady state phylogenies in a finite run time. Combining the results, one obtains a fast algorithm to sample food-web topologies from the exact matching-model steady state. Specific statistical properties are then analytically derived from the algorithm. This stochastic analysis is the key for obtaining the formulae for the correct re-normalization of model parameters. Results are verified by simulations. Readers unfamiliar with basic stochastic methods (e.g., Bailey, 1964; Feller, 1971) might skip the analytic parts of this paper without loss. Concluding remarks discuss conceivable applications of the theory to other ecological and biological networks.

2. The matching model

2.1. Definition

In the matching model (Rossberg et al., 2006a), each species i is characterized by a logarithmic size parameter s_i in the range [0,1] and two vectors of size n containing values +1 and −1, that is, $\vec{v}_i, \vec{f}_i \in \{-1, +1\}^n$, which describe abstract traits of the species. The first vector $\vec{v}_i$ describes traits determining vulnerability against foraging, the second vector $\vec{f}_i$ foraging strategies and preferences. The strength of a trophic link from a resource i to a consumer j is thought to be an increasing function of the number $m_{ij} := (\vec{v}_i \cdot \vec{f}_j + n)/2$ of matches between the vulnerability traits of i and the foraging traits of j, or, equivalently, of the overlap $x_{ij} := \vec{v}_i \cdot \vec{f}_j / \sqrt{n}$. A link is

considered to be present if x_{ij} exceeds some threshold $x_{ij} \geq x_0$ and $s_i \leq s_j + \lambda$, where the model parameter λ sets a lower bound for the predator/prey size ratio.

Matching-model food webs evolve by speciations, extinctions and invasions, which are modeled by a simple birth–death–invasion process (Bailey, 1964). Speciations from any species in the web occur at a rate r_+ per species. The traits of the new species j are obtained from the traits of the ancestral species i with some mutations: Each of the n foraging traits flips (from −1 to +1 or vice versa) with probability p_f, and each of the vulnerability traits flips with probability p_v. The size parameter mutates as $s_j = s_i + \Delta s$, where Δs is normally distributed with mean zero and variance D. If s_j exceed the range [0,1], it is projected back into this range by repeated application of the operations $s_j \rightarrow -s_j$ and $s_j \rightarrow 2 - s_j$. The extinction rate for each species is $r_- (<r_+)$. New species invade at a rate r_1. The traits of invading species are chosen from the single-species steady-state distribution of the speciation process: foraging and vulnerability traits are distributed evenly over $\{-1, 1\}^n$ and size parameters evenly over [0,1].

2.2. Basic properties

To provide a background for the theory developed in Sections 3 and 4, some basic, known properties of the matching model are explained in the following.

2.2.1. Clades
The analysis of the matching model is simplified by dividing the set of member species of a web into clades of species that all derive from the same invading species (Rossberg et al., 2006b). The number of species in a clade is described by a simple birth–death process (Bailey, 1964). If $r_- < r_+$, which is here assumed, clades have a finite lifetime (for the life-time distribution, see Bailey, 1964). The contribution of clades to the overall stochastic properties of the food-web steady state is proportional to their lifetime. The distribution for the number of species in a clade at a moment chosen randomly (evenly) over its life time, with clades weighted by their lifetime, can be obtained by considering the birth–death process where, immediately after the extinction of the last species of a clade, a new clade with a single species is generated, or, equivalently, the steady state of a birth–death process where the extinction of the last species is forbidden. Denoting the probability for having a clade of size k in the steady state by p_k, and equilibrating probability flows $\phi_{k \rightarrow k+1}$ from k to $k + 1$ and backwards ($\phi_{k+1 \rightarrow k}$), one obtains a condition

$$\phi_{k \rightarrow k+1} = k r_+ p_k = (k+1) r_- p_{k+1} = \phi_{k+1 \rightarrow k}. \qquad (1)$$

This is solved by

$$p_k = -\frac{\rho^k}{k \ln(1-\rho)}, \qquad (2)$$

where the abbreviation $\rho = r_+/r_-$ has been introduced and an appropriate normalization was applied. The moment generating function for p_k is given by

$$m(z) = \sum_k p_k z^k = \frac{\ln(1-\rho z)}{\ln(1-\rho)}, \tag{3}$$

where z is a formal variable. In particular, the mean size of a clade is $m'(1) = -\rho/[(1-\rho)\ln(1-\rho)]$.

New clades are generated at a rate r_1, and existing clades go extinct at a rate

$$r_0 = r_- \quad p_1 = -\frac{r_+}{\ln(1-\rho)}, \tag{4}$$

independent from each other. As a result, the total number of clades is Poisson distributed with mean r_1/r_0, and the moment generating function for the number of clades is

$$m_c(z) = \exp\left[\frac{r_1}{r_0}(z-1)\right]. \tag{5}$$

The moment generating function $m_S(z)$ for the total number of species S in a matching-model web can now be obtained using the composition theorem for moment generating functions (Feller, 1971): If N is the sum of N_1 independent realizations of N_2, and N_1 and N_2 are random numbers with moment generating functions $m_1(z)$ and $m_2(z)$, respectively, then N has the moment generating function $m(z) = m_1(m_2(z))$. Since S is the sum of the sizes of the constituent clades,

$$m_S(z) = m_c(m(z)) = \left(\frac{1-\rho}{1-\rho z}\right)^\kappa, \tag{6}$$

with $\kappa := r_1/r_+$. That is, S follows a negative binomial (or Polya) distribution. The mean number of species is $\langle S \rangle = m_S'(1) = \kappa\rho/(1-\rho)$ (here and below, $\langle \cdot \rangle$ is used to denote expectation values).

2.2.2. Phylogenetic correlations of links

Phylogenetic relations between species lead to phylogenetic correlations between link strengths (as shown empirically by Cattin et al., 2004; Bersier and Kehrli, 2007). Denote the νth component of $\vec{v}_i$ by $v_i^{(\nu)}$ and the νth component of $\vec{f}_i$ by $f_i^{(\nu)}$. Then

$$\begin{aligned} \text{cov}(x_{hi}, x_{jk}) &= \frac{1}{n}\text{cov}(\vec{v}_h \cdot \vec{f}_i, \vec{v}_j \cdot \vec{f}_k) \\ &= \frac{1}{n}\sum_{\nu=1}^n \text{cov}(v_h^{(\nu)} f_i^{(\nu)}, v_j^{(\nu)} f_k^{(\nu)}) \\ &= \frac{1}{n}\sum_{\nu=1}^n \text{cov}(v_h^{(\nu)}, v_j^{(\nu)})\,\text{cov}(f_i^{(\nu)}, f_k^{(\nu)}), \end{aligned} \tag{7}$$

because all n components evolve independently, and vulnerability traits evolve independent of foraging traits in the model. Since all vulnerability traits evolve according to the same rule, $\text{cov}(v_h^{(\nu)}, v_j^{(\nu)})$ is equal for all ν, and $\text{cov}(f_i^{(\nu)}, f_k^{(\nu)})$ as well. Thus

$$\text{cov}(x_{hi}, x_{jk}) = \text{cov}(v_h^{(1)}, v_j^{(1)})\,\text{cov}(f_i^{(1)}, f_k^{(1)}), \tag{8}$$

that is, the covariances between links have a tensor-product structure, with the first factor depending only on phylogenetic correlations between resources, and the second factor only on phylogenetic correlations between consumers. Ives and God-fray (2006) derived such a tensor-product structure under the assumption that link strength is determined by a single vulnerability traits and a single foraging trait alone. The analysis above shows that this assumption is not necessary.

If species h and j belong to different clades, then $\text{cov}(v_h^{(1)}, v_j^{(1)}) = 0$. To derive this covariance for two species from the same clade, note that a straightforward induction shows that the probability p that $v_h^{(1)} = v_j^{(1)}$ is

$$p = \tfrac{1}{2}[(1-2p_v)^{l_{hj}} + 1], \tag{9}$$

where l_{hj} is the degree of relation, that is, the number of speciation events that separates h and j. Thus, $\text{cov}(v_h^{(1)}, v_j^{(1)}) = 2p - 1 = (1-2p_v)^{l_{hj}}$, and

$$\text{cov}(x_{hi}, x_{jk}) = (1-2p_v)^{l_{hj}}(1-2p_f)^{l_{ik}}. \tag{10}$$

This result had been derived in the limit $n \to \infty$ before (Rossberg et al., 2006a), and is here generalized to arbitrary $n > 0$. For $n \to \infty$, the multivariate central limit theorem applies, and elements of the overlap matrix $x_{ij} = \vec{v}_i \cdot \vec{f}_j/\sqrt{n}$ are multivariate normally distributed with mean zero and the above covariance matrix. In particular, each element x_{ij} has unit variance.

3. Generating exact steady-state matching-model samples

3.1. Outline of the algorithm

This section describes an algorithm that generates random food-web topologies sampled from the exact steady state of the matching model for $n \to \infty$. The algorithm has the following structure:

1. Sample the number of clades and the size of each clade.
2. Sample the degrees of phylogenetic relations between clade members.
3. Sample the size parameters of all species.
4. Sample the link strengths between species.
5. Threshold the link strengths to get a binary food web.

Technically, the most complex part of the algorithm is to sample the phylogenetic relations in Step 2. The procedure and its theoretical basis are described below. Another technical complexity is the computation of the Cholesky decompositions of covariance matrices, which is needed to obtain random variables with the corresponding covariance structure. But for this packaged libraries are available (Anderson et al., 1999).

3.2. Clade numbers and clade sizes

This step is based on Section 2.2.1. The number of clades c is sampled from a Poisson distribution with mean r_1/r_0, where r_0 is given by Eq. (4), e.g., using the method of Ahrens and Deiter (1974). Next, the number of species k_i ($i = 1, \ldots, c$) in each clade is sampled from the log-series distribution Eq. (2). A simple algorithm for this is to sample a random number X uniform in [0,1] and add successive probabilities p_k until the sum exceeds X. Then k_i is given by the number of addends minus one.

3.3. Backward phylogenies

A simple idea to sample the degrees of phylogenetic relations between species in a clade (together with the clade's size) would be to initiate a clade with a single species, generate its phylogenetic history by simulating the corresponding branching process until the extinction of the clade, then fixing a moment in time uniformly distributed over the clade's lifetime, and finally determining the degree of relation of all species present at this moment. Computationally, however this procedure is awkward, because it requires keeping track of the full phylogenetic history (topology and timing), even though most information it contains is never used. And mathematically the method is, in this form, wrong, because it does not weight clades by their lifetime as would be required.

A computationally simpler approach is to develop the phylogenies backward in time, starting from the given number of species k_i in the clade, until all k_i species are connected (Hein et al., 2005). This requires a description of the dynamics of the birth–death process backward in time.

The goal here is to reconstruct the phylogenetic relations of the $k_i > 0$ species present when the web is sampled, and these are fully determined by the process that started when the size of the clade was $k = 1$ for the last time. Thus, only phylogenies with clade sizes $k > 0$ are of interest here, and one may analyze the backward evolution of the clade conditional to $k > 0$.

First, consider the clade size k at two moments separated by a short time interval $\Delta t > 0$. By the definition of the birth–death process, the conditional probability that a clade that contains k species before the interval contains $k + 1 > 0$ species after the interval Δt is

$$P(k + 1|k; \Delta t) = r_+ k \, \Delta t \tag{11}$$

to lowest order in Δt. The probability that it contains $k - 1 > 0$ species is

$$P(k - 1|k; \Delta t) = r_- k \, \Delta t. \tag{12}$$

Since the situation $k - 1 = 0$ is excluded, $P(0|1; \Delta t) = 0$. In the remaining cases, k remains unchanged: $P(k|k; \Delta t) = 1 - P(k + 1|k; \Delta t) - P(k - 1|k; \Delta t)$.

If and only if the number of species k follows the steady-state distribution p_k given by Eq. (2) before Δt it follows this distribution also after Δt, because only then upward and downward probability flows are equilibrated. Since we assume k_i to follow the steady-state distribution for the reasons explained in Section 2.2.1, we can assume k to be steady-state distributed at any earlier time, too.

Using Bayes' theorem, the probability that there were $k + 1$ species before the interval Δt when there are k species afterwards can therefore be computed as

$$
\begin{aligned}
P(k + 1|k; -\Delta t) &= P(k|k + 1; \Delta t) \frac{p_{k+1}}{p_k} \\
&= r_-(k + 1) \, \Delta t \frac{k\rho}{k + 1} \\
&= r_+ \, k \, \Delta t
\end{aligned} \tag{13}
$$

to lowest order in Δt. Correspondingly,

$$P(k - 1|k; -\Delta t) = r_- \, k \, \Delta t \tag{14}$$

for $k - 1 > 0$. That is, when going backward in time, new species appear (reverse extinctions) at a rate $r_+ k$ in a clade containing k species, and each of the k existing species is *absorbed* by another species (reverse speciation) at a rate r_-. Due to the Markov property of the process, this species will be absorbed by any of the $k - 1$ other species with equal probability.

The degrees of relations l_{hj} between the k_i clade members can therefore be obtained using an algorithm as sketched by the pseudo code in Fig. 2. Lines 5 and 6 of the pseudo code implement the Gillespie algorithm (Gillespie, 1977) for random point-processes. Some additional bookkeeping, not shown in Fig. 2, is required to decide when all relevant degrees have been calculated (Fig. 2, line 4) and to keep track of the sets of descendants of each species.

3.4. Sampling of size parameters

With a given degree matrix l_{hj}, it is now possible to sample the size parameters for all species in a clade. First, observe that the projection of the size parameters into the range $[0,1]$ by repeated substitutions $s_j \to -s_j$ and $s_j \to 2 - s_j$, which, in the original description of the model, is to be done after every mutation, can equivalently be postponed to after the last speciation. Therefore, the size parameters are first sampled for an evolution without the projection.

Then, the difference $s_i - s_j$ between the size parameters of two species i and j is normally distributed with mean zero and a variance that increases by D with every speciation separating i and j, that is, $\mathrm{var}(s_i - s_j) = Dl_{ij}$. Now, choose an arbitrary member h of the clade as a reference species, and observe that

$$
\begin{aligned}
Dl_{ij} = \mathrm{var}(s_i - s_j) &= \mathrm{var}[(s_i - s_h) - (s_j - s_h)] \\
&= \mathrm{var}(s_i - s_h) - 2\mathrm{cov}(s_i - s_h, s_j - s_h) + \mathrm{var}(s_j - s_h) \\
&= Dl_{ih} - 2\mathrm{cov}(s_i - s_h, s_j - s_h) + Dl_{jh}
\end{aligned} \tag{15}
$$

```
1:  start with a clade containing k_i species
2:  for all species s in the clade do
3:      l_ss ← 0
4:  while some degrees l_vw between the original k_i species remain undefined do
5:      sample a random number X ∈ [0, 1[
6:      if X < (1 + ρ)^{-1} then
7:          select a species s at random from the clade
8:          select another species r at random from the clade
9:          [absorb s into r as follows:]
10:         for all descendants v of s, including s do
11:             for all descendants w of r, including r do
12:                 l_vw ← l_vs + l_wr + 1
13:                 l_wv ← l_vw
14:         add the descendants of s to the descendants of r
15:         remove s from the clade
16:     else
17:         add a new species s to the clade
18:         l_ss ← 0
```

Fig. 2 – Algorithm to compute the phylogeny of clade i backward in time.

implies that the covariance matrix for differences relative to s_h has the form

$$\text{cov}(s_i - s_h, s_j - s_h) = D \frac{l_{ih} + l_{jh} - l_{ij}}{2}. \tag{16}$$

The standard method to sample a vector $\mathbf{y}$ from a zero-mean, multinormal distribution with a given covariance matrix is to compute the lower Cholesky transform $\mathbf{C}_L$ of the covariance matrix, sample a corresponding vector $\mathbf{x}$ of independent standard normal random variables, and to obtain the desired random vector as $\mathbf{y} = \mathbf{C}_L \mathbf{x}$. This method can here be used to sample the size-parameter differences relative to s_h.

The size parameter s_f of the clade founder species is distributed uniformly over the unit interval [0,1]. Relative to this value, s_h is shifted by some symmetrically distributed random number Δs. But the final projection onto [0,1] will transform the density of $s_f + \Delta s$ back to a uniform density over [0,1] for any symmetrically distributed Δs (up to possible endpoint effects of measure zero). Thus, s_h can also directly be sampled uniformly from [0,1]. Adding s_h to the differences sampled above and applying the final projection onto [0,1] yields all size parameters of the clade.

3.5.   Sampling of link strengths and topology

Link strengths with a covariance structure as computed in Section 2.2.2 can be obtained as follows: Denote by $C_v^{(g)}$ the lower Cholesky transform of the matrix $\{(1 - 2p_v)^{l_{ij}}\}$ of the gth clade, and by $C_f^{(h)}$ the lower Cholesky transform of $\{(1 - 2p_f)^{l_{ij}}\}$ for the hth clade. Sample a $k_g \times k_h$ matrix $\mathbf{X}$ of independent standard normal random variables (k_g and k_h are the sizes of clades g and h). Then, a random matrix $\mathbf{X}'$ with covariances between the rows corresponding to the first factor of Eq. (10) is obtained as $\mathbf{X}' = C_v^{(g)} X$, and a random matrix with the full tensor product form of Eq. (10) is obtained as

$$\mathbf{X}'' = \left(C_f^{(h)} X'^T\right)^T = C_v^{(g)} X C_f^{(h)\,T}. \tag{17}$$

This is the matrix of overlaps x_{ij} between the vulnerability traits of the members of clade g and the foraging traits of the members of clade h in the limit of an infinite number of traits $n \to \infty$. Computation of the overlaps for all pairs of clades, thresholding, and application of the size constraint $s_i \le s_j + \lambda$ yields the food-web topology.

3.6.   Testing the algorithm

As a numerical test of the validity of the algorithm, the statistical properties of samples generated by this algorithm were compared with the statistical properties of samples generated by a direct simulation of the matching model using the code of Rossberg et al. (2006a).

Means and covariance matrices of 13 food-web properties were computed following the scheme of Rossberg et al. (2006a), that is, from 1000 food-web samples, standardized for better comparison with empirical data and with the web size fixed at the empirical value. The reader is referred to the original work for the precise definition of the food-web properties and the details of the evaluation procedure. The

standardization of food webs is not immediately required for a comparison of the two methods, but using the same evaluation scheme as in previous work helps putting the small differences found (see below) into context. In any case, the question at hand is not the accuracy of the new algorithm, but if it is conceptually correct. Conceptual errors would be reflected in drastically different properties, irrespective if webs are standardized or not. Fixing the web size avoids blurring the food-web properties by the large but trivial fluctuations of size (Rossberg et al., 2006b).

I used the parameter set ($r_1 = 0.48, r_- = 1, 1 - r_+ = 1 - \rho = 0.0082, \lambda = 0.068, p_v = 0.008, p_f = 0.39, D = 0.05^2, (2\pi)^{-1/2} \int_{-\infty}^{x_0} \exp(-x^2/2)\,dx = 0.29$) that was obtained by fitting the model to empirical data for a Caribbean reef (Opitz, 1996). This data set belongs to those which are difficult to reproduce by simpler models (Rossberg et al., 2006a). Table 1 lists sample means and standard deviations for the 13 properties considered, and gives Student's t for the differences between the means obtained by using the algorithm above and means obtained by direct simulations. Some statistically significant deviations can be identified. For example, VulSD, the coefficient of variation of the number of a species' consumers (Williams and Martinez, 2000) is clearly larger for the direct simulation. These deviations are most likely due to the fact that directs simulations only approximate the two limits of an infinite relaxation time and an infinite number of traits.

Overall, however, the differences are small. The χ^2 statistic obtained from model means and covariances in comparison with the empirical data as a measure for the goodness of fit is $\chi^2 = 7.5$ for the direct simulation, for which parameters had been fitted, and 8.0 for the algorithm introduced here (8 degrees of freedom). For comparison, the best fit for the niche model of Williams and Martinez (2000) yields $\chi^2 = 79.1$, and for the nested-hierarchy model of Cattin et al. (2004) one obtains $\chi^2 = 169$ (12 degrees of freedom in both cases, see Rossberg et al., 2006a for details).

4.   Sub-sampling of matching-model food webs

From a given matching-model food web (hereafter called the *large web*), select species at random, each with probability q (assume $0 < q < 1$). What will the resulting sub-web look like? How good can this sub-web be approximated by another matching model web (hereafter called the *small web*) obtained with a different set of model parameters (Fig. 1)? More specifically, how good can the distribution of random sub-webs obtained from large webs sampled from the matching-model steady state with one set of parameters be approximated by the distribution of small webs sampled from the matching model with another set of parameters? In the following, I will first compare the statistical properties of matching-model webs and sub-webs in order to derive good parameters for the small webs, given the parameter set for the large webs (below, primed symbols correspond small webs, unprimed symbols to large webs). Then, more complex properties of small webs and sub-webs of large webs are compared numerically, to verify the accuracy to which one approximates the other.

Table 1 – Comparison of sample means and standard deviations of food-web properties obtained from the exact steady state and from direct simulations with empirical data. Student's t compares the two mean values

Food-web property	Simple explanation	Empirical value	Exact		Simulation		t
			Mean	S.D.	Mean	S.D.	
C	Directed connectance	0.237	0.234	0.038	0.233	0.038	0.6
T	Fraction of top predators	0	0.011	0.023	0.015	0.028	−3.5
GenSD	Variability of generality	0.90	0.88	0.11	0.87	0.11	2.0
VulSD	Variability of vulnerability	0.64	0.58	0.11	0.61	0.11	−6.1
MxSim	Trophic similarity among species	0.585	0.592	0.047	0.597	0.048	−2.4
Cannib	Fraction of cannibal species	0.438	0.358	0.078	0.364	0.081	−1.7
aChnLg	Mean food-chain length	13.4	12.8	1.7	12.5	1.7	3.9
aChnSD	Variability of chain length	2.88	2.88	0.28	2.83	0.28	4.0
aChnNo	$\log_{10}$ number of chains	7.30	6.78	0.72	6.72	0.76	1.8
aLoop	Number of loops	38	46	22	42	21	4.2
aOmniv	Degree of omnivory	1.63	1.67	0.22	1.67	0.22	0
Ddiet	Deviation from intervality	0.336	0.357	0.097	0.350	0.091	1.7
Clust	Clustering coefficient	0.669	0.581	0.073	0.583	0.075	−0.6

4.1. Clade numbers and clades sizes

Deciding for a single species if it will be part of the sub-web of a large web or not corresponds to sampling a Bernoulli random variable which is 1 with probability q and otherwise zero. It has the moment generating function $m_B(z) = qz + (1 - q)$. The size S' of the selected sub-web is the sum of such Bernoulli variables. Its moment generating function can be obtained from the moment generating function Eq. (6) for the size S of the full web using the composition theorem as

$$m_{S'}(z) = m_S(m_B(z)) = \left(\frac{1 - \rho}{1 - \rho(qz + 1 - q)} \right)^\kappa$$
$$= \left(\frac{1 - \rho'}{1 - \rho' z} \right)^\kappa \qquad (18)$$

with

$$\rho' = \frac{q\rho}{1 - \rho + q\rho}. \qquad (19)$$

That is, the distribution of the number of species in the sub-web and, as a more detailed analysis shows, also the number of clades and their size distribution, is perfectly reproduced by the small web with the appropriate choice of ρ' and with $\kappa' = \kappa$. It is not difficult to see that $\rho' < \rho$, and that, in the limit $\rho \to 1$ at fixed q, also $\rho' \to 1$, with $(1 - \rho)/(1 - \rho') \to q$. Typical values of ρ obtained from field data are close to one. Thus, the limit $\rho, \rho' \to 1$ is often a good approximation. We shall sometimes invoke it below to simplify results.

Furthermore, as expected, $\langle S' \rangle = q\langle S \rangle$. On the other hand, because from some clades no species are selected, only a fraction $\log(1 - \rho')/\log(1 - \rho)$ of the clades in the large web is also contained in the sub-web and in the small web.

4.2. Phylogenetic degree distributions

The statistical properties of matching-model webs depend on the structure of phylogenetic trees, which, in turn, can be described in terms of the matrices of phylogenetic degrees l_{ij}. These matrices have above been defined for single clades, but the definition can be extended to the full set of species of a web by setting $l_{ij} = \infty$ whenever i and j are from different clades. A simple characterization of the distribution of these matrices is the probability distribution $P_{deg}(l)$ to have $l_{ij} = l$ for two different species i and j randomly picked from the full set of species.

Assume, for simplicity, that the web consists of a large number of clades, such that the total size S of the web is mostly uncorrelated with the size of a single, randomly picked clade. In this case, the probability that a randomly picked species i comes from a clade of size k, which is $P(\text{pick } i \text{ from given clade}|\text{the given clade has size } k) \times P(\text{a clade has size } k)$, can be approximated as $\langle k/S \rangle p_k = k \langle 1/S \rangle p_k$, with p_k denoting the probability for a clade of size k, given by Eq. (2). Similarly, the probability that a second randomly picked species j comes from the same clade as i, and this clade has size k, can be estimated as $k(k - 1)\langle 1/S(S - 1) \rangle p_k$. Thus, for a fraction

$$P_{same} = \left\langle \frac{1}{S(S - 1)} \right\rangle \sum_k k(k - 1) p_k$$
$$= -\frac{\langle 1/S(S - 1) \rangle \rho^2}{(1 - \rho)^2 \ln(1 - \rho)} \qquad (20)$$

of all disjoint pairs, i and j will come from the same clade. They come from different clades and yield $l_{ij} = \infty$ with probability $P_{deg}(\infty) = 1 - P_{same}$. Since the small web exactly reproduces the clade size- and number distribution of the sub-web, this part of the phylogenetic degree distribution is exactly reproduced as well.

The degree distribution for the case that i and j are from the same clade can be computed by analyzing the backward branching process described in Section 3.3, and paying special attention to the events involving i, j and the lineages of their ancestral species. For simplicity, call the species that are part of the lineages of i and j black species, and all other members of the clade white species. Going backwards in time, a clade always contains exactly two black species, up to the moment where the lineages of i and j join, and the phylogenetic degree l_{ij} is decided. l_{ij} is given by the total number of absorptions (time-reversed speciations) of black species until then.

As the clade evolves backward in time, distinguish two types of dynamics: (Type 1) time intervals without the

absorption of black species and (Type 2) events where black species are absorbed.

At the beginning of the backward evolution, the probability distribution g_k that the clade under consideration has size k (with $k \geq 2$) is given by

$$
\begin{aligned}
g_k &= k(k-1)\left\langle \frac{1}{S(S-1)} \right\rangle \frac{p_k}{P_{\text{same}}} \\
&= N_g(k-1)\rho^k,
\end{aligned}
\tag{21}
$$

where $N_g = (1-\rho)^2/\rho^2$ and Eqs. (2) and (20) have been used to simplify the result. Under Type 1 dynamics, the rate of change of the distribution g_k is determined by upward ($k \to k+1$) and downward ($k \to k-1$) probability flows. As argued in Section 3.3, new species (which are all white) appear at a rate $r_+ k$ if there are k species now, thus

$$
\phi_{k \to k+1} = r_+ k g_k,
\tag{22}
$$

just as in Eq. (1). The downward flow corresponds to absorptions. Under Type 1 dynamics, only absorptions of white species occur, and thus

$$
\phi_{k \to k-1} = r_-(k-2)g_k.
\tag{23}
$$

Comparing upward and downward flows for g_k as given by Eq. (21), it is easily verified that $\phi_{k \to k+1} = \phi_{k+1 \to k}$, that is, Eq. (21) describes the steady state of Type 1 dynamics. g_k was initiated in the steady state and, as is shown below, g_k remains in the steady state until the coalescence of the two lineages.

Intervals of Type 1 dynamics are interrupted by absorptions of black species, i.e., Type 2 dynamics, at a rate $2r_-$. When a black species is absorbed and the clade has size k, it is an absorption by the other black species, and hence the coalescence of the two lineages, with probability $1/(k-1)$. Averaging over all k yields

$$
P_{\text{coal}} = \sum_{k=2}^{\infty} \frac{g_k}{k-1} = 1 - \rho.
\tag{24}
$$

On the other hand, with probability $(k-2)/(k-1)$, the absorbing species is white and becomes black (the bearer of a lineage). Since k is decremented by one in this process, the probability to have a clade size $k-1$ when going back from Type 2 to Type 1 dynamics, conditional to still having two black species, is

$$
\begin{aligned}
[g_{k-1}]_{\text{after}} &= \left[g_k \cdot \frac{k-2}{k-1} \cdot \frac{1}{1-P_{\text{coal}}} \right]_{\text{before}} \\
&= [N_g(k-2)\rho^{k-1}]_{\text{before}} \\
&= [g_{k-1}]_{\text{before}},
\end{aligned}
\tag{25}
$$

if the steady-state distribution Eq. (21) is assumed. Thus, both Type 1 and Type 2 dynamics leave the initial distribution $g = g_k$ unchanged. Due to the general diffusive nature of master equations, g will relax to the steady-state form even if the initial condition slightly deviates from it, as one must expect if the simplifying assumption of a large number of coexisting clades made above is not perfectly met.

At each Type 2 episode, coalescence of the two lineages occurs with probability P_{coal}. Thus, the probability of coalescence in the lth Type 2 episodes (with $l \geq 1$) follows a geometric distribution

$$
P_{\text{deg},1}(l) = (1 - P_{\text{coal}})^{l-1} P_{\text{coal}}
\tag{26}
$$

with moment generating function

$$
m_{\text{deg},1}(z) = \langle z^l \rangle = \frac{P_{\text{coal}} z}{1 - (1 - P_{\text{coal}})z}.
\tag{27}
$$

In particular, the mean degree of relation between two different species of the same clade is $1/P_{\text{coal}}$. Finally, one obtains

$$
P_{\text{deg}}(l) = P_{\text{same}} \cdot P_{\text{deg},1}(l)
\tag{28}
$$

for $l < \infty$.

These considerations hold for two species picked at random from the large web, and as such for the random sub-web of species sampled with probability q, but also for a small matching-model web designed to approximate the sub-web. In the latter case, the coalescence probability P'_{coal} is given by Eq. (24), with ρ replaced by ρ'. Thus, average degrees are by a factor $P'_{\text{coal}}/P_{\text{coal}} \approx 1/q$ larger in the sub-web than in the small web. Other model parameters must be adjusted to compensate for this.

Eq. (26) was verified numerically by comparing the theoretical distribution $P_{\text{deg},1}(l)$ for values of ρ ranging from 0.1 to 0.98 with numerical estimates. In order to obtain an estimate of $P_{\text{deg},1}(l)$, 10^5 clades with the steady-state size distribution Eq. (2) were evolved backward in time by the algorithm given in Section 3.3, and the number of occurrences of phylogenetic degrees l was counted. Numerical results excellently reproduced the theoretical predictions. Examples of numerical and theoretical degree distributions are shown in Fig. 3.

4.3. Adjusting other model parameters

The difference Δs in size parameter between two related species is given by adding l independent mutations y, where l is the
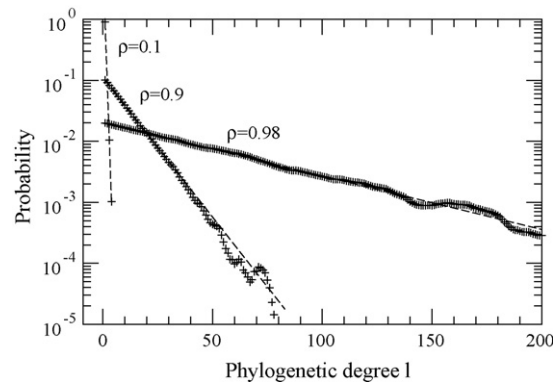

Fig. 3 – The distribution of the phylogenetic degree of relation between random pairs of species (dashed lines: theory; +: simulation) for various values of ρ.

degree of relation and y is normally distributed with variance D (moment generating function $m_y(e^t) := \langle e^{ty} \rangle = \exp(Dt^2/2)$). Using the composition theorem, the moment generating function of Δs for general l can be obtained as

$$
\begin{aligned}
m_{\Delta s}(e^t) &:= \langle e^{t\,\Delta s} \rangle = m_{\mathrm{deg},1}(m_y(e^t)) \\
&= \frac{P_{\mathrm{coal}} \exp(Dt^2/2)}{1 - (1 - P_{\mathrm{coal}})\exp(Dt^2/2)}.
\end{aligned}
\tag{29}
$$

The expected variance is therefore $\mathrm{d}^2 m_{\Delta x}(e^t)/\mathrm{d}t^2|_{t=0} = D/P_{\mathrm{coal}}$. Equating variances for disjoint pairs of related species from the sub-web and from the small web yields

$$
D' = D\,\frac{P'_{\mathrm{coal}}}{P_{\mathrm{coal}}}.
\tag{30}
$$

In general, the higher moments of Δs for the two webs will differ. However, Eq. (30) shows that, as web sizes increase and P_{coal} decreases, D will decrease, too, with the ratio D/P_{coal} fixed. Assuming that both P_{coal} and D are small

$$
m_{\Delta s}(e^t) \approx \frac{1}{1 - (Dt^2/2P_{\mathrm{coal}})},
\tag{31}
$$

that is, the distributions of Δs for sub-webs and small webs are nearly identical.

In order to adjust the covariances between trait overlaps given by Eq. (10), the trait flipping probabilities p_v and p_f in the small model are chosen such that the expectation values of the factors $(1 - 2p_v)^{l_{hj}}$ and $(1 - 2p_f)^{l_{ik}}$ entering Eq. (10) remain unchanged for disjoint pairs of species chosen at random. Noting that $\langle (1 - 2p_v)^l \rangle = m_{\mathrm{deg},1}(1 - 2p_v)P_{\mathrm{same}}$ with $m_{\mathrm{deg},1}(z)$ given by Eq. (27), one obtains

$$
\begin{aligned}
p'_v &= \frac{p_v P'_{\mathrm{coal}}}{P_{\mathrm{coal}} + 2p_v(P'_{\mathrm{coal}} - P_{\mathrm{coal}})} \\
&\approx \frac{p_v}{q + 2p_v(1 - q)}
\end{aligned}
\tag{32}
$$

and similar expressions for p'_f. The approximation in the last step is valid for ρ and ρ' near 1. It shows that, as q decreases from 1 to 0, p'_v increases from p_v to $1/2$, corresponding to a loss of correlations between the few remaining species in the sub-web. Thus, it is likely that for the small empirical food webs that had been investigate in the early states of food-web theory, absence of phylogenetic correlations as realized in the cascade model (Cohen et al., 1990) was a good approximation.

4.4. Testing the theory

To measure the accuracy of the approximation of sub-webs by small webs, means and variances of 15 food-web properties of sub-webs of 1000 samples of large webs are compared with those obtained form 1000 samples of small webs. For technical reasons, the parameters for the small webs are fixed and those of the corresponding large webs computed thereof, rather than *vice versa*. In order to maximize the accuracy of characterizations, the sampled webs are not standardized. Of all sampled (sub- and small)

webs, only those of a fixed size ($S = 50$) are taken into consideration, again to avoid blurring properties. The steady-state algorithm is easily modified to avoid most of the calculations for webs with other values of S.

The parameter set used here ($r_1 = 1.5, r_- = 1, 1 - r_+ = 1 - \rho = 0.03, \lambda = 0.01, p_v = 0.01, p_f = 0.3, D = 0.05^2, (2\pi)^{-1/2} \int_{-\infty}^{x_0} \exp(-x^2/2)\,\mathrm{d}x = 0.2$) is modified from the set used above in order to allow a fast evaluation of large webs, while remaining within the empirical parameter range (see Rossberg et al., 2006a). To put the results into context, two different parameterizations are chosen for the large webs. The parameterization denoted as ''good'' relates primed and unprimed values as given by Eqs. (19), (24), (30), (32), and the corresponding equation for p_f (all other parameters remain unchanged). The ''bad'' parameterization adjusts only ρ, keeping D, p_v and p_f at the numerical values for the small webs. Sub-webs are obtained from large webs by picking species at random with probability $q = 0.1$.

Table 2 displays the results of this numerical test. Student's t is computed for the differences between ''good'' sub-webs and small webs, and ''bad'' sub-webs and small webs. Some statistically significant differences between ''good'' sub-webs and small webs can be found. The trophic similarity among species MxSim (Williams and Martinez, 2000) seems to be particularly sensitive to the distinction between full webs and sub-samples. Remarkably, the value for random assemblies is somewhat larger than for exact matching-model webs. This is just what one would expect, because in real assemblies combinations of trophically similar species are suppressed by competitive exclusion.

The overall agreement between ''good'' sub-webs and small webs is excellent, in particular compared to the results for ''bad'' sub-webs, which drastically differ. Of the 15 properties, only 3 have absolute t values larger than 3 for the ''good'' sub-webs, while there are 11 for the ''bad'' sub-webs. The results demonstrate that the matching model realizes the scaling property to a good approximation. ''Bad'' differ from ''good'' sub-webs by exhibiting much weaker phylogenetic correlations. Table 2 does therefore also provide insights regarding the dependence of specific food-web properties (and their variability) on such correlations.

5. Final remarks: the matching model as a tool box

The analysis of the matching model presented above split the model into several components. By re-arranging these components, models for other biological networks can be obtained where the matching of the properties of individual units and phylogenetic relations between these units play a role. The main components are:

1. Links are determined by large numbers of properties on both sides of the link. This describes links between complex entities that are established for reasons that can differ case by case. Mathematically, it leads to a statistical independence of links between quadruples of units. For example, if links were determined by a single foraging trait and a single

Property	Simple explanation	Small webs		"Good" sub-webs			"Bad" sub-webs		
		Mean	S.D.	Mean	S.D.	t	Mean	S.D.	t
C	Directed connectance	0.108	0.020	0.107	0.021	−0.6	0.105	0.010	2.2
T	Fraction of top predators	0.080	0.057	0.080	0.056	0	0.074	0.038	2.8
I	Fraction of intermediate species	0.64	0.12	0.62	0.11	2.5	0.80	0.06	−40
B	Fraction of bottom species	0.283	0.093	0.296	0.095	−3.0	0.120	0.045	50
GenSD	Variability of generality	1.25	0.22	1.25	0.22	−0.2	0.87	0.10	49
VulSD	Variability of vulnerability	0.678	0.111	0.679	0.113	−0.2	0.677	0.065	0.1
MxSim	Trophic similarity among species	0.558	0.054	0.590	0.057	−13.0	0.366	0.033	95
Cannib	Fraction of cannibal species	0.200	0.065	0.197	0.066	1.2	0.200	0.057	0
aChnLg	Mean food-chain length	6.54	1.65	6.52	1.71	0.3	7.45	1.33	−13.0
aChnSD	Variability of chain length	2.04	0.31	2.02	0.32	1.6	2.25	0.29	−15.3
aChnNo	$\log_{10}$ number of chains	4.33	0.67	4.36	0.71	−0.8	4.43	0.44	−3.7
aLoop	Number of loops	2.54	2.15	2.78	2.43	−2.4	1.46	1.29	13.6
aOmniv	Degree of omnivory	0.88	0.24	0.85	0.23	2.8	1.24	0.22	−36
Ddiet	Deviation from intervality	0.124	0.064	0.113	0.061	3.9	0.205	0.055	−30
Clust	Clustering coefficient	0.346	0.085	0.350	0.092	−0.9	0.241	0.035	36

Table 2 – Comparison of small matching-model webs with corresponding sub-samples of large matching-model webs, one with a "good" and another with a plausible but "bad" parameterization

vulnerability trait only (i.e., $n = 1$), then a situation in which $A \overset{\text{eats}}{\to} C$, $A \overset{\text{eats}}{\to} D$, and $B \overset{\text{eats}}{\to} C$ would imply that $B \overset{\text{eats}}{\to} D$, because either all traits are +1, or all traits −1. With $n \to \infty$, it follows from the multivariate normality of x_{ij} (Section 2.2.2) that this is the case only in the presence of phylogenetic correlations.

2. Neutral evolution of the units, where different kinds of properties evolve at different rates.
3. "Big eats small" and an evolution of size.

The final component is probably a particularity of food webs. Using the other two components, one might, for example, model pollinator networks by equipping pollinators with "pollinator traits" and plants with "susceptibility traits", and determining pollination interactions based on trait matching. Model parameters can be estimated from field data and then be scaled up or down to larger or smaller networks by the methods described here. Thinning of pollinator networks is a matter of great concern in conservation biology (Fontaine et al., 2006).

Another example would be niche overlap graphs between plants. In this case, the traits at both ends of a link would be of the same kind. Even applications to regulatory networks of cells are conceivable. Enzymes with similar properties due to common ancestors co-exists with similar roles in a single cell, and a key-lock match between two enzymes is thought to be required to activate interactions. Generally, only sub-units of cellular regulatory networks are known well. The theory presented here could contribute to getting the big picture for these networks, too.

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