# An elementary dynamic model for non-binary food webs

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## Abstract

Paine [Ecology 69 (1988) 1648] called for a "dynamic rather than static" food web theory which should also take into account the "interaction strength" between the nodes. Here we face the challenge: an elementary food web model is presented which is both, dynamic and non-binary. We introduce the complexity measure for non-binary food webs "*medium articulation*" which resolves a contradiction in the discussion of stability of ecosystems. We propose a possible standard for establishment of food webs which avoids arbitrariness of both, nodes and links. After consideration of non-binary webs, binary webs are deduced by removing small fluxes and setting remaining fluxes to 1. Comparing both network types, it is argued that non-binary webs are more important than binary webs.
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## 1. Introduction

A food web is the pattern of flows of energy and matter between suitably chosen compartments within an ecosystem. Often compartments represent "trophic species" containing all species which share the same set of prey and predators. However, up to now there seems to be no common agreement about what to merge into one node. It has been proposed to be here as explicitly as possible (Cohen et al., 1993). Food webs are basic to ecology and important for scientific and practical reasons. The qualitative information about "who eats whom" is the presupposition for advanced studies on population biology. "Biological concentration of toxins and pollutants could

be better predicted if food webs were known better. Strategies for integrated pest management, control of disease vectors, industrial waste-water treatment, and wildlife conservation" (Cohen et al., 1993) are examples for practical problems which should benefit from improved food web theory. A food web "allows a reader to assimilate much complex information rapidly" (Paine, 1988). This could help to better understand the often dominating role of indirect effects in the ecosystem answer to manipulation experiments (Pimm, 1991).

Most food web models use only binary information: linkage or not (Cohen and Newman, 1985; Williams and Martinez, 2000; Pimm et al., 1991). The cascade model (Cohen and Newman, 1985) assigns each species a "niche value" and allows only predation of species with a lower niche value. Therefore, this does not yield a food web which expresses a cycling of matter in the ecosystem, but a cycle-free digraph. The niche model (Williams and Martinez, 2000)

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additionally allows cannibalism and, to some degree, predation of species with a higher niche value, thus yielding more web-like structures.

A more quantitative description is obtained with non-binary food webs, where the fluxes $t_{ij}$ from node $i$ to $j$ are measured as accurately as possible. Today most of the "students of food webs" agree upon "the real goal of measuring links quantitatively" (Cohen et al., 1993).

All these models give only a static characterisation of food webs, or more precisely, a static description of food web topology, i.e. of the structure of linkage of the nodes. In contrast, food webs with a given topology are often simulated dynamically using differential equations. Two recent examples are van Nes and Scheffer (2003) and Jordáne et al. (2003). The well-known Lotka-Volterra cascade model (Cohen et al., 1990) also fits into this category. It deduces the topology of links from a refined version of the cascade model (Cohen and Newman, 1985), and models the dynamics of the interactions with Lotka-Volterra terms, that is to say that the topology remains fixed. In order to incorporate also spatial dependencies, instead of studying the corresponding differential equations often the simpler cellular automata models are used (Spencer, 1997; Keitt, 1997). Recently, five different modelling techniques have been compared to make predictions on a short time scale (Moisen and Frescino, 2002).

However, all these dynamical models are dynamic only on a short time scale, but static on a longer time, for instance, the time scale of evolution. On such longer time scales typically also the topology of the underlying food web changes (changes in the number of nodes and links). The problem "What happens to food webs (or generally to ecosystems) on longer time scales?" has been tackled under the question for goal functions of ecosystems (Jørgensen, 1997). We have argued that no universal goal function can exist that describes the direction of development of all natural systems (Wilhelm and Brüggemann, 2000).

However, to investigate basic mechanisms of evolution, the corresponding dynamic models should be characterised by food webs with variable topology and variable connectance $C$ (number of actual links divided by the maximal possible number). Such dynamic models should demonstrate a self-organisation of food web topology. As result of this self-organisation one should obtain food webs with the same topological features as observed in empirical webs. In the following we present a simple model which fulfills these requirements, but at first a useful measure that characterises non-binary food webs is introduced.

## 2. The complexity measure "medium articulation"

In discussion of stability and maturity of ecosystems, an interesting contradiction arise. Some authors state that the more connections there are in a food web, the more stable the corresponding ecosystem (Rutledge et al., 1976; McCann et al., 1998; Polis, 1998). (Some of the confusion about stability has been clarified by Pimm (1991) who has given precise definitions for resilience, persistence, resistance, variability and stability in the mathematical sense, all covering different aspects of "stability".) Using the mathematical definition for local stability of a steady state May (1972) found the opposite: highly connected systems tend to be unstable. In this sense it has been argued that in ecosystems "autocatalytic cycles" arise so that food webs of mature undisturbed ecosystems are characterised by very "articulated" structures (Hirata and Ulanowicz, 1984). However, "real systems may be expected to range somewhere between these extremes" (Pahl-Wostl, 1995).

Recently, we proposed a new information theoretic measure, called "medium articulation" (MA) which resolves this contradiction (Wilhelm and Brüggemann, 2001). In the same way as has been done for other complexity measures (Lopez-Ruiz et al., 1995; Shiner et al., 1999), we combined a measure which is zero in the minimally articulated case, i.e. each node has inputs from and outputs to each other node (the mutual information $I = \sum_{ij} T_{ij} \log[T_{ij}/(\sum_k T_{kj} \sum_l T_{il})]$ with $T_{ij} = t_{ij}/\sum_{kl} t_{kl}$), and a measure which is zero in the maximally articulated case, i.e. each node has exactly one input and one output, but the network is still connected (the redundancy $R = -\sum_{ij} T_{ij} \log[T_{ij}^2/(\sum_k T_{kj} \sum_l T_{il})]$) yielding the measure MA which is zero in both extremes and has its maximum in between (with a medium number of in- and outputs): $MA = IR$. (For a detailed discussion of $I$ and $R$ see Pahl-Wostl, 1995.) With the same idea of multiplication, one can define other

complexity measures (CM) for non-binary webs (for example, the simple generalisation: $CM_1 = MA_g = I^a R^b$ $(a, b > 0)$, using the Kullback-entropy $D = \sum_{ij} T_{ij} \log(T_{ij}n^2)$: $CM_2 = DR$, or using terms without logarithms: for example, $CM_3 = F_1 F_2$ with $F_m = \sum_{ij}(T_{ij}^m - \sum_k T_{kj} \sum_l T_{il})^2$, $(m = 1, 2)$).

The minimally and the maximally articulated case correspond each with one well-known link-species scaling law, namely the constant connectance hypothesis that states that trophic links increase approximately to the square of the nodes (minimally articulated webs), and the contradicting linear "link-species scaling law", which asserts that links increase linearly with the nodes (maximally articulated webs) (Martinez, 1992; Solow and Beet, 1998). Martinez (1992) underlined this contradiction and found by linear regression of empirical food web data points a medium exponent of 1.54. Food webs with MA = $MA_{max}$ scale with an exponent of 1.5 (Wilhelm and Brüggemann, 2001). In the next section we show that the measure MA can be used to describe the development of food webs on long time scales.

## 3. Dynamic description of ecosystem development—the elementary model

As mentioned in the introduction, ecosystem models that study basic mechanisms of evolution should be characterised by variable topology of the underlying food web. For the sake of generality and clarity non-binary models should be preferred. The following elementary model fulfills these requirements. We consider a fixed number of nodes $n$ and normalised fluxes $T_{ij}$ ($0 \leq T_{ij}$, $\sum_{ij} T_{ij} = 1$) of mass or energy from node $i$ to node $j$ (suitably averaged over time, for example, 1 year). Because of a mutation, one arbitrary flux is changed according to: $T_{ij} = x/n^2$, where $x$ represents an equally distributed stochastic variable $x \in [0, 2a]$. At each time step ($t \in \mathbb{N}$) $z$ mutations arise. After the $z$ mutations all fluxes are normalised again. Thus, the model contains three parameters: $n$, $a$, $z$. In the following discussion we set $z = 1$, which can be interpreted as a complete relaxation of the disturbance across the whole ecosystem after each mutation. This normalisation represents one of the simplest kinds of system response. For instance, a mutation could cause the hare to run faster. The fox now cannot catch the hare as

efficiently as before and the flux (biomass or energy) from hare to fox decreases. Of course also other fluxes will change, e.g. the fox eats other prey, and/or the hare now eats more grass. Normalisation means that we assume a corresponding change of all fluxes: the sum of all fluxes is fixed, so if a flux gets larger because of a mutation, all others have to get smaller. The normalisation procedure is justified because there is an upper limit of cycling velocity in ecosystems.

To ensure that the sum of influxes equals the sum of effluxes for all nodes, one can add for each node just one appropriate influx or efflux to the exterior. Because the impact of these $n$ "outer" fluxes to all measures considered here, can, at least for sufficiently large $n$, be neglected compared with that of the $n^2$ "inner" fluxes, subsequently only these inner fluxes are considered.

Fig. 1 shows the evolution of all $n^2$ fluxes. Two different worlds are seen: Fig. 1A ($a > 1$) shows a kind of "red queen world" (In the kingdom of the red queen one has to run as fast as possible in order to remain at the same place Carroll (1994); biological example in Cooper and Lenski (2000).): as long as a flux is not mutated it becomes smaller and smaller, whereas Fig. 1B ($a < 1$) represents a "wu wei world" (in Chinese Taoism wu wei means "non-action"): without mutation a flux becomes larger and larger.

Fig. 2 shows the distribution of fluxes for different values of $a$. Because $\langle x \rangle = a$, $a = 1$ leads to an equal distribution of all fluxes: $T_{ij} \approx n^{-2} \, \forall i, j$. For $a \neq 1$ two different kinds of distribution arise. Closer inspection shows that both distributions are essentially power-laws with cutoffs. For $a > 1$ all resulting $\alpha < 1$, and for $a < 1$ all $\alpha > 1$ (Wilhelm and Hanggi, submitted). There are reasons to believe that our terrestrial ecosystems exist in a "red queen world", for instance, the many examples of "arms race" in evolution. With this assumption our model hypothesises that the amount of fluxes in food webs should be distributed according to a power-law with exponents $\alpha < 1$, or more precisely with $\alpha = 1 - \varepsilon$ ($0 < \varepsilon \ll 1$). Both kinds of distribution agree with the qualitative summary of McCann et al. (1998): "Data on interaction strengths in natural food webs indicate that food web interaction strengths are indeed characterised by many weak interactions and a few strong interactions". Moreover, there is some evidence that the amounts of fluxes in food webs follow a power-law (Ulanowicz, 2002).
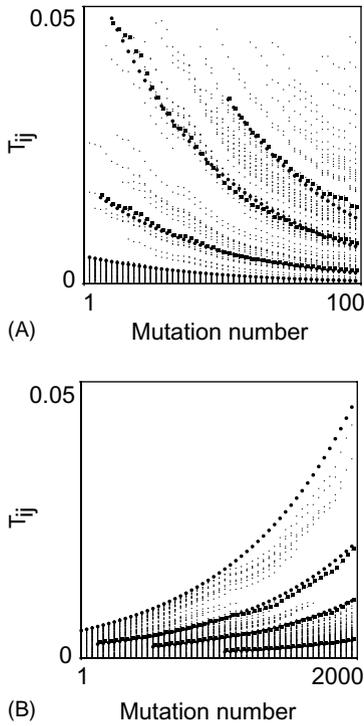
(A)    Mutation number



(B)    Mutation number

Fig. 1. Evolution of all $n^2$ fluxes for $n = 20$ ("random initial condition": $t_{ij} \in [0, 1]$, equally distributed $\forall i, j$, and normalised: $\sum_{ij} T_{ij} = 1$). (A) $a = 10$. (B) $a = 0.55$. If a thread of points stops, at this time the corresponding flux is mutated. The squares show the evolution of three selected fluxes, the dots the evolution of all remaining fluxes, and the circles the first approximation $T_{ij}(t) = T_{ij}(0)(1 + (a - 1)/n^2)^{-t}$ of the selected fluxes and the maximum fluxes of the initial values.

However, for future clarification of this feature it is necessary to establish a standard of food web assembly. Of course the amounts of the fluxes between the nodes strongly depend on the resolution. This dependence has been the topic of many debates about food webs (Paine, 1988; Cohen et al., 1993; Solow and Beet, 1998). It is important to use the same resolution for all compartments. Consequently, I propose to consider compartments which contain nearly the same quantity of, for example, mass or energy. Otherwise the amount of the fluxes primarily depends on the arbitrary assignment of matter into compartments, which cannot be a sound basis for the proposed statistics. This "equal quantity proposal" avoids the arbitrariness of the nodes in food webs and clarifies discussion of
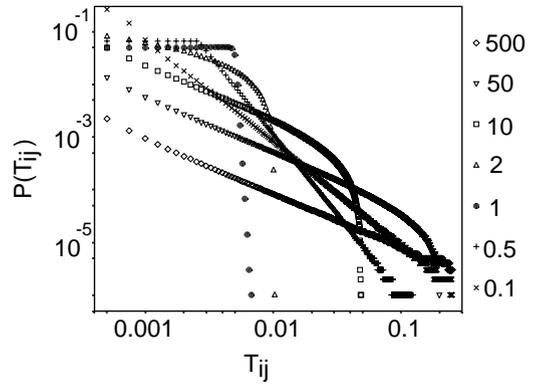


Fig. 2. Flux-distributions for different $a$-values ($n = 20$). For $a < 1$ the fluxes are equally distributed for values $T_{ij} < 2a/n^2$ and distributed according to the power-law $P(T_{ij}) \sim T_{ij}^{-\alpha}$ ($\alpha = f(a)$) for $T_{ij} > 2a/n^2$. For $a > 1$, one obtains the power-law $P(T_{ij}) \sim T_{ij}^{-\alpha}$co with the cutoff co $= 2a/n^2 - T_{ij}$, because usually no flux can be larger than $2a/n^2$.

resolution and lumping (Sugihara et al., 1989; Solow and Beet, 1998).

Fig. 3A shows the complexity measure MA during evolution of the network. In the present model the amount of a flux after a mutation is independent of its previous amount, thus for all initial conditions the same MA is reached, MA only depends on $a$. Fig. 3B shows for different $n$ the optimal $a$-values $a^*$ in order to reach maximum values for MA. Fig. 3C demonstrates the astonishing result that, using $a^*$, the difference $MA_{max} - \langle MA \rangle$ disappears in the limit $n \to \infty$. Thus, already the elementary mechanism is able to yield webs with maximal complexity, according to the measure MA.

Thus far, discussion has focused on a web with fluxes from each node to every other node. However, very small fluxes will probably not be observed in reality, or may simply be neglected if deemed irrelevant. Thus, it is appropriate to remove the small fluxes: all fluxes smaller than the parameter "*cut*" are set to 0. This procedure avoids the arbitrariness of links in food webs, the connectivity becomes a clear function of *cut*. A binary food web (mathematically: a digraph) is obtained if we set all remaining fluxes to 1.

The most discussed digraph measure in food web theory, and the central one for several general graph and digraph studies, is the connectance $C$. Fig. 4A confirms that the present model can reproduce the
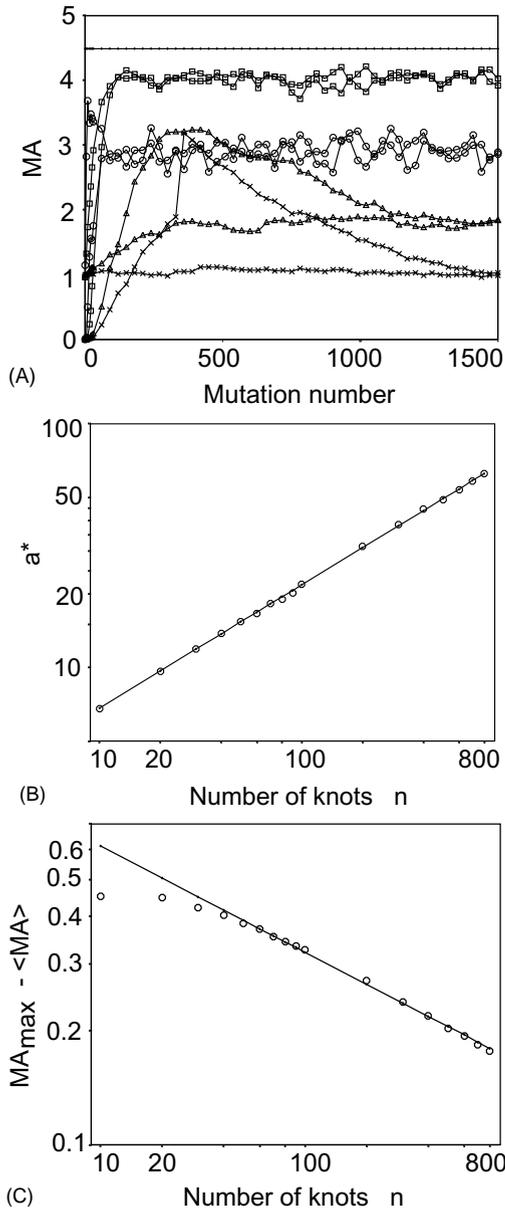
(A)

(B)

(C)

Fig. 3. Medium articulation of the non-binary networks. (A) Self-organisation of the network ($n = 20$): MA = MA($t$), $a = 1$ (crosses), 2 (triangles), 10 (squares), 30 (circles). For each $a$ two different initial conditions are used: the "random initial condition" (RIC) and the "one flux initial condition" (OFIC: one arbitrary $T_{ij} = 1$, all others equal 0). Using RIC, for $a = 1$ MA does not change, the web remains random. The straight line indicates $MA_{max} = (\log n)^2/2$ (Wilhelm and Brüggemann, 2001). (B) The optimal $a$-values $a^* = (2.14 \pm 0.04)n^{0.505 \pm 0.003}$. (C) Using $a^*$, the difference dif = $MA_{max} - \langle MA \rangle$ (averaged over 100,000 mutations) disappears in the limit $n \to \infty$: dif = $(1.16 \pm 0.02)n^{-0.280 \pm 0.004}$.
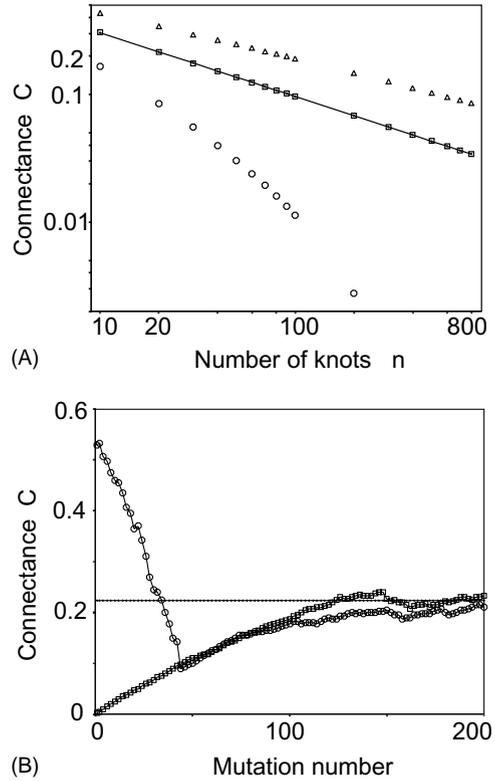
(A)

(B)

Fig. 4. Connectance of the binary networks ($a = a^*$). (A) Different "link-species scaling laws": cut = $0.2n^{-b}$, $b = 1$ (circles), 1.5 (squares), 2 (triangles). cut = $cut_{lin} = 0.2n^{-1.5}$ yields the linear link-species scaling law $C = (0.969 \pm 0.002)n^{-0.5013 \pm 0.0007}$. (B) Self-organisation of the network ($n = 20$) $C = C(t)$ for RIC (circles) and OFIC (squares) (cut = $cut_{lin}$). The straight line indicates $C = 20^{-0.5}$.

realistic "link-species scaling law" (Martinez, 1992) $C = n^{-0.5}$, that is the number of links $L$ increases according to $Cn^2 = L = n^{1.5}$. Fig. 4B shows the self-organisation of $C$ yielding a steady state which is independent of the initial conditions, $C$ depends only on $a$ and *cut*.

Table 1 shows a first comparison of real food webs with simulated webs on the basis of some digraph measures. Except for $D$, GenSd, VulSd, all measures vary between 0 and 1. Column 3 corresponds to the mechanism described above (here denoted as *mech*1), with cut = $cut_{lin}$ (see Fig. 4A). For the sake of comparison, columns 4 and 5 contain the values for random and regular networks with the same connectance (Watts and Strogatz, 1998). For column 6 the basic mechanism

Table 1
Comparison of empirical and simulated food webs

| Measure | Empirical webs[a] | Mech1 | Rand$_1$ | Reg$_1$ | Mech2 | Rand$_2$ | Reg$_2$ |
|---|---|---|---|---|---|---|---|
| Con | | 0.69 | 0.68 | 1.00 | 0.12 | 0.92 | 1.00 |
| $C$ | | 0.22 | 0.22 | 0.22 | 0.28 | 0.28 | 0.28 |
| Cliq | | 0.21 | 0.22 | 0.38 | 0.40 | 0.28 | 0.40 |
| $D$ | | 2.16 | 2.15 | 2.73 | 1.97 | 1.90 | 2.26 |
| Ci | | 0.01 | 0.01 | 0.00 | 0.03 | 0.02 | 0.00 |
| MA$_n$ | | 0.94 | 0.94 | 0.99 | 0.85 | 0.91 | 0.98 |
| Gen | 0.12–0.18 | 0.22 | 0.22 | 0.22 | 0.28 | 0.28 | 0.28 |
| Vul | 0.10–0.24 | 0.22 | 0.22 | 0.22 | 0.28 | 0.28 | 0.28 |
| GenSd | 0.73–1.42 | 0.42 | 0.41 | 0.11 | 0.54 | 0.35 | 0.09 |
| VulSd | 0.54–1.41 | 0.41 | 0.41 | 0.11 | 0.48 | 0.35 | 0.09 |
| MxSim | 0.52–0.76 | 0.35 | 0.36 | 0.67 | 0.45 | 0.41 | 0.74 |
| MSim | | 0.15 | 0.15 | 0.14 | 0.22 | 0.20 | 0.19 |
| Can | 0.03–0.66 | 0.21 | 0.22 | 0.00 | 0.38 | 0.28 | 0.00 |
| Omn | 0.40–0.76 | 0.84 | 0.85 | 1.00 | 0.87 | 0.95 | 1.00 |
| Omne | | 0.01 | 0.01 | 0.02 | 0.03 | 0.02 | 0.03 |

Parameters: $n = 20$; mech1: $a = a^* = 9.692$, cut $=$ cut$_{lin} = 0.0022$; mech2: $a = 10$, cut $= 0.001$. Con: fraction of connected networks (from each node each other node can be reached), only connected networks were considered for calculation of all subsequent measures. $C$: connectance, Cliq: clustering index (number of connections between all neighbours of one node $i$ divided by the maximal possible number: $cc(i) = nn(i)/nn(i)_{max}$, averaged over all nodes) (Watts and Strogatz, 1998), $D$: diameter (smallest number of links between two nodes $i$ and $j$, averaged over all pairs $(i, j)$) (Watts and Strogatz, 1998), Ci: cycling index $= n^{-1} \sum_k$ (number of cycles of length $k$/maximal number of length-$k$ cycles), MA$_n$: medium articulation/maximal possible medium articulation, Gen: generality (normalised average number of prey species of a predator (Schoener, 1989)), Vul: vulnerability (normalised average number of predators of a prey species (Schoener, 1989)), GenSd and VulSd: standard deviation of normalised generality and vulnerability, respectively (Williams and Martinez, 2000). MxSim: maximum similarity $= n^{-1} \sum_i \max s_{ij}$ ($s_{ij}$: number of the joint predators and prey of $i$ and $j$ divided by their total prey and predator number (Williams and Martinez, 2000)), MSim: mean similarity $= \sum_i \sum_{j \neq i} s_{ij}/(n(n-1))$, Can: fraction of cannibals among all species (Williams and Martinez, 2000), Omn: fraction of omnivores (an omnivor consumes at least two species, and at least one of these also consumes the other (Williams and Martinez, 2000)), Omne: exact fraction of omnivory (quantifies the exact number of omnivory relationships for each species).
[a] Schoener (1989), Williams and Martinez (2000).

has been modified to obtain _mech_2: for each time step, the clustering coefficient $cc(i)$ for each node $i$ is calculated (see table legend). The flux $T_{ij}$ which is mutated connects with higher probability nodes with high $cc(i)$. If the network is not connected, a random mutation (as in the basic mechanism) occurs. Columns 7 and 8 again contain the corresponding random and regular networks.

Evidently, _mech_1 leads to random networks and _mech_2 leads to small-world (SW) networks, where _cliq_ is larger than in the corresponding random networks, but the diameter $D$ is not. It has been speculated that a small $D$ has a big influence on the dynamic behaviour of the networks, for example, facilitating high homeostasis (Watts, 1999). In contrast to the SW model (Watts and Strogatz, 1998) which always starts with regular networks, our models simulate true self-organisation processes, where the final structure is independent of the initial conditions.

## 4. Discussion

The present model is a very elementary one and as such not very realistic for a detailed simulation of the evolution of food webs. However, in the sense of monk William of Ockham (Ockham's razor), one should always start with the simplest models and add successively more and more realistic features, thus increasing the complexity of the model. We have shown that already our simple model produces networks with many characteristic features of real food webs. For instance, the measure MA, which seems to be maximised in real food webs (Wilhelm and Brüggemann, 2001), is also maximised during the evolution process in our model. Moreover, power-law distributions of the amount of fluxes as observed in our model can also be found in real food webs (Ulanowicz, 2002).

An according analysis shows that our model is quite robust, that means all the results depend very weakly

on all the parameters (Wilhelm and Hanggi, submitted).

It has been demonstrated that empirical food webs are not completely random, for non-binary food webs by Ulanowicz and Wolff (1991), and later for binary food webs by Solow and Beet (1998). Recently, small-world patterns have been identified in empirical food webs (Montoya and Solé, 2002), although in contrast to our approach, all links were taken as undirected.

A comparison of *mech*1-networks with the corresponding random networks shows that the binary measures are not sensitive enough to distinguish them. This is in accordance with results of Ulanowicz and Wolff (1991). The medium articulation MA, for example, taken for the digraphs, is the same in both network classes, in contrast to the non-binary webs where the random network ($a = 1$) has another MA than $a \neq 1$-networks (Fig. 3A). Clearly, too much information has been neglected in extracting a digraph from the more general non-binary web via cutting off the small fluxes and equalising the remaining ones. Therefore, a subtle analysis should use all the information (empirical examples in Riemann et al., 1986; de Ruiter et al., 1995; Lyche et al., 1996; Ulanowicz, 1997) by analysing the corresponding statistics (Fig. 2) and appropriate measures (such as MA).

The most restricting assumption in the presented model is that of a constant number of nodes $n$. However, this is also a characteristic feature of all previous food web models (Cohen and Newman, 1985; Cohen et al., 1990; Williams and Martinez, 2000). Furthermore, the connectance $C$ is a crucial parameter in these models and in other network models, such as the SW model (Watts and Strogatz, 1998; Watts, 1999). Models also exist with variable $C$ (e.g. Bornholdt and Rohlf, 2000), but these are not discussed in ecology. A binary network model with a growing number of nodes has been proposed (Barabási, and Albert, 1999), here $L$ grows linearly with $n$. This model yields a so-called "scale-free" structure, where the probability of the number of connections per node declines in a power-law like manner. It was found that "The scale-free property is common but not universal" (Strogatz, 2001). Food webs seem to possess quite skewed distributions (Montoya and Solé, 2002; Matutinovic, 2002). The present model, like the SW model, generally yields Poisson distributions,

but for high *cut*-values, distributions are also shifted to highly skewed ones.

Three points, listed with descending importance, summarise our proposals for future food web theory: (i) establishment of empirical non-binary food webs with the same resolution for all nodes ("equal node webs"); (ii) discussion of non-binary webs (comparison of empirical data with appropriate simulations, best as self-organisation result of dynamical models as our elementary one); (iii) discussion of the deduced digraphs. In a forthcoming paper we have used a published simple non-binary food web to deduce the corresponding equal node web (Wilhelm, submitted). There we have also discussed in detail the relationship between non-binary webs and the corresponding binary webs.

Our model can be extended to the most general case of variable $C$ and $n$, to cover questions such as species–area relationships (Harte et al., 1999) or Elton's hypothesis "that ecological stability should depend on biological diversity" (Tilman et al., 1998), where the focus is upon discussion of the number of nodes itself (Tilman et al., 1998; Harte et al., 1999; McCann, 2000).

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