

Ecological Community's "Trophic Level Extreme" from Vulnerability Link Distributions & Energetic Pathways

Luca R. Valandro¹, Roberto Caimmi², Yiannis G. Matsinos³, Emanuele L. Secco^{4,*}

¹Former PhD at Vallisneri Biology Department, Padua University, IT

²G. Galilei Physics and Astronomy Department, Padua University, IT

³Department of Environment Biodiversity Conservation Lab, Aegean University, GR

⁴School of Mathematics, Computer Science and Engineering, Liverpool Hope University, UK

Abstract Complexity of complete ancient and modern food webs assumed to capture essential forests network trophic topology scales similarly to that of ancient and modern lake webs and communities from variable environments. Reasonably these groupings and patterns are not exclusively driven by environmental fluctuating conditions. Unexpectedly, disparate aquatic and terrestrial communities can belong to the same connection trend with network size whose nodes represent the number of trophic species. Although some aquatic communities can host apex predators at higher trophic levels than terrestrial ones, it is not clear if this relates to different connectance or hierarchical structure. **OBJECTIVES** - In this study we analyzed, reviewing literature trophic webs, extreme number of trophic levels data and their relationship with trophic link distributions (vulnerability and surrogate energetic parameters). Furthermore, we report about a gap on the number of energetic pathways at a threshold modal trophic level. General differences, among aquatic and terrestrial communities, in primary consumers fractions or percentages were tested. **METHODS** - A new network approach to food webs was presented to interpret maximum chain length or extreme trophic levels from matrix information and few assumptions. Two opposite logarithmic trends were analyzed, and sigmoid models were utilized to predict missing predatory links in large cumulative food networks. **RESULTS** - The main results are the presentation of two opposite trends of link density vs topological connectance in log-log correlation analysis where communities belonging to different eco-regions of the richest lake in terms of trophic species (i.e., Lake Malawi-Nyasa-Niassa) were submitted to further scrutiny for the interpretation of their maximum chain length. *Herbivore's Fraction*⁻¹ equal the number of trophic levels in newly defined size ambivalent communities that are characterized by relatively small number of species but displaying the same complexity pattern of species rich ones. **CONCLUSION** - Maximum number of trophic levels of ecological communities from different habitats could be associated with extrapolated link density obtained by the trends of vulnerability link and surrogate energetic link distributions. Top-down and bottom-up control were discussed under this new perspective where ubiquitous anti-predatory strategies, inferred by reduction in trophic links, were also estimated. This wide new perspective could be preparatory for the interpretation of the effects of changing scenarios or contexts and habitat/species safeguard.

Keywords Networks, Connectance, Network size, Trophic biodiversity, Trophic levels

1. Introduction

In ecology the issue of how and how much predation and competition affect the structuring of ecological communities has involved many food web ecologists in recent years.

Pressed by abrupt and unprecedented anthropogenic and environmental perturbations, there is an urgency to disentangle the ecological complexity of such peculiar natural networks [1]. Trophic chains and trophic webs have a long tradition in ecology and indeed, were addressed and

drafted by authors from Sir Charles Darwin to Bruckner, Elton (food cycle) and Lindeman to mention the most popular [2,3]. Top predators, intermediate species and basal species present often constant proportions in small webs or slight scaling [4]. In general, in most predation networks abundances are inversely related to their trophic position in the food web, *FW* [5,6]. The species position in the network can change during ontogeny [7,8] or contexts but it seems to be rather constant at least in certain *FWs* with season [9]. However seasonal variability has been shown to be much greater than spatial variability in determining relative position of species in the Trophic Level, *TL*, stable isotopes measurements [10].

After different correlation and topological analysis of the food webs literature data, we have selected some general ecological perspectives about *FWs* structural complexity

* Corresponding author:

secco@hope.ac.uk (Emanuele L. Secco)

Received: Sep. 30, 2021; Accepted: Nov. 5, 2021; Published: Dec. 15, 2021

Published online at <http://journal.sapub.org/zoology>

that could be preparatory for the management of different ecosystems in rapidly changing climatic scenarios.

Unexpectedly disparate aquatic and terrestrial communities can belong to the same connectional trend with network size whose nodes represent the number of trophic species.

Although some aquatic communities can host apex predators at higher Trophic Levels than terrestrial ones it is not clear if there are general connectional differences or hierarchies. Better understanding of how communities are shaped, considering also ancient fossil communities, has an appeal that goes beyond food webs beauty. Complex ecological communities have undoubtedly aesthetic valence but we urge to avert ephemeral mandalas and search implications for a sustainable exploitation of services and humans minimising risks of being parasitized.

• Definition of trophic network composite parameters

Typical structural food web parameters are network Size, S , and trophic Links, L , and many composite parameters have been proposed by *FW* ecologists [11-14]. In this analysis, we present empirical correlations between a basic modified parameter of communities, linkage density *bottomless*, LD_{bl} , or reconnecting with our previous analysis [15]:

$$m_{bl} = \frac{L}{(S - B)}$$

in which all links are spread between consumers, and topological connectance defined as:

$$m_{bl}^* = \frac{(S - B)(S - B - 1)}{2 \cdot (S - B)}$$

i.e. the maximum number of potential links of the web for consumer species. This parameter is considered more suitable for comparing topological links from aquatic and terrestrial habitats with slightly comparable but different number of resources (trophic aggregation).

Producers or number of basal species, B , are those species that start the flux of energy with no incoming links. Top predators' species, *Top* or T , having no outgoing links, are only by definition not predated by other species, while intermediate species, *Int*, display both ingoing and outgoing links [6]. Interestingly in trophic chains connectance or connectedness, defined as:

$$C' = \frac{m}{m^*}$$

is identical to:

$$C_{bl} = \frac{m_{bl}}{m_{bl}^*}$$

namely, the bottomless connectedness for the *FWs* with the same S . Mainly bottomless parameters were chosen in the present analysis considering that they could be of greater value while focusing on link distribution among higher Trophic Levels species. In order to quantify a flexible attribute of ecological organization of real communities, we focused on the predator-prey interactions while neglecting

sometimes 'dead-ends' trophic species which are not directly sustaining predators at the highest Trophic Levels; some basal species nodes could represent parts of primary producers and become a misleading indicator by inflating the consumers network size and lessening C' .

Following an analogous definition [15], although utilizing a parameter of greater variance than $L \cdot S^{-2}$, its average value for certain communities attested close to 0.5 that could be of theoretical significance as a threshold or bound.

Plotting didactically m_{bl} vs m_{bl}^* , allows to quickly capture concomitantly constant un-weighted connectance (*i.e.*, slopes of the lines, excluding cannibalistic loop in Figure 1) and constant linkage density (green dashed line) sampled ecological communities in small intervals.

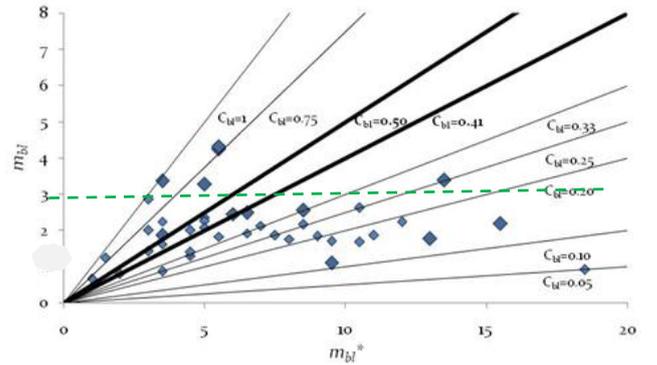


Figure 1. Effective link density vs topological normalized connections. Data for the communities from constant environments are represented by bigger diamonds. All communities belonging to the approximate interval, $0.05 < C_{bl} < 0.96$ can be graphically represented by the family of lines passing through the origin. Hypothetical mean ($C_{bl} = 0.5$) and median ($C_{bl} = 0.41$) *Cbl* lines and values have been bolded. Average connectedness $C_{bl} = 0.40$ (number of communities = 40), for bottomless communities (excluding basal species), was slightly higher compared to the $C' = 0.30$ value for the same 40 communities that was identical to C' for the whole sample of collected *FWs* ($n = 113$). Interpretation of the constant Link Density communities (dashed green line) was tentatively re-examined in alternative to *FWs* pictorial constraints. Raw data reported in [16], collected in [17,18]

We suggest to avoid connectivity denomination for either C' or C_{bl} in particular when they are not explicitly defined, since this term after 1984 has become even more fundamental in landscape ecology [19,20]. We opted for another connectional parameter that at least in ideal food chains does not vary increasing the number of trophic levels (*bottomless link density*: $m_{bl} = 1$, $\forall TL \in \mathbb{N}^e$) and is at least unitary with short-circuit or food web-like structure.

Interestingly the significant trend of increasing m_{bl} with N - number of trophic levels or height - or maximum chain length, *MCL*, was not apparent when plotting Average max number of Chain Length, *ACL*, ($n = 40$ homogeneous community selected by [16]) although $r = 0.781$ and in a revised sample [5] the correlation of these two food web lengths was even higher with $r = 0.938$ ($n = 98$, one-tailed $p < 0.001$, $d.f. = n - 2$).

Indeed, communities of different sizes can be characterized by equal C_{bl} values (Table 1, Appendix A).

1.1. Simplifying the Ecological Complexity

Ecological analogies with digital librarianship warn us about writing a manuscript without a proper software or permanent cross reference tool that automatically update number and position of references. If anthropization inflicts drastic changes at every scale, from local to planetary, it is unlike that we could tell how ecosystems will react or if community will persist or reassemble when biotic interactions (disordered or mismatched references) will be lost or greatly rearranged without understanding the basic semantic of simple topological networks.

- **Species aggregation, body size trait/predator prey ratios to predict community trophic levels**

Un-lumping basal trophic levels in *FWs* do not increase the average number of *TLs* but this procedure can clearly diminish them [21]. If the communities have constrained topological links, then we expect a strong sensitivity of *MCL* to m_{bl} . Indeed, the empirical observation that most communities have short chains, their “extreme length limit” does not imply an energetic limitation allowing to reach the top of the chain (see [22] and references therein).

In spite it was shown that increasing the number of *TLs* will delay the recovery time from perturbation (resilience) of the *FW* [23] and dynamical instability is reasonably dependent on trophic architecture. However, efforts to make ‘atomistic’ dynamic models less phenomenological must be acknowledged (wider list of hypotheses in [12,24,25]).

Recently McGarvey et al. [26] with trophic energetic efficiency considerations and by extending allometric scaling of production rate versus body size, could explain why pelagic ecosystems could sustain the 5th trophic level with a minimally rescaled sample of those communities [27]. The proposal of body size-food web structure integration is not new in food web literature [28,29] but it is original how the more robust empirical *FW* components and groups are assembled and how body size affects the variability and persistence of food webs [30-33]. In dealing with interaction strength and stability in a real food web, predator-prey body mass ratios have been proposed as a surrogate-correlate of the interaction strength (e.g., [32]). This approach, considering the occasional occurrence of complex ‘anomalous’ (not allometric) trends, needs careful examination.

Information being scarce and rather variable about species abundances (trivariate analysis in Ings *et al.* [34]) or energy fluxes between *TLs*, most of the literature concentrated on theoretical modelling in search for robust approximations or static analysis of ‘first-generation’ food webs [35,36]. In this context, linkage density, as a partial indicator of food web complexity ($S \cdot C$), has been demonstrated by N.D. Martinez using the Kendall’s nonparametric tests, to increase with S in communities where the number of species, $S > 54$, and widely thought not to be scale invariant [4]. Significant trend of normalised number of nonzero links, L/S , and %*B* has been also observed in [5,37] but L/S was shown to be larger in food

webs with large S because of the uneven aggregation between the communities (see also the sampling effort bias in [38]).

Surprisingly, recent analysis found that the functional properties of *FWs* were preserved over a large portion of the aggregation gradient [39]. Definitely not only body-size could interpret *MCL* as parsimoniously proposed [37].

1.2. Topological Structure of Ecological Networks: Communities from Stable vs Variable Environments

Topological indications of ecosystem persistence or health could be derived from the calculation of fine-scale structural parameters in comparable contexts with only one main or few environmental or relational variables perturbations or most diversified cross-habitat comparisons in either ‘constant’ or ‘variable’ environments or gradients [34]. Pioneering papers by J.E. Cohen [29] and F. Briand [17] evidenced the significant difference of Connectance, C , between communities from stable environments and those from fluctuating ones. It was defined as:

$$C = \frac{\text{number of nonzero interactions } A_{ij} \text{ in the community matrix}}{S \cdot (S-1)}$$

where n replaces S (number of nodes or Species) for a more intuitive denomination that does not generally interfere with statistical symbols as does n with sample size. As F. Briand theorised, the greater connectedness in communities from constant environments might be even associated with high interaction strength, violating the condition for dynamical stability [40]; being the probability of environmental disruption low, this behavior appears acceptable.

Schriever [41] by means of a multivariate approach analyzed effects of the environmental variability on ponds concluding that *MCL* responded to both multiple environmental variables (e.g., hydroperiod, T) and species assemblage. Therefore, interpretation of food webs structure should sometimes not disregard the historical contingency.

Remarkably *MCL* significantly correlated with S in none but short marine estuarine group ($r = 0.815$, two tailed $p = 0.001$, $n = 12$) [5] reinforcing the fact that the overall *LD-MCL* correlation is not obvious. In a sample of insect dominated communities, (see par. 1.3, Hypothesis of a trophic level threshold for trophic pathways), when considering only independent observations, even the modal chain length, lost statistical significance in the log-log correlation with S (Bengtsson J., personal communication).

Here we expand the ecological implications of the empirical correlation analysis between *LD* and *MCL* delimiting *LD* intervals of validity (see list of parameters in Appendix A).

1.3. Topological Structure of Ecological Networks: Aquatic vs Terrestrial Communities

Higher degree of trophic specialization in large terrestrial communities should allow more Trophic Levels in a food chain from a simple energetic calculation assuming constant ecological efficiencies and an estimated five times greater

photosynthetic production [see [26]]. Theoretically more biomass would be available for sustaining further Trophic Levels with their emergent ecological patterns from less sideways routes. Despite higher average feeding specialization (i.e. lower connectance) in terrestrial communities than in aquatic ones, diet breadth variation was recognized to be dependent not only on species richness and habitat type but also on the variability in the resources and sampling effort (see analysis of insect herbivores in [42]).

Only in lakes a latitudinal gradient of the scaling of LD , generality (gen) and vulnerability ($vuln$) with S was evidenced [43].

The terrestrial food webs are typically considered shorter because of different organism size and dynamics of the bottom resource and primary producers (phytoplankton *vs* plants) and an inferior ecological efficiency at the base of the trophic pyramid [15], [44].

Interestingly we were expecting to find communities differences more easily identifiable from charismatic species studied in greater detail while herbivorous richness and intensity are becoming central for answering many ecological issues [e.g. [45], see reference 46 therein].

• 'Size Ambivalent' Communities (SAC)

Apart from the Malaysian Rainforest and Canadian Willow Forest, terrestrial communities, from the Briand collection [17], were large according to our group size classification ($S \geq 15$). These two small communities (low S) of first-generation food webs are characterized by the same logarithmic trend of realized links *vs* maximum potential links of large communities but belonging to the small size group ($S < 15$). Their structural link density scale as if they were somehow large or 'size-ambivalent'. A similar trend has been exhibited by the aquatic Pamlico River and the Marshall Reefs. Such communities belong to the same global pattern of increasing MCL with m_{bl} as anticipated in our abovementioned paper [15], till a critical linkage density (m_{bl}) of around 2.5 close to the most common region for the 40 communities (see par. 1.3, Hypothesis of a trophic level threshold for trophic pathways and par 3.1, Herbivores diversity and proportion as a proxy for TLs). We have introduced SAC notwithstanding the dubious uniformity of aggregation of the trophic species/functional groups of this collection of food webs since after redrawing these food webs interesting values of $C_{bl} \sim 0.4$ were obtained (see Figure 1).

For this subgroup of communities "extreme trophic levels" were derived without the need to know all links but only a fraction of species, namely it holds:

$$MCL = 1 / \underline{H}$$

where \underline{H} = Number of herbivore species / S .

In SAC $Log LD_{bl} = 0.3$ the sample link density mode, typical of species rich communities could indicate, under certain assumptions, a constraint rather than a trivial artifact (see averaging procedure in par. 3.1, Herbivores diversity and proportion as a proxy for TLs).

• Functional diversity, trophic interactions in modern or ancient webs

Attempting to address the elucidation of the profound macroscopic differences between aquatic and terrestrial communities in less habitat specific terms than T.W. Schoener [5] did, we presented different pattern of trophic levels correlation with LD between aquatic and terrestrial community webs not mentioning 'obvious' hypothetical causes like water limitation or more TLs in the latter communities being functionally rich or peculiar [15]; furthermore adaptation to land and environmentally huge differences (e.g., ecological efficiency, oxygen availability, and basal groups peculiarities) were expected to be somehow reflected also in the community structure and predator-prey flexible interactions.

Interestingly analysis of fossil ancient food webs from the 48 Myr-old Messel deposit found a 5% of specialists in Messel Lake while 14% of taxa feeding on one taxon was reported for Messel Forest with almost all parameters of the trophic structure of the Messel Lake web that fit within the ranges observed for extant webs [45]. Investigations of the topological structure of terrestrial and aquatic communities (see [44,46]), by comparative analysis, are making scientists foresee some theoretical-empirical rules of their functioning, from pattern to processes (e.g., see detritus-based subwebs by Rossi *et al.* [47]).

Schalk *et al.* [48] studying tropical pond communities concluded that unrestricted diets and plasticity enables consumers to exploit a broad range of resources and promote species coexistence suggesting that high diversity in tropical ponds does not necessarily translate into specialization of trophic function.

Traditionally whenever two or more species are preyed upon by exactly the same set of predators, and prey upon exactly the same set of prey, in each food web, trophically identical species were lumped together as one [49]. This analysis showing the singularities of different groups of freshwater ecosystems focused on lentic and lotic communities from different biomes but of comparable network size ($8 < S < 23$). Commenting on how a brief appearance of an opportunistic top predator could reshape the community structure, top down cascades were observed in aquatic ecosystems [50,51] but also in terrestrial ones [52,53].

Mathematical modelling that incorporates both top-down and bottom-up cascades are promising tools to interpret different propagating effects in FWs [54,55] and especially widespread anthropogenic impacts at all TLs [56].

• Hypothesis of a trophic level threshold for trophic pathways

The isometric trend for lakes and environmentally hyper-variable communities, after calculation of bottomless parameters, could suggest the presence of some sort of compartmentalization to counteract the higher risks of predation expected as indicated by their high relative link density. An opposite hypothesis conceives many lake's

vulnerable species saved from extinctions as a consequence of the weakening of the intensity of such predatory links due to the high number of alternative preys. On average there could be a tendency of reduced risk of species extinction when the number of trophic pathways is greater. However, we have drawn indication of a limit to the number of trophic pathways with *TLs* from a collection of insect food webs [57] after excluding gall *FWs* with parasites; without such exclusion a perfect linearity of trophic pathways vs *TLs* was observed ($R^2 = 0.99$). To complicate the interpretation, link relevance in terms of energy flows does not necessarily parallel strong interactions *sensu* R.T. Paine [58].

Figure 2 summarizes different trends of link density where m_{bl} can either increase or decrease with network size.

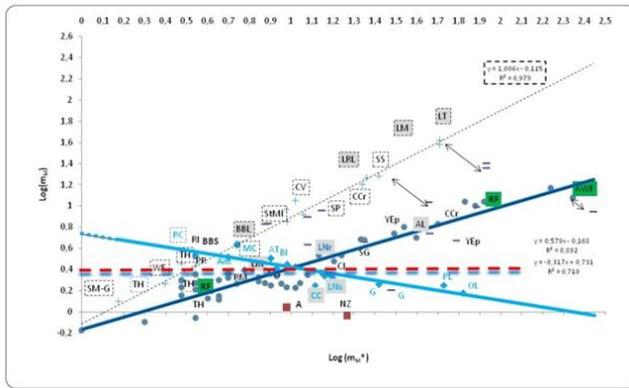


Figure 2. Across habitats invariance and scaling of connectedness. Bottomless link density (m_{bl} or LD_{bl}) vs topological connectance (m_{bl}^* , LD_{bl}^*) for the 40 communities (in red Arctic sea and salt meadows New Zealand communities) collected in [17] and [18]. Labeled in dark blue trend for communities from ‘variable environment’ (ii) and in light blue opposite trend for most communities (bold) from constant environment (iii). **CC:** Crocodile Creek, **LNs:** Lake Nyasa sandy, **LNr:** Lake Nyasa rock. Another collection of recalculated comprehensive food webs bottomless parameters were added [57]. **AT:** Arctic tundra, **PL, OL:** Pine and Oak logs, **TH:** Tree Holes, **G:** Grassland, **LRL:** Little Rock Lake and other large lakes’ food webs in grey (**AL:** Ancient Messel Lake fossil community, **Rain Forest** and **Ancient Messel Forest (AMF)** in green (data of comprehensive food webs from [1]; ancient food webs from [45]). With *Plus* indicator all isometric C_{bl} food webs, mainly lakes and creeks (i). *Minus* indicator for linkage density of ‘comprehensive food webs’ (e.g. *Ythan Estuary* with parasites, *YE*). Dark blue dots for variable communities with refuges (rainforest, ancient lake - not corrected), **LNr**, **Reef Marshal**, **RM** and **Sea Grass**, **SG**. In red a dashed line threshold for m_{bl} around 2.5 links / trophic species

A pattern of constant connectance was deduced by calculating this parameter for certain cumulative ‘comprehensive food webs’, namely it holds:

$$(i) C_{bl} = 10^{-0.115} = 0.77 \sim 3/4$$

(environmentally hyper-variable communities - *dashed line*)

$$(ii) C_{bl} = 10^{-(0.42 \log LD^* + 0.163)}$$

(heterogeneous environmentally variable communities - **LNr**- *dark blue*)

$$(iii) C_{bl} = 10^{-(1.339 \log LD^* - 0.748)}$$

(open-space environmentally constant communities - **CC**, **LNs**- *light blue*)

Our choice, to focus only on few parameters of predator-prey interactions, without considering parasitic and collaborative networks, derived that none of us, neither our small group of authors, could dream of winning such a triathlon competition. The huge effort in addressing such a broad research area and the conflicting effects on performance of trying to improve in more than one field all at once, parallel different group of muscles trained during swimming, cycling, running, that cannot excel in all three sportive disciplines.

• **Functional diversity in different habitats**

Species richness follows an inverse biogeographic trend with latitude and its correlation with habitat heterogeneity and environmental gradient of energy were reported for mammalian, fish and bird species though more robust analysis are underway [59]-[61].

Trophic species rich communities are more frequent in the dark blue trend (see Figure 2) of heterogeneous variable habitat (ii) whereas ‘open-space communities’ are found mostly in the light blue trend (iii). Clearly pattern differences are not only in relation to observing large or small networks but conservation or management decisions could benefit from network analysis starting from basic parameters and simplest *FWs* snapshots (see [6]).

2. Perspective from an Innovative Methodology

Max chain length occurs at the crossroad of energetic and connectational parameters. Conceptual basis for bridging energetic and connectational aspects of food webs combining reductionist premises and parameters to holistic observed complex ecological networks were provided [15]. Recently it was stated that complex ecosystem networks consist of a multitude of weak connections dominated by a relatively few strong flows and trophic depth (a measure of number of *TLs*) was formalized and presented, under certain assumptions on the degree of organization of the ecosystem, in a linear correlation with trophic breadth [62]. Here, in a functional topological framework, a new set of parameters were defined by us to address analytically the issue of linkage density and levels complexity of trophic webs. F_{Skc_y} , the complement of the relative cumulative fraction of species (*in + out*) normalized by the total number of *vuln* and *gen* links, points to testing species and trophic transactions (*sensu* [63]) interplay.

Without measuring directly energetic fluxes of environmental networks, we could extrapolate both connectational and indirect energetically related parameters, oriented by an analogous contextual alternating role of forms and contents in social sciences. This procedure allowed us to progress further towards the integration of energetic and connectational aspects of food webs and to circumscribe hypothesis discriminating macro-descriptors of exemplary lacustrine food webs from the same location,

the African Malawi-Nyasa-Niassa lake [64].

The functions $FSck_{vuln}$ and $FSck_{gen}$ were defined as:

$$FSck_{vuln} = 1 - \sum_{k=1}^{k=10} \frac{S_k}{(S-T)}$$

$$FSck_{gen} = 1 - \sum_{k=1}^{k=10} \frac{S_k}{(S-B)}$$

where to each k (number of link-in or vulnerability link) corresponds a certain number of nodes or species in the $S \times S$ matrix that are counted and summed up from LD_1 till LD_{10} where all predatory links are exhausted. Top predators were not subtracted from the denominator assuming that also top predators are somehow vulnerable and they were not counted in LD_0 associating always 1 to $FSck$ initial condition. The function $FSck_y$ was calculated according to the following form:

$$FSck_y = 1 - \sum_{k=1}^{k=10} \frac{S_k}{(2L)}$$

where in this case to each k corresponds a certain number of nodes or species that are 'interwoven' by a certain number of total ingoing and outgoing links (see Figure 3).

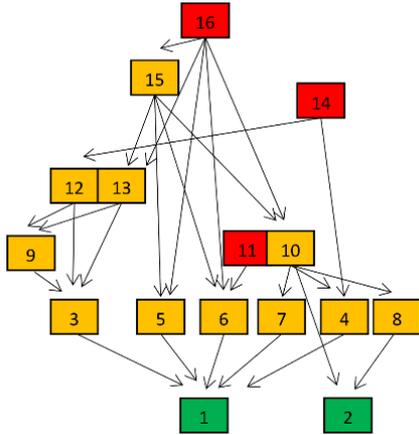


Figure 3. Lake George FW. Nodes are trophic species, links represent predator-prey relationship. Green nodes indicate plants or single cell producers. Intermediate Species and Top Predators are reported in orange and red color, respectively

3. Results

In Figure 4 structural parameters, the cumulative fraction of species presenting average community vulnerability at each k number of predators (green thick trend), are plotted in relation to another newly defined parameter (yellow thick trend) whose complement of cumulative fraction of species intercept at $MCL+1$. We propose a critical LD for LN_s at 3 instead of 4 (Figure 4). In CC and LN_s habitats belonging to the opposite pattern of connectance and species richness of Figure 2 with respect to LN_r , MCL could be more precisely associated with a minimum of predatory pressure (highest filled red dots) and an inversion of the blue, yellow LD_s

thresholds. It is important to note that Int average 'vuln' is also much greater in LN_r than in LN_s and CC and C_{bl} value of LN_r is about two times greater (see Table 1, Appendix A) although all these communities were sampled in the same location. We hypothesise a minimization of predatory pressure for all communities not only from compartmented habitats and energetic constraints categorisation of extrapolated $LD_{y-y} < LD_{v-y}$ for LN_s and CC or $LD_{y-y} > LD_{v-y}$ in the case of LN_r (Figure 4). Computed structural parameters are reported for the three communities investigated in greater detail from the Lake Nyasa-Malawi-Niassa (known in Tanzania-Malawi-Mozambique respectively), the southernmost lake of the Eastern Africa Rift system (Table 1, Appendix A). More typical parameters of food web literature, $\%T$, $\%B$ and $\%Int$ are associated with LD_{y-y} and only $\%Int$ is concordant (Table 2, Appendix A).

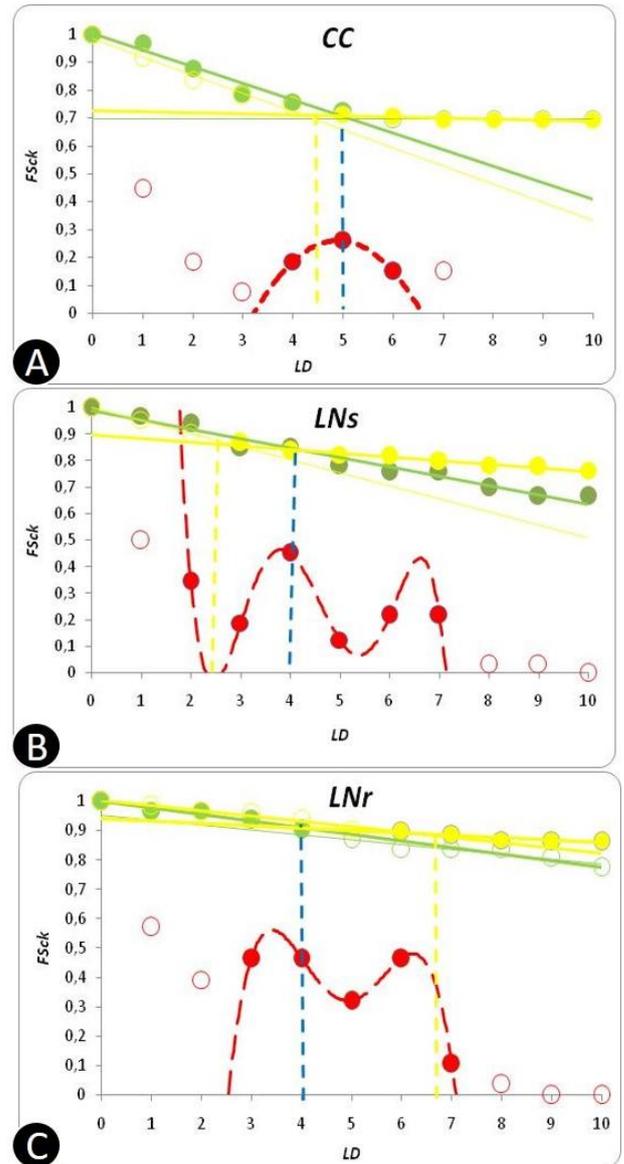


Figure 4. Structural and surrogate energetic parameters of exemplary food webs

To summarize some definitions, we have drawn an anonymous food web with $S = 16$ and $L = 25$, $TLs = MCL = 5$ (depending on the different first level attribution). $C = 2 \cdot 25 / (16 \cdot 15)$, $C_{bl} = 2 \cdot 25 / (14 \cdot 13)$, $LD = m = \text{number of links} / 16$ and $LD_{bl} = m_{bl} = 25 / 14$.

Simplified schematic food web / ecological Network

1. Basal species (only *vuln* links)
 2. Basal species (only *vuln* links)
 3. Intermediate species (*vuln* and *gen* links)
 4. Intermediate species (*vuln* and *gen* links)
 5. Intermediate species (*vuln* and *gen* links)
 6. Intermediate species (*vuln* and *gen* links)
 7. Intermediate species (*vuln* and *gen* links)
 8. Intermediate species (*vuln* and *gen* links)
 9. Intermediate species (*vuln* and *gen* links)
 10. Intermediate species (*vuln* and *gen* links)
 11. Top predator (only *gen* links)
 12. Intermediate species (*vuln* and *gen* links)
 13. Intermediate species (*vuln* and *gen* links)
 14. Top predator (only *gen* links)
 15. Intermediate species (*vuln* and *gen* links)
 16. Top predator (only *gen* links)
- Predator-prey adjacency square matrices, allows to draw the FW starting from A_{ij} elements (1 trophic relationship: 0 no link between the trophic species)
 - Calculate composite network parameters and fractions
 - Apply our new method described in par. 2 to species rich communities
 - Links are not weighed but trophic position can be calculated (simplified FW from [65])

A newly defined parameter $FSck_y$ (yellow dots), complement of the Fraction of Species k-connected (*in+out*) normalized for the total number of effective matrix *gen* and *vuln* links is plotted (par. 2). By fitting initial values (low LDs hollow yellow dots) of this newly defined $FSck_y$ and final values (high LDs filled yellow dots), LD_{y-y} is obtained by extrapolating a LD value from the two linear fitting equations. The intercept of the $FSck_{v-y}$ and $FSck_{y-y}$ trend lines individuate different linkage density thresholds. The Maximum Chain Length values are in relation to $LD_{v-y} - 1$. This parameter corresponding to the abscissa value where the trend of the complement of the cumulative fraction of vulnerable species ($FSck_v$, low LDs , green filled dots) intersects the trend of the complement of the cumulative fraction of the species with link-in plus link-out normalised by total number of links (pred+vuln) $FSck_y$ (high LDs , filled yellow dots). Interestingly to this value corresponds a minimum of predatory pressure for arbitrarily simulated (shadowed red dots) $FSck_g$ according to absence of vulnerable species (or a single species) at that LD_{vuln} . Hollowed red dots were those $FSck$ predatory values not included in the trend. Lake Nyasa-Malawi-Nyassa food web swampy *CC* (A), sandy *LN*s (B) and rocky *LNr* habitat (C). Data from Cohen [18] taken from Fryer [64].

3.1. Connectance, Linkage Density and Height of Ecological Networks

Searching for connectational thresholds, we fitted community's *Height* (MCL) vs LD_{bl} with a nonlinear polynomial model of the 4th order by interpolating average linkage density values for each TL (Figure 5). Highest MCL values are of extreme environment communities, with different network sizes, and possibly more subjected to climate warming threat.

• Herbivores diversity and proportion as a proxy for TLs (obvious for chains)

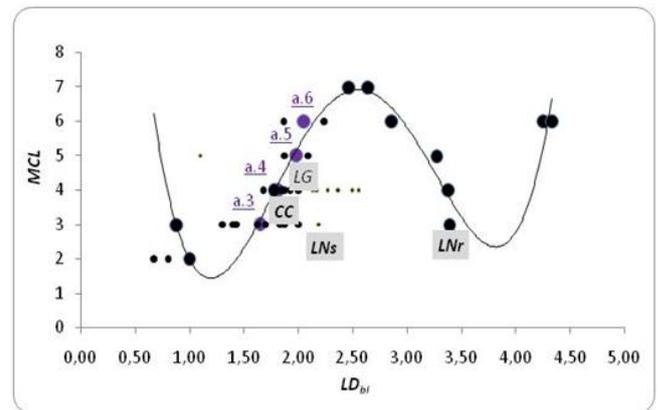


Figure 5. Maximum chain length vs link density. Maximum number of trophic levels, MCL , as a function of LD_{bl} ($n=16$ communities). To draw the fitting curve, data approaching to LD_{bl} equal two, where averaged for each trophic level a.3, a.4, a.5 and a.6. Mostly terrestrial communities with LD_{bl} closer to the abscissa of MCL_{max} were excluded from LD_{bl} average calculation corresponding to $MCL=4$ (also Lake Abaya [5] was not considered). Only exemplary lacustrine FWs (*LNr*, *LN*s, *CC* and *LG*) were indicated in grey in the graph. Communities not averaged (smallest dots). MCL of Ross Sea was taken from [26]. Large size black dots for communities that were included in the polynomial fitting (data from [27])

Arctic and Antarctic communities display also large number of average trophic levels (ACL) and a significantly reduced $\%H$ (the ratio of herbivorous and detritivorous species to other consumers). Consumption by Herbivores in terrestrial ecosystems was shown to be on average three times smaller than in aquatic ecosystems for a given level of primary productivity [66] and size-consumption scaling of herbivores could indirectly explain MCL in our lake case study. In fact, management of terrestrial ecosystems is starting to tackle both herbivores diversity and secondary productivity in different ecosystems [56]. Furthermore J. Lubchenco & B.A. Menge [67] attributed to herbivores a potential controlling role of intertidal community succession.

With selected literature data at hand [27] we refer to broad categorization of herbivores in a unifying perspective for community's "extreme trophic levels" approximation. We would expect a faster decrease in ACL with $\%H$ in terrestrial than in aquatic communities. Future refined studies, analogously for predators, could consider mobility of the species, contrasting browsers *versus* grazers,

ectotherm *versus* endotherm herbivores and integrating different species traits into ecological networks.

• Stratigraphy in food webs (trophic levels)

According to the results of Figure 4 we defined a new synthetic species density Y_{N-1} parameter computed as the number of species at the level $N-1$ divided by the Potential contiguous Weighted inter-level interactions, $PcWii$ (Table 3, Appendix B). The greater variability of this partial 'vertical' community parameter should probably be intended as a measure of independence from and adaptability to the environment and not of instability of the communities with greater height (number of TLs). Furthermore, energy-limited communities belong to the main axis of an ellipse where increasing C_{bl} could lead to a constant increase of the Y_{N-1} parameter. $S_{N-1} / (PcWii)$ is plausibly minimized for all three species rich communities of Lake Nyasa-Malawi-Niassa and maximized for mostly terrestrial communities at $C_{bl} \sim 0.2$ (values in Table 1, Appendix A). In this regard it was shown that an increase of percent omnivory, consequent to habitat coupling in relative smaller lakes, brings about a shortening of food chain length after increasing the accessibility of preys lower in the food web [25]. A food web could shrink in terms of species reducing its ACL but increasing connectance and hence lengthening their chains in favorable conditions like those occurring during seasonal or inter-annual favorable conditions [see [68]]. Other considerations about habitat type, stability and complexity were discussed by Shurin *et al.* [44].

4. Discussion & Conclusions

Comparative analysis and modelling of Ecological Networks offer a new perspective for a better understanding of communities as a whole. Rational management of natural reserve areas [69-70] and more in general unravelling the complexity of real ecological communities could be addressed with different network approaches possibly having matured awareness of potential pitfalls [1,34,62].

Efforts to make coherent the trophic level concept are encouraging and constructive [35,51]. Often its heuristic power becomes evident only above a threshold where certain structural parameters cannot be much relaxed otherwise S.H. Cousin's considerations cannot go unheeded [7]. Whenever possible existing food webs should be updated, and homogeneity of data more than exhaustiveness of resolution pursued to meet more functional than compile project's aim.

Gaining insight on the relationship between trophic web structural parameters and indexes of stability, persistence or services/health (indirect measure is easily obtained from catches estimated by fisheries) of an ecosystem should complement traditional ecological studies in responsible decisions of re-wilding and re-wiring.

Therefore, a list of key points re-analyzed follows:

- Architecture and patterns of ecological networks are meaningful for the interpretation of many different general ecological outcomes of trophic species number (coexistence) and connectance that could help explaining the reported constant [13,70-72], power law C findings [12,13,40] and also opposite link density (LD or m) pattern in diverse aquatic and terrestrial habitats [68,73].
- All-seasons communities belonging to the 'hyper-variable' trend, free to increase their S , optimize their connective network ($C \sim 0,75$) reflecting opportunistic foraging if not methodological biases. Species normally attract and interact with other species and adding 'guardians' to 'rebel species' could avert monopolization of the habitat (e.g., *Pisaster* starfish-effect on a strong competitor for space, *Mytilus* [58]). According to Martinez [13] larger communities do not display smaller C values after normalization is carried out (see also Figure 2).
- A fossil paleo-community structure, Messel Shale, featuring lake and forest food webs, belonged to the same trend of link density vs topological links of extant communities from variable environments with lake having ~ 3 times more strictly specialist fossil taxa [45]. It could be interesting to extend this analysis by Dunne *et al.* with different indicators of specialization (see different ranking in our case study Table 2).
- After recognizing the presence of at least two different linear patterns of link density with food web size, log-log scale, we focused our analysis on species and link distribution of three exemplary lentic communities from the same location (LNr and LN_s , CC). A new adjustable tool (Figure 4) was used to integrate trends of link distribution with effective network size and complexity (see degree distribution in [1,34,74]). Manipulative experiments have shown that the introduction of a generalist predator will often weaken other competition-based coexistence mechanisms resulting, whether by habitat segregation or indirect interspecific interactions, in competitive exclusion [75]. Satiation of the predator or switching may be more relevant for the dark blue pattern (Figure 2), where piscivorous fishes especially those that consume prey whole and provide extended parental care regularly experience long periods of empty stomachs [76].
- 'Comprehensive FW' increasing the reliability of patterns led us to estimate relative 'missing links' between mainly terrestrial communities and mainly lacustrine ones (data file kindly provided by Prof. J. Dunne); our attempt to convert communities from different trends resulted in an increase in the LD parameter of ~ 5 times (i.e. range from 2.6 to 10.3) or a corresponding reduction in topological links of around 20 - 40 links/species after antilog transformation of the $\log L - \log L^*$ data trend

(references in Appendix C; see also [77]).

- The simulation of low exerted predation pressure at low k -species vulnerability to support the localisation of maximum effective TL s where ‘predatory pressure’ is reasonably reduced for all communities suggests a more relevant bottom-up TL control in the sandy zone or creek than in the rocky zone of this great African lake (Figure 2; FW s in [64]); burrowing could help prey hiding only from visual predators some of which ambush, whilst rocky barricades with their numerous refuges could allow a more efficient and reliable top-down control (Figure 4).
- ‘Predatory pressure’ should be intended not as interaction strength or intensity but simply indicative of a niche or network condition where few consumers (Top or Int) realising predatory links of degree k pander vulnerability.

Most species, when not masking, interact in a food web by attractive and deterrent signals.

Defenses of plants are much more common on land environment [78] and indeed feedbacks are widespread at different levels of biological organization [79,88].

4.1. Examples of Camouflage in FW s

As an unusual example of anti-predatory tactic, animal changes in brightness could reduce detection probability of crabs [80,88] and notwithstanding ubiquity of mimetism (e.g., Figure 6) the adaptive significance of carapace geometric patterns is still under field and laboratory experimentation.

Different camouflage strategies minimize signal to noise ratio [81], both background sand matching in estuarine cryptic juveniles and possibly displaying disruptive markings in *Carcinus aestuarii* juveniles frequenting structurally more heterogeneous habitats have been observed in the western side of the North Adriatic Sea (45° N, 12° E) (Valandro L.R., in preparation). Quantification of effectiveness of resultant avoiding predation by field experiments or going further the commonness of camouflage in both aquatic and terrestrial habitat, and different contexts, could quite soon open up innovative research avenues with integrative methodologies at the moment only prudentially listed in food web modelling [26]. All species are likely vulnerable at some stage including apex predators.

Furthermore, cannibalism and damages by bigger conspecifics should necessarily be included in network modelling functional responses, returning species identity relevance, here only indirectly manifested.

All species are vulnerable and mimetism is ubiquitous but never obvious. In Figure 6, panel A a cryptic *Carcinus* juvenile with three white triangles and a black spot in the dorsal side of the carapace remains motionless but only partially under the sand. If conspicuous to visual predators such white triangles or dark spots when not corresponding to any search image of their natural predators could be

interpreted as a ‘cognitive mimetism’ allowing the crab to avoid recognition by visual predators or harassers. A spotted newborn lamb (Figure 6, panel B) and a copepod (Figure 6, panel C) are common species of terrestrial and freshwater habitats.

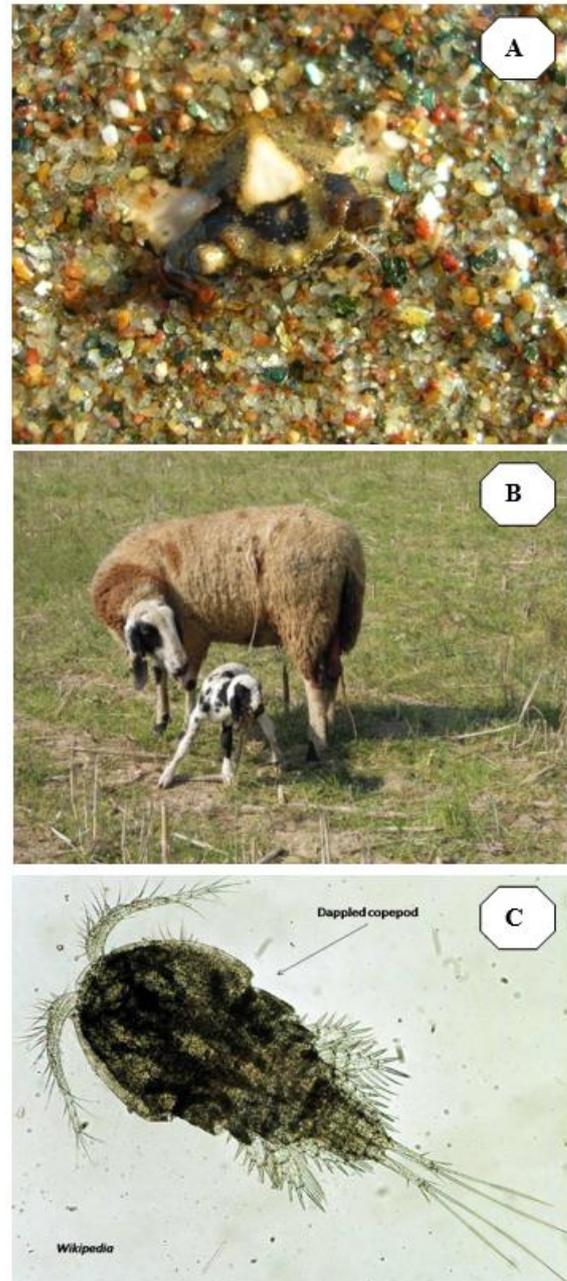


Figure 6. *C. aestuarii* juveniles (estuarine-marine), newborn lamb (terrestrial) and a Cyclopoid copepod (freshwater) on panel A, B and C, respectively - 6C adapted from <https://it.m.wikipedia.org/wiki/Cyclops> US Environmental Protection Agency

Consumers interact less effectively with camouflaged species especially during development, whereas community predation pander vulnerability mainly in crowded habitats. Camouflage is a ubiquitous mode to avoid predation and we would expect to behold its optimal modulation at different trophic levels in different contexts.

4.2. Anti-Predatory Perspective and Fraction of Primary Consumers

Notwithstanding our awareness of possible consistent subsidies among habitats, aquatic and terrestrial communities have been compared from an anti-predator perspective and empirical data [66] were confirmed with food web parameters different trends (ACL vs $\%H$).

Whenever herbivory seems to play a role of a determinant parameter in structuring food web complexity, herbivores and animals mobility trait could be crucial to reveal the mechanisms.

The upland moa, an extinct though quite generalist herbivore of New Zealand, was probably migrating seasonally thus becoming the "highlander" of the flightless moas; it had probably a speckled appearance (not unique to *Megalapteryx didinus*) and it could be interesting to prosecute the reconstruction of terrestrial ecological networks of moas from coprolites, gizzard contents, isotope analysis to contrast what we envision was the more wide, complex and persistent heterogeneous habitat according to the framework here proposed or see inverse primary consumer size- ACL hypothesis [82]. Size of large and mega herbivores is often also anti-predatory but it seems reasonable that avoiding human hunting was pivotal more than avoiding predation by Haast eagle or protecting eggs considering that, although exceptionally coloured, eggs of *M. Didinus* were the smaller and thinner among the moa species [82].

Longer lower limbs in hominid populations could allow to reach easily and more economically terrestrial and aquatic feeding sites. However, approximate average specific power calculations were provided considering arm movement biomechanics and length to be a driver for human evolution in hunters and fishermen [84] and postponing prey target size or sportive launching accuracy to future analysis.

Whether networks of mutualists are possibly more often impacting communities on longer temporal scales, we expect active involvement of abundant parasites and virioplankton in particular to exert their multiple effects in shorter timescales [85].

4.3. Trophic Levels Extreme from Cumulative Distributions of Links

The analysis of link distribution and the definition of two parameters with energetic and vulnerability connotation ($FSck_y$, $FSck_{vuln}$) provide a new interpretation for maximum chain length of food webs (Table 1, Appendix A). Energy trends in combination with vulnerability patterns seem to individuate the "trophic level extreme" of a food web that is already implicit in the matrix information; in this approach overall distribution of links enriches the framework and could add directional predictive power by changing the fraction of species involved after different perturbations or somehow changed ecological contexts. Community Height (MCL) is possibly not energetically constrained in LNr

where *aufwuchs* (algae plus microfauna) is omnipresent [64]. Analogously to other food webs of the dark blue trend of Figure 2, although environmentally variable, they could have continuous high-quality food supply. The observed greater MCL for CC could be in relation to the reduction in Top specialisation as compared with LN s (see Table 2, Appendix A and Figure 4) by a reduced vulnerability of the further stratified community [see [36]] the extra carnivorous cyclopoid copepods node. Other herbivorous cyclopoid species are abundant in Lake Nyasa sandy and rocky shores but *Macrocyclops* was exclusive of Crocodile creek ecological region [64]. Interestingly a shorter modal chain in CC was reported [57] giving credit to Briand & Cohen food web structure simplification and supporting the Eltonian general observation of low number of TL s especially at warmer tropical latitudes. However a deeper analysis is needed to explain the low C value of *Crocodile Creek* community and the text paper from which the food webs were originally taken [64] reporting generalist species in the weedy lentic CC in order to survive shortage of food during flooding events of the rainy season.

The number of TL s increases with link density between intervals at least in this small sample (Figure 5). We expect highest Height of whole ecological communities as already presented for zooplanktonic lacustrine food webs at low zooplankton Species Packing (range of SP in Table 3, Appendix B). A concomitant large network size and high ACL is theoretically allowed for LD^{-1} close to 1 (trophic chain-like efficient energy transfers) and $LD^{-1} \sim C_{cr}$ (data not shown) analysing data from lake Okeechobee, part of a vast protected aquatic ecosystem including the Florida Everglades [68].

To our knowledge not many conclusive results have been obtained by the exploration of ecological networks assembling process [41]; however, data are growing from frequent cases of species extinctions or threatening invasions.

It would be interesting to investigate the temperature effect on disparate lentic ecological networks and macro-descriptors. Hierarchical communication among sub-webs and the whole food web in lentic systems from the same location could also be a topic to investigate with long temporal series datasets from experimental surveys and satellites. Probabilistic (trait matching) and Bayesian approaches have been recently addressed in the ecological network discipline. Further work, assisted by new algorithmic techniques and programs and including in models organism traits [86-87] will tell us how much mathematical ecologists are bringing us closer to bio-signalling and biocenosis' understanding and safeguard.

ACKNOWLEDGEMENTS

We would like to acknowledge Prof. JH Cohen for authorizing us to utilize matrix data of communities from Ecologists Co-operative Web Bank (ECOWEB TM) and Prof.

J Dunne for providing taxonomical information of the comprehensive FWs. Prof. A Minelli improved the structure of the manuscript and provided crucial bibliographic information and discussions about complexity of organisms at different levels of organization. Prof. L Colombo, Prof.

J Reynolds and Prof. TW Schoener commented the manuscript with clarifying feedbacks. We are indebted to Prof. B Patten for improving a preliminary version of this work. Many thanks also to Dr. William Irwin for his suggestions.

Appendix A

Parameters of exemplary regions of Lake Nyasa-Malawi-Niassa

Table 1. Food webs bottomless parameters of different lentic habitats from the same location (Malawi-Nyasa-Niassa)

FWs habitat	S_{bl}	C_{bl}	LD_{bl}	$FSkc_v=FSkc_y$	LD_{y-y}	LD_{v-y}	ACL	MCL
Lake Malawi-Nyasa sandy	32(37)	0.15	2.37	0.84	2.86	4.09	2.87	3
Lake Malawi-Nyasa rocky	28(31)	0.25	3.39	0.91	6.77	4.14	3.13	3
Crocodile Creek	28(33)	0.14	1.86	0.71	4.21	5.25	2.85	4
Parameter averages	29(34)	0.18	2.54	0.820	4.61	4.49	2.95	3.33

The relative fraction of species values with k -vulnerability, $FSkc$, are in grey. The same holds for the cumulative fraction of species, normalized for the total number of links instead of number of S_{bl} , $FSkc_y$. Extrapolated link density LD_{vuln-y} are obtained by the intersection of the initial trend of $1-FSkc_{vuln}$ function (green line upper left) and the terminal part of the $1-FSkc_y$ function (yellow line lower right) of Figure 3. MCL from Briand & Cohen [27]. Focus on link density and maximum chain length correspondence framed. All structural parameters point to a separate ranking of LN_s , CC , and LN_r FWs two groups. Smaller value/values of the term were underlined to support exemplarity of the LN_s , CC , and LN_r FWs two groups. Within parentheses, first column, the total number of species, including basal species. ACL values from Begon *et al.* [16]. Data for calculations of $FSkc$ parameters taken from: Cohen [18] Ecologists Co-operative Web Bank ECOWebTM originally reported in Fryer [64].

Food Webs structural parameters of three Lake Nyasa habitats

Food web number 33, 38, 39 of the Briand and Cohen collection - Smaller value/values of the term were underlined to support exemplarity of the LN_s , CC and LN_r FWs two groups. The differences between $\%Top$ species are very small while $\%Top_{bl}$ are inverted after the exclusion of the resources from total number of trophic species. $\%Top$ is higher in the rocky ecological region of the Great African lake (54.8%) and smaller in the sandy and crocodile swampy areas respectively (54.1 and 54.5). Average $\%Top$ is 54.47 ($n=3$). $\%Top_{bl}$ were 60.7, 62.5, and 64.3 ($Average = 62.50\%$; $n=3$).

Table 2. Food Webs structural parameters of different lentic habitats from the same location (12° S, 34° E)

FWs habitat	$\%B$	$\%Int$	$\%Spec$	$\%Spec2$	$\% \frac{Top_{spec2}}{Top}$	$\% \frac{Top_{spec}}{Spec}$	$\% \frac{Top_{spec2}}{Spec2}$
Lake Malawi Nyasa sandy	13.5	34.4	50.0	78.1	70	54.2	56.0
Lake Malawi Nyasa rocky	9.7	39.3	42.8	46.4	23.5	25.0	30.8
Crocodile Creek	15.2	35.7	51.7-64.3	82.7	66.7	46.7	54.5
Parameter averages	12.80	36.83	52.37	69.07	53.40	41.97	47.10

Data taken from Cohen [18] Ecologists Co-operative Web Bank ECOWebTM originally reported in Fryer [64]. The $\%$ of specialist species with one or two ingoing predatory links ($Spec2$) discriminate clearly the two groups (LN_r and CC , LN_s) analogously to $\%Top_{spec}/Top$ with one or either one and two predatory links.

Appendix B

Further structural parameters definition and intervals

Table 3. Further structural parameters definition and intervals

COMPOSITEPARAMETERS	DEFINING EQUATION	INTERVAL
Potential interactions (no diagonal links)	$L^* = S(S - 1)/2$	3-528
Connectedness bottomless	$C_{bl} = 2L / [S_c(S_c - 1)]$	(0.05) 0.12 ^(a) -0.96
Link density bottomless	$LD_{bl} = L/S_c$	1.1-4.3
Link packing	$LP = L/ACL$	0.67-30.35
Species packing	$SP = S_c/ACL$	1.0-11.1
Percentage of herbivores and detritivores	$\%H = H / (S_c H)$	16.7-400
Potential contiguous inter-level interactions	$Pc(W)_{ii} = S_{N-1}S_{N-1} + S_{N-1}S_{N-2}$	2-240
Synthetic species community density	$Y_{N-1} = S_{N-1} / Pc(W)_{ii}$	0.04-0.50

L : Effective trophic links, H : number of primary consumers, S_i : Consumer trophic species, $N = MCL = TLs$. Data from Begon *et al.* [16] originally taken from Briand [17]. (a) value if not considering case study number 40 (Salt Meadows of New Zealand). Species community density is defined as the ratio of S_i at the trophic level approaching MCL and $P_c(W_{ij})$

Appendix C

Authors and acronym of 'comprehensive trophic networks'

Coachella Valley, CV (Polis 1991), St. Martin Island, StMI (Goldwasser & Roughgarden 1993), G, UK Grassland (Memmott *et al.* 2000), SP, Skipwith Pond (Warren 1989), Bridge Brook Lake, BBL (Havens 1992), Little Rock Lake, LRL (Martinez 1991), Canton Creek, CCr, and Stony Stream, SS (Townsend *et al.* 1998), Chesapeake Bay, CB (Baird & Ulanowicz 1989), St. Mark's Estuary, StME (Christian & Luczkovich 1999), Ythan Estuary, YE (Hall & Raffaelli 1991), Caribbean Reef (Opitz 1996).

'Comprehensive trophic networks' references

Baird D & Ulanowicz RE. The seasonal dynamics of the Chesapeake Bayecosystem. *Ecol. Monogr.* 1989, **59**: 329-364.

Christian RR & Luczkovich JJ. Organizing and understanding a winter's Seagrass foodweb network through effective trophic levels. *Ecol. Modell.* 1999, **117**: 99-124.

Goldwasser L & Roughgarden JA. Construction of a large Caribbean foodweb. *Ecology* 1993, **74**:1216-1233.

Hall SJ & Raffaelli D. Food-web patterns: lessons from a species-rich web. *J. Anim. Ecol.* 1991, **60**:823-842.

Havens K. Scale and structure in natural food webs. *Science* 1992, **257**:1107-1109.

Memmott J, Martinez ND, Cohen JE. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *J. Anim. Ecol.* 2000, **69**:1-15.

Opitz S. Trophic interactions in Caribbean coral reefs. *ICLARM Tech. Rep.* 1996, **43**: 341pp.

Polis GA. Complex desert food webs: an empirical critique of food web theory. *Am. Nat.* 1991, **138**: 123-155.

Townsend CR, Thompson RM, McIntosh AR, Kilroy C, Edwards E & Scarsbrook MR. Disturbance, resource supply, and food-web architecture in streams. *Ecol. Lett.* 1998, **1**:200-209.

Warren PH. Spatial and temporal variation in the structure of a freshwater food web. *Oikos* 1989, **55**:299-311.

of fourteen researchers. *Food webs* 2015, 4: 14-24.

- [4] Martinez ND. Scale dependent constraints on food web structure. *Am. Nat* 1994, 144: 935-953.
- [5] Schoener TW. Food webs from the small to the large. *Ecology* 1989, 70(6): 1559-1589.
- [6] Cohen JE, Briand F, Newman CM. *Community Food Webs: Data and Theory*. New York: Springer-Verlag; 1990.
- [7] Cousins SH. The decline of the trophic level concept. *Trends Ecol. Evol.* 1987, 2: 312-316.
- [8] Deb D. Scale-dependence of Food Web Structures: Tropical Ponds as Paradigm. *Oikos* 1995, 72: 245-262.
- [9] Akin S, Winemiller KO. Seasonal variation in food web composition and structure in a temperate tidal estuary. *Estuar. Coas* 2006, 29: 552-567.
- [10] Quillfeldt P, Ekschmitt K, Brickle P, McGill RA, Wolters V, Dehnhard N, Masello JF. Variability of higher trophic level stable isotope data in space and time - A case study in a marine ecosystem. *Rapid Commun. Mass Spectrom* 2015, 29(7): 667-74.
- [11] Yodzis P. The connectance of real ecosystems. *Nature* 1980, 284: 544-545.
- [12] Pimm SL. *Food webs*. New York; Ed. Chapman & Hall; 1982.
- [13] Martinez ND. Constant connectance in community food webs. *Am. Nat.* 1992, 140: 1208-1218.
- [14] Banasek-Richter C, Bersier L-F, Cattin M-F, Baltensperger R, Gabriel J-P, Merz Y, Ulanowicz RE, Tavares AF, Williams DD, de Ruiter PC, Winemiller KO, Naisbit RE. Complexity in quantitative food webs. *Ecology* 2009, 90(6): 1470-1477.
- [15] Valandro L, Caimmi R, Colombo L. What is hidden behind the concept of ecosystem efficiency in energy transformation? *Ecol. Model.* 2003, 170: 185-191.
- [16] Begon M, Harper JL, Townsend CR. *Ecology: Individuals, populations and Communities*. Third edition, Oxford: Blackwell Science; 1996.
- [17] Briand F. Environmental control of food web structure. *Ecology* 1983, 64(2): 253-263.
- [18] Cohen JE. 1989 *Ecologists Co-operative Web Bank (ECOWeBTM)*, New York, Rockefeller University.
- [19] Merriam G. Connectivity: a fundamental ecological characteristic of landscape pattern. In: Brandt J and Agger P. (eds) *Proceedings of first international seminar on methodology in landscape ecology research and planning*, vol I. Roskilde Universitessforlag GeoRuc, Roskilde, Denmark, 1984. p.5-15.
- [20] Hodgson JA, Thomas CD, Wintle BA, Moilanen A. Climate change, connectivity and conservation decision making: back to basics. *J. Appl. Ecol.* 2009, 46: 964-969.
- [21] Leguerrier D, Degré D, Niquil N. Network analysis and inter-ecosystem comparison of two intertidal mudflat food

REFERENCES

- [1] Dunne AJ, Williams RJ, Martinez ND. Food-web structure and network theory: The role of connectance and size. *Proc. Natl Acad. Sci. USA* 2002, 99: 12917-12922.
- [2] Egerton FN. Understanding food chains and food webs, 1700-1970. *Bull. Ecol. Soc. Am.* 2007, 88(1): 50-69.
- [3] Laymann CA, Glery ST, Buhler S, Rossi R, Penland T, Henson MN, Bogdanoff AK, ..., Archer SK. A primer on the history of food webs ecology: Fundamental contributions

- webs (Brouage Mudflat and Aiguillon Cove, SW France). *Estuar. Coast. Shelf Sci.* 2007, 74(3): 403-418.
- [22] Hairston NG Jr, Hairston NG Sr. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *Am. Nat.* 1993, 142: 379-411.
- [23] Pimm SL, Lawton JH. Number of trophic levels in ecological communities. *Nature* 1977, 268: 329-331.
- [24] DeAngelis DL, Bartell SM, Brenkert AL. Effects of nutrient recycling and food-chain length on resilience. *Am. Nat.* 1989, 134(5): 778-805.
- [25] Tunney TD, McCann KS, Lester NP, Shuter BJ. Food web expansion and contraction in response to changing environmental conditions. *Nature Com.* 2012, 3:1105.
- [26] McGarvey R, Dowling N, Cohen J. Longer food chains in pelagic ecosystems: trophic energetics of animal body size and metabolic efficiency. *Am. Nat.* 2016, 188(1): 76-86.
- [27] Briand F, Cohen JE. Environmental correlates of food web chain length. *Science* 1987, 238: 956-960.
- [28] Kerr SR. Theory of size distribution in ecological communities. *J. Fish. Res. Board Can.* 1974, 31(12): 1859-1862.
- [29] Cohen JE. *Food Webs and Niche Space*. Princeton: Princeton Univ. Press; 1978.
- [30] Yodzis P, Innes S. Body size and consumer-resource dynamics. *Am. Nat.* 1992, 139: 1151-1175.
- [31] Emmerson MC, Raffaelli D. Predator-prey body-size, interaction strength and the stability of a real food web. *J. Anim. Ecol.* 2004, 73:399-409.
- [32] Warren PH, Spencer M. Community and food-web responses to the manipulation of energy input and disturbance in small ponds. *Oikos* 1996, 75(3): 407-418.
- [33] Tucker MA, Rogers TL. Examining predator-prey body size, trophic level and body mass across marine and terrestrial mammals. *Proc. R. Soc. B* 2014, 281: 1797.
- [34] Ings TC, Montoya JM, Bascompte J, Blüthgen N, Brown L, ..., Woodward G. Ecological Networks - beyond food webs. *J. Anim. Ecol.* 2009, 78:253-269.
- [35] Williams RJ, Martinez ND. Limits to trophic levels and omnivory in complex food webs: Theory and data. *Am. Nat.* 2004, 163: 458-468.
- [36] Dunne J. The Network Structure of Food Webs. Workshop on Theoretical Ecology and Global Change at The Abdus Salam International Centre for Theoretical Physics, Trieste; 2009.
- [37] Warren PH. Spatial and temporal variation in the structure of a freshwater food web. *Oikos* 1989, 55:299-311.
- [38] Bersier LF, Sugihara G. Scaling regions for food web properties. *Proc. Natl Acad. Sci. USA* 1997, 94: 1247-1251.
- [39] Gauzens B, Legendre S, Lazzaro X, Lacroix G. Food-web aggregation, methodological and functional issues. *Oikos* 2013, 122:1606-1615.
- [40] May RM. *Stability and Complexity in Model Ecosystems*, Princeton, NJ: Princeton University Press; 1973.
- [41] Schriever TA. Food webs in relation to variation in the environment and species assemblage. A multivariate approach. *Plos ONE* 2015, 10(4): e0122719.
- [42] Forister ML. et al. The global distribution of diet breadth in insect herbivores. *Proc. Natl Acad. Sci. USA* 2015, 112(2): 442-447.
- [43] Cirtwill AR, Stouffer DB, Romanuk TN. Latitudinal gradients in biotic niche breadth vary across ecosystem types. *Proc. R. Soc. B* 2015, 282: 20151589.
- [44] Shurin JB, Gruner DS, Hillebrand H. All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proc. R. Soc. B* 2006, 273: 1-9.
- [45] Dunne JA, Labandeira CC & Williams RJ. Highly resolved early Eocene food webs show development of modern trophic structure after the end-Cretaceous extinction. *Proc. R. Soc. B* 2014, 281: 20133280.
- [46] Chase JM, Leibold MA, Downing AL, Shurin JB. The effect of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology* 2000, 81(9): 2845-2497.
- [47] Rossi L, Di Lascio A, Carlino P, Calizza E, Costantini ML. Predator and detritivore niche width helps to explain biocomplexity of experimental detritus-based food webs in four aquatic and terrestrial ecosystems. *Ecol. Complex.* 2015, 23: 14-24.
- [48] Schalk CM, Montaña CG, Winemiller KO, Fitzgerald LA. Trophic plasticity, environmental gradients and food-web structure of tropical pond communities. *Freshw. Biol.* 2017, 62(3): 519-529.
- [49] Briand F. Structural singularities of freshwater food webs. *Verh. Internat. Verein Limnol.* 1985, 22: 3356-3364.
- [50] Carpenter SR, Chisholm SW, Krebs CJ, Schindler DW & Wright RF. Ecosystem experiments. *Science* 1995, 269: 324-327.
- [51] Christensen V, Guénette S, Heymans JJ, Walters CJ, Watson R, Zeller D & Pauly D. Hundred-year decline of North Atlantic predatory fishes. *Fish Fish.* 2003, 4: 1-24.
- [52] Spiller DA & Schoener TW. Effects of top and intermediate predators in a terrestrial food web. *Ecology* 1994, 75: 182-196.
- [53] Polis G, Sears ALW, Huxel GR, Strong D, Maron J. When is a trophic cascade a trophic cascade? *Trends Ecol. Evol.* 2000, 15: 473-475.
- [54] Leroux SJ, Loreau M. Consumer mediated recycling and cascading trophic interactions. *Ecology* 2010, 91: 2162-2171.
- [55] Heath MR, Speirs DC, Steele JH. Understanding patterns and processes in models of trophic cascades. *Ecol. Lett.* 2013, 17(1): 101-114.
- [56] Gandiwa E. Top-down and bottom-up control of large herbivore populations: a review of natural and human-induced influences. *Trop. Conserv. Sci.* 2013, 6(4): 493-505.
- [57] Schoenly K, Beaver RA, Heumier TA. On the trophic relations of insects. A food web approach. *Am. Nat.* 1991, 137:597-638.

- [58] Paine RT. Food webs: linkage, interaction strength and community infrastructure. *J. Anim. Ecol.* 1980, 49: 667-685.
- [59] Kerr JT, Packer L. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 1997, 385: 252-254.
- [60] Guegan JF, Lek S, Oberdorff T. Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature* 1998, 391: 382-384.
- [61] Hurlbert AH. Species-energy relationship and habitat complexity in bird communities. *Ecol. Lett.* 2004, 7(8): 714-720.
- [62] Ulanowicz RE, Holt RD, Barfield M. Limit on ecosystem trophic complexity: insights from ecological network analysis. *Ecol. Lett.* 2014, 17: 127-136.
- [63] Borrett SR, Patten BC. Structure of pathways in ecological networks: relationships between length and number. *Ecol. Modell.* 2003, 170: 173-84.
- [64] Fryer G. The trophic interrelationships and ecology of some littoral communities of Lake Nyasa with especial reference to the fishes and a discussion of the evolution of a group of rock frequenting Cichlidae. *Proc. Zool. Soc. Lond.* 1959, 132: 153-281.
- [65] Burgis MJ., Dunn IG., Ganf GG., McGowan LM. & Viner AB. Productivity Problems of Freshwaters, Kajak Z. & Hillbricht-Ilkowska A. eds. Warsaw: Polish Scientific Publishers; 1972, Lake George, Uganda: Studies on a tropical freshwater ecosystem; pp.301-309.
- [66] Cyr H, Pace ML. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* 1993, 361: 148-150.
- [67] Lubchenco J, Menge BA. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.* 1978, 48: 67-94.
- [68] Carney HJ, Havens KE, Bersier L. Nonlinear scale dependence and spatiotemporal variability in planktonic food webs. *Oikos* 1997, 79: 230-240.
- [69] Coll M, Libralato S. Contribution of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. *Fish Fish.* 2012, 13: 60-88.
- [70] Soler GA, Graham JE, Thomson RJ. et al. 2015 Reef fishes at all trophic levels respond positively to effective marine protected areas. *PLoS ONE* 10(10): e0140270.
- [71] Sugihara G, Schoenly K., Trombla A. Scale invariance in food web properties. *Science* 1989, 245: 48-52.
- [72] Havens KE. Unique structural properties of pelagic food webs. *Oikos* 1997, 78: 75-80.
- [73] Buzhdygan OY, Rudenko SS. Trophic Network assessment of grassland ecosystem status. *Biol. Syst.* 2016, 8(1): 143-154.
- [74] Poisot T, Gravel D. When is an ecological network complex? Connectance drives degree distribution and emerging network properties. *PeerJ* 2014, e251: 1-11.
- [75] Holt RD, Lawton JH, Polis GA, Martinez ND. Trophic rank and the species-area relation. *Ecology* 1999, 80: 1495-1504.
- [76] Arrington DA, Winemiller KO, Loftus WF, Akin S. How often do fishes "run on empty"? *Ecology* 2002, 83(8): 2145-2151.
- [77] Nakazawa T, Ushio M, Kondoh M. Scale dependence of predator-prey mass ratio: determinants and applications. *Adv. Ecol. Res.* 2011, 45: 269-302. (doi.org/10.1016/B978-
- [78] Vermeij GJ. Plant defences on land and in water: why are they so different? *Annals of Botany*, 2016, 117: 1099-1109.
- [79] Smith MJ, Sander E., Allesina S. Stability and feedback levels in food web models. *Ecol. Lett.* 2015, 18, 593-595.
- [80] Stevens M, Lown AE, Wood LE. Color change and camouflage in juvenile shore crabs. *Front. Ecol. Evol.* 2014, 2, 1-14.
- [81] Cuthill IC. Camouflage. *J. Zool.* 2019, 308, 75-92.
- [82] Ayal Y., Groner E. Primary consumer body size and food-chain length in terrestrial communities. *Israel. J. Ecol. Evol.* 55(4), 239-343.
- [83] Gill BJ. Eggshell characteristics of moa eggs (Aves: Dinornithiformes). *J. R. Soc. N. Z.* 2007, 37, 139-150.
- [84] Secco EL, Valandro L, Caimmi R, Magenes G, Salvato B. Optimization of two-joint arm movements: a model technique or a result of natural selection? *Biol. Cybern.* 2005, 93(4), 288-306.
- [85] Wommack KE, Colwell RR. Virioplankton: Viruses in Aquatic Ecosystems. *Microbiol. Molec. Biol. Rev.* 2000, 64, 69-114.
- [86] Eklöf A, Tang S, Allesina S. Secondary extinctions in food webs: a Bayesian network approach. *Methods Ecol. Evol.* 2013, 4, 760-770.
- [87] Bartomeus I, Gravel D, Tylianakis JM, Aizen MA, Dickie IA, Bernard-Verdier M. A common framework for identifying linkage rules across different types of interactions. *Funct. Ecol.* 2016, 30, 1894-1903.
- [88] Soto-Ortiz L. The Regulation of Ecological Communities Through Feedback Loops: A Review, *Research in Zoology.* 2015; 5(1): 1-15. doi:10.5923/j.zoology.20150501.01.