

**IDEA AND
PERSPECTIVE**

Limits on ecosystem trophic complexity: insights from ecological network analysis

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Abstract

Articulating what limits the length of trophic food chains has remained one of the most enduring challenges in ecology. Mere counts of ecosystem species and transfers have not much illuminated the issue, in part because magnitudes of trophic transfers vary by orders of magnitude in power-law fashion. We address this issue by creating a suite of measures that extend the basic indexes usually obtained by counting taxa and transfers so as to apply to networks wherein magnitudes vary by orders of magnitude. Application of the extended measures to data on ecosystem trophic networks reveals that the actual complexity of ecosystem webs is far less than usually imagined, because most ecosystem networks consist of a multitude of weak connections dominated by a relatively few strong flows. Although quantitative ecosystem networks may consist of hundreds of nodes and thousands of transfers, they nevertheless behave similarly to simpler representations of systems with fewer than 14 nodes or 40 flows. Both theory and empirical data point to an upper bound on the number of effective trophic levels at about 3–4 links. We suggest that several whole-system processes may be at play in generating these ecosystem limits and regularities.

Keywords

Connectivity, ecosystem roles, food chain length, network complexity, system flexibility, system roles, trophic breadth, trophic depth, window of vitality.

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AN ENDURING QUESTION IN ECOLOGY: WHAT LIMITS FOOD CHAIN LENGTH?

One of the most important, unanswered questions in ecology remains, ‘What limits the number of trophic levels in an ecosystem?’ (May 1999). Empirical and applied studies of trophic cascades (Terborgh & Estes 2010; Estes *et al.* 2011; Carpenter *et al.* 1985) reveal that ecosystems often comprised effectively just a few trophic levels—e.g. producers, herbivores and predators—even though complete food webs reveal a much more tangled network of trophic interactions among species. At first glance, a deceptively simple answer might seem to suffice—the necessary thermodynamic losses that accompany each trophic transfer do not allow for an indefinite number of transfers. While this statement is surely true, it is hardly the final word. Pimm & Lawton (1977), e.g. suggested a limit to the number of observed trophic transfers at about 5, but noted that, even beyond this number of transfers, there appears to be sufficient energy and material to build further levels. Indeed, some food chains can reach considerably longer lengths (see Table 3.3 in Moore & de Ruiter 2012). Hastings & Conrad (1979) suggested an evolutionary argument: carnivores that attack other carnivores can also likely consume herbivores. Evolution of body size at low trophic levels can also influence food chain length (Ayal & Groner

2009); some herbivores (megaherbivores) evolve to sizes whereby they largely escape predation, thus truncating the food chain. Also, if consumers are likely to feed across trophic levels, food chain length is reduced.

Pimm & Lawton (1977) concluded that limits to the number of trophic levels arise from dynamical considerations—and in particular by the ability of ecosystems to recover after perturbations—rather than from thermodynamics. Their conclusions are sensitive to assumptions about local density dependence (Sterner *et al.* 1997), but more generally dynamical constraints could encompass a broad range of spatial and temporal processes, such as colonisation-extinction dynamics, disturbance and the effects of coupling heterogeneous habitats or detrital and producer pathways by mobile consumers (Rooney *et al.* 2006). These processes could lead to a limitation on the number of trophic levels reflecting ecosystem size and variability (Post 2002; Holt *et al.* 2010; McHugh *et al.* 2010; Calcagno *et al.* 2011; Takimoto *et al.* 2012.)

It is still true, however, that for almost any food web, any ecologist can identify feeding pathways longer than three. Analyses of unweighted trophic interactions reveal no obvious limit to trophic pathway length (Whipple & Patten 1993). Many lengthy feeding pathways have been documented, particularly in aquatic ecosystems (e.g. Fig. 7.2 in Holt 1993). Baird & Ulanowicz (1989), e.g. enumerated

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pathways of length 8 in the Chesapeake ecosystem, while the recent compilation by Moore & de Ruiter (2012) reveals some food chains of length 9. In fact, Bondavalli & Ulanowicz (1999) have identified feeding pathways as long as 12 in the Florida Bay ecosystem. However, many consumers above the second trophic level are omnivorous and cannot be assigned uniquely to a given trophic level (Cousins 1985). Usually, a predator receiving resources at some high level draws most of its sustenance from lower levels (Ulanowicz & Kemp 1979; Ulanowicz 1995a). In effect, rarefied feeding at high levels is massively subsidised by consumption at lower ones. When Baird & Ulanowicz (1989) summed up the amounts being transferred between trophic levels, they discovered that only miniscule resources make it beyond the fifth level. Connection webs can mask tremendous heterogeneity in the magnitudes of flows across different pathways.

We suggest that characterising and understanding the limits to trophic levels in ecosystems require one to quantify the magnitudes and asymmetries among flows (see also Raffaelli 2002; Williams & Martinez 2004; Benke 2011). We will build on a formal approach pioneered by Bersier *et al.* (2002) to define a set of network measures that can be applied either to quantified or to qualitative ecosystem networks. We demonstrate how these measures are interrelated, and suggest that all trophic networks can be characterised by two virtual dimensions—a *width*, which we suggest typifies the effective number of parallel pathways in the structure, and a *depth*, which reflects the effective number of transfers any element experiences during its passage through the ecosystem and is a measure of the effective number of trophic levels in the system. Using this approach, we will show that complex webs often have relatively short effective food chain lengths, and also that the ratio of width to depth for each network varies surprisingly little among ecosystems. We conclude with a phenomenological perspective on the factors that may lead to limits on these structural features of flow networks, including the number of trophic levels.

IDENTIFYING CONSISTENT, WEIGHTED FOOD WEB METRICS

To build towards an understanding of weighted food web metrics, it is useful to begin with simpler, unweighted metrics. For any food web we can make simple counts of the number of nodes N and of the number of flows F connecting nodes to each other and to the external environment. From these quantities, the average number of flows into or out of each node, the link-density C , is defined as F/N (flows per node). We suggest that C serves as a measure of the *width* of the network (see below). A measure of the *depth* of the network is the number of nodes divided by the width, and is given by $R = N/C$. These unweighted measures can be assessed for any food web.

To make more intuitive the characterisation of C as a measure of width and R of depth, consider the *pedagogical* example in Fig. 1, which depicts an idealised, closed unweighted network. This idealised ensemble has 6 nodes (N) and 12 flows (F), and therefore a width of $C (= F/N = 2)$ parallel pathways and a trophic depth of $R (= N/C = 3)$ levels. In this

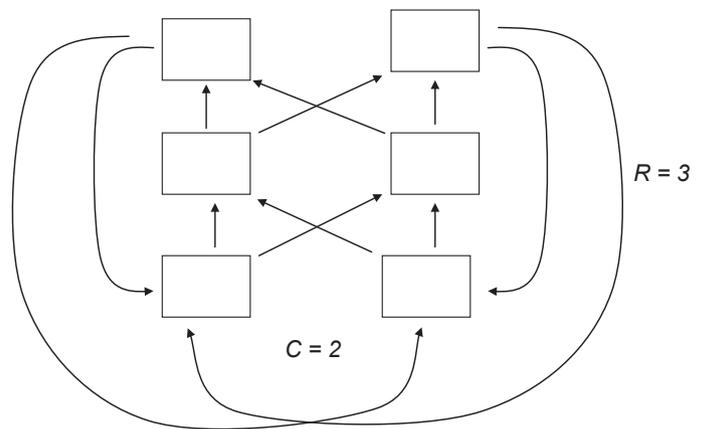


Figure 1 An idealised, closed flow network. There are three trophic levels (roles, R), with two nodes per level. A flow issues from every lower node to each node at the next higher level, and flows connect each top node to each bottom node. Connectivity (C) is 2. All flows are equal. The number of nodes N is RC , and the total number of flows F is NC .

example, each node is connected to all those at the next higher level by flows of a quantity (e.g. energy, mass), and there are return flows from each node in the highest trophic level to every node at the lowest level. For simplicity, all flows are assumed equal in magnitude. The upward flows might represent the flow of, say, nitrogen up a food chain, while the downward returns consist of the same element flowing from the top predator to the detritus pool at the bottom. C is the number of nodes at each trophic level, but since adjacent levels are fully connected, it is also the link-density (Pimm *et al.* 1991), or the average of the number of inputs or outputs per node. In general, nodes per trophic level and link-density are not equal, and we use C strictly to denote the latter (i.e. F/N). The quantity $R (= N/C)$ is the number of trophic levels for this network, or what, more generally, might be called the number of effective ‘system roles’ (Zorach & Ulanowicz 2003). R is a measure of how many distinct functions are present in the network. In this example, network roles can be identified with the separation into trophic levels, because within any level, all nodes are equivalent (i.e. any pair of them may be swapped without any change in topology or function). The total number of nodes N equals RC (in the example, 6), and the total number of flows F is $NC = RC^2$ (here $F = 12$).

Real networks are neither as simple nor as regular as this idealised example: flow magnitudes may vary greatly, as can the number of nodes at each level, and there can be complex flow patterns. Accounting for strong flow asymmetries and network heterogeneities should yield more robust quantitative measures of food web structure (Banašek-Richter *et al.* 2004). Bersier *et al.* (2002) made a general suggestion that one can identify continuous metrics that correspond to the discrete metrics of qualitative food web analyses. Along those lines Zorach & Ulanowicz (2003) set about to identify for quantitative flow webs a set of continuous metrics f , r , c and n that match one-for-one the integer values F , R , C and N , and that are interrelated in a parallel fashion (i.e. $n = rc$ and $f = nc = rc^2$). These corresponding metrics quantify the

effective number of flows, roles, link-density and nodes, respectively, for networks that may exhibit wide variations in flow magnitudes. An important requirement on any suggested formulae for f , r , c , and n is that, when they are applied to simplified, equally weighted and uniformly connected idealised networks (e.g. that shown in Fig. 1), the formula must generate the correct values of F , R , C and N . We will use the example of Fig. 1 to illustrate that this holds.

The measure for the effective number of flows, f , should reflect the fact that not all flows are equally weighted. In particular, the effective number of flows should correspond roughly to the number of large transfers. Here, a useful measure is analogous to a very familiar one used in ecology to estimate the effective number of *species*, taking into account variation in their abundance—namely, the Shannon diversity index, $H = -\sum_k p_k \ln(1/p_k)$, where p_k is the relative abundance of species k (density or other measure such as biomass or energy; the subscript k goes from 1 to S , where S is the number of species). The effective number of species is then $s = e^H$, which can be rewritten as $\prod_k (1/p_k)^{p_k}$.

This formula for the effective number of species thus is of the form

$$g = \prod_{k=1}^K G_k^{p_k} \quad (1)$$

which is a weighted geometric mean of G_k , with weights p_k . If the p_k are all equal ($1/K$) this equation gives the standard geometric mean. The total number of items is K , and G_k is a measure of a quantity of interest pertaining to item k ; the weighted geometric mean of G_k gives the effective value (g) of the quantity of interest as weighted over all items. For the effective number of species s , $G_k = 1/p_k$, which would be the number of species if the total abundance were partitioned among species into amounts all equal to the abundance of species k . The geometric mean of G_k is taken over all species after weighting according to each species' relative densities.

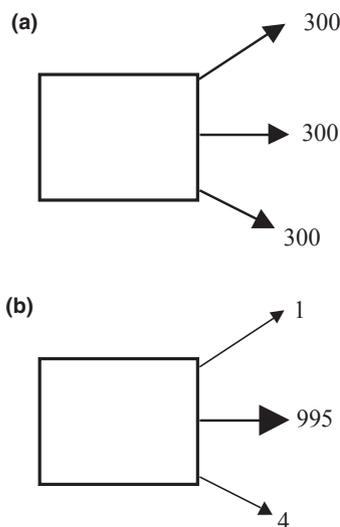


Figure 2 Two nodes, each with three outflow edges of (a) equal magnitude and (b) highly disparate magnitudes. The quantity f (effective number of flows, see text) varies from 3 in the homogeneous case (a) to ~ 1 in the highly skewed configuration (b).

Using a weighted geometric mean de-emphasises rare species (with high G_k) so that this diversity measure is affected more by common species. All of our effective network measures follow the form of eqn 1, where the index k will pertain to each flow. Because the convention is to denote flows by both origin, i , and destination, j , the single subscript k will be henceforth replaced by the indices (i, j) . Thus, G_{ij} will be the function of the flows that represents the network quantity of interest (e.g. link-density or number of roles), and the weightings p_{ij} will be the fraction of the total flow represented by the flow from node i to node j .

As a measure of the effective number of flows, f , the Shannon index can be applied to flows exactly as it is applied to species' abundances. Consider the partial network in Fig. 2a, with three equal flows, each accounting for 1/3 of the total. Destination j is left unspecified. Substituting the value 1/3 for each p_{ij} yields $H = \ln(3)$ and thus $f = e^H = 3$, identical to the number of arrows. Now consider the configuration in Fig. 2b. It also has three output flows, but the largest accounts for 99.5% of the total. H now equals 0.0340, and the effective number of flows is $f = e^H = 1.035$, reflecting the fact that the output is basically just the single large flow. In general, simple topological counts overestimate the number of effective link-ages between nodes.

Fig. 2 depicts only a single node of a flow network. To characterise a complete flow network and build towards our generalised network metrics, we start by labelling the N nodes from 1 to N . The magnitude of the flow from node i to j is denoted by T_{ij} . The total flow in the entire network is denoted $T_{..}$ (a dot in the place of a subscript indicates summation over that index, from 1 to N), which we use to normalise all flows. An appropriate estimator of a flow's importance (p_{ij}) is the fraction of the overall flow comprised by that flow, which is $t_{ij} = T_{ij}/T_{..}$. For the effective number of flows, as in the Shannon diversity index, G_{ij} is just the reciprocal of the weightings, or $1/t_{ij}$, and so the effective number of flows in the network becomes

$$f = \prod_{i,j} (1/t_{ij})^{t_{ij}}, \quad (2)$$

where the product in eqn 2 is over all combinations $i, j = 1, N$ for which $t_{ij} > 0$. To see that this give a sensible result, note that for the pedagogical example of Fig. 1, $t_{ij} = 1/12$ for all i, j , so $f = F = 12$.

To gauge link-density c , we first define the total outflow from node i as t_i (sum of t_{ij} over all j) and the total inflow to node j as $t_{.j}$ (sum of t_{ij} over all i). Link-density can be defined as either a measure of the average number of input flows per node, or the average number of output flows per node (or a measure that combines both). For outflows, a measure of the number of output links from node i is the its total outflow t_i , divided by an individual outflow t_{ij} . This quotient can be used as G_{ij} in eqn 1 to yield an effective value of link-density using all nodes and flows. Using the same logic, the appropriate function for G_{ij} for inflows becomes $t_{.j}/t_{ij}$. In general, these two estimates of G_{ij} are not equal, and so to account for both inputs and outputs, we suggest that one take the standard geometric mean of these two quantities (the square root of the

product). The appropriate G_{ij} for link-density we propose is thus $\sqrt{t_i t_j} / t_{ij}$, and our weighted measure of the link-density accordingly becomes

$$c = \prod_{i,j} \left(\frac{\sqrt{t_i t_j}}{t_{ij}} \right)^{t_{ij}} \quad (3)$$

Applying this metric to the pedagogical example of Fig. 1, note that $c = C = 2$.

With weighted metrics for flows and link-density now in hand, we can define the remaining metrics by analogy with their unweighted counterparts. In unweighted networks, $F = NC$ and $N = RC$, so we suggest that the effective number of nodes, n , is f/c , and the effective number of roles, r is n/c or f/c^2 . As a result,

$$r = \prod_{i,j} \left(\frac{t_{ij}}{t_i t_j} \right)^{t_{ij}} \quad (4)$$

Note that in the example of Fig. 1, these metrics match their intuitive, unweighted counterparts: $r = R = 3$ and $n = N = 6$.

It is useful to reflect on potential interpretations of the metric r . As mentioned above, the term ‘role’ is a measure of how many distinct functions (i.e. groups or clusters of nodes that mostly share nodes to which they are linked by input and output flows) are present in the network. In this sense, r measures the number of effective trophic levels in that ecosystem; it is also the average number of flows through which an aliquot of medium passes before leaving the system or being recycled. More accurately, the effective number of trophic levels should be $r - 1$, because non-living pools of energy or material play an identifiable role in any ecosystem, but the convention is to exclude such pools when counting trophic levels (Williams & Martinez 2004). In eqn 4, r is taken as the weighted mean of $G_{ij} = t_{ij}/(t_i t_j)$. If a unit of flow is chosen randomly, t_{ij} is the probability that it goes from node i to node j , t_i is the probability that it is in a flow out of node i , and t_j is the probability that it is in a flow into node j . The quantity G_{ij} is the ratio of the first of these probabilities – which is a joint probability, to the product of the other two (i.e. its marginal probabilities). If all flows were independent, G_{ij} would always be 1, making $r = 1$. In such a case, where a randomly chosen unit of flow came from provides no clue as to where it is flowing. At the other extreme, where a flow originates might fully determine its destination (e.g. because each node would have at most one input and one output), in which case $t_{ij} = t_i = t_j$, so that $r = f$. The measure r , therefore, gauges the overall departure of the system from independence among flows, or the amount of trophic structure inherent in the network.

The link-density in eqn 3 is high if each flow tends to be a small fraction of its source node’s output and recipient node’s input, which is the case if most nodes tend to have many inputs and outputs. Eqn 3 thus provides a measure of the average number of different pathways an aliquot of medium can take through the system.

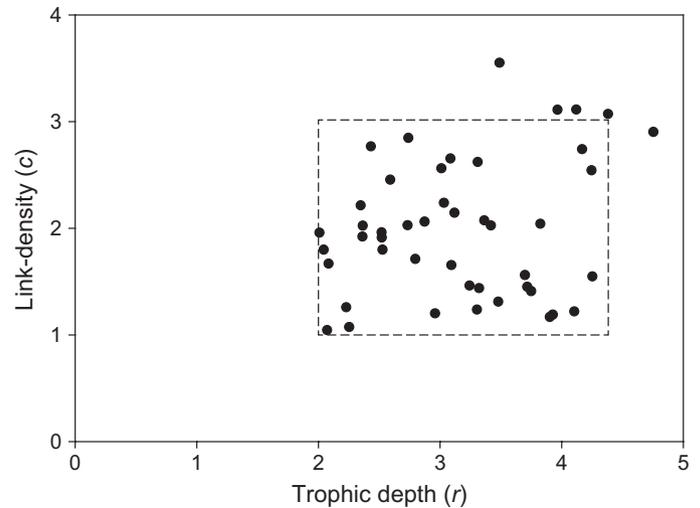


Figure 3 Effective trophic depths and link-densities of 46 ecosystem trophic networks. Dashed line refers to the limits of the ‘window of vitality’ as explained in the text.

Since $f = rc^2$, for networks with the same effective number of flows, a high r implies a low c and vice versa. Insofar as structure is quantified by r , the fraction of f attributed to organised structure can be defined as $a = \ln(r)/\ln(f)$, where $0 \leq a \leq 1$ for all real networks. When a is near zero, connections among nodes are nearly random (in the sense noted above that knowledge of where an input flow comes from gives no knowledge as to where it is going); as a approaches 1, the network resembles a set of closed, isolated cycles of same-magnitude flows.

Finally, we note that $r = f^a$, an expression that compactly relates the number of trophic levels to both the number of effective flows and to our scaled measure of organisation.

A CONSTRAINED ‘WINDOW OF VITALITY’

We have now developed a set of measures f , n , c and r (viz., the effective number of flows, effective number of nodes, effective link density, and effective trophic depth of a flow network) that take into account quantitative heterogeneities in flow magnitudes, and which generalise the integer indices F , N , C and R as obtained from box and arrow counts in connectivity webs. We have further shown how these measures are interrelated. As an illustration of the potential utility of these measures, we now employ them as phenomenological tools for characterising patterns in ecosystem networks. We will then suggest some directions of potential explanations for the patterns we observe.

The data on network flows comprise a collection of 46 quantified networks of trophic flows, estimated for a range of marine, estuarine, freshwater and terrestrial ecosystems (the networks are compiled and publicly accessible at <http://www.cbl.umces.edu/~ulan/ntwk/EcoLets.htm>). We begin by plotting c vs. r for these systems (Fig. 3). While r and c theoretically can assume any value in the positive quadrant, actual ecosystems appear to occupy only a small subspace of this quadrant (see also Ulanowicz 2002; Zorach & Ulanowicz 2003; Solé &

Valverde 2004). Roughly, most ecosystems in this sample have values of $r < 4.5$ and $c < 3.0$ (dashed line). Ulanowicz (1997a) called this region the ‘window of vitality’, and we will use this phrase to describe the observed bounds on ecosystem properties.

Explaining why real ecosystems are confined to such a small region of parameter space requires identifying factors that might contribute to upper and lower limits on r and c . The minimal values of c and r are easy to identify and explain. The lower limit on c should be unity, because $c < 1$ would imply that the corresponding network is not connected. A connected network has at least one pathway between every pair of nodes: $c < 1$ might arise if one pools data from spatially disjoint ecosystems. Similarly, one expects that $r \geq 2$, because all ecosystems contain at least one pair of ‘complementary coupled processes’, such as autotrophy-heterotrophy or oxidation–reduction (Fiscus 2001). These are absolute minima. As we shall see presently, the r and c for real networks might not approach these extremes.

Delimiting what sets upper bounds on link-density and trophic level is more challenging. Some insights come from general systems theory applied to ecological networks. The basic insight is that too high a proliferation of links can lead to instability. Regarding link-density, Kauffman (1991) observed that networks with fewer than two connections per node were almost always persistent, whereas those with more than three per node proved ephemeral. Pimm (1982); [p89] suggested a putative upper limit to stable networks of three links per node, and Wagensberg *et al.* (1990) cited the limit of 3 links per node as a ‘magic number’. May (1972) had provided a heuristic criterion for the stability of randomly assembled food webs, based on Wigner’s (1958) semicircle criterion for the stability of randomly assembled linear dynamical systems. Ulanowicz (2002) used this May–Wigner heuristic criterion as a dimensional template (independently of May’s dynamical assumptions) to formulate a phenomenological upper bound

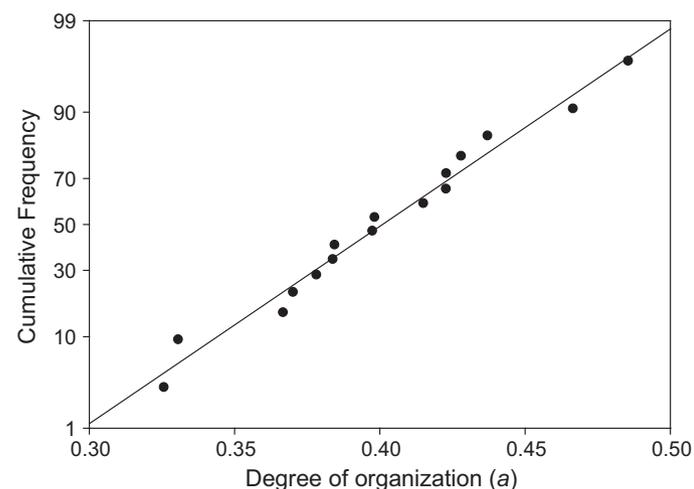


Figure 4 The cumulative distribution of the degrees of organisation (a) for the 16 ecosystem flow networks among the networks in Figure 3 with $N \geq 13$ compartments (using a scale for which a Gaussian distribution gives a straight line).

on c of $e^{(3/e)}$ (≈ 3) links per node. Higher values for link-density might require special structural attributes of webs, such as nestedness, or coupling between fast and slow components of ecosystems (McCann 2011). Allesina & Tang (2012) have demonstrated that with correlated interaction coefficients and a wealth of predator–prey interactions, the maximal c permitting ecosystem stability could exceed the above value. Our overall conclusion that the weighted index c should be low broadly matches the expectation that system persistence may depend upon many interactions being weak, rather than strong, as has been noted by McCann *et al.* (1998) and others.

THE LIMIT ON TROPHIC DEPTH

Only the right-hand side of the region of persistence remains to be elucidated—the upper limit on r —which caps the number of effective trophic levels and resembles a mean food chain length (Moore & de Ruiter 2012). As noted above, one rarely encounters individual species feeding on average well above trophic level 5, and the calculated r for observed networks usually falls below 5. Beyond these observations, what empirical evidence might help define the upper limit on r more closely?

It turns out that the degree of organisation, a , for the 46 networks exhibits a significant cluster around $a \approx 0.4$ (Ulanowicz 2009a). Robert Christian (personal communication) noticed that all outliers away from this cluster (nearly all in the direction of larger a) are very simplified networks with few components ($N < 13$). Furthermore, Bersier & Sugihara (1997) independently observed that communities with fewer than 12 members behaved qualitatively differently than more fully articulated ones. When networks with $N < 13$ are excluded, the clustering becomes more pronounced (see Fig. 4, where systems appear normally distributed within a modest range of a , from about 0.3 to 0.5).

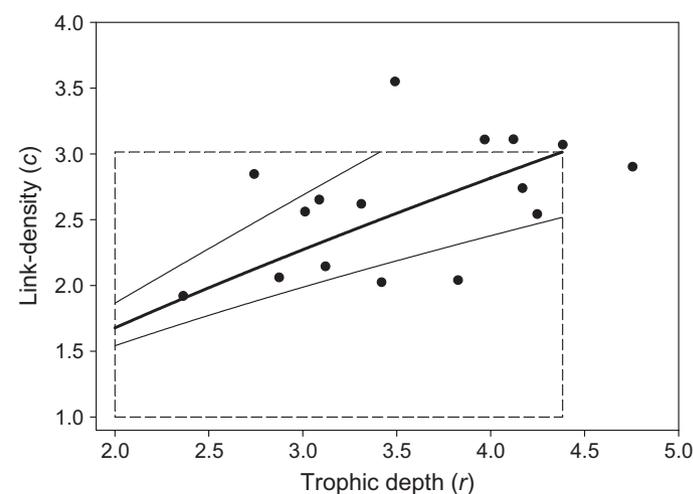


Figure 5 Link-density (c) vs. trophic depth (r) for 16 ecosystem trophic networks having $N \geq 13$. The bold solid curve indicates all networks with $a = 0.401$; the dashed box approximates the ‘window of vitality’. The lighter parallel curves indicate one standard deviation in a above and below the mean (0.36 and 0.44) and yield values for r_{\max} of 3.4 and 5.8 respectively.

Box A Linked Limits on r and c

It was observed in Fig. 4 that the value of a is roughly constant ($a \approx A = 0.4$) across a wide range of ecosystems. The degree of organisation, a , in its turn is defined in terms of r and c :

$$a = \frac{\ln(r)}{\ln(f)} = \frac{\ln(r)}{\ln(r) + 2\ln(c)}, \quad (\text{A1})$$

so that solving for c yields

$$c = r^{(1-a)/(2a)}. \quad (\text{A2})$$

Eqn A2 relates three fundamental attributes of an ecosystem network: link-density, effective trophic level and the overall degree of organisation in the network. So if there is rough constancy in the quantity a , there is an emergent relationship between r and c .

Eqn A2 shows that, given that a is assumed essentially be a constant (call it A), the quantity c increases monotonically with r , and whenever $1/3 < A < 1$, that rate of increase in c decreases with increasing r . Furthermore, any attractor point $a = A$ will be represented by a monotonic curve in the plane defined by possible combinations of r and c . (More generally, if persistent ecosystems match a range of values for a , then this would define a corresponding band of values for the interrelationships of r and c .) Thus, it is that the arc of eqn A2 as it traverses the window of vitality might be termed an attractor of ‘balanced development’ (Fig. 5). Presumably, sparser ecosystems (with fewer components, connections and trophic levels) would lie on the curve closer to the left end of the window, and the system would progress along the attractor curve as the system becomes more complex (both r and c increase), approaching the right end in the limit, which becomes the simultaneous limit to both network breadth and depth.

The average a for the 16 systems of Fig. 4 is $A = 0.401$. The exponent in eqn A2 thus becomes 0.75. In Fig. 5, the attractor line enters the window of vitality at the point $r = 2$ and $c = 1.68$ along the left boundary and intersects the upper limit on c ($c_\omega = 3.0$) at a corresponding value of r (call it $r_\omega = 4.38$), which represents the maximal number of roles feasible for persistent systems. Accordingly, the upper limit on trophic level would be about one less than this, or 3.4, a value that remains well below Pimm & Lawton’s (1977) ad-hoc upper limit of 5. If instead of the average a we use values one standard deviation above and below the mean for the networks shown in Fig. 4 (about 0.36 and 0.44), the maximal value of r (for $c \approx 3$) would range from about 3.4 and 5.8, the latter of which exceeds most observed food chain lengths.

We note that the clustering in Fig. 4 seems to be around a particular attractor point, call it $a = A$. By ‘attractor point’ we simply mean that for a given set X of possibilities for a variable x , one hypothesises that there are processes that tend to guide the system over time towards a smaller contained subset, Y . In the Discussion, we will examine some possible processes that could generate such an attractor, but for now we take the observation of bounded variation in a as an empirical observation, and draw consequences out of that observation.

In Box A, we argue that the clustering of a represents an empirical constraint between r and c , such that the upper bound on c ($c_\omega \approx 3$) implies as well an upper limit on r of $r_\omega \approx 4.38$, implying that the effective trophic levels of real ecosystems rarely, if ever, exceed about 3.4 transfers ($r_\omega - 1$).

The clustering of a similarly suggests a relationship between the minimum c and the minimum r . Given a minimum r of 2 and assuming that a is fixed at its mean value 0.401 (as in Box A) gives a minimum c of 1.68 (which is greater than the topological minimum of $c = 1$ for a connected graph). Therefore, it appears that link-densities in real ecosystems with at least a moderate number of compartments (i.e. ≥ 13) are rarely less than about 1.7, and for moderately diverse ecosystems we could tentatively raise the floor of the

‘window of vitality’ to this value, consistent with the points in Fig. 5.

Although numerous trophic pathways of considerable length (> 5) may be identified in individual trophic networks, our results indicate that there rarely are much more than 3–4 effective trophic roles in any ecosystem. The available data thus support the assertions of Hastings & Conrad (1979) and Rooney *et al.* (2006) that trophic cascade analysis based on three to four trophic levels usually suffices for ecosystem management.

LIMITS TO OVERALL ECOSYSTEM COMPLEXITY

The foregoing results confirm the common experience among system ecologists that by parsing ecosystems to finer and finer resolution (e.g. with each of thousands of biological species occupying its own node), one does not thereby increase the number of trophic roles—although the topological complexity of highly resolved ecosystem networks may increase appreciably, the weighted complexity does not keep pace. In practical terms, as one resolves the network into a larger number of components, the resulting configurations become ever sparser and remain dominated by a relatively few large exchanges.

Because the upper-right corner of the window of vitality represents the approximate bound on complexity that persis-

tent ecosystem networks appear to reveal, it deserves further consideration. One may designate this point as $\Omega = (r_{\omega}, c_{\omega})$. We recall that the effective number of (virtual) nodes is $n = cr$. It follows, therefore, that the maximum n is $n_{\omega} = c_{\omega}r_{\omega} = 13.23$. Similarly, one may calculate the corresponding maximum number of effective flows as $f_{\omega} = n_{\omega}c_{\omega} = 39.9$. In rough numbers, the most complex ecosystem networks in nature out of the set we have examined rarely have more than a dozen major players and some 40 dominant flows.

At first encounter, such low limits for n_{ω} and f_{ω} seem absurd. After all, local communities comprise many thousands of microbial and eukaryotic species, each in principle represented by its own node. But ecosystems tend to be dominated by only a few nodes. Borrett (2013), e.g. reported that 4 or fewer nodes accounted for over 50% of the throughflow in each of a collection of 45 trophic networks. That high-dimensional systems should be equivalent to ones having but few effective nodes and flows is indicative, we suggest, of the high degree of functional redundancy in ecosystem networks. It appears that ecosystems are governed at most by a dozen or so nodes and a score or two of individual transfers.

Several of the data points in Fig. 5 lie a bit outside the suggested limits. This may of course reflect the inherent noise of ecological data, arising in part from temporal variation in the exogenous environment, or from inherent stochasticities in population and community processes, or from variability in ecosystem structure itself. Finally, there is the measurement problem. Practitioners who empirically estimate ecosystem networks are usually pleased to obtain values for trophic flows that are within 25% of the actual values (and even the qualitative connectance webs may be incomplete, such that not all nodes and flows will be measured). Another reason is that some of the logic leading to the suggested limits may need to be modified. For instance, ecosystems, as noted above, may have special structural features that allow them to surpass the threshold on link-density (Allesina & Tang 2012), or species may have strong direct density dependence that can permit long food chains to persist stably (Sternier *et al.* 1997).

However, it is useful to take the patterns at face value and scrutinise the outliers for unusual features. The only ecosystem lying to the right of r_{ω} is the Charca de Maspalomas (Almunia *et al.* 1999). This system builds to an annual eutrophic catastrophe and recovers thereafter—a phenomenon the investigators termed ‘pulse eutrophication’. Usually disturbances are thought to constrain food chain length, but this system suggests that, at times, longer chains can be sustained in systems with high temporal variability. In some circumstances, resource pulses can permit species to persist in environments where otherwise they would go extinct (Holt 2008; Hastings 2012), and such mechanisms could potentially help sustain longer food chains.

The system with highest c is the St. Marks Estuary (Baird *et al.* 1998). None of the factors that contribute to c (eqn 3) for this system is unusually large, but the aggregate c of this habitat does significantly exceed those of the other 15 systems. Further inquiry reveals that Baird *et al.* had estimated separate spatially and temporally articulated networks for their

system, and these were then condensed into a single annual composite flow network that was used here. It appears that the system never exhibited redundancies in any of the separate networks that were comparable to those that appeared in the composite as the result of aggregation.

Our scrutiny of these two outliers suggests that the limits we have established might serve as useful diagnostic tools to highlight either interesting ecological problems or potential methodological issues. Further analytic developments of the network metrics we have presented here will need to encompass temporal and spatial heterogeneities, aggregation across scales, and the vicissitudes of sampling, and should be applied to a wide range of ecosystems from many different biomes. It also would be instructive to consider how these metrics might be systematically influenced by productivity (Arim *et al.* 2007), ecosystem size and stability (Sabo *et al.* 2010) and meta-community dynamics (Calcagno *et al.* 2011), and to assess as well the use of stable isotope techniques to characterise efficiently empirical estimates of r in ecosystem analyses (Hagy 2002; Vander Zanden & Fetzer 2007).

CLUSTERING OF THE DEGREE OF ORGANISATION, a

Our estimation of the maximum number of roles (*viz.*, effective trophic levels) depended on the observation of clustering in our measure of aggregate system organisation. Explanations in general for observations of an empirical pattern of clustering around a small number of values out of a larger array of potential values, for any particular system attribute, tend to follow three lines of thought:

- (1) There could be historical contingencies, making the clustering a sheer accident of how systems arose.
- (2) There could be external constraints (boundary conditions) that simply prevent a system from moving outside a given subdomain.
- (3) There can be processes that either move systems from extremes towards intermediate values, or eliminate systems with extreme values.

It is not clear to us what the first two of these might correspond to for ecosystems, so we focus on the third possibility. Consider a thought experiment: one imagines that initially a number of ecosystems are arrayed somewhat uniformly across the entire spectrum of values for the metric in question, and then seeks forces that trim the tails of this distribution. These tail-trimming forces could be internal or external. In the former, dynamical processes contained within each of the original systems may arise which push their states towards intermediate values. As an example of the latter, by analogy, in evolutionary biology, stabilising selection within a population culls extreme values of a trait, favouring intermediate values. The mechanics of such normalising selection are well understood (Bell 2008). Analogues of selection at the community and ecosystem level are much less well articulated, in part because evolutionary biology and ecosystem ecology have developed largely within separate conceptual domains (see, however, Wicken & Ulanowicz 1988; Loehle & Pechmann 1988; Holt 1994; Levin 1999), but also because many ecologists and evolutionary biologists remain uncomfortable invoking

ing analogues of selection at the community or ecosystem level (exceptions include DeAngelis *et al.* 1986; Wilson & Sober 1989; Swenson *et al.* 2000; Wright 2008.)

Nevertheless, a standard assumption in community ecology is that, during community assembly, some configurations of species interactions may prove infeasible (i.e. some of the set of species placed together inevitably face extinction), or are not likely to persist, even if feasible (e.g. unstable dynamics lead to such extreme fluctuations in abundance that extinctions occur). In either case, across an array of communities a kind of differential mortality eliminates configurations of species that are unstable and cannot co-exist locally. Ginzburg *et al.* (2010) have argued that (phenomenological) allometric relationships in life histories could likewise be the result of population stability thresholds. Even when a system is inherently persistent, it might exist in a spatial context of a multiplicity of other such systems, and the pattern of dominance by some systems over others could change across the landscape. In a meta-community context of recurrent colonisation and extinctions, communities that suffer catastrophic collapses are less likely to emit colonising propagules that become incorporated into new communities, and some alternative states can come to predominate over others, in effect via a higher scale competition among communities (Shurin *et al.* 2004).

Rather than pursue such mechanistically detailed scenarios, we turn instead to a phenomenological examination of some factors that could lead to clustering. In part, the clustering reflects the limits on r and c noted above. For example, when r is minimum (≈ 2) and c is maximum (≈ 3), the minimal value of a becomes 0.238. One notes, however, from the definition of a ($= \ln(r)/[\ln(r) + 2\ln(c)]$), that a draws near to one as c goes to 1 for *any* value of r . So what is preventing the quantity a from approaching 1?

We reason that at small values of a , the increase of organisation can become significant because of the almost countless possibilities for further organisation. Beyond the cluster, however, the options for further organisation decrease markedly, because the secondary and redundant transfers (which contribute mostly to c) wane. The system becomes 'brittle' and subject to catastrophe that would reduce a radically. We begin to discern that the cluster is the result of countervailing tendencies towards either disorganisation or organisation.

Regarding the first tendency, the second law of thermodynamics operates at all levels to decrease a . Moreover, the variety of perturbations that can reduce a are legion—fires, floods, drought, pollution, etc. So, it comes as no surprise that natural ecosystems have less organisation than might be logically possible.

Less obvious is why systems with low a would exhibit a strong inclination to increase in organisation, or be replaced by other systems with a higher value. In this regard, we suggest as a major player the phenomenon of 'centripetality' that arises out of any autocatalytic dynamic, including those found in community and ecosystem processes (Ulanowicz 1997b). Kauffman (1995) demonstrated how, with a sufficiently large collection of processes, there exists an overwhelming probability for autocatalytic sets of processes to appear spontaneously. Once an autocatalytic configuration has come into existence,

it will exert a selective pressure upon its constituent components and processes that will favour the import of ever more material and energy into its orbit (Ulanowicz 1997b). This tendency to pull ever more resources into autocatalytic structures is aptly described as 'centripetality'. Bertrand Russell (1960) called this same centripetal pull 'Chemical Imperialism', and he declared it to be the fundamental drive behind all of evolution.

Centripetality among autocatalytic configurations in otherwise disorganised (low a) systems would cause the catalytic structures to grow at the expense of non-participating processes (i.e. centripetality pulls resources away from non-participants). The growing prominence of the autocatalytic participants relative to other system elements contributes to an increase in the value of a (Ulanowicz 2009b). In fact, the closer a network is to $a = 0$, the larger becomes the proportion of candidate processes available to engender autocatalysis.

Unlike the action of the second law, however, the effect of centripetality is not uniform at all levels of a . At lower values of a , where autocatalytic cycles tend to be short, the entry of a new component into the cycle is likely to speed up the circulation. For example, the appearance of bacteria is virtually certain to speed up recycling between autotrophs and detritus. Likewise, the introduction of an herbivore increases recycling under certain conditions (Loreau 2010; p243). The case seems less clear for the enhancement of cycling by carnivores. Carnivorous plants are known to increase productivity and recycling in oligotrophic communities (Ulanowicz 1995b), but carnivores do not in general seem to augment recycling. We have uncovered only one example in which secondary carnivory magnifies recycling. Hilderbrand *et al.* (1999) describe how the contribution of brown bears (*Ursus arctos*) feeding on salmon enhances the cycling of nitrogen in a terrestrial ecosystem. It also might be noted that if top predators effectively limit the abundance or activity of herbivores, this could reduce the total consumption of plant production by herbivores, thereby shunting more primary production into detrital food chains, which can be relatively short.

The diminishing influence of new higher levels on matter and energy circulation surely reflects in part the fact that each transfer is accompanied by losses, which diminishes the strength of centripetality and works against the inclusion of yet another compartment into the cycle. This is a form of the classic assumption, noted above, that thermodynamics may constrain food chain length. Moreover, a long cycle may become vulnerable to the spontaneous appearance of shorter, very rapidly recycling circuits near its base. The accompanying centripetality of the newcomer would very rapidly bleed the longer cycle of its sustenance. Thus, beyond a certain point, progressively longer cycles become increasingly vulnerable to replacement by newly emergent shorter ones, as happens frequently in eutrophication (Ulanowicz 1986). That the point at which longer cycles become invulnerable might lie not much beyond length three accords with suggestions by Hastings & Conrad (1979) and Rooney *et al.* (2006) that concatenations of trophic exchanges much longer than three contribute little to the sustained functioning of ecosystems, and the observation by Williams & Martinez (2004) (using a

quite different approach) that mean flow-based trophic levels of species are < 3 , with maxima of about 4.5.

It is becoming clearer, we suggest, why trophic levels remain within bounds. As Pimm & Lawton (1977) surmised, the constraints are surely not entirely due to thermodynamic losses. We suggest that the topology of interacting trophic processes plays a decisive role, as does the centripetality generated by autocatalytic cycles. A fuller analysis of this hypothesis would require the articulation of detailed processes, which goes beyond the scope of what we have attempted to provide here.

MECHANISTIC THEORY VS. PHENOMENOLOGY

We have presented a set of interrelated metrics that permit one to characterise compactly major features of ecosystem flow networks, and shown that use of these metrics can reveal intriguing patterns in ecosystem organisation. We then presented some ideas about why these patterns are found, which although quantitative, are primarily phenomenological in nature, not mechanistic in detail. The conclusions drawn here rest ultimately upon two phenomenological observations. The first empirical formulation was inspired by work in population ecology, namely May's (1972) application of the Wigner semi-circle rule to develop a criterion for dynamical stability in randomly assembled networks. Ulanowicz (2002) used dimensional arguments (independent of dynamical theory) to create an analogous (phenomenological) index that conveniently delimited the stability of weighted digraphs.

The second observation is straightforwardly empirical: the degree of organisation (as measured by a) in known flow networks appears to cluster tightly around 40%. Such an attractor had not been anticipated, and its discovery provides future grist for the theoretical mill, including further exploration of autocatalysis (broadly conceived) as a generator of patterns in ecosystem structure (DeAngelis *et al.* 1986). We suggest that phenomenological observation both feeds and prunes theoretical constructs. Whole-system regularities alone, however, seldom provide satisfactory explanations to ecologists, who experience and try to explain nature first-hand at the level of the organism, and then build up to more complex ecosystems via population and community processes. Like the counter-vailing tendencies in a Hegelian dialectic, population biology and ecosystem phenomenology require one another to drive forward the science of ecology.

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AUTHOR CONTRIBUTIONS

RU designed the framework and wrote the initial drafts. RH provided narrative on mechanisms. MB extended the mathematical framework and provided pedagogical examples.

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