Least-inference methods for constructing networks of trophic flows

Robert E. Ulanowicz[a], *Ursula M. Scharler*[b,c,*]

[a] *University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, 1 Williams Street, Solomons, MD 20688-0038, USA*
[b] *School of Biological and Conservation Sciences, Howard College Campus, University of KwaZulu-Natal, George Campbell Building, 4041 Durban, South Africa*
[c] *Department of Aquatic Ecology and Water Quality Management (AEW), Wageningen University and Research Centre, Ritzema Bosweg 32-A, 6703 AZ Wageningen, The Netherlands*

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ABSTRACT

The construction of material and energy budgets within ecosystems has long been accomplished via manual calculation. Recently, optimization techniques have been adapted to automate the procedure, but these methods require assumptions that may not square with biological reality. Two algorithms are developed to construct ecosystem budgets under minimal inference. Although the methods do not recapitulate the model used to generate the input data, analysis reveals that the results do not differ statistically from networks that were constructed manually.

1. Introduction

The recent demand by management for mitigation strategies that encompass whole ecosystems has fueled a search for new quantitative whole-system methods. Heretofore, ecosystems science developed around various methods for modeling and simulating ecosystems processes; however, simulation modeling becomes fraught with problems associated with stability and prediction whenever multiple coupled processes are involved (Platt et al., 1981). Ecological network analysis (ENA) has evolved as a complementary alternative to simulation modeling for the study of individual ecosystem components, groups of components, or the quantification of attributes of the system as a whole (Wulff et al., 1989; Higashi and Burns, 1991; Fath and Patten, 1999; Ulanowicz, 2004; Jørgensen and Fath, 2006).

ENA requires that one first quantify the stock of each ecosystem component (or node) as well as the various exchanges among those nodes. That is, one must identify and quantify a network that answers the questions, "Who eats

* *Corresponding author at*: School of Biological and Conservation Sciences, Howard College Campus, University of KwaZulu-Natal, George Campbell Building, 4041 Durban, South Africa. Tel.: +27 31 2601605.
E-mail addresses: ulan@cbl.umces.edu (R.E. Ulanowicz), scharler@ukzn.ac.za (U.M. Scharler).

whom?" and "By how much?" Furthermore, most (but not all) ENA methods require the balance of medium around each node. The analysis packages themselves are often available online (Ulanowicz, 2002; Christensen and Pauly, 1992; NOAA, 2004; Allesina and Bondavalli, 2004; Fath and Borrett, 2006), so that the major task facing most ENA investigators is the accumulation of the necessary data.

Ideally, ENA should rely on field data to quantify each and every stock and transfer comprising the particular community under study. As this is a virtual impossibility, even for systems of modest complexity, the investigator is forced to create networks based on partial data. The rest of the values must be inferred via the assumption that, over a sufficient interval, outputs should balance inputs around each compartment (Polovina, 1985; Ulanowicz, 1989; Hart et al., 1997). Usually, the available information consists of: (1) the population densities expressed in terms of some chosen material element (e.g., carbon, nitrogen, phosphorus) or the amount of bound energy in each node; (2) information on the topology of transfers (who eats whom); and (3) some quantitative knowledge about the physiological requirements of each species. With such information, it usually becomes possible to create a fully balanced network.

One usually begins with the density of a population and some estimate of its consumption per unit density. The product of these yields the approximate demand that the compartment makes on all its possible sources. If, in addition, one also has information on the losses via respiration and excretion per unit of stock, then one may subtract those losses from the total demand to estimate the potential secondary production of that population, i.e., how much input that species is capable of providing to all its predators. Finally, one uses the known prey–predator connections (feeding topology) to match up the rates of availability (supplies) with the various demands.

This apportionment of sources to supplies is known as balancing the network, and it originally was accomplished either by trial and error or with the help of a spreadsheet. Today there are algorithms that can handle this task (Polovina, 1985; Christensen and Pauly, 1992; Vezina and Platt, 1988). Most of these methods are variational in nature. That is, some goal function, such as deviation from suggested parameters, is minimized subject to the constraints that inputs and outputs must balance around each node. There are, however, drawbacks to optimization techniques: (1) the object function is often chosen for mathematical convenience, rather than to satisfy biological reality, and the particular choice could bias the results arbitrarily. (2) Furthermore, solutions to optimization problems very often lie on a "vertex of the constraint polyhedron" (Cheung, 1985), which is a mathematician's way of saying that one or more of the known exchanges are forced to zero in the solution. (3) Finally, optimization routines often are computationally demanding.

Because (1) and (2) can introduce unwanted (and often unknown) bias into the final result, the question arises whether there exist methods that require as little mathematical inference as possible. By obviating the complexities associated with optimization techniques, it is possible that both fidelity to nature and computational efficiency could be improved. Two such potential methods are considered below,
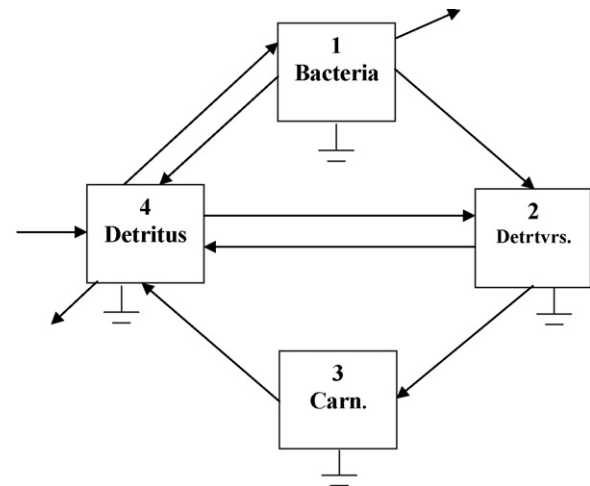

Fig. 1 – **The topology of the exchanges of energy within the Cone Spring Ecosystem (Tilly, 1968). Arrows not originating from a box represent exogenous inputs. Arrows not terminating in a box portray exogenous outputs. Ground symbols depict dissipations.**

but it is helpful first to describe a very simple network example with which to test and illustrate each method.

2. The Cone Spring example

One of the iconic examples from the early days of network analysis is the very simple five-component budget for energy flow in the ecosystem of Cone Spring, Iowa (Tilly, 1968). For illustrative purposes, only the four-component detritus sub-web need be considered. This consists of (1) bacteria, (2) detritivores (small animals that eat detritus and attached bacteria) and (3) carnivores (animals that prey on detritivores), as well as a pool of (4) non-living detritus that supports all of the foregoing. The topology of the transfers of energy among the four components is depicted in Fig. 1.

The stocks of bound energy and the associated physiological ratios for the detrital sub-graph are all given in Table 1.

There are 14 flows depicted in Fig. 1. Eleven of the ratios among these flows are specified in Table 1. In addition, the flows around each of the four components must balance (any three of which are linearly independent). Hence, the system is determinate (14 unknowns and 14 independent constraints)

	Stocks (U)	C/U	I/U	E/U	R/U
Table 1 – Stocks of energy (kcal m^{-2}) and physiological constants (y^{-1}) for the detrital-based community in the Cone Spring Ecosystem (Fig. 1)					
Bacteria	116.3	44.64	0.00	2.19	28.09
Detritivores	60.0	39.73	0.00	0.00	30.23
Carnivores	17.0	21.76	0.00	0.00	11.94
Detritus	357.4	32.13	26.63	2.41	8.70

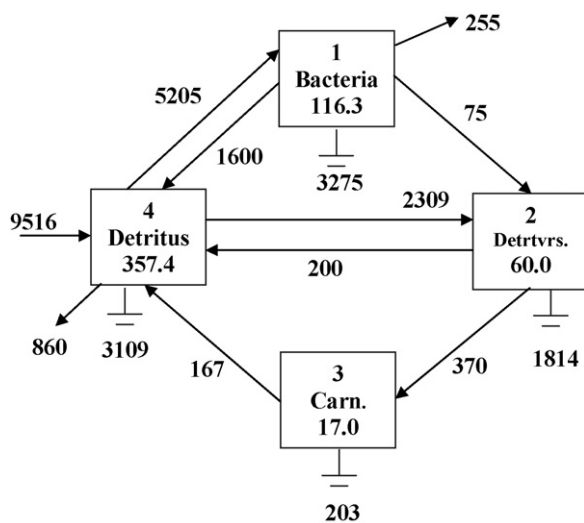U: Stock, C: consumption, I: external input, E: export, R: dissipation (respiration).

Fig. 2 – The magnitudes of the trophic exchanges of energy (kcal m^{-2} y^{-1}) in the Cone Spring Ecosystem (Tilly, 1968). The numbers inside each box represent the stocks of energy in kcal m^{-2}.

and may be solved exactly to yield the exchanges shown in Fig. 2.

It is convenient to use a determinate set of data as the benchmark with which to illustrate the balancing of the network, because then any discrepancies can be attributed exclusively to inaccuracies in the balancing algorithm and not to ambiguities in the flow structure or to defects in the original data.

It is always helpful to run an initial check on the overall balance of the system. That is, the external inputs should roughly balance the external outputs, $\sum_{i=1}^{n} I_i = \sum_{i=1}^{n} (E_i + R_i)$, where I_i is the external input to compartment i, E_i is the export from that compartment, and R_i is its rate of dissipation. Here the overall balance is perfect, but if imbalance should be severe (say, >10–20%), then it would behoove the investigator to recheck the data. The methods to be described will work, even when the overall imbalance is large, but results obviously will be more satisfactory if one starts with a system that is balanced overall.

Before implementing a compartmental balancing technique, it is necessary first to check the given data for consistency. One begins by summing up the overall internal demands, D, as

$$D = \sum_{i=1}^{n} (C_i - I_i),$$

where C_i is the consumption by compartment i, and I_i the external input to compartment i originating outside the system, e.g., migration, litter import, or energy from the sun. The accumulated available supplies, S, that constitute medium (e.g., carbon) that is available for internal consumption, are summed as

$$S = \sum_{i=1}^{n} (C_i - E_i - R_i),$$

Table 2 – Internal demands (D_j) and internal availabilities (S_i) (kcal m^{-2} y^{-1}) for each member of the detrital-based community in the Cone Spring Ecosystem

	D_j	(D_j/D)	S_i	(S_i/S)
Bacteria	5205.0	(0.52)	1675.0	(0.17)
Detritivores	2384.0	(0.24)	570.0	(0.06)
Carnivores	370.0	(0.04)	167.0	(0.02)
Detritus	1967.0	(0.20)	7514.0	(0.75)
Totals	9926.0	(1.00)	9926.0	(1.00)

Corresponding fractions of total demands [D_j/D] or availabilities [S_i/S] follow in parentheses.

where C_i is the consumption, R_i the respiration, and E_i the material export by compartment i to the outside of the system. With a system in overall balance, the aggregate demands equal the total available supplies. If the overall balance is only approximate, however, one takes the geometric mean between them, $G(= \sqrt{DS})$, to be the metric of total internal system activity.

It is also necessary to check whether sufficient potential supplies are available to meet the demand by each component. That is, for each node i, one checks whether

$$\sum_{j} (C_j - E_j - R_j) \geq (C_i - I_i), \tag{1}$$

where j is summed over all prey (sources) available to taxon i. If any taxon fails this test, then the data pertaining to it as predator and those associated with all its prey need to be re-examined. In the determinate case of Cone Spring, $D = G = S = 9926$ kcal m^{-2} y^{-1}, and all inequalities (1) are satisfied. For reference in what follows, Table 2 lists the internal demands and availabilities for each compartment of the Cone Spring network.

3. Joint apportionment (MATBLD)

Having outlined how to estimate the demands and availabilities proper to each compartment, attention now turns to possible least inference schemes for apportioning the availabilities among the demands according to the given topology. Perhaps the simplest scheme would be to assign availabilities according to respective demands. That is, the amount of the internal activity that flows from i to j might be jointly proportional to the product of the fraction of all supplies proper to prey i times the fraction of community demand made by predator j([D_j/D] × [S_i/S]). In fact, if $D = S = G$, and if each compartment contributes to all the others (i.e., all possible flows i, j are nonzero), then the suite of flows,

$$T_{ij} = \left(\frac{D_j}{D}\right)\left(\frac{S_j}{S}\right) G, \tag{2}$$

would exactly balance the network. Of course, ecosystems are virtually never so densely connected, so that many T_{ij} are observed to be zero. Whenever flows are missing, the sum of all the nonzero T_{ij} as calculated by (2) will fall short of the total
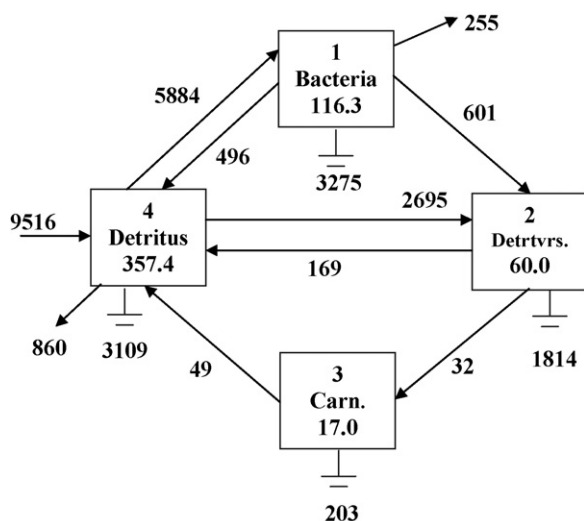
Fig. 3 – The Cone Spring detrital community as in Fig. 2, only with internal flows as estimated by joint distribution, MATBLD.

Fig. 4 – The Cone Spring detrital community of Fig. 3 after balancing by the method of Allesina and Bondavalli (2003).

estimated internal transfers. It becomes necessary to "inflate" them by the ratio of the original G (9926) to the summed T_{ij} (6583 in this instance) to yield an inflation factor (=1.508). Once the T_{ij} have been inflated by this ratio, the system can be balanced, and the ensuing G is 9920 kcal $m^{-2} y^{-1}$, which is about the same as the original the value (Fig. 3).

It is immediately apparent that these estimated flows do not balance around each compartment. (The surpluses in compartments 1 and 2 roughly balance the deficits in 3 and 4.) The entire system can be made to balance, however, using the dynamical assumption of linear donor-control (Ulanowicz, 1989). It is well known that a system wherein each flow out of an arbitrary compartment is proportional to the current stock of that compartment will remain inherently stable (positive semi-definite). That is, starting with a system of all positive flows, the dynamics will never drive any flow negative. Now, the balanced steady-state endpoint of the linear donor-control dynamics can be calculated via matrix operations. Allesina and Bondavalli (2003) noted how, when the direction of each flow is reversed, a balance also can be struck in the opposite direction. Importantly, they discovered that the statistical reliability of a balance consisting of the average of those cast in both directions is greater than can be achieved by equilibrating the system in either direction alone. Accordingly, Fig. 4 depicts the results of balancing the network using the method of Allesina and Bondavalli.

4. Construction by reverse mold-filling (MATLOD)

Comparison of Fig. 4 with Fig. 3 reveals that some constraints beyond simple joint dispersal are at work in the Cone Spring Ecosystem. But one is left to wonder whether joint apportionment is really the method of least inference? Here it is useful to recall that early networks were balanced by trial and error using spreadsheet calculations. Might this approach be mim-
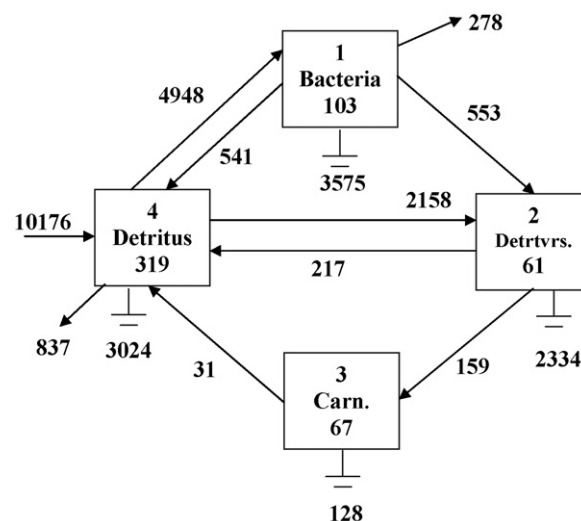
icked in algorithmic fashion? To do so, one begins with the assumption that no distinction whatsoever exists among all possible flows. That is, one begins to add some small uniform amount, δ, to all allowed flows in some arbitrary sequence. Each time δ is added to a flow, it is also subtracted from the availability of its donor and the demand by its recipient. This process is iterated until one of two conditions occurs for a particular flow:

(1) The addition of δ to that flow exhausts the availability of its donor, or
(2) The addition of δ to the flow in question satiates all remaining demand by the receptor.

Whenever either condition (1) or (2) is encountered, the particular flow in question is deleted from the sequence of flows during all subsequent iterations. Uniform additions to flows continue until no flows remain in the sequence. At that point, availabilities will have been matched with demands to the fullest extent possible under the uniform apportionment scheme. The availabilities and demands that remain at termination will represent the remaining imbalances among the compartments.

This "loading" method bears some resemblance to what happens when a fluid is poured into a concave mold. The initial fluid runs down to the deepest and narrowest segment of the mold. The fluid level continues to rise until the lip of that segment is reached, whereupon the additional fluid begins to spill out over a larger area of the mold. This continues until the mold is filled. Just prior to the endpoint the fluid is being applied over the whole area of the mold. The algorithm just described strongly resembles the mold-filling process in reverse.

Loading the Cone Spring topology matrix via the reverse mold-filling algorithm, results in the values shown in Fig. 5.

As happened with MATBLD, the direct output of MATLOD does not balance around each node. There is a significant deficit around the bacteria and a commensurate surplus for
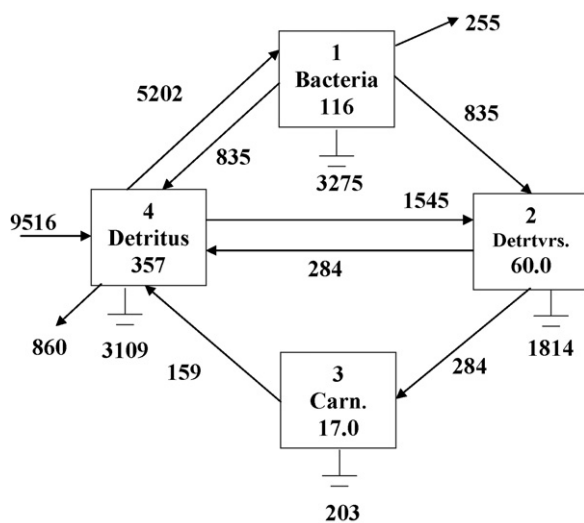
Fig. 5 – The Cone Spring detrital community (Fig. 2) that results when internal flows are estimated using the reverse mold-filling algorithm, MATLOD.
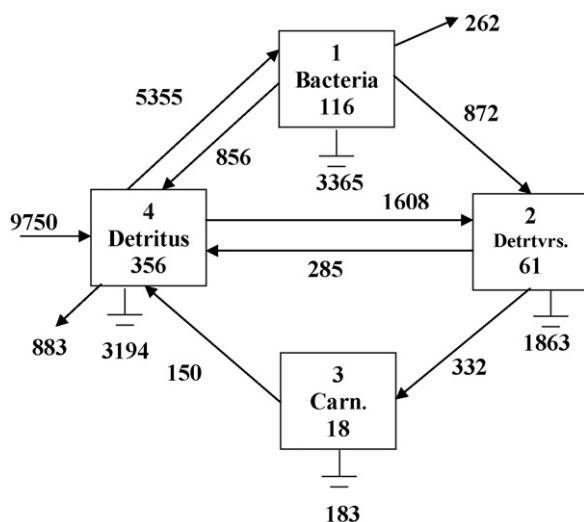

Fig. 6 – The Cone Spring detrital community created by MATLOD (Fig. 5) after application of the balancing method of Allesina and Bondavalli (2003).

the detritus. Again, the system must be brought into balanced by the Allesina–Bondavalli algorithm (Fig. 6).

5. Applications to diverse ecosystems

When the original estimates of flows in the Cone Spring detrital system (Fig. 2) are compared with the results generated by MATBLD and MATLOD (Figs. 4 and 6), it becomes obvious that constraints are at work in the actual system to apportion activities in ways that diverge from the patterns of simple joint or uniform distributions. Knowing such differences can assist an investigator in identifying and articulating the active agencies that influence trophic patterns in ecosystems (see Section 6 below).

The starting data are not precise, however. They themselves are (sometimes rough) estimates and usually bear the unavoidable systematic or arbitrary biases of those who put the network together. The larger question arises, therefore, as to whether the outputs from MATBLD and MATLOD are any poorer representations of reality than the constructs achieved through ad hoc or variational schemes? To explore this issue requires that one examine the differences between the networks that currently populate the literature and their counterparts as would result from the application of the algorithms proposed here.

Accordingly, the two methods described above were applied to 25 published networks of trophic exchanges that had been estimated either "by hand" or with the aid of optimization routines. That is, the availabilities (S_i) and demands (D_j) of each compartment in every chosen network were calculated using the reported topology of each network. Similarly, the physiological rate parameters (consumption, respiration, production, and egestion) were calculated from the given data. Doing so provided the data required to start both the joint and even fill methods for matching supplies with demand. The resulting flows were compared with those given in the original networks.

The flows between compartments generated by both MATBLD and MATLOD were correlated with the flows given in the literature. The intercept of the correlation was constrained to be zero, because the object of the exercise was to examine how well the correlations correspond to a 1:1 line. In general, the chosen networks were a mixture of many small flows and markedly fewer large ones. The likelihood therefore existed that the few large flows might dominate the correlations, resulting in unrealistically high R values (Table 3). Therefore, the data were log-transformed to examine the correlation in the absence of such bias.

By and large, the trophic exchanges generated by MATLOD resulted in better correlations with the published data, although both methods were rather effective in reproducing the original flows. Networks consisting of a comparatively high number of exchanges all correlated very well. Only 4 networks generated using MATBLD and 2 using MATLOD resulted in Rs smaller than 0.8. Both methods reproduced larger transfers better than smaller flows.

Both MATBLD and MATLOD balance the flows after generating them, so that inflows equal outflows for each compartment. The balancing routine changes the flows to some extent in order to achieve balancing (see Allesina and Bondavalli, 2003). To test whether the correlation results were in part due to the balancing of the networks, the original published flow values were correlated to unbalanced flows generated by MATBLD and MATLOD. The correlation coefficients showed hardly any change for most flows, especially for those flows generated by MATLOD (Table 3). Unbalanced MATLOD generated flows actually showed higher overall correlation coefficients with original flows than did balanced MATLOD generated flows. The correlation coefficients of unbalanced MATBLD generated flows and original (=untransformed) published flows were in general slightly lower compared to balanced MATBLD generated flows (Table 3).

A t-test was performed pairing the untransformed published trophic exchanges with the corresponding flows

Table 3 – Simple linear correlations of published trophic transfers with those generated by MATBLD or MATLOD										
Ecosystem	Published vs. balanced MATBLD		Published vs. balanced MATLOD		Published vs. unbalanced MATBLD		Published vs. unbalanced MATLOD		n	References
Name (#compartments)	Original	log	Original	log	Original	log	Original	log		
	R	R	R	R	R	R	R	R		
Kromme estuary, South Africa (16)	0.98	0.71	0.99	0.88	0.97	0.68	0.99	0.94	44	Baird and Ulanowicz (1993)
Kromme estuary, South Africa (25)	0.99	0.73	0.98	0.74	0.98	0.71	0.98	0.75	98	Scharler and Baird (2005)
Swartkops estuary, South Africa (25)	1.00	0.79	0.99	0.78	0.99	0.77	0.99	0.78	104	Scharler and Baird (2005)
Sundays estuary, South Africa (25)	0.99	0.86	0.98	0.85	0.98	0.84	0.98	0.85	99	Scharler and Baird (2005)
Crystal River Creek, USA (21)	1.00	0.85	1.00	0.92	0.97	0.82	1.00	0.93	82	Homer and Kemp (unpublished data)
Chesapeake Bay, USA (15)	0.98	0.87	0.99	0.91	0.96	0.92	0.99	0.95	47	Baird et al. (1991)
Chesapeake Bay, USA (36)	0.96	0.93	0.99	0.95	0.92	0.94	0.99	0.99	122	Baird and Ulanowicz (1989)
Lower Chesapeake Bay, USA (34)	0.96	0.91	0.98	0.94	0.87	0.98	0.98	0.99	115	Hagy (2002)
Middle Chesapeake Bay, USA (34)	0.93	0.89	0.97	0.95	0.83	0.95	0.96	0.99	149	Hagy (2002)
Upper Chesapeake Bay, USA (34)	0.89	0.83	0.94	0.86	0.79	0.95	0.94	0.98	158	Hagy (2002)
Somme Estuary, France (9)	0.94	0.9	0.91	0.87	0.95	0.91	0.94	0.92	24	Rybarczyk et al. (2003)
Dublin Bay, Ireland (7)	0.96	0.88	0.99	0.91	0.97	0.88	0.99	0.91	12	Wilson and Parkes (1998)
Dublin Bay, Ireland (15)	1.00	0.86	0.99	0.93	1.00	0.98	0.99	0.98	31	Foley (unpublished data)
Narragansett Bay, USA (32)	0.96	0.88	0.99	0.96	0.96	0.85	0.99	0.99	158	Monaco (1995)
St. Marks estuary, USA (51)	0.95	0.85	0.98	0.91	0.82	0.90	0.98	0.93	270	Baird et al. (1998)
Maspalomas lagoon, Spain (21)	0.86	0.69	0.91	0.80	0.75	0.99	0.93	1.00	55	Almunia et al. (1999)
Mondego estuary, Portugal (43)	0.99	0.91	1.00	0.84	0.99	0.96	1.00	0.96	348	Patrício et al. (2004)
Everglades Graminoids dry, USA (66)	1.00	0.91	0.99	0.98	0.98	0.97	0.99	0.97	793	Ulanowicz et al. (2000)
Everglades Graminoids wet, USA (66)	0.99	0.93	0.97	0.91	0.98	0.97	0.97	0.97	793	Ulanowicz et al. (2000)
Florida Bay dry, USA (125)	0.96	0.88	0.99	0.90	0.82	0.98	0.99	0.98	1969	Ulanowicz et al. (1998)
Florida Bay wet, USA (125)	0.94	0.88	0.99	0.90	0.80	0.98	0.99	0.98	1938	Ulanowicz et al. (1998)
Cypress Wetlands dry, FL, USA (68)	0.94	0.89	0.94	0.89	0.89	0.97	0.94	0.97	554	Ulanowicz et al. (1997)
Cypress Wetlands wet, FL, USA (68)	0.95	0.92	0.98	0.94	0.89	0.98	0.98	0.98	545	Ulanowicz et al. (1997)
Mangrove estuary dry, FL, USA (94)	0.96	0.85	0.98	0.89	0.90	0.98	0.98	0.99	1339	Ulanowicz et al. (1999)
Mangrove estuary wet, FL, USA (94)	0.96	0.86	0.98	0.90	0.90	0.98	0.98	0.99	1340	Ulanowicz et al. (1999)

Original: Untransformed data; log: log-transformed data; n: number of transfers; intercept = 0.

Ecosystem	Published vs. balanced MATBLD			Published vs. balanced MATLOD		
Name (#compartments)	t	d.f.	p	t	d.f.	p
Kromme estuary, South Africa (16)	−0.548	43	0.59	0.095	43	0.93
Kromme estuary, South Africa (25)	0.104	97	0.92	0.367	97	0.72
Swartkops estuary, South Africa (25)	0.626	103	0.52	0.448	103	0.66
Sundays estuary, South Africa (25)	0.345	98	0.73	0.493	98	0.62
Crystal River Creek, Control, USA (21)	0.479	81	0.63	0.409	81	0.68
Chesapeake Bay, USA (15)	0.658	46	0.51	−0.194	46	0.85
Chesapeake Bay, USA (36)	−0.101	121	0.92	−0.093	121	0.93
Lower Chesapeake Bay, USA (34)	−0.206	114	0.84	−0.259	144	0.80
Middle Chesapeake Bay, USA (34)	−0.409	148	0.68	−0.618	148	0.54
Upper Chesapeake Bay, USA (34)	0.196	157	0.85	0.255	157	0.80
Somme Estuary, France (9)	0.873	23	0.39	0.524	23	0.61
Dublin Bay 7 UB	−0.248	11	0.81	−0.082	11	0.94
Dublin Bay, Ireland (7)	−0.02	11	0.98	0.009	11	0.99
Dublin Bay 15 UB	−0.219	30	0.83	−0.192	30	0.85
Dublin Bay, Ireland (15)	−0.073	30	0.94	−0.073	30	0.94
Narragansett Bay, USA (32)	0.178	157	0.86	0.089	157	0.93
St. Marks estuary, USA (51)	0.385	269	0.70	0.007	157	0.99
Maspalomas coastal lagoon, Spain (21)	0.688	54	0.49	0.56	54	0.58
Mondego estuary, Portugal (43)	1.094	347	0.28	0.713	347	0.48
Everglades Graminoids, dry season, USA (66)	−0.082	792	0.94	−0.092	792	0.93
Everglades Graminoids, wet season, USA (66)	0.042	792	0.97	−0.043	792	0.97
Florida Bay, dry season, USA (125)	1.584	1968	0.11	0.267	1968	0.79
Florida Bay, wet season, USA (125)	1.103	1937	0.27	0.261	1937	0.79
Cypress Wetlands, dry season, FL, USA (68)	−0.079	553	0.94	−0.014	553	0.99
Cypress Wetlands, wet season, FL, USA (68)	0.153	544	0.88	0.138	544	0.89
Mangrove estuary, dry season, FL, USA (94)	−0.356	1338	0.72	0.003	1338	1.00
Mangrove estuary, wet season, FL, USA (94)	−0.352	1339	0.73	0.061	1339	0.95

Table 4 – Paired t-test on untransformed published flows and their counterparts generated by MATBLD and MATLOD

generated by MATBLD and MATLOD. The comparison revealed no statistically significant differences (Table 4). Hence, it can be concluded that both methods work at least as well at matching supplies and demands as do the conventional ad hoc or variational methods.

6.   Discussion and conclusions

Comparison of the network generated by MATBLD (Fig. 4) with the original flows (Fig. 2) reveals some significant differences. Most notably, the throughput of carnivores (3) has decreased by almost 50%, whereas its stock has almost quadrupled. The retention time by the carnivores has thus lengthened drastically (from 16 days to 22 weeks). The detritivores now process far more via the bacteria, which for their part recycle less directly back to the detrital pool.

The network constructed using the reverse mold-filling algorithm (Fig. 6) likewise differs from the original (Fig. 2). In particular, one notes on Fig. 5 the equiponderance of flows from the bacteria to the detritivores and detritus (835 kcal m^{-2} y^{-1}), as well as those from the detritivores to the carnivores and detritus (284 kcal m^{-2} y^{-1}). These uniformities presumably result because the availabilities of the donors involved all become exhausted at the same point in the algorithm. As with the joint apportionment, reverse mold-filling shunts more energy from bacteria to the detritivores and recycles less from the bacteria back to the detritus than occurred in the original network. Unlike the joint distribution algorithm, the mold-filling method did not dilate

the retention time of the carnivores to an unusual extent (20 days).

Neither method of construction recapitulated the small flow from bacteria to detritivores present in the original system (Fig. 2). Presumably, this constriction in the actual ecosystem is the result of constraints particular either to this example or to this biotic process. The mold-filling, as might have been expected, tended to even out flows over the suite of internal transfers, whereas the joint apportionment generated more disparities in the pattern of assignations. Unfortunately, the more heterogeneous latter pattern did not compare well to the original system.

Such discrepancies notwithstanding, the flows generated by the two proposed algorithms compared well with the original (published) flows. Because the published networks also reflect explicit and tacit approximations, it becomes difficult to say which of the two algorithms generates networks closer to reality. Suffice it to conclude that the methods in both MATLOD and MATBLD compare favorably with estimation techniques now commonly in use.

It may be possible to shorten the computational time required by the reverse mold-filling scheme by conducting a conditional search between the remaining availabilities and demands to locate exactly which constraint will next be satisfied and by which amount. All flows could then be adjusted simultaneously by that quantity. The conditional search could then be iterated until no possible combinations remain to be satisfied. Such an alternative algorithm will be explored under future work. The assumption made under both MATBLD and MATLOD – that all biomass in the system is

available as food for consumers – also bears further examination. As currently implemented, the algorithms disregard any strategies on the part of prey and plants to avoid being consumed. Therefore, adding natural mortality rates to the starting system information might improve the estimation schemes.

Although the suggested algorithms did not reproduce all flows in the Cone Spring test network well, several did match closely. The attempts to recapitulate a collection of networks that had been constructed 'by hand' generally produced good agreement. It should be stressed once again that the two methods employed here minimize the suppositions (explicit or tacit) usually made in constructing networks. They produce results that are as "untouched by human hands" as possible. The facts that they are also simple and easy to use should go a long way towards facilitating the construction of additional quantitative trophic networks and thereby make the network approach more attractive to use and easier to implement by whole-system ecologists.

The software to calculate trophic exchanges with either the MATBLD or MATLOD method can be requested from the authors.

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