



HAL
open science

ANALYSIS OF ECOLOGICAL NETWORKS: LINEAR INVERSE MODELING AND INFORMATION THEORY TOOLS

Valérie Girardin, Théo Grente, Nathalie Niquil, Philippe Regnault

► **To cite this version:**

Valérie Girardin, Théo Grente, Nathalie Niquil, Philippe Regnault. ANALYSIS OF ECOLOGICAL NETWORKS: LINEAR INVERSE MODELING AND INFORMATION THEORY TOOLS. International Workshop on Bayesian Inference and Maximum Entropy Methods in Science and Engineering, Jul 2023, Ghent, Belgium. 10.3390/psf2023009024 . hal-04801116

HAL Id: hal-04801116

<https://hal.science/hal-04801116v1>

Submitted on 25 Nov 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

ANALYSIS OF ECOLOGICAL NETWORKS: LINEAR INVERSE MODELING AND INFORMATION THEORY TOOLS

Valérie Girardin ¹, Théo Grente ^{1,2,*}, Nathalie Niquil ³ and Philippe Regnault ⁴

¹ Laboratoire de Mathématiques Nicolas Oresme, CNRS 6139, Normandie Université, UNICAEN

² France Énergies Marines

³ Laboratoire BOREA MNHN, CNRS 7208, IRD 207, UNICAEN

⁴ Laboratoire de Mathématiques de Reims, CNRS 9008, Université de Reims Champagne Ardenne,

* Correspondence: theo.grente@france-energies-marines.org

Abstract: In marine ecology, the most studied interactions are trophic, in networks called food webs. Trophic modeling is mainly based on weighted networks, where each weighted edge corresponds to a flow of organic matter between two trophic compartments, containing individuals of similar feeding behaviors and metabolisms, and with the same predators.

To take into account the unknown flow values within food webs, a class of methods called Linear Inverse Modeling has been developed. The total of linear constraints, equations and inequations, defines a multidimensional convex bounded polyhedron, called a polytope, within which lie all realistic solutions to the problem. To describe this polytope, a possible method is to calculate a representative sample of solutions by using the Monte Carlo Markov Chain approach.

In order to extract a unique solution from the simulated sample, several goal (cost) functions –also called Ecological Network Analysis indices– have been introduced in the literature as criteria of fitness to the ecosystems. These tools are all related to information theory. Here are introduced new functions that potentially provide a better fit of the estimated model to the ecosystem.

Keywords: Divergence; Entropy; Linear inverse modeling; Trophic systems

1. Introduction

The description of ecosystems is often based on networks of interactions, of different types. For terrestrial ecosystems, recent developments concern different types of interactions, sometimes gathered into a common model called multiplex [11]. In marine ecology, the most studied interactions are trophic, i.e. interactions between predators. These highly complex food webs have been described by numerous models widely used to describe the impact of human activities on marine ecosystems; see [1] and [13]. They are also important tools for the sustainable management of marine and coastal environments [19].

There are many ways to model food webs. Flows from preys to predators can be represented by non-quantified interactions and then the model is a graph (web) with vertices (the species) and edges (the interactions). Trophic modeling for ecosystem-based management of fisheries and other management questions is mainly based on weighted networks; see for example the Ecopath-Ecosim-Ecospace model [5]. Each link corresponds to a flow of organic matter between two trophic compartments, collecting individuals of similar feeding behaviors and metabolisms, and with the same predators.

In ecology, field studies are often associated to laboratory experiments to estimate some flows within food webs, and many flow values remain unknown, which the Linear Inverse Modeling (LIM) takes into account; see [22]. LIM relies on the principle of steady state for the biomass of all compartments, i.e., the sum of the inflows and outflows through the components of the system equals the rate of change in their standing stocks, most often considered negligible or null. This yields a set of linear equations, the Mass Balance

Citation: Girardin, V.; Grente, T.; Niquil, N.; Regnault, P. Analysis of ecological networks: linear inverse modeling and information theory tools. *Proceedings* **2023**, *1*, 0. <https://doi.org/>

Published:

Copyright: © 2024 by the authors. Submitted to *Proceedings* for possible open access publication under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

Equations (MBE), describing the steady state or mass balance. Then, constraints are added from field measurements of mass transfers like local estimations of primary production, respiration or diet contents, etc.. Additional constraints come from experiments or study of other ecosystems. All these constraints constitute a set of linear inequalities that impose linear combinations of flows to be between certain values. The total of MBE and inequalities defines a bounded multidimensional polyhedron, called a polytope, within which lie all realistic solutions to the problem.

A first idea to describe the polytope was to select a single solution inside this space of possible solutions, assuming a least square of the flows; see [31]. Then, methods were developed to describe the solution space by calculating a representative sample of all possible solutions by the Monte Carlo approach, see [16], and more efficiently the Monte Carlo Markov Chain (MCMC) approach, see [17] and [27]. Further, Linear Inverse Modeling Monte Carlo Markov Chain (LIM-MCMC) methods involve mass balanced models (the biomass of each species is assumed constant) that consider the uncertainty in the estimations and link them to the variability of the living; see [22,27]. As such, a range of possible results is provided, that makes LIM-MCMC advantageous by allowing to include uncertainties in the data; see [12].

Still, the question remains to extract a unique solution from this simulated sample. In [3], we proposed a numerical optimization of some pertinent goal functions that directly yields a unique functioning point of the ecosystem, with a low computing time. This straightforward approach allowed us to infer properties on the stability of the selected state, and hence on the evolution of the ecosystem. Precisely, the assumption is that the biomasses are the stationary state of a dynamical system determined by the constraints on the flows. Determining the stability of this fixed point informs on how the biomasses will vary. In this sense, this approach is data-driven by the information on both the biomasses and the biological constraints.

Such an optimization may also be inferred in a probabilistic framework, where the flows are all seen as random variables. MCMC thus amounts to simulating samples drawn from the probability density functions (pdfs) of the flows, while the optimization can be processed in the space of pdfs satisfying the biological constraints.

In ecology, Ecological Network Analysis (ENA) indices, and have been introduced in the literature as criteria of fitness to the ecosystems; see [3,15,17,29]. They are all related to Shannon information theory. Some are based on Shannon entropy, while others are based on Kullback-Leibler divergence [18] or Shannon mutual information. In this paper, we present several of these classical goal (cost) functions. Then we consider goal functions that take into account reference distributions that may not belong to the polytope but are of interest, for instance resulting from previous studies of the same ecosystem. We also consider goal functions based on Rényi entropy and divergence, that may fit better to particular food systems by adjusting the associated parameter. Their potential optimization opens the way to a better fit of the chosen unique solution among the MCMC sample.

2. The constraints, the polytope of solutions, and the probabilistic framework

2.1. The constraints

We will denote by V the set of all vertices of the trophic network (directed graph), and E is the set of all oriented edges – denoted by ij when going from vertex i to vertex j , with $|E| = n$.

In many situations, all biomasses B_i of the species can be measured with accuracy. On the other hand, the flows F_{ij} between the species (or compartments) are much more difficult to evaluate. Therefore, we will adopt here the standard viewpoint that the biomasses are given and the flows between nodes are unknown.

Mathematically, the flow is a vector $F = (F_{ij})_{ij \in E}$ of dimension $n = |E|$ with non negative components - also called flows, satisfying Kirchoff law on all vertices,

$$\sum_{j \in N^+(i)} F_{ij} - \sum_{j \in N^-(i)} F_{ji} = 0, \quad i \in V, \quad (1)$$

where the successors and predecessors of a vertex i are $N^+(i) = \{j \in V : ij \in E\}$ and $N^-(i) = \{j \in V : ji \in E\}$.

The flows F_{ij} satisfy biological constraints. For example, a fish cannot eat more than a certain percentage of its biomass. These constraints are numerous thanks to the important knowledge that has been acquired over the years on the functioning of species ecosystems and can be summarized as a system of linear equations and inequations over the flux space.

2.2. The polytope of solutions

The set \mathcal{S} of solutions F to the constraints system is a convex subset of \mathbb{R}^n , where n is the number of edges of the graph. Precisely, for any such ecosystem,

$$\mathcal{S} = \{F = (F_{ij})_{ij \in E} \in \mathbb{R}^n : F_{ij} \geq 0, AF = b, GF \leq h\}, \quad (2)$$

where A and G are matrices of sizes $m \times n$ and $k \times n$ and b and h vectors of sizes m and k , where m and k are, respectively, the number of equality and inequality constraints (with $m < n$ so that the system $AF = b$ is under-determined).

The defined domain is the intersection of hyperplanes and half-spaces and hence is a convex polyhedron. In addition, biological constraints encompass bounds on flows, so \mathcal{S} is bounded. The same is true for most alike ecosystems. Such bounded polyhedrons are called polytopes. Apart from the MBE which involve many flows in the same equation, most constraints involve a small number of flows. Therefore matrices A and G are mainly composed of 0 and a few 1.

2.3. The probabilistic framework

The problem can also be presented in terms of pdfs, or proportions. Let $f_{ij} = F_{ij}/F_{..}$ denote the proportion of flows from vertex (i.e., compartment) i to vertex j with respect to the total flow in the system, where $F_{..} = \sum_{ij \in E} F_{ij}$. The marginal distributions $(f_{i.})_{i \in V}$ and $(f_{.j})_{j \in V}$, where $f_{i.} = \sum_{j \in N^+(i)} f_{ij}$ and $f_{.j} = \sum_{i \in N^-(j)} f_{ij}$ represent the proportions of, respectively, outflows and inflows of trophic compartments. The polytope of admissible flows defined by (2) is identified to

$$\mathcal{S} = \{f = (f_{ij})_{ij \in E} \in \mathbb{R}^n : 0 \leq f_{ij} \leq 1, Af = a, Gf \leq g\}, \quad (3)$$

where $a = b/F_{..}$ and $g = h/F_{..}$.

Actually, \mathcal{S} can be considered, and hence MCMC applied, in a smaller space. Let d be the rank of A , that is the dimension of the subspace of \mathbb{R}^n defined by the system $Af = b$. One way to present this is to write $f = f_p + \tilde{A}x$ where f_p is a particular solution in \mathcal{S} , and \tilde{A} is the orthonormal matrix obtained from A , e.g., through the well-known QR-decomposition. Indeed in this subspace, only inequality constraints remain, say $\tilde{G}x \leq \tilde{h}$ with $\tilde{G} = G\tilde{A}$ and $\tilde{h} = Gf_p - h$, that define the volume delimited by the intersection of hyperplanes. MCMC methods are then applied to the latter system, that is in a smaller space.

3. The Goal Functions

In ecological studies, goal functions appear either as indices of the behavior of the system, or as a means of comparison between estimated solutions. Actually, they are potential tools for determining one solution from the MCMC numerous simulated ones.

Many goal functions can be considered in relation to ecosystems. They are either statistical tools, information theory quantities, or purely ecological indexes. The most classical are the mean, the quadratic energy, and the so-called ENA, all quantities derived from entropy. An important characteristics is whether the goal function includes information from the constraints or not. Further, only convex (or concave) functions yield a unique optimum corresponding to a unique functioning state of the system.

The natural setting is to give all these functions in terms of the pdfs f . Indeed, the advantage of considering pdfs for ENA indices, computed in different situations, is that

different ecosystems can be compared. This makes it possible to compare different stations or different time periods. For example, [20] compare seven spatial sub-sections of the Seine estuary at two time periods; they were thus able to describe the change in the functioning of the estuary's food web, linked to the construction of the Le Havre port extension called Port2000, but also to the change in the precipitation regime that occurred over the same period. Such comparisons are essential in the search for indicators of marine ecosystems health.

3.1. Classical ENA

The most usual function is the empirical mean of all flux,

$$E(f) = \sum_{ij \in E} f_{ij}. \quad (4)$$

The quadratic energy, giving rise to the least squares method, is also classical, with

$$Q(f) = \sum_{ij \in E} f_{ij}^2. \quad (5)$$

Various functions involving the concept of entropy of distributions have been considered in the literature on ecosystems, under various specific names. See [4] and the references therein for a synthesis of these Shannon entropic indices, and [6] for details and more on information theory tools. Shannon's definition of entropy \mathbb{S} gave birth to information theory; see [26] and [6]. It was introduced in the field of ecological systems by [21], through the so-called Mc Arthur index C ,

$$C(f) = \mathbb{S}(f) \quad (6)$$

$$= - \sum_{ij \in E} f_{ij} \log(f_{ij}) = - \sum_{ij \in E} \frac{F_{ij}}{F_{..}} \log\left(\frac{F_{ij}}{F_{..}}\right). \quad (7)$$

Note that the basis of the logarithm is non pertinent, since only comparison or optimization are to be considered.

The mutual information is also a classical tool in information theory. It was introduced in ecology by [14], that calls it ascendancy, as

$$A(f) = \sum_{ij \in E} f_{ij} \log\left(\frac{f_{ij}}{f_{i.} f_{.j}}\right) = \sum_{ij \in E} \frac{F_{ij}}{F_{..}} \log\left(\frac{F_{ij} F_{..}}{F_{i.} F_{.j}}\right). \quad (8)$$

The ascendancy can be written $K(f|(f_{i.}) \otimes (f_{.j}))$, that is the Kullback-Leibler divergence with respect to the product distribution $(f_{i.}) \otimes (f_{.j}) = (f_{i.} f_{.j})$. This function is neither convex nor concave, which hinders it from being used as an optimization function; see [3].

While A/C also serves to measure the degree of constraint of the system, in order to keep a balance between A and C , [9] prefers

$$G_{A/C}(f) = \frac{A(f)}{C(f)} \log\left[\frac{A(f)}{C(f)}\right], \quad (9)$$

for which we fail to find an interpretation in terms of pdfs.

The symmetrized conditional entropy becomes in ecology the system redundancy (overhead), introduced in [30] as the negative quantity $\Phi = C - A$, that is to say

$$\Phi(f) = - \sum_{ij \in E} f_{ij} \log\left(\frac{f_{ij} f_{ij}}{f_{i.} f_{.j}}\right) = - \sum_{ij \in E} \frac{F_{ij}}{F_{..}} \log\left(\frac{F_{ij}^2}{F_{i.} F_{.j}}\right). \quad (10)$$

Several indices drawn from overhead and ascendency have been proposed as health indicators based on marine ecosystem functioning; see [24] and [10].

Note that in the literature, these ENA indices have sometimes been multiplied by $F_{..}$, to make them depend on the total mass of the system. Then they can only be used as tools in analyzing the system, and neither for determining a flow solution to the constraints nor for comparing two systems.

3.2. Goal function involving a reference

An added value to determining a pertinent solution in \mathcal{S} is to incorporate information on the system that is not given in terms of the set of MBE and inequalities. In this aim, the following goal functions involve some reference pdf, say f^* , known a priori to be informative on the behavior of the ecosystem. In particular, a solution to the problem obtained in a previous study, or a previous year, may not be solution to the present, but can be considered as a reasonable reference. Another natural way is to consider the middle of the constraint intervals, in particular to take into account regular feeding habits of most species; see [3].

The most classical tool in information theory is the Kullback-Leibler divergence

$$\mathbb{K}(f|f^*) = \sum_{ij \in E} f_{ij} \log \left(\frac{f_{ij}}{f_{ij}^*} \right), \quad (11)$$

where $f^* = (f_{ij}^*)$ is some reference pdf of flows that makes sense in terms of the ecosystem. Note that [4] considers it as a "structural term".

The divergence is not a mathematical distance because it is not symmetric in f and f^* . Still, it is nonnegative and null only if $f = f^*$, and minimizing K determines the projection in terms of divergence of the reference f^* on the set \mathcal{S} of solutions f to the constraints; see [6] and [7].

It is worth remembering that the entropy \mathbb{S} in Equation (6) is, up to constants, the Kullback-Leibler divergence with respect to the uniform distribution on the flows, with $f_{ij}^* = 1/n$. This uniform distribution is well-known to maximize the entropy when no information is a priori available.

A simple generalization of the quadratic function Q is the well-known χ^2 -distance

$$\chi^2(f) = \sum_{ij \in E} \frac{(f_{ij} - f_{ij}^*)^2}{(f_{ij}^*)^2};$$

see [3] for an application, where for both for \mathbb{K} and χ^2 , we have chosen f^* for each flow as the middle of the interval defined by the inequality constraints.

3.3. Rényi goal functions

Shannon type entropy quantities have been generalized to many others, that – to the best of our knowledge – have not yet been used in ecological networks. For a better fit of the goal function to the problem through the choice of a parameter s , we propose to consider the family of Rényi entropy, introduced in [23], and defined for positive $s \neq 1$ by

$$R_s(f) = \frac{1}{1-s} \log \left[\sum_{ij \in E} (f_{ij})^s \right], \quad (12)$$

with associated divergence

$$R_s(f|f^*) = \frac{1}{1-s} \log \left[\sum_{ij \in E} \frac{(f_{ij})^s}{(f_{ij}^*)^{s-1}} \right]. \quad (13)$$

The value of the parameter s has to be chosen. In a first stage, $s = 1/2$ and $s = 2$ can illustrate the role of the regions separated by the threshold $s = 1$. Note that Shannon entropy appears as the limit of Rényi entropy when s tends to 1; see [6].

Similarly to the Shannon case, Rényi mutual information is Rényi divergence with respect to the product distribution (f_i, f_j) ,

$$A_s(f) = R_s(P|(f_i) \otimes (f_j)) = \frac{1}{1-s} \log \left[\sum_{ij \in E} \frac{(f_{ij})^s}{(f_i, f_j)^{s-1}} \right]. \quad (14)$$

The associated quantities $A_s(f)/R_s(f)$ and $R_s(f) - A_s(f)$ may also be of use in further studies.

4. Conclusion

Classically in ecology, ENA indices are used to bring more information on an estimated model, or as a tool for comparing two of them. Considering them as goal (cost) functions in [3] opens the field to full mathematical optimization methods, as soon as the convexity of the function is assessed. Adding to the collection divergence-like functions, that take into account reference pdfs, should lead to a better fit to a priori information on the ecosystem. Tools from extended information theory, such as Rényi's, also may yield an optimized solution that is a better fit to certain complex systems, by a pertinent choice of the parameter.

A fully determined food web model (one in which all the flows are known, mainly from mean of observations) is presented in [2], that describes the eight habitats of the Sylt-Romo Bight. These food webs are composed of 56 living compartments and 3 non-living compartments. In [25], the known flows are replaced with inequalities at four decreasing levels of information block per block. Then a unique solution is chosen within the LIM-MCMC sample by optimizing a variety of goal functions. Some technical issues of computation time regarding the R package `limsolve` used in this paper made the randomization difficult. This will be corrected by using a new version of `limsolve` updated in C++, that will appear soon; see [8]. Then, a meaningful comparison of goal functions on the ecosystems of [2] at decreasing levels of information will be conducted by the authors.

Abbreviations

The following abbreviations are used in this manuscript:

MBE	Mass-Balance Equations
pdf	probabilistic density function
ENA	Ecological Network Analysis
LIM	Linear Inverse Modeling
MCMC	Monte-Carlo Markov Chain

References

1. Belgrano, A., Scharler, U. M., Dunne, J., & Ulanowicz, R. E. (Eds.). (2005). Aquatic food webs: an ecosystem approach. *Oxford University Press*.
2. Baird, D., Asmus, H., & Asmus, R. (2007). Trophic dynamics of eight intertidal communities of the Sylt-Rømø Bight ecosystem, northern Wadden Sea. *Marine Ecology Progress Series*, 351, 25-41.
3. Caputo, J. G., Girardin, V., Knippel, A., Nguyen, M. H., Niquil, N., & Noguès, Q. (2021). Analysis of trophic networks: an optimisation approach. *Journal of Mathematical Biology*, 83, 1-29.
4. Christensen, V. (1995). Ecosystem maturity—towards quantification. *Ecological modelling*, 77(1), 3-32.

5. Christensen, V., & Walters, C. J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecological modelling*, 172(2-4), 109-139. 239
6. Cover, T.M., & Thomas, J.A. (2006) *Elements of information theory*, 2nd edition. 240
7. Csiszár, I. (1975). I-divergence geometry of probability distributions and minimization problems. *The annals of probability*, 146-158. 242
8. Dien, M., Girardin, V., Grente, T. Niquil, N., Noguès, Q. & Regnault, P. *samplelim*: an updated mirror algorithm for Linear Inverse Modeling applied in metabolic networks, *work in progress*. 244
9. Fath, B. D. (2015). Quantifying economic and ecological sustainability. *Ocean & Coastal Management*, 108, 13-19. 246
10. Fath, B. D., Asmus, H., Asmus, R., Baird, D., Borrett, S. R., de Jonge, V. N., Ludovisi, A., Niquil, N., Scharler, U.M., Schückel, U., & Wolff, M. (2019). Ecological network analysis metrics: the need for an entire ecosystem approach in management and policy. *Ocean & Coastal Management*, 174, 1-14. 248
11. Fontaine, C., Guimarães Jr, P. R., Kéfi, S., Loeuille, N., Memmott, J., van Der Putten, W. H., ... & Thébaud, E. (2011). The ecological and evolutionary implications of merging different types of networks. *Ecology letters*, 14(11), 1170-1181. 249
12. Grami, B., Rasconi, S., Niquil, N., Jobard, M., Saint-Béat, B., & Sime-Ngando, T. (2011). Functional effects of parasites on food web properties during the spring diatom bloom in Lake Pavin: a linear inverse modeling analysis. *PLoS One*, 6(8), e23273. 252
13. Jørgensen, S. E., & Fath, B. D. (2011). Fundamentals of ecological modelling: Applications in environmental management and research. *Elsevier*. 253
14. Hirata, H., & Ulanowicz, R. E. (1986). Large-scale systems perspective on ecological modelling and analysis. *Ecological modelling*, 31(1-4), 79-104. 254
15. Johnson, G. A., Niquil, N., Asmus, H., Bacher, C., Asmus, R., & Baird, D. (2009). The effects of aggregation on the performance of the inverse method and indicators of network analysis. *Ecological modelling*, 220(23), 3448-3464. 255
16. Kones, J. K., Soetaert, K., van Oevelen, D., Owino, J. O., & Mavuti, K. (2006). Gaining insight into food webs reconstructed by the inverse method. *Journal of Marine Systems*, 60(1-2), 153-166. 256
17. Kones, J. K., Soetaert, K., van Oevelen, D., & Owino, J. O. (2009). Are network indices robust indicators of food web functioning? A Monte Carlo approach. *Ecological Modelling*, 220(3), 370-382. 257
18. Kullback, S., & Leibler, R. A. (1951). On information and sufficiency. *The annals of mathematical statistics*, 22(1), 79-86. 258
19. Langlet, D., & Rayfuse, R. (2018). The ecosystem approach in ocean planning and governance: Perspectives from Europe and beyond (p. 492). Brill. 259
20. Le Guen, C., Tecchio, S., Dauvin, J. C., De Roton, G., Lobry, J., Lepage, M., Morin, J., Lassalle, G., Raoux, A. & Niquil, N. (2019). Assessing the ecological status of an estuarine ecosystem: Linking biodiversity and food-web indicators. *Estuarine, Coastal and Shelf Science*, 228, 106339. 260
21. MacArthur, R. (1955). Fluctuations of animal populations and a measure of community stability. *ecology*, 36(3), 533-536. 261
22. Niquil, N., Saint-Béat, B., Johnson, G. A., Soetaert, K., Van Oevelen, D., Bacher, C., & Vézina, A. F. (2011). Inverse modeling in modern ecology and application to coastal ecosystems. *Treatise on estuarine and coastal science*. Academic Press, Waltham, 115-133. 262
23. Rényi, A. (1959), On the dimension and entropy of probability distributions, *Acta Mathematica Academiae Scientiarum Hungarica*, 10(1-2), 193-215. 263
24. Safi, G., Giebels, D., Arroyo, N. L., Heymans, J. J., Preciado, I., Raoux, A., Schückel, U., Tecchio, S., de Jonge, V.N. & Niquil, N. (2019). Vitamine ENA: a framework for the development of ecosystem-based indicators for decision makers. *Ocean & Coastal Management*, 174, 116-130. 264
25. Saint-Béat, B., Vézina, A. F., Asmus, R., Asmus, H., & Niquil, N. (2013). The mean function provides robustness to linear inverse modelling flow estimation in food webs: A comparison of functions derived from statistics and ecological theories. *Ecological modelling*, 258, 53-64. 265
26. Shannon, C. E., Weaver, W. (1949), *The Mathematical Theory of Communication*, *Urbana, University of Illinois Press*. 266
27. Van Oevelen, D., Van den Meersche, K., Meysman, F. J., Soetaert, K., Middelburg, J. J., & Vézina, A. F. (2010). Quantifying food web flows using linear inverse models. *Ecosystems*, 13, 32-45. 267
28. Peterson, C. H., & Lubchenco, J. (1997). *Marine ecosystem services* 177-195. Island Press, Washington, DC. 268
29. Ulanowicz, R. E. (2018). Biodiversity, functional redundancy and system stability: subtle connections. *Journal of the Royal Society Interface*, 15(147), 20180367. 269

-
30. Ulanowicz, R. E., & Norden, J. S. (1990). Symmetrical overhead in flow networks. *International Journal of Systems Science*, 21(2), 429-437. 298
299
 31. Vézina, A. F., & Platt, T. (1988). Food web dynamics in the ocean. 1. Best-estimates of flow networks using inverse methods. *Marine ecology progress series*. Oldendorf, 42(3), 269-287. 300
301
 32. Vézina, A. F., & Pahlow, M. (2003). Reconstruction of ecosystem flows using inverse methods: how well do they work?. *Journal of Marine Systems*, 40, 55-77. 302
303
 33. Vézina, A. F., & Pace, M. L. (1994). An inverse model analysis of planktonic food webs in experimental lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 51(9), 2034-2044. 304
305