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Network construction, evaluation and documentation: A guideline

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ABSTRACT

Network analysis of complex systems is a rapidly growing field. Both theoretical and empirical network studies have permeated many different ecological, biological, social, and economic fields, investigating the interrelationships between nodes as structural and functional attributes in static, time-dynamic, or spatially explicit formats. We consider the network construction phase as a vital, but neglected component, and therefore provide recommended guidelines, describe how to evaluate the resulting network model quality, and highlight tools to assess their plausibility. Thereby we stress the importance of constructing multiple plausible networks to comply with basic scientific standards, and to pave the way for better informed evaluations. Finally, we provide recommendations for the management and policy arena where we advocate a thorough interrogation of network analyses outcomes (metrics) especially with regard to their sensitivity to the construction process, and a focus on relative changes between and within systems (e.g. as indication of vulnerability), rather than strict benchmarks.

1. Introduction

Network modelling and analyses are tools to investigate the complexity of biological, ecological, social and economic structures as integral systems (Capra and Luisi, 2014; Estrada, 2012; Newman, 2003). A core advantage of an integral view is that it provides context for individual species in ecosystems, for individuals in societies, or individual economic activities in cities, countries and the globe. Context renders a comprehensive view of the system that is inclusive of the wider impacts and roles of system components. Whole system properties can emerge from the system components' interactions, and these emergent properties are therefore only understood from analyses at this level (Capra and Luisi, 2014; Fath and Patten, 1998; Jørgensen, 2012; Ulanowicz, 1986, 2009a). The many different types of interactions within systems (trophic, behavioural, energy, water, money, etc.) facilitate the co-existence of several networks operating in parallel within a system (Golubski et al., 2016; Olff et al., 2009; Treml et al., 2015; Zand et al., 2017). All networks, however, consist of nodes (e.g., vertices, compartments) that are linked by edges that can be weighted and directed.

The construction and analysis of network models is a growing approach to study many types of complex systems, identified as network science (Brandes et al., 2013; Newman 2010). Network ecology is the use of network models to investigate ecological and evolutionary questions, and it is a proper subset of network science (Fig. 1). Network ecology is rapidly expanding into many different fields in ecology and socio-economics (Borrett et al., 2014), as well as socio-ecology (e.g. Sayles and Baggio, 2017; Treml et al., 2015). In the wider ecological field, it has found applications to ecosystem service assessments (Dee et al., 2017), to habitat connectivity in the life-history of single species (Buddendorf et al., 2017), the interplay between human consumption and environmental issues (Dai et al., 2012), the importance of functional traits in ecosystems (Gravel et al., 2016), and landscape connectivity (Fletcher et al., 2011).

A key challenge for the success of network science lies in the model construction and evaluation steps. Model quality is essential. The challenge of quality network construction is a theme apparent from fields as diverse as archaeology (e.g. Groenhuijzen and Verhagen, 2017), waste water treatment works (Martin and Vanrolleghem, 2014), epidemiology (Eames et al., 2014; Pellis et al., 2015), neural networks (Peng et al., 2006; Tsoulos et al., 2008), geomorphic systems (Phillips, 2012), healthcare systems (Zand et al., 2017), or effects of natural disasters (Zheng et al., 2017). For example, in the social sciences, the construction process has explored methodology regarding peer reputation networks (Azzedin and Ridha, 2008; Pujol et al., 2002), or how the behaviour of social network site users generates certain types of networks (Krasnova et al., 2010). The definition and measurement of interactions, and how

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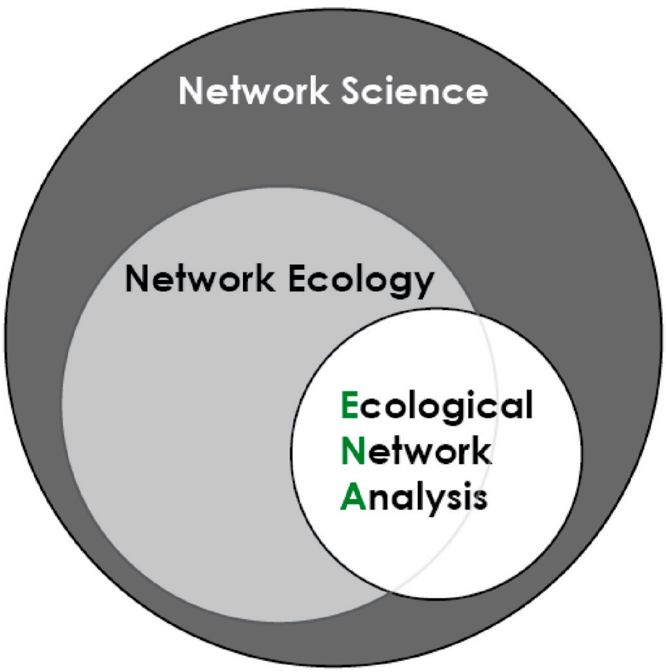


Fig. 1. Ecological Network Analysis is embedded in the broader field of network science and it partially overlaps with the growing domain of a more general network ecology that includes epidemiology, organism movement across landscapes, or combining trophic and nontrophic networks in multi-layer networks.

to manage data gaps has also received attention in social networks (Eames et al., 2014). The dramatic recent increase in the amount of genetic sequencing data has opened opportunities for big data analyses, necessitating considerable attention also in the field on network construction methodologies and evaluation for instance in genealogy (e.g. Cassens et al., 2005), for gene regulatory networks (e.g. Chai et al., 2014; Chen and VanBuren, 2012), and co-expression networks (e.g. Kumari et al., 2012; Tang et al., 2011).

While network construction is a widely discussed topic in different disciplines, in this paper we focus on directed, weighted networks, which have been the subject of analyses by methods collectively known as Ecological Network Analysis (ENA) (Borrett et al., 2018; Lindeman, 1942; Patten et al., 1976; Scharler and Fath, 2009; Ulanowicz, 1986, Figs. 1 and 2). Two types of directed, weighted networks have been most prominent - the construction of trophic ecosystem networks (energy and nutrient networks) and socio-economic networks (e.g. urban metabolism, sectorial water-use, monetary exchanges) (Fig. 3), though we believe that much of the methodology may be more broadly applicable. Application of ENA has brought new insights into ecosystem functioning and hypothesized emergent properties over the past decades. For instance, the understanding that overfishing decreases the mean trophic level of the fishery as large predators are overfished first (Pauly et al., 1998) was revealed by calculating trophic levels of target fish species from the analyses of trophic networks. The concept of "Fishing down the food web" is now firmly embedded in the literature, explaining the diminished resource of sought after higher trophic level predatory fish (e. g. tuna) in fisheries catches. Other, longer established ecological theory on community motifs (Holt, 1997) have been investigated in the Big Cypress Preserve ecosystem (Florida, USA), and revealed beneficial relations between species by examining both direct and indirect effects (Ulanowicz and Puccia, 1990) that were not apparent from the known biology and ecology of the involved species alone (Bondavalli and Ulanowicz, 1999). As an example, an 'intraguild predation' configuration (alligators and snakes feed on frogs, alligators also feed on snakes), revealed mutualistic relations between predators (alligators) and their

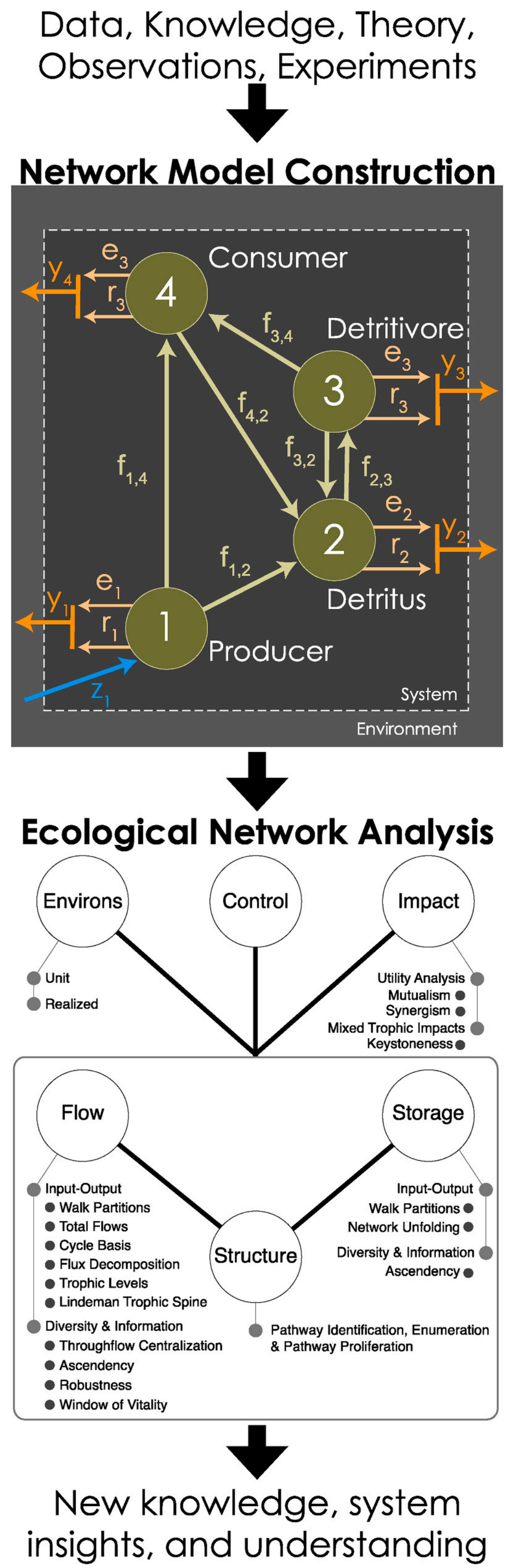


Fig. 2. Workflow diagram depicting data requirements, a flow model (z: import flow across system boundary, f: flow between nodes, e: export across system boundary, r: respiration flow, y: e + r), and a conceptual model of the universe of Ecological Network Analysis (ENA) methods (Fath and Patten, 1999; Lindeman, 1942; Ulanowicz, 1986; Ulanowicz and Abarca-Arenas, 1997; Borrett et al., 2018; Borrett and Scharler, 2019).

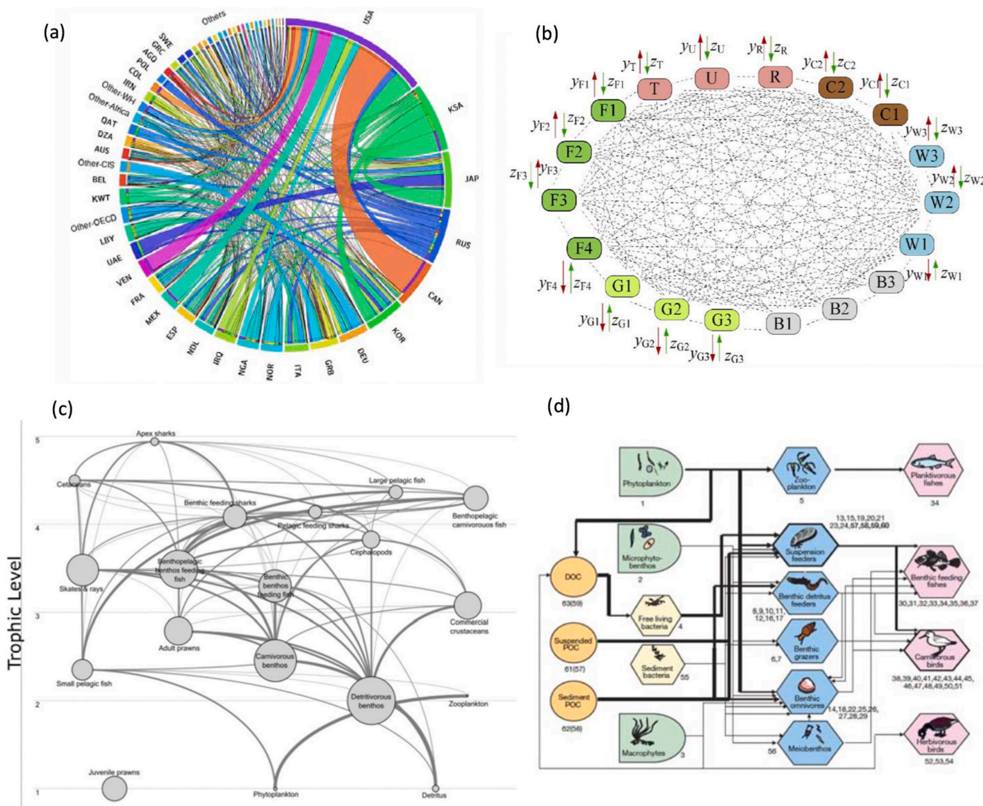


Fig. 3. Various types of ecosystem and socio-economic networks compatible with Ecological Network Analysis (ENA). (a) Crude oil trade network 2012. Coloured line (thickness depending on trade volume) depicts oil trade between two countries (Kharrazi and Fath, 2016), (b) Conceptual model of Beijing's carbon metabolic network. z and y are im- and export vectors respectively. F:forest, G: grassland, B:barren earth/rock, W: water bodies, C: cultivated land, R: rural, U: urban, T: transportation and infrastructure (Xia et al., 2016), (c) Ecopath biomass flow diagram of the Thukela Bank ecosystem, South Africa (adapted from Ayers et al., 2013), (d) Carbon flow diagram of an aggregated Sylt-Rømø Bight food web (Baird et al., 2012).

prey (frog). This motif of trophic interaction is only a particular portion of their feeding interaction within the food web, and alligators had further net positive indirect effects on 11 of their prey groups, although direct effects of predators on their prey are negative. The consequences of these deeper insights into relations between species is a changed perception of importance of this species within the context of the trophic web. This has added information on the ecosystem next to other important concepts such as species diversity, predation or habitat modification.

Methods and metrics emerging from ecological networks have been applied to socio-economic systems with increasing enthusiasm (Tang et al., 2021). For instance, a study on carbon emissions, sequestrations and fluxes of the Beijing Metropolitan area revealed positive and negative direct and indirect relations between the city's components (Xia et al., 2016). One of the main findings were that change in land-use and economic sectors over 20 years highlighted that urban expansion caused a decline in mutualistic relations between metropolitan sectors overall.

Even though ENA is used widely in multiple different fields (Borrett et al., 2018), there are as yet insufficient guidelines on how to generate input data, the construction process itself, and how to evaluate the quality of the network model. It is essential for practitioners to recognize that the construction of network models is fundamentally a modelling step and as such, the process should follow best ecological modelling practices. This is reminiscent of efforts in other areas of ecological modelling (e.g. Grimm et al., 2010; Jakeman et al., 2006; Parrott, 2017; Schmolke et al., 2010; Hipsey et al., 2020) which provide guidelines for model development, evaluation, model description, validation and documentation, amongst others, and are applicable to decision support models, individual- and agent-based models, and more generally, environmental models. Unfortunately, the direct application of these existing guidelines to specifically network models is not always clear due to model differences. Thus, this paper provides an overview of adapted and additional guidelines and principles to the construction of network models of ecosystems and socio-economic systems.

There are several existing recommendations but little overarching consensus on what makes a quality ecosystem network model. Instead, as we already know from other modelling studies, the sufficiency or success of the model is dependent on research questions and hypotheses, the system, and data availability. Such ambiguity is in conspicuous contrast to more established guidelines for generating ecological datasets (e.g. Underwood, 1997). At present, the available guidelines are few and are a loose conglomerate of descriptions of data required, how to construct the network from the data, and how to generate possible network solutions of the available data (Ayers and Scharler, 2011; Dame and Christian, 2006; Fath et al., 2007; Heymans et al., 2016; Lassalle et al., 2014; Link, 2010; van Oevelen et al., 2010; Ulanowicz, 1986; Ulanowicz and Scharler, 2008). All of this documentation describes specific possible steps within the process of generating networks, but it does not give complete guidance on multiple critical topics including: how to design fieldwork to obtain data appropriate for constructing networks; how to transform the data into the correct format (conceptually and practically); how to identify links; how to deal with missing data; and lastly, but perhaps most importantly, how to evaluate whether a network model is a sufficient or plausible representation of the system. In multilayer networks, multi- and hypergraphs (Delmas et al., 2018; Golubski et al., 2016; Lin and Sutherland, 2013; Pilosof et al., 2017), increased types of interactions can be modelled within the same system. A guided construction process is thus valuable for the current mainstream of network models, as well as for networks expanded into different dimensions which we will see increasing in future.

The last publication explicitly focused on the construction of weighted ecological network models, and specifically for ecosystems, was published more than 10 years ago (Fath et al., 2007). Since then, considerable progress has been made to reveal and solve flaws in network construction processes, with many useful developments in the field. This paper seeks to capture these developments and common practices to provide guidance during the network construction process, and present a more unified approach. It is divided into four sections that each deal with a different aspect of this process (Fig. 4) and includes (1) network construction, (2) evaluation, (3) documentation, and (4) utility of network models (including interpretation of ENA results). This paper is intended as a reference, and for first entry researchers and more senior students to become acquainted with concepts of ecosystem and socio-economic network construction methodology.

2. Network construction

Data requirements for network construction are generally high. To start, the investigator has to identify the system components and represent them as compartments or **nodes**, and then determine how the nodes interrelate with others in the system to map the network **edges** or links (Fig. 4). This requires knowledge on the inputs into, and outputs from each node. In ecosystem networks, it is thus imperative to know the intake (consumption), and the proportions to which the intake is divided into outputs of production (e.g. somatic production, reproduction, natural mortality), unassimilated consumption (faeces), and metabolic cost (respiration) (Odum 1971). The outputs that are useable in the system (production and unassimilated consumption), are furthermore divided along links to various other nodes in the system, representing their consumers and detritus nodes respectively. This concept is similarly applied to socio-economic networks, where inputs into and outputs from nodes may be virtual-water, carbon sequestration and emission in urban environments, money or commodity trade flows. Ecosystems are thermodynamically open (Jørgensen et al., 1999) and therefore receive and produce boundary flows as imports and exports. In food webs, gross production of primary producers is often treated as an import and

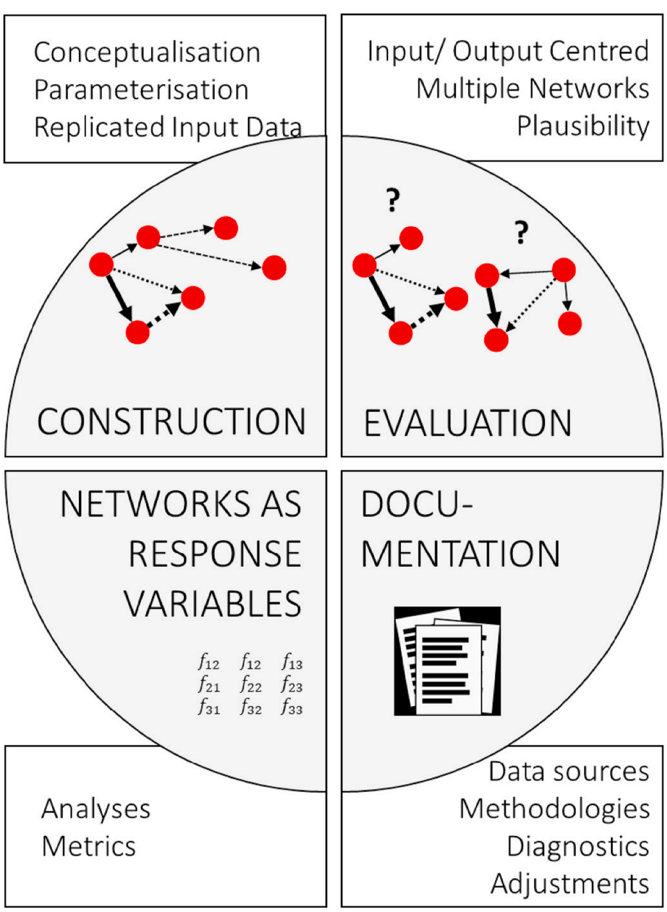


Fig. 4. Main phases of network construction and analyses in clockwise orientation. Each point is explained in the main text.

respiratory losses as boundary losses. Boundary flows can also include migratory movements or long distance transport processes. Socio-economic network models do not always incorporate boundary flows (e.g. raw materials feeding into a trade network of the product). The inclusion of natural resources as boundary flows could certainly be added to highlight resource dependency, applicable to much of the global economic activity. To move from a single network representing a temporal or spatial snapshot towards dynamic networks over time and space, data requirements increase according to the extent of the temporal and spatial frame.

It is no surprise that historically network construction has been guided by data availability. Some of the first available ecological networks, Silver Springs (Odum, 1957) or Cone Springs (Tilly, 1968), are therefore rather small with a total of five highly aggregated nodes (e.g., multiple species and resources grouped together). These early networks illustrate perfectly the ambition at the time to characterise ecosystem processes at a level beyond that of species and communities, even if comprehensive datasets were not available. Although present day ecosystem networks are better resolved with a larger number of nodes that may reach >120, this is likely far less than the number of species present. Availability of suitable data for network construction remains an issue as it can influence how well the network model represents the system, and has consequences for analyses outcomes (e.g. Abarca-Arenas and Ulanowicz, 2002; Allesina et al., 2005; Baird et al., 2009; Gauzens et al., 2013; Johnson et al., 2009; Jordán and Osváth, 2009). Continuous datasets in time and over spatial extents are especially rare for ecosystems, but not necessarily for socio-economic systems (Fang et al., 2014; Kharrazi et al., 2017; Zhang et al., 2017). Therefore few time-series and spatially explicit networks have found their way into the ecological literature (but see Christian and Thomas, 2003; Chrystal and Scharler, 2014; Haraldsson et al., 2018; Scharler, 2012; Steenbeek et al., 2013; de la Vega et al., 2018).

2.1. Existing network construction processes and software

Several network construction techniques for ecosystems became mainstream in the 1980s. Ecosystem and socio-economic networks in the early decades were constructed mainly by arranging gathered data into spreadsheets, that allowed the verification of mass-balance by comparing inputs and outputs (e.g. Ulanowicz, 1986). For the early, small networks (Silver Springs (Odum, 1957), Cone Springs (Tilly, 1968)) this was manageable, but far less practical for larger networks. A plain text format (SCOR) comprised the input structure for the NETWRK software facilitating the network analysis (Ulanowicz and Kay, 1991). This was later translated into an Excel front end, and the calculations to the GUI operated software WAND (Allesina and Bondavalli, 2004), used by ecologists, but did not change the way networks were constructed. Subsequently, a more objective method was developed which systematically assigns weights to interactions within the constraints of node consumption and production (MATLOD, Ulanowicz and Scharler, 2008). Building partially on this methodology, an expanded version constructing stoichiometric multitrophic networks has recently been applied to semi-terrestrial and marine environments (Scharler et al., 2015; Scharler and Ayers, 2019).

A similar bioenergetics food web modelling approach (Ecopath) was conceived in the early 1980s (Polovina, 1984). Subsequently it was developed into the software package Ecopath with Ecosim (EwE) that also enabled a network construction process (Christensen and Pauly, 1992). The construction process in EwE is facilitated by a user-friendly interface where standardized and available data are entered, and the software will calculate missing data through mass-balance and other modelling assumptions. Recently, the mass balance algorithms have been translated into R (R Core Team, 2018), which makes this approach further accessible through the package Rpath (Lucey et al., 2020). The direct incorporation of additional information on diet (McCormack et al., 2019) and diet uncertainty analysis (Bentley et al., 2019) promise to advance realistic representations of trophic webs.

An alternative network construction methodology is that of Linear Inverse Modelling (LIM) (Niquil et al., 1998; van Oevelen et al., 2010; Vézina and Platt, 1988). Here networks flows are inferred from equalities and inequalities describing stocks and flows of (typically) undersampled food webs. The method provides either a single network solution or a range of solutions presented as an ensemble of possible networks within the range of the input data. In addition, stoichiometric and isotope data can be used in this approach (van Oevelen et al., 2010). This method was recently advanced by generating multiple plausible networks to certain specifications regarding the flow ranges (Hines et al., 2018; Waspe et al., 2018).

All of the described approaches result in networks with weighted links that represent how much energy or material (depending on model currency) is transferred from one node to another in the selected model time step. With the exception of the multi-solution linear inverse modelling approach, their common disadvantage is that the variability of data used to construct the networks is largely lost, because the result is a single network per point in time or space. When networks represent only a single version of a system, statistical analyses are largely infeasible (but see Kones et al., 2009). There have been few attempts to reflect this variability of input data (e.g. Ayers and Scharler, 2011), but Hines et al. (2018) and Waspe et al. (2018) started to address this issue systematically within the LIM framework. This framework already provides the possibility to produce an ensemble of plausible network models based on known data, and Hines et al. (2018) illustrate how they can be constructed from already existing single networks. For instance, networks can be replicated retrospectively by applying a user defined range of flow values, e.g. ±50% of a nominal estimated value or a user can specify a range defined by empirically known data variability (Hines et al. 2015, 2018; de la Vega 2018; Bentley et al., 2019). An ensemble of plausible networks is then generated based on one or more new flow ranges, and the group of networks is returned to enaR for subsequent analysis (Borrett and Lau, 2014; Lau et al., 2017b). As each model parameter is being randomly sampled from the empirically estimated range, it appears that these plausible models act like replicate samples of the system. As a result, network analysis results can be compared more rigorously by comparing their density distributions that result from a given uncertainty or range of flow values, which lets the user draw more robust conclusions. For example, Hines et al. (2015) applied this uncertainty technique in an ENA application to determine the impact of sea water intrusion on microbially mediated nitrogen removal pathways in the Cape Fear Estuary, NC, USA. This work was able to robustly conclude that while the sites experiencing different salinity regimes had the same N_2 removal capacity, the same coupled steps in the nitrogen cycle used to achieve the removal were utilised in substantially different magnitudes. More generally, these uncertainty analyses allow for a deeper understanding of networks in terms of their function and behaviour (Ma et al., 2018). This constitutes a large, and absolutely necessary, step towards a more comprehensive representation of systems as networks.

Waspe et al. (2018) expanded the methodology of van Oevelen (2010) and Hines et al. (2018), to preserve the entire empirically measured range of the input data during the initial network construction phase, in the R package FlowCAr. The networks generated in this way are diagnosed to be representative of the entire range of empirically measured input data. They are subsequently packed into a format readable by enaR for network analysis, and the calculated ENA metric distributions plausibly represent the range of empirical measurements.

Another way of constructing networks, and especially for time-series networks, is to extract snapshots from time-dynamic simulations that are conducted in software such as Stella (isee systems), Econet (Kazanci, 2007), EwE (Christensen et al., 2005), Vensim (Ventana Systems, Inc.), and others. Care should be taken that all data needed for an ENA are able to be extracted from networks generated this way (Fath et al., 2007). As an example, Econet (Kazanci, 2007; Schramski et al., 2011) uses basic input data (stocks, flows) which are converted into differential equations. The goal is to arrive at a steady state system to be used subsequently for analyses. Although simulated Ecosystem Networks have played a prominent part in the network literature (e.g. the cascade model (Cohen and Newman, 1985), niche model (Williams and Martinez, 2000); Allesina et al. (2008)), there are few similar approaches to construct weighted versions of networks. A notable exception is the method introduced by Fath (2004) on cyber-ecosystem assembly.

Then how to start the network construction process? Regardless of which methodology is used to construct networks, the basic data needs are very similar. Two fundamental steps of the process are the system *conceptualization* (referring to structure, purpose, and ecosystem boundaries), and the subsequent data requirements and parameterisation.

2.2. *Conceptualization*

2.2.1. *System boundary*

As with most modelling, one of the first steps to constructing a network model is to conceptualize the system which starts by identifying its boundaries (Haefner, 2005; Fath et al., 2007). This process begins with deciding or inferring from data what system elements are inside the system of interest, and what elements fall outside the system. In this process, the modeller will determine (1) the spatial scale and resolution of the system, and (2) the timescale it represents (day, season, year, …). For instance, should the spatial resolution adhere to natural boundaries such as watersheds or to political boundaries? Should the network model include features such as the littoral zone of lakes and estuaries, or the benthic environment for an open ocean ecosystem or lake? Sometimes the system boundary is determined by data availability, which may lead one to restrict its physical or temporal dimension, for instance to the pelagic or benthic realm, to municipalities, or certain economic sectors, or a particular season or decade.

2.2.2. *Structure of networks (nodes, links, resolution)*

The next step in system conceptualization is the definition of the basic structure of a network, created by deciding on the network nodes and edges (Fig. 4). For example, how many nodes will be used to represent the ecosystem elements (e.g., species, functional groups, nonliving resources), and what are the interlinkages or edges among the nodes? In network models used for ENA, a single directed edge between two nodes represents the energy or matter transfer even if it arose from multiple ecological processes. Again, the node and edge conceptualization should be guided by the research questions and data availability, and overall lead towards an appropriate representation of the system. Some system components represent highly important functions (e.g. primary producers in ecosystem, or water sources in virtual water networks), that it would be unreasonable to dismiss them. This may require efforts to close the data gap from direct (e.g. fieldwork, data banks) or indirect sources (e.g. literature, expert opinion). Once constructed, scientists should use sensitivity and uncertainty analyses to judge the model sufficiency and analytical consequences of the heterogeneity of data abundance, and quality in terms of sensitivities of model output uncertainties to those of the input data.

Increasing the model resolution (resolution refers to the degree of aggregation or disaggregation) by increasing the number of nodes and links is only feasible if data are available for parameterisation. The resolution of networks has received considerable attention (see Section 1), as network structure, and thus analysis outcomes are generally sensitive to the number and proportional weight of links (Haller-Bull and Rovenskaya, 2019). Socio-economic network models are usually more aggregated compared to those of ecosystems, due to the more intense aggregation of data sources. In economic systems, the reporting of trade flows is more readily available as aggregated datasets with nodes representing sectors incorporating many different types of factories, or economic activities (e.g. transport, agriculture, annual trade volume). This results in a higher degree of aggregation of commodity flows, and therefore a higher connectivity of the network. In ecology, the recognized importance of taxonomic and functional biodiversity lead to a tendency to disaggregate nodes where possible. Overall, it is essential to have all critical components of the system represented in the model – even if in more aggregated nodes – than to completely omit key elements.

The structure of network models can differ due to underlying system differences, and also due to differences in research questions and system conceptualization. A particular system can thus be represented by different network models. This has made comparisons challenging. In the past, researchers have tried to standardise network structure by resolving different networks to the same number of nodes, even going to the extreme of featuring nodes as placeholders for temporarily absent species (e.g. Baird et al., 2011). However, such practice may conceal real differences between networks, for instance the absence and presence of migratory species (Horn et al., 2019), or of seasonally active economic sectors.

In trophic webs, direct flows between nodes are largely unidirectional and not reciprocated by return flows. Exchanges between highly aggregated nodes (nodes to represent groupings of functionally similar species) may appear bidirectional (represented by two single direction edges in opposite direction). For instance, exchanges between living nodes and non-living nutrient pools or detritus may be bidirectional. In economic networks, bidirectional flows between any two particular nodes are more common. This observation may be a consequence of a relatively high degree of aggregation in currently available empirical economic and socio-economic network models, or it could reflect a higher interaction incidence in comparison to trophic webs. Economic networks structures are subject to, and therefore a result of anthropogenic concepts, some of which may differ substantially from that of ecosystems (e.g. Fang et al., 2014; Huang and Ulanowicz 2014; Xia et al., 2016). For instance, they lack the strong metabolic constraints of ecosystems. Also, trading networks seldom incorporate the commodity source as opposed to ecosystem networks, which feature energy or nutrient imports across the system boundary to depict their connectedness to other environments and external sources. In reality, this is an important feature for certain economic sectors and for those warrants consideration.

2.3. Basic data requirements and parameterisation (node and link weights)

Efforts put into data gathering will be reflected in the outcomes of model analyses, and both small and large links deserve attention. Large links usually emanate from high biomass (e.g. detritus, trees), or high turnover (e.g. phytoplankton, bacteria) nodes, and a high variability in their value will result in the same for calculated ENA metrics (e.g. Ludovisi and Scharler, 2017). It is important to consider which weak (or small weight) links of a system to include as their absence or presence change the network structure, and therefore can change system function and the analytic results. For example, the number and magnitude of weak links in networks has an influence on network metrics, as they are calculated from the flow distribution within weighted, directed networks.

Incomplete system specific data availability for nodes and links can be supplemented, depending on the type of missing information. If only some part of the data requirements are missing, they can often be estimated by mass balance equations so that inputs equal outputs (of energy, material, trade flows, wealth accumulation etc.), from expert opinion, or information from the literature.

A balance of node inputs and outputs (i.e., sum of inputs = sum of outputs) is required for many different types of network analyses, and can be balanced by using the equations in Box 1.

Historically, model balance was achieved manually, e.g. by assessing and comparing inputs and outputs on a spreadsheet. This approach is cumbersome, but has the advantage that experts can apply their system knowledge to determine the reasonableness of the necessary changes. Several automated procedures are available to balance all nodes simultaneously for the entire network (e.g. Allesina and Bondavalli, 2003; Christensen et al., 2005; Lau et al., 2017a; van Oevelen et al., 2010). However, one should be cognisant that these balancing methods tend to change all of the original flow values in the model, some values can exceed what is biologically reasonable to achieve such balance, and they typically disregard the underlying data certainty or quality. Practitioners should compare the balanced and original network model to assess the algorithmic changes, and changes to the original input data. Some of the changes could result in ratios of stock to flow that turn out to be unreasonable for certain nodes. Another solution, therefore, is to add an in- or decrease of stocks to assist in the balancing procedure. Ulanowicz (2004) suggested this could take the form of adding a vector each that represent the stock increase as an added input, and the stock decrease as an added output (Box 1). More information on model evaluation is provided in the following section (Section 3. Evaluation).

Network data can be represented as matrices and vectors (Box 2). A flow matrix indicates not only the presence or absence of a flow (edge) from source node *i* to receiver node *j*, but in weighted networks the amount transferred via a particular link per unit time is stated. For clarity, care should be taken to specify the flow direction as both row-to-column and column-to-row orientations are used in the literature (see e.g. Scharler and Fath, 2009).

For certain links, databases and online tools are available to identify feeding links and sometimes estimate flow values (e.g. Brey, 2001; Froese and Pauly, 2000; Gray et al., 2015; Pasquaud et al., 2007; Poelen et al., 2014). Short of direct measurements, respiration rates in ecosystems can be estimated from body size and environmental data (e.g. Brey, 2001; Brown et al., 2004), and a popular estimate of production values

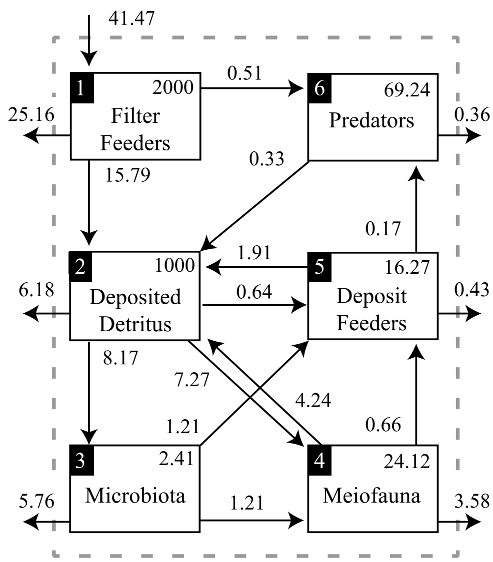
Box 1

Mass Balance:	Inputs	=	Outputs
Ecosystems	Boundary Inflow + Consumption	=	Production (somatic and reproduction) + Respiration + Unassimilated Food + Boundary Outflow
Socio-Economic Systems	Boundary Inflow + Nodal Input of Intra-System Origin	=	Use by Sector (e.g. investment, water) + Flow to Other Nodes + Boundary Outflow
Adding stock in- and decrease to the equation (applicable to both Ecosystems and Socio-Economic Systems)	Boundary Inflow + Nodal Input + Storage Increase	=	Nodal Output + Storage Decrease + Boundary Outflow

Box 2
Example of flow matrix and vectors of a trophic network.

South Carolina oyster reef model represented as a (a) graph and (b) set of matrices (Dame and Patten, 1981). The matrices include the internal flow matrix (F), the boundary input (z), respiration (r), and export (e) flows, the storage or biomass of each node (X), and a vector indicating the truth status as to if each nodes is living (Living). The matrices are oriented from row to column, and flows units are kcal m^{-2} d^{-1}, and biomass is kcal m^{-2}.

(a) Graph Representation



(b) Matrix Representation

$$\mathbf{F} = \begin{bmatrix} 0 & 15.79 & 0 & 0 & 0 & 0.51 \\ 0 & 0 & 8.17 & 7.27 & 0.64 & 0 \\ 0 & 0 & 0 & 1.21 & 1.21 & 0 \\ 0 & 4.24 & 0 & 0 & 0.66 & 0 \\ 0 & 1.91 & 0 & 0 & 0 & 0.17 \\ 0 & 0.33 & 0 & 0 & 0 & 0 \end{bmatrix}$$

Inputs

Outputs

$$\mathbf{z} = \begin{bmatrix} 41.47 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \quad \mathbf{r} = \begin{bmatrix} 25.16 \\ 6.18 \\ 5.76 \\ 3.58 \\ 0.43 \\ 0.36 \end{bmatrix} \quad \mathbf{e} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\mathbf{X} = \begin{bmatrix} 2000.00 \\ 1000.00 \\ 2.41 \\ 24.12 \\ 16.27 \\ 69.24 \end{bmatrix} \quad \textbf{Living} = \begin{bmatrix} \text{TRUE} \\ \text{FALSE} \\ \text{TRUE} \\ \text{TRUE} \\ \text{TRUE} \\ \text{TRUE} \end{bmatrix}$$

are Production/Biomass ratios from the literature. Whenever literature data are used, data sources for the same species in the same environment (e.g., biogeographic region, type of habitat, temperature) are preferable. Information on the presence and absence of trophic links is also often gathered from the literature (e.g. stomach contents, feeding experiments, isotope data), and measured data include observations, or the analyses of stomach content, isotopes or fatty acids. Although literature data can give an indication of the feeding guild of a species, they might not be an accurate representation of the feeding interaction of every system the species occurs in.

Overall, it is imperative to keep in mind that literature data are estimates and may therefore introduce bias into the network construction process. This applies to both ecosystem and socio-economic networks. Usually, a combination of methods to parameterise the network are applied and for socio-economic networks existing data recorded in open-access databases, for instance municipal records, or trade relations for certain sectors, are readily available data sources.

An empirical sampling design that connects directly to network construction is a preferable approach to generating data. In practice, however, this is not always feasible and networks are constructed from measured and literature data, and expert opinion to fill gaps. For ecosystems, important data sources are those obtained by continuous data recorders, long-term government datasets (e.g. fisheries records), or open access databases. When data are gathered specifically for constructing networks, such actions may be classified according to their resource investment. These include (1) *Extreme* Investment when data are actually measured for nodes and links for which no data are available, or (2) *Moderate* Investment that includes estimating some data that are missing. We speak of (3) *Minimal* Investment when balance adjustments within the range of input data from which the networks were constructed are sufficient. A recently developed methodology assists in the decision making for diverting resources to measure certain links over others, depending on their importance (Kazanci et al., 2020). This is a useful guide applicable especially in resource constrained, or data constrained environments.

For network science to move from largely descriptive studies to hypothesis driven research, adequate initial data gathering that enables researchers to pose and answer hypotheses is a requirement and thus combined efforts by data scientists and empirical scientists are essential (e.g. Delmas et al., 2018). A step-by-step summary of network construction guidelines is provided in Box 3.

3. Evaluation

Evaluation of constructed network models has historically been a neglected topic. This is in part because the most commonly used model verification and validation methods in ecological modelling compare the temporal output of dynamic models to observed field data, but these methods do not apply to static models like most of the ENA network models. This is further complicated by a lack of data for validation (especially for early networks) and lack of evaluation on how network analyses outcomes are affected by the network construction process. Today, the desire to use network models and ENA in system management and policy making (Dame and Christian, 2008; Fath et al., 2019; Goerner et al., 2009; Heymans et al., 2016; Kharrazi et al., 2013; Safi et al., 2019; Xia et al., 2016) makes model evaluation essential. The evaluation should be conducted on both the input data and the network analyses outcomes, and can be treated as input data and analyses output

Box 3
Guide - Network Construction:

1. Define the research question.
2. Identify the system ***boundaries*** (political, geographic, economic, social, time scale).
3. Define the ***network structure*** (nodes, links) that is in accordance with the research question.
4. Generate or find existing data to ***quantify nodes and links.***
5. ***Construct multiple plausible networks*** to represent the data and model uncertainty, either by utilising the range of input data, or apply sensitivity and uncertainty analysis post-construction.
6. Depending on the type of analysis, ***balance*** the networks so that inputs equal outputs.

centered validations. Such evaluations have been described for various software and different modelling frameworks (e.g. Bennett et al., 2013; Costanza et al., 1992; Grimm et al., 2010; Heymans et al., 2016; Jakeman et al., 2006; Schmolke et al., 2010). Here we add points that are specific to system network models.

3.1. Input data centered

The field or literature data used for network construction should always be evaluated for their fit for the model purpose, and especially when the goal is management or policy relevant research (Costanza et al., 1992). When considering the relevance of the data for node and flow values of the network, modelers should keep in mind that the input data themselves may not be a good representation of the system (e.g. Bennett et al., 2013), due to inadequately describing the system when data are used from studies not designed for this purpose. For instance, literature metabolic ratios for fauna specific to certain latitudes are less likely to be representative for those occurring at different latitudes, or between vastly different phyla or feeding guilds (e.g. detritivores and carnivores). Should it not be possible to construct replicate plausible network models of a system to reflect the system variability itself, researchers can conduct extensive sensitivity and uncertainty analyses to judge the network model quality and the dependency of the ENA results on less well known inputs.

The final network model parameterisation can be compared to the original input data using various descriptive and statistical methods to evaluate differences of single node and flow values. An automated assessment of the amount of system specific data used for network construction is incorporated in the software Ecopath (Christensen et al., 2005), through a measure called 'pedigree' that represents the proportion of system specific input data in the network model. Even though the amount of system specific data used for network construction is not a full guarantee for a good quality network, it serves as a broad gauge of how well the network model could represent the system. Also incorporated into the EwE software is a data check before mass balancing for the entire network, called PREBAL (Link, 2010). With this tool, certain attributes across nodes and trophic levels can be checked for their correspondence with known general ecosystem attributes.

At all times, and notwithstanding the software used, an assessment of correspondence between balanced networks with original input data of node and flow data, and data variability, should be conducted.

3.2. Analyses outcome centered

Once ENA has been applied to the network, the network analyses outputs – the analytic results – need evaluation. For example, practitioners should consider if the results show artefacts from an ill-defined network. Because the network construction process is influenced by data availability, it may become apparent only after analyses that the degree of node aggregation prevented detection of a system feature of interest. In this case, the network topology may have to be re-evaluated for its fitness for purpose. Such considerations are important also when comparing networks. While it is important to maintain the same model assumptions and approach (e.g., node aggregation decisions), real differences between the systems should not be masked by trying at all costs to keep the structure the same. Here again, multiple plausible networks representing the system are useful, and a knowledge of the system by experts in different fields may provide deeper insights into the accuracy of results. How convincingly results can be communicated to people outside the field (e.g. stakeholders) is another desirable check. It requires a deep understanding of the intricacies of the network and how its quantitative structure resulted in certain metric values.

A second powerful approach is to validate selected network analysis results with an independent method. For example, Deehr et al. (2014) validated their fisheries models of Core Sound, North Carolina by comparing the ENA predicted node trophic levels calculated by Ecopath with an independent estimate of the node trophic levels from isotope analysis. Conducting internal checks by using different types of analyses on the same dataset to calculate nutrient limitations of nodes in several networks was applied to a mangrove ecosystem by Scharler et al. (2015). Strong agreement between the independent methods was used as convincing evidence of the trophic models' quality.

We suggest the guidelines listed in Box 4 to evaluate the representativeness of constructed networks:

4. Model reporting/documentation

Scientific reporting aspires to be replicable, transparent, and accessible. To achieve this, scientists working with network analysis must (1) document the network construction itself including adjustments to primary data and evaluations of input data and analyses outcomes, and (2) consider the publication and accessibility of the network models.

Scientific writing conventions require methodologies to be described in enough detail to be replicated by other investigators. This is true for modelling studies as much as it is for experimental work. The documentation of modelling decisions, the use of large amounts of data, and clarifications on any necessary data transformations and calculations are often voluminous, but necessary. It is difficult to identify a single common documentation format because networks may have very different structures, data sources, and purposes. However, this does not preclude the documentation of network construction and evaluation to be presented in detail and to standardise documentation where possible (e.g. Ayers and Scharler, 2011; Bonet et al., 2014; Grüss et al., 2017; Gurney et al., 2014; Hoch et al., 1998; Schmolke et al., 2010). Articles that present new network models must include a full description of the network construction to enable peer review and evaluation.

Beyond individual publications, there are several collections of previously published networks that are available for additional research. These network data can be stored in different formats. For instance, Ulanowicz maintained a collection in a data format referred to as SCOR formatting (Ulanowicz and Kay, 1991). A collection of over 100 ecosystem networks, which partially overlap with Ulanowicz's set are distributed with enaR in the R *network* data format (Borrett and Lau, 2014; Lau et al., 2017a, https://github.com/SEELab/enaR). Ecopath

Box 4
Guide - Network Evaluation:

- Evaluate input data to be ***representative*** for the ecosystem, or socio-economic system.
- Evaluate whether the networks correspond to the ***research question***. This also applies for intersystem comparisons.
- Construct ***multiple plausible network models, parameterisations, or replicates*** to represent the known data uncertainty or variability.
- Use ***networks*** for further analyses, i.e. before and after balancing, check for node and system attributes to be realistic (biologically or economically), and corresponding to field and literature data, expert opinion or complementary analyses outcomes, where applicable.
- After analyses, ***check*** whether ***analysis outcomes***, unexpected or not, are an artefact of their sensitivity to the network construction process. Validate analytical results when possible using an independent method.

with Ecosim networks are stored in Ecobase (http://sirs.agrocampus-ouest.fr/EcoBase/) allowing for submission of new networks and extraction of existing ones. Another more recent development is that of *mangle*, a development and storage for binary food webs in R (Poisot et al., 2016). Such repositories are useful for cross-system research, network construction and common storage format. However, the network model information may differ within and between databases according to purpose. A list of commonly used network construction methodologies, model databases and software are provided in Box 6.

In addition to evaluation of the science, clear documentation of the network construction process may ultimately benefit the research field to enable new participants and the emergence of stronger community standards. This is especially important for addressing common data challenges, including that of missing data, applying conversion factors, and how to distinguish between plausible and possible network models. Above all, documenting the methods used during the entire network construction process adds credibility to the process and final network structure, and increases the potential applications of networks and their analyses in management and policy making (Costanza et al., 1992).

We recommend that clear documentation of the network construction and evaluation process should be included in ENA publications as part of a best practice. It will allow the approach to become more rigorous, and the results to be better interpretable. The communication of the variability and uncertainty of the analysis outcomes plays an important role in providing realistic recommendations to stakeholders and facilitate application (Saltelli et al., 2020). Box 5 provides basic guidelines we can provide for information on the accuracy, validation, variability and uncertainty of the network construction phase.

5. Networks as response variables

How scientists construct, evaluate, and document network models is critical to create a successful ecological network science. Once networks are constructed and deemed sufficiently representative of the system, researchers can use them as experimental response variables, providing information at system components and whole ecosystem levels (see Memmott, 2009). Network metrics describe various features of the system. In the ENA framework, these metrics are frequently labelled as either structural (e.g., the number of nodes, edge density) or functional (e.g., total system throughflow, Finn Cycling Index); nevertheless, the functional metrics often incorporate both structure *and* function (e.g. Bersier et al., 2002; Delmas et al., 2018; Kazanci and Ma, 2015; Ulanowicz, 1986). Weighted networks are used to calculate the latter, because a considerable amount of information is inherent in the distribution of link weights within networks (e.g. Allesina et al., 2009; Bersier et al., 2002).

Comparing two or more models of a system under different conditions is one way network models can function as response variables. In this application, analyses are focused on the whole system response to the conditional change. For example, Deehr et al. (2014) compared trophic network models parameterized with data from sites where shrimping was allowed and sites where shrimping was excluded to identify the ecosystem impact of the fishing activity. De la Vega et al. (2018) compared network models of the Sylt-Romo bight ecosystem parameterized with data from different seasons. By applying the uncertainty analyses to generate multiple plausible model given the data uncertainty, the authors discovered that some whole-system network metrics such as flow diversity and effective link density varied seasonally as expected, while other indices such as the average mutual information showed no significant seasonal variations. Multiple recent applications of the uncertainty analysis (Hines et al., 2015; de la Vega et al., 2018; Bentley et al., 2019) have directly compared the distribution of analytical results. Statistical difference was inferred if the 95% confidence intervals did not overlap. This is a useful, but conservative approach. In some cases it might be possible to use a nonparametric statistical approach to compare the distributions. We suggest a nonparametric test because the observed distributions of network metrics from flows of multiple plausible networks in general often do not follow a simple distribution pattern.

Whereas for decades theory has far outrun applications in the network analysis field, many efforts have arisen in recent years to use ecosystem and socio-economic networks in management, and to investigate how they could shape policy making (Fath et al., 2019; Heleno et al., 2014; Pincetl et al., 2012; Safi et al., 2019; Zhang et al., 2013; Longo et al., 2015). Parallel to this is an increased effort to understand how input data and ENA output relate, and therefore how network analysis metrics can be meaningfully applied (Borrett and Osidele, 2007; Christian et al., 2009; Kaufman and Borrett, 2010; Ludovisi and

Box 5
Guide - Network Documentation:

- List ***methodologies for measured data*** used in the construction phase.
- Identify all ***literature sources*** and those from ***expert opinion*** used in the calculations.
- List ***pre-and/or post-balance diagnostics***, and ***adjustments*** that were necessary to balance the network. This can include a measure of divergence of the balanced model from the nominal model, which flows adjustments were made, and how the remaining discrepancy is justified.
- ***Publish*** final model flow information, for example include flow matrices and vectors in appendices.

Box 6
Summary of ENA software tools and model databases:

Software	Source	Reference
Netwrk 4.2	Available from RE Ulanowicz	Ulanowicz and Kay (1991)
WAND	No longer available	Allesina and Bondavalli (2004)
EcoNet	http://eco.engr.uga.edu	Kazanci (2007), Schramski et al. (2011)
Ecopath with Ecosim	http://ecopath.org	Christensen and Pauly (1992)
MATLOD	Available from RE Ulanowicz	Ulanowicz and Scharler (2008)
Rpath	https://github.com/NOAA-EDAB/Rpath	Lucey et al. (2020)
LIM	https://cran.r-project.org/web/packages/LIM/index.html	Soetart and van (2015)
NEA.m	https://github.com/SEELab/NEA	Fath and Borrett (2006)
enaR	https://github.com/SEELab/enaR	Borrett and Lau (2014)
enaUncertainty	Part of enaR, https://github.com/SEELab/enaR	Hines et al. (2018)
FlowCAr	https://zenodo.org/record/1408672	Waspe et al. (2018)
LINX	https://www.mathworks.com/matlabcentral/fileexchange/72143-linx/	Kazanci et al. (2020)
Model Database	**Source**	**Reference**
>100 ecosystem models distributed with enaR	https://github.com/SEELab/enaR	Borrett and Lau (2014)
Ecobase	http://sirs.agrocampus-ouest.fr/EcoBase/	

Scharler, 2017). Although the ENA metrics generally have thorough theoretical underpinnings, one challenge to their use in management is that the correspondence between any metric value and desired system states (e.g., healthy, sustainable, resilient) is not always immediately apparent. A key challenge for using ENA metrics for ecosystem and economic system management is to determine which ENA metric values are most sensitive to certain system states (Fath et al., 2019).

Few ENA metrics are well benchmarked and interpretations largely remain relative among networks. This relative comparison, however, is a powerful tool. For example, it can be used to track system function over time (Christian and Thomas, 2003; Schückel et al., 2015; Luong et al., 2014), and compare differences among systems or subsystems (Baird et al., 2011; Pezy et al., 2017; Scharler and Baird, 2005). Such relative indicators may overall be a better guide for change than metrics benchmarked against absolute values because they track trajectories of individual systems.

One example of metric benchmarking has been applied to the metric termed system's robustness (Ulanowicz, 2009b) that considers the information inherent in the weighted flow structure of networks. This has been adopted by ecologists and economists alike (e.g. Goerner et al., 2009; Kharrazi et al., 2017; Mukherjee et al., 2015; Scharler et al., 2018). It has been proposed as a way of identifying the optimal functioning state as a dynamic tension between system needs both for efficiency and resilience, the latter of which is expressed as redundant (or parallel) transfers within the network. Ecosystem networks constructed from empirical data have been shown to congregate at a point that is indicative of high robustness, signifying an advantage for ecosystems with a considerable proportion of redundant flows in addition to favouring efficiency (Ulanowicz, 2009b). Economic networks seem to feature many more redundant pathways and thus have their highest robustness at different proportions of flow redundancy and efficiency compared to ecosystem networks. This, however, may be an artefact as a result of high node aggregation.

The interpretation of the network metrics can depend on model characteristics, as well as management goals. This further implies that scientists and managers applying ENA need to carefully consider their results and cannot always depend on previous ecological interpretations of the metrics. Context dependency of a desired state is an important consideration when using ENA metrics. Many of the metrics characterise the *state* of the system in a Driver-Pressure-State-Impact Response (DPSIR) frame (Burkhard and Mueller, 2008; Lewison et al., 2016), and do not characterise the desirability of the state. For example, an increase in the node or total system throughflow might be desirable in marine fisheries models tracing carbon or energy (Deehr et al., 2014), but it would be undesirable in models tracing toxins in the food web (Taffi et al., 2015).

6. Conclusions

The overarching goal of this paper is to improve the development of weighted network models of ecosystems and socio-economic systems, the application of ecological network analysis, and its use for system management by considering guidelines for best practices. Specifically, we considered key elements of network construction, model evaluation, documentation, and scientific applications. We highlighted challenges in the network construction process, and identified points that might result in unrealistic or not-for-purpose networks. More broadly, it is useful to recognize that network construction is a specific form of modelling, and that it should thus adhere to the best-practices prescribed for general modelling activities including robust forms of model evaluation (e.g., verification, validation, sensitivity and uncertainty analysis). The construction process is time-consuming, and yet critical as a strong foundation for credible network analysis results, and for the field to move into more rigorous hypothesis testing and policy and decision making realms.

As we seek greater management applications of ecological network analysis, the critical gap between theoretically oriented network analysis and its application becomes more apparent. This highlights a key direction for future research and development. A closer collaboration between theorists and empirical scientists can alleviate some of the remaining challenges, especially for checking the quality of constructed networks, filling crucial data gaps and the interpretation of calculated metrics against a backdrop of empirical knowledge of the system. Overall, adhering to basic scientific standards of assessing data quality, reporting methodology, hypothesis testing and more thorough interpretation of metrics will already make the field more appealing to stakeholders.

Standardized protocols provide for a certain efficiency and accessibility. The network model databases mentioned are highly useful to access a large number of networks, especially for assessments across different systems. In the absence of a single agreed-upon standard format for model presentation, it is useful to create interchangeable formats in various databases that allow access by different users for different types of analyses in different software. Besides such technical issues, the most critical challenges at present are the data verification of constructed networks and the interpretation of metrics in ways that increase our understanding of system function for management actions, and eventually for policy making.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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