Flipbook-ENA: Towards a dynamic Ecological Network Analysis under changing environmental conditions

Joel Habedank [a,*], Sabine Horn [a], Dan Baird [b], Peter Lemke [a], Jasmin Renz [c], Vera Sidorenko [a], Karen H. Wiltshire [a]

[a] *Wadden Sea Station Sylt, Alfred-Wegener-Institute, Helmholtz Centre for Polar and Marine Research, Hafenstraße 43, 25992, List, Germany*
[b] *Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland, 7620, Stellenbosch, South Africa*
[c] *German Centre for Marine Biodiversity Research (DZMB), Senckenberg Research Institute, Hamburg, Germany*

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ABSTRACT

Changes in abiotic parameters can affect ecosystem structure and function. Network models with subsequent Ecological Network Analysis (ENA) are often used for the quantification of ecosystem-wide properties with descriptive system indices. However, dynamic abiotic alterations of an ecosystem cannot be resolved with the "state of the art" ENA as the methodology of analyses is static in both space and time. In this study, we present a new, almost dynamic ENA "Flipbook-ENA" which allows for the trend analysis of system indices over a defined range of abiotic factors. Flipbook-ENA enables an approximation of the dynamic system response by discretizing the continuous influence of abiotic factors and by calculating the corresponding changes in the model for each discretization step. ENA indices are therefore obtained as a discrete function of the abiotic conditions. We applied this new concept to two aquatic food web models as case studies, using temperature as the influencing abiotic factor. Flipbook-ENA can be considered an enhancement of ENA flexibility, also facilitating the provision of a quantitative assessment basis for socially, economically and ecologically-balanced management of ecosystems in unstable environmental conditions under the pressure of climate change.

1. Introduction

Changes in the abiotic environment (e.g. temperature, light availability, salinity, nutrient concentration) alter the structure and function of ecosystems in direct and indirect ways (cf. Bornette and Puijalon, 2011; Dunson and Travis, 1991). Increasingly, in the Anthropocene, modifications of ecosystem structure are occurring outside the actual ecologically defined boundaries, via changed ecological, economic, and social parameters and due to the high degree of interconnectedness of socio-ecosystems (cf. Daily and Matson, 2008; Peterson et al., 2010; Westman, 1977). The consequences manifest as a complex permutation of internal and external interactions/intercorrelations on multiple scales. Hence, examining the influence of both natural and anthropogenically-induced changes in abiotic factors on ecological systems is crucial for developing effective ecosystem-based management, particularly in addressing future challenges to Earth's sustainability (cf. UNESCO, 2017).

The understanding of the complex overall influence of abiotic factors on ecosystems is dependent upon structural and functional effects on the specific entities and processes in the system. Ecosystem models can help to investigate and provide a mechanistic understanding of how these abiotic conditions influence ecosystem dynamics (Shugart, 1990).

A class of models that has become popular in recent decades is ecological network models (Borrett & Lau, 2014; Ulanowicz, 2004; Wulff et al., 1989). Based on the mathematical concept of network theory, these models describe the internal and external (e.g. trophic and energetic) relationships of an ecosystem, simplified by a graph consisting of vertices (compartments) with directed and weighted edges (links between compartments) (for a detailed overview refer to Kay et al., 1989; Ulanowicz, 2004). Network models explicitly describe the flows of matter or energy units. In ecological contexts, the changes in biomass and its corresponding flow, particularly in relation to food webs, is a common consideration (Ulanowicz, 2004). Ecological networks are applied in food web representations via trophic interactions between species of a community (Delmas et al., 2019), in the assessment of different keystone species concepts (Jordán & Scheuring, 2002) and in

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* Corresponding author.
E-mail address: joel.habedank@awi.de (J. Habedank).

the more holistic consideration of the robustness of an ecological network (Pocock et al., 2012).

Ecological network models allow for the analyses of the direct and indirect relationships of energy and matter of an ecosystem (Fath et al., 2007). One method of analyzing these networks in terms of their structure, flows and storage is the Ecological Network Analysis (ENA) (Fath et al., 2007; Fath & Patten, 1999; Scharler & Borrett, 2021; Ulanowicz, 1986, 2004; Wulff et al., 1989). ENA includes both compartment-specific and system-wide indices enabling the assessment of ecosystem function and provides a quantitative basis for ecosystem management questions (Fath et al., 2019; Safi et al., 2019). According to the European Marine Strategy Framework Directive (MSFD), some of the ENA indices are "potential candidate indicators […] to assess the health status of coastal food webs" (Horn et al., 2021) and therefore of particular interest to various stakeholders (OSPAR-Commission, 2010; Schückel et al., 2022).

ENA enables quantitative structural and functional analyses of specific ecosystem properties such as those in Chesapeake Bay (Baird & Ulanowicz, 1989), the Ems estuary (de Jonge et al., 2019; de Jonge & Schückel, 2019), different South African estuaries (Scharler & Baird, 2005) or the Sylt-Rømø Bight (Baird et al., 2004, 2008, 2012). The influence of abiotic factors on ecosystems has also been investigated using ENA. For example, de la Vega et al., (2018) considered temperature to investigate the seasonal biomass flow dynamics for the Sylt-Rømø Bight (SRB) food web model in northern Germany. Baird et al., (2019) extended analyses of this temperature dependency of the food web model and investigated its structure and function under different temperature scenarios. The influence of other abiotic factors such as salinity (Hines et al., 2015) and nutrients (Schückel et al., 2015) has been analyzed using ecological network models with a subsequent ENA.

Ecological network analyses can currently only be carried out for a specific point in time (snapshot of the system) for investigation of the properties and functions of ecological networks. This is mainly because the availability of measured data for implementing an ecological network is often limited. For instance, time series of energy flows and organism stock numbers, which are necessary for a dynamic implementation, are rarely available. However, this form of static computational snapshot is inadequate in the context of continuous trends in e.g., for understanding how a system may change in response to alterations of the abiotic environment. Thus, in the context of for example climate change, the development of the network analyses under the influence of a continuous abiotic stressor is urgently required.

Approaches combining dynamic shifts of an abiotic factor with the analysis concept of ENA have so far been rarely applied (Horn et al., 2021). Indeed, the analysis of a time-varying factor continuously influencing a system by using ENA raises some difficulties: (i) ENA is based on static network models which must be in steady state for many ENA indices and thus making it difficult to directly incorporate continuous influences; (ii) physiological responses of species (e.g., respiration, consumption, egestion) related changes in abiotic conditions are not well studied and formalized; (iii) missing quantification of the direct influence of abiotic factors on network compartments (single species or groups of species) and their interrelationships, as well as resulting propagating indirect effects, and (iv) the time scales of a response of particular ecosystem process (e.g. metabolic rates) or the ecosystem structure on abiotic shifts are not always known.

In this study, we present a concept for integrating shifts of abiotic factors into a static ecological network model. This substantially enhances the applicability using ENA by providing an assessment of dynamic network changes due to abiotic influences. Our approach provides a trend analysis of ENA indices with regard to changing abiotic conditions of the ecosystem, yet retaining all strengths of ENA. Alterations of the ecological network functions under changing abiotic conditions can thus be considered in an almost dynamic way. After introducing the new concept here, we present the application of the methodology to two regionally distinct marine ecological systems, focusing on the influence of temperature as an external driver.

2. Materials and methods

2.1. Background: Equilibrium equation of the metabolic rates

Ecological network analysis is based on the network definition as well as on underlying formal assumptions of the analysis technique. First, the network must be defined by describing the standing stocks of the compartments, the flows between them and the respective external import and export flows per compartment. Based on this status information of the individual compartments, an overall picture of the entire network can be obtained.

In order to quantify the internal fluxes per compartment, their underlying metabolic rates must be defined. According to Crisp, (1971), the individual metabolic rates of a species can be determined by means of the energy-balanced equation

$$C = P + E + R, \tag{1}$$

where C denotes the consumption, P the production, E the egestion and R the respiration of the considered compartment. More specifically, in terms of the primary producers, it yields

$$GPP = NPP + R \tag{2}$$

(Crisp, 1971). Whereby, GPP represents the gross primary production, NPP the net primary production and R the respiration of the organisms. All further steps of the ENA and its extension presented in this paper are based on this metabolic equilibrium for each model compartment.

2.2. Background: Steady state versus continuous influence

ENA allows the structural and functional investigation of relationships in ecological network models. The input and output flows defining the interactions of each compartment in the network must be in steady state for most ENA indices (cf. Section 2.6), otherwise imbalances in the flows can significantly bias the indices leading to a distorted interpretation of the system relationships (cf. Baird et al., 2009; Kay et al., 1989). Based on the internal metabolic equilibrium of each compartment (see Eq. (1) and Eq. (2)), the inclusion of a compartment into the network is then determined by adding external influences (from outside the system as well as connections between the compartments).

The steady state represents a balance between the sum of all input and output flows to each compartment (vertex) i of the network with a total number of N compartments. The input of each compartment is therefore equal to the respective output. Thus, the entire network is in a steady state. It yields

$$I_i + \sum_{k=1}^{N} S_{ki} = \sum_{j=1}^{N} S_{ij} + U_i + R_i \qquad \text{with} \quad \forall i \in [1, \ldots, N], \tag{3}$$

where the left side of Eq. (3) represents all input flows and the right side all output flows (Ulanowicz, 2004). I_i denotes the external import of the respective compartment i, S_{ki} and S_{ij} the incoming and outgoing network-internal transfer flows such as consumption or egestion. The rate of export of non-dissipative energy units to not further specified external outside (higher trophic levels, etc.) is denoted by U_i. Dissipative energy, for instance generated by respiration of organisms in an ecosystem, is represented by R_i.

The explicit integration of an abiotic factor into the network model affects all compartments and their relations with each other and with their environment, individually and collectively. In order to allow for a comprehensive analysis of dynamic shifts of abiotic factors and their superposition as well as their additive effects, they must be integrated as a continuous influence on the network in steady state. However, this is difficult to accomplish due to the overlap of two different modeling

concepts.

The network model described by ENA is in steady state and therefore represents a static model (Kay et al., 1989; Ulanowicz, 2004). It describes a specific state of the system at a certain point in time. Simply speaking, it can be thought of as a "snapshot" of the system. However, an abiotic factor is typically variable and needs to be included as a dynamic influence describing a continuous trajectory in time. This is not a problem in dynamic models (e.g., represented by Ordinary Differential Equations; Caldwell & Ram, 1999). Nevertheless, merging these two different concepts may cause issues in terms of integrating an abiotic factor into an ecological network model with ENA. The challenge arises when attempting to incorporate a dynamic external factor into a static model system, as the latter is unable to directly respond to external forcing in a spatially or temporally continuous manner (Horn et al., 2021). The implementation of dynamic abiotic factors on the individual compartments not only results in the overall structural and functional effect on the considered network, but also as indirect propagating influence effects and their superimposition.

2.3. Integration concept and workflow

To enable the analyses of effects of varying abiotic factors on a static modelled ecological network, with subsequent ENA, we here present a concept for integrating these influences into the model. The basic idea is to discretize the continuous influence of the abiotic factor and to calculate and analyze the corresponding response in the model for each discretization step. The result is an improved development of ENA indices with regard to the abiotic factor variation. Metaphorically-speaking, the original "snapshot" type analysis describing the basic steady-state model, becomes multiple "shots" which as a sequel of shots become "flip-book"[a] like, depicting the more continuous effects of the abiotic factor at a higher or lower frame rate depending on the required resolution. While the concept does not allow for a totally dynamic integration, it does however, hugely increase the resolution. Thus, it can provide a better assessment of the underlying structural and functional effects of a dynamic abiotic factor on a static network model and actual trends in ENA indices.

We need to stress that in this work, we do not consider the influence of abiotic conditions on the fluctuation of the system around the equilibrium (steady state). Instead, we focus on the influence of abiotic factors on a new adopted equilibrium. When integrating different abiotic conditions, we always assume that the system is in a steady state.

In order to integrate dynamic shifts of the abiotic factors into the network model and to analyze it with ENA, several construction steps were considered. The workflow used consists of three components: preparation, implementation, and evaluation. The actual integration step is located between model preparation and evaluation using ENA (Fig. 1). For the preparation step, a basic network model of the ecosystem has to be designed following the guidelines of Fath et al. (2007). Following this step, a reference file for the response of individual model compartments to the specific external factor and the range of the abiotic factor was required. The operation range of the abiotic factor was initialized as a vector, which also defined the discretization steps.

In the integration step, the abiotic influence was implemented into the base network by means of a loop over the individual discretization steps of the external factor to be included (cf. "2. Integration" in Fig. 1). The number of loop passes was defined by the chosen discretization density. In each loop pass, fluxes were first updated according to the applied abiotic factor value. All internal and external fluxes of the respective sensitive compartments were adjusted according to the aforementioned processes in the steady state condition in Eq. (3). A

detailed description of the direct and indirect flux adjustments of the network using the example of temperature can be found in the following Section 2.5.

The steady state condition (cf. Eq. (3)) of the updated network model was no longer satisfied after adjusting the network fluxes. This is due to the fact that the individual flows react differently to shifts of an acting abiotic factor and therefore do not change proportionally to each other. To allow an analysis of the network using all ENA indices, the model was rebalanced by the routine *balance()* included in the enaR package version 3.0.0 (Borrett & Lau, 2014; Lau et al., 2017). During the balancing process, the steady state condition is established between all input and output fluxes at each model compartment according to the balancing routine employed. In our study, we used the AVG2 method as described in Allesina & Bondavalli (2003). Subsequently, the integration step was completed by an uncertainty analysis according to Hines et al., (2018) in order to quantify uncertainties in the model construction, the model integration of abiotic factors and successive model balancing. The quantification of uncertainty was done using the enaR function *enaUncertainty()*. This function utilizes the adapted Linear Inverse Modeling (LIM) technique in combination with Monte Carlo sampling, which quantifies the uncertainty range in the calculated model fluxes (Hines et al., 2018).

Each loop pass yielded an ensemble of balanced models defined by the uncertainty analysis. Consequently, each discretization step of the range of the abiotic factor resulted in an ensemble of possible network models that quantify the defined uncertainty. In the final evaluation step, (cf. "3. Evaluation" in Fig. 1), the models of the ensemble were structurally and functionally evaluated using various ENA indices (Kazanci & Ma, 2015; Ulanowicz, 2004) provided in the enaR package. The concept therefore allows an investigation of the development of ENA indices in relation to shifts in the considered abiotic factor. Code examples for the application of the concept described here can be found in the supplementary material.

2.4. Temperature dependence

Temperature has a major influence on many physical and biogeochemical properties of the oceans, especially in the context of climate change (IPCC AR6 WG 1, 2021; IPCC AR6 WG II, 2022) and can therefore directly and indirectly affects biodiversity and the structure of entire ecosystems (cf. Doney et al., 2012; Scavia et al., 2002; and references therein). The temperature dependence of individual species compartments or, more specifically, their metabolic rates is often described in ecosystem models using Q_{10} coefficients (cf. Archibald et al., 2022; Laufkötter et al., 2015). According to Prosser (1961), temperature dependencies of a metabolic rate (production, consumption, respiration, egestion, etc.) using Q_{10} values can be quantified as

$$R = R_0 \cdot Q_{10}^{\frac{T-T_0}{10}}, \qquad (4)$$

where R_0 denotes the metabolic rate at reference temperature T_0, R the adapted metabolic rate at the considered ambient temperature T and Q_{10} a factor that describes the ratio of two (metabolic) rates at an increased temperature of $10°$.

The temperature dependence described by Eq. (4) accounts for an exponential relationship characterized by the Q_{10} value. An exponential curve fitting of dependence behavior is not necessarily realistic, especially at higher temperatures. Baretta & Ruardij (1988) therefore propose a correction to flatten the temperature dependence towards higher temperatures. This correction can be expressed as

$$R_T = \frac{\mu \cdot R}{\mu + R - 1}. \qquad (5)$$

The parameter μ represents a constant, which describes the maximum correction factor of the adjusted metabolic rate R and is assumed to be $\mu = 3 \, [\text{mgC}/\text{m}^2\text{d}]$ (Baretta & Ruardij, 1988). In the

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[a] flip-book: "a series of illustrations of an animated scene bound together in sequence so that an illusion of movement can be imparted by flipping them rapidly" after (Merriam-Webster, 2024)
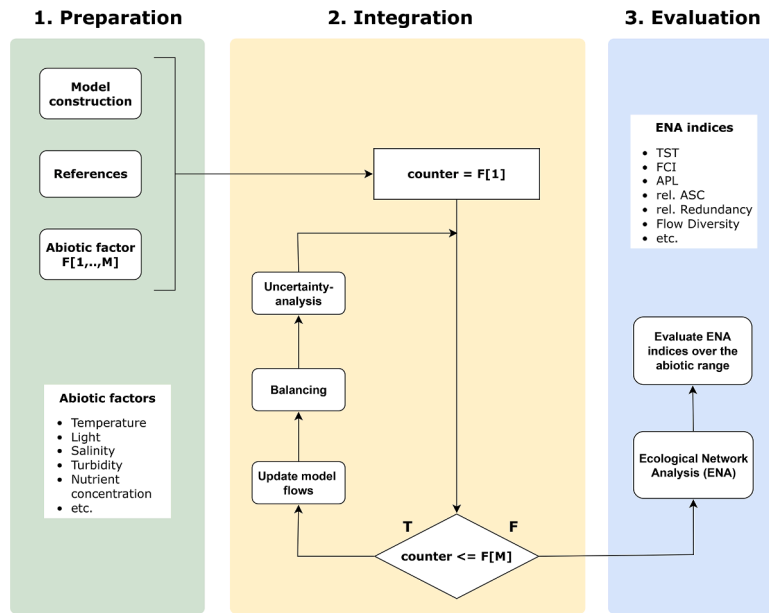
Fig. 1. Schematic workflow for incorporating a continuous abiotic factor into a static network model with a subsequent Ecological Network Analysis (ENA). In the first preparation step, some preconditions must be created. In addition to the formulation of the basic model, a reference file describing the response of the individual compartments to the specific abiotic factor and the range of the abiotic factor $F[1,..,M]$ must be defined. The integration is therefore calculated along the defined range using a for-loop, resulting in an ensemble of balanced models per abiotic discretization step according to the uncertainty analysis. Finally, the structural and functional influence of the abiotic factor under consideration is evaluated using ENA from the enaR package.
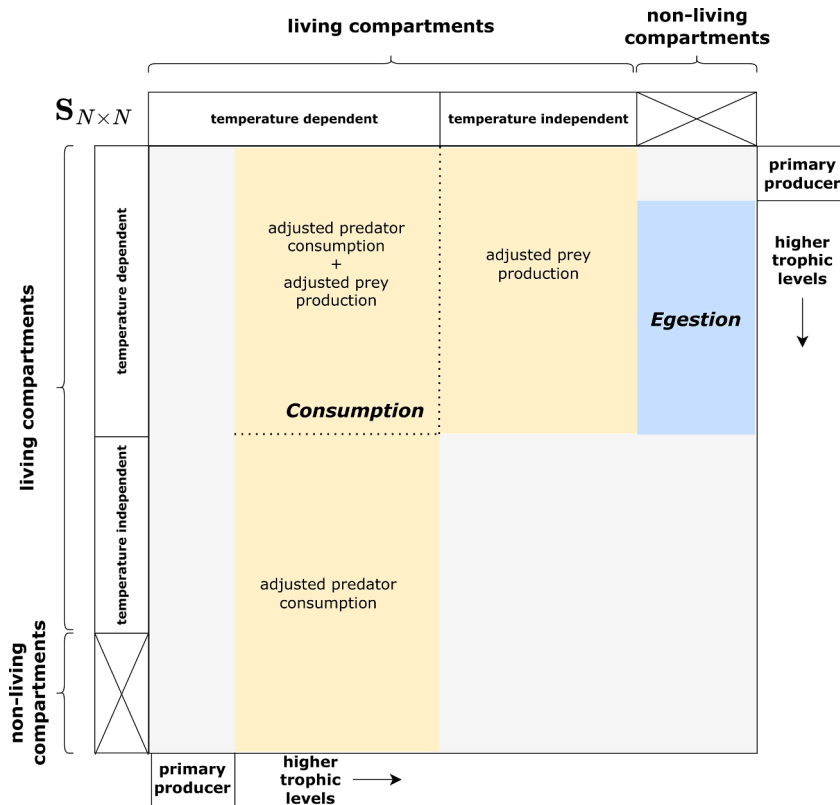

Fig. 2. Scheme for adjusting the flow matrix $S_{N \times N}$ (reading direction: row (donor) to column (acceptor)) in response to changes in temperature. The adjusted egestion is shown in blue and the consumption of the higher trophic levels in yellow. Gray areas of the flow matrix remain unchanged, as the flows localized here are temperature-independent. The area containing the consumption flows is divided by a dotted line into three different sub-areas. According to Eq. (6), these subareas represent the direct temperature effects and/or indirect effects that are included in the flow adjustment due to their temperature dependence of the donors and acceptors.

following, we denote the corrected metabolic rate at ambient temperature T as R_T.

2.5. Adjustment of model flows due to their temperature dependence

The relationships between the different compartments of the model and their external connections must be adjusted with respect to the temperature dependence of each compartment. At the network level, an adjustment of the individual fluxes represents an adjustment of the network to the initial state and the change in temperature. Therefore, it was assumed that changes in temperature directly affect the compartments and also propagate indirectly through the network. Accordingly, even compartments which are not directly influenced are affected by the individual change in their adjacent compartments and beyond. Consequently, there is an overlap of temperature dependency levels at a considered compartment of the network.

Prior to the quantification of the indirect effects, the direct temperature influence must be included. For this purpose, the model flows of each compartment (cf. Eq. (3)) were adjusted based on the temperature dependencies of the respective underlying metabolic rates (cf. Eq. (1) and Eq. (2)). The metabolic rates were calculated according to the general temperature dependency equations shown in Section 2.4.

Except for respiration (R) and GPP, all metabolic rates were assigned to internal flows between two compartments of the network. They were arranged according to the respective transform or flow matrix $S_{N \times N}$ which describes the internal flows (cf. Eq. (3)) of the N-dimensional network. The production P (or NPP for the primary producers) was only used to calculate consumption and is therefore not denoted as an extra network flow. All metabolic rates shown in Eq. (1) and Eq. (2). were assumed to be temperature dependent hereafter.

The metabolic rates of the respective temperature-dependent compartments were calculated according to the adjusted Q_{10} relation in Eq. (5). The respiration R and the egestion E were directly assigned to the respective flows. The latter one is an internal flow, which can be found in the flow matrix $S_{N \times N}$ (cf. Fig. 2). Metabolic rates of non-temperature-dependent compartments (i.e., endothermic compartments) remained unchanged.

In addition to egestion, the flow matrix $S_{N \times N}$ also contains the consumption relationship between the individual compartments of the model. The consumption rates C were not assigned to the respective flows directly after their temperature adjustment, but were corrected afterwards. Therefore, the consumption flow C_{ij} from donator (prey) i to acceptor (predator) j (without the number of primary producers L) is expressed as

$$C_{ij} = \frac{P_i^T}{P_i^{T_0}} \cdot C_j \cdot \alpha_{ij} \qquad \text{with} \quad \forall i, j \in [1, ..., N-L], \tag{6}$$

where for $P_i^T = P_i^{T_0}$ holds

$$C_{ij} = C_j \cdot \alpha_{ij} \tag{7}$$

(adapted after Baird et al. (2019)). The consumption flow is composed of the temperature-adjusted consumption C_j of the acceptor j and the respective percentage contribution α_{ij} of the donor i to the diet of the acceptor. In addition, the product is corrected by the ratio between the reference production of the donor $P_i^{T_0}$ at T_0 and its adjusted production P_i^T at the considered ambient temperature T. Consequently, the temperature dependence of the metabolic rates is incorporated twice in the consumption flows between the different compartments; directly via the adjusted consumption of the acceptor and indirectly via the production of the donor (cf. Fig. 2).

The adjustments of the consumption flows did not always follow the same updated scheme. Depending on whether the metabolism of the donor and/or the acceptor is temperature-dependent, there are three different options to update the consumption flows (Eq. (6)), which are

shown in Fig. 2. For instance, the consumption between a temperature-dependent acceptor and a temperature-independent donor is shown in the lower left rectangle in Fig. 2. The "adjusted acceptor consumption", P_i^T is equal to $P_i^{T_0}$, which leads to the updating scheme according to Eq. (7). Therefore, the consumption flow of the acceptor was not indirectly affected by adjusting the production of the donor.

Eq. (3) shows, in addition to the flows resulting from the adjustments of metabolic rates, that there are also exchange flows of import I_i and export of non-dissipative energy U_i per compartment i. Except for GPP, which is directly temperature-dependent and accounted for in the import flow of the primary producer, the rest of the external flows do not depend directly on temperature. However, as a result of the restoration of the necessary steady state, an indirect adjustment of the external fluxes was carried out due to the subsequent balancing routine described in Section 2.3. The adjustment of the metabolic rates therefore has an indirect effect on the exchange of the network with the non-modeled environment.

2.6. Ecological network analysis (ENA)

The influence of temperature on the network model was analyzed structurally and functionally using ENA. The analyses comprise several analytical approaches, which are mainly divided into the analysis of the structure, the flows and the storage values of the considered network (Kazanci & Ma, 2015). The input information on the structure for the two example models below was provided in the usual SCOR format (Ulanowicz & Kay, 1991). The subsequent network analysis was conducted in R (version 4.2.2; R Core Team, 2023) with the package enaR (version 3.0.0 Borrett & Lau, 2014; Lau et al., 2017).

We investigated the effect of temperature adaptation on a selection of six indices representing the system structure and functioning (de Jonge & Schückel, 2021; Safi et al., 2019):

The Total System Throughflow (TST) quantifies the sum of flows of material or energy through all compartments of the system in the respective system currency. It describes the sum of all individual flows over all compartments (sum of all compartment inflows or outflows) (Fath et al., 2019) expressed as

$$TST = \sum_{i=1}^{N} \left(I_i + \sum_{k=1}^{N} S_{ki} \right) = \sum_{i=1}^{N} \left(\sum_{j=1}^{N} S_{ij} + E_i + R_i \right) \qquad \text{with} \quad \forall i$$
$$\in [1, ..., N]. \tag{8}$$

The Average Path Length (APL) describes the average number of compartments of the system through which a unit of material or energy flows before it leaves the defined system. The APL is calculated by dividing TST by the total external input over all compartments

$$APL = \frac{TST}{\sum_{i=1}^{N} I_i}. \tag{9}$$

According to Fath et al., (2019), the APL can be considered as a metric of the quantity of system activity generated by a considered unit passing through the modeled system.

The Finn Cycling Index (FCI, Finn, 1976) quantifies the fraction of the TST that does not pass through the network directly but remains longer in the system due to network cycles. It therefore corresponds to the proportion of the TST that passes through the same compartment more than once before it leaves the system and its expressed as

$$FCI = \frac{\sum_{i=1}^{N} TST_{c_i}}{TST} = \frac{1}{TST} \cdot \sum_{i=1}^{N} F_i \cdot \left(\frac{c_{ii} - 1}{c_{ii}} \right), \tag{10}$$

where TST_{c_i} denotes the fraction of cycled TST at compartment c_i. The total input or output at compartment i of the network in the steady state is therefore expressed as

$$F_i = I_i + \sum_{k=1}^{N} S_{ki} = \sum_{j=1}^{N} S_{ij} + E_i + R_i. \tag{11}$$

According to de Jonge & Schückel (2021), the FCI can be used as a metric for assessing the recyclability of the considered network currency. This ability of the network to use the respective currency effectively leads to increased independence of the system from external inflows (de Jonge & Schückel, 2021). In addition, the FCI is often used in the literature as an indicator for evaluating the development status of an ecosystem (Wulff & Ulanowicz, 1989) and the system resilience against perturbations (Saint-Béat et al., 2015).

The equation for quantifying the <u>Flow Diversity (H)</u> is derived from the Shannon index for diversity applied to the individual flows of the network model (MacArthur, 1955). The flow diversity can be calculated as

$$H = -\sum_{i,j} \left(\frac{F_{ij}}{F_{..}} \right) \cdot \log_2 \left(\frac{F_{ij}}{F_{..}} \right), \tag{12}$$

where F_{ij} denotes a flow from donor i to acceptor j. The dot represents the summation over the full range of the respective index. $F_{..}$ defines the summation of all network flows over i and j. The flow diversity H provides therefore an overview of the structural and functional complexity of the considered ecosystem. (Scharler & Fath, 2012)

The <u>relative Ascendency (rel. A)</u> describes the portion of the system's capacity (DC) that is used by the ascendency (A). Therefore, the rel. A is expressed as

$$rel. A = \frac{A}{DC}. \tag{13}$$

The development capacity (DC) is defined as

$$DC = -\sum_{i,j} F_{ij} \cdot \log_2 \left(\frac{F_{ij}}{F_{..}} \right), \tag{14}$$

and represents the maximum development capacity of the system. By definition, the DC represents the upper limit of the ascendency. The ascendency (A) combines the overall activity of a system and its organization. Thus, it represents a measure of the organization level and efficiency of the considered flows. The ascendency can be calculated as

$$A = \sum_{i,j} F_{ij} \cdot \log_2 \left(\frac{F_{ij} F_{..}}{F_{i.} F_{.j}} \right), \tag{15}$$

where $F_{i.}$ denotes the overall output of compartment i and $F_{.j}$ is the overall input to compartment j.

The ratio between the ascendency and the development capacity has been used to quantify the functional state of a system in terms of its efficiency and resilience (Fath et al., 2019). It therefore describes how a given unit of system currency is processed based on network organization and activity relative to its maximum capacity. The relative ascendency has been used to define a measure of <u>robustness</u> of a system. The robustness describes and captures the trade-off between the system organization and its degrees of freedom to react on system perturbations (Goerner et al., 2009). According to Fath et al., (2019) it can be expressed as

$$robustness = -a \cdot ln(a), \tag{16}$$

where a denotes the relative ascendency $rel.A = A/DC$.

The robustness is often used as an indicator to assess the ecosystem health and to quantify the "sustainability" at network level. Sustainable ecological networks are therefore located in a "window of vitality" defined by the balance between efficiency and the degree of freedom (Ulanowicz et al., 2009). This position guarantees a degree of organization adapted to external and internal properties, as well as the necessary network resilience.

2.7. Case studies

We applied the presented concept to two already published case study models to test methodical feasibility of our approach. The case studies serve as examples of methodological application and do not claim to be complete ecological investigations.

The modeled networks were chosen based on data availability for the approach. Decisive for case study selection were the available Q_{10} values for all network compartments and their corresponding reference temperatures.

2.7.1. Sylt-Rømø Bight

The first case study examined the structural and functional temperature dependence using ENA of the food web of the Sylt-Rømø Bight (SRB) at Danish-German border. The SRB model was originally implemented by Baird et al. (2004) and has since been extended in several subsequent studies (cf. Baird et al., 2008, 2012, 2019; de la Vega et al., 2018). The original model was aggregated into functional groups according to (de la Vega et al., (2018) and is comprised of 25 compartments (22 living and three non-living compartments). It includes sedimentary as well as benthic and pelagic pathways, which represent the internal and external fluxes of biomass as the systems currency.

The temperature dependencies of the individual model compartments were integrated according to the concept in Section 2.4. Each aggregated compartment includes several species exhibiting different abundances and, hence, biomass. The temperature dependence of the aggregated compartments was determined by the species with the highest cumulative biomass. The Q_{10} values and corresponding reference temperatures were taken from (de la Vega et al., 2018) and the sources cited therein (see supplementary material).

2.7.2. Ems estuary

The second case study was a food web model of the lower reaches of the Ems estuary on the northwest German coast of the North Sea near the Dutch border (de Jonge et al., 2019). The Ems estuary model was implemented to investigate the effect of spatial scaling, species aggregation and the balancing procedure on ENA indices (de Jonge et al., 2019). The model was aggregated into 24 compartments, with 21 living and three non-living compartments after de Jonge et al. (2019). The internal and external exchange fluxes in this network model also represent sedimentary, benthic and pelagic processes.

The temperature dependence of the metabolic processes was assigned according to the species with the highest cumulative biomass in a compartment. The Q_{10} values and corresponding reference temperatures were taken from the literature (see supplementary material).

2.7.3. Additional model settings

The same methodological parameterization was used for both case studies. Based on the annual average temperatures of both model regions (SRB: 9.89 °C (Baird et al., 2019); Ems: 10.48 °C (Baretta & Ruardij, 1988)), a temperature range of 9 °C to 15 °C was defined. The upper bound was chosen to include the global sea surface temperature (SST) increase of around 1 °C to 3.7 °C expected by the IPCC (Pachauri et al., 2015) and a scenario of +5 °C to investigate the structural and functional sensitivity of the system (Baird et al., 2019). In order to achieve sufficient resolution over the temperature range increments of 0.5 °C were used.

To quantify the uncertainty of the temperature dependent flow adjustments, the function *enaUncertainty()*, described in Section 2.3, was applied. The function is based on the Monte Carlo sampling technique and was defined with a sampling size of 10 000 model runs per temperature step. A variability of the flows of ± 50% was assumed, which follows a uniform distribution. By considering flow variability, it was possible to quantify the flow uncertainties and the sensitivity of the network to changes in its parameterization (Hines et al., 2018).

3. Results

The flipbook concept revealed trends in different ENA indices in relation to an increase in temperature. Fig. 3 shows a selection of six ENA indices and their development over the considered temperature range. Three indices were taken from flow analysis (TST, APL, FCI; cf. left side of Fig. 3) and three from information theory (H, rel. A, robustness; cf. right side of Fig. 3) to cover a range of the different index concepts of ENA with the method presented here.

The indices of the flow analysis mostly indicate an increasing linear trend for both case studies (cf. Fig. 3). The TST, APL and FCI of the SRB model show a linear increase over the investigated temperature range, with variations in the interquartile magnitude around the mean. The quantiles of the TST and APL are lower than those of the FCI, indicating a greater variability of the distribution of the Finn Cycling Index around its mean. The flow indices of the Ems model (cf. Fig. 3; blue) show a weak increasing trend in APL and FCI and a stronger trend in the Total System Throughflow (TST). Moreover, their variability around the mean value is smaller for APL and TST than for the FCI over the investigated temperature range.

Compared with the structural analysis, the development of the Sylt-Rømø Bight and Ems model indices derived from the information theory do not show a linear trend in all the examined indices. Fig. 3 indicates that the flow diversity of the SRB model shows a constant trend over the temperature range. The Ems model, on the other hand, demonstrates a slight increase in flow diversity H. In both case studies, the directly dependent indices of relative ascendency the rel. A and robustness show a slight saturating decrease and saturating increase, respectively. The interquartile range of rel. A and the robustness is higher than that of flow diversity H in both model examples, but especially for the Ems model.

Changes in temperature affect food webs, which is reflected not only in the ENA indices but also in the underlying biomass flows. Fig. 4 shows these differences in temperature response of the individual compartments of both networks as changes in nodal throughflow. For increasing temperatures, most compartments exhibit an increase in nodal throughflow in both models. However, there are exceptions such as the suspended POC and the zooplankton in the SRB model. Both compartments exhibit a very small range of variation. As shown in Fig. 4, the primary producers and detritus compartments, however, undergo the largest change during temperature variations in the SRB and Ems model.

4. Discussion

Flipbook ENA was developed here to enable a more continuous evaluation of the effects of environmental trends and changes on marine food webs. For the first time, we applied it to investigate drivers of ecological networks over a range of temperatures using the Sylt-Rømø Bight and the Ems food web model. The method significantly increases the power of the basic ecological network analysis, which operates on static snapshots of the networks.

4.1. Temperature dependence of case study networks

Both case studies revealed a similar trend for the investigated ENA indices over the defined temperature range (cf. Fig. 3). The shifts or its trends in indices in response to the increase in temperature shown for the Sylt-Rømø Bight model, are consistent with the study of Baird et al., (2019). However, in their work, the temperature was only increased by $+3\,°C$ and $+5\,°C$ degrees compared to the base model, so only a selective evaluation of the influence was possible. By using Flipbook-ENA it is now possible to describe a higher resulting trend in the temperature dependence over a defined range of temperatures.

The Ems model shows a similar trend in the ENA metrics as the Sylt-Rømø Bight model, although mostly with different magnitudes. While both networks are comparable in species composition, they differ in terms of network structure and reaction of metabolic processes to temperature changes. Flipbook-ENA indicated clear differences in the adjustment of biomass fluxes over the temperature range for both net-
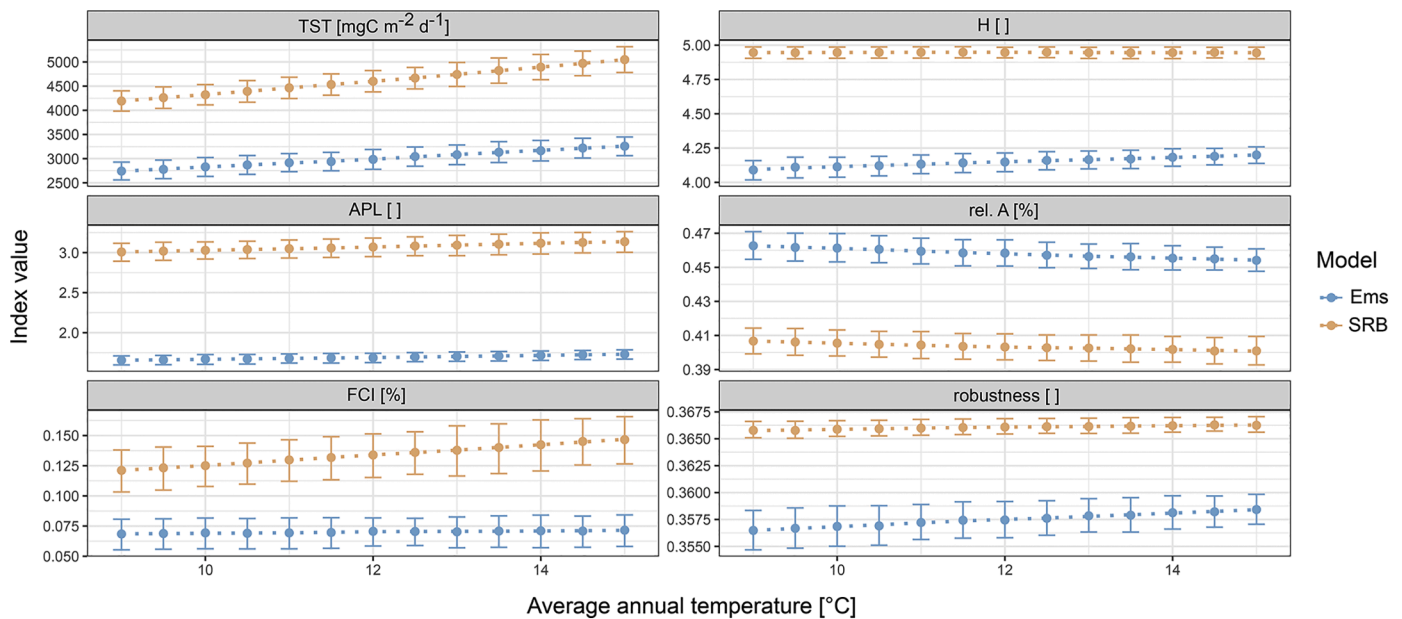

Fig. 3. Different ENA indices over temperature range with an average annual temperature increase for the Ems (blue) and SRB model (orange). The individual points represent the average value over the examined uncertainty ranges (10,000 model runs per temperature step) of the different fluxes, the dotted functions denote a trend line. The uncertainty bars indicate their corresponding 0.25 and 0.75 quantiles. Acronyms: TST = Total System Throughflow; APL = Average Path Length; FCI = Finn Cycling Index; H = flow diversity; rel. A = relative ascendency (cf. Section 2.6).
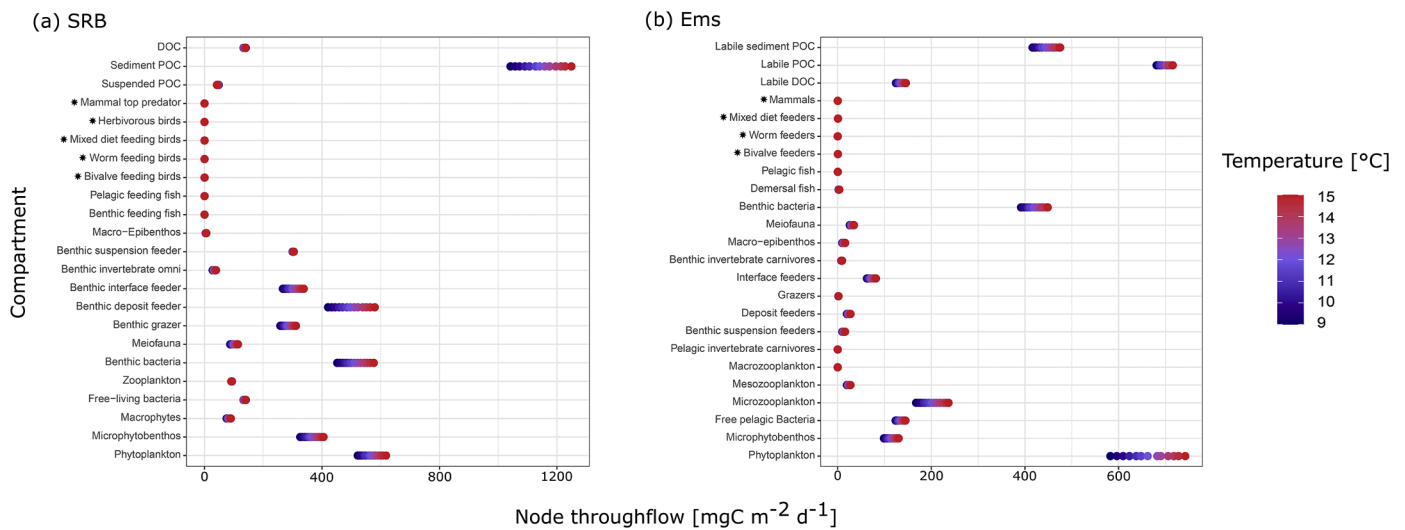
Fig. 4. Node throughflow variations per compartment of Sylt-Rømø Bight (a) and Ems (b) model over considered temperature range from 9 °C to 15 °C. Black stars denote non-temperature-dependent compartments. A broad color gradient shows a high variation of nodal throughflows and thus a strong temperature dependence. Narrower temperature dependencies of throughflows are characterized by a weak to no color gradient. Temperature-dependent compartments with node throughflows close to zero already have very low biomass fluxes in the basic model (see supplementary material).

works across all trophic levels (cf. Fig. 4) despite similar aggregation. These mainly result from differences in the network topology (different node degrees, influences of adjacent nodes, etc.) and inclusion of indirect effects of the approach. The concept therefore ensures that each compartment retains its' individual dependency and response to temperature variations.

Flipbook-ENA allows the comparison of trends between the two case studies, as this approach comprises a sequence of networks over the entire temperature range including its uncertainty per temperature increment. However, we do not recommend a direct comparison of the metric values in total or even per temperature step because a large number of the ENA indices significantly depend on the model implementation and on the aggregation of the model compartments in particular (cf. Abarca-Arenas & Ulanowicz, 2002; Baird et al., 2009). A specific example of the aggregation effect with regard to the Ems model used here can be found in de Jonge et al., (2019).

4.2. Temperature integration via Q_{10} values

ENA is based on energy fluxes (often biomass), defined by the metabolic rates of each compartment, between compartments of the investigated network. The abiotic factor temperature alters the weighted link value from one compartment to another and is defined by the direct temperature dependence of the metabolic rates of the different compartments. Thus, the direct influence of temperature on the metabolism of the compartment also determines the direct influence on the interaction of two neighboring compartments as well as the indirect influence over more than the adjacent node. Consequently, the implementation of temperature dependence in the model on a metabolic scale influences the functional behavior on network scale and its results.

Regardless of their spatial and temporal resolution, many models implement temperature dependence of their model entities and units using the Q_{10} representation (Archibald et al., 2022; Laufkötter et al., 2015). The temperature dependence by the Q_{10} value is modeled as an exponentially-increasing function on the community or, more specifically, on a functional group level. The calculation is therefore quite straight forward and simple if the corresponding metabolic rates are available (cf. Section 2.4). However, this simplification also leads to a few general problems as described below:

The assumption of the Q_{10} value as a constant for temperature dependence of metabolism within a defined species community is too

simplistic, both physiologically and with regard to the dependence on the influence of external factors. From a purely physiological point of view, metabolic rates (production, respiration, consumption, egestion, etc.) have a different sensitivity to changes in temperature and can only be minimalistically described by one common constant per functional group as is also used in this study. In addition, metabolic rates are closely related to species properties such as the size of the organism (Gillooly et al., 2001). Barton & Yvon-Durocher, (2019) show an example of size dependent metabolic rates in phytoplankton. Thus, temperature dependence varies even within the same community or even taxa (Anderson et al., 2021) and is shaped by the adjacent thermal environmental conditions and their physiological responses (Boersma et al., 2016; Chen, 2022).

The Q_{10} application of metabolic temperature dependence presents a broad challenge in terms of scaling, encompassing both temporal and intra as well as inter-specific aspects. This issue is particularly evident in the connection between an organism's metabolic rate and the fundamental physico-chemical processes (Chaui-Berlinck et al., 2002). The criticism extends to the upscaling of Q_{10} values in ecological models due to the challenge of transferring the metabolic temperature response of an individual organism to the community level.

At the intraspecific level, the temperature dependence of metabolic rates can be described by a unimodal function with negative skewness - characterized by a temperature optimum and the temperature range or niche considered (cf. Archibald et al., 2022; Barton and Yvon-Durocher, 2019; Chen, 2022; Montagnes et al., 2003). The community response to thermal changes is based on the assumption that the individual thermal curves, which occupy different niches along the temperature range, are arranged in a substitutive manner. This results in a distribution of occupied niches whose cumulative total response according to the respective temperature increases under the assumption of a continuous increase in metabolic rates with increasing temperature ("hotter is better"-hypothesis) (Barton & Yvon-Durocher, 2019). Based on these assumptions the overall thermal response of the community can be described by an exponential relationship (cf. Eppley, 1972; Gillooly et al., 2001; White et al., 2012).

Modeling the metabolic community response to temperature change using exponential correlation has been applied in a variety of models but has also been criticized (cf. Baretta & Ruardij, 1988; Mundim et al., 2020). A major point of criticism is the monotonicity of the exponential relationship resulting in unrealistically high metabolic rates at higher

temperatures (Chen, 2022). To avoid overestimation, we have included a saturation of the temperature dependence at higher temperatures according to Baretta & Ruardij (1988) in our concept (cf. Section 2.4). A uniform parameterization of the maximum correction factor (μ = const. for all species) allows the saturation of the metabolic rates, but this does not change between the individual species or compartments due to the lack of available data. Consequently, there is no overestimation of temperature dependence at high temperatures, but saturation is applied uniformly in a simplified manner to all compartments. Nor is there any recognition of shifts related to frequency of temperature hits which an organism will be adapted to see (Amorim et al., 2023; Boersma et al., 2016).

Modeling using Q_{10} can be calculated straightforward and has sufficient data availability. Although, there are more advanced approaches to model metabolic temperature sensitivity (Chaui-Berlinck et al., 2002; Chen, 2022; Grimaud et al., 2017; Mundim et al., 2020), these require other or additional parameters such as optimal temperature or the metabolic niche of the species. The procurement of data for new potential parameterizations is challenging, especially in network models which contain a large number of different compartments or even species. Thus, complex network models need to focus on the trade-off between simplification and data availability on temperature dependencies.

In general, the approach used in our study is not limited to the implementation of the temperature dependence via the Q_{10} representation. Its modular design also enables the integration of other more advanced temperature dependency concepts (see section below).

4.3. The flipbook as an ENA enhancement

Flipbook-ENA is neither completely static nor continuous. It is an in-between of model classes. It is basically a frequent succession of adapted network models with subsequent ENA - a sequence of snapshots. Freely translated from the field of image technology: it is a flipbook, a juxtaposition of individual images that are viewed continuously as a sequence. Depending on its frequency, a continuous representation will be approached, but will not be reached. This basic idea allows a trend analysis of ENA indices under the influence of an abiotic forcing without discarding the model's theoretical basis.

By defining the unit of the model, the network is tailored to a specific research question. Subsequently, direct external influences on the network, such as temperature, can be investigated with Flipbook-ENA. Indirect external effects that do not directly affect the metabolism of the modeled compartments, on the other hand, cannot be represented. An example related to temperature dependence are shifts in nutrient availability or changes in hydrodynamics under increasing temperatures.

The concept presented in this paper is not limited to temperature dependence, but can be applied to other abiotic factors (salinity, light availability, turbidity, etc.). Moreover, it is not important how exactly the considered network is constructed as long as the requirements for an ENA are met. All advantages of the ENA are retained and the ability to observe the structure and function of networks over a range of abiotic forcing factors is added.

Flipbook-ENA is based on the adjustment of the biomass flows of the network in response to one specific external factor. Consequently, there is a lack of superimposition of multiple abiotic factors via compartment-specific response functions and the adaptation of biomass stocks to changes in abiotics. However, the latter is not so relevant for trend analysis of many structural and functional indices as they are only based on the adjusted biomass flows between the compartments (cf. Kazanci & Ma, 2015). The superimposition of several abiotic factors or the modification of the network topology (e.g., due to extinction and invasion of species or changes in feeding behavior) in response to abiotic shifts could be considered in the future. The combined effects of multiple abiotic factors (nutrient concentration, salinity, light availability, turbidity) may be used to simulate the influence of their positive and

negative interference on food webs at different spatial and temporal scales. This would lead to non-linear responses at both the species and network level, which would also be reflected in the ENA indices under consideration.

The approach introduces uncertainties arising from the network implementation, which are already known from the standard ENA. For instance, a significant source of uncertainty is the aggregation of Multiple species into one network compartment of the model (cf. Abarca-Arenas & Ulanowicz, 2002; Baird et al., 2009; de Jonge et al., 2019; Giacomuzzo & Jordán, 2021). The type of aggregation and the resulting structure of the network have therefore an influence on the evaluation and development of several ENA indices (Baird et al., 2009) and other general network characteristics (Giacomuzzo & Jordán, 2021).

The different uncertainties are quantified within the working flow of this concept by the function *enaUncertainty()* after Hines et al. (2018) based on the Monte Carlo sampling technique (cf. Section 2.3). Uncertainty in network flows arises from several sources. The main sources of uncertainty are the experimental data used to calculate the flows and the inclusion of temperature dependence through the simplified Q_{10} representation. In addition, the applied balancing routines also creates variation that affects the calculation of the ENA indices (Allesina & Bondavalli, 2003; Baird et al., 2009). The uncertainty analysis applied in the concept does not allow for the quantification of individual sources of these uncertainties, instead it covers the cumulative uncertainty. Therefore, due to the relatively dispersed variation, the quantification of the metric considered in each abiotic step is not recommended. Instead, we recommend a trend analysis for the entire abiotic range. Reducing that variation is achievable through experimental measurements of the included data sources, with a focus on species-specific metabolic responses to changes in the influencing abiotic factors.

4.4. Comparison with other modeling approaches

Flipbook-ENA allows us to approximate the dynamic development of the network via the abiotic factors, i.e., indirectly over time. A method to model dynamic ecological networks, which are continuous over time, is Ecopath with Ecosim (EwE). This widely used method was mainly developed for the evaluation of fisheries policies and their assessment (Christensen et al., 2005). EwE combines network analysis based on storage and flows of different network units (Ecopath) with the capability of time dynamic modeling (Ecosim) to predict potential future scenarios (Christensen & Walters, 2004).

A comparison of our Flipbook-ENA concept with EwE shows a few general differences arising from the model purpose and its corresponding approach. EwE is used here as a comparison because it applies a similar base model. According to Dame & Christian (2006), "manual" network construction followed by ENA (the basis of Flipbook-ENA) focuses on the structural and functional investigation and evaluation of a particular network snapshot, whereas EwE generally focuses more on the dynamics of the network system. EwE therefore targets the prediction of possible future scenarios, particularly with regard to the standing stocks (biomasses) of the network compartments. The different model purpose also results in the different model approach. Flipbook-ENA is a static model that approximates the dynamic development via an abiotic factor in order to recognize a trend while EwE is a continuous model based on differential equations.

In addition to the differences in model theory, there are also differences in the inclusion of abiotic factors. In EwE, effects of abiotic factors only change certain model parameters, but not the overall metabolism of all compartments of the network (Horn et al., 2021). In contrast, Flipbook-ENA allows to selectively modify the overall metabolism of all model compartments directly based on various metabolic processes. Additionally, it is possible to determine the specific and different dependencies of the individual compartments and their metabolic rates individually by means of various mathematical implementation options. Flipbook-ENA thus offers a high degree of specification of abiotic

influence at different network scales.

In order to generate the high level of specification of the concept presented here, extensive data sets are required. While EwE allows the estimation of some parameters of the model especially in the area of metabolic rates, the "manual" network generation with subsequent ENA requires more empirical data for the construction process (Heymans & Baird, 2000). However, the internal parametrization routines of EwE have shortcomings especially with respect to the implementation of the abiotic dependence of metabolic rates. For example, respiration is not directly implemented and used, instead it only plays a role in balancing (Christensen et al., 2005). The application of both concepts is therefore based on a trade-off between the resolution of the abiotic dependence of the network and the parametrization effort with regard to the data acquisition.

In contrast to Flipbook-ENA, where the basic network model is approximately dynamized but the ENA remains unchanged, other approaches (cf. Kazanci & Ma, 2012; Shevtsov et al., 2009) adapted the ENA to dynamic network models. The advantage of utilizing a dynamic network model with adapted ENA is that it eliminates the necessity of assuming a forced steady state, thereby obviating the need to balance the model. This approach inherently acknowledges the lack of balance in ecological networks. However, this method requires considerable efforts in the model implementation, parameterization, and simulation compared to Flipbook-ENA. Vice versa, Flipbook-ENA allows the integration of abiotic factors into already existing static network models. When abiotic data and the corresponding metabolic responses of model compartments are available, this method can be implemented with relatively little effort, while simultaneously utilizing all "conventional" ENA options. The use either of one of the two approaches depends on the data availability and also the research question.

4.5. Flipbook-ENA's potential in times of global ecosystem change

The two case studies have demonstrated the potential of Flipbook-ENA to investigate and quantify dynamic abiotic shifts in ecological networks. Our concept enhances ENA with the option of a trend analysis of the various ENA-indices, which allows the quantification of the changing network properties and functions. This quantification enables the analysis of the influence of changing abiotic conditions as well as the prediction of possible consequences of certain assumed scenarios. For instance, with regard to temperature, Flipbook-ENA permits the simulation of different IPCC scenarios (cf. IPCC AR6 WG 1, 2021; IPCC AR6 WG II, 2022) to be examined on an ecological network.

Flipbook-ENA allows to analyze the influence of different abiotic factors on a structural and functional level. The method provides the framework which can be extended to other abiotic factors such as nutrient availability, salinity or light availability. This potential for easy adaptation is crucial because understanding how ecosystem networks change in times of global change requires examining multiple abiotic factors, rather than focusing solely on one. Only investigating multiple factors and their combinations enables a comprehensive analysis, better understanding, and consequently realistic predictions.

It is essential to consider the ecosystem as a network to evaluate and assess stressor-induced changes in ecosystems (c.f. Horn et al., 2021; Woodward et al., 2010). Consequently, the evaluation of networks is based on the quantification of topological and functional properties. Flipbook-ENA reinforces the advantage of "state of the art" ENA to quantify complex network properties of ecosystems and make them accessible for management strategies. In contrast to a fixed static network, Flipbook-ENA facilitates the quantitative assessment by various stakeholders (from science, industry and policy) to quantitatively assess the state of an ecosystem, using the comprehensible indices of ENA. As a result, it will be possible to conduct trend analyses and predictions on the alteration of ecosystem networks due to global change. These insights are crucial for formulating and implementing targeted management response strategies.

5. Conclusion

For the first time, Flipbook-ENA allows an investigation of dynamic shifts of abiotic factors (temperature, salinity, nutrient concentration, etc.) on static ecological networks using the Ecological Network Analysis (ENA). The resulting trend analyses of ENA indices, allow both the structural and functional understanding of networks as well as a prediction of their change. The method, as developed in this study, improves the predictive ability of the "state of the art" ENA to analyze important ecosystem management parameters. This capability enables the testing of different alteration scenarios of ecological networks under various stressors, which is essential for recommending actions to stakeholders. Flipbook-ENA presents a first step towards a holistic dynamic ecosystem analysis in times of global change.

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CRediT authorship contribution statement

Joel Habedank: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Visualization. **Sabine Horn:** Conceptualization, Resources, Validation, Writing – review & editing, Supervision. **Dan Baird:** Resources, Validation, Writing – review & editing. **Peter Lemke:** Writing – review & editing, Supervision. **Jasmin Renz:** Validation, Writing – review & editing. **Vera Sidorenko:** Conceptualization, Writing – review & editing. **Karen H. Wiltshire:** Conceptualization, Validation, Writing – review & editing, Supervision.

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.

Data Availability

All model data used and the corresponding R scripts can be found in the published supplementary material.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2024.110834.

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