Original Articles

Robustness of macroscopic-systemic network indices after disturbances on diet-community matrices

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ABSTRACT

The macroscopic ecosystem properties of thirteen trophic networks based on Ulanowicźs *Ascendency* and Odum's indices were re-estimated for (1) previously published data ("Baseline"), (2) after simulated modifications in the percentage of assimilated food ("AssimScenario") and (3) after simulated reductions of the number of links of consumers ("DietScenario"). The community matrices of "Baseline" models were constructed using the classic stomach content analysis (SCA), and both model simulated scenarios ("AssimScenario" and "DietScenario") represent two ways to include the information given by stable isotope analysis (SIA). The macroscopic-systemic network indices of the studied ecological systems along the Chilean coast concerning growth, organization, development, maturity, health, complexity, and resistance against disturbances were confirmed, regardless of whether the community matrices were constructed using SCA or SIA. SIA is recognized as a useful technique for the quantification of the energy webs in ecosystems; nevertheless, it reduces the richness and complexity of trophic connections, linearizing the relationships. The reduction of the complexities of community matrices constructed by SIA could be avoided, if the *Ecopath with Ecosim* software is used due to a modification of the percentage of assimilated food during the input data and balancing procedure ("AssimScenario"). The SCA still offers a chance for an approach to trophic complexity, increasing our prediction capacity. Consequently, energy webs and trophic networks should not be considered as the same but as complements of each other. Hence, the use of both techniques is recommended.

1. Introduction

Ecological network analysis (ENA) has been widely applied in recent years, including for estuarine, oceanic and coastal ecosystems (Christian et al., 2005). ENA appeared as an alternative or complementary strategy to reductionist abstractions (where isolation is the principal rule), integrating a finite set of "core" variables that represent and describe the dynamics and structures of the ecosystems to which they belong (Pickitch et al., 2004). The application of ENA based on food webs has proven to be an efficient tool for the estimation of the macroscopic or emergent properties of ecosystems; for assessing the structure, dynamics and overall health of ecosystems (Costanza and Mageau, 1999); as well as for predicting the propagation of direct and higher order effects and system recovery times (as a measure of stability) in response to human disturbances (e.g., Monaco and Ulanowicz, 1997; Jørgensen, 2000; Ortiz, 2008). The principal features of ENA include (1) the interactions in a food web being represented as flows of energy or matter and (2) the species or some subset of the species have to be aggregated into functional groups, which is principally explained

by data availability, software limitations (Cohen et al., 1993; Morris et al., 2005) and the ecological questions to be explored.

Professor Robert Ulanowicz has dedicated valuable research time to developing a theoretical framework called *Ascendency*, which describes the growth and development of ecosystems at the systemic approach (Ulanowicz, 1986, 1997). The main macroscopic descriptors associated with this analysis are *Ascendency* (A), *Total System Throughput* (TST), *Overhead* (Ov), *Development Capacity* (C), A/C and Ov/C ratios. *Ascendency* (A) is obtained by quantitatively scaling the number of flows measured as the *Total System Throughput* (TST) and the organization quantified as the *Average Mutual Information* (AMI) (Ulanowicz, 1986, 1997). Therefore, *Ascendency* integrates both the size and organization of the systems based on information theory. *Ascendency* and *Overhead* have been related to system "stability" (Christensen, 1995; Cropp and Gabric, 2002) and maturity (Ulanowicz and Abarca-Arenas, 1997; Perez-Espana and Arreguin-Sanchez, 2001; Fath et al., 2001; Cropp and Gabric, 2002). *Overhead* corresponds to the difference between the *Development Capacity* and *Ascendency* and indicates the multiplicity of informational pathways, which may be closely related to the resistance

system's robustness to perturbations (Christensen, 1995; Angelini and Petrere, 2000). The *Development Capacity* quantifies an upper limit of *Ascendency*, and the A/C ratio describes the network efficiency (used as the maturity index) (e.g., Baird and Ulanowicz, 1993; Costanza and Mageau, 1999). However, the A/C and Ov/C ratios can also be used as indicators of ecosystem development (Kaufman and Borrett, 2010) and an ecosystem's ability to resist disturbances (Ulanowicz, 1986, 1997). *Ascendency* has been widely used to describe and compare a variety of ecosystems characterized by different geographic locations, spatial sizes and complexities (Monaco and Ulanowicz, 1997; Niquil et al., 1999; Heymans and Baird, 2000; Ortiz and Wolff, 2002; Arias-González et al., 2004; Patrício and Marques, 2006; Ortiz, 2008; Panikkar and Khan, 2008; Ortiz et al., 2009, 2013, 2015, 2016; Li et al., 2009; Kaufman and Borrett, 2010; Li and Yang, 2011; Díaz–Uribe et al., 2012; Bayle-Sempere et al., 2013; Cáceres et al., 2016; González et al., 2016; Rodríguez-Zaragoza et al., 2016; Ibarra-García et al. (2017)). Likewise, the four indexes given by Odum (1969) regarding the ecosystem development and maturity were also considered in the current work: (1) the total primary production/total respiration ratio (TPP/TR ≈ 1 for mature ecosystems); (2) the total primary production/total biomass ratio (TPP/TB tends to lower values of mature ecosystems); (3) the total biomass/total system throughput ratio (TB/TST increases via energy storing in mature ecosystems); and (4) the food web connections(FWCo tends to be higher in mature ecosystems).

The application of Ulanovicz's and Odum's theoretical frameworks requires information about population dynamics (i.e. biomass, consumption, mortality and productivity) and those regarding the feeding relationships of the species or functional groups in the network. To date, two analytical techniques have been used to build food webs: (1) traditional stomach content analysis (SCA), commonly describing the proportion or percentage of each type of food found (Cortés, 1997); and (2) stable isotopic analysis (SIA), determining the isotopic ratios of $\delta^{13}C$ in the tissues, which is used to evaluate trophic relationships. This technique assumes that during the ingestion of food and excretion of wastes, there is an enrichment of the heavier isotope $\delta^{13}C$ (by fractionation) (Olive et al., 2003). Therefore, a predator will have a higher proportion of the heavy isotope than the prey on which it feeds (Fry and Sherr, 1984; Domi et al., 2005; Boecklen et al., 2011). Recently, the SIA has become popular among scientists in the biology, ecology and conservation fields as a technique to assess the flow of carbon and nitrogen in the ecosystems as well as other processes (Peterson and Fry, 1987). Although some authors have proposed using SIA to "re-construct diets" (Tieszen et al., 1983; Samelius et al., 2007; Boecklen et al., 2011), others recognize the complementarity of both techniques (Whitledge and Rabeni, 1997; Burns et al., 1998; Beaudoin et al., 1999; Grey et al., 2002; Hollows et al., 2002; Ruiz-Cooley et al., 2006; Dehn et al., 2007; Drazen et al., 2008; Polito et al., 2011). A comparison between both techniques shows that the SIA tends to reduce the number of diet items in the organisms compared to the traditional SCA (Hollows et al., 2002; Dehn et al., 2007; Drazen et al., 2008; Muñoz et al., 2011). One explanation for this would be that most consumers are not sufficiently selective at any moment to capture their food, interacting with other organisms during their feeding. Therefore, the SIA could be hiding or underestimating the complexity of the trophic webs because it only quantitatively describes the assimilated food (energy converted in somatic tissue), which is just a fraction of the total stomach content.

Along the Chilean coast (SE Pacific), thirteen trophic webs have been constructed to assess and compare the size, organization, complexity and healthy properties of benthic/pelagic ecological systems using the Ulanowicz's and Odum's theoretical frameworks (see Fig. 1). For these trophic webs, the predation and herbivore relationships were determined using the traditional SCA. Therefore, the objective of the current work is to compare the macroscopic or emergent properties of these thirteen trophic webs with the properties of new trophic networks in which the percentage of unassimilated foods was modified and the items of food of some organisms or groups were intentionally reduced,

both simulating the outcomes of SIA. To do so, new mass-balance models for these thirteen previously published models were obtained using the software *Ecopath with Ecosim* v.6.0 (Polovina, 1984; Christensen et al., 2004). Likewise, the implications of the outcomes obtained for SCA and SIA using generalized Lotka-Volterrás prey-predator equations will also be analysed.

2. Materials and methods

2.1. Multispecies modelling and macroscopic ecosystemic properties

All models were re-analysed using the *Ecopath with Ecosim* software (v. 6.0) (EwE) (www.ecopath.org). *Ecopath* was first developed by Polovina (1984) and was further expanded to include several additional routines (Christensen and Pauly, 1992; Walters et al., 1997). The *Ecopath* model combines a steady-state description of the matter/energy flows within an ecological system at a particular time with Ulanowicz's (1986, 1997) and Odum's (1969) system analyses for the calculation of the macroscopic properties of the ecosystem. EwE is based on a series of linear equations, assuming mass-balanced compartments in the model. The general equation (Eq. (1)) can be expressed as follows:

$$\frac{B_i}{dt} = P_i - (B_i * M2_i) - P_i * (1 - EE_i) - EX_i \tag{1}$$

where biomasses (B) (g wet weight [ww] m^{-2}) is at a steady-state, P_i is production (g ww m^{-2} year^{-1}), $M2_i$ corresponds to predation mortality (year^{-1}), EE_i equals the ecotrophic efficiency (%) that quantifies the proportion of the production utilised in the system, 1- EE_i is the other mortality of i (year^{-1}), and EX_i corresponds to the export (g ww m^{-2} year^{-1}). For all re-analysed models, several field studies were carried out to select the variables (species and or functional groups) of each ecological system and to estimate the biomass (B_i), catches (Ca_i), turnover rates (P_i/B_i), consumption rates (Q_i/B_i) and food items of the selected variables. For estimations of turnover rates (P_i/B_i), between 8 and 10 length frequencies were obtained by sampling, which were used to calculate the initial growth parameters (K and Loo) adjusted to the von Bertalanffy growth function. Once the growth parameters were estimated, the instantaneous rate of the total mortality (Z_i) was estimated using the length-converted catch equation (Sparre and Venema, 1998). It is important to mention that Z is an approximation of P/B (after Allen, 1971). Consequently, the production (P_i) was estimated as $P_i = B_i * P_i/B_i$. The consumption rates (Q_i/B_i) were estimated for the 24-hour cycle following the procedure given by Cerda and Wolff (1993). To determine the food spectrum of the principal benthic species, the stomach and gut were extracted, the gut content was classified to the lowest possible taxonomic level, and the frequency of occurrence of each food item was calculated. Predation mortality ($M2_i$) depends on the predator activity, is defined as the sum of consumption by all predators (j) preying on a species or functional group (i) and can be expressed as:

$$B_i * M_i = B_j * \frac{Q_j}{B_j} * \frac{D_{ji}}{C_{ji}} \tag{2}$$

where Q_j/B_j equals the consumption/biomass of predator j (year^{-1}), and D_{ji}/C_{ji} corresponds to the fraction of prey i in the dietary spectrum of predator j. Even though for each variable in the models the key input parameters are B_i, P_i/B_i, Q_i/B_i and EE_i, at least three of these parameters must be known for each group. The fourth is estimated by the models. In the current work, all trophic models and scenarios were balanced following the six rules given by Heymans et al. (2016) in terms of fulfilling the laws of thermodynamics (Appendix A).

The ecosystem and network macroscopic properties estimated were the *Total System Throughput* (TST), which quantifies the sizes and metabolic activities of an ecosystem (Ulanowicz, 1986, 1997) corresponding to the sum of all exchanges within the ecosystem and with the outside world (see Eq. (3)).