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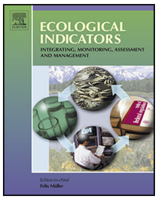

Review

Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review

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ABSTRACT

In the context of present global changes, interest in understanding how systems respond to anthropogenic environmental pressures and stress has increased. Indices that characterize ecosystem state are helpful tools for the interpretation of ecosystem responses. The central question is how to link these responses to ecosystem structure and functioning and to quantify ecosystem persistence, resistance or resilience. Quantification and characterization of trophic networks by ecological network analysis (ENA) indices is proceeding rapidly, especially in the field of coastal ecology. In this contribution, we review several theories that relate ecosystem structure and function to stability. The structure and functioning of ecosystems change during the maturation of ecosystems. In the first section, the maturation of ecosystems is described using thermodynamics. In the second and third parts of this paper, we define some concepts for analysing structure and functioning of food webs and discuss their relation to stability. In the last section, we describe three ENA indices and their link to stability. We demonstrate that ENA provides powerful tools for describing local stability, combining quantitative and qualitative concepts. However, it remains incomplete for describing real conservation cases that combine local and global stability.

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1. Introduction

Species diversity had a buffering impact on resistance and resilience of coastal ecosystem functions and services provided to human (Worm et al., 2006). Biodiversity loss, due in particular to species extinction, is now recognized as a major driver of the accelerating declines of ecosystem functions (Cardinale et al., 2011; Hooper et al., 2012). by altering the performance of ecosystems (productivity, decomposition) (Naeem et al., 1994), modifying biogeochemical cycles (Loreau et al., 2001), by the extinction of multiple species through cascading effects (Pimm, 1991; Myers et al., 2007). Modern changes in biodiversity are largely due to impacts of human activities (e.g. habitat loss, climate change, invasive species, overexploitation, pollution) and have occurred more quickly over the past 50 years than at any other time (Millennium Ecosystem Assessment, 2005). The maintenance of functional ecosystems and the services they provide is critical and the conservation of species diversity appears essential to achieve this objective (Chapin et al., 2000).

Stability refers to the ability of an ecosystem to maintain its state over time, against external and internal forces that drive it away from that state. Two kinds of stability can be distinguished: local and global stability. The local stability corresponds to the maintenance of the original state after small perturbations (Pimm, 1991), or small changes away from its equilibrium state (Chen and Cohen, 2001). On the contrary, global stability deals with all possible perturbations (Pimm, 1984). The range of all values of perturbations from which the ecosystem returns to the original state, is called basin of attraction and constitutes the threshold from which the ecosystem shifts from one state to another one (May, 1977; Scheffer et al., 2001). Regime shifts have been already observed in nature, like for example coral reef damage (Bellwood et al., 2004; Hughes et al., 2010) or lake and estuary eutrophication (Baird et al., 2004)).

Trophic interactions, represented through food webs, are one of the major ways by which species are organized in an ecosystem (Elton, 1927). Food webs integrate population dynamics, community structure, species interactions, biodiversity, ecosystem productivity and community stability in their description of community and ecosystem structure (Link et al., 2005). A stable food web is not a static entity. Food webs can show clear variability over a large range of temporal scales, from seasonal (e.g.Baird and Ulanowicz, 1989; Lobry et al., 2008) to year-to-year changes (Heymans et al., 2007). Beyond this apparent variability, an ecosystem can show recurring states at particular periods of time. Such a system is regarded as stable. When studying the dynamics of food webs to relate the complexity and the stability of ecosystems, two schools of thought have emerged among ecologists. The first one holds that complex ecosystems are more stable than simpler ones, based on the observations of the longevity of natural complex communities in nature (Odum, 1953, Elton, 1958, MacArthur, 1955). In contrast, May (1972, 1973) demonstrated via mathematical modelling that complexity does not necessarily lead to the stability of ecosystems. This demonstration paved the way for a number of dynamical models which showed that for a given complexity, both stable and unstable food web can exist (Kondoh, 2005). Consequently, it is crucial to determine the architecture of the food web that provides stability to the ecosystems.

Food webs can be described by qualitative (diversity, number of flows and feeding topology) or quantitative (magnitude of flows) features (Legendre and Niquil, 2013). Indices derived from Ecological Network Analysis (ENA), which combines the qualitative and the quantitative aspects of ecosystem dynamics, can be considered to be emergent properties of systems (Ulanowicz, 1986). ENA is defined as "a systems-oriented methodology to analyze within system interactions used to identify holistic properties that are otherwise not evident from the direct observations" (Fath et al., 2007). The rapid development of the use of ENA, especially in coastal ecology (Christian et al., 2005), has led to interpretations of these food web properties in terms of their potential for local stability. Highlighting holistic properties of food webs, ENA indices appear to be a potentially powerful tool to assess ecosystem stability, with possible applications in management (Heymans et al., 2014). By their holistic approach and integrative approach of the functioning of the whole ecosystem, the trophic networks and especially the ENA indices can be used as health indicators by the Marine Strategy Framework Directive to access the state of marine ecosystems. Thus the understanding of the relation between ENA indices and ecosystem stability becomes crucial for the next decades.

The aim of this review was to synthesize current theories which link food web structure and functioning to stability properties of ecosystems. We focused on local stability and specifically analyzed ecosystem response to one important type of perturbation, the