Enhanced resilience and resistance assessment with virtual ecoexergy for a subtropical lake ecosystem under the intermittent impact of hurricanes and droughts

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ABSTRACT

Ecosystem growth and development constrained by material, energy, and information flows can be well described by the use of ecoexergy in the context of thermodynamic laws. However, ecosystems are not only physically open to the environment but also ontic to all species and processes involved in an ecological network. Essential exchange of mass, energy, and information through an ecological network may happen both directly and indirectly, which in turn affect the ecosystem resilience and resistance when facing stresses and/or disturbances. The complexity of how the cycling of matter, energy, and information via commensalism or mutualism over relevant species in an ecological network could affect the ecosystem resilience and resistance has not yet been well explored quantitatively. This paper defines a virtual ecoexergy concept and develops a quantitative way to address the possible contributions from commensalism or mutualism between any paired species indirectly in an ecosystem under a decadal impact of intermittent droughts and hurricanes. The key terminology of the biomass equivalence rule that addresses these indirect contributions in an ecological network was introduced as an integral part of virtual ecoexergy concept to facilitate the applications. The case study in Lake Okeechobee (Florida) confirms a big difference in terms of resilience and resistance when the virtual ecoexergy is taken into account through the biomass equivalence rule. With the inclusion of the concept of virtual ecoexergy associated with mutualism or commensalism, the lake's ecological stability condition would not be underestimated during an ecosystem succession and recovery process when facing continuous hurricane and drought impacts in the 2000s. The enhanced resilience with the consideration of the virtual ecoexergy is about 12 times larger than the conventional resilience in this real-world case study.

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1. Introduction

An ecological community can be defined as a group of trophically similar interacting species living in the same environment with actual or potential relationships to compete for the same or similar resources in a local area. Ecosystem growth and development constrained by the material, energy, and information flows can be well described by the concept of ecoexergy in the context of thermodynamic laws (Jørgensen, 1992). However, ecosystems are not only physically open to the environment but also ontic to all species and processes involved in an ecological network. Ecological stability in terms of resilience and resistance is one of the most important properties in ecosystem health assessments. Essential exchange of mass, energy, and information directly and indirectly through an ecological network may occur in both direct and indirect ways such that resilience and resistance may be enhanced to some extent, although the contribution from information is uncertain.

There is a close connection between the measure of additional information (Kullback's measure) and exergy (Svirezhev, 2000 Svirezhev and Steinborn, 2001). Ecoexergy originated from the exergy concept in thermodynamics laws, which indicates the maximum useful work that brings one system into equilibrium because everything without outside forces in the universe would naturally tend toward an equilibrium status. By contrast, ecoexergy is mainly defined to address the information embedded in the biomass and genome directly, which has been regarded as a thermodynamically oriented ecological indicator in environmental assessment and management. According to Jørgensen and Fath (2006), ecoexergy is equal to the multiplication of work capacity expressed as biomass in an ecosystem and the "Kullbach's Measure of Information". Ecoexergy expresses the work capacity, presuming a reference environment that represents the same system (ecosystem) at the same temperature and pressure at the thermodynamic equilibrium, which means that all the components are inorganic at the highest possible oxidation state and homogeneously distributed in the system (Jørgensen et al., 2004). Ecoexergy has successfully been used to develop structurally dynamic models (Jørgensen, 2002) and as a holistic

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ecological indicator (Jørgensen et al., 2004). Ulanowicz et al. (2009), however, proposed his information theory providing a uniform way to quantify both essential attributes, effective performance and reserve capacity, resulting in a single metric that gauges system sustainability (robustness) in terms of the tradeoff allotment of each. With the concept of reserve capacity, Jørgensen and Ulanowicz (2009) considered network calculations and ascendancy based on ecoexergy, and it is advisable in such cases to explore how changes in a flow variable, like ascendency, might capture network adaptations. Currently, the organizational aspect of exergy is expressed as Kullbach's measure of information based on the genetic complexity of the organism only. Yet it does not address the base of: 1) how to link it with network adaptations facing natural hazards and human disturbances ending up flow topology changes and 2) how the ecologiclal stability can be assessed in terms of resilience and resistance with respect to such network adaptations in an ecological network facing multiple stressors. Nevertheless, current ecoexergy can be compared with diversity measures in an ecosystem for biodiversity and ecosystem studies. For instance, ecoexergy-based indices (ecoexergy and specific ecoexergy) and the Margalef and Shannon–Wiener indices were computed and tested in terms of the differences in their responses to change in benthic communities across three tropical reservoirs located in the basin of the Paraopeba River, Minas Gerais State-Brazil, characterised by different degrees of anthropogenic disturbance (Molozzia et al., 2013).

In literature, ecological stability has been assessed in terms of resilience and resistance (Jørgensen and Mejer, 1977; Mitchell et al., 2000). The principle of ecological stability can be applied to multiple fields, such as evolutionary biology (Borrelli et al., 2015), forest management and utilization (Larsen, 1995), conservation management in terms of response and stability of ecosystems to disturbances (Mitchell et al., 2000). In essence, the cycling of matter, energy, and information via an ecological network is relevant to ecosystem stability. This cycling might be seriously disturbed by human acitvties and natural hazards and could be further complicated when considering different classes of relationships between two organisms/species via predation, mutualism, commensalism, or parasitism in an ecological network. When facing a series of extreme events (i.e., natural hazards or human activities), the dynamics of species population in an ecosystem must be assessed by the cascade effects of stresses or disturbances throughout an ecosystem network, and the ecosystem resilience and resistance may be evaluated in association with possible reserve capacity or mutualism/commensalism during the ecosystem succession and recovery. Note that in the context of ecological stability, ecological resilience is the time required for an ecosystem to return to an equilibrium or steady-state following a perturbation (Gunderson, 2000; Holling, 1973) or, alternatively, as the capacity of a system to absorb disturbance and reorganize while undergoing change so as to retain essentially the same function, structure, identity, and feedbacks (Walker et al., 2004). Ecological resilience in this study refers to the first definition, understanding that ecological resistance is the property of communities or populations to remain essentially unchanged when subject to disturbance (D'Antonio and Thomsen, 2004).

Generally, resilience describes how soon an ecosystem structure or function can recover from disturbances, and resistance indicates the capacity of an ecosystem to retain its fundamental structure processes and function under stresses or disturbances (Chambers et al., 2014; Mejer and Jørgensen, 1979). To quantify those standards, representative species are chosen as ecological indicators, and ecosystem resilience and resistance are then calculated based on their population or biomass concentration. As Nielsen (2016) indicated, complexity in ecology arises not merely from the number of components and the direct interactions, such as flows between them, and transactions in general may consider that both could be material and immaterial in character. Although a means currently exists to quantify the immaterial in character, both ecological resistance and resilience may be enhanced by possible mutualism and commensalism in an ecological network, and the quantitative method to characterize the

enhanced resistance and resilience relative to traditional resistance and resilience has not yet been well developed in the literature. To bridge the gap, the new concept of "virtual ecoexergy" with the aid of the biomass equivalence rule may be defined as the potential contributions via commensalism or mutualism in an ecological network to enhance the understanding of network adaptation from resistance to resilience. Without considering the possible contributions from the ecological network indirectly via commensalism or mutualism in terms of virtual ecoexergy, the ecological resilience and resistance associated with network adaptation might otherwise be largely underestimated.

The objective of this study was thus to develop the concept of virtual ecoexergy with the aid of the biomass equivalence rule as a theoretical foundation for deriving the enhanced resistance and resilience, and to account for the possible contribution to resistance and resilience from mutualism or commensalism in an ecological network facing stress and undergoing network adaptation. The practical implementation was assessed by a case study in Lake Okeechobee (Florida, USA) where the ecosystem was disturbed by continuous hurricanes and droughts in the 2000s. This analysis addressed the following science questions: 1) How can virtual ecoexergy be calculated based on the biomass equivalence rule in a typical food web throughout various stages of influences of natural disasters such as hurricanes and droughts in a lake ecosystem? 2) Can we quantify the integral utility matrix in a lake ecosystem that experienced an ecosystem succession and recovery processes under stressed conditions driven by commensalism and/or mutualism among a few species? and 3) Can the cascade effects of intermittent natural disasters such as hurricanes and droughts in a lake ecosystem be well addressed by the ecosystem stability change in terms of both enhanced resistance and enhanced resilience? Our hypotheses were that the use of virtual ecoexergy with the aid of the biomass equivalence rule may better represent the basic nature of ecosystem stability from resistance to resilience, in which the use of the integral utility matrix is deemed a good tool to delineate the potential contributions from the commensalism and/or mutualism between two species.

2. Methodology

2.1. Virtual ecoexergy

The exergy of a system is a measure of its deviation from thermodynamic equilibrium within an environment and represents the maximum capacity of energy to perform useful work as the system proceeds to equilibrium (Ludovisi, 2006). Jørgensen (1988) pointed out the possible use of exergy to assess the structural changes in ecosystems. Jørgensen (1990) and Patten (1991) emphasized the concept of network ecology to illustrate the indirect connection to the life of the organisms in the ecosystem. The concept of ecoexergy to describe the dynamics of ecosystems was further developed and applied by Jørgensen (1995, 2002); Susani et al., 2006). The ecoexergy can be simply calculated as (Jørgensen, 1992):

$$E_x = \sum_{i=1}^{N} \beta_i c_i \tag{1}$$

where: E_x = the total exergy of the system summed over all components (or organisms), which stands for the total exergy of an ecosystem based on the total density of all organisms involved in terms of detritus equivalent (kJ/m³), N = the total number of organisms involved in an ecosystem (unitless), β_i = a weighting factor of the ith component in the ecosystem dependent on the amount of information that the components carry ($\beta = 1$ for detritus; see Table 1 for the remaining weighting factors) (unitless), and c_i = the concentration of the components (mg/L).

When considering different species' ecoexergy, the higher the total amount of ecoexergy, the further the ecosystem has diverged from equilibrium status (the physical envrionment), meaning the ecosystem