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Resource pulses can increase power acquisition of an ecosystem

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ABSTRACT

Pulsing is prevalent in nature. As resource pulse has been recognized as one of the major factors influencing ecosystem structures and processes, it is important to investigate why nature pulses and what benefits an ecosystem obtains from pulsed resources. The main question of this study was that if a system could be exposed to either constant external resources or pulsed external resources of the same temporal average intensity, which resources would maximize power acquisition of a system. To answer the question, this study tested how matching of pulsed resources affects total empower acquisition of a system using numerical simulation models and a refined dynamic emergy accounting method. A producer–consumer model system was built and simulated by varying phases and frequencies of pulsed energy sources. It was hypothesized that matching of frequency and phase among two or more pulsed energy sources increases the empower acquisition of a system, compared with a system under constant energy sources. The simulation results showed that in systems of two energy sources, matching phases and frequencies of the pulsed energy sources involved in primary production is critical to increase total empower acquisition and consumer energy storage. The primary mechanism was that the matching of pulsed resources in phase and frequency promotes energy acquisition of primary producers that is further efficiently transferred for the production of consumers. Energy acquisition of consumers was strongly correlated with total empower acquisition of the system presumably because the consumers are in the high energy hierarchical position controlling the producers thus contributing to the total empower acquisition through the system.

1. Introduction

1.1. Hypotheses on the self-organization of ecosystems

Goal functions for the self-organization of ecosystems have long been discussed among ecologists particularly who have studied energetics or system-level properties. Lotka (1922) stressed that a prevailing system tends to increase total available energy flux through the system during natural selection. Later, the hypothesis of the maximum power principle (MPP) proposed by Lotka (1922) has been partially supported and complemented by Odum. Odum proposed the maximum empower principle (MEP) that hypothesizes natural selection goes to a system that maximizes empower, the quality-corrected energy flux (Brown et al., 2004). He suggested empower instead of power as the maximized flow because the quality difference among various energy types (Odum, 1988) has been a problem in defining energy terms, especially when many energy sources of different qualities drive a process (Patterson, 1996). Although the MPP or MEP has been hypothesized as a goal function for the self-organization of an ecosystem, only a few empirical or modeling studies on the hypothesis have been reported (e.g., Cai et al., 2006; DeLong, 2008). The scarcity of the studies on the MPP or MEP may be attributed to the difficulty in identifying and quantifying available energy flux through complex energy networks (Cai et al., 2004).

Meanwhile, Ulanowicz (1997) proposed ascendency as a hypothesis on the development of ecosystems. Ascendency, an index encompassing both qualitative and quantitative aspects of system development, is defined as the multiplication of average mutual information and total system throughput. Although the ascendency includes mutual information as a factor of system development, it appears that both the MPP and ascendency hypotheses agree that a critical component of self-organization in a prevailing system is the total energy flux through the system.

1.2. Pulsing paradigm and resource pulse

Resource pulse has been acknowledged to be an important factor that influences ecosystem structures and processes (Chesson, 2003; Ostfeld and Keesing, 2000; Yang et al., 2008). Some ecologists

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defined resource pulses as episodes of resource availability characterized by low frequency, large magnitude, and short duration (Yang et al., 2008). Those episodic resource pulses may affect individual- or community-level behavior in an ecosystem. From a more general perspective, Odum et al. (1995) suggested the prevalence of pulsing trends in external resources or internal variables in comparison with the traditional steady-state paradigm for the succession of an ecosystem. While many pulsing trends have been observed in nature (e.g., solar radiation, nutrient pulse, flood pulse, population oscillation), the fundamental reasons for or benefits from the pulsing trends have not been explained well.

Considering that many external resources are supplied to an ecosystem with variable temporal pulsing patterns (e.g., daily insolation, seasonal fluctuation of food sources, episodic precipitation), one may expect that the pulsed resource environment benefits ecosystems or individual organisms. For instance, an ecosystem may better obtain total energy flux under pulsed resource supplies. Regarding the resource pulsing, there have been studies about the matching of pulse frequencies between external resources and system components for system performance. For example, Campbell (1984) found that system-level production is likely to be maximized under the matching of frequencies between external resource and internal oscillation. In a similar context, Lodge et al. (1994) emphasized the importance of synchrony of nutrient supply with plant uptake to minimize competition between microbes and plants. The effects of matching of pulsing traits such as frequency and phase between different external resources, however, have not been studied well. When an energy transformation process in a system occurs by using more than two pulsed external resources, matching of a trait such as phase or frequency among the pulsed resources may benefit the system. If the average energy intensities are the same between a constant external resource and a pulsed one, would the ecosystem draw more energy flux under the matching of the two pulsed external resources than that of the two constant external resources? The effects of matching between pulsed resources seem to be equivocal because matching of two or more fluctuating resources yields not only high production under the resources' highest points but also low production under the resources' lowest points.

1.3. Dynamic emergy accounting

Dynamic emergy accounting (Odum, 1996) is a useful tool for understanding time-dependent emergy by simulating emergy, unit emergy value (UEV), and relevant currencies such as energy, matter, and money. While emergy synthesis as a snapshot represents total emergy directly or indirectly contributed to make a product at a certain time, dynamic emergy accounting shows how emergy or UEV changes over time. Since Odum introduced the method for dynamic emergy accounting (Odum, 1996; Odum and Odum, 2000b), however, there have been only a few studies related to it (e.g., Tilley, 2010; Tilley and Brown, 2006; Vassallo et al., 2009). As Tilley (2010) discussed, the dynamic emergy accounting method introduced by Odum (1996) conflicts with the concept of emergy so it is necessary to refine the method to accurately simulate the trajectories of emergy or UEV.

1.4. Study plan

This study aims to investigate how the matching of pulsed external energy sources influences empower (emergy/time) acquisition of an ecosystem using a numerical simulation model. First, I refined Odum's dynamic emergy accounting method for the simulation of emergy. Second, I built a simple producer–consumer model system and tested how the matching of pulsed energy sources affects empower acquisition of the system by varying phase difference and frequency combination among the sources. I hypothesized that a system under pulsed external energy sources draws more empower through the system under the frequency and phase matching, compared with a system under constant external energy sources, when the temporal average intensities between the pulsed and constant energy sources are the same.

2. Theory

2.1. Odum's dynamic emergy accounting method

Odum and Odum (2000b) suggested a dynamic emergy accounting method by three conditional equations derived from the diagrams in Fig. 1 as follows:

$$\frac{dQ}{dT} > 0 : dEm_Q = Em_J - Em_H \quad (1)$$

where $Em_J = Tr_J \cdot J$ and $Em_H = Tr_Q \cdot K2 \cdot Q \cdot F$

$$\frac{dQ}{dT} = 0 : dEm_Q = 0 \quad (2)$$

$$\frac{dQ}{dT} < 0 : dEm_Q = Tr_Q \cdot dQ \quad (3)$$

where Em_X is the emergy of X, Tr_X is the transformity (or UEV) of X.

2.2. Inconsistencies in the Odum's method

2.2.1. The depreciation pathway

When $dQ/dT > 0$, or Q is accumulated, the emergy of the depreciation pathway $K1 \cdot Q$ was considered zero in Eq. (1) because heat sink is a necessary process to maintain Q but does not carry emergy. Odum and Odum (2000b), however, stated regarding Eq. (3) that "When the change in emergy storage is negative, the loss in emergy is the loss of the energy times the transformity of the storage, whether it is due to depreciation loss or whether it is due to the transfer of useful energy out." This statement is not compatible with Eq. (1). That is, the depreciation pathway $K1 \cdot Q$ was regarded as carrying emergy in Eq. (3) but not in Eq. (1). Because heat sink is necessary to maintain Q but does not carry emergy, emergy is not lost through the depreciation pathway.

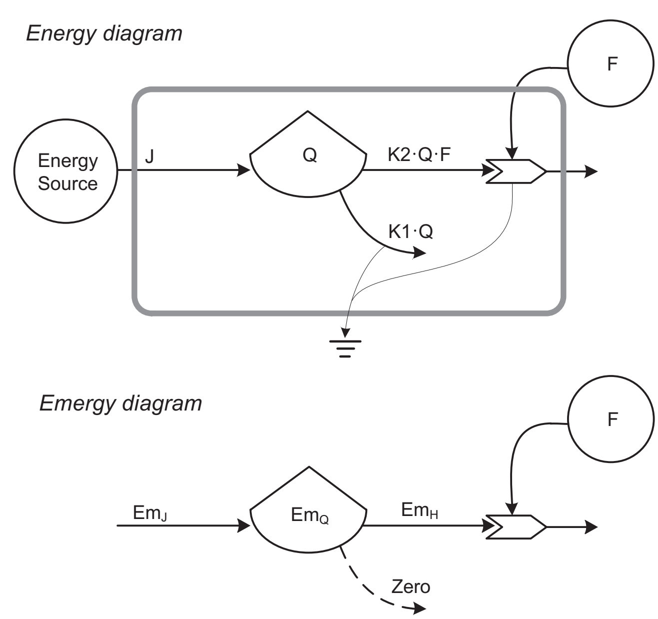

Fig. 1. Odum's energy and emergy systems diagrams for the dynamic accounting method (Odum and Odum, 2000b).