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Relationships between renewable emergy storage or flow and biodiversity: A modeling investigation

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ABSTRACT

In this study we investigate the relationships of emergy storage or flow to biodiversity using three different models—a dynamic simulation model, a static scenario model, and a modified ecological network model. These models attempt to explain how disturbance regime, latitude, and trophic complexity are related to observed patterns of renewable emergy flows and storages and biodiversity. A prior hypothesis, which this work seeks to examine, suggests that as renewable emergy flow increases biodiversity will increase. In this regard, we simulate how H.T. Odum's original CLIMAX model, which tracks forest biomass and diversity over 100 years of succession, responds to a periodic disturbance. The static scenario model compares emergy flow, storage and diversity in five forest eco-regions along the east coast of the United States. An emergy flow matrix ecological network model was used to simulate biodiversity in a mature forest ecosystem and in a typical suburban forest system to investigate how the complexity of a forest system will affect emergy throughput. Comparisons were made for the Shannon diversity index and transformity at the individual trophic level. These comparisons seek to further our understanding of the relationship of emergy and biodiversity and to validate the use of renewable emergy flow to explain ecological phenomena (e.g., biodiversity increasing as latitude decreases, biodiversity increasing through the stages of forest succession).

1. Introduction

Odum (1996) suggests that biodiversity (i.e. genetic variety in the flora and fauna of a given region) and emergy (i.e. cumulative available energy used-up to produce a component of an observed system) are interrelated, and that as the renewable emergy flow captured by a system increases biodiversity will increase proportionately. Moreover, Odum (1988, 1996) suggests that a system will self-organize to best take advantage of emergy of the available energy signature,[1] maximizing the emergy flow through the system over time (i.e. the Maximum Empower Principle). While he did not explicitly state that the product of self-organization for maximum empower in a natural system is the further development of genetic diversity through evolution, this is a logical conclusion given the accepted paradigm (in this work) that systems self-organize under the constraint to maximum empower in evolutionary competition (Lotka, 1922a,b; Odum, 1996) and, less contentiously, the evolution of genetic diversity over time. Jorgensen and Svirezhev (2004) and Jorgensen (2008) presents a similar theory of thermodynamics and evolution, suggesting that systems self-organize to maximize entropy and eco-exergy (i.e. environmentally derived available energy including the genetic information per unit biomass).

Biodiversity can be calculated in different ways; simple species counts per area and species richness combined with evenness, when considered together in the Shannon-Wiener Diversity Index (Shannon, 1948). In more recent research, phylogenetic analysis (Purvis and Hector, 2000) has been used and diversity has been considered at different scales, i.e. alpha, beta, and gamma diversity (Whittaker, 1960). The frequency of connections between species and the degree of connectedness in an ecological network have been evaluated using information theory (Ulanowicz, 1997, 2001, 2004; Fath and Patten, 1998; Fath et al., 2007).

Emergy is an accounting system for available energy that has the virtue of placing all forms of energy (and matter) on a common basis; the amount of cumulative available energy (i.e. exergy) in solar equivalents required for what is currently observable. The method is applicable to both natural and human systems, because all action depends on the transformation of available energy potentials (Franzese et al., 2014; Brown et al., 2015). Odum developed

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[1] The energy signature of a system is the set of energy sources that affects it (Kangas, 2004).

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the method; he and his students and colleagues demonstrated its applicability (Odum, 1996, 2007), including its use as a tool for evaluating diversity, both at the genetic (Odum, 1996) and at the system level (Brown et al., 2006).

There is evidence that the biodiversity in an ecosystem increases the resilience of that system (Holling, 1973; Folke et al., 2004; Bastian, 2013). It has been observed that the emergy flow and the area examined increase exponentially, as the number of species found increases arithmetically ((Odum 1996), from Keitt, 1991). Previous work has theorized how stored emergy and the emergy of genetic information relate to biodiversity (Campbell and Brown, 2012). A strong correlation between stored emergy and biodiversity has not been observed in the real world, but the building of genetic information is an iterative process, with current information dependent on prior generations, possibly correlating to the building of natural capital (defined here as ecological assets independent of economic value), measured through emergy accounting (Campbell and Brown, 2012; Odum, 1996). Renewable emergy is a measure of the resource base available to support species and more emergy flow (i.e. empower) will allow a greater number of species to exist within the system and consequently the development of greater complexity. The emergy needed to develop genetic material is generally very high because genetic material tends to develop over a long period of time and require the support of the entire population (Lee et al., 2013; Givnish et al., 2014; Lanfear et al., 2014).

In this paper, we will demonstrate that the annual flow of renewable emergy is related to the amount of biological diversity in terrestrial ecosystems. To support our thesis, we developed or modified three models that represent a temporal perspective, a spatial perspective and a network perspective on the relationship between emergy and diversity. The temporal model is a slight modification of Odum's (1996) CLIMAX mini-model in which we add a forced disturbance that partially destroys biomass. The spatial model relates the annual renewable emergy of five contiguous forest regions located along the east coast of the United States from Florida to Maine to the amount of vertebrate and plant diversity found in those forests. The network model is an ecological network model based on Ulanowicz's (1997, 2000) ascendency theory in which we contrast the total system empower and ecosystem diversity of a natural forest with a theoretical suburban forest.

Existing ecological theories inform the interpretation of the results of our models. In particular, we consider our results in the context of the intermediate disturbance hypothesis (IDH), top down regulation of trophic systems, and ascendancy theory. These theories can be influential in ecological systems, affecting the emergy-biodiversity observations we attempt to simulate in our work. The intermediate disturbance hypothesis states that maximum diversity occurs at the median frequency of disturbance to the system (Connell, 1978). Top down regulation theory states that top level trophic species have a disproportionate influence on lower trophic level species, as evidenced by trophic cascades, such as the classic example of the depletion of the sea otter population off the coast of the Western United States triggering an explosion of the sea urchin population, with devastating consequences for kelp in the region (Estes and Palmisano, 1974). Ascendancy theory (Ulanowicz 1997, 2000) applies information theory to ecology, measuring the organization and activity in ecological networks and states that "In the absence of major perturbations, ecosystems exhibit a propensity towards configuration of ever-greater network ascendancy" (Ulanowicz, 2000). These are in addition to the theories that we seek to investigate (1) that renewable emergy inflow to a system is related to its biodiversity and (2) a fundamental principle of Energy Systems Theory that all systems self-organize to maximize empower.

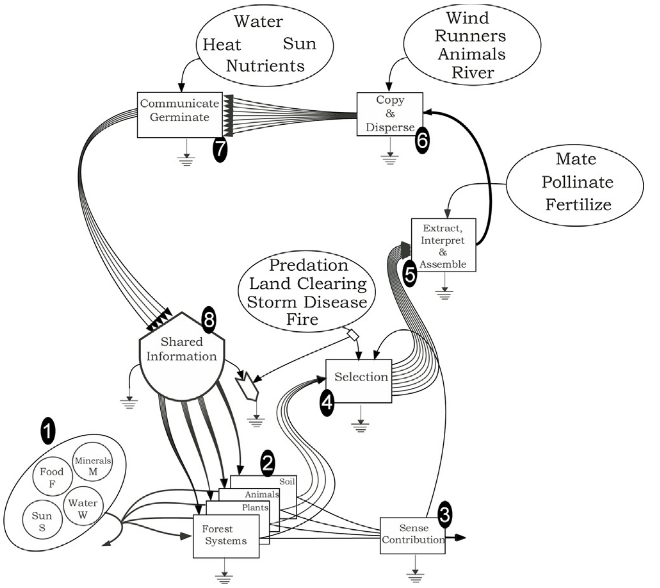

Fig. 1. Diversity Evolution Cycle Model showing the cycling of information in an ecological system to develop and support species.

2. Models

2.1. *What is the emergy of a species?*

Fig. 1 is an Energy Systems Language diagram of the cycle necessary to create, maintain and use information for operating living systems based upon a diagram published by Odum (1996). Operation of the entire information cycle requires energy and material resources entering at Stage 1. Darwinian evolution can be conceptualized as an information cycle. Beginning with the sub-systems of an ecosystem (i.e., plants, animals, soil) labeled as Stage 2, the various energies and material resources (Stage 1) are required to operate each stage as well as maintain the overall organizational structure. Those components of the ecosystem that are most successful in terms of longevity or dominance contribute significantly to the surrounding ecosystems (Stage 3). There exists a multitude of natural and anthropic selection mechanisms (e.g., predation, human-forced land clearing, floods, disease, fire, and insect infestation) that determine which components of each ecosystem become a part of the future ecosystem, which is often called natural selection. Those components that survive the selection process will then go through reproduction Stage 5, which has unique mechanisms of action. Stage 5 is also where novelty and innovative plans for life arise, Corning (2008) referred to this as synergy. Those individuals that survive selection and produce progeny have created unique copies of their genes that are then dispersed across the landscape by various processes (e.g., wind, animals, rivers) as shown in Stage 6. By Stage 7 the new carriers of the new genetic material and life-plans are embedded in the original or new ecosystems, increasing the amount of shared genetic information (Stage 8) available for future ecosystems and information cycles to use.

Like other structures, information is thermodynamically distant from equilibrium and thus is continuously lost by error generation, dispersal, depreciation and destruction. This feature of the second law is represented in the information cycle (Fig. 1) by heat sinks connected to each stage of the cycle. Work that consumes resources irreversibly is required not only to make the living systems and their environments function, but also to carry out each stage of the information cycle. If information is not cycled through this multi-stage loop, the shared information will shrink, degrade, and be lost or forgotten. Thus, the information cycle captures the

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