

Emergy and ecosystem complexity

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Abstract

The question “What drives complexity?” is addressed in this paper. To answer this question, we explore the way energy and material resources of different quality flow through ecosystems and support, directly and indirectly, ecosystems growth and development. Processes of resource transformation throughout the ecosystem build order, cycle materials, generate and sustain information. Energy drives all these processes and energetic principles explain much of what is observed, including energy degradation according to the laws of thermodynamics. Emergy, a quantitative measure of the global environmental work supporting ecosystem dynamics, is used here in order to provide a deeper understanding of complexity growth and decline in ecosystems. Ecosystem complexity is discussed in this paper in relation to changes in structure, organization and functional capacity, as explained by changes in energy, empower, and transformity.

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1. Introduction

The living and non-living parts and processes of the environment as they operate together are commonly called ecosystems. Examples are forests, wetlands, lakes, prairies, and coral reefs. All parts of ecosystems are interconnected, each receiving energy and materials from the other, interacting through feedback mechanisms to self-organize in space, time, and connectivity. Ecosystems circulate materials, transform energy, support populations, join components in network interactions, organize hierarchies and spatial centers, evolve and replicate information, and maintain structure in pulsing oscillations. The parts are organized in an energy hierarchy as shown in aggregated form in Fig. 1, representing the system diagram of Silver Springs ecosystem, Florida. Numbers on pathways are energy flows. As energy flows from driving energy sources on the left to higher and higher order ecosystem components, it is transformed from sunlight to plant biomass, to 1st

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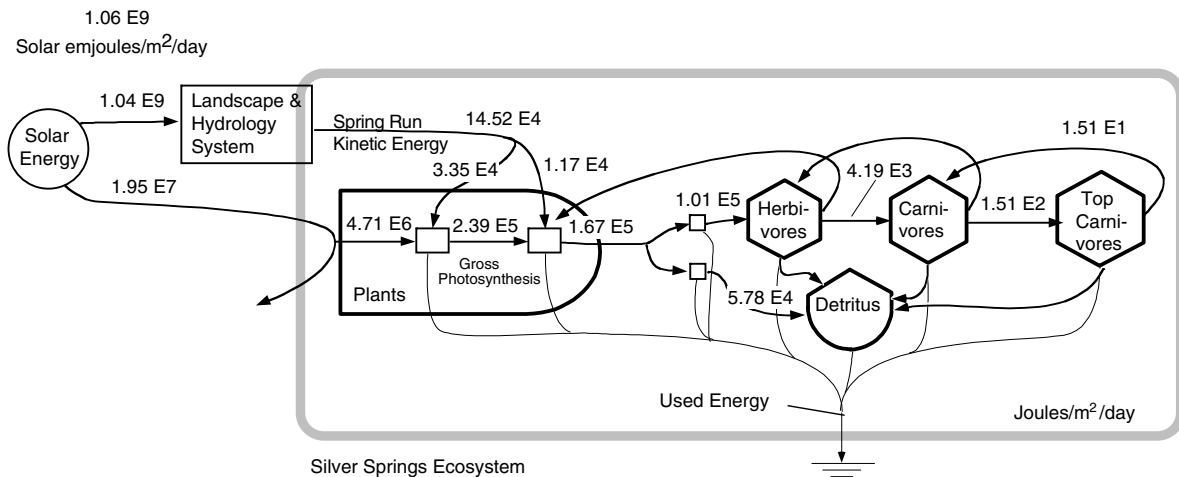


Fig. 1. Aggregated systems diagram of the ecosystem at Silver Springs, Florida, showing decreasing energy with each level in the metabolic chain [1,2].

level consumers, to second level and so forth. At each transformation, second law losses decrease the available energy, but the “quality” of energy remaining is increased.

Given next are definitions and a brief description of energy synthesis theory [2,3], systems ecology [4] and the information concept, that are used throughout this paper as the conceptual framework for a deeper understanding of ecosystem complexity. Readers who are already familiar with energy accounting methods may skip next Section 1.1.

1.1. Energy and transformity: concepts and definitions

While it is true that all energy can be converted to heat, it is not true that one form of energy is substitutable for another in all situations. For instance, plants cannot substitute fossil fuel for sunlight in photosynthetic production, nor can humans substitute sunlight energy for food or water. It should be obvious that the quality that makes an energy flow usable by one set of transformation processes makes it unusable for another set. Thus, quality is related to a form of energy and to its concentration; where higher quality is somewhat synonymous with higher concentration of energy and results in greater flexibility. So, wood is more concentrated than detritus, coal more concentrated than wood, and electricity more concentrated than coal. As a consequence, the quality (concentration, wave-length, pulsing, etc.) of incoming energy makes it able to drive different forms of complexity in recipient systems.

Odum [2,3] introduced the concept of energy in order to account for the quality of incoming energy and resources, i.e. for the environmental services supporting a process as well as for their convergence through a chain of energy and matter transformations in both space and time. By definition, energy is the amount of energy of one type (usually solar) that is directly or indirectly required to provide a given flow or storage of energy or matter. The units of energy are emjoules (abbreviated eJ) to distinguish them from energy joules (abbreviated J). Solar energy is expressed in solar energy joules (seJ, or solar emjoules). The flow of energy per unit time is empower. Solar empower is solar emjoules per time (e.g. seJ/s).

The solar energy required to generate a unit flow or storage of available energy is called solar transformity and is expressed as solar energy joules per joule of output flow (seJ/J). The transformity of solar radiation is assumed equal to one by definition (1.0 seJ/J). Transformities of the main natural flows in the biosphere (wind, rain, ocean currents, geological cycles, etc.) are calculated as the ratio of total energy driving the biosphere, as a whole, to the actual energy of the flow under consideration [2]. The total energy driving the biosphere is the sum of solar radiation, deep heat, and tidal momentum and is about $15.83 \text{ E}24 \text{ seJ/yr}$, based on a re-evaluation and subsequent recalculation of energy contributions done in the year

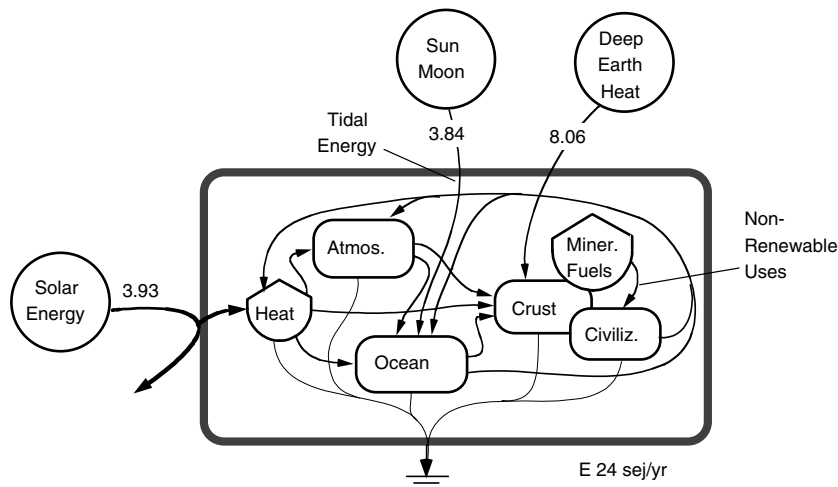


Fig. 2. The main components of the biogeosphere showing the driving energies and the interconnected cycling of energy and matter. The total energy driving the biogeosphere is the sum of solar, tidal and deep heat sources totaling 15.83 E24 sej/yr.

2000 [5]¹. This total energy is used as a driving force for all main biosphere scale processes (winds, rains, ocean currents, and geologic cycles), because these processes and the products they produce are coupled and cannot be generated one without the other (Fig. 2).

Table 1 lists transformities (seJ/J) and specific emergies (seJ/g) of some of the main flows of energy driving ecological processes. Transformities and specific emergies given in the last column are ratios of the biosphere driving energy in the 2nd column to the annual production in the 3rd column. Fig. 2 shows in an aggregated way the energy of the main biosphere flows. These emergies in turn drive processes on smaller space-time scales, like processes in ecosystems as well as in human-dominated systems [6–9]. The total energy driving a process becomes a measure of the self-organization activity of the surrounding environment, converging to make that process possible. It is a measure of the environmental work necessary to provide a given resource. For example, the organic matter in forest soil represents the convergence of solar energy, rain, and winds driving the work processes of the forest over many years that has resulted in layer upon layer of detritus that ever so slowly decomposes into a storage of soil organic matter. It represents part of the past and present ecosystem's work that was necessary to make it available.

1.2. Example transformities in ecosystems

Example transformities of main ecosystem components are given in Tables 2–4. Table 2 lists components and processes of terrestrial ecosystems giving several transformities for each. Within each category transformities vary almost one order of magnitude reflecting the differences in total driving energy of each ecosystem type. The table is arranged in increasing quality of products from gross production to peat. Transformities increase in like fashion. An energy transformation is a conversion of one kind of energy to another kind. As required by the second law, the input energies (sun, wind, rain, etc.) with available potential to do work are partly degraded in the process of generating a lesser quantity of each output energy. With each successive step, a lesser amount of higher quality resources are developed.

When the output energy of a process is expressed as a percent of the input energy, an efficiency results, Lindeman [16] efficiencies, in ecological systems, are an expression of the efficiency of transfer of energy between trophic levels. Table 3 lists transformities of trophic levels in the Prince William Sound of Alaska

¹ Prior to 2000, the total energy contribution to the geobiosphere that was used in calculating energy intensities was 9.44 E24 seJ/yr. The increase in global energy reference base to 15.83 E24 seJ/yr changes all the energy intensities, which directly and indirectly were derived from the value of global annual empower. Thus, to be consistent and to allow comparison with older values, energy intensities calculated prior to the year 2000 are multiplied by 1.68 (the ratio of 15.83/9.44).

Table 1
Emergy of products of the global energy system (after Odum et al. [5])

Product and units	Emergy ^a (E24 seJ/yr)	Production units/yr	Emergy/unit
Global latent heat, J	15.83	1.26 E24	1.3 E1 seJ/J
Global wind circulation, J	15.83	6.45 E21	2.5 E3 seJ/J
Hurricane, J	15.83	6.10 E20	2.6 E4 seJ/J
Global rain on land, g	15.83	1.09 E20	1.5 E5 sej/g
Global rain on land (chem. pot.), J	15.83	5.19 E20	3.1 E4 seJ/J
Average river flow, g	15.83	3.96 E19	4.0 E5 sej/g
Average river geopotential, J	15.83	3.40 E20	4.7 E4 seJ/J
Average river chem. potential, J	15.83	1.96 E20	8.1 E4 seJ/J
Average waves at the shore, J	15.83	3.10 E20	5.1 E4 seJ/J
Average ocean current, J	15.83	8.60 E17	1.8 E7 seJ/J

^a Main empower of inputs to the geobiospheric system from Fig. 2, not including non-renewable consumption (fossil fuel and mineral use).

Table 2
Summary of transformities in terrestrial ecosystems

Ecosystem	Transformity (seJ/J)	Reference
<i>Gross primary production</i>		
Subtropical mixed hardwood forest, Florida	1.03E+03	[10]
Subtropical forest, Florida	1.13E+03	[10]
Tropical dry savanna, Venezuela	3.15E+03	[11]
Salt marsh, Florida	3.56E+03	[2]
Subtropical depressionnal forested wetland, Florida	7.04E+03	[7]
Subtropical shrub–scrub wetland, Florida	7.14E+03	[7]
Subtropical herbaceous wetland, Florida	7.24E+03	[7]
Floodplain forest, Florida	9.16E+03	[12]
<i>Net primary production</i>		
Subtropical mixed hardwood forest, Florida	2.59E+03	[10]
Subtropical forest, Florida	2.84E+03	[10]
Temperate forest, North Carolina (<i>Quercus</i> spp)	7.88E+03	[13]
Tropical dry savanna, Venezuela	1.67E+04	[11]
Subtropical shrub–scrub wetland, Florida	4.05E+04	[7]
Subtropical depressionnal forested wetland, Florida	5.29E+04	[7]
Subtropical herbaceous wetland, Florida	6.19E+04	[7]
<i>Biomass</i>		
Subtropical mixed hardwood forest, Florida	9.23E+03	[10]
Salt marsh, Florida	1.17E+04	[2]
Tropical dry savanna, Venezuela	1.77E+04	[11]
Subtropical forest, Florida	1.79E+04	[10]
Tropical mangrove, Ecuador	2.47E+04	[14]
Subtropical shrub–scrub wetland, Florida	6.91E+04	[7]
Subtropical depressionnal forested wetland, Florida	7.32E+04	[7]
Subtropical herbaceous wetland, Florida	7.34E+04	[7]
<i>Wood</i>		
Boreal silviculture, Sweden (<i>Picea aibes</i> , <i>Pinus silvestris</i>)	8.27E+03	[15]
Subtropical silviculture, Florida (<i>Pinus elliotti</i>)	9.78E+03	[15]
Subtropical plantation, Florida (<i>Eucalyptus</i> & <i>Malaleuca</i> spp.)	1.89E+04	[15]
Temperate forest, North Carolina (<i>Quercus</i> spp)	2.68E+04	[13]
<i>Peat</i>		
Salt marsh, Florida	3.19E+04	[2]
Subtropical depressionnal forested wetland	2.52E+05	[7]
Subtropical shrub–scrub wetland	2.87E+05	[7]
Subtropical wetland	3.09E+05	[7]

Table 3

Summary of transformities in a marine ecosystem, Prince William Sound, Alaska (after Brown et al. [17])

Item	Transformity (seJ/J)
Phytoplankton	1.84E+04
Zooplankton	1.68E+05
Small nekton (molluskans, arthropods, small fishes)	1.84E+06
Small nekton predators (fish)	1.63E+07
Mammals (seal, porpoise, belukha whale, etc.)	6.42E+07
Apex predators (killer whale)	2.85E+08

Table 4

Solar transformities of ecosystem components of the Silver Springs, FL (after Odum [18], updated according to Odum et al. [5])

Item	Transformity (seJ/J)
Solar energy	1
Kinetic energy of spring flow	7170
Gross plant production	1620
Net plant production	4660
Detritus	6600
Herbivores	127,000
Carnivores	4,090,000
Top carnivores	40,600,000

calculated from a food web and using Lindeman efficiencies of about 10% [17]. The transformity, which is a ratio of the energy input to the available energy output, is an expression of quality of the output energy; for the higher the transformity, the more energy is required to make it.

Table 4 gives transformity values for the aggregated system diagram of Silver Springs, Florida, shown in Fig. 1. The data were taken from Odum's earlier studies on this ecosystem [18]. Solar energy drives the system directly (i.e. through photosynthesis) and indirectly through landscape processes that develop aquifer storages, which provide the spring run kinetic energy. Vegetation in the spring run use solar energy and capitalize on the kinetic energy of the spring, which brings a constant supply of nutrients. Products of photosynthesis are consumed directly by herbivores and also deposited in detritus. Herbivores are consumed by carnivores which are, in turn, consumed by top carnivores. With each step in the food-chain, energy is degraded.

2. Hierarchical organization of ecosystems

A hierarchy is a form of organization resembling a pyramid, where each level is subordinate to the one above it. Depending on how one views a hierarchy, it can be an organization, whose components are arranged in levels from a top level (small in number, but large in influence) down to a bottom level (many in number, but small in influence). Or one can view a hierarchy from the bottom, where one observes a partially-ordered structure of entities in which every entity, but one is successor to at least one other entity; and every entity except the highest entity is a predecessor to at least one other. In general, in ecology we consider hierarchical organization to be a group of processes arranged in order of rank or class in which the nature of function at each higher level becomes more broadly embracing than at the lower level. Thus, we often speak of food-chains as hierarchical in organization.

Most, if not all systems form hierarchical energy transformation series, where the scale of space and time increases along the series of energy transformations. Many small-scale processes contribute to fewer and fewer of larger scale ones (Fig. 3). Energy is converged from lower to higher order processes, and with each transformation step, much energy loses its availability (a consequence of the 2nd Law of Thermodynamics), while only a small amount is passed along to the next step. In addition, some energy is fed back, reinforcing power flows up the hierarchy. Note in Fig. 3, the reinforcing feedbacks by which each transformed power flow feeds backward so that its special properties can have amplifier actions.

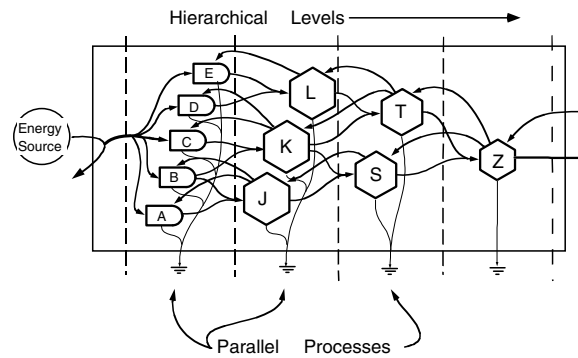


Fig. 3. Diagram of the organization of systems showing the convergence of energy and matter into higher and higher levels via parallel and hierarchical processes.

2.1. Transformities as indicators of hierarchical position

Transformities are quality indicators, by virtue of the fact that they quantify the convergence of energy into products and account for the total amount of energy required to make something. Quality is a system property, which means that an “absolute” scale of quality cannot be made, nor can the usefulness of a measure of quality be assessed without, first defining the structure and boundaries of the system. For instance, quality as synonymous with usefulness to the human economy is only one possible definition of quality, a “user based quality.” A second possibility of defining quality is one, where quality increase with increases of input. That is, the more energy invested in something the higher its quality. We might describe this type of quality as “donor based quality”.

Self-organizing systems (be they the biosphere or an ecosystem) are organized with hierarchical levels (Fig. 3) and each level is composed of many parallel processes. This leads to two other properties of quality: (a) *Parallel quality*, and (b) *Cross quality*. In the first kind, “parallel quality”, quality is related to the efficiency of a process that produces a given flow of energy or matter within the same hierarchical level (comparison among units in the same hierarchical level in Fig. 3). For any given ecological product (organic matter, wood, herbivore, carnivore etc.) there are almost an infinite number of ways of producing it, depending on surrounding conditions. For example, the same tree species may have different gross production and yield different number and quality of fruit depending on climate, soil quality, rain, etc. Individual processes have their own efficiency, and as a result, the output has a distinct transformity. Quality as measured by transformity in this case relates to the energy required to make like products under differing conditions and processes. Note in Table 2, where several transformities are given for each of the ecosystem products listed.

The second definition of quality, “cross quality”, is related to the hierarchical organization of the system. In this case, transformity is used to compare components or outputs from the different levels of the hierarchy, accounting for the convergence of energy at higher and higher levels (comparison of transformity between different hierarchical levels, in Fig. 3). At higher levels, a larger convergence of inputs is required to support the component (a huge amount of grass is needed to support a herbivore, many kg of herbivore are required to support a predator, many villages to support a city, etc.). Also, higher feedback and control ability characterize components at higher hierarchical levels, so that higher transformity is linked to higher control ability on lower levels. Higher transformity, as equated with higher level in the hierarchy, often means greater flexibility and is accompanied by greater spatial and temporal effect.

Transformities can therefore play sometimes the role of efficiency indicators and sometimes the role of hierarchical position indicators. Both of these aspects are strongly related with the complexity of an ecosystem. This is completely true in systems selected under maximum power principle constraints [4,19,20] and is therefore true in untouched and healthy ecosystems. Things are different in an ecosystem stressed by an excess of outside pressure. Relations among components are likely to change, some component may also disappear and the whole hierarchy be altered and simplified. The efficiency of a given process may change (no matter if it decreases or increases) and some patterns of hierarchical control of higher to lower levels may diminish or

disappear due to the simplified structure of the system. These performance changes translate into different values of the transformities, the variations of which become clear measures of lost or decreased system's integrity and complexity.

3. The information cycle

Ecosystems create, store and cycle information. The cycles of material, driven by energy are also cycles of information. Ecosystems, driven by a spectrum of input resources generate information accordingly, and store it in different ways (seeds, structure, biodiversity). Information depreciates by developing unrepaired errors. Considered to be sustainable in the long run, an information storage has to be supported by a duplication and testing cycle. Energy is required to maintain information with a cycle of repeated duplication, reusing, retesting and selecting to eliminate errors, a process that sometimes adds improvements. The circular life history diagrams taught in biology courses are examples. Very large energy is required to generate the systems information the first time, especially genetic information.

The energy cost of the generated information can be measured by a transformity value and may be a measure of healthy ecosystem dynamics. Odum [2] suggested transformities for various categories of information within ecosystems given in Table 5. In healthy ecosystems (as well as in healthy human-dominated systems such as a good University) suitable energy input flows contribute to generating, copying, storing and disseminating information. In stressed ecosystems, such as those, where some simplification occurs due to improper loading from outside, the cycle of information is broken or impaired. In this case, the ecosystem exhibits a loss of information, which may manifest itself in simplification of structural complexity, losses of diversity, or decreases in genetic diversity (reduced reproduction).

There are two different concepts of information shown in Table 5. The first aspect refers to the energy required to maintain information, as in the maintenance of DNA in leaves (i.e. copying), and the maintenance of information of the population of trees (energy in seed DNA, which is the storing and disseminating information). The second concept is related to generating new information. When a species must be generated anew the costs are associated with developing one from existing information sources, such as trees within the same forest. However, the energy required to generate biodiversity at the global scale, that is to generate all species anew, required billions of years and a huge amount of total energy.

4. Energy, information and complexity

Complexity of systems has long been represented by “information-theory” measures. For example, complexity in bits is the number of yes–no decisions required to define a configuration and is expressed on a logarithmic scale. In short, the information-theory measure is the logarithm of the possibilities among the parts and connections.

Since the possible arrangements and connections increase roughly as the square of the number of items, the energy requirement to generate and maintain such storage may be proportional. However, information-theory measures do not differentiate between useful complexity that operates a system and happenstance

Table 5

Transformities of information in forest components and the energy to generate global biodiversity (after Odum [2] and Ager [21])

Item	Solar transformity	Units
<i>Forest scale</i>		
DNA in leaves	1.2E+07	seJ/J
DNA in seeds	1.9E+09	seJ/J
DNA in species	1.2E+12	seJ/J
Generate a new species	8.0E+15	seJ/J
<i>Global scale</i>		
Generate global biodiversity	2.1E+25	seJ/species

complexity with the same number of parts that cannot do anything. The contribution of complexity to the system is best evaluated from its emergy content and empower required to sustain it.

There is great complexity at the small-scales of molecules and heat, where information-theory measure on a logarithmic scale is molecular entropy. Information-theory measures do not distinguish the same complexity on small molecular scale from that found on a large ecological scale. Instead, emergy does increase with scale of the units.

4.1. Changes in emergy signatures

A histogram showing all emergy inputs ordered by quality by means of their transformity values is called an *emergy signature*. A signature is a picture of the driving forces, which support a system development. Changes in ecosystem complexity can result from alterations in driving energy signature, or inflows of a high quality stressor such as pollutants, or unsustainable activity like over harvesting. In each case, there is a consequent change in the pattern of energy flows supporting organization. Fig. 4a and b shows respectively the emergy signatures of one hectare of fully natural mangrove ecosystem and one hectare of a industrialized corn production in Florida. The signature of the mangrove ecosystem shows only environmental driving forces, while the industrialized corn is mostly driven by fossil fuels, goods, labor and services (as indicated by a shift of the columns to the right). The total emergy inflow to the corn is only 2.3 times the total emergy supporting the mangroves. This fact suggests that an ecosystem development is not only driven and determined by the total emergy inflow, but also by the quality of the different flows. In the first case, the ecosystem is driven towards ecological biodiversity and complexity, with an average transformity of $2.47E+04$ seJ/J; in the second case, the system is pushed towards a state with lower diversity and higher net productivity per hectare. However, the higher transformity characterizing industrialized agriculture, $1.26E+05$ seJ/J, indicates a lower global scale conversion efficiency. Expanding the scale, Fig. 5a and b shows respectively the emergy signatures of Nicaragua and Italy, two countries with very different level of economic development. Again, the total emergy per

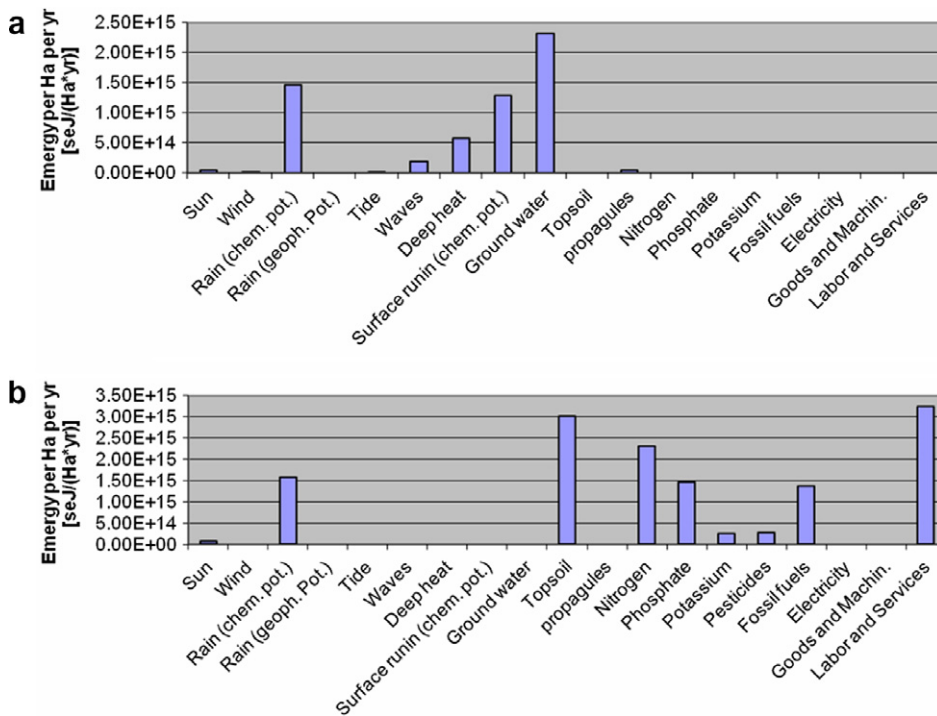


Fig. 4. Emergy signature of driving energies for 1 hectare of typical mangrove ecosystem [7] and 1 hectare of corn production in Florida [8].

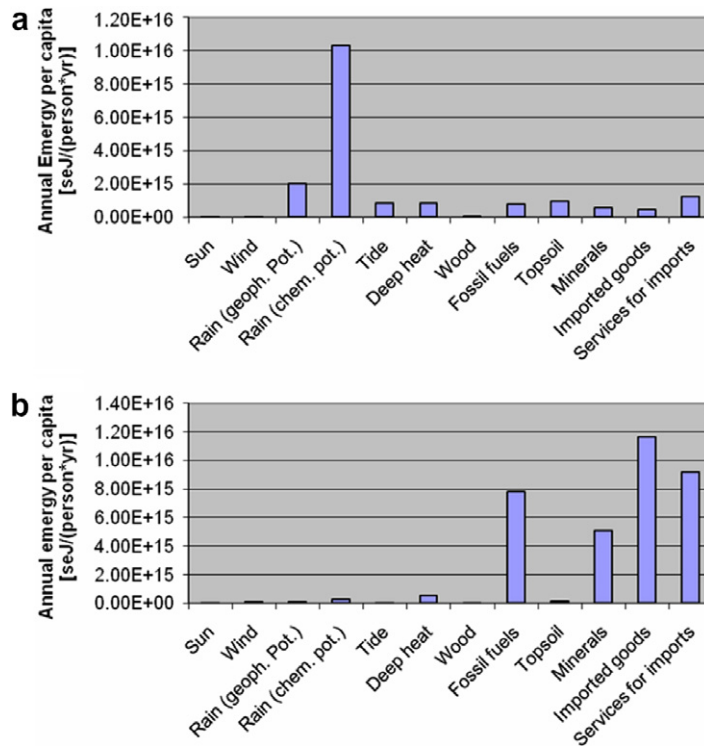


Fig. 5. Energy signatures for driving energies of Nicaragua 1999 [22] and Italy 2000 [23].

capita is not that different (Italy's value is only twice that for Nicaragua), but the energy signatures are very different. Nicaraguan signature indicates a rural country, mainly supported by fully environmental energy flows, while instead the opposite is true for Italy. In the first case, we have a nation rich with environmental complexity, while in the Italian case we have a nation characterized by environmental simplification and higher technological complexity. In a similar way, Odum et al. [24] and Huang et al. [25], explore trends of structural, economic, and social organization in world urban development.

4.2. Stressors

An energy signature could therefore change over time, resulting in ripples that could propagate through the whole system. If the change in signature is outside the normal range of fluctuations in the driving energy pattern, the effect is a change in the flows of energy and material throughout the system. In general, chemicals, including metals, pollutants and toxins have high transformity (see Table 6) and as a result of an excess concentration, they are capable of instigating significant changes in ecosystem processes, which often result in declines in ecosystem complexity. As transformities (emergy intensities) increase, their potential effect within ecosystem also increases. Effects can be both positive and negative. Transformity does not suggest the outcome that might result from the interaction of a stressor within an ecosystem, only that with high transformity, the effect is greater.

The ultimate effect of a pollutant or toxin is not only related to its transformity, but more importantly to its concentration or empower density (emergy per unit area per unit time, i.e. $\text{seJ}/\text{m}^2 \cdot \text{day}$) in the ecosystem. Where empower density of a stressor is significantly higher than the average empower density of the ecosystem, it is released into, one can expect significant changes in ecosystem function. For instance, because of the very high transformities of most metals like those at the bottom of Table 6, their concentrations need be only in the parts per billion range to still have empower densities greater than most natural ecosystems. For instance, using the transformity of mercury in Table 6, and the exergy of mercury [27], one can convert the

Table 6

Transformities of selected metals as global flows to atmosphere and storages within a river ecosystem

	Annual releases to atmosphere ^a (seJ/J)	River ecosystem ^b (seJ/J)
Aluminium	9.65E+06	3.30E+07
Iron	8.46E+07	6.19E+07
Chromium	2.59E+10	1.99E+10
Arsenic	8.56E+11	–
Lead	2.39E+12	3.59E+10
Cadmium	1.52E+13	8.78E+10
Mercury	6.85E+14	–

^a Not including human release.^b Genoni et al. [26].

transformity to a specific emergy of 3.7 E17 seJ/g. Using this specific emergy, and a mercury concentration of 0.001 ppb (the level the EPA, the US Environmental Protection Agency, considers to have chronic effects on aquatic life) the emergy density of the mercury in a lake would be 3.7 E12 sej/m². This emergy density is about two orders of magnitude greater than the empower of renewable sources driving the lake ecosystem. Genoni et al. [26] measured concentrations of 25 different elements in trophic compartments and in the physical environment of the Steina River in Germany. They calculated transformities of each element based on the global emergy supporting river ecosystem, which cycles the elements and their Gibbs energy. They suggested that the tendency to bioaccumulate was related to transformity of the elements and the transformity of accumulating compartments (i.e. metals and heavy elements accumulated in high transformity compartments).

Bioaccumulation of stressors may lead to simplified ecosystems by endangering some species or causing its extinction. Often the signs are subtle enough that change is difficult to detect. In other circumstances, indicators are not sensitive enough to detect change or to discern changes from “normal variability”. Network analysis of the flows of emergy on pathways of ecological systems may add insight into changes in ecosystem performance and integrity. Using the data from Silver Springs in Fig. 1, a network analysis of changes in emergy flows and cycling given in Table 7 shows changes in overall cycling emergy of about 15% at the top end of the food-chain and diminishing effect cascading back downward toward the bottom. The analysis uses a matrix technique to assign emergy to pathways and includes cycling, so that feedbacks within the system are accounted for. Evaluation of the changes in pathway emergy may provide a tool that can help in measuring changes in overall ecosystem behavior with alterations of components or elimination of trophic levels within the system.

Table 7

The effect of changes in system organization resulting from loss of top carnivore (Silver Springs, Florida data)

Item	Transformity ^a (seJ/J)	Pathway emergy with top carnivore ^b (seJ/m ² /da)	Pathway emergy without top carnivore ^c (seJ/m ² /da)	Percent change
Solar energy	1	–NC–	–NC–	–NC–
Kinetic energy of spring flow	7170	–NC–	–NC–	–NC–
Gross plant production	1620	3.87E+08	3.84E+08	0.8%
Net plant production	4660	4.71E+08	4.68E+08	0.6%
Detritus	6600	6.67E+08	6.58E+08	1.4%
Herbivores	127,000	5.32E+08	5.20E+08	2.3%
Carnivores	4,090,000	6.13E+08	5.20E+08	15.2%
Top carnivores	40,600,000	6.13E+08	0	100.0%

NC=no change.

^a After [18], updated according to Odum et al. [5].^b Emergy on pathways of the system depicted in Fig. 5. Emergy is calculated using a network analysis method [28].^c Emergy on pathways of the system depicted in Fig. 5 when the top carnivore is excluded. Emergy is calculated using a network analysis method [28].

5. Summary and conclusions

Emergy and transformity are useful measures that may be applied to concepts of ecosystem complexity. Transformity measures the convergence of biosphere work into processes and products of ecosystems and as such offers the opportunity to scale ecosystem and their parts based on the energy required to develop and maintain them. Ecosystems are composed of physical structure (i.e. wood, biomass, detritus, animal tissue, etc.) and information found in both its genetic makeup as well as relationships and connections between individuals and groups of individuals. Declines in ecosystem complexity are manifested in changes in the quality and quantity of relationships and connections between individuals. Stressors may change driving energies pathways, and connections.

When one component in a system is affected, the energy and matter flows in the whole system change, which may translate into declines in ecosystem integrity and complexity. We suggest in this paper, that changes in ecosystem structure and functions are reflected in changes of emergy flows and the corresponding transformities of system components.

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