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Explanations of ecological relationships with energy systems concepts

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Abstract

In order to compare aspects of systems ecology theory, this paper is one of a group by different authors arranged by Sven Jorgensen to explain the quantitative relationships in the same set of recently published papers. Energy concepts were used to identify and explain the results as systems designs and hierarchical structures self organized for maximum empower. To clarify the discussion, each explanation includes an energy systems diagram of the main parts and processes related in the paper, required by the theory, including connections with the controls from the surrounding system—the next larger scale. Whereas most of the papers explain mechanisms and relationships of parts, energy systems diagramming and synthesis shows how these designs are adaptations to increase function on several scales. Human understanding of phenomena is aided by simplified overview models that include the phenomena of special interest and their empower interactions on smaller and larger scales.

Keywords: Energy systems; Mechanism; Ecosystem

1. Introduction

Ecological concepts which have been formulated as energy systems theory relate the spatial, temporal, hierarchical, and informational patterns that follow from the concepts of energy laws and energy hierarchy for all scales. Structure and functions of a system are represented by diagrams in energy systems language to show energetic, material, hierarchical, and kinetic properties at the same time without the semantic confusion of using words alone. When appropriately drawn, scale of turnover time and territory increases from left to right. The conventions used in drawing also define the differential equations with the constraints of the thermodynamic involved. The energy systems theories and the energy systems symbols were explained in many published books and papers starting in 1966 (Odum, 1967, 1971, 1983). Energy concepts were given in detail in 1996, and the mathematical-simulation aspects of the energy systems language updated in 2000.

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1.1. Energy concepts and the maximum empower principle

In this paper the observed patterns found in ecosystems are explained by the principles by which energy is assigned in self organization. A principle tenet of these theories is the maximum empower principle. Systems self organize designs and populations that maximize their contribution to the empower of the surrounding system. Only in early growth stages where resources are in excess does this mean for a unit to maximize its power by operating alone. After an initial time of competition, units and relationships form connecting designs that contribute to the larger system's energy use and efficiency and receive reinforcement that insures their continuation and dominance.

Misunderstanding about the maximum power principle is sometimes a question of scale. Self organization maximizes empower at all scales and at the same time. Maximizing power might imply priority in self-organizing to send more energy flow toward the bottom of energy transformation chains where power is larger. This is avoided by expressing energy flows as empower = flow of emergy. By referring all flows to the energy of one kind that has to be used up by all the necessary pathways to make something, emergy puts all scales on a comparable basis. No scale is inherently more important than another. But the scale of study and explanation may be determined by the time and space scales of the human existence and interest.

Whereas many of the selected ecological papers proposed mechanisms at smaller physiological, organismal, or species population level, energy systems theory always explains the consequence of such mechanisms within the system of the next larger scale to which organisms and populations are controlled and adapt in the longer run.

When something at one scale is controlled by a mechanism on a larger scale, it may be described as having purpose beyond the small scale. Some people attack that language as teleological and therefore unscientific, but to deny teleology is to deny that each scale of interest is controlled by the next larger one. In self-organization energy transformations link scales together symbiotically, maximizing empower at all scales.

2. Explanations of published results

Each of the numbered sections that follow reviews the observational results of a recent paper, represents the phenomena with an ecosystem energy diagram, and relates the facts and each author's ideas to expectations of energy systems concepts.

2.1. Allocation of biomass to maximize early growth

McConnaughay and Coleman (1999) grew three species of annual plants for 57 days in gradients of light, water, and nutrients to see how the plants allocated their newly grown biomass to leaves, shoots, and roots. The experiments tested the hypothesis that plant biomass was allocated to minimize limiting factors. More leaves were formed where the light was less; more roots were formed when nutrients were less. Water gradient had little effect on biomass allocation.

2.1.1. Explanations

The authors found evidence of photosynthate allocation for maximum growth, which is an example of the maximum power principle. Expectation of the theory of maximum empower, is that species normally found where resources are initially in excess (light, nutrients) will have mechanisms (from previous evolutionary adaptation) to maximize their net growth (overgrowth ability). Fig. 1 is an energy systems model of these experiments aggregated according to the factors, mechanisms, and consequences mentioned by the authors. Note the many autocatalytic loops which reinforce their input functions. Such intercoupled autocatalytic processes have the property of passing energy to cogenerate units cooperatively. Even without a special mechanism at the split of photosynthate (Switch box Sw in Fig. 1), qualitative tracing of the model's pathways shows which parts grow most for each input condition: leaves have first priority on photosynthate when nutri-

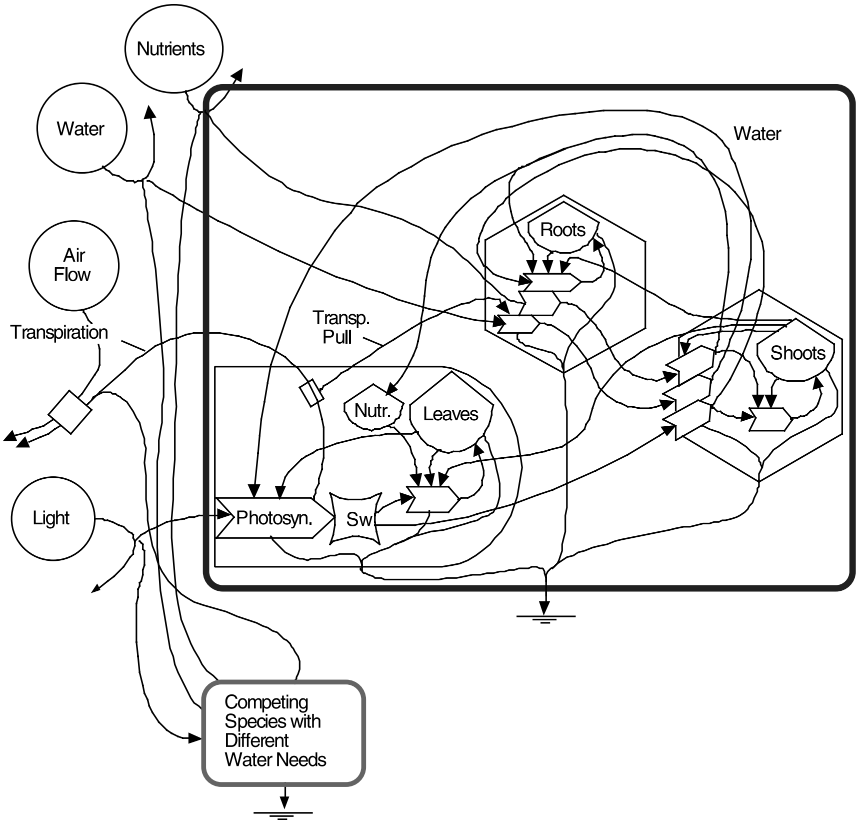

Fig. 1. Energy systems model of the main structures and processes involved by McConnaughay and Coleman (1999) in the study of biomass allocation by plant seedlings as limited by light, nutrients and water.

ents are in excess (light limiting). With nutrients low, more photosynthate passes to small roots and faster turnover. With age, more organic storage develops in shoots with their lesser depreciation rate.

Where water conditions differ in nature, maximum growth (maximum empower) is often accomplished more by species replacement and overgrowth than by physiological adaptation of the same species. Note alternate species included in Fig. 1. Even among the three similar species studied, the responses to different water conditions were very different.

Some of the known adaptive mechanisms for maximizing production were not monitored and thus are not included in the model. For example, changing chlorophyll is a principal mechanism of adaptation to light; changes in leaf reflectance of infra-red energy and stomatal behavior can conserve water; and changed ratios of nutritive elements can substitute in part for a limiting element.

2.2. Reality of prey–predator model with spatial and stochastic properties

Donalson and Nisbet (1999) found interesting time series when the Lotka–Volterra prey–predator model was simulated with stochastic births and deaths and a spatial dimension. However, models with mean intrinsic rate of reproduction constant are models with unlimited energy not valid in nature. Adding stochastic variation as if there is inherent randomness is not realistic either, if variation in the real world comes from energy constrained oscillations of the smaller scale. Is understanding aided by complex simulations designed to mimic the real world without the

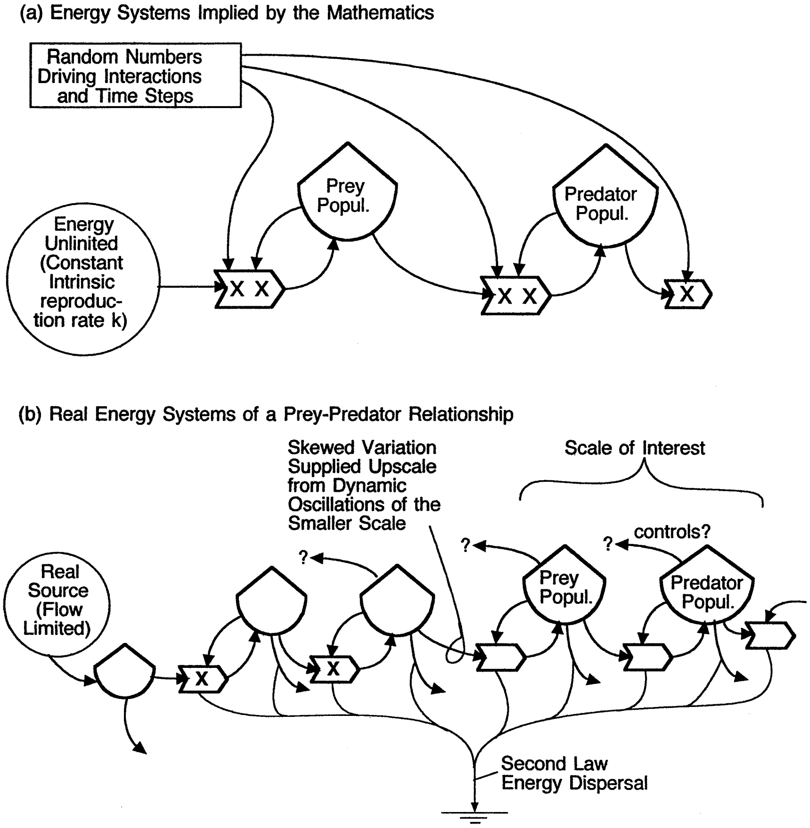

Fig. 2. Energy systems diagrams comparing the energy sources of real world prey–predator relationships with the unrealistic energy implied in the simulation models of Donalson and Nisbet (1999).

fundamental constraints of energy? Fig. 2 compares the unlimited energy system implied by the mathematics with the real energetics of prey–predator relationships.

2.3. Variation in number of species with latitude and area

Some empirical equations for the change in species number with latitude and with area were combined by Lyons and Willig (2000) and compared with biogeographic data on ranges of marsupials and bats. Energy systems theory accounts for the fewer species in higher latitudes as the necessary priority for energy use is for the physiological and behavioral adaptations to live with less favorable temperatures and seasons. As a result, less energy is available for the mechanisms of species interaction and niche separation necessary to prevent competitive elimination. The energy systems theory finds the increase of energy needed to support species rising in proportion to the inter-species interactions (Odum and Pigeon, 1970; Odum, 1971). Where available, energy is supplied in proportion to area; the area required is proportional to the species number squared. Or conversely, the species increase with the square root of the area. Fig. 3 diagrams the area effect (Odum, 2000).

2.4. Variation of diversity and the area occupied by species with latitude

Taylor and Gaines (1999) use models to relate the diversity decrease with latitude to the larger territories of species at higher latitudes. An energy support theory to explain the diversity change with latitude was given in the preceding

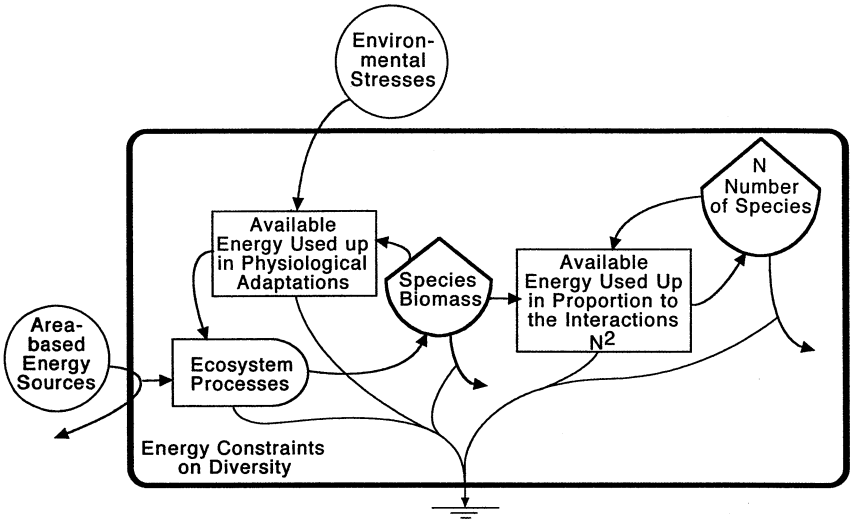

Fig. 3. Energy systems diagram showing the energy basis for species number and the role of area and the stress of less favorable environment of higher latitudes as studied by Lyons and Willig (2000).

paragraph. The smaller area per species in the tropics is explained by the larger number of species of similar functions available to divide up the energy available for diversity support. Fig. 4 is a modification of Fig. 5 to show the area per species quotient. Thus, the diversity gradients follow from the energy flows rather than being the cause.

2.5. Effect of chemical substances on food benefits to herbivores

Schmidt (2000) studied the effect of nutrition-retarding and toxic substances on the fox squirrel tendency to move out of those feeding areas with carnivore risk. Nutrition-retarding substances caused animals to adjust their time at risk to

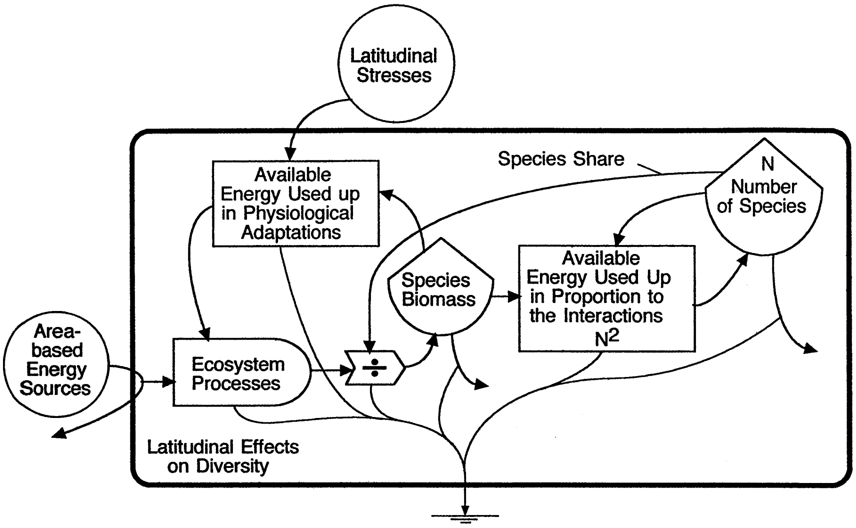

Fig. 4. Energy systems diagram of energy supporting diversity from Fig. 3 modified to include the effect of species number on the geographic area per species studied by Taylor and Gaines (1999).

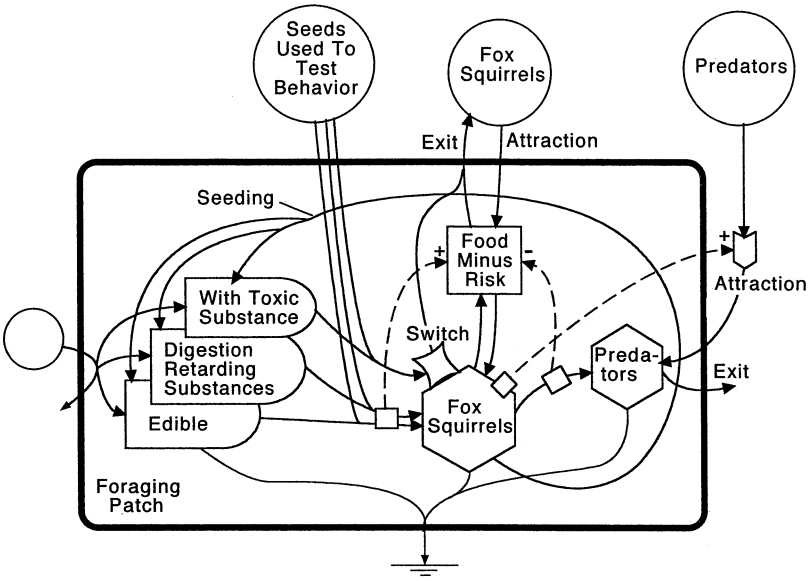

Fig. 5. Energy systems diagram of the relationship of fox squirrels and the plant food as affected by carnivore risk, toxic substances, and digestibility limiting substances as studied by Schmidt (2000).

optimize their net energy benefit, but toxins caused animals to move promptly. Energy systems theory judges feeding mechanisms in the whole relationship of the species involved, thus modeling at a larger scale. Energy hierarchy concepts predict that toxic substances have higher transformity and consequently greater unit effect, as observed. And more of the plants' energy would be required to make higher transformity substances. By making higher transformity inhibitors, plants could use resources to provide sustaining control mechanisms. Furthermore, plants insure their prevalence by feeding those species that contribute needed services such as dispersing seeds in appropriate ratios. Where toxics do occur (as in polluted areas), species that use energy to maintain toxic sensing mechanisms will prevail. Fig. 5 shows the relationships in the author's model of the mechanisms and their energy basis.

2.6. *Benefits of feeding behavior of deer mice using cover from predators*

Morris and Davidson (2000) tested three aspects of deer mice behavior to see if their feeding choices were beneficial to reproductive success. The mice chose areas with more forest cover from carnivores and minimized their time and feeding effort in less secure areas. An energy systems view expects appropriate populations of plant food, prey, and predator populations that keep the whole system at maximum performance. The behavior fits their participation in a habitat of complex mature ecosystem, not a role competing for maximum growth in simpler open ecosystems. This paper finds that some of the control of rates is inherited and/or learned behavior in the herbivore population. Fig. 6 diagrams the parts, energy flows, and sensing-behavioral pathways of the ecosystem studied in the paper.

2.7. *Increase of net productivity by increasing species evenness*

Wilsey and Potvin (2000) obtained some increase in net production of plants by planting species in early grassland succession to increase evenness indexes. This result is to be expected where self organization for maximum empower is given an opportunity to reinforce the better adapted species earlier. See principal pathways of reinforcement of production in Fig. 7.

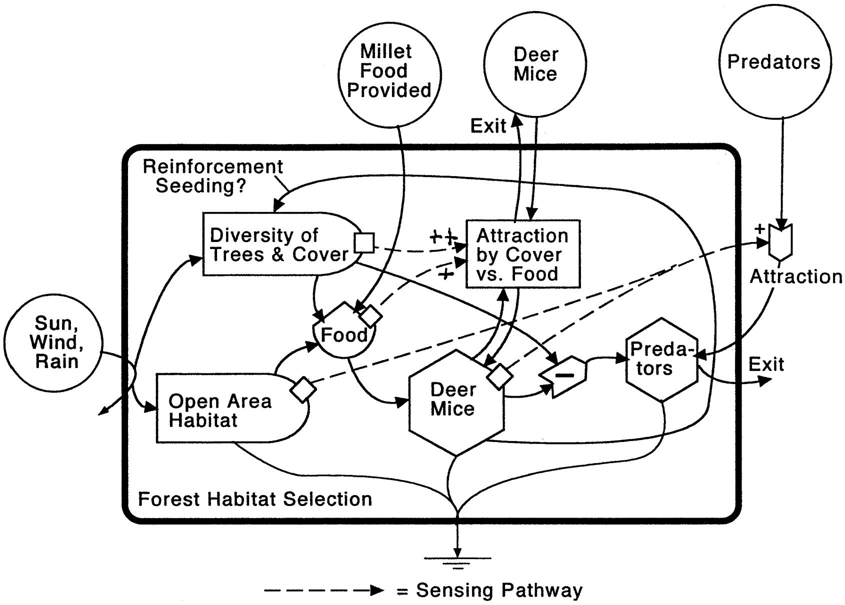

Fig. 6. Energy systems diagram showing the behavior of deer mice adapting to food supply and cover protection from weasels as studied by Morris and Davidson (2000).

2.8. Systems understanding of nitrogen dynamics in a woodland stream

Mulholland et al. (2000) used N^{15} tracer to estimate many of the rates of nitrogen processing in a forest stream in Tennessee. An overview summary of the authors' data on nitrogen flows is given in energy systems language to suggest the dynamic relationships of self-organization and its left–right energy hierarchy structure (Fig. 8a). For example, the expected concentration of nitrogen storage and lower turnover time was found in the snail *Elimia* (top of the series on the right). The simplification in Fig. 8b shows the 'competition–cooperation' design in which producers and consumers compete for nitrate while also reinforcing

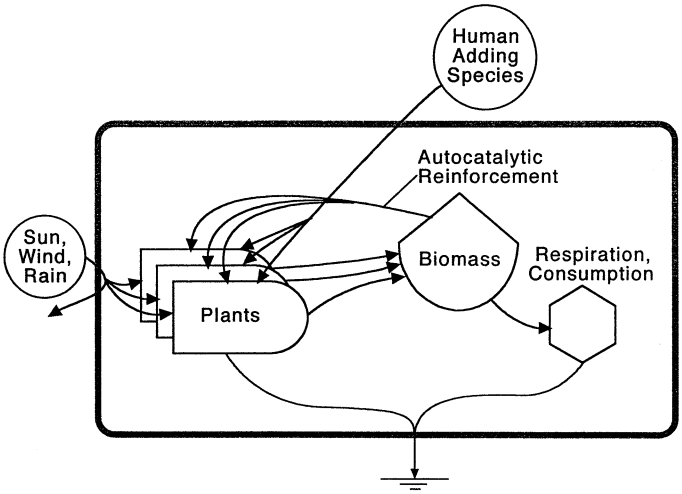

Fig. 7. Energy systems diagram showing the way starting an even distribution of plants can accelerate self organization for increased empower as studied by Wilsey and Potvin (2000).

each other with closed loop recycle. This comp–coop mechanism is a common design known to self regulate for maximum performance.

2.9. Adaptive fit of controlling bird consumers to climatic cycles on tropical dry islands

Grant et al. (2000) showed Galapagos finches adapting their breeding efforts, populations, and control of arthropods, increasing in years when higher sea temperature produces higher atmospheric vapor pressures, cloud cover shading, lower temperatures, and rain. With the pulsing that favors maximum power provided by El Nino, the finch populations contribute to ecosystem performance by adjusting their load and their services to the cycle without developing a destructive prey–predator cycle. Fig. 9 shows the system as discussed by the authors, including a possible adaptive mechanism, the negative sensing of higher land temperature when sea temperatures and clouds are less.

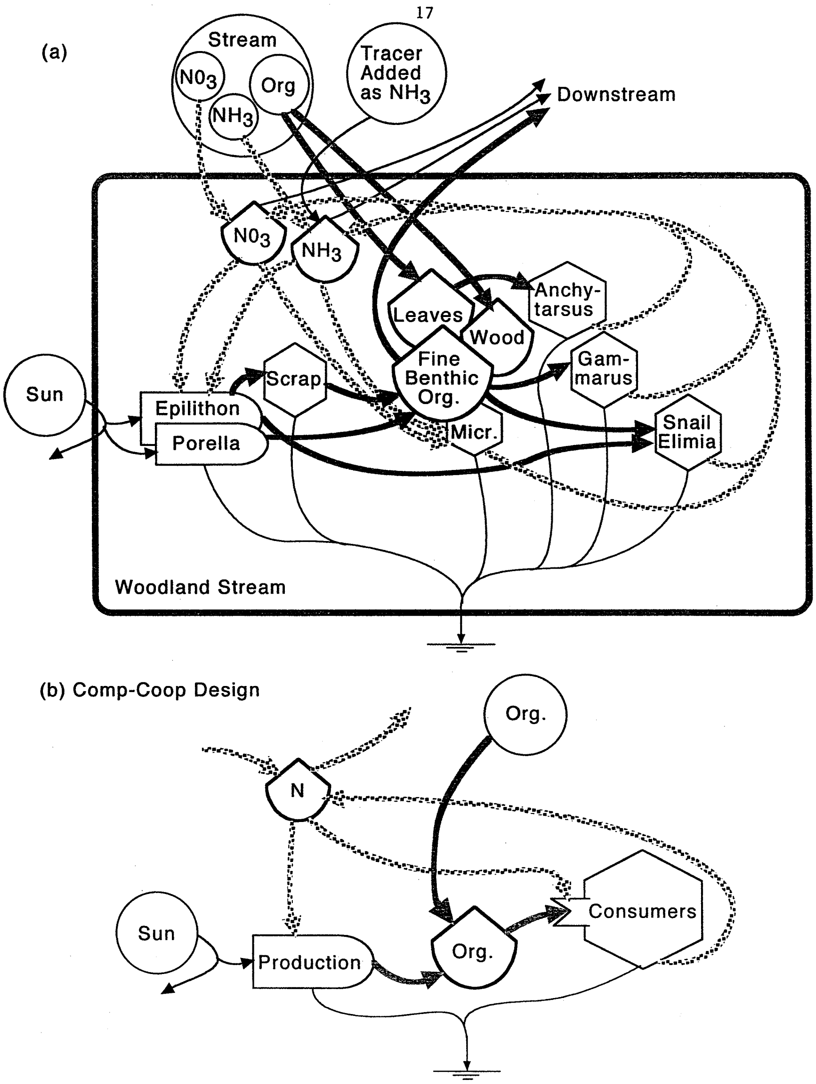

Fig. 8. Energy systems diagram of the Tennessee woodland stream ecosystem with some nitrogen flows as studied by Mulholland et al. (2000).

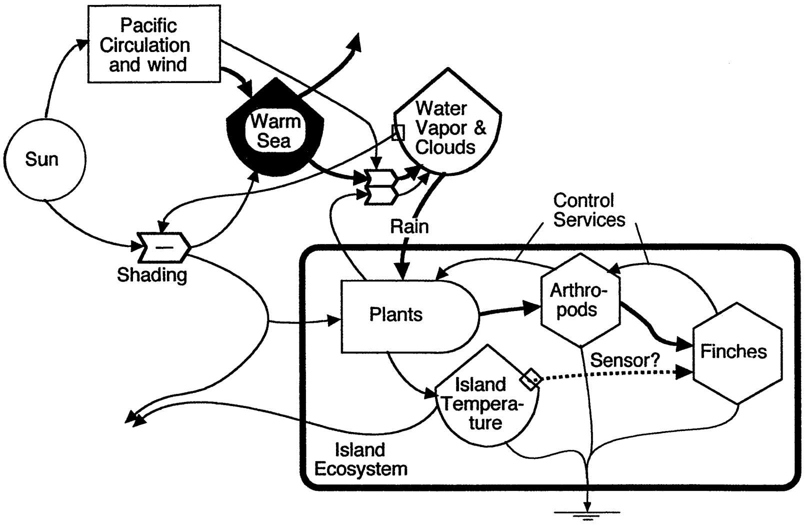

Fig. 9. Energy systems diagram showing the role of carnivorous finches adapting the Galapagos Island dry forest to increased resources of a warmer sea as studied by Grant et al. (2000).

2.10. Adaptive mechanisms connecting harrier predators and herbivorous voles to an ecosystem simplified by human agriculture

Salamolard et al. (2000) found hawk reproduction adjusting to vole populations and thus controlling the load on the plant production. Except when regional agriculture reduced diversity, predators could switch to alternate food with less prey–predator oscillation. Drawing an energy systems view in Fig. 10 shows how these design mechanisms limit overgrazing and help sustain the system productivity.

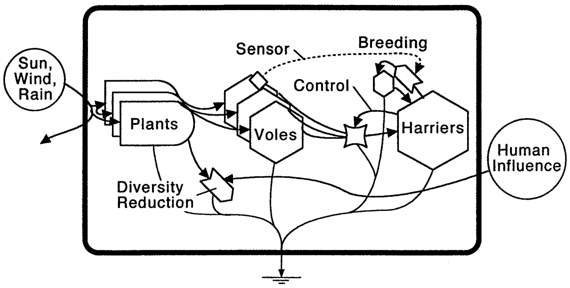

Fig. 10. Energy systems diagram showing the interplay of vole prey, harrier predators, and human influence in sustaining an ecosystem in France as studied by Salamolard et al. (2000).

2.11. Self regulation within a parasitic flea population, limiting its load on the host population

Tripet and Richner (1999) found intra-specific competition regulating the concentrations of bird fleas developing on host birds (blue tits). A stable parasite population did not overload the birds physiology and helped sustain the host population's role in the ecosystem (Fig. 11).

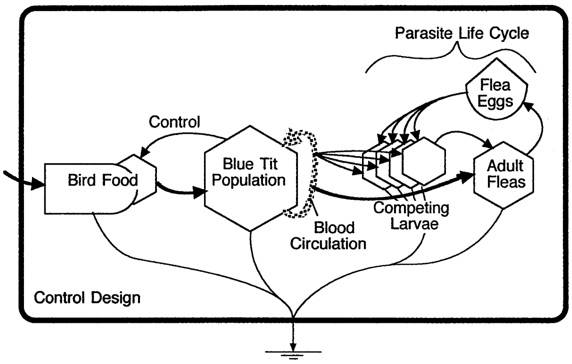

Fig. 11. Energy systems diagram showing the density dependent larval survival self regulating bird fleas and their control of bird functions in ecosystems as studied by Tripet and Richner (1999).

2.12. Self organization of chemosynthetic methane ecosystem on the sea floor

Smith et al. (2000) studied a methane-using ecosystem in a sea bottom briny pool in a low oxygen zone at 650 m in the Gulf of Mexico. The ecosystem was dominated by mussels, with endosymbiotic organisms converting the methane to metabolizable organic matter. The energy systems diagram in Fig. 12 may help in understanding the processing of materials and energy and the hierarchy of organization ending on the right in the largest *Bathymodiollus* mussels.

3. Commentary

Hopefully, the use of energy systems diagrams and concepts helps people to understand the meaning of scientific measurements and the way they may fit into and receive reinforcement by the larger systems of which they are part. Phenomena at all scales are interconnected, and full explanations are not possible by limiting the work of a discipline to one scale of time and space. Reading a paper so as to connect the author's results and his explanations with energy principles, and diagram the essence with aggregated simplicity, is hard work but fun. In the dozen papers reviewed here several maximum power designs were found, which should be looked for in any system.

The process of systems diagramming makes a reader dig critically in ways simple reading of a paper may not. Authors may enjoy seeing their work through a different lens. Hundreds of papers were diagrammed and discussed earlier in the book systems ecology (Odum, 1983).

However a National Science Foundation officer once told me that scientists do not like to have their work diagrammed by others because the model generated may have different aggregation, scales, and choice of pathways and parts included. If a consensus with an author is to be achieved he or she needs to collaborate in making the diagram. However, many if not most ecologists believe their science can make progress by measurements and hypotheses expressed only in words, without the rigor of energy-constrained, multiple scale, and mathematically drawn systems models. It would be a good policy if papers in ecological journals were not accepted until authors include their own diagrams, thus forcing authors to rigorously show how their ideas may fit their results on a systems basis.

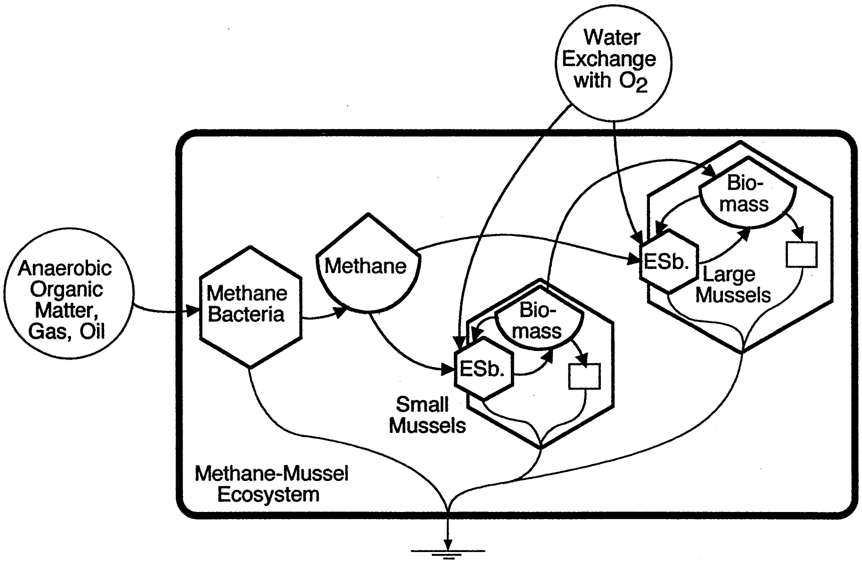

Fig. 12. Energy systems diagram showing the hierarchical series of the methane-based mussel ecosystem of brine pools on the sea bottom of the Gulf of Mexico as studied by Smith et al. (2000). Abbreviation Esb = endosymbiont.

In recent years with the development of emergy and transformity, we recognize explicitly what was subconscious earlier, that the diagrams laid out in energy transformation series represent energy hierarchy and are also the separation of scales of time and space from left to right. The analyses given here show an objective way to explain how mechanisms have purpose on the next scale, a perspective that Evelyn Hutchinson once called teleological mechanisms. It is too bad when people are taught that it is wrong to propose systems hypotheses and blind themselves to what may be most important and interesting in their own work.

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