

See: Ulanowicz, R.E. pp. 481-483. Theoretical Ecology

McGraw-Hill Yearbook of Science & Technology



1987

COMPREHENSIVE COVERAGE OF
RECENT EVENTS AND RESEARCH AS
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McGRAW-HILL ENCYCLOPEDIA OF
SCIENCE AND TECHNOLOGY

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**McGRAW-HILL YEARBOOK
OF SCIENCE & TECHNOLOGY**

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1234567890 DODO 8932109876

The Library of Congress has cataloged this serial
publication as follows:

McGraw-Hill yearbook of science and technology.
1962- . New York, McGraw-Hill Book Co.

v. illus. 26 cm.

Vols. for 1962- compiled by the staff of the
McGraw-Hill encyclopedia of science and
technology.

1. Science—Yearbooks. 2. Technology—
Yearbooks. 1. McGraw-Hill encyclopedia of
science and technology.

Q1.M13 505.8 62-12028

ISBN 0-07-046182-1
ISSN 0076-2016

Theoretical ecology

Environmental legislation and common discourse of an ecosystem, attributes without rigorous definitions. It is now possible, however, to define and measure a related property called ecosystem ascendancy, which in a single index quantifies both the magnitude of system activity and the degree of organization inherent in the pattern of interactions among taxa. The increase of ecosystem ascendancy describes the process of community growth and development, and the limits to this increase are reflected in various components of the measure. Ascendancy is an admixture of ideas from thermodynamics, economic input-output analysis, information theory, and cybernetics. That the index rests upon such firm theoretical foundations contributes to the power of ascendancy to unify several hypotheses of development pertaining both to ecosystems and to other cybernetic ensembles.

Growth and development are processes. It is only natural, therefore, that their mathematical definitions be related to the magnitudes and the juxtaposition of the constituent ecological processes. The most concrete measure of any process is the amount of material or energy transfer which accompanies the change; for purposes of description this intensity may be assumed to reflect and integrate all the more detailed aspects of the process. For example, the measured feeding rate of a herbivorous copepod in the ocean characterizes and embodies the densities and relative distributions of the predator and its prey, the feeding behavior of the herbivore, the morphologies and genetic makeups of copepod and phytoplankton, and so forth.

Derivation of ascendancy. In a community of n species there are at most n^2 bilateral exchanges of a

given medium, and these flows may be regarded as a network connecting the compartments. The network of energy flowing among the five "taxa" of the Cone Spring ecosystem is depicted in Fig. 1. The size of the network (that is, the exchanges as distinct from the contents of the nodes) is taken to be simply the aggregation of all the existing flows. Mathematically, if T_{ij} represents the magnitude of the flow from species i to species j , then the total amount of flow associated with the ecosystem becomes Eq. (1), where T_{0j} represents the inputs to

$$T = \sum_{i=0}^n \sum_{j=1}^{n+2} T_{ij} \quad (1)$$

species j from outside the system (for example, primary production, or advection of medium into the ecosystem), $T_{i,n+1}$ the output of useful medium from taxon i (such as by advection, or harvest by humans), and $T_{i,n+2}$ the amount of medium dissipated by i . In input-output analysis, T is called the total system throughput, and in economics a partial sum of T for the network of a national economy is the gross national production. There is strong and familiar precedent for reckoning community size in terms of total flow activity.

Although the mathematical description of network organization is moderately complicated, the underlying idea is nonetheless straightforward. A network is said to be organized or well articulated when an event (output) at any given compartment engenders other events (inputs) at only a limited number of other nodes (taxa). That is, if one knows that a quantum of medium has left a particular taxon, then one knows with relative confidence which species will receive the flow. Such articulation has been equated with the average mutual information of the flow structure as defined by Eq. (2), where K is a scalar constant. For example, knowledge that a

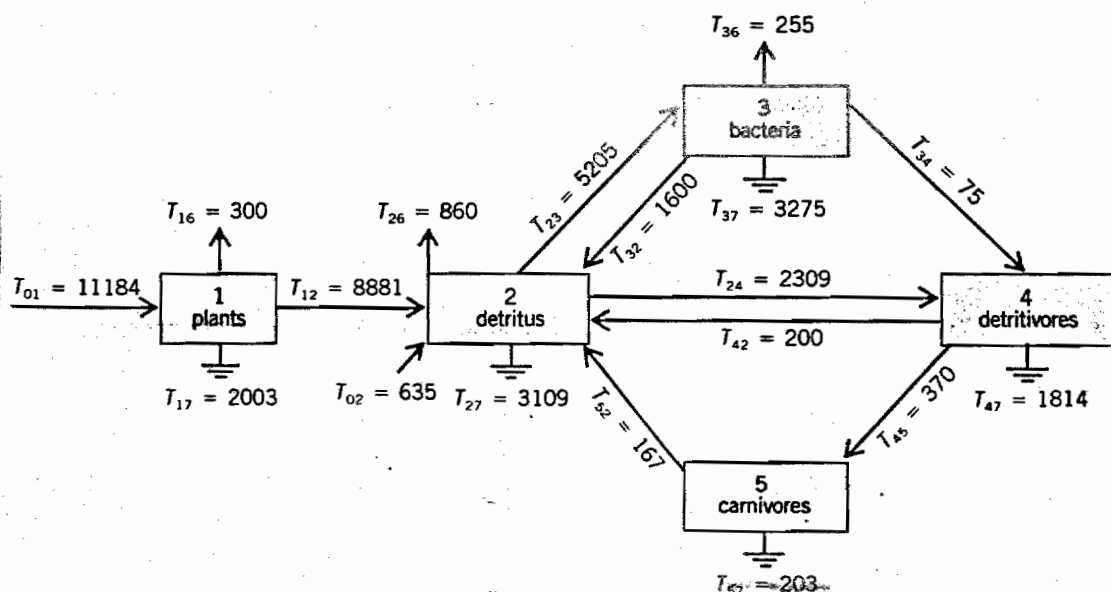


Fig. 1. Schematic of the flows of energy ($\text{kcal/m}^2 \cdot \text{y}$) between the major components of the Cone Spring ecosystem. Ground symbols represent dissipations.

$$A = K \sum_{i=1}^n \sum_{j=1}^n (T_{ij}/T) \log \left(T_{ij} T / \left[\sum_{k=1}^{n+2} T_{ik} \right] \left[\sum_{m=1}^n T_{mj} \right] \right) \quad (2)$$

quantum of flow has left a particular compartment in the hypothetical network in Fig. 2a gives one no idea as to which node the medium will enter next. The configuration is totally inarticulated, and A for the system is identically zero. By contrast, the network in Fig. 2b has the same total flow as 2a; however, knowing where the output exits tells one unequivocally where it is going. The value for A in Fig. 2b ($K \log 4$) is the maximum possible for a network of four compartments. Real four-component networks of flow would possess values for A intermediate to these theoretical extremes.

The usual convention in information theory is to set $K = 1$, but the scalar constant may be used to give physical dimensions to the system being studied. By setting $K = T$ the factor of organization is scaled by an index of size, and the product becomes the network ascendancy.

Because growth may be regarded as an increment in size, and development as an augmentation of organization, growth and development become two aspects of a unitary process—the increase of ascendancy. Ecosystems may be said to grow and develop insofar as their associated networks of material or

energy flows increase in ascendancy.

Community reconfiguration. No real system can grow and develop without bounds, and the limits on increasing A are readily apparent. To visualize the constraints, it helps to imagine an ecosystem recovering from a major environmental shock which has obliterated all but a few of the original species. Initially the surviving taxa have ample resources opened to them by the sudden demise of their competitors. As Alfred Lotka observed, the advantage, under conditions of abundance goes to those species best able to increase their throughputs. Consequently, initial recovery occurs largely as increasing total activity T . Available resources are finite, however, and medium cannot be recycled indefinitely because of obligatory losses at each transfer. Inevitably, the rise in T begins to slow, and the subsequent increase in ascendancy occurs mostly through the reconfiguration of the flows.

To follow the effects of community reconfiguration upon A , it is helpful to expand A into four intrinsically nonnegative terms, as in Eq. (3). The mathe-

$$A = C - (E + S + R) \quad (3)$$

matical forms of C , E , S , and R derive from information theory, and all bear some resemblance to that for A given above. Only their qualitative characteristics will be described below.

The quantity C exceeds the value of A for all real configurations; it represents the capacity of the existing system for development. During the intermediate stages of ecological succession, ascendancy increases mostly as a result of increasing capacity. A larger number of species and a more equitable distribution of activity among the taxa both serve to augment C . In the example of the recovering ecosystem, new species are continually arriving from less disturbed communities, and the available resources become spread over a more diverse ensemble of living things. This trend toward greater diversity cannot continue forever, because an increasing n and a finite T guarantee that some compartments eventually will share in only a minuscule fraction of the overall activity. Such insubstantial species are always subjected to the chance of extinction by the small perturbations which are a part of any real environment.

During the final stage of development, A increases primarily because of decreases in any of the last three terms, which collectively are called the system overhead. The first overhead term, E , is generated by the exports of usable medium, the $T_{i,n+1}$, whence a diminishing E mirrors the tendency for mature systems to become more self-contained. In principle, nothing prohibits E from shrinking to zero; however, most real systems are themselves components of hierarchically larger systems. Should the outputs of the smaller system be cybernetically linked to its own inputs in the next hierarchical order, then reduction of E beyond a certain amount could imperil the system's own inputs. The most poignant example of this limitation comes from international economics, where a cutback in oil ex-

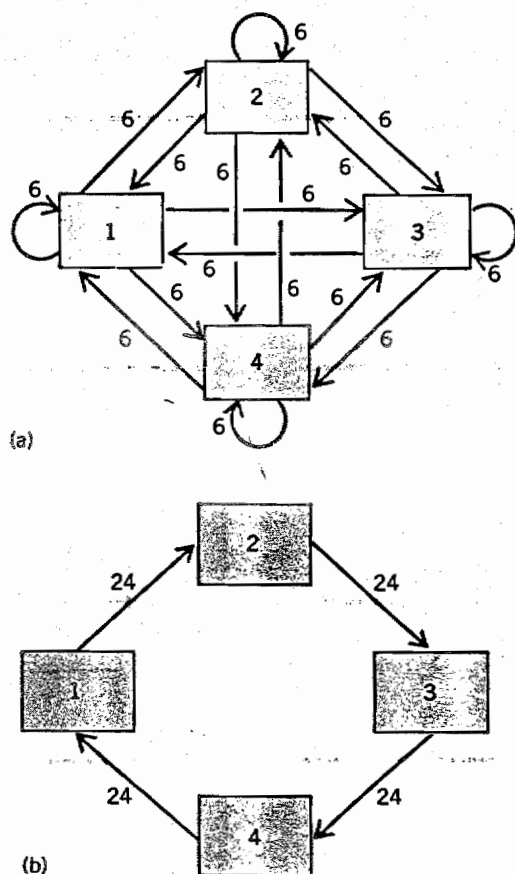


Fig. 2. Hypothetical ecosystem networks. (a) Network of inarticulated flows. (b) Network of maximally articulated flows.

ports by producer states depressed the global economy and eventually worked hardships upon the oil producers.

The dissipation of medium (the $T_{i,n+2}$) gives rise to S , which by the second law of thermodynamics is guaranteed to remain positive in real networks. Ilya Prigogine was the first to formalize the tendency for systems developing near their limits to minimize their dissipation. However, decreasing dissipation as a way of increasing A is effective only during the latter stages of development. During initial growth, A is increased more rapidly by inflating T and C at the relatively minor concomitant expense of increasing S .

The last term, R , reflects the redundancy of pathways connecting any two species. In the absence of disturbances, competition should diminish flows along the less efficient pathways, resulting in the relatively less diverse and more streamlined configurations often observed in mature ecosystems. But researchers have pointed out a connection between redundant pathways and ecosystem reliability. When some of the several pathways connecting two taxa are differentially perturbed, the less impacted routes may compensate for the disturbance. All real systems are subjected to some degree of environmental disturbance; hence R may decrease only to that level which, on the average, is sufficient to compensate for the vicissitudes of the given environment.

No real course of system evolution can be cleanly divided into the three phases as discussed; any one of the ways of increasing A may be occurring at any time. What is apparent at all times, however, is that the flow (and the occasional ebb) of the process called growth and development may be charted in strict quantitative fashion. The phenomenon central to the temporal behavior of ecosystems and connecting them with the actions of economic communities, ontogenesis, or social and political systems is now subject to scrutiny by numbers—a significant step toward a powerful and comprehensive theory of living systems.

For background information see ECOLOGICAL SUCCESSION; ECOSYSTEM; INFORMATION THEORY (BIOLOGY) in the McGraw-Hill Encyclopedia of Science and Technology.

[ROBERT E. ULANOWICZ]

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Thermoregulation

It has long been known that day-flying butterflies regulate their body temperatures by taking advantage of sunshine for basking. Night-flying Lepidoptera (usually moths) do not have such a readily available heat source. However, they also require often quite

specific and high body temperatures in order to generate sufficient work output from their flight muscles so that they can stay airborne. This article examines comparative aspects of moth thermoregulation in the contexts of body mass and habitat.

Sphinx moths. Most sphingids are fast-flying, narrow-winged, nocturnal moths that feed on nectar while they hover. The majority of species are tropical, and they range in weight from about 200 mg to over 6 g. In most species, flight is not possible until the temperature of the thorax (which contains the flight muscles) is near 104° F (40°C), and thoracic temperature (T_{th}) is regulated [maintained independent of ambient temperature (T_a)]. The T_a at which sphinx moths fly ranges from near 50°C (10°C) to 95°F (35°C). Resting moths have body temperature similar to that of their environment, and before starting to fly they warm up by a process like shivering, during which the upstroke and downstroke muscles of the wings are contracted nearly simultaneously, rather than alternately as in flight. During flight no heat is produced specifically for thermoregulation. Rather, all of the heat that then elevates body temperature is a by-product of the flight metabolism.

The internally generated heat during flight does not automatically result in optimum muscle temperatures. Because of their large mass, vigorous flight metabolism, and flight at high ambient temperature, these moths more commonly produce excess heat during flight. But the moths stabilize thoracic tem-

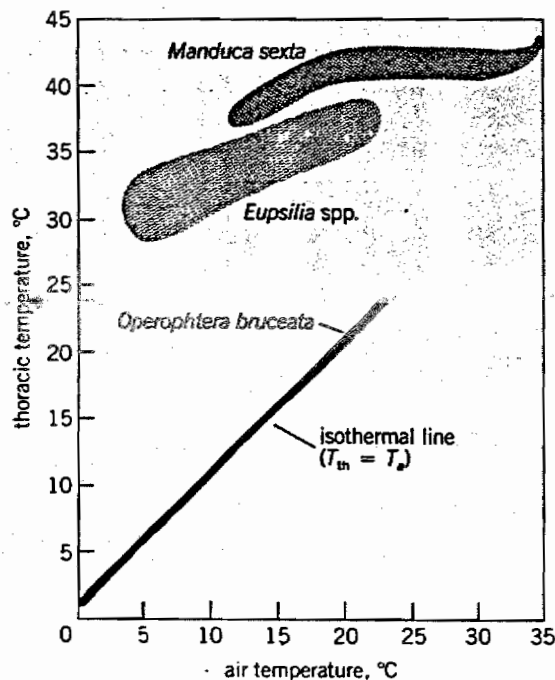


Fig. 1. Thoracic muscle temperatures during free flight of a sphinx moth, *Manduca sexta*; a winter noctuid moth, *Eupsilia* spp.; and a winter geometrid moth, *Operophtera bruceata*. The thoracic temperatures indicated also reflect the range of ambient temperature over which the moths were able to remain in continuous free flight. °F = (°C × 1.8) + 32. (After B. Heinrich and T. P. Mommson, *Flight of winter moths near 0°C*, *Science*, 228:177–179, 1985)