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Proceedings of the Royal Society of London. Series B, Biological Sciences, Vol. 232, No. 1267. (Nov. 23, 1987), pp. 181-192.

Proc. R. Soc. Lond. B **232**, 181–192 (1987)
Printed in Great Britain

Life and the production of entropy

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(*Communicated by R. M. May, F.R.S. – Received* 20 *November* 1986 – *Revised* 22 *June* 1987)

It appears that living communities serve to augment the rate of entropy production over what it would be in the absence of biota. This hypothesis might be tested by comparing the spectra of electromagnetic fluxes incident to and emanating from the surface of the Earth. An added measure of the value of stored energy to ecosystems is derived by using the economic theory of discounting.

Introduction

Thermodynamics is considered by many to be the keystone of modern science. There are certainly few other principles that have generated more controversy than the second law of thermodynamics. Yet the increase of entropy in the universe is an observation that has withstood the most stalwart of challenges. In the words of Eddington (1948),

> If someone points out to you that your pet theory of the universe is in disagreement with Maxwell's equations – then so much the worse for Maxwell's equations. . . . But if your theory is found to be against the second law of thermodynamics I can give you no hope; there is nothing for it but to collapse in deepest humiliation.

Earlier, it was thought that the process of life was a contradiction of the second law. Certainly, progressive order in ontogeny and phylogeny, when considered separately, appears to contradict the second law. However, such order never occurs in isolation, and when accurate account is made of all processes obligately coupled to the evolution of order, the final result is always that, on balance, the disorder in the Universe has increased. The universal increase of entropy is unavoidable.

Not all controversy over life and entropy has ceased, however. Classical thermodynamics does not explicitly refer to time. Time as used in thermodynamics is ordinal, but not cardinal in that it considers only the ultimate ends of processes and not the rates at which those ends are achieved. That life creates entropy hardly any serious thermodynamicist will dispute. However, whether living systems augment or diminish the rate of entropy production is an unresolved and highly intriguing question, as we hope to demonstrate.

By way of background, Prigogine (1945) employed some of the newly formulated concepts in irreversible thermodynamics (Onsager 1931) to recast the LeChâtelier–Braun principle for systems constrained to remain slightly away from thermodynamic equilibrium. Such systems, according to Prigogine (1945), will take on the configuration of forces and flows that minimizes its rate of entropy production. The Prigogine principle was broad in the sense that it applied to an arbitrary ensemble of physical processes, but it was restricted in its application by the severe constraint that the system remain very near to equilibrium.

Although the Prigogine hypothesis was formulated for physical systems, it none the less held great appeal for those seeking a 'principle of organization' for living systems. Their idea was that if there were no way around the second law, then at least living entities would make the least concessions possible to entropy. That is, life would represent another 'hang-up' in the degradation of energy (Dyson 1971). The full suite of investigators and philosophers who have argued that living systems operate near enough to equilibrium so as to minimize their rates of dissipation is too numerous to list (see, for example, Gladyshev 1982; Johnson 1981; Schneider 1987).

However, to operate near equilibrium is to behave in a very conservative fashion, and Lotka (1922), for example, argued that when excess resources were available, those adopting a conservative behaviour would lose out to more expansive competitors. Specifically, Lotka maintained that under such conditions the survival advantage goes to the population that has the greatest rate of resource utilization (i.e. the greatest rate of useful output such as growth and maintenance). To behave conservatively in an expansive milieu is to have a 'death wish' (H. T. Odum, personal communication). Needless to say, the rates of dissipation of expansive systems are hardly minimal (Odum & Pinkerton 1955), and Trincher (1965) pointed to the high rates of dissipation during embryogenesis as contradicting the Prigogine principle.

The question we consider here is whether living communities create more or less entropy than would appear at the same location in the absence of any living organisms. The question is stated in a comparative rather than an optimal or extreme sense. We do not mean thereby to exclude the possibility of optimal behaviour, but as will be seen, the comparative issue is difficult enough without complicating matters further.

We begin our discussion with the working hypothesis that living systems create more entropy than their non-living complements when observed over an appropriate interval of ecological time. An appropriate ecological interval is one that is long with respect to the temporal scale of physiological processes occurring among the constituent organisms, but short in relation to the time it takes the system to return to its 'climax' after pertubation (the successional timescale). For most systems the appropriate interval would be one or a few annual cycles.

We then present three propositions outlining heuristic reasons favouring the validity of the working hypothesis (see also Kay 1984). None of these arguments is rigorously conclusive, however, and in a fourth proposition we outline an experimental programme for actually putting the hypothesis to the test. Finally, we recognize that the extension of the working hypothesis to cover longer timescales over which long-term storages occur becomes problematical. To address the role of long-term biological storage in quantitative fashion, we suggest that elements from the economic theory of discounting be employed to estimate the value to the ecosystem of biologically stored energy and materials.

THE SECOND LAW

Proposition 1

The second law, in combination with the observed increase in order of living systems, implies that life increases the amount of entropy generated in the universe.

It is commonly accepted that living systems possess an inherent order. Order is a result of work. No work can be accomplished without the generation of even greater disorder (entropy). It is also widely held that species of organism evolve, and that the direction of evolution is predominantly (although not always) in the direction of greater order. Also, such order as exists in organisms must be continuously renewed at the expense of generating even more disorder. Thus, the well-known Bernal cells (Schmidt & Silveston 1958) enhance both the heat flow through and the rate of dissipation by the fluid system in which they arise. Some (Ulanowicz 1980, 1986) even hold that structural order is the obverse of a complementary order in the underlying dynamics (the dissipative structures of Prigogine). Hence, the very existence of order in life (and *a fortiori* its contingent nature) argues that life increases the amount of entropy being generated over what would otherwise appear in its absence.

The immediate evidence to sustain this proposition appears in the evolution of heterotrophy. Predation usually requires the development of physiological or behavioural programs, which are usually more expensive to maintain (i.e. generate more dissipation) than the corresponding defences to predation adapted by the prey. Another example is the increased metabolic demand occasioned by the appearance of homeothermy among some living organisms. The argument for increasing order at higher trophic levels has some theoretical foundations (Ulanowicz 1972; May 1973; Hirata & Fukao 1977; Nisbet & Gurney 1976). Now if living systems were constituted so as to decrease entropy production, the emergence of heterotrophs then would be retrogressive. However, if all life serves to increase the rate of entropy production, the emergence of heterotrophs poses no anomaly, but rather underscores a uniform tendency in nature.

POSITIVE FEEDBACK

Proposition 2

Positive feedback, a fundamental element of the life process, serves to augment the total dissipation by a living system.

Positive feedback, or autocatalysis, is not limited to living systems and is observed in chemical, nuclear, meteorological and other systems as well. But it is a ubiquitous characteristic of living systems (Eigen 1971). By way of the simplest example, if activity by entity A engenders an increase in the activity of another entity B, which is similarly coupled back to A, then A and B are engaged in autocatalysis. In general the autocatalytic cycle may have other intermediates, i.e. it may be a closed cycle of three or more catalytic links.

Without limits, positive feedback would result in an orgy of ever-increasing activity. In reality some factor always interferes with the behaviour of one or more of the participants so as to establish an upper limit on group activity. Typically, the constraint appears either as a finite rate of supply to one or more of the interacting group, or there is attenuation of feedback due to increased dispersal of effect along the causal loop. That is, the effect of activity at any point in the cycle cannot all be directed towards increasing the activity of the next downstream participant. Often, a growing circuit of autocatalysis is eventually opposed by a corresponding cycle of negative feedback (Allen & Starr 1982). The functions of positive and negative feedback remain reasonably distinct, however. Positive feedback induces growth and is a primary agent behind the formation of structure, whereas the role of negative feedback remains largely regulatory in nature.

It is important to notice that positive feedback serves as a mechanism for selection among its constituents. Any chance alteration in one of the components of a cycle that serves to decrease its activity will be propagated around the loop to reflect negatively upon itself. Conversely, any random improvement at any point will be self-rewarded. In more extreme cases actual participants in a loop may be replaced by newer arrivals better able to promote the positive feedback. Once established, autocatalysis serves as a pressure to incrementally transcend its own limits, either 'improving' or replacing its constituents (Ulanowicz 1986).

Now the aggregate dissipation by the members of a positive feedback loop is a monotonically increasing function of the total activity (i.e. the total amount of flow in the system) of the loop. This assertion is not immediately evident. Do not some of the 'improved' elements in the loop serve to increase activity by decreasing losses? Local improvements in efficiency are certainly conceivable, but the increased loop activity engendered elsewhere by such gain will result in still greater dissipation at the other sites where efficiencies have not improved. It is even possible to imagine a sequence of such local improvements whereby all the elements in the loop are eventually replaced by more efficient counterparts. In the end, the ratio of dissipation to total activity will have decreased, but the absolute amount of dissipation will none the less have risen. A quantitative example of why dissipation in a system increases monotonically is given by Ulanowicz (1987).

To summarize, positive feedback, or autocatalytic behaviour, drives the participating elements to the highest levels of activity possible under the prevailing circumstances. But higher activity in cyclically catalytic systems implies greater dissipation, and increased dissipation, with only rare exceptions (e.g. lasers), implies more entropy. Hence, positive feedback is a mechanism for the generation of entropy.

Causal loops have been of interest in ecology for several decades (Hutchinson 1948). That some degree of positive feedback exists in ecosystem is guaranteed by the observation that much material, and some energy, cycle within living communities. Odum (1969) identifies a greater degree of cycling as a distinguishing characteristic of more mature ecosystems. Finn (1976) and Patten (1985) have quantified the degree of cycling in systems, and Ulanowicz (1983) has outlined a method for analysing the structure of cycling in ecosystems. The observation of Trincher (1965) of high dissipative rates during embryogenesis is very likely the manifestation of Eigen's (1971) 'hypercycles' (positive feedback) at work in the developing organism.

It was remarked earlier that autocatalytic behaviour is not unique to living systems. It has been studied extensively in chemical systems (see, for example, Glansdorff & Prigogine 1971). The thermonuclear (autocatalytic) reactions of stars are quantitatively one of the largest sources of dissipation in the universe. Meteorological organization is often the result of positive feedback (e.g. convective thunderstorms and hurricanes), and Paltridge (1979) has made some bold efforts at predicting climatological change by invoking the principle of maximal dissipation. With all the potential for autocatalytic dissipation by non-living systems, why should one persist in maintaining that life augments dissipation?

To take these points in order, chemical oscillations exist in isolation only under laboratory conditions. In nature they have been either outcompeted by, or incorporated into, living systems. Thermonuclear reactions and violent meteorological phenomena (e.g. hurricanes and tornadoes) are largely incompatible with life, and do not coexist in a given locale with living communities for any length of time. Only the smaller scale, weakly autocatalytic meteorological phenomena pose any threat to the hypothesis, and this conflict will be addressed later under Proposition 4. Hence, in those locations where life occurs, it serves to augment dissipation over the natural background.

ENTROPY PRODUCTION AS A CONSEQUENCE OF UTILIZATION EFFICIENCY

Proposition 3

Living systems generate more entropy because they are more effective in utilizing energy than are the ambient physical systems.

At first glance, this sounds like self-contradiction. The problem lies in the ambiguities associated with the concept of 'efficiency.' It usually connotes conservative behaviour (a first-law notion), which in turn is often paired with minimizing losses, including dissipation. But these concerns are largely quantitative, and it should be remembered that entropy (a second-law concept) has a prominent qualitative dimension.

Specifically, the entropy of a given unit of energy varies in inverse proportion to its ability to do work, as Gibbs and Helmholtz have pointed out. Low entropy energy has a greater capacity to do work. If two systems receive the same quantity of energy at the same entropy, that system which extracts the most work from its input before releasing it to its environment (as it inevitably must) can be said, in the second law sense of the word, to be the more efficient utilizer. Having extracted more work from the given amount of energy, the quality of the release is less, i.e. its entropy is higher.

But are living systems more efficient at extracting energy from their inputs? To answer this question one needs to observe the dissipative outputs of living and non-living systems, an experiment considered in Proposition 4.

GLOBAL BALANCE

Proposition 4

Living systems generate more entropy than their ambient environment by projecting a lower albedo at shorter electromagnetic wavelengths and generating greater emission at longer wavelengths.

This last statement provides less a reason why life augments the production of entropy than it gives a way of testing the central hypothesis. So many arguments involving entropy and living systems remain hypothetical and untestable because there exists no feasible way to measure the entropy (or derivative properties such as free energy) of an organism alive in its environment. It is difficult enough to quantify the entropy of most simple substances. To apply the cryogenic techniques commonly used for inert materials to a living being is nonsensical. To attempt such a measurement one must first remove the living creature from its biotic environment and kill it in the course of measuring the variation of its heat capacity at low temperatures. Both acts destroy the order and organization necessary for the existence of the entity as a living being. It is doubtful that any entropy measured by this procedure would be of much value for inferring anything about the organization of the creature *in situ*, *in vivo*.

The situation is not hopeless, however. The biotic realm interacts with the abiotic, and the former leaves the traces of its activities upon the latter. One seeks to remove the observer to a location where he would see only the effects of the life process upon some abiotic medium. In particular, the biosphere is a closed system with practically no exchange of material with extraterrestrial sources. However, energy does enter and leave the Earth, primarily as electromagnetic radiation. The radiation back into space is generally of lesser quality than when it impinged upon the Earth, and living systems have contributed to that degradation to some degree (Kay 1984).

If one knows the history of the spectral distribution of the incoming and outgoing radiative fluxes, it is an uncomplicated matter to calculate the entropic change that must have occurred at the surface. The electromagnetic flux may be considered as the flow of a Bose–Einstein gas.

If $e(\lambda,t)\,\mathrm{d}\lambda\,\mathrm{d}t$ represents the amount of radiation in the differential wavelength band between λ and $\lambda+\mathrm{d}\lambda$ that passes a given area during the interval t and $t+\mathrm{d}t$, then the temperature of this 'gas' may be taken as $hc/k\lambda$, where h is Planck's constant, c is the speed of light and k is the Boltzmann constant. The flow of entropy associated with this photon stream is found by dividing the energetic flux by its associated temperature;

$$s(\lambda,t)\,\mathrm{d}\lambda\,\mathrm{d}t = e(\lambda,t)\,\mathrm{d}\lambda\,\mathrm{d}t/T = (k/hc)\,e(\lambda,t)\,\lambda\,\mathrm{d}\lambda\,\mathrm{d}t, \tag{1}$$

where s is the entropic flow corresponding to e. The total entropy flux is found by integrating s over all wavelengths,

$$s(t)\,\mathrm{d}t = (k/hc)\left\{\int_0^\infty e(\lambda,t)\,\lambda\,\mathrm{d}\lambda\right\}\mathrm{d}t. \tag{2}$$

Of course, the integral in brackets cannot and need not be measured over the entire spectrum, and practical limits might run from *ca.* 50 μm in the infrared to about 0.2 μm in the ultraviolet. (Call these λ_1 and λ_2, respectively.) Denoting the incoming and outgoing fluxes by the subscripts i and o, respectively, the instantaneous generation of entropy at the surface of the Earth, S, becomes

$$S(t)\,\mathrm{d}t = \{s_0(t) - s_i(t)\}\,\mathrm{d}t = (k/hc)\left\{\int_{\lambda_1}^{\lambda_2} (e_0 - e_i)\,\lambda\,\mathrm{d}\lambda\right\}\mathrm{d}t. \tag{3}$$

Now it is well-known that biota capture energy and retain it for a while before releasing it back to the environment in degraded form. Therefore the instantaneous flux should be averaged over a long enough interval, τ, to smooth any diurnal or seasonal variations in the $S(t)$ of a relatively stable ecosystems:

$$\bar{S} = (k/\tau hc)\int_0^{\tau}\int_{\lambda_1}^{\lambda_2} (e_0 - e_i)\,\lambda\,\mathrm{d}\lambda\,\mathrm{d}t. \tag{4}$$

If e is measured in joules per cubic metre per second, then the average flux, $\overline{S}$ has the dimensions joules per square metre per second.

The question at hand is whether or not the $\bar{S}$ measured over those areas of the Earth's surface that are dominated by dense biosystems (e.g. tropical rainforests) would exceed the same measurement taken over a relative desert at the same latitude. The correct answer can be supplied by a well-planned research programme implementing appropriate remote sensing technology. There are, however, several casual observations that would indicate that the forest is more dissipative than the desert.

To anyone baking in a desert at midday it might seem hard to imagine that a forest canopy could be more dissipative. However, objective measurements probably would show otherwise. To begin with, the desert surface is more reflective than a leaf canopy. Reflection of electromagnetic radiation occurs without change in wavelength and virtually no change in entropy. (There is a general tendency in desert surfaces towards lighter, more reflective colours. Bleaching in the sun is more than a simile.) The absorbed fraction of incident radiation quickly heats the surface to a temperature exceeding that of a forest leaf. The flux of back radiation is high, but because of the elevated temperature of the surface, the quality factor of this flux remains higher than what comes off the forest canopy. In addition, the desert surface cools rapidly after sunset, and at night the intensity of reradiation falls off quickly. The backradiation from the biome, however, does not fall as rapidly at night, the forest temperature does not plummet, and the reradiation of physically absorbed heat is augmented by the release of chemical energy via the continuous respiration of autotrophs, bacteria and heterotrophs. Hence, when integrated over the diurnal cycle, the dissipation of the forest probably exceeds that of the desert. Similar arguments apply to the seasonal variations in the entropy productions.

Some might argue that a more equitable comparison would be made between living and non-living systems, both having similar physical characteristics, by comparing a living and an artificial turf, for example. It is our opinion that the foregoing arguments comparing entropy production in forests with those in deserts apply to the turfs as well, albeit with markedly diminished difference in dissipation rates. Such difference would increase, however, as the living turf developed towards the next successional stage and as the pigment in the artificial medium faded. An exception to the hypothesis might appear in those (relatively unusual) circumstances where reduced temperature or excessive moisture inhibited heterotrophy, and the system accumulated energy over the long term as thick sod or peat (but more about that in the next section).

There remains the possibility that any augmented entropy production by living systems will be a 'signal' lost in the 'noise' of the variations in the dissipations effected by the abiotic surroundings. The signal might be especially confounded by meteorological advection along the surface. The dissipations resulting from the weakly autocatalytic meteorological events (thunderstorms) are likely to be co-correlated with the biological signal, however, so it would probably be best to schedule measurements to avoid such cloud as far as possible.

The compilation of maps of entropy creation as it occurs on the Earth's surface by using remote sensing data appears to afford the best way to determine the relative amount of entropy created by the life process.

CAVEAT

The preceding arguments have all been cast in the context of current thermodynamic theory. Hardly anyone believes that living processes contravene the principles of thermodynamics, but there are many who feel that this branch of physical science must in some way be extended before it can provide a sufficient description of biological phenomena.

One particular shortcoming of present thermodynamics has already been mentioned: thermodynamic time is ordinal, but not cardinal. That is, for any two times t_1 and t_2, it matters greatly whether t_1 comes before or after t_2. However, the magnitude of the duration between t_1 and t_2 is unimportant to the description of the system. This is because classical and near-equilibrium thermodynamics deal with systems that are at equilibrium or at steady-state, respectively. In the latter condition, for example, one makes an entropy balance on the system by measuring the rates of entropy influx and efflux to calculate by difference the rate of entropy production. At first glance it might seem that by measuring rates one is implicitly accounting for the cardinal nature of time. This is not entirely the case. Such measurements provide no information on how long the energy or material spent inside the compartment. Did the energy emanating from the system pass quickly through the compartment, or did it enter at some time in the distant past? Of course, one is justified in asking whether the residence time of the energy is of any importance at all.

There appear to be good reasons for believing that the time energy spends within an ecological system is a key indicator of the degree of maturity of the system (Hannon 1979; Cheslak & Lammarra 1981; Higashi & Patten 1987). Both succession and evolution appear to favour the development of species that retain captured energy for progressively longer periods. The turnover times of oaks and tigers exceed those of blue–green algae and ctenophores, for example. The latter are representative of 'r-strategists', organisms that thrive in the early stages of system development where resources are abundant but the environment is quite erratic. By contrast, the former 'K-strategists' are the products of resource-limited, highly competitive, albeit more predictable environments.

How does one go about accounting for the delay in the passage of medium through a system? One lead is provided by the economic theory of discounting. When an individual acquires an economic resource there follows a (conscious or otherwise) decision of how and when to spend that capital. One must weigh the advantages of spending it now against the future benefits and risks of disposing of it at some later time. When there is a strong reason to liquidate the asset immediately, whether because there is little need for it at a later time or because conditions in the future seem quite uncertain, then one spends the resource as soon as possible and discounts its future value.

Different individuals and corporations have unique histories and present circumstances, so it follows that the degree to which they discount the future value of a resource will vary. Each is said to regard the same resource with a different discount rate, r. In the simplest case, this discount rate is unchanging with time, so that the future value of the commodity is seen to decline in the fashion of a negative exponential, $V\mathrm{e}^{-rt}$, where V is the present value of the resource, r is the constant discount rate and t is time into the future.

It should be strongly emphasized that discounting need not be a conscious process. Organisms evolving in a particular environment may acquire teleonomic growth or behaviour patterns (see Mayr 1974) that evince an implicit discounting process. In this sense 'r-strategists', face an abundant set of resources and a very precarious future, may be said to strongly discount the future value of the resources to themselves. (There is, however, a significant investment in reproduction, otherwise the species would cease to exist.) These species store little, are small, respire heavily, excrete profusely and in general are characterized by short turnover times. At the other extreme are the 'K-strategists', which evolve elaborate structural and behavioural attributes that give them an advantage in a more resource-limited, competitive environment. They discount incoming resources to a lesser extent, investing them into biomass, structure and intricate behaviour. The trend in both succession and evolution appears to be in the direction of organisms that progressively discount resources to a lesser degree (i.e. the discount rate, r decreases with development).

Metabolic data often afford an approximate estimate of the energy discount rates exhibited by many living species. To see this, one may assume that an amount of biomass, B, of a particular species possesses ρ units of energy in each unit of B, i.e. ρ is a specific energy or energy density. If the ρB units of energy are not immediately used, they will be discounted to $\rho B\mathrm{e}^{-rt}$ for future use at time t. But the same biomass requires a continuous expenditure of ω units of energy per unit time per unit of B to maintain the biomass for future use. The total expenditure, ωBt, to carry B until time t must likewise be discounted by e^{-rt}. The parameters, ρ, ω and r are all assumed to be constant. The average, long-term discount rate is then defined such that the accumulated value of the investment (the energy expended to maintain B) should equal the accumulated value of preserving B into the indefinite future, or

$$\int_0^\infty \omega B t\, \mathrm{e}^{-rt}\, \mathrm{d}t = \int_0^\infty \rho B\, \mathrm{e}^{-rt}\, \mathrm{d}t. \tag{5}$$

Solving this equation yields $r = \omega/\rho$. That is, species with low discount rates are characterized by low metabolic rates or high specific energies or both.

Ulanowicz (1972) and May (1973) have given systems-theoretic reasons why the energy density should increase as one ascends the trophic ladder, whereas Odum (1969) cites a decrease in ω as an indicator of maturation in ecosystems. Our r accounts for both of these ideas simultaneously.

The estimated discount rate becomes equal to the respiration rate when expressed as a fractional loss per unit time. Thus Wiegert (1975) reports a value of 11.3 per year for the ω/ρ of algal communities, whereas Jorgensen (1979) reports a range in the same quotient of about 0.37–3.7 per year for fish. Usually, the variation in ω among different taxa (Jorgensen 1979) exceeds the corresponding variation in ρ (Slobodkin & Richman 1961). One expects the discount rate to be inversely related to the average life-span of the given species, and perusal of the latter references tends to support this notion.

More accurate estimates of discount rates involve a suite of process rates and development times (Hannon 1984).

The physicist might well ask what relevance biological discount rates have to entropy or entropy production. It should be remembered that entropy is an inverse measure of value: the higher the entropy the lower the value of the associated energy for doing physical work. But entropy describes only part of the value of an energy resource in a biological context. The duration that a quantum of energy spends in a living system is also related to its value. An appropriate balance of biologically valued energy entering and leaving a living system should help to define a more accurate qualitative conclusion regarding the role of life in the dynamics of the universe. We feel that the discounting process gauges how living systems respond to the inevitability that they must increase the universal disorder: as a system matures and develops increasingly complex structure, the increase in entropy production continues, albeit in decelerating fashion, as reflected by the continual decline in the natural discount rate.

Conclusions

The available indications are that the life process tends to augment the production of physical entropy in the universe, although the data to substantiate this hypothesis are yet to be taken. Regardless of the outcome on this issue, it is unlikely to be the final word on the subject. Entropy is an inverse measure of the value of energy in a physical context. The efficacy of a given amount of energy might be quite different in the biological context where storage and delays become prominent factors in the value calculus.

When we speak of life, we must necessarily speak of values. Hence appropriate value measures for ecosystems should be pursued. A first task towards elucidating value might be to measure physically the discount rates of various species in an appropriate ecosystem.

R. E. U. acknowledges the helpful discussion with Trevor Platt about measuring entropy production rates by using remote sensing, thanks G. D. Canaday, B. Hayden and T. Heimer for typing and editing the manuscript. Robert Herendeen and James Kay were most helpful in criticizing the draft manuscript. We thank Professor D. R. Wilkie of the University College, London, for his help in preparing the final manuscript.

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