Entropy Production in Ecosystems

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Abstract. We present an extremely minimal ecosystem model which takes account of thermodynamic constraints on the organisms' metabolism. This suggests a way to test the application of a hypothesised principle of Maximum Entropy Production to ecosystems. It also puts definite physical bounds on the rates at which matter can flow through the system and paves the way for more detailed models that have thermodynamic principles built in from the start. In providing the background for this model we point out some connections between thermodynamic principles and autopoiesis.

1 Introduction

Artificial life has had some successes at emulating many aspects of life in abstract and simulation models. In order to do this some aspects of life in the physical world are included in the model and the remainder assumed irrelevant for the study in question. Most ALife studies have ignored thermodynamic issues such as energy use and entropy production, yet if one considers living organisms as self-sustaining processes such issues are fundamental.

The idea that ecosystems act so as to maximise a thermodynamic quantity such as energy flow has been a running theme throughout the ecological literature [17]. In a parallel series of developments, notions of a principle of Maximum Entropy Production (MEP) have been discussed for complex non-linear systems that are maintained in a steady state out of thermodynamic equilibrium by external forces. So far the most successful applications of this idea have been to large-scale models of planetary climates driven by energy input from the sun [13, 6]. It has been hypothesised that the MEP principle might be general enough to apply to apply to living systems as well. In particular, MEP is thought to hold arbitrarily far from equilibrium, making its applicability to living systems uniquely plausible.

We present an extremely simple model of an ecosystem which takes account of thermodynamic constraints on the organisms' metabolism. We find that there is a peak in entropy production at a particular value for the rate of matter flux through the system. This demonstrates a way in which the hypothesised principle of Maximum Entropy Production could be tested experimentally in ecological systems. It also puts definite bounds on the rates of flux that can be achieved and paves the way for more detailed models that have thermodynamic constraints built in from the start.

A further contribution of this paper is a clarification of the fundamental interrelationship between the autopoietic perspective and thermodynamics in section 2.1.

2 Background

2.1 Thermodynamics Applied to Life

Organisms have low entropy compared to their surroundings. We can relate this to their structure by considering Boltzmann's result that the entropy S of a system is proportional to the logarithm of the number W of physical microscopic states compatible with the system's macroscopic state: $S = k_{\mathrm{B}} \log W$.[1] Structure is a macroscopic property. We can think of it as a set of constraints on the system's microscopic state. On a microscopic level one can only talk about state: there is an atom here, another there and so on, and the concept of structure is not relevant. But moving to a macroscopic level and throwing away some information we are able to structural statements such as "there is a membrane here, beyond which the concentration of this compound is higher." This statement is macroscopic: there are many possible ways in which the atoms could be arranged which are compatible with the concentration being higher behind the membrane. We can think of these as a vast number of hypotheses about the system's (unobservable) microscopic state. These hypotheses can in principle be enumerated, and so the structure has an entropy. The autopoietic concept of organisation works at an even higher level, providing constraints on structure.

Without the constraint of the membrane (or more strictly, without the constraint of our knowledge of the membrane) there would be an even greater number of possible microstates, and hence a greater entropy. This is true for any constraint, because all constraints rule out some of the possible states. Any structured system will therefore have a lower entropy than its constituent matter would have in thermal equilibrium. Structure is central to the theory of autopoiesis [9, 10], and to our knowledge this particular connection with thermodynamics is new to the literature on autopoiesis.

Morowitz [12] gives an estimate of $10^{-10^{11}}$ for the probability of a living *Escherichia coli* cell spontaneously arising due to a thermal fluctuation in an equilibrium system. Equivalently, if we take all the atoms that make up an *E. coli* cell, then for every arrangement of those atoms that constitutes an *E. coli* cell there are $10^{10^{11}}$ which do not. Applying Boltzmann's formula, this corresponds

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[1] Jaynes [4] provides a clear elucidation of how this formula can be generalised to the information entropy $-k_{\mathrm{B}} \sum_i p_i \log p_i$ of the maximum entropy probability distribution of microstates compatible with the macroscopic constraints. Jaynes' clear and extensive writing on the nature of entropy has played a significant part in developing this work.

to an entropy difference of about 3.2×10^{-12} JK^{-1} between an *E. coli* cell and its constituent matter in the equilibrium state[2].

In order to maintain this low-entropy structure processes must continually take place that reduce the organism's entropy, countering its tendency to increase. According to the second law of thermodynamics this can only be done by increasing the entropy of the environment, so that the total entropy of the system and its environment increases. Schrödinger [18] described this as "feeding on negative entropy" in the environment. We can also think of this as the organism performing work in order to maintain its structure. This work is done by physical and chemical processes that occur due to constraints imposed by the organism's organisation itself, giving rise to the Work-Constraint cycle described by Kauffman [5] and the self-referentiality that is central to the idea of autopoiesis, as discussed in [11, 15].

Chemotrophic organisms achieve this reduction of internal entropy by altering chemical concentrations in their environment, taking in food and converting it to waste. Plants absorb high-energy (and thus low-entropy) photons, emitting radiation at a lower temperature, and most animals feed on low-entropy matter from other organisms, producing higher entropy waste. The model presented here deals only with chemotrophic organisms, although the other types should be straightforward to add.

2.2 Maximum Entropy Production

The historical origins of the MEP principle are complex [8] and its applicability and justification are still debated but perhaps one of its earliest and most impressive application is Paltridge's [13] model of the Earth's climate, which accurately reproduces features of the Earth's climate using a simple 10-box model.

In [6] this is distilled to a two-box model which despite its extreme simplicity reproduces well the values of the latitudinal heat transfer rates of the atmospheres of Earth, Mars and Titan. Entropy is produced in the atmosphere due to the transfer of heat from the high temperature (T_H) equator to the low temperature (T_C) poles. If the heat is transported at a rate F then entropy is produced at a rate $F \cdot (1/T_\mathrm{C} - 1/T_\mathrm{H})$, which increases with F but decreases as the two temperatures become closer together. A higher heat transfer rate increases T_C while decreasing T_H, so there is a kind of tradeoff in which both very low and very high transfer rates produce little entropy. At the extreme of zero heat transfer the temperature difference is maximised but the F term is zero, whereas in the upper limit heat transfer is maximised but the temperatures are equal, so again there is no entropy production. In between is a value for F which maximises the entropy production, and the MEP hypothesis predicts that the observed value will tend to be close to this value. By making this assumption the model is able to make good predictions while essentially ignoring all the complex mechanisms by which the heat transfer takes place.

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[2] For comparison, a similar difference in entropy is involved in heating 2.3×10^{-13} kg of water from 300 to 301 K (the per kilogram entropy change is given by heat capacity of water $\times \ln(T_\mathrm{final}/T_\mathrm{initial})$). An *E. coli* cell weighs about 10^{-15} kg.

There is no widely accepted theoretical justification for the MEP principle but Dewar [1, 2] has given some interesting arguments that it could arise from information theory in a similar way to the second law itself [4]. If this is the case then the Maximum Entropy Production principle would apply to any physical system in a steady state, including not only planetary atmospheres but ecosystems as well, with the maximisation taking place subject to whatever constraints are acting on the system.

For a planet's atmosphere the relevant constraint is the effect the flow rate has on the temperature gradient. Our model shows that in an ecosystem an analogous constraint can be imposed by a relationship between the rate at which processes take place and the difference in chemical potential that drives them.

The idea that a thermodynamic maximisation principle might apply to ecosystems has many precedents in the ecological literature [17], beginning with Lotka's 1922 proposal of a maximum energy flux principle [7]. Schneider and Kay [16] have suggested that life is the result of a physical principle whereby nonequilibrium systems "take advantage of all available means" to resist externally applied gradients. Predictions from these ideas have usually taken the form that a particular quantity such as energy flux or surface temperature will increase or decrease over time (see [19] for an investigation into several such "goal functions" using a population-based food web model). In contrast, because our model exhibits a tradeoff closely analogous to that in [6] applying the MEP hypothesis predicts a specific numerical value for the rate of matter flow through the system.

2.3 Chemical Potential

Heat transfer in the Earth's atmosphere is powered by a temperature difference between the equator and the poles. Chemical potential is somewhat analogous to temperature, and we can think of chemotrophic ecosystems as being powered by a difference in this quantity. Just as the temperature of a system increases with energy added to the system, the chemical potential of a substance within a system increases with each mole of that substance added to the system. Concentrations tend to flow from areas of high chemical potential to areas of low chemical potential, so that in thermochemical equilibrium the chemical potentials are equal in all areas of the system.

This is also true for chemical reactions: if there is a reaction that converts between two substances X and Y, it will take place in the direction that moves the two chemical potentials together, so that at equilibrium they are equal. If the system is isolated this corresponds to a maximum of the system's entropy; if it is held at constant temperature and pressure then it corresponds to a minimum of Gibbs free energy within the system and a maximisation of the entropy of the system and its surroundings. If there is a mixture of X and Y in which the chemical potential μ_X of X is greater than that of Y (μ_Y) then X will tend to be spontaneously converted into Y, producing entropy. Work can be done by coupling this spontaneous reaction to another one.

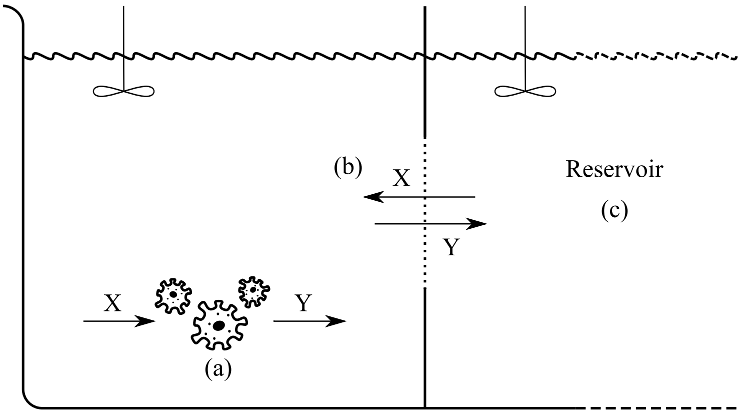

Fig. 1. Important features of the ecosystem model. (a) The system consists of a chemical mixture containing a population of organisms that metabolise by converting food X into waste Y. (b) A membrane allows X and Y to flow in and out of the system at rates which depend on the difference in chemical potential on either side of the membrane. (c) On the other side of the membrane is a well-mixed reservoir in which the chemical concentrations of 'food' X and 'waste' Y are held at constant non-equilibrium values.

All chemical reactions can take place in both 'forward' and 'backward' directions in this way but some reactions are experienced as unidirectional because the equilibrium point is such that when the chemical potentials are equal the proportions of reactants are vanishingly small compared to the products.

In an ideal solution the relationship between chemical potential μ_{X} and concentration N_{X} is given by $\mu_{\mathrm{X}} = \mu_{\mathrm{X}0} + RT \ln N_{\mathrm{X}}$, where $\mu_{\mathrm{X}0}$ is a constant that depends only on the temperature and the nature of X, and $R = N_{\mathrm{A}} k_{\mathrm{B}} = 8.31 \mathrm{JK}^{-1} \mathrm{mol}^{-1}$ is the gas constant. However, the exact form of this relationship does not matter for what follows. This model is quite general in that all that is required for it to work is that the chemical potential is an increasing function of the concentration.

3 The Model

The basic components of an ecosystem are a population of organisms and a source of work, in this case a difference between chemical potentials. In order for interesting behaviour to take place there must be feedback between the organisms and their environment. Perhaps the simplest way to achieve this is to imagine that food is transported into the system and waste out by diffusion (figure 1).

The system contains a population of organisms (which need not be of the same species) whose metabolism is very simple, with individuals maintaining their structure by converting 'food' X into 'waste' Y. The system is coupled via a membrane to a reservoir in which the concentrations of X and Y remain constant, either because the reservoir is very large or because they are held constant by an externally powered process. The concentrations in the reservoir are such that there is a greater proportion of X than there would be at chemical equilibrium. X and Y diffuse through the membrane at rates that are proportional to the difference in their chemical potentials on either side of the membrane.

In what follows we take the system boundary to be to the left of the membrane in figure 1, so that it includes the metabolism of all the organisms but not the membrane itself. This is by analogy to studies such as [13] and [6], which calculate the entropy produced inside the Earth's atmosphere, excluding the absorption of Solar radiation; the justification for this an important open quesion for the theory of MEP. The system is open to matter flow, since matter flows in in the form of X and out in the form of Y. If we assume that the system reaches a steady state, so that the flow in is equal to the flow out, then it meets Dewar's [1] criteria for an analysis in terms of Maximum Entropy Production.[3]

3.1 Population Metabolic Rate

In traditional ecosystem models the focus tends to be on the numbers of individuals or the biomass of each species. These are treated as dynamical variables, with rates of change that depend on the population numbers of other species, so for instance the population of a predator species will grow more rapidly if there are more of its prey species present.

However, in this model the focus is on the flow of matter through the system, and the relevant variable to represent this is the *Population Metabolic Rate* M. We define this as the total rate at which food is converted into waste within the system. This takes place due to the combined effect of each individual's metabolism. There will of course be many other processes occurring within each organism's metabolism and within the system as a whole. In this scenario these are all ultimately powered by the conversion of X into Y and we can use the total conversion rate M to summarise the operation of the whole system.

Population metabolic rate is not necessarily directly related to population size. An organism can sustain itself either by having a structure that decays very slowly and using slow, efficient processes to maintain it or by having a rapidly decaying structure which must be renewed at a faster rate, so for a given population metabolic rate the population could consist of a small number of rapidly metabolising individuals or a large number that metabolise slowly; or there could be a small number which metabolise slowly as adults but which have a high rate of turnover. Like the two-box climate model in [6] this model is not concerned with what is inside the system, only with the rate at which it operates.

Another difference between this model and traditional models in ecology is that rather than treating the population metabolic rate as a dynamical variable it

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[3] Dewar's framework is very general in that the flows in and out can be of matter rather than energy and they do not have to be fixed externally. In order to perform an analysis along the lines of [6] the system must also be free to take on a range of possible steady states, a requirement that is often expressed as needing many degrees of freedom. Our hope is that the complexity of biological organisms and ecosystem structure provide enough degrees of freedom to meet this requirement.

is left unconstrained. This gives the system a range of possible steady states (one for each value of M) which enables the use of the Maximum Entropy Production principle to choose between them.

3.2 Mechanics of the Model

Because the concentrations of X and Y are held constant on the reservoir side of the membrane, their chemical potentials remain constant in the reservoir also. Their values $\mu_{\mathrm{X}}^{\mathrm{res}}$ and $\mu_{\mathrm{Y}}^{\mathrm{res}}$ are parameters in the model. Since the proportion of 'food' X compared to 'waste' Y is assumed to be higher than it would be in equilibrium, $\mu_{\mathrm{X}}^{\mathrm{res}} > \mu_{\mathrm{Y}}^{\mathrm{res}}$. The chemical potentials μ_{X} and μ_{Y} within the system are variables that depend on the population metabolic rate and the rate of diffusion through the membrane.

The rate at which the fluids X and Y flow through the membrane are given by the difference in chemical potential of the fluid on the two sides of the membrane, multiplied by a diffusion constant D, which can be different for X and Y. Let the concentrations of X and Y within the system be N_{X} and N_{Y}, measured in moles. Their rates of change are given by

$$\begin{aligned} \dot{N}_{\mathrm{X}} &= D_{\mathrm{X}} \left(\mu_{\mathrm{X}}^{\mathrm{res}} - \mu_{\mathrm{X}}\right) - M \\ \dot{N}_{\mathrm{Y}} &= D_{\mathrm{Y}} \left(\mu_{\mathrm{Y}}^{\mathrm{res}} - \mu_{\mathrm{Y}}\right) + M \ . \end{aligned} \tag{1}$$

The rate of diffusion through the membrane is positive for X and negative for Y. In the steady state $\dot{N}_{\mathrm{X}} = \dot{N}_{\mathrm{Y}} = 0$ and the diffusion term will be balanced by the population metabolic rate M, from which we can obtain the chemical potentials as functions of M: $\mu_{\mathrm{X}} = \mu_{\mathrm{X}}^{\mathrm{res}} - M/D_{\mathrm{X}}$ and $\mu_{\mathrm{Y}} = \mu_{\mathrm{Y}}^{\mathrm{res}} + M/D_{\mathrm{Y}}$. As M increases the two potentials move closer together, and if no metabolism takes place then the system will be in equilibrium with its surroundings ($\mu_{\mathrm{X}} = \mu_{\mathrm{X}}^{\mathrm{res}}$, $\mu_{\mathrm{Y}} = \mu_{\mathrm{Y}}^{\mathrm{res}}$).

The total entropy produced per mole of X converted to Y is given by $\Sigma = (\mu_{\mathrm{X}} - \mu_{\mathrm{Y}})/T$, which as a function of M is

$$\Sigma = \frac{1}{T}\left(\mu_{\mathrm{X}}^{\mathrm{res}} - \mu_{\mathrm{Y}}^{\mathrm{res}} - \left(\frac{1}{D_{\mathrm{X}}} + \frac{1}{D_{\mathrm{Y}}}\right) M\right) \ . \tag{2}$$

Σ is closely analogous to the inverse temperature difference $(1/T_{\mathrm{C}} - 1/T_{\mathrm{H}})$ between the two heat baths in a classical heat engine or in the two-box climate model in [6]. It represents an upper limit on the amount by which an organism can reduce its structural entropy by metabolising one mole of X into Y. Equivalently, the upper limit on the amount of work that can be performed per mole metabolised is $T\Sigma$. Σ decreases with M (figure 2a), so that a slow population metabolic rate will result in a greater ability to do work per mole metabolised. M has a maximum value of $M_{\max} = (\mu_{\mathrm{X}}^{\mathrm{res}} - \mu_{\mathrm{Y}}^{\mathrm{res}})/(\frac{1}{D_{\mathrm{X}}} - \frac{1}{D_{\mathrm{Y}}})$ at which Σ becomes zero and no work can be done. Converting X to Y faster than this rate would require work to be done rather than being a source of work.

The total entropy production due to metabolism is given by

$$\sigma = M\Sigma = \frac{1}{T}\left(\left(\mu_{\mathrm{X}}^{\mathrm{res}} - \mu_{Y}^{\mathrm{res}}\right) M - \left(\frac{1}{D_{\mathrm{X}}} + \frac{1}{D_{\mathrm{Y}}}\right) M^2\right) \ . \tag{3}$$

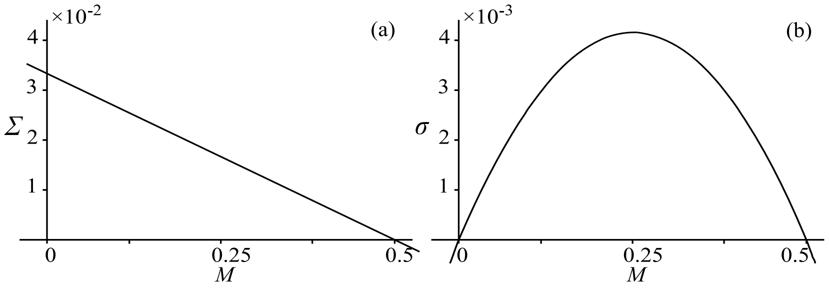

Fig. 2. (a) $\Sigma = (\mu_X - \mu_Y)/T$ tails off with increasing metabolic rate M. Σ is proportional to the difference in chemical potential between X and Y, which is equal to the maximum amount of work that can be done by converting one mole of X into Y. With $M > M_{\max} = 0.5$ work would have to be done to perform the conversion since $\Sigma < 0$. (b) The total entropy production $\sigma = M\Sigma$ rises to a peak and then falls off with increasing M. The values used for these plots are $\mu_{\mathrm{X}}^{\mathrm{res}} - \mu_{\mathrm{Y}}^{\mathrm{res}} = 10$, $D_{\mathrm{X}} = D_{\mathrm{Y}} = 0.1$ and $T = 300$.

This function is zero at $M = 0$ and $M = M_{\max}$, with a maximum in between at $M_{\mathrm{MEP}} = \frac{1}{2}(\mu_{\mathrm{X}}^{\mathrm{res}} - \mu_{\mathrm{Y}}^{\mathrm{res}})/(\frac{1}{D_{\mathrm{X}}} - \frac{1}{D_{\mathrm{Y}}})$. From a global point of view there is therefore a tradeoff between slow and fast population metabolic rates (figure 2b). A slow population metabolism leaves a large difference in potential between food and waste but produces a sub-optimal amount of work because it occurs slowly, whereas a fast population metabolic rate leaves too small a difference in potential to perform as much work as the optimal rate.

The MEP principle suggests a hypothesis that real systems would tend to have a population metabolic rate close to M_{MEP} but it does not provide an explanation in terms of mechanisms that take place within the system, just as MEP based atmospheric models predict rates of heat transfer without specifying the mechanisms by which the heat transfer takes place (see [6] for an interesting discussion of this in relation to the Martian atmosphere). We leave open the question of what ecological or evolutionary processes might occur to drive an ecological system toward a state of maximum entropy production.

4 Extensions and Applications

4.1 Experimental Testing

A model along these lines could be used to test the application of MEP to ecosystems experimentally. In our model food and waste enter and exit the system via diffusion through a membrane but a similar calculation can be performed for a chemostat-like bioreactor in which a constant inflow of food is balanced by a constant outflow of the system's contents (a mixture of food and waste). This leads to a nonlinear decline in Σ with M but the analysis is qualitatively the same and one can find a value M_{MEP} for which σ is maximised. It should therefore be possible to perform a bioreactor experiment in which a measured value of M, which can be calculated from the amount of unused food in the system's outflow, is compared against the value predicted using the MEP principle.

In order for the MEPP to apply the organisms' growth must be constrained by the rate of food availability and/or waste disposal, and not significantly constrained by other factors. We suspect that this is not normally the case in a bioreactor since the aim is usually to produce as high a growth or reaction rate as possible so high concentrations of food are used, leading to a population metabolic rate that is constrained only by physiological factors. In order to test the applicability of MEP to biological populations it will probably be necessary to perform a specialised bioreactor experiment in which the nutrient inflow is very dilute and the system run until the population reaches a steady state. It may also be important to use species for which the bioreactor is a close approximation to their natural environment because an environment to which the organisms are not well adapted could induce additional constraints their growth.

4.2 More Detailed Models

This model was kept as minimal as possible and represents perhaps the simplest possible ecosystem, with a single environmental feedback caused by a single metabolic process which converts a single reactant into a single product.

Real systems of course contain multiple species with dissimilar metabolisms. Real metabolisms are also more complex, performing multiple reactions at rates that can vary depending on circumstances. More complex reactions result in more complex biochemical feedbacks, including nutrient cycling. Real organisms can also use photosynthesis or prey on other organisms. It should be relatively straightforward to add each of these features to the model, which could then be used as a powerful tool to study the interaction between metabolism and environment at a very fundamental physical level, allowing studies along the lines of [3] but rooted in a model constrained by real physics. It should also be possible to add photosynthesis and organisms that can feed on other organisms, resulting in a more widely applicable ecosystem model.

A general ecosystem model built on sound energetic principles would be an extremely useful tool for simulating processes such as ecosystem succession [19] or artificial ecosystem selection [14]. The current natural tool for such studies is the generalised Lotka-Volterra equations, which are unsatisfying as they do not model the abiotic environment and include no energetic constraints.

5 Conclusion

We have presented a simple model that illustrates the relationship between the rate of chemical processes in an ecosystem and its rate of entropy production. This shows that the applicability of a principle of Maximum Entropy Production to living systems could be tested and opens up a range of possibilities for new research directions.

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