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Thermodynamics and environmental constraints make the biosphere predictable – a response to Volk

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Abstract In his critique of Kleidon (Clim Change 66:271–319, 2004), Volk (Clim Change 85:3–4, 2007) concludes that maximum entropy production (MEP) has no great relevance for biological evolution and the time history of life on Earth. I think that most of his points are not justified but rather reflect (a) a lack of appreciation of the central importance of entropy production as the "universal currency" that measures what keeps systems working, including the biosphere, (b) a misunderstanding of how biotic activity is embedded in the global entropy budget, and (c) a lack of distinction between optimal environmental conditions that maximize productivity and result from environmental tradeoffs versus optimal function of organisms to some internal tradeoffs. The examples that he uses to support his conclusions show flaws in that these mostly discuss single environmental effects and immediate system responses. Optimal environmental conditions, however, requires at least two effects that result in a trade-off, so it is not surprising that his examples seem to contradict optimality and MEP. And the immediate response of a system to change can be very different than the response in steady state, for which MEP applies. This is specifically important to be considered in the context of the "cheater" problem. In summary, I do not think that Volk makes convincing arguments that contradict MEP, although I certainly agree that there is a lot more work to be done to fully recognize the great importance that thermodynamics and MEP play in shaping the Earth's biosphere and its evolutionary history.

1 Introduction

In his response to Kleidon (2004) (abbreviated K04 in the following), Volk (2007) criticizes the application of the principle of maximum entropy production (MEP) to

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biospheric activity. Volk uses several examples that seem to be in contradiction to what would be implied by MEP. However, most of Volk's objections are flawed and explained in detail below. I am nevertheless grateful for Volk's critique, because it reveals to me that more explanations are necessary, especially in terms of the fundamental roles of thermodynamics, optimum environmental conditions, and in terms of how systems react to instantaneous perturbations compared to their response in steady state.

In the following, I prefer the use of the term "biosphere", as opposed to Volk's use of the term "biota". I see the distinction between these terms as the biota referring to the sum of all organisms (as in Volk), but "biosphere" referring to the biota plus the environmental constraints that limit its activity. Volk's critique has stimulated me to make this distinction, because it is the addition of the environmental constraints that in my view make the biosphere predictable. This is analogous to the distinction between a large number of molecules versus the ideal gas, which is subjected to the constraints of energy- and mass conservation. It is only through the consideration of the constraints that the large number of molecules become a predictable ideal gas.

2 Clarifying the application of MEP to the biosphere

Volk uses the example of a "black carpet" mutation to counter the application of MEP to the biosphere. By covering the Earth with a black nonproductive tissue, this mutation, he argues, would maximize entropy production but would be out-competed by ordinary trees. This example, however, does not counter MEP, but rather reflects a lack of understanding of how biotic activity is embedded in the overall entropy budget of the Earth system.

Let us first consider a simpler example of MEP, that of poleward heat transport (as in K04), to better understand how a thermodynamic process (i.e. poleward heat transport) is embedded in the global entropy budget. For a given amount of absorbed solar radiation, the state of MEP for poleward heat transport results from the trade-off between the heat flux – which depletes the temperature gradient – and the temperature gradient between the equator and the poles – which drives the heat transport flux (see Fig. 2 in K04). Hence a state of MEP is associated with an intermediate value of heat transport that maintains a temperature gradient in steady-state. Planetary entropy production increases with increasing values of heat transport, and it would be maximized in the absence of a temperature gradient. However, this planetary MEP state is not achievable in steady state by a heat flux that is driven by temperature gradients! The poleward heat flux at a state of MEP is the best it can do, and it maximizes planetary entropy production "to the extent possible".

In the "black carpet" mutation example Volk argues that MEP would imply that this mutation would become dominant as it results in a planetary MEP state. Here we also have to distinguish between the particular thermodynamic process (biotic activity), its rate of entropy production, and its effect on the planetary entropy budget. The growth and maintenance of a non-productive "black carpet" would come at a huge energetic cost, but since this tissue would not enhance photosynthesis (and hence biotic entropy production), it is likely not just improbable, but impossible to form and sustain in a steady state. Even if it were possible, it would maximize planetary entropy production, but not biotic entropy production. And this is not the application of MEP to the biosphere that was described in K04. MEP applied to the biosphere implies that biotic entropy production is maximized with respect to its environmental constraints, and that this then maximizes planetary entropy production to the extent possible, just as it is the case for poleward heat transport.

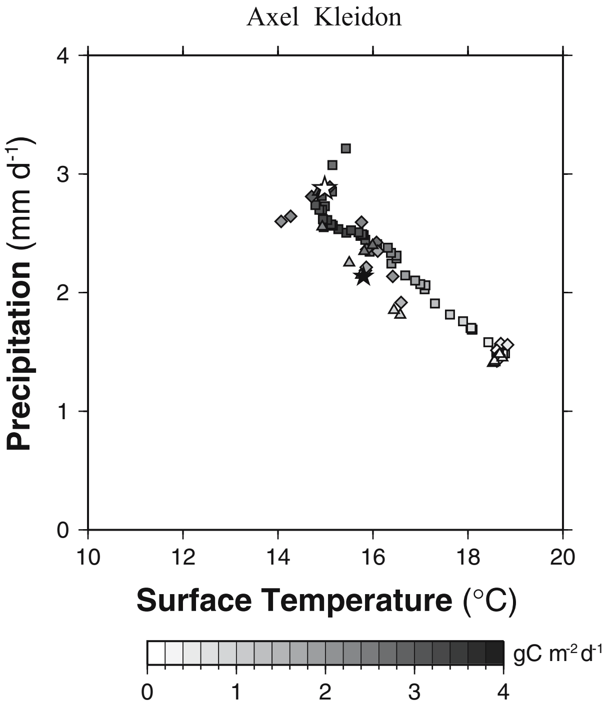
Another way to look at the application of MEP to the biosphere is in terms of the amount of information necessary to describe its form and function. A state of MEP means predictability with the least amount of information, which ultimately means that environmental constraints are sufficient to describe the form and function of the biosphere. That we can characterize the complex and diverse terrestrial biosphere by a few terrestrial biomes at the global scale to a very good approximation is a reflection of this predictability. But what this actually means is that we do not need much detailed information of the actual plants that form these biomes, and this is because the biota is optimally adapted to its environment by maximizing its activity. Hence its form and function is predictable by its environmental constraints.

This MEP perspective of the biosphere can explicitly be tested with numerical simulation models. Kleidon (2006) conducted a wide range of sensitivity simulations with respect to vegetation parameters such as maximum stomatal conductance, canopy roughness, and the partitioning of biomass between above- and belowground compartments, and evaluated the associated climates in terms of terrestrial productivity (taken as a proxy for biotic entropy production). This setup can be viewed as an extension of the Kleidon et al. (2000) study which was used in K04 (but only considered the end-members of a "Desert World" and a "Green Planet").

In principle, vegetation parameters are free to vary and evolve within certain ranges. For instance, the boreal forest has a relatively high surface roughness compared to a forest that would be formed by the acacia trees of the African savanna, which have relatively smooth canopies. Likewise, the partitioning of biomass between roots, leaves and structures can in principle vary greatly among ecosystems. Yet all of these parameters are associated with various trade-offs that are related to the energy- and water balance, and they affect the photosynthetic constraints of the amount of absorbed light and the uptake of carbon dioxide through plant leaves. When the simulated climates are evaluated in terms of their effect on productivity, these suggest that the present-day climate is very close to optimum conditions, the terrestrial biosphere is close to maximizing its productivity (Fig. 1), and associated vegetation parameters are consistent in their values to observed ranges. In this comparison we need to keep in mind that the environmental constraints simulated by climate models are tuned to represent the present-day climate to a reasonable extent, irrespective of its effects on vegetation productivity and the global entropy budget. It is therefore anything but trivial that both studies (Kleidon et al. 2000; Kleidon 2006) show consistent effects that support the notion that present-day vegetation productivity is very close to maximum productivity.

Following the example of poleward heat transport and its effect on planetary entropy production, we would now expect that the MEP state of the terrestrial biosphere would enhance planetary entropy production as well. In this context Volk criticizes that the effects of terrestrial vegetation on the planetary entropy budget as estimated in K04 are small. Given that the model itself and the model setup were quite constrained in that it included many fixed boundary conditions (such as fixed sea-surface temperatures and fixed atmospheric carbon dioxide concentration) and

Fig. 1 Sensitivity of land averaged global mean temperature and precipitation rate to vegetation parameters (stomatal conductance, canopy roughness, root-shoot partitioning) and its effect on terrestrial productivity (*colored shades*). Each symbol represents one simulation with different vegetation parameters. The *white star* denotes the "Control" simulation, the *black star* the simulation of a "Desert world". After Kleidon (2006)



empirical parameterizations, especially with respect to subgrid-scale convection and cloud parameterizations that may not even be thermodynamically consistent, it is, again, quite surprising that these effects point in the predicted direction. It that sense I nevertheless agree with Volk in the sense that more work needs to be done to test these models in terms of their thermodynamic consistency, and in terms of loosening up the fixed boundary conditions in the models that are not fixed in the real world. This would then allow us to test the hypotheses formulated in K04 more rigorously and address Volk's concerns more satisfactorily.

3 Consequences of a single effect versus multiple effects that result in optimality

In addition to this misunderstanding of how to apply MEP to the biosphere, Volk uses several examples of biotic effects that he claims disprove MEP. These examples are flawed in that these examples take only one environmental effect into account. The problem with this "single-effect reasoning" is that it cannot result in optimum environmental conditions. An optimum is generally associated with a trade-off between at least two effects.

One example in Volk is the production of dimethylsulfide (DMS) production by plankton. Since DMS acts as cloud condensation nuclei in the atmosphere, it enhances cloud albedo and decreases absorption of solar radiation. Volk argues that as a consequence, the production of DMS decreases planetary entropy production. Another example of this "single effect reasoning" is shown in Volk's Fig. 1: a light-colored lichen on a darker rock surface. The lighter-colored lichen acts to decrease the absorption of solar radiation under the same amount of incoming solar radiation. Volk then argues that because of the decreased amount of absorbed solar radiation, the rate of entropy production would be decreased.

Both examples of Volk cannot result in trade-offs and environmental optima as such since only a single effect is considered. In contrast, one important example in K04 that includes trade-offs and optimality is the planetary albedo and its relation to surface temperature: Warmer temperatures result in less highly-reflective snow and sea-ice cover, but increase reflective cloud cover. As a consequence of the two contrasting effects, an optimum albedo should exist at which absorption of solar radiation, and therefore entropy production, is maximized. The effect of nutrient cycling used in K04 can easily be extended to this view as well: With a given amount of nutrients being available, an increase in biomass allows for more absorption of light but is associated with more of the nutrients being locked away in biomass, thus decreasing the availability of nutrients in the soil. Hence, there should be an optimum in the nutrient cycling rate at which growth, and hence biotic entropy production, is maximized. Many more examples can be set up, but the important point is that all examples of optimality require a view of biotic effects that at least consider two effects on environmental conditions, not just one as in Volk's examples.

So which trade-offs in the environment are left out in Volk's examples? The role of the biota in altering aerosols, cloud condensation nuclei (CCN) and cloud formation, for instance by DMS, has certainly more dimensions than just to raise the cloud albedo. Shaw (1983) mentions the role of the particle diameter, and the lifetime of the aerosol in shaping the response of the planetary albedo to aerosols. Adding more, or larger, CCN to the atmosphere could also lead to faster condensation and shorter lifetime of clouds. In that case, the planetary albedo may decrease and entropy production would increase. Cloud effects are still highly uncertain (IPCC 2001), but I would argue that Volk's example of DMS is certainly incomplete and as such is not a disproof of MEP. The other example of Volk, the presence of light-colored lichen, has other relevant implications that were left out. Lichen play an important role in the overall enhancement of silicate rock weathering, which had profound effects on the Earth's climate evolution, surface temperature (Schwartzman and Volk 1989), and quite likely cloud cover. But these other effects and their associated consequences on entropy production were not considered in Volk's example.

Volk's examples therefore do not contradict MEP since these isolated cases do not have the sufficient complexity to reveal trade-offs and optimal conditions in the environment. After all, I do not claim that *every* biotic effect in *every* situation results in enhanced biotic entropy production. In fact, biotic effects that increase entropy production for certain conditions are very likely to decrease it in others, otherwise we would not get optimum states. But this requires a more inclusive perspective of more than just one cause and effect as in Volk's reasoning.

4 Immediate versus steady-state consequences

Another aspect that is problematic in Volk's examples is that he uses examples where he only considers the immediate response rather than the response in steady-state. One example in Volk is discussed in the context of the "black carpet" mutation, which relates to the "classic" cheater problem that has been used by critics in the discussion of the Gaia hypothesis (e.g. in the recent debate, Kleidon 2002; Kirchner 2002, 2003; Lenton 2002; Volk 2002, 2003a, b; Lovelock 2003; Lenton and Wilkinson 2003). A cheater in this context is an organism, where it benefits from the optimized environment without contributing to the cost of maintaining the optimum. This reasoning, however, is based on the immediate response of the biosphere to the perturbation (i.e. the introduction of the cheater). The response of the biosphere in steady state is very different, because the response in steady state includes feedbacks that take place on *all* temporal and spatial scales.

To demonstrate this critical distinction of immediate versus steady-state consequences, I use again the example of poleward heat transport. As discussed above, the MEP state results from a trade-off between the thermodynamic force (the equator-pole temperature gradient ΔT) and flux (the poleward heat transport Q). Let us now imagine what would happen to a small perturbation to the MEP steady state. A small increase in the heat flux ΔQ applied over a very short time period would seem to proportionally increase entropy production since the temperature gradient does not react instantaneously to this perturbation. Hence, one could argue that an increase in heat flux would increase entropy production. This line of reasoning, however, is flawed when we consider the system in steady state. If the perturbation ΔQ is sustained over sufficiently long time, the steady-state equator-pole temperature gradient reacts to the altered heat flux and would be decreased. The associated steady state would be associated by a lower rate of entropy production. The decrease in the temperature gradient would then result in a negative feedback as the diminished temperature gradient would result in less generation of motion, thereby reducing the heat flux and returning to the MEP state (Ozawa et al. 2003). This actually points out that the common definition of a steady state in terms of energy- and mass balances is insufficient, since a whole range of solutions can satisfy the energy- and mass balances. The negative feedbacks associated with MEP suggest that the dynamics are such that it is the steady state that maximizes entropy production which characterizes the steady state that emerges from the system dynamics.

The same line of reasoning applies to the cheater problem. Imagine a region in which the biota is optimally adapted to its environment. A cheater enters the region. If the cheater becomes dominant, it will alter the environment to some sub-optimal state. A neighboring region with a similar environmental setting, but where the cheater is absent and the conditions are optimal, the associated higher productivity of the biota would result in a higher ability to reproduce and/or to develop higher and denser canopies. And this will prevent the cheater from ever becoming dominant in the steady state!

Related to this is also an example in Volk's discussion section. There he writes that "...if a plant could live just as well with fewer light-absorbing chlorophyll molecules, ..., it would do so and, as a lower entropy producer, would soon out compete the higher entropy producers". This is incorrect. Entropy production is likely to be higher of a more efficient species – after all, plants use up their assimilated carbon. So if a plant species "A" is more efficient than another species "B" under the same environmental conditions, then this means that this particular species achieves the same productivity with less efforts (e.g. it has lower maintenance costs), but it will nevertheless allocate all carbon to some function. For instance, it can devote more resources to growth and/or reproduction (which is essentially growth by the next generation of plants). Anyway, it would surely result in more growth, either by the same plant or by its offsprings, and it is at least as productive as species "B", if not more. And if it is more productive, then it respires more as well in the steady-state, hence produces more entropy than species "B"!

Another example that Volk uses to "disprove" MEP is anthropogenic global warming. I am somewhat surprised that he uses this example because I discuss anthropogenic global change in K04. As explained in K04, MEP applies to steady states. The current transition into the anthropocene is driven mainly by dissipating the free energy from the depletion of fossil fuel stores. This is clearly not a steady-state. It is either a temporary phenomenon that ends once fossil fuels are depleted (and humans return to their caves), or a transition to a human-dominated future. If we assume that the pre-industrial steady-state is a planetary MEP state, then the system will return to this state in either case, either through the biotic processes that acted and regulated the environment in the past (on a slower time scale of oceanic uptake and silicate weathering), or through conscious human decision making (e.g. through carbon sequestration). The latter should be the case because the pre-industrial planetary MEP state with conditions that maximize biospheric activity should also be best for humans (approximately).

Hence, these examples that Volk uses to disprove MEP are flawed by "immediate response" thinking, in contrast to "steady-state" thinking that result in quite different functional consequences that are consistent with what would be expected from MEP!

5 Conclusions

Volk's conclusion that "...maximum entropy production...has no relevance for discussions of biological evolution or the time history of the effects of life on the global system" is unjustified. His reasoning is based on a lack of understanding of how MEP applies to the biosphere. The examples that he uses to substantiate his criticism are either such that they cannot lead to optimal states by setup because they are too simple by only considering a single environmental effect or he discusses only their immediate consequences, rather than the consequences for the steady state.

The alternative view of "by-products" that Volk proposes lacks the ability of quantitatively predict the present-day shape and the past evolution of the biosphere. And it may even violate thermodynamics as it is not based on a solid thermodynamic foundation that tells us what is impossible, possible, or probable. On the other hand, if we want to understand the clear trends in the evolution of the biosphere, e.g. the evolution to more complex life, from single to multiple to many cells, in terms of energetically more expensive metabolisms from mollusks to humans (Zotin 1984), we need to approach this from a thermodynamic perspective. These trends clearly resemble trends towards higher order, or states of lower entropy as these are less probable arrangements of the Earth's carbon dioxide molecules than in thermodynamic equilibrium. The increasing "ordering" of the biosphere can only be achieved through increasing work to build and maintain these structures. Hence, this implies that biotic entropy production has substantially increased through time! Whether biotic (and planetary)entropy production was at a maximum throughout most of Earth's history for the given, but changing environmental settings is an open, challenging perspective that certainly would need a lot more work to address.

Yet this perspective of entropy production and its maximization is clearly of great relevance to understand biospheric evolution. Volk's view of "by-products" and "entropy production can be either increased or decreased" is clearly ignorant about the profound importance of thermodynamics in the shape, structure and evolution of the Earth's biosphere!

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