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14 Biotic Entropy Production and Global Atmosphere-Biosphere Interactions

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Summary. Atmospheric conditions constrain biotic activity through incoming solar radiation, temperature, and soil water availability on land. At the same time atmospheric composition and the partitioning of energy fluxes at the surface are strongly affected by biotic activity, thereby modifying the environmental constraints. Here we review the foundations for atmosphere-biosphere interactions, focusing on the role of biogeophysical effects of terrestrial vegetation and the emergent feedbacks of the coupled atmosphere-biosphere system. We then investigate atmosphere-biosphere interactions from a perspective of entropy production and discuss the applicability of the hypothesis of Maximum Entropy Production (MEP) to biotic activity as a dissipative process within the Earth system. Specifically, we suggest two examples demonstrating the existence of MEP states associated with biotic activity and the Earth's planetary albedo. We close with a discussion of how this research can be extended and what the implications of biotic MEP states would be for understanding the dynamics of the Earth system.

14.1 Introduction

The biota plays an important role in the climate system. For instance, the strength of the atmospheric greenhouse, in terms of atmospheric concentrations of carbon dioxide, is closely linked with the global carbon cycle, which is affected by biotic activity through photosynthesis, respiration, and enhancement of rock weathering on geologic time scales (see also Schwartzman and Lineweaver, this volume). Over land, the absorption of solar radiation and the subsequent partitioning into radiative and turbulent heat fluxes is strongly affected by terrestrial vegetation. For instance, the presence of a rainforest leads to a darker and aerodynamically rougher surface with a higher capacity to evaporate water. These aspects affect the physical functioning of the land surface. However, biotic processes such as photosynthesis and respiration are also strongly constrained by the atmospheric environment, through temperature and the availability of light and water. This leads to the notion of atmosphere-biosphere interactions, with atmospheric conditions constraining biotic activity but biotic effects moderating atmospheric conditions, resulting in emergent feedbacks. In addition, both, an abiotic surface as well as a biotically influenced surface are consistent with the constraints imposed by

Table 14.1. Albedoes for different surfaces and cloud types (after Hartmann 1994)

	typical value (in %)
bare surfaces:	
water	7–12
moist soil	10–25
dry soil	30–35
vegetated surfaces:	
short green vegetation	17
Extratropical forests	10–15
Tropical forests	13–18
snow- and ice-covered surfaces:	
sea ice, no snow cover	30
old, melting snow	50
fresh, dry snow	80
forest with surface snow cover	25
clouds:	
high (cirrus)	21
medium (cumulus)	48
low (stratus)	69

the surface energy- and water balances, so that there are potentially many possible states and we may ask whether the biotic state is the most probable state. This then relates to the question of how atmosphere-biosphere interactions affect the rate of entropy production, and how the MEP principle can be applied to understand the emergent outcome of atmosphere-biosphere interactions.

Let us first briefly motivate the reasoning why biotic activity should affect the rate of entropy production at the planetary scale. Consider the planetary rate of entropy production, as approximated by

$$\sigma_{EARTH} = I_0(1 - \alpha_P)(1/T_R - 1/T_{SUN}) \tag{14.1}$$

with I_0 being the mean solar irradiation at the top of the atmosphere, α_P the planetary albedo, T_R the effective radiative temperature of Earth, and T_{SUN} the emission temperature of solar radiation. The radiative temperature T_R is mainly constrained by the planetary energy balance, since absorption of solar radiation balances the emission of terrestrial radiation at the effective radiative temperature T_R in steady state. The planetary albedo plays a crucial role in determining σ_{EARTH}. It is not a fixed property, but results from the dynamics of the energy- and water balances, specifically the amount and type of clouds, the type of vegetative cover on land, and the abundance of snow or ice at the surface or the lack thereof (Table 14.1). Considering that many processes affect the planetary albedo, we may argue that many degrees of freedom are associated with total absorption of solar radiation, and that the Maximum Entropy Production (MEP) principle should be applicable.

Noting that vegetated surfaces are generally cooler than non-vegetated surface, Ulanowicz and Hannon (1987) and Schneider and Kay (1994) both argued that biotic influences on physical processes make them more efficient (by lowering surface temperature), resulting in higher rates of entropy production. Given that the biosphere is inherently diverse, with differing functional responses to environmental conditions of a large number of individuals, we may take their perspectives further and ask how the MEP principle should be applicable to atmosphere-biosphere interactions at the global scale.

In this chapter, we first review the basics of photosynthetic activity as the main energy source of the biota and how it is constrained by the climatic conditions at the surface. We then discuss the consequences of photosynthetic activity for energy- and water partitioning and how these effects impact the rate of biotic entropy production. Finally, we propose how *MEP* may be applicable to biotic activity in an Earth system context and how the emergent behavior may share similarities with the Gaia hypothesis of Lovelock and Margulis (1974) (also Toniazzo et al., this volume).

14.2 Photosynthetic Activity and Climatic Constraints

The majority of biotic activity results from photosynthesis and the derived organic carbon compounds. The assimilates from photosynthesis are used to maintain existing living tissues or allocated to growth and reproduction. Eventually, organic carbon compounds are respired – either by the photosynthesizers through autotrophic respiration, or by heterotrophic respiration at various trophic levels of the food chain. In the following we focus on the climatic constraints on photosynthesis as the primary process supplying energy to the biota.

14.2.1 Climatic Constraints on Biotic Productivity

The net conversion of carbon dioxide into organic carbon by photosynthesis can be expressed as

$$\mathrm{CO_2 + H_2O + energy \rightarrow HCO_2 + O} \tag{14.2}$$

The conversion of one mol of CO_2 into organic carbon requires roughly 479 kJ of energy (Larcher 1995). This energy is derived from the absorption of solar radiation by chlorophyll, particularly wavelengths between 380 nm and 710 nm. This band of radiation is also referred to as photosynthetically active radiation, or *PAR*. *PAR* represents roughly 50% of the incoming solar radiation, I_S. The amount of absorbed *PAR*, or *APAR*, depends on the photosynthesizing biomass, C_{GREEN}, and the efficiency of its conversion into organic carbon depends on limiting factors imposed by the availability of nutrients and the temperature of the environment. A large fraction of up to 75% for tropical rainforests (Larcher 1995) of the resulting gross uptake of carbon by photosynthesis (or gross primary productivity, *GPP*) is consumed by autotrophic respiration (RES_A). Net primary production, or *NPP*, describes the net carbon uptake by photosynthesizers that is not consumed by autotrophic respiration (i.e., $NPP = GPP - RES_A$).

NPP is commonly used to describe biotic activity. It can be estimated from the amount of *APAR* by (Monsi and Saeki 1953; Monteith 1977; Field et al. 1998)

$$NPP = \varepsilon APAR \tag{14.3}$$

where ε is the average light use efficiency. The light use efficiency includes the environmental constraints on biotic activity imposed by temperature, and water and nutrient availability. By explicitly expressing the climatic effects on *NPP* through temperature and water availability, (14.3) can be expanded to:

$$NPP = \varepsilon_{MAX}\, f(C_{GREEN})\, g(T_S)\, h(W_S) PAR \tag{14.4}$$

where ε_{MAX} is the maximum light use efficiency (reflecting the biochemical efficiency of the conversion and other limitations not considered here, e.g., by nitrogen or phosphorus availability), W_S is the available soil moisture within the rooting zone (for terrestrial vegetation) and f, g, h some functional relationships.

Oceanic productivity is primarily limited by the availability of nutrients. Nutrients originate from deep ocean water where dead organic material is decomposed. Consequently, regions in which surface water mixes with deep water show a high productivity, such as the upwelling regions at the western shores of continents and in regions where the depth of the mixed layer shows large seasonal variations (as in the mid-latitudes), which allows for mixing with deeper water.

On land, geographic variations in productivity can be categorized in water-limited environments - mainly in the tropics – and in temperature-limited environments – mainly in temperate and polar regions. Water limitation to *NPP* arises from the uptake of atmospheric carbon dioxide through the plant's stomata being strongly coupled to the loss of water by transpiration. Consequently, productivity decreases with a decrease in precipitation, shaping the transition of vegetation types from rainforests to savanna to desert along moisture gradients. In polar regions, temperature limits the rate of photosynthesis, and the strong seasonality in solar radiation leads to a limited length of the growing season. This limitation is reflected in the transition of vegetation types of lower productivity towards colder regions, from temperate forests to boreal forest to tundra.

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14.2.2 Dynamic Constraints of Terrestrial Energy- and Water Exchange

The temperature- and water constraints of terrestrial productivity are governed by the surface energy and water balance. The surface energy balance links the net radiative fluxes of solar and terrestrial radiation with the turbulent fluxes of sensible and latent heat. The net radiative energy flux, R_N,available for partitioning is the sum of the absorption of short wave radiation from the sun at the surface, I_S, reduced by the net emission of infrared radiation, $Q_{LW}(T_S)$, depending on the surface temperature, T_S, and the strength of the atmospheric greenhouse effect:

$$R_N = I_S(1 - \alpha_S) - Q_{LW}(T_S) \tag{14.5}$$

with α_S being the albedo of the surface. This net radiative flux is partitioned into the sensible and latent heat fluxes, SH and LH, and the heat flux heating the ground, $c\,dT_S/dt$:

$$R_N = SH + LH + c\,dT_S/dt \tag{14.6}$$

where c is the effective heat capacity of the soil. The chemical energy stored during photosynthesis and released by respiration is comparably small and is neglected here. If water availability is not limiting the latent heat flux (as is the case over the oceans) then the Bowen ratio, defined as $B = SH/LH$, can be approximated by the equilibrium Bowen ratio, B_e. The equilibrium Bowen ratio sets a fixed proportion of the two heat fluxes depending on surface temperature, with the partitioning shifting towards increased latent heat flux with increasing surface temperature. It is given by (Hartmann 1994):

$$B_e^{-1} = \lambda/c_p\ \partial q_{\mathrm{SAT}}/\partial T\ \approx \lambda^2/(c_p R T_S^2)\, q_{SAT}(T_S) \tag{14.7}$$

where λ being the latent heat of fusion, c_p the specificy heat capacity of the air, R the gas constant for water vapor, and q_{SAT} the saturated specific humidity, which increases roughly exponentially with T_S.

Over land, the latent heat flux is often limited by the amount of available water, so that the equilibrium Bowen ratio only serves as an upper limit for the latent heat flux. The surface water budget describes another partitioning taking place at the surface and imposes an important constraint on the latent heat flux. The incoming flux of water (that is precipitation P and snowmelt SM) is partitioned into the fast surface and slow drainage runoff R, the evapotranspiration ET (with latent heat flux $LH = \lambda ET$) and the change in soil water storage within the rooting zone dW_S/dt:

$$P + SM = ET + R + dW_S/dt \tag{14.8}$$

Equations (14.5), (14.6) and (14.8) represent the dynamical formulation of the constraints on terrestrial NPP. These constraints, however, are not fixed, but affected by the biota, leading interacting dynamics of the atmosphere-biosphere system and emergent feedbacks.

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14.3 Biogeophysical Effects and Feedbacks

14.3.1 Vegetation Effects on Land Surface Characteristics

Biotic activity affects the physical exchanges of energy and water primarily at the land surface. Terrestrial vegetation modifies the physical aspects of land surface exchange by a series of characteristics (e.g., Kleidon et al. 2000; Bonan 2002; Pitman 2003):

- *Surface albedo:* vegetated surfaces are generally darker than non-vegetated surfaces, leading to increased absorption of incoming solar radiation at the surface (Table 14.1).
- *Albedo of snow cover:* the vertical structure of forests, particular coniferous forests in the boreal regions, leads to a masking effect of surface snow cover, effectively reducing the overall surface albedo in the presence of snow cover (Table 14.1). This leads to enhanced absorption of solar radiation, particularly during spring time, accelerating the rate of snow melt.
- *Surface roughness:* vegetated surfaces are aerodynamically rougher because of their heterogeneous canopy structure, leading to a shift in the energy balance towards greater turbulent fluxes of sensible and latent heat, reducing net radiative loss by terrestrial radiation.
- *Bowen ratio:* vegetated surfaces generally show higher fluxes of LH and reduced SH because of the direct coupling of carbon uptake with transpiration by stomatal functioning, leading to a lower Bowen ratio.
- *Rooting zone depth:* vegetation can more effectively take up soil moisture for transpiration through the vertical extent of the rooting zone, therefore enhancing the ability of a land surface to maintain ET during dry episodes, with further consequences on energy partitioning and surface temperature.

The magnitude of these effects on climate, and therefore on the climatic constraints for terrestrial productivity, can be estimated by extreme climate model simulations of a “Desert World” and a “Green Planet” (Fraedrich et al. 1999; Kleidon et al. 2000). In the “Desert World” simulation, land surface characteristics representative of a desert (i.e., high albedo, low roughness, low ability to transpire water) were prescribed to all land surfaces with no permanent ice cover. Compared to the simulated climate of the “Present-Day”, the surface receives less solar radiation in the “Desert World” climate, the surface energy balance is shifted towards more loss by terrestrial radiation and reduced rates of latent heat flux (Table 14.2). As a consequence of less evapotranspiration, precipitation over land is reduced by more than 30% . At the other extreme of a “Green Planet”, land surface characteristics were prescribed to be representative of a rainforest (i.e., low albedo, high roughness, high ability to transpire water). When compared to the “Present-Day” climate, the simulated climate of the “Green Planet” shows the same differences,

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but of opposite sign: the surface energy balance is shifted towards more turbulent fluxes and evapotranspiration. Consequently, precipitation is enhanced by 30% . Net solar radiation at the surface, however, is slightly reduced as a consequence of increased cloud cover. Note that the land surface parameters in the "Green Planet" simulation do not reflect carbon constraints. That is, the land surface characteristics of a rainforest would not be sustained by the productivity of the vegetation in all areas of the simulated climate of the "Green Planet". On the other hand, some regions of the "Desert World" scenario would exhibit climates that would sustain vegetation, and it has been shown that the present-day vegetation-climate state is likely a reproducible state independent of initial conditions (Claussen 1994; Claussen 1998).

Table 14.2. Components of the surface energy budget, water cycle and terrestrial productivity averaged over land for a "Desert World", the "Present-Day", and the "Green Planet" (after Roeckner et al. 1996; Fraedrich et al. 1999; Kleidon et al. 2000; Kleidon 2002). Negative components represent net loss of energy from the surface. Terrestrial productivity has been normalized to yield 100% for the "Desert World" climatic conditions

	"Desert World"	"Present-Day"	"Green Planet"
Energy balance: (in W/m^2)			
net solar radiation	124	130	129
net terrestrial emission	-74	-62	-53
sensible heat flux	-22	-17	-8
latent heat flux	-18	-44	-60
Water cycle:			
precipitation (in 10^{12} m^3/yr)	71	108	137
evapotranspiration (in 10^{12} m^3/yr)	31	73	108
precipitable water (in kg/m^2)	16	18	21
cloud cover (in %)	51	53	58
Terrestrial productivity: (in %)	100	250	255

14.3.2 Climate Feedbacks of Terrestrial Vegetation

When the simulated climates are used to calculate terrestrial productivity from climatic constraints (following the approach in Sect. 14.2), the "Present-Day" climate allows for a terrestrial productivity 2.5 times the one corresponding to the "Desert World" climatic conditions (Table 14.2). This suggests that the overall feedback associated with biogeophysical effects is positive, that is, that the changes in the simulated climates that result from the inclusion of biotic effects lead to less climatic constraints and allow for

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a higher productivity (Betts 1999; Kleidon et al. 2000; Kleidon 2002). Note that the difference in productivity for the "Present Day" and the "Green Planet" climate is only marginal despite considerable differences in the simulated climates. This is due to the fact that the increased productivity in marginal areas is offset by the reduction in productivity in highly productive areas due to increased cloud cover.

The effects of terrestrial vegetation can be understood in terms of two *biogeographical* feedbacks (since most changes in land surface characteristics are usually associated with changes in vegetation type which take place on time scales of decades to centuries):

- *boreal forest feedback:* In temperature-limited environments, the presence of forest leads to a lower surface albedo in the presence of snow (Table 14.1). This leads to the following feedback loop which reinforces the presence of forest (Bonan et al. 1992): + forest → − surface albedo (if snow is present); + absorption of solar radiation → + temperature; + snow melt → + length of growing season → + productivity to sustain forest. Ultimately, the amount of snowfall and the seasonality in solar radiation set an upper limit to the strength of this feedback. Climate model simulations have also shown that this feedback is amplified by changes in sea-ice at the hemispheric scale.
- *water cycling feedback:* In water-limited environments, the presence of vegetation allows for a lower surface albedo and better access soil moisture through a root system, both of which act to enhance evapotranspiration. The presence of vegetation is reinforced by the following feedback (Charney 1975; Milly and Dunne 1994; Eltahir 1998; Kleidon and Heimann 2000): + vegetation → + evapotranspiration/latent heat flux; − sensible heat flux → + water vapor in the planetary boundary layer; − boundary layer growth → + precipitation → + water availability → + productivity to sustain vegetation. Additional physical feedbacks lead to enhanced net radiation at the surface, reinforcing increased evapotranspiration (Charney 1975; Eltahir 1998, see also Table 14.2): + evapotranspiration → + water vapor in the planetary boundary layer → + enhanced absorption of longwave radiation → + incoming longwave radiation at the surface → + net radiation at the surface → + available energy for evapotranspiration; and: + evapotranspiration → − surface temperature → − emission of terrestrial radiation → + net radiation at the surface → + available energy for evapotranspiration. Negative feedbacks that set limits to these loops are through decreased water vapor pressure deficit in the planetary boundary layer, therefore reducing the atmospheric demand for evapotranspiration, and increased cloud cover which reduces incoming surface solar radiation (see also Table 14.2).

Both of these feedback loops extend the boundary of vegetation types towards the more limited side, therefore extending the overall area available for biotic productivity.

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These feedbacks have been suggested to be important for understanding the climate system response to global change, for instance during glacial-interglacial cycles. During the Mid-Holocene (approx. 9000 years before present), the time that the Earth was closest to the sun on its orbit (i.e., perihelion) was during the northern hemisphere summer, so that the northern hemisphere received more solar radiation in summer. Foley et al. (1994) demonstrated that the northern shift of the boreal forest zone during that time was amplified by the boreal forest feedback, resulting in a simulated climate which is in better agreement with paleo-reconstructions. During the same period, reconstructions suggest that the Sahara desert was much reduced in size (as for instance depicted by cave paintings in the Sahara, leading to the notion of a "green" Sahara with abundant wildlife,). Kutzbach et al. (1996) and Claussen and Gayler (1997) demonstrated that this reconstruction is reproduced with climate model simulations if the water recycling feedback associated with the shift of vegetation zones is included in the model. The boreal forest feedback has also been suggested as a potentially important factor for initiating ice ages (deNoblet et al. 1996; Gallimore and Kutzbach 1996), while the water recycling feedback (associated with deep rooted vegetation) has been suggested to be important for sustaining Amazonian rainforest cover during the last glacial maximum (Kleidon and Lorenz 2001).

14.4 Biotic Entropy Production and MEP

Biotic activity, mainly represented by photosynthesis and subsequent respiration of organic carbon, allows organisms to perform work and therefore leads to entropy production. Photosynthesis absorbs and utilizes a certain fraction of incoming low entropy solar radiation, that is, it converts solar energy into carbohydrates at a certain rate, Q_{GPP}. These carbohydrates are eventually respired, releasing carbon dioxide and heat roughly at the surface temperature T_S of the Earth. In steady state, the conversion of solar energy into carbohydrates by photosynthesis balances the production of heat by respiration (neglecting the effect of carbon burial), leading to a rate of biotic entropy production of:

$$\sigma_{BIO} \approx Q_{GPP}(1/T_S - 1/T_{SUN}) \qquad (14.9)$$

Equation (14.9) determines the overall biotic entropy production from the differences of energy fluxes at the biosphere-environment boundary, rather than summing up all factors that lead to entropy production within the biosphere. With this expression we also neglect contributions of other metabolisms that are not related in the processing of carbohydrates derived from photosynthesis.

Previous work by Ulanowicz and Hannon (1987) and Schneider and Kay (1994) suggests that terrestrial vegetation acts to enhance the rate of entropy production by lowering the surface albedo and surface temperature. Here we suggest that the biota does not only increase the rate of entropy production, but that there are distinct macroscopic states of maximum entropy production associated with biotic activity.

14.4.1 Conditions for Biotic MEP States

As discussed in the introduction to the book (Kleidon and Lorenz, this volume), MEP applies to open thermodynamic systems which (a) do not have fixed boundary conditions and (b) have sufficient degrees of freedom (see also Dewar 2003, and Dewar, this volume). Biotic entropy production depends primarily on biotic productivity Q_{GPP}, which in turn depends on incoming solar radiation, water availability and surface temperature (in a similar way as expressed in 14.4). The extreme climate model simulations discussed in the previous section illustrate that none of these factors is fixed, but strongly affected by the presence of terrestrial vegetation (Table 14.2). Consequently, biotic productivity on land is indeed subject to open boundary conditions. Furthermore, the terrestrial biota is inherently diverse, that is, there are many different ways for individual organisms to use assimilated carbon to grow, reproduce, and respond to environmental conditions (e.g., with respect to stomatal functioning, Buckley et al. 1999). Kleidon and Mooney (2000) used an individual-based modeling approach to demonstrate this functional diversity for terrestrial vegetation (Fig. 14.1). They developed a model of an individual plant, which simulates the growth and phenology as a function of environmental conditions, and then used it in a Monte-Carlo setup to estimate the range of plant growth strategies that lead to reproductive success under given climatic conditions. The simulated large-scale pattern from this modeling approach reproduced the observed features of plant species richness very well, with characteristic gradients in diversity along moisture and temperature gradients. The functional diversity of organisms as simulated by their approach is interpreted here as degrees of freedom associated with the macroscopic process of biotic activity. These biotic degrees of freedom also introduce flexibility to the macroscopic processes of water and carbon cycling.

We can also understand the applicability of MEP to the biota in terms of macroscopic reproducibility (see also Dewar, 2003; Dewar, this volume; Lineweaver, this volume). When addressing the role of the biota at the macroscale, we do not require microscopic reproducibility, but are interested in the reproducibility of the macroscopic state. This may be illustrated as follows: Given certain values of annual mean precipitation and temperature, we can with high certainty predict whether this climate would likely lead to a tropical rainforest, a grassland, a tundra, or a desert. The vegetation type in turn determines the macroscopic state of the land surface, in terms of its surface albedo, its aerodynamic roughness, and its rooting zone depth. What we do not know is whether the community at the microscale at a certain location

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is composed of species A, B, and C at a given time t. But for the macroscopic description of the land surface and for the functional consequences for the global biogeochemical cycles of water and carbon, this information is not required, except to the extent to which sufficient biotic degrees of freedom are represented. Macroscopic reproducibility then tells us that the MEP state is the most likely macroscopic state, that is, the macroscopic MEP state can be reproduced by the vast majority of microstates which in our case would be the compositions of communities formed by individual plants.

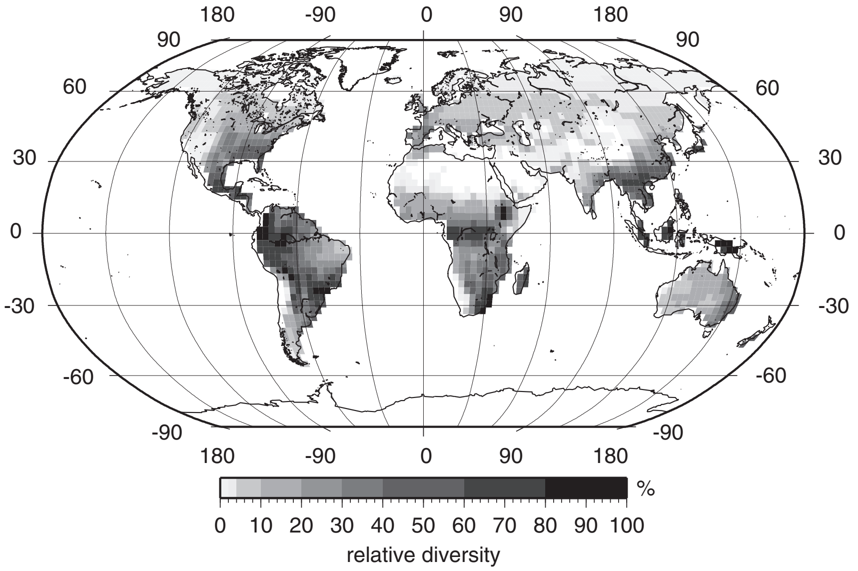

Fig. 14.1. Simulated plant functional diversity by a modeling approach of Kleidon and Mooney (2000). A simulation model of a generic plant was used in conjunction with a Monte-Carlo simulation to estimate the range of feasible plant growth strategies that lead to reproductive success under different climatic conditions. The geographic variation of diversity is interpreted here as biotic degrees of freedom, which are a necessary requirement for MEP to apply to biotic activity

14.4.2 Biotic States of MEP

We suggest two MEP states relevant to atmosphere-biosphere interactions at the large scale, which are both related to the Earth's albedo. As discussed in the beginning of this chapter, the Earth's planetary albedo is not fixed, but variable and flexible, determined primarily by the surface albedo and the extent of cloud and snow cover. The planetary albedo plays a crucial role of the overall rate of entropy production of planet Earth (14.1), and

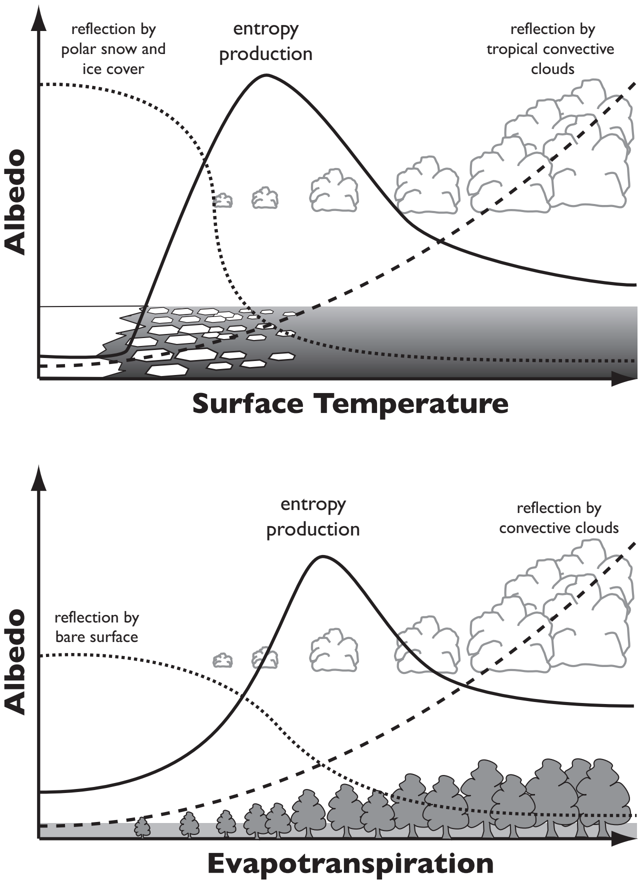

Fig. 14.2. Conceptual diagrams of how the (*top*) planetary albedo and (*bottom*) land surface albedo exhibit a minimum with respect to surface temperature and land surface evapotranspiration. A minimum in the overall albedo leads to a maximum in absorption of solar radiation and therefore to a maximum in entropy production (*solid lines*). Since surface temperature is related to the strength of the atmospheric greenhouse, which in turn is affected by the biota through its effects on biogeochemical cycles, there are potentially many possible states with a range of global mean temperatures that satisfy the constraints of global energy- and carbon balance. Likewise, the energy- and water budget constraints on land surface functioning permit potentially many states with differing rates of evapotranspiration, ranging from a bare surface to a fully vegetated one. The MEP principle in these two cases states that the state of MEP is the most likely macroscopic state of the system. See text for further explanations

small changes in the planetary albedo can dwarf the contributions of other processes to the overall entropy budget of Earth (see Kleidon and Lorenz, this volume). The two states of MEP can be explained as follows (Fig. 14.2):

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- *biotic MEP and carbon cycling:* Biotic activity affects atmospheric concentrations of carbon dioxide (and methane), and therefore the strength of the atmospheric greenhouse effect and surface temperature. To illustrate the state of MEP, let us think of surface temperature as an external control parameter at the planetary scale for a moment, meaning that we have multiple potential steady states with different values of surface temperature that satisfy the constraints of the global energy and carbon budget. We would likely expect the following effects of surface temperature on planetary albedo (Fig. 14.2): With decreasing surface temperature, the extent of snow cover would increase in the polar regions, leading to an increase in planetary albedo. On the other hand, increasing surface temperature leads to a lower equilibrium Bowen ratio (14.7), which leads to a moister boundary layer and less boundary layer growth. This should result in an increase in convective clouds, particularly in the tropics, and an associated increase in planetary albedo. Taken together, these two lines of reasoning suggest that there is a minimum planetary albedo at which the absorption of solar radiation is at a maximum. This, in turn, would lead to a state of maximum entropy production of the Earth system. Surface temperature of course is not an external control parameter, but at the planetary scale is determined largely by the absorption of solar radiation at the surface and the strength of the atmospheric greenhouse, which is affected by the extent of biotic carbon cycling and the biotic enhancement of rock weathering (see e.g., Schwartzman and Lineweaver, this volume). This leads then to a connection between a planetary state of MEP associated with absorption of solar radiation and biotic carbon exchange.
- *biotic MEP and water cycling:* The examples of a “Desert World” and a “Green Planet” suggest a state of MEP associated with evapotranspiration (which, as explained above, is directly linked to the productivity of terrestrial vegetation). Let us again view evapotranspiration as an external parameter for a moment that we can adjust, meaning that there are many macroscopic states of the land surface that satisfy the energy- and water balance. We get the following effects of the magnitude of evapotranspiration on net albedo: Increasing evapotranspiration allows for higher productivity, therefore allowing for a lower surface albedo to be maintained through more green biomass at the surface. This leads to increased absorption of solar radiation. On the other hand, increased evapotranspiration leads to a moister boundary layer with less boundary layer growth, resulting in increased formation of convective clouds. This leads to an increase of the net albedo of the atmospheric column and reduces the amount of incoming solar radiation at the surface. Therefore, there should be a state of MEP associated with evapotranspiration. This MEP state can be illustrated at a qualitative level by the extreme climate model simulations of a “Desert World”, the “Present-Day”, and a “Green Planet”. Table 14.2 clearly shows the trend towards higher cloud

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cover with increasing presence of terrestrial vegetation as suggested in Fig. 14.2b. Note however that the vegetation state of a "Green Planet" does not account for productivity constraints on land surface parameters, that is, rainforest characteristics are prescribed even in desert climates, which could not be maintained in steady state due to lack of productivity. This lack of constraint may explain the absence of a peak in biotic productivity.

14.4.3 Biotic MEP and Gaia

If we accept biotic MEP as an emergent property of atmosphere-biosphere interactions in steady-state, then this can have important implications for the adaptability of climate system functioning to change. This is illustrated by the sensitivity of a simple coupled climate-carbon cycle model (Kleidon 2004) to a prescribed external change in solar output of solar radiation (i.e., the solar luminosity, which affects I_0 in 14.1). This model implements the line of reasoning described above for biotic MEP and carbon cycling (as shown in Fig. 14.2a). When the model is forced by changes in solar luminosity (which was 70% of today's value some 4 billion years ago) and it is assumed that biotic activity adjusts to a maximum in entropy production, then the resulting simulated surface temperature is insensitive to these changes (Fig. 14.3). The resulting evolution of atmospheric carbon dioxide concentrations associated with the MEP state is roughly similar to what reconstructions suggest about the past evolution of the atmospheric greenhouse (e.g., Kasting 1993; Catling, this volume). The homeostatic outcome of this simple model shares similarity to the Gaia hypothesis, which states "environmental homeostasis for and by the biosphere" (Lovelock and Margulis 1974; see also Toniazzo

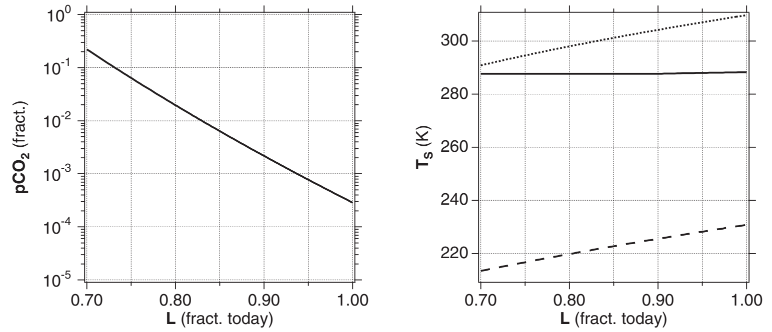

Fig. 14.3. Sensitivity of (*left*) atmospheric carbon dioxide concentrations pCO_2 and (*right*) surface temperature to variations of solar luminosity at a state of biotic MEP as simulated by a simple climate-carbon cycle model. Solar luminosity is expressed as a fraction of the present-day value. Also shown are the simulated temperatures for $pCO_2 = 1$ (*dotted line*) and $pCO_2 = 10^{-6}$ (*dashed line*). After Kleidon (2004)

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et al., this volume). The important difference is, however, that the emergent outcome of this example is the result of MEP as a physical selection principle, and biotic processes being viewed as representing additional degrees of freedom for climate system processes.

14.5 Conclusions

In this chapter we discussed the role of the biota for present-day climate system functioning, focusing on the role of terrestrial vegetation. We illustrated how climatic conditions constrain photosynthetic activity, and that these constraints are not fixed, but an emergent outcome of atmosphere-biosphere interactions and biotic feedbacks. For terrestrial vegetation, the overall feedbacks can be described by two positive feedbacks: the boreal forest feedback for temperature-limited regions and the water cycling feedback for water-limited regions. We showed that biotic entropy production at the large scale in steady-state can be approximated by the gross primary productivity, and that the two feedbacks are consistent with the notion that biotic effects enhance entropy production. The existence of a maximum in biotic entropy production was qualitatively demonstrated with two examples involving carbon exchange and evapotranspiration. Both examples specifically emphasize the role of convective clouds to understand biotic MEP states in the coupled atmosphere-biosphere system. We also illustrated that *if* we assume that the biosphere adjusts to MEP when environmental conditions (such as solar luminosity) change, then the outcome can lead to environmental homeostasis. This notion naturally needs to be substantiated, for instance with further modeling studies using process-based simulation models of the biosphere and the Earth system. Nevertheless, the perspective we promote here seems to be a promising path to appreciate the role of biodiversity in the functioning of the Earth system from a fundamental, thermodynamic perspective and to understand the ability of the Earth system to adapt to global changes.

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