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Stochastic Thermodynamics of Ecosystems

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Abstract

We investigate the thermodynamics as well as the population dynamics of ecosystems based on a stochastic approach in which the biomasses of the several species of the ecosystem are treated as stochastic variables. The several species are connected by feeding relationships that are understood as unidirectional processes in which a certain amount of biomass is exchanged between species. We show that the equations for the averages in the biomass of species are those given by the deterministic approach. We determine the fluxes of mass, energy, and entropy as well as the rate of the entropy production. In the stationary state, the entropy production and the input of energy into the ecosystem are both found to be proportional to the organic mass generated by the autotrophs per unit time per unit mass of the autotrophs.

Keywords Stochastic thermodynamics · Ecosystems · Food webs

1 Introduction

An ecosystem consists of organisms that live in the same space, interacting with each other and with the physical environment [1–8]. The organisms of distinct species are connected with each other through a feeding relationship structured in a hierarchy of trophic levels, called a food web [3–9]. In the first trophic level, one finds the organisms that produce organic matter from inorganic substances. These are the autotrophs. In the other levels, we find the heterotrophs, which obtain organic matter by feeding on the autotrophs and on other heterotrophs. In the second level, there are the species that eat the autotrophs and are food for the species of the third level. The species of this level are, in turn, food for the upper level, and so on. The top level consists of species that are not food for any other species and are represented by the apex predators.

The feeding relationship induces a change in the number of individuals of each species, which for that reason evolves in time and may reach a stationary state. Many approaches have been employed in the theoretical study of the sizes of populations in food webs and its evolution in time [10–13]. We point out the deterministic approaches in which the number of individuals of each species obeys an ordinary differential equation of first order in time. This approach was employed by Lotka [14, 15] and by Volterra [16] in their study of a predator–prey system. The Lotka-Volterra model was extended to several interacting species by May in his studies of the stability in multispecies community models [17]. The extended model was then used by other investigators as a model for food webs [18–21].

The structure composed of the organisms and the abiotic environment is maintained active by the consumption of light energy by the autotrophs that transform inorganic substances into organic matter through photosynthesis. The heterotrophs obtain organic matter by feeding on the autotrophs and on other heterotrophs. These organisms convert the nutrients into matter that are used again by the autotrophs completing the cyclic transformation of matter. The transformation of matter induced by the input of energy in an ecosystem was pointed out by Lotka [14, 15] and by Lindeman [22], and the role of the flow of energy through the system was emphasized by Odum [4, 6]. The flow of energy acts to organize the system [23], and an ecosystem is regarded as a thermodynamic system which transforms matter and maintain the living structure through the flow of energy.

The continuous flow of energy through the system shows that the equilibrium thermodynamics cannot be applied because in thermodynamic equilibrium, there can be no macroscopic flow of any kind and particularly of energy. Therefore, it is necessary to resort to theories that take into

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account the irreversible character of the processes as pointed out by Prigogine and Wiame [24]. Such a theory was developed by De Donder [25] and by Prigogine [26–29] in which entropy production, entropy flux, and energy flux are central concepts. Irreversible thermodynamic was then applied to the ecosystem by making it consistent with the dynamic equations for the population, usually represented by the Lotka-Volterra equations [30–39].

An inherent characteristic of species populations is fluctuations, which are manifest when a species become extinct in a certain region because by chance its number decreases and vanishes. Fluctuations in space and time are essential features of stochastic thermodynamics [40–43]. This theory is based on a probabilistic approach to thermodynamics and provides a stochastic dynamics from which we obtain the time evolution of the thermodynamic quantities. Like statistical mechanics the states of the system are defined by a set of random variables over which a probability distribution is defined. We wish here to apply the stochastic thermodynamics to the ecosystem and thus explain through this theory the flows of matter and energy and their connection with the flow of entropy and the production of entropy.

From the present approach, we obtain the relation between the flux of entropy, the flux of energy and the flux of matter. It is singular when compared to other approaches in the thermodynamic treatment of unidirectional processes and on the use of the biomass of each species as the dynamic variable, which fits the conservation of mass, instead of the number of individuals of each species. One of the main results coming from the present approach is that at the stationary state, the entropy production, which equals the flux of entropy to the environment and the input of energy are both proportional to the quantity of organic matter generated by the autotrophs per unit time per unit mass of the autotrophs.

2 Deterministic Dynamics

2.1 Dynamic Equations

An example of a food web is that consisting of plants, herbivorous, and carnivorous living in a given region. The first trophic level of the food web consists of plants , which generate organic matter using light energy through photosynthesis. In the second trophic level, we find the herbivorous which eat plants and are the food for the first carnivorous. The herbivorous as well as the first carnivorous are the food for the second carnivorous. There might be other carnivorous trophic levels until the top level of the food web, consisting of the apex carnivorous.

A food web is represented by a set of nodes and connections between them, as shown in Fig. 1. Each node of the food web represents an animal species , except the bottom node, which represents the plants. The feeding connection between the nodes is represented by an arrow which points from an organism eaten to the animal eating it. Several arrows may point to a node meaning that the species at the node eats several species. A node may also be at the tail of several arrows meaning that the species is the food of several species.

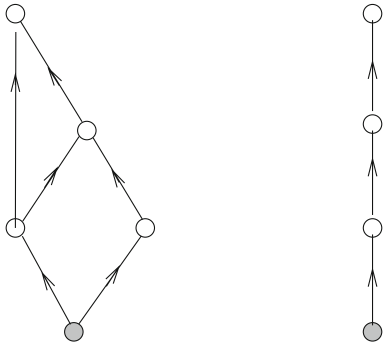

Fig. 1 Representation of two food webs with four trophic levels. The gray circle represents the plants, and the other circles represent the animal species. An arrow represents the process of feeding and points from an organism eaten to the animal eating it

Instead of using the numbers of individual of each species as the dynamic variables as is usual in population dynamics, we employ here the biomasses of the several species. We denote by M_i, the biomass of the animal species i, $i = 1, 2, \ldots, n$, and by M_0 the biomass of the plants. The biomasses M_i vary in time according to the feeding processes represented by the arrows in Fig. 1. In this process, a certain amount of the biomass of a species is transferred to the biomass of the species eating it. In addition to this type of process, there is another type involving only the animals, which is the spontaneous transformation of organic to inorganic matter, which embraces many actions, such as the death of animals. A third type of process involves only the plants and corresponds to the transformation of inorganic substances into organic matter through photosynthesis.

To set up the equation that gives the time variation of M_i, we consider first the contribution coming from the feeding process. We assume that this process is analogous to an autocatalytic reaction, which means that the contribution associated with species i and j is proportional to the product $M_i s_j$, where s_j is the fraction in mass of specie j, to be defined more precisely later. The contribution coming from the transformation of the biomass of species i into inorganic matter is proportional to M_i, as it is understood as analogous to a spontaneous reaction. Adding these two contributions, we get the following equation

$$\frac{dM_i}{dt} = \sum_{j=0}^{n} \nu_{ij} b_{ij} M_i s_j - c_i M_i, \tag{1}$$

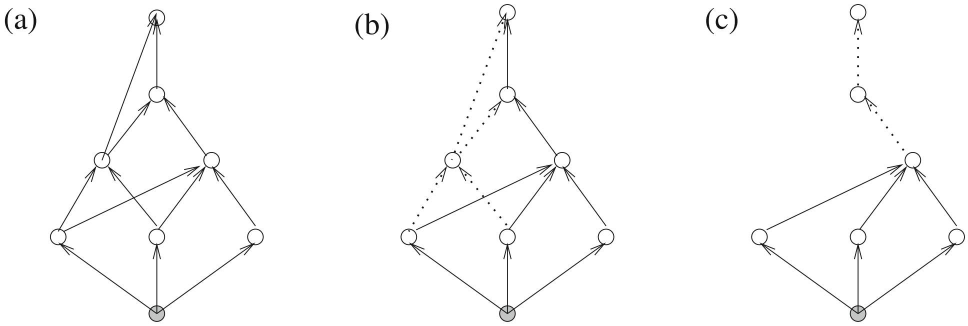

Fig. 2 **a** Representation of a food web with five trophic levels. **b** Representation after one of the species of the third level becomes extinct. **c** Representation after the species of the fourth level becomes extinct. As a consequence, the apex predator of the fifth level also becomes extinct by the suppression of its prey

where $b_{ij} > 0$ is the feeding rate constant, $c_i > 0$ is the decomposition rate constant, and $\nu_{ij} = +1$ if i feeds on j, and $\nu_{ij} = -1$ otherwise. We remark that c_i cannot be zero for the apex carnivorous; otherwise, its number would increase without bounds.

The third process, which involves only the plants, is represented by a constant Q, which is the rate at which organic matter is produced by the plants. The equation that gives the time variation of M_0 is

$$\frac{dM_0}{dt} = -\sum_{j=1}^{n} b_{0j} M_j + Q. \tag{2}$$

It is more convenient to write the dynamic equations in terms of the mass fraction s_i defined as the ratio $s_i = M_i/M$ between M_i and the total mass M of the ecosystem, which is the sum of the masses of the living organisms and the mass of the inorganic matter. If we denote by M_{n+1} the mass of the inorganic matter then

$$\sum_{i=0}^{n} M_i + M_{n+1} = M. \tag{3}$$

Dividing (1) and (2) by M, we find

$$\frac{ds_i}{dt} = \sum_{j=0}^{n} \nu_{ij} b_{ij} s_i s_j - c_i s_i, \tag{4}$$

valid for $i = 1, 2, \ldots, n$, and

$$\frac{ds_0}{dt} = -\sum_{j=1}^{n} b_{0j} s_0 s_j + q, \tag{5}$$

where $q = Q/M$. The equation for the fraction s_{n+1} of inorganic matter is unnecessary because

$$\sum_{i=0}^{n} s_i + s_{n+1} = 1. \tag{6}$$

There are some immediate consequences of the dynamic equations that are worth mentioning, which are illustrated in Fig. 2. If the biomass fraction s_k of species k vanishes, then it remains zero forever, which means that the species becomes extinct. Indeed, if $s_k = 0$, then it follows from (4) that $ds_k/dt = 0$ and s_k will not change from its zero value.

If one animal species becomes extinct, then the food web that remains is the one we obtain by removing all the arrows that are connected to it, as shown in Fig. 2. Indeed, if k is the species going extinct, then $s_k = 0$. Setting $s_k = 0$ in the other equations is equivalent to set $b_{ik} = 0$, which corresponding to erasing the corresponding arrow.

If all prey of a species k disapear, then the species k becomes extinct. In other words, if all arrows pointing to k are erased, then $s_k = 0$. Indeed, if all prey of k disappears, then all positive terms on the right-hand side of the (4) disappear, remaining only negative terms, so that $ds_k/dt < 0$ and s_k eventually vanishes.

2.2 Food Chains

We consider here food chains, which are food webs such that each animal has just one prey like that shown on the right panel of Fig. 1. The species $i + 1$ feeds on the species i. To turn the model simpler, we set $b_{i+1,i} = b$, except $b_{10} = a$, and $c_i = c$. The equations become

$$\frac{ds_1}{dt} = as_1s_0 - bs_1s_2 - cs_1, \tag{7}$$

$$\frac{ds_i}{dt} = bs_is_{i-1} - bs_is_{i+1} - cs_i, \tag{8}$$

$$\frac{ds_n}{dt} = bs_ns_{n-1} - cs_n, \tag{9}$$

$$\frac{ds_0}{dt} = -as_0s_1 + q. \tag{10}$$

The nonzero stationary solution is determined by the set of equations

$$as_0 - bs_2 = c, \tag{11}$$

$$bs_{i-1} - bs_{i+1} = c, \tag{12}$$

$$bs_{n-1} = c, \tag{13}$$

$$as_0s_1 = q. \tag{14}$$

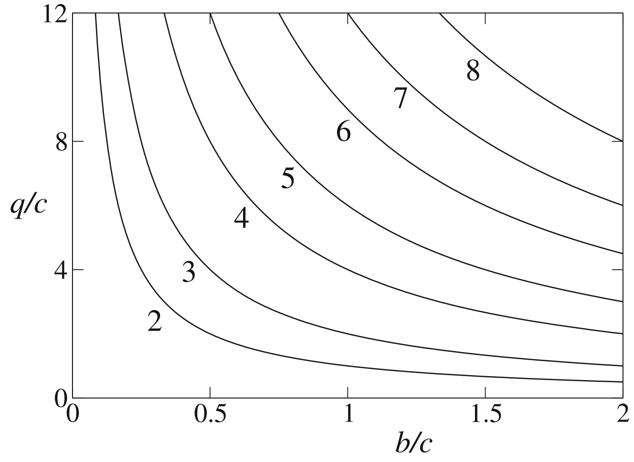

Fig. 3 Diagram in the space of parameters q/c versus b/c for the food chain with n animal species. The number next to a line corresponds to the number n of animal species. A line n determines the boundary of the region $\mathcal{R}_n$ of the occurrence of the positive solution $s_i > 0$, for $i = 0, 1, 2, \ldots, n$, which occurs at the right and above the line n

It is straightforward to solve this system of equations. For n even, the solution is

$$s_0 = \frac{2bq}{nac} \tag{15}$$

$$s_\ell = (n - \ell + 1)\frac{c}{2b}, \qquad \ell \text{ odd}, \tag{16}$$

$$s_\ell = \frac{2q}{nc} - \frac{\ell c}{2b}, \qquad \ell \text{ even}. \tag{17}$$

The fractions s_0 and s_ℓ for ℓ odd are all positive. The smaller fraction s_ℓ for ℓ even is s_n. Thus, the condition that all s_ℓ be positive is given by $s_n > 0$, or

$$\frac{2q}{nc} > \frac{nc}{2b}, \tag{18}$$

which defines the region $\mathcal{R}_n$ in the space of parameters where the full positive solution exists. The boundary of this region is given by

$$\frac{2q}{nc} = \frac{nc}{2b}, \tag{19}$$

valid for $n = 2, 4, 6, \ldots$ and is shown in Fig. 3.

Let us consider now the case n odd. In this case, the solution of the system of linear equation is

$$s_0 = \frac{(n+1)c}{2a} \tag{20}$$

$$s_\ell = \frac{2q}{(n+1)c} - \frac{(\ell - 1)c}{2b}, \qquad \ell \text{ odd}, \tag{21}$$

$$s_\ell = (n + 1 - \ell)\frac{c}{2b}, \qquad \ell \text{ even}. \tag{22}$$

The fractions s_ℓ for ℓ even are all positive. The smaller fraction s_ℓ for ℓ odd is s_n. Thus, again, the condition that all s_ℓ be positive is given by $s_n > 0$, or

$$\frac{2q}{(n+1)c} > \frac{(n-1)c}{2b}, \tag{23}$$

which defines the region $\mathcal{R}_n$ where the full positive solution exists. The boundary of this region is given by

$$\frac{2q}{(n+1)c} = \frac{(n-1)c}{2b}, \tag{24}$$

valid for $n = 1, 3, 5, \ldots$ and is shown in Fig. 3.

It is worth mentioning that as one approaches the boundary of $\mathcal{R}_n$, given by (19) for n even and by (24) for n odd, the fraction that vanishes is that corresponding to the apex predator, which becomes extinct at the boundary of $\mathcal{R}_n$.

3 Stochastic Dynamics

3.1 Fokker-Planck Equation

The dynamic approach that we have presented above describes a deterministic motion. In the following, we present a stochastic approach to the thermodynamics of an ecosystem. The mass fraction now becomes a stochastic variable, which we denote by x_i. We use the notation x to represent the collection of all fractions x_i. We begin by setting up a master equation that gives the evolution equation of the probability distribution of $P(x)$ of the mass fractions.

The ecosystem to be described here by the master equation is understood as composed by $n + 2$ components, as shown in Fig. 4, each one labeled by an integer i from 0 to $n+1$. The component $i = n + 1$ represents the surroundings consisting of inorganic matter. The component $i = 0$ represents the plants that transform inorganic matter into organic matter. The components from $i = 1$ to $i = n$ represent each one an animal species that eats another animal or the plants.

We remark that the mass of the surroundings consists of inorganic matter. The plants transform the inorganic matter into the organic matter, a process represented by the lowest vertical arrow in Fig. 4. The solid arrows represent the process of feeding, which transfers biomass from the species being eaten to the eating species. The processes represented by dashed arrows correspond to the decomposition of animals, understood as the transformation of organic to inorganic matter deposited in the surroundings.

To set up a master equation, one needs to introduce the rates at which mass is transferred from one component to another, associated with each process. We suppose that the amount of mass transferred is the *same* at each time a process

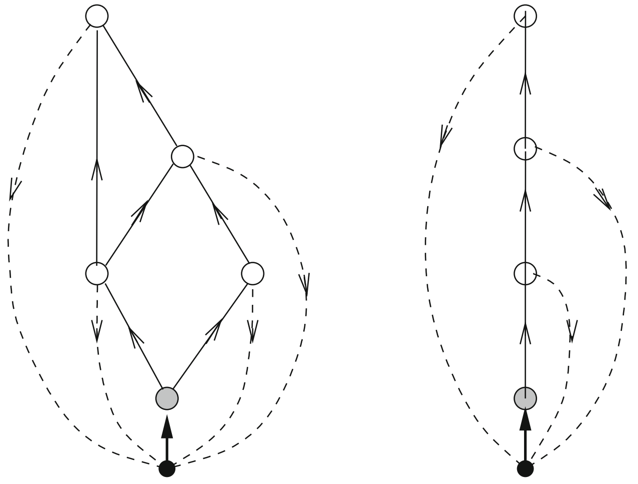

Fig. 4 Representation of the processes of transfer of masses occurring in an ecosystem. The black small circle represents the surroundings containing inorganic matter. The gray circle represents the plants, and the other circles represent the animal species. The solid arrow at the bottom, pointing from the black to the gray circle, represents the process of production of organic matter by the plants through photosynthesis. The other solid arrows represent the process of feeding. A solid arrow points from an organism eaten to the animal eating it. The dashed arrows represent the spontaneous decomposition of animals, that is, the transformation of organic into inorganic matter

occurs. The rate of mass transfer is then understood as this constant amount of mass, which we denote by m, multiplied by the rate at which a process occurs, or the frequency of the occurrence of a process. By this procedure, we simplify the model, which otherwise would be complicated because the individuals of distinct species have different masses. This is possible by performing an rescalling of the rates of transition.

As the mass transferred in each process is the same and equal to m, the biomass M_i increases or decreases by the amount m in each process. Thus, the mass fraction increases or decreases by an amount $\varepsilon = m/M$. A processes represented by an arrow in Fig. 4 from j to i corresponds to a decrease of the fraction x_j by an amount ε and an increase of the fraction x_i by the same amount. We represent this process by the transition

$$x \to x^{ij}, \tag{25}$$

where x represents the vector

$$x = (x_0, \dots, x_i, \dots, x_j, \dots, x_{n+1}), \tag{26}$$

and x^{ij} is the vector

$$x^{ij} = (x_0, \dots, x_i + \varepsilon, \dots, x_j - \varepsilon, \dots, x_{n+1}), \tag{27}$$

obtained from x by replacing x_i by $x_i + \varepsilon$ and x_j by $x_j - \varepsilon$. The transition $x \to x^{ij}$ occurs with a probability per unit time equal to $w_{ij}(x)/\varepsilon$ where $w_{ij}(x)$ represents the change per unit time in the mass fraction by an amount ε. It may depend on x and is given by

$$w_{ij} = b_{ij} x_i x_j, \tag{28}$$

if $i = 1, \dots, n$ and $j = 0, 1, \dots, n$, where b_{ij} is the feeding rate constant. We remark that b_{ij} is nonzero only when there is an arrow from j to i. When $i = n + 1$ and $j = 1, \dots, n$ then

$$w_{n+1,j} = c_j x_j, \tag{29}$$

where c_j is the decomposition rate constant. When $i = 0$ and $j = n + 1$ then

$$w_{0,n+1} = q, \tag{30}$$

where q is the rate in which the organic matter is produced by the plants.

Once we are given the transition rates, the master equation reads

$$\frac{d}{dt} P(x) = \frac{1}{\varepsilon} \sum_{ij} \{ w_{ij}(x^{ji}) P(x^{ji}) - w_{ij}(x) P(x) \}, \tag{31}$$

where i and j take all values from 0 to $n + 1$.

As ε is small compared to x_i we may expand the right-hand side of the master equation in powers of ε. Up to linear terms in ε, we find

$$\frac{dP}{dt} = \sum_{ij} \{ -D_{ij} w_{ij} P + \frac{\varepsilon}{2} D_{ij}^2 w_{ij} P \}, \tag{32}$$

which is a Fokker-Planck equation, and we are using the abbreviation

$$D_{ij} = \frac{\partial}{\partial x_i} - \frac{\partial}{\partial x_j}. \tag{33}$$

The presence of the quantity ε in the last term of the Fokker-Planck indicates that ε is a measure of the fluctuations, that is, the covariances of x_i are proportional to $\varepsilon = m/M$. In an equivalent manner, we may say that the amplitudes of the fluctuations in M_i is proportional to $\sqrt{M}$.

From (32), we may determine the time evolution of the average $\langle x_i \rangle$. It is given by

$$\frac{d}{dt} \langle x_i \rangle = \sum_j \langle w_{ij} - w_{ji} \rangle, \tag{34}$$

where we have performed an integral by parts, and assumed that the integrated part vanishes. Taking into account that the probability distribution is very sharp at the mean values $s_i = \langle x_i \rangle$, we may replace $\langle w_{ij}(x) \rangle$ by $w_{ij}(s)$ and write

$$\frac{ds_i}{dt} = \sum_j \{w_{ij}(s) - w_{ji}(s)\}. \tag{35}$$

We remark that this is a closed set of equations for s_i and determine s_i as a function of time. These equations for $i = 0, 1, \ldots, n$ coincide with the deterministic (4) and (5), and we may say that within the present stochastic approach, the dynamic variables of the deterministic approach can be understood as the average values of the stochastic variables.

3.2 Entropy Flux

The entropy S of the ecosystem is defined by

$$S = -k \int P \ln P dx, \tag{36}$$

where k is the Boltzmann constant and the integration is performed over the space x. Its time evolution is

$$\frac{dS}{dt} = -k \int \frac{\partial P}{\partial t} \ln P dx. \tag{37}$$

Using the master (31), we find

$$\frac{dS}{dt} = \frac{k}{\varepsilon} \sum_{ij} \int w_{ij}(x) P(x) \ln \frac{P(x)}{P(x^{ij})} dx. \tag{38}$$

The rate of entropy production Π is defined by the following formula [44]

$$\Pi = \frac{k}{\varepsilon} \sum_{ij} \int w_{ij}(x) \times \times \{P(x) \ln \frac{P(x)}{P(x^{ij})} - P(x) + P(x^{ij})\} dx, \tag{39}$$

and we remark that Π is nonnegative because if we let $\xi = P(x)/P(x^{ij})$ we see that the integrand is proportional to $\xi \ln \xi - \xi + 1 \geq 0$. This formula for the entropy production rate is distinct from the Schnakenberg formula [45], and is appropriate for the unidirectional transitions that we consider here. The time variation of the entropy of the system is equal to the production of entropy minus the flux of entropy *from* the system *to* the outside Ψ, that is,

$$\frac{dS}{dt} = \Pi - \Psi. \tag{40}$$

From the expressions of dS/dt and Π, we find the following expression for the flux of entropy associated with unidirectional processes,

$$\Psi = \frac{k}{\varepsilon} \sum_{ij} \int w_{ij}(x) \{P(x^{ij}) - P(x)\} dx. \tag{41}$$

We point out that the rate of entropy production vanishes when all states are equally probable.

The entropy flux can be expressed as an average

$$\Psi = \sum_{ij} \Psi_{ij}, \tag{42}$$

where

$$\Psi_{ij} = \frac{k}{\varepsilon} \langle w_{ij}(x^{ji}) - w_{ij}(x) \rangle, \tag{43}$$

In the limit $\varepsilon \to 0$, Ψ_{ij} can be written as

$$\Psi_{ij} = -k \langle D_{ij} w_{ij} \rangle, \tag{44}$$

Let us determine the entropy flux Ψ_{ij} for each one of transitions $j \to i$. For the feeding processes, represented by solid arrows in Fig. 4, the transition rates are given by (28), and the entropy flux is

$$\Psi_{ij} = -k b_{ij}(s_j - s_i), \qquad i = 1, 2, \ldots, n, \tag{45}$$

and we recall that $b_{ij} > 0$ if there is an arrow from j to i, and vanishes otherwise. For the process of decomposition, represented by dashed arrows in Fig. 4, the transition rates are given by (29), and the entropy flux is

$$\Psi_{n+1,j} = k c_j. \tag{46}$$

an we recall that $c_j > 0$. For the process of transformation of inorganic matter into organic matter by the plants, represented by the small vertical arrow, the transition rate is given by (30), and flux

$$\Psi_{0,n+1} = 0, \tag{47}$$

which means that there is no flux of entropy associated with the input of energy when inorganic matter is transformed into organic matter by the plants.

3.3 Heat Flux

Let $\mathcal{E}(x)$ be a state function, which we wish to identify with the energy function. The time variation of its average $U = \langle \mathcal{E} \rangle$ is

$$\frac{dU}{dt} = \int \frac{\partial P}{\partial t} \mathcal{E} dx. \tag{48}$$

Using the master (31), we find

$$\frac{dU}{dt} = \Phi, \tag{49}$$

where

$$\Phi = \frac{1}{\varepsilon} \sum_{ij} \int w_{ij}(x) P(x) \{\mathcal{E}(x^{ij}) - \mathcal{E}(x)\} dx \tag{50}$$

is the heat flux from the outside to the system. It can be written as an average,

$$\Phi = \sum_{ij} \Phi_{ij}, \tag{51}$$

where

$$\Phi_{ij} = \frac{1}{\varepsilon} \langle w_{ij}(x) \{\mathcal{E}(x^{ij}) - \mathcal{E}(x)\} \rangle. \tag{52}$$

The quantity Φ_{ij} is the heat flux associated to the transition j to i. In the limit $\varepsilon \to 0$, it can be written as

$$\Phi_{ij} = \langle w_{ij} D_{ij} \mathcal{E} \rangle \tag{53}$$

which is nonzero only when there is an arrow from j to i. In other cases, Φ_{ij} vanishes.

3.4 Relation Between the Entropy and Energy Fluxes

We did not give the precise form of the energy function. To this end, we introduce a connection between entropy flux and heat flux. Following Clausius, we postulate a relation between the entropy flux Ψ_{ij} and the heat flux Φ_{ij}, which is

$$\Psi_{ij} = -\lambda_{ij} \Phi_{ij}, \tag{54}$$

where λ_{ij} is a constant, and the negative sign is introduced because Φ_{ij} is positive when heat is introduced into the system and Ψ_{ij} is negative when entropy is introduced into the system.

To determine the actual expression of $\mathcal{E}(x)$ and the coefficients λ_{ij}, we proceed as follows. We observe first that the coefficient $\lambda_{0,n+1} = 0$ must be zero in view of the relation (47). Using the expressions (44) and (53), the relation (54) reads

$$k \langle D_{ij} w_{ij} \rangle = \lambda_{ij} \langle w_{ij} D_{ij} \mathcal{E} \rangle, \tag{55}$$

which is fulfilled if

$$D_{ij} \ln w_{ij} = \frac{\lambda_{ij}}{k} D_{ij} \mathcal{E}. \tag{56}$$

Taking into account that $\ln w_{ij}$ is linear in $\ln x_i$ and $\ln x_j$, then we wee that $\mathcal{E}$ can be chosen to be of the form

$$\mathcal{E} = E \sum_{i=0}^{n} \ln x_i, \tag{57}$$

where E is a positive constant.

The explicit expression for the energy fluxe for the first type of transition is are

$$\Phi_{ij} = b_{ij} E (s_j - s_i) \qquad i = 1, 2, \ldots, n. \tag{58}$$

For the second type of transition, it is given by

$$\Phi_{n+1,j} = -c_j E. \tag{59}$$

For the third type of transition, it is given by $\Phi_{0,n+1} = Eq\langle 1/x_0 \rangle$, which we write as

$$\Phi_{0,n+1} = E \frac{q}{s_0}, \tag{60}$$

Comparing these expressions with (45), (46) and bearing in mind the relation (54), we may choose λ_{ij}, $j \neq n+1$, to be all the same and equal to $\lambda = k/E$, that is,

$$\Psi_{ij} = -\lambda \Phi_{ij} \tag{61}$$

valid for all transitions, except $n+1 \to 0$, in which case the coefficient $\lambda_{0,n+1} = 0$ and $\Psi_{0,n+1} = 0$ but $\Phi_{0,n+1} \neq 0$ and given by (60).

The flux $\Phi_{0,n+1}$ given by (60) is the input of energy per unit time introduced into the ecosystem. Let us use the abbreviation $\varphi = \Phi_{0,n+1} = Eq/s_0$ for this quantity and the abbreviation Φ' for the sum of all the heat fluxes Φ_{ij}, except φ, so that

$$\Phi = \Phi' + \varphi. \tag{62}$$

If we multiply Φ' by $-\lambda$, we get the total entropy flux Ψ, that is

$$\Psi = -\lambda \Phi', \tag{63}$$

which follows from the relation (61). Therefore

$$\Psi = -\lambda(\Phi - \varphi). \tag{64}$$

In the stationary state $\Phi = 0$, and we reach the result

$$\Psi = \lambda \varphi. \tag{65}$$

Bearing in mind that $\varphi = Eq/s_0$ and that $\lambda = k/E$, we find

$$\Psi = k\frac{q}{s_0} > 0, \tag{66}$$

that is, the ecosystem is continuously producing entropy which is throwing away at a rate given by (66). We remark that the input of energy into the ecosystem

$$\varphi = E\frac{q}{s_0} \tag{67}$$

is also the heat flux *through* the ecosystem.

The flux of entropy given (66) as well the input of energy given by (67) are proportional to

$$\frac{q}{s_0} = \frac{Q}{M_0}. \tag{68}$$

This quantity is the rate at which organic matter is being produced by the plants divided by the mass of the plants, or the rate of creation of organic matter per unit mass of the plants.

4 Discussion and Conclusion

We presented a stochastic approach to the population dynamics as well as to the thermodynamics of ecosystems. The stochastic dynamics led to a description in terms of a master equation, which in turn was approached by a Fokker-Planck equation. In the present stochastic approach, the fluctuations in the populations of the several species are measured by a parameter ε which is inversely proportional to the total mass of the ecosystem. One could, for that matter, replace the total mass by any other quantity that measures the size of the ecosystem, such as the total number of individuals or the area of the ecosystem. Thus, a prediction of the stochastic approach is that if the area is small, the fluctuations will be relatively greater and the extinction by fluctuations will be more probable.

The dynamics are understood as a consequence of processes involving the several species that are analogous to chemical reactions. The creation of an individual of a certain species is analogous to an autocatalytic reaction. As a consequence, if for some reason the number of individuals of a certain species vanishes, then it becomes zero forever; that is, the species becomes extinct. With the deterministic approach, this occurs, for example, when the feeding rate constant associated with a species is decreased. Observing Fig. 3, if the parameter b is decreased, the apex carnivorous is extincted as one cross each one of the transition lines.

When ε is small, which we consider to be always the case, the equations for the main values of the number of individuals of each species coincide with the dynamic equations of the deterministic approach. Thus, we may understand the evolution of a population as given by the deterministic equations supplemented by the stochastic fluctuations. The fluctuations may lead to the extinction of a species, which is not the absolute type of extinction explained above and predicted by the deterministic approach. If by fluctuations the number of individuals vanishes, then the species becomes extinct, a type of extinction that we call extinction by fluctuations. If a small group of individuals of the extincted species is introduced, then the number of individuals may grow and the species is restored. In the case of the absolute extinction, this is not feasible, that is, the small group of individuals will disappear instead of growing.

A single main feature resulting from the present thermodynamic approach concerning a food web consisting of plants, animals, and environment is as follows. The plants transforms inorganic substances into organic matter through photosynthesis, inducing a flux of matter and energy across the ecosystem. Simultaneously, entropy is being generated and throwing away into the environment. The entropy flux to the environment Ψ, given by formula (66), and the input of energy per unit time to the ecosystem φ, given by (67), are both proportional to $q/s_0 = Q/M_0$, which is understood as the quantity of organic matter generated by the plants per unit time per unit mass of the plants.

Author Contributions Both authors contributed equally.

Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing Interests The authors declare no competing interests.

References

1. E. Warming, Oecology of plants: an introduction to the study of plant communities (Clarendon Press, Oxford, 1909)
2. A.G. Tansley, Ecology **16**, 284 (1935)
3. C. Elton, Anim. Ecol. (Macmillan, New York, 1927)
4. E.P. Odum, Fundamentals of ecology, (Saunders, Philadelphia, 1971)
5. R. MacArthur, Ecology **36**, 533 (1955)
6. E.P. Odum, Basic ecology (CBS College Publishing, New York, 1983)
7. R.E. Ricklefs, G.L. Miller, Ecology (Freeman, New York, 2000); 4th ed
8. R. Ricklefs, The economy of nature (Freeman, New York, 2008); 6th ed
9. R.T. Paine, American Naturalist **100**, 65 (1966)
10. R.M. May, Stability and complexity in model ecosystems (Princeton University Press, Princeton, 1973)
11. J. Maynard Smith, Models in ecology (Cambridge University Press, Cambridge, 1974)

12. S.L. Pimm, Food webs (Chapman and Hall, London, 1982)
13. P. de Ruiter, V. Wolters, J.C. Moore, Dynamic food webs: multispecies, assemblages, ecosystem development, and environment change (Elsevier, Amsterdam, 2005)
14. A.J. Lotka, Proc. Natl. Acad. Sci. **8**, 147 (1922)
15. A.J. Lotka, Elements Phys. Biol. (Williams and Wilkins, Baltimore, 1925)
16. V. Volterra, Leçons sur la Théorie Mathématique de la Lutte pour la Vie (Gauthier-Villars, Paris, 1931)
17. R. May, Math. Biosci. **12**, 59 (1971)
18. S.L. Pimm, Theoretical Population Biology **16**, 144 (1979)
19. S.L. Pimm, J.C. Rice, Theor. Popul. Biol. **32**, 303 (1987)
20. J.C. Moore, P.C. de Ruiter, H.W. Hunt, Science **261**, 906 (1993)
21. P.C. de Ruiter, A.-M. Neutel, J.C. Moore, Science **269**, 1257 (1995)
22. R.L. Lindeman, Ecology **23**, 399 (1942)
23. H.J. Morowitz, Energy Flow Biol. (Academic Press, New York, 1968)
24. I. Prigogine et J.M. Wiame, Experientia **2**, 451 (1946)
25. T. De Donder, L'Affinité (Gauthier-Villars, Paris, 1927)
26. I. Prigogine, Étude thermodynamique des phénomènes irreversibles (Desoer, Liège, 1947)
27. I. Prigogine, Introduction to thermodynamics of irreversible processes (Thomas, Springfield, 1955)
28. P. Glansdorff, I. Prigogine, Thermodynamic theory of structure, stability and fluctuations (Wiley, London, 1971)
29. G. Nicolis, I. Prigogine, Self-organization in nonequilibrium systems (Wiley, New York, 1977)
30. A.I. Zotin, R.S. Zotina, J. Theoret. Biol. **17**, 57 (1967)
31. R. Feistel, W. Ebeling, Studia Biophysica **86**, 237 (1981)
32. D. Assimacopoulos, Appl. Math. Modelling **10**, 234 (1986)
33. P. Auger, Dynamics and thermodynamics in hierarchically organized systems (Pergamon Press, Oxford, 1989)
34. C.G. Chakrabarti, S. Ghosh, S. Badhra, J. Biol. Phy. **21**, 273 (1995)
35. Y.M. Svirezhev, Ecol. Model. **132**, 11 (2000)
36. S.E. Jørgensen, Y.M. Svirezhev, Towards a thermodynamics theory for ecological systems (Elsevier, Amstgerdam, 2004)
37. K. Michaelians, J. Theor. Biol. **237**, 323 (2005)
38. C.G. Chakrabarti, K. Ghosh, Ecol. Model. **220**, 1950 (2009)
39. S.N. Nielsen, F. Müller, J.C. Marques, S. Bastianoni, S.V. Jørgensen, Entropy **22**, 820 (2020)
40. T. Tom, M.J. de Oliveira, Phys. Rev. E **82**, 021120 (2010)
41. T. Tom, M.J. de Oliveira, Phys. Rev. E **91**, 042140 (2015)
42. T. Tom, M.J. de Oliveira, J. Chem. Phys. **148**, 224104 (2018)
43. T. Tom, C.E. Fiore, M.J. de Oliveira, Phys. Rev. E **107**, 064135 (2023)
44. T. Tom, M.J. de Oliveira, J. Stat. Mech. (2024) 093202
45. J. Schnakenberg, Rev. Mod. Phys. **48**, 571 (1976)