

Mass and Energy Flow in Closed Ecosystems: Do Ecological or Mathematical Constraints Prevail?

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Hirata & Fukao (1977, *Math. Biosci.* **33**, 321–334) showed that the model of mass and energy flow in closed ecosystems presented by Ulanowicz (1972, *J. theor. Biol.* **34**, 239–253) and May (1973, *J. theor. Biol.* **39**, 155–163) was physically inconsistent and proposed an improved version of it. It is shown here that the model of Hirata and Fukao is also physically and ecologically inconsistent, and that the problem lies in the very methodology followed by these authors, which consists in letting the flows be determined by mathematical constraints on the allocation of mass and energy within the recipient trophic levels. A brief comparison between ecological and economic models is made in this respect.

An alternative framework to account consistently for coupled mass and energy flows in ecosystems is proposed, based on the principle that the allocation of mass and energy within the recipient trophic levels is subject to the constraints of coupling between mass and energy.

Introduction

The coupling of matter and energy flows is a fundamental feature of ecosystems (Morowitz, 1968). Most ecosystem models, however, describe a single type of flow, either of matter (nutrient) or of energy. Ulanowicz (1972) and May (1973) presented a model of mass and energy flow in closed ecosystems dealing explicitly with the aspect of coupling. Although mathematically elegant, the model was shown by Hirata & Fukao (1977) to be physically inconsistent, since mass actually circulated in the wrong direction under stable equilibrium conditions, that is, when the specific energy of the various trophic levels increased along the food chain. Hirata and Fukao then proposed a modified model which corrected this inconsistency essentially by adding a nutrient pool with zero energy. Although the energy content of the nutrient pool is likely not to be exactly zero (some energy remains bounded to decomposition products), it is very close to zero indeed (e.g. Finn, 1980), and this basic property of ecosystems is evidently a necessary counterpart to the absorption of energy by auto-

trophs. In Ulanowicz and May's model, there was a contradiction between the fact that energy was absorbed in the autotroph compartment and the fact that energy was more and more concentrated along the food chain and then fed back to the autotrophs; their model resolved this contradiction by letting matter flow in the opposite direction, i.e. down the food chain.

Hirata and Fukao's solution was free of this obvious physical mistake, and was subsequently followed in a few other model studies (Hirata, 1980a; Koukios *et al.*, 1987). Hirata and colleagues (Hirata & Fukao, 1978; Hirata, 1979, 1985; Hirata & Sugai, 1988) applied the same methodology in the field of economy with models of production processes. Although such models have never been applied as they stood to real data, they have important implications for the functioning and organization of ecosystems, for they suggest general constraints on such features as the specific energies, respiration rates or biomass ratios of successive trophic levels (May, 1973).

However, it is shown in this paper that Hirata & Fukao's (1977) (hereafter H-F) ecosystem model is

also physically and ecologically inconsistent, and that the problem lies in the very methodology originally put forward by Ulanowicz (1972), which they preserved in their model. Differences in that respect between ecological and economic models are briefly discussed, and finally a consistent framework for the formulation of coupled matter and energy flows in ecosystems is proposed.

Physical and Ecological Inconsistency of the H-F Model

The methodology followed by Ulanowicz, May, and H-F to derive their models is simple in its principle, and can be summarized by the three following steps.

(i) The model is formulated in terms of coupled equations for mass and energy flows. In the H-F model, these have the form:

$$\frac{dM_i}{dt} = \gamma_i m_{i-1,i} - m_{i,i+1} - (p_i M_i + q_i M_i^2) + (\varepsilon_i - s_i) M_i \quad (1)$$

$$\frac{dE_i}{dt} = \gamma_i e_{i-1,i} - e_{i,i+1} - \lambda_i (p_i M_i + q_i M_i^2) + (\sigma_i - r_i) M_i \quad (2)$$

where M_i and E_i are the mass and energy, respectively, contained in trophic level i ($i > 0$), and $m_{i,j}$ and $e_{i,j}$ are the mass and energy flows, respectively, from level i to level j .

In these equations, the first term represents the food assimilated and is associated with a coefficient of assimilation efficiency γ_i ($0 < \gamma_i \leq 1$); the second term represents the losses to the next trophic level; the third term represents a density-dependent death rate; and the fourth term represents the exchanges with the nutrient pool (for mass) or the external world (for energy) associated with energy fixation (σ_i) and respiration (r_i); thus, $\sigma_1 = \sigma > 0$ for level 1 (autotrophs) but $\sigma_i = 0$ for all other levels (heterotrophs), and ε_i and s_i are the rates at which mass (under the form of oxygen, carbon dioxide, etc) flows in and out during these processes.

Dynamical equations for level 0 (nutrient pool) are unnecessary since the ecosystem is assumed to be closed with respect to matter and the energy of level 0 is assumed to be zero. Thus systems (1-2) need only be completed by the following equations:

$$\sum M_i = Q \quad (3)$$

$$E_0 = 0. \quad (4)$$

(ii) Each trophic level is assumed to have a constant specific energy or energy content per unit mass λ_i . Energy and mass are thus related by:

$$E_i = \lambda_i M_i \quad (5)$$

$$e_{i-1,i} = \lambda_{i-1} m_{i-1,i}. \quad (6)$$

(iii) After multiplication of (1) by λ_i , the two equations (1) and (2) must be equivalent. Setting the right-hand sides of (1) and (2) equal to each other, and using (5) and (6), leads to the equation:

$$\gamma_i \lambda_{i-1} m_{i-1,i} - r_i M_i = \gamma_i \lambda_i m_{i-1,i} - \lambda_i (s_i - \varepsilon_i) M_i, \quad (7)$$

which H-F then solve for the flow $m_{i-1,i}$. Thus:

$$m_{i-1,i} = a_i M_i, \quad (8)$$

where

$$a_i = [\sigma - r_i - \lambda_i (\varepsilon_i - s_i)] / \lambda_i \quad (9)$$

$$a_i = [\lambda_i (\varepsilon_i - s_i) - r_i] / [\gamma_i (\lambda_i - \lambda_{i-1})] \quad (i > 1). \quad (10)$$

Equation (8) tells us that the mass flow from one trophic level to the next is a linear function of the mass of the recipient trophic level. To ensure that the flow rate a_i as given by eqn (10) be positive, H-F further formulate the so-called "energy condensing condition":

$$\lambda_i (s_i - \varepsilon_i) > r_i, \quad (11)$$

which in turn requires that $\lambda_i > \lambda_{i-1}$, that is, specific energy must increase as one goes up the trophic ladder.

From an ecological point of view, the outcome of the H-F model under the form of eqns (8) and (10) appears pathological in several respects.

(i) As in the case of Ulanowicz's or May's model, this model leads to strictly linear recipient-controlled flows between trophic levels. If this result were correct, it would condemn virtually all ecosystem models developed so far, which are usually based on donor-controlled, or at least shared donor-recipient-controlled, flows. A considerable body of empirical evidence and theoretical arguments has led to the conclusion that the control of trophic interactions is shared and variable (e.g. Odum & Biever, 1984; McQueen *et al.*, 1986; Hunter & Price, 1992; Power, 1992), and that donor control may be a good approximation in ecosystems near equilibrium (e.g. Patten, 1975; Strong, 1992). The H-F model is unable to accommodate this elementary ecological realism.

(ii) Again as with Ulanowicz's or May's model, this model is structurally unstable for changes in the specific energy λ_i near $\lambda_i = \lambda_{i-1}$, where flows become indeterminate [eqn (10)]. While there is some tendency towards increasing specific energies up the food chain, it is certainly unreasonable to expect this tendency to

be verified in all cases and for all species. The basic assumption of a constant specific energy for each trophic level is itself no more than a convenient abstraction, since specific energy is likely to vary among species, or even individuals, as well as in time, as a result of variations in chemical composition (in particular, varying amounts of lipids, sugars and proteins). Any realistic model should be robust against such variations.

(iii) As H-F showed, the stability of the model depends critically on the density-dependent parameters q_i . Again this shows a weakness of the model—most ecosystem models do not need an additional density dependence to be stable. Linear donor-controlled models, for instance, are always stable (Hearon, 1968; Mazanov, 1976). This weakness is a consequence of the first one: it is well known that recipient control is destabilizing, and thus density-dependent terms were added *ad hoc* to stabilize an otherwise unstable model.

These obvious weaknesses are all the more alarming since they are not found in models of material flows in closed ecosystems, as Nisbet & Gurney (1976), Parker (1978), Nisbet *et al.* (1983), or Hirata (1980*b*) himself showed. Why would coupling with energy flows lead to such discrepancies? The cause lies again in a physical inconsistency in the model, which appears in eqn (7).

(i) *Either* the mass and energy balance implied in (1) and (2) is correct, and then eqn (7) is incorrect. In the description of their model, H-F associate the fourth term in both eqns (1) and (2) with respiration. But then the mass and energy flows associated with respiration must match each other, that is:

$$r_i M_i = \lambda_i (s_i - \varepsilon_i) M_i, \quad (12)$$

and eqn (7) reduces to:

$$\gamma_i \lambda_{i-1} m_{i-1,i} = \gamma_i \lambda_i m_{i-1,i}, \quad (13)$$

which is a contradiction since H-T assume that $\lambda_i \neq \lambda_{i-1}$.

(ii) *Or* equation (7) is correct, and then the mass and energy balance implied in (1) and (2) is incorrect. In this case, there is an excess mass flow equal to $\gamma_i (1 - \lambda_{i-1}/\lambda_i) m_{i-1,i}$, which must either return directly to the nutrient pool or be compensated for by a decrease in the respiration rate. It is the latter alternative that H-F assume implicitly with their so-called "energy condensing condition" (11), which seems to imply that the excess mass flow is subsumed under the term $s_i - \varepsilon_i$ (or that r_i is reduced accordingly). But if that is the case, $s_i - \varepsilon_i$ (or r_i) can no longer be considered constant, and eqn (7) must be regarded as

the equation expressing the dependence of $s_i - \varepsilon_i$ (or r_i) on $m_{i-1,i}$ and M_i . Thus eqn (7) has to be solved for $s_i - \varepsilon_i$ (or r_i) instead of $m_{i-1,i}$.

The conclusion of the above is that the *a priori* mathematical constraints imposed on the allocation, at each trophic level, of the mass and energy flow coming from the lower trophic level among the categories of non-assimilated food, material losses and respiration lead to a physical contradiction when $\lambda_i \neq \lambda_{i-1}$. This physical contradiction can only be removed when at least one of these mathematical constraints is relaxed, that is:

- (i) γ_i for the mass flow [eqn (1)] is different from that for the energy flow [eqn (2)];
- (ii) and/or the material loss rate per unit mass ($s_i - \varepsilon_i$) is not constant;
- (iii) and/or the respiration rate per unit mass (r_i) is not constant.

Elementary physiological mechanisms ensure that these constraints are relaxed in actual fact. Digestion is a complex and selective process during which only part of the ingested substances are assimilated with their associated chemical energy. That part which is not assimilated is egested with a specific energy that is different from that of the food consumed. Thus assimilation efficiency is not the same in terms of mass and in terms of energy; it depends on the chemical nature of the substances assimilated. Also, respiration is a complex phenomenon involved in the homeostatic response of organisms to their environment; it varies depending on the balance of energy exchanges in all forms, including radiation, heat of evaporation, etc (Månsson & McGlade, 1993). Therefore it is unlikely to occur at a constant rate per unit mass.

In fact, this is implied in the H-F model itself, although H-F avoid facing the problem. A density-dependent death term is contained in eqns (1) and (2); but the dead biomass has to be freed from its energy through respiration by decomposers before returning to the nutrient pool. This non-linear respiration term, which would be hard to reconcile with the linear flows coming out of the model, is simply ignored in the model, which does not include decomposition explicitly. This is an additional flaw of the H-F model, which lacks an energy balance at the ecosystem level. At equilibrium, the total respiration in the ecosystem should balance the energy absorbed by photosynthesis, a feature that is not explicitly present in the H-F model.

The above has an implication that is fatal to the very methodology followed by Ulanowicz, May and H-F in their models: *the equivalence between the*

coupled mass and energy flow equations [eqns (1) and (2)] cannot be used to determine the flows $m_{i-1,i}$. This equivalence simply ensures a correct coupling between the allocations of mass and energy at each trophic level, and therefore should be used instead to express the constraints linking assimilation, material losses and respiration for a given flow $m_{i-1,i}$.

This conclusion is consistent from an ecological point of view. The models of Ulanowicz, May and H-F imply that all mass and energy flows in ecosystems are determined by mathematical constraints on the allocation of mass and energy within the recipient trophic levels, which turns reality upside down. They picture ecosystems as some sort of chemical engineering device in which the trophic levels have fixed characteristics that determine the flows from below. The present conclusion, which puts reality right again, is that, for a given mass and energy flow from the lower trophic level, the coupling between mass and energy imposes some ecological constraints on their allocation within the recipient trophic level. Ecosystems are living systems in which flows are determined by complex biological interactions between organisms, and recipient trophic levels must be able to adapt to independently fluctuating flows, which are the rule in nature. Although the allocation of mass and energy within recipient trophic levels is subject to some basic physiological constraints, such as a minimum level of respiration due to basal metabolism, it must be flexible enough to adjust to variable flows, in particular under the form of variable respiration rate and assimilation efficiency.

A Brief Comparison Between Ecological and Economic Models

Since the very methodology followed by H-F in their ecological model was shown to be incorrect, an obvious question that poses itself is whether the economic models of production processes that Hirata and colleagues (Hirata & Fukao, 1978; Hirata, 1979, 1985; Hirata & Sugai, 1988) developed suffer from the same deficiencies. Ironically, although they were built after the principle of the ecological model, these models turn out to provide acceptable solutions. How can the same methodology deliver such contrasting results? Although a detailed discussion of the economic models is beyond the scope of the present paper, a brief comparison between the ecological and economic models is interesting to help understand the basic differences between ecosystems and economic systems.

Hirata & Sugai (1988) formulated an abstract flow-based model which is suitable for that purpose, and which is rewritten here as:

$$\frac{dM_i}{dt} = m_{i-1,i} - m_{i,i+1}$$

$$\frac{dE_i}{dt} = e_{i-1,i} - e_{i,i+1} + \phi_i(M_1, \dots, M_n),$$

where $\phi_i(M_1, \dots, M_n)$ represents the exchange of energy with the external world. For the sake of clarity, the variables mass and energy have been kept, but in Hirata & Sugai (1988) mass could be replaced by anything that circulates within the system, and energy could be replaced by anything that flows through the system. This system describes a closed chain, and basically reduces to a generalized version of Ulanowicz's and May's model.

Applying exactly the same recipe as above, and under the same assumptions (5) and (6), Hirata & Sugai (1988) derive the flows as:

$$m_{i-1,i} = \phi_i(M_1, \dots, M_n) / (\lambda_i - \lambda_{i-1}).$$

In the case of a production process, more work or energy is added at each production stage, so that $\phi_i(M_1, \dots, M_n)$ is positive and the value or energy content of a unit mass necessarily increases, i.e. λ_i is always greater than λ_{i-1} . Therefore eqn (15) is always physically consistent. By comparison, in the case of an ecosystem, more energy is dissipated at each trophic level, so that $\phi_i(M_1, \dots, M_n)$ is negative and mass flows in the wrong direction if $\lambda_i > \lambda_{i-1}$, as it happened in Ulanowicz's and May's model.

The physical consistency of eqn (15) in the case of a production process does not guarantee its economic consistency, however. This equation could as well be reversed and, for instance, express ϕ_i as a function of $m_{i-1,i}$. This would be an ecologically more consistent formulation of the equation in an ecosystem model, where respiration should be expressed as a function of the flow rather than the reverse, as is argued above. The real question is to identify the dependent and independent variables in the equation. Under the present mode of production, the economic production process consists in the production of an additional value through the incorporation of work in a certain quantity of materials. The initial quantity of materials and its associated value, and the working force and its associated value, are given at the onset of the production process, while the value of the products at the end of the process is a variable. Therefore, the main dependent variable in eqn (15) should actually be λ_i . This is basically what Sushil (1991)

proposed, although with a different methodological approach.

Consistent Formulation of Coupled Mass and Energy Flows in Ecosystems

Here a consistent formal framework is outlined, to account for coupled mass and energy flows in ecosystems, based on the ecologically reasonable principle that the allocation of mass and energy within the recipient trophic levels, not the flows from the lower trophic levels, is subject to the constraints of coupling. To that end, a model for the closed food-chain ecosystem examined by May and H-F is reformulated.

It must be understood that no ecosystem is perfectly closed and that reduction of its complex trophic structure to a simple food chain is by no means trivial (Burns, 1989). Both the assumption of a closed material cycle and the classical food-chain metaphor introduced by Lindeman (1942) are taken up here because they lead to transparent model formulation and results. For the sake of simplicity, it is also assumed that each trophic level includes its associated decomposition process. Modelling the latter explicitly is possible, but requires particular assumptions on the specific energies of the biomasses delivered by the various trophic levels to the decomposition processes and makes the constraints imposed by the coupling of mass and energy flows less transparent. These complexities are unnecessary for the present purpose, which is to present a methodological framework rather than a detailed model of a particular ecosystem. The same methodology can be applied to any other system configuration.

Månsson & McGlade (1993) have recently called attention to more fundamental problems in the reduction of ecological processes to energy flows due to the various forms and uses of energy in ecosystems. A detailed examination of these problems is beyond the scope of the present paper; in the present context it suffices to notice that it is both conceptually and empirically possible to distinguish the chemical energy that is associated with material flows in trophic interactions from other energy sources, since heterotrophs (unlike autotrophs) are unable to transform radiation or heat into other forms of energy. It is common practice to consider only that energy which comes from ingested food in an animal's energy budget, and we may make the same restriction in ecosystem models, as has been implicit in previous works.

The model is as follows:

$$\frac{dM_1}{dt} = m_{0,1} - m_{1,2} - m_{1,0} \quad (17)$$

$$\frac{dM_i}{dt} = \gamma_i m_{i-1,i} - m_{i,i+1} - m_{i,0} \quad (2 \leq i \leq n) \quad (18)$$

$$\sum M_i = Q \quad (19)$$

$$\frac{dE_1}{dt} = \Phi - e_{1,2} - r_1 \quad (20)$$

$$\frac{dE_i}{dt} = e_{i-1,i} - e_{i,i+1} - r_i \quad (2 \leq i \leq n)$$

$$E_0 = 0,$$

with $m_{n,n+1} = e_{n,n+1} = 0$.

In this model, n is the number of trophic levels, level 0 is the nutrient pool, level 1 represents the autotrophs, levels $i > 1$ represent the heterotrophs, Φ is the flow of energy fixed by photosynthesis, r_i is the flow of energy dissipated by respiration, and all the other variables and parameters are as in the H-F model above. Note that a fraction $(1 - \gamma_i)$ of the mass flow from trophic level $i - 1$ returns directly to the nutrient pool, but that the totality of the energy flow is respired by the heterotrophs, as required by (22).

The overall mass balance is ensured by the conservation relation (19), and the overall energy balance is respected, since

$$\frac{d\left(\sum_i E_i\right)}{dt} = \Phi - \sum_i r_i$$

Thus, at equilibrium, the total respiration in the ecosystem balances the energy absorbed by photosynthesis, as it should.

Using (5) and (6), the equivalence between the mass- and energy-flow equations for each trophic level leads to the following constraints:

$$r_1 = \Phi - \lambda_1(m_{0,1} - m_{1,0}) \quad (24)$$

$$r_i = (\lambda_{i-1} - \lambda_i \gamma_i)m_{i-1,i} + \lambda_i m_{i,0} \quad (2 \leq i \leq n) \quad (25)$$

These constraints say that:

- (i) the respiration of autotrophs (and their associated decomposers) must balance the difference between the energy fixed by photosynthesis and the energy contained in the primary production transferred to the upper trophic levels;
- (ii) the respiration of heterotrophs at each trophic level (and their associated decomposers) must balance the total energy contained in the matter that is not assimilated and the matter that is remineralized.

These constraints are ecologically quite reasonable and transparent.

One further constraint is nested in (25), for the first term in the right-hand side of (25) must be non-negative to have any physical meaning. Therefore, it is necessary that:

$$\lambda_i/\lambda_{i-1} \leq 1/\gamma_i \quad (26)$$

This inequality sets an upper limit on the increase in specific energy as mass ascends the trophic chain. This result again makes sense from a thermodynamical point of view: as energy is progressively dissipated along the food chain, any concentration of energy per unit mass must be performed against the thermodynamical tendency towards dissipation of energy. Thus such a concentration in ecosystems results from an active biological process, not from a passive thermodynamical constraint as implied in Ulanowicz's, May's and H-F's models.

It must be stressed that the constraints (24) and (25) are quite general and independent of the particular form of the flows between trophic levels. As an example, assume that the λ_i s and γ_i s are constant and the flows are linear donor-controlled. Equation (25) then says that respiration at any trophic level occurs in part at a constant rate per unit mass due to intrinsic characteristics of that trophic level [the second term in the right-hand side of (25)], but also adjusts in part to flows determined by the lower trophic level [the first term in the right-hand side of (25)]. The qualitative difference between these two terms, however, will manifest itself only in the dynamical properties of the system away from equilibrium. At equilibrium, the masses of all trophic levels are proportional to each other in a linear donor-controlled system; therefore even the first term in the right-hand side of (25) will appear as a linear term in M_i , and the whole of respiration will appear as occurring at a constant rate per unit mass.

In conclusion, the approach presented here to model coupled mass and energy flows in ecosystems is both ecologically consistent and flexible, and thus avoids the critical weaknesses of the previous models developed by Ulanowicz, May and H-F. The model examined as an illustration of this methodology, however, rests on several simplifying assumptions. The challenge is now to apply this approach to actual ecosystems. I suspect that such an exercise would bring to light insufficiencies in our knowledge of some basic ecological processes, in particular the dynamics of animal energy budgets, and would thus stimulate the development of a better understanding of the functioning of ecosystems.

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