



# Thermostatistical distribution of a trophic energy proxy: Extension for modelling energy pyramids at the inter-taxocene scale and under non-stationary conditions



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## ABSTRACT

The theory of food chains, and therefore the assembly and modifications of trophic pyramids depending on environmental influences, is an essential part of modern ecosystem ecology. A general model of energy pyramids based on a fruitful but simple analytical connection between ecology and conventional physics has been proposed by Rodríguez et al. (2015a). However, this model has several drawbacks. Among them: it has only been tested for isolated taxocenes and under stationary ecological conditions (SEC). Besides, it has not been tested if the internal distribution of typical species groups within the obtained pyramids follows the expected pattern according to the well-known trophic habits of these typical groups of species. This article starts with a brief summary of the most relevant drawbacks of our conventional point of view about trophic pyramids in order to highlight the differences, as well as the advantageous coincidences, of the above-mentioned new model in comparison with our orthodox point of view about trophic pyramids. This summary connects with a description of the obstacles that should be surpassed in order to develop a more general model (i) valid at the inter-taxocene scale and (ii) fully useful to model systems under non-stationary ecological conditions (NSEC). The article proposes two simple mathematical modifications of the original model in order to achieve items (i) and (ii). In subsequent sections, the effectiveness of these modifications is tested by using field data from 25 samplings belonging to 6 different taxocenes, by including a majority of zooplankton data from a human-made highly eutrophic reservoir (Acton Lake; Hueston Woods State Park, Ohio, U.S.A.) with frequent and contingent episodes of NSEC. According to our results, it is not possible to reject either the hypothesis about the validity of modifying the original equation to model ecosystems as a whole under NSEC or the hypothesis that typical species groups follow a distribution within their respective pyramid in agreement with the expected pattern according to their trophic habits. In summary, this article is an additional step in favor of the usefulness of rescuing and expanding the original epistemological roots of ecosystem ecology in connection with conventional physics.

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## 1. Introduction and theoretical foundation

*1.1. Conventional insight about ecological pyramids from the point of view of physics, and its methodological consequences to obtain reliable quantitative models*

Every ecosystem is a sort of metastable "bubble" of high levels of ecological information (species diversity) and low internal entropy,

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surrounded by a cosmic ocean of entropy due to the pro-entropic influence of the second law. The basic requirement to keep such bubbles open everywhere is a constant flow of high quality energy that is degraded to sustain a given amount of standing biomass and intensity of dispersal activity, understood as a combination of individual dispersal and reproduction at the population scale. That is to say, ecosystems are far-from-equilibrium open systems.

Disregarding the particular internal differences between ecosystems, we obtain two general types of possible energy flow conditions: (a) Energy input (in J/s)  $\neq$  energy output (non-stationary ecological conditions: NSEC). (b) Energy input = energy output (stationary or quasi-stationary ecological conditions: SEC). Under SEC, the state variable values of the system do not change over time. This is the most important requirement for physical equilibrium (Callen, 1985, p. 13). As a result, SEC is equivalent to an open equilibrium (Montero and Morán, 1992). This implicitly means that many principles and methods of conventional physics (i.e., classical thermodynamics as well as Newtonian mechanics and its application to thermodynamics in the form of statistical physics, aka thermostatics) are fully valid to explain important topics of ecosystem functioning (e.g.: Rodríguez et al., 2012, 2013a,b).

The above-mentioned energy flow is essential from the genetic, evolutionary and ecological point of view. So, the ecosystem have been regarded (e.g., Margalef, 1968) as the functional unit of the biosphere and, therefore, as the essential study unit of ecology. This has had a strong influence on ecology development. It is possible to assert that modern ecology was born from a combination of several clusters of concepts at the ecosystem level; for example: life-history theory either in its original (Elton, 1927) or in its more modern and interdisciplinary version (MacArthur and Wilson, 1967; Pianka, 1970; Reznick et al., 2002); ecological niche, food chains and pyramid of numbers (Elton, op. cit.); trophodynamics itself (Lindeman, 1942), as well as the earliest proposals about species diversity and its measurement as a key issue to understand ecosystem dynamics (MacArthur, 1955; Margalef, 1957). The final classic effort in this field was performed by some reference publications (e.g., Margalef, 1963; Odum, 1968, 1969) aimed to achieve the integration of all these concepts based on the ecological effects of energy flow. Paradoxically, this approach centered in energy and interdisciplinary links between biology and physics is not in the mainstream of ecological thinking right now. This situation is a sort of contradiction with the fact that ecological pyramids deploy a fractal and omnipresent behavior based on the equivalent role of food chain dynamics, which can be regarded as the central theory of ecology (Fretwell, 1987). Perhaps, the above-mentioned circumstances explain some of the well-known epistemological difficulties for ecology advancement in the last decades (e.g., Lawton, 1999; Belovsky et al., 2004; Scheiner, 2013).

However, even the classical understanding based on typical ecological pyramids with only four trophic levels has some methodological difficulties whose analytical effect seems to have been neglected by conventional ecology. For example, "the concept of trophic level is not primarily applicable to individual species . . . it is important to emphasize that the concept of trophic level is not primarily intended for categorizing species. Energy flows through the community in stepwise fashion due to the second law of thermodynamics, but a given population of a species may be (and very often is) involved in more than one step or trophic level" (Odum, 1968, pp. 11, 13). Furthermore, conventional pyramids are constructed according to a categorical or nominal statistical scale (i.e., the ordination criterion is a qualitative one: who eats who) of very low trophic resolution resulting in that, for example, ants, locusts, nectarivorous bats, rabbits, buffaloes and elephants are all of them exactly at the same energy level (herbivores or primary consumers). But this generalization offers a very coarse trophodynamic classification that is hardly acceptable in terms of quantitative energy measures.

The above-mentioned categorical distribution secondarily becomes an ordinal scale, that is to say, that the higher the trophic level the larger and less available the energy amount per individual. This could be a better and more accurate quantitative criterion to model ecological pyramids. Unfortunately, it is only a secondarily-derived assumption with greater difficulties for being assessed in practice (i.e., starting from quantitative field data) within the methodological framework of orthodox ecology. In addition, conventional ecological pyramids are of three main types: number, biomass and energy pyramids. But, if the pyramid shape really depends on energy dissipation due to the influence of second law, then any type of ecological unit or indicator distributed by following an energy gradient could deploy a similar behavior at any scale.

Finally, given the fractal structure of ecosystems (Brown et al., 2002; Miller, 2008), we get trophodynamic insights from samples selected according to certain criteria trusting that the more inclusive structure is reflected in the composition of these selected parts (Margalef, 1963, p. 358). So, a simple question emerges: How does a general fractal spectrum of several concurrent taxocenes can be linked to each other in order to get quantitative models of ecological pyramids at the inter-taxocene scale? After all, starting from the previous quote from Odum (1968, pp. 11, 13), an ecological pyramid is a graphical representation that unifies many food chains in a quite simple arrangement by "diluting" the underlying real structure of a given food web. The set of issues analyzed in this section could explain those difficulties linked to obtain a reliable and reproducible quantitative model of ecological pyramids.

### 1.2. Summary of a recent attempt of "epistemological rescue" starting from physics, and its link with the hypotheses of this work

According to Rodríguez et al. (2012), it is possible to use an advantageous proxy (because it does not require direct energy measurements, and it is in simultaneous agreement with well-known principles of ecology and physics; see Rodríguez et al., 2013a,b) of total trophic energy per plot:

$$E_{eTp} = N_p \cdot E_{ep} = N_p \left( \frac{1}{2} m_{ep} \cdot I_e^2 \right) \quad (1)$$

where  $E_{eTp}$ : total eco-kinetic energy per plot in ecoJoule ( $J_e$ :  $\text{kg} \cdot \text{d}^2$ ; where  $\text{d}$ : dispersal units, the unit in which  $I_e$  is expressed);  $N_p$ : total number of individuals per plot;  $E_{ep}$ : mean eco-kinetic energy per individual per plot;  $m_{ep}$ : mean fresh standing biomass per individual per plot, and  $I_e$ : an indicator of dispersal activity intensity with the appropriate statistical features to homeomorphically replace physical velocity ( $v$ ) in the classical equation to assess mechanical kinetic energy ( $E = \frac{1}{2} m \cdot v^2$ ; see structural equivalence between  $E$  and  $E_{ep}$ ).

Additionally, according to Rodríguez et al. (2015a), the Boltzmann distribution of molecular energy values in the equilibrium state (Eq. (2); Aguilar, 2001) can be transformed to an analogue equation (Eq. (3)) to describe the observed distribution of  $E_{eTp}$  under SEC:

$$N_i = \left( \frac{N}{\sum_{\varepsilon_i=0}^{\varepsilon_i=x} e^{-\varepsilon_i/k_B T}} \right) \cdot e^{-\varepsilon_i/k_B T} \quad (2)$$

where  $N$ : total number of molecular kinetic energy values ( $E$ , see above) included in the observed distribution;  $k_B$ : Boltzmann's constant ( $1.3806504 \times 10^{-23}$  J/K/molecule);  $T$ : temperature in Kelvin;  $e$ : Euler's number 2.71828;  $N_i$ : number of  $E$  values associated to  $\varepsilon_i$ ;  $\varepsilon_i$ : lower limit of the class of  $E$  values for which the expected value of  $N_i$  is calculated. The term  $\sum \exp. -\varepsilon_i/k_B T = Z$  (Eq. (2)) is

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