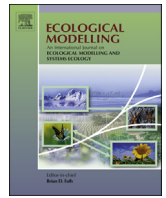




ELSEVIER

Contents lists available at [ScienceDirect](http://www.sciencedirect.com)

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Thermostatistical distribution of a trophic energy proxy with analytical consequences for evolutionary ecology, species coexistence and the maximum entropy formalism



Ricardo A. Rodríguez^{a,*}, Ada Ma. Herrera^a, Rodrigo Riera^b, Juan D. Delgado^c,
 Ángel Quirós^d, María E. Perdomo^d, Jacobo Santander^e, Jezahel V. Miranda^e,
 María J. Fernández-Rodríguez^c, Antonia Jiménez-Rodríguez^c,
 José Ma. Fernández-Palacios^f, Rüdiger Otto^f, Carlos G. Escudero^f,
 Rafael M^a. Navarro-Cerrillo^g

^a 6203, Apartment A, Lucy Street, Tampa, FL 33619, USA

^b Centro de Investigaciones Medioambientales del Atlántico C.I.M.A., C/Arzobispo Elías Yanes n° 44, La Laguna, Tenerife, E-38206, Spain

^c Departamento de Sistemas Físicos, Químicos y Naturales, Facultad de Ciencias Experimentales, Universidad Pablo de Olavide, Sevilla E-41013, Spain

^d Parque Nacional Los Caimanes, Carretera Central n° 716, Santa Clara CP-50100, Cuba

^e Parque Nacional Sistema Arrecifal Veracruzano, C/Juan de Grijalva n° 78, Veracruz, Mexico

^f Departamento de Parasitología, Ecología y Genética, Universidad de La Laguna, Tenerife E-38071, Spain

^g Escuela Técnica Superior de Ingenieros Agrónomos, Universidad de Córdoba, Dpto. Ingeniería Forestal, Avda. Menéndez Pidal s/n°, Apdo. 3048, Córdoba 14080, Spain

ARTICLE INFO

Article history:

Received 14 July 2014

Received in revised form 10 October 2014

Accepted 10 October 2014

Available online xxx

Keywords:

Ecosystem ecology
 Ecological state equation
 Ecological pyramid
 Food chain
 Partition function
 Physics

ABSTRACT

Conventional thermodynamics and statistical mechanics deal with the study of physical systems under equilibrium conditions (EC). Internal EC at a temperature that differs from the environment temperature are sustained, in general, by some type of artificial boundaries imposed with research aims or with quotidian utility goals in many kind of domestic appliances; the typical example of academic lab is a closed system immersed in a thermal bath which keeps the temperature constant. However, the ecosystem is a far-from-EC open system. Therefore, conventional thermodynamics and statistical mechanics tend to be orthodoxly regarded as limited to explain the ecosystem functioning since, at the first glance; there seem to be several essential functional differences between it and the previously-mentioned kind of physical systems. This viewpoint averse to conventional physics is paradoxical in regard to the current ecological paradigm given the fully thermodynamic foundation of ecosystem ecology. However, additional evidence in favor of the usefulness of conventional physics to describe the ecosystem functioning have recently been published, pointing out to the possibility that the analytical approach to ecology based on our undergraduate knowledge of physics, unfortunately, could have been hastily neglected before producing its most valuable results. This paper, fully based on the above-mentioned evidence, performs an unavoidable additional step in order to complete such a proposal by showing that the Boltzmann distribution of molecular energy values can be simply and successfully adapted to model the distribution of values of a proxy for trophic energy across an increasing gradient of energy levels, in a very similar fashion to that of a standard trophic pyramid. Starting from this result and by using a balanced combination between plausible theoretical considerations and abundant empirical data, we analyze why this approach is in agreement with well-known ecological principles, at the same time that we explore the general empirical advantages and aftermaths derived from this suggestion. Finally, the article explores the usefulness of the thermo-statistical modeling of eco-kinetic energy per plot to understand those essential physical factors that: promote biological evolution, facilitate species coexistence, can explain the holes in the fossil record, and enhance our current viewpoint about the ecological meaning of entropy. In summary, this article provides simply understandable additional information that indicates, despite its far-from-EC nature, any natural ecosystem is not far away from the most orthodox principles of conventional physics.

© 2014 Elsevier B.V. All rights reserved.

* Corresponding author. Tel.: +1 786 479 6354.

E-mail address: arodveg@gmail.com (R.A. Rodríguez).

1. Introduction

Trophodynamics is an essential part of conventional theoretical ecology (e.g., Lindeman, 1942; Odum, 1968; Fretwell, 1987). Nevertheless, it has been regarded as empirically difficult from its very beginning (Elton, 1927, p. 70). In practice, 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).

The role of trade-offs (e.g., Ben-Hur et al., 2012; Rodríguez et al., 2013a) to support species coexistence (Tilman, 2000) reveals the influence of gradients that keep the energy flow. Such gradients are reflected in typical statistical distributions useful as indicators of underlying patterns. This yields a fruitful analytical sequence: gradients to sustain energy flows → trade-off via adaptive responses → distributions that reflect patterns far away from statistical uniformity. Therefore, a lot of effort have been devoted to study statistical distributions in ecology, e.g.: (a) energy, biomass and abundance distributions along a decreasing ordinal gradient of energy availability (i.e., the well-known trophic pyramids); (b) species-abundance distribution (e.g., Banavar et al., 2010; Sonnier et al., 2010) and (c) distribution of groups of sites over shared species (e.g., Kelly et al., 2011).

However, there is a break in continuity from (a–c): our orthodox understanding of trophic pyramids is based on conventional thermodynamics; meanwhile the more recent proposals (b–c) are based on non-conventional approaches, as the maximum entropy formalism (MaxEnt) initially proposed to develop a “subjective statistical mechanics . . . independently of any physical argument, and in particular independently of experimental verification” (Jaynes, 1957, p. 620).

MaxEnt has been broadly used to explore and forecast statistical distributions (additional examples: Shipley et al., 2006; Williams, 2010) despite its limitations (e.g., Marks and Muller-Landau, 2007; Haegeman and Loreau, 2008 Yackulic et al., 2013). This paradoxical combination of successes and drawbacks is normal in developing approaches; even so, it highlights the importance of developing alternative proposals.

Any model not based on classical statistical mechanics lies in a simple idea: classical statistical mechanics describes equilibrium closed systems, but the ecosystem is a far-from-equilibrium open system; that is why ecologists must avoid the negative effects from the analytical trap of the closed systems (Margalef, 1991, pp. 884, 894–895, 904–905) because “conventional physics is of little help in describing how ecosystems develop” (Ulanowicz, 2004, p. 341).

Nevertheless: (a) time-independence is the main requirement for equilibrium (Callen, 1985 p. 13) and state variables do not change with time neither under equilibrium nor under stationarity in open systems. (b) Stationarity involves gradients that are absent in equilibrium but, with constant gradients, the exchange system ↔ environment does not imply change since stationarity is equivalent to an “open equilibrium” (energy gains ≈ energy losses). (c) The standard thermostatical approach regarding ideal gas requires neither intermolecular attraction nor repulsion, meanwhile, the ecosystem embraces mutualism and competition, respectively; but it is plausible to assume that stationarity involves a mutual cancelation between these opposite inter-specific relationships in the large spatial scale. These items explain why, according to Montero and Morán (1992), stationarity in open systems is analytically equivalent to equilibrium in isolated systems. Besides, the increase of species diversity (H) has an anti-thermic effect; i.e., the increment of H reduces population fluctuations and dispersal activity in a similar way as low

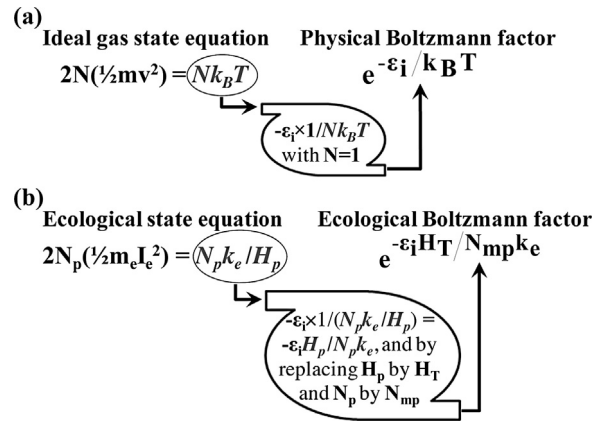


Fig. 1. Equivalence between IGSE ↔ physical Boltzmann factor (a) and ESE ↔ ecological Boltzmann factor (b) that supports the transformation from Eqs. (5) to (6) starting from an algebraic inversion of the physical Boltzmann factor based on the anti-thermic effect of H_T , concurrently with a scale expansion from individuals to plots (by replacing $N = 1$ by N_{mp}). N : number of molecules. m : molecular mass. v : molecular velocity. k_B : Boltzmann constant. T : temperature. ϵ_i : energy level. e : Euler's number. N_p : number of individuals per plot. m_e : mean individual biomass. I_e : dispersal indicator (Eq. (2)). k_e : ecological equivalent of the Boltzmann constant. H_p : species diversity per plot. H_T : total species diversity per survey. N_{mp} : mean number of individuals per plot at the survey level.

temperature reduces molecular motion; (Margalef, 1991; Odum, 1972; Rodríguez et al., 2012, 2013a).

The set of premises in the previous paragraph was the foundation to obtain an ecological state equation (ESE, Rodríguez et al., 2012; see Fig. 1, below) by replacing the variables of ideal gas state equation (IGSE, see Fig. 1, below) by ecological variables with an equivalent analytical meaning. This procedure for obtaining the ESE is based on an initial assumption of meaning equivalence between a mixture of species that includes several populations of individuals with particular values of mean biomass and a mixture of gases that includes several populations of molecules with particular values of molecular mass.

The ESE is valid despite body size, taxon or environment type (Rodríguez et al., 2013a), because the mantissa of the ecological equivalent ($k_e = 1.3806504 E \phi J_e \times \text{nat}/\text{individual}$, it indicates the average rate in which an individual exchange information by eco-kinetic energy $-E_e$, see Eq. (1), below— across the set of plots, and vice versa, within a stationary ecosystem) of the Boltzmann constant (k_B) is the same for all ecological assemblages but ϕ varies along a succession of integer values ($-x_i, \dots, 0, \dots, +x_i$). This points out to the nature of k_e as a “universal ecological constant” in a similar fashion as k_B in physics. This result implies additional aftermaths whose analysis surpasses the limits of this manuscript.

The above-mentioned exchange (i.e.: $m_e^{-1}, I_e^{21}, H_p^{-1}$ or, alternatively: m_e^1, I_e^{21}, H_p^1) supports the constant value of $k_e = m_e \times I_e^2 \times H_p$. Hence, k_e also explains the hump-backed curve (Hooper et al., 2005; Graham and Duda, 2011) between production (total energy per plot, Eq. (1), below) and diversity in coherence with an r - K continuum (Pianka, 1970) along the gradient of H_p values. In other words, the exchange of energy by information at the intra-ecosystem scale means a unimodal distribution of energy per plot (i.e., $m_{\min} \leftrightarrow H_{p \min}$, and $I_e^2_{\min} \leftrightarrow H_{p \max}$, $\therefore (m_e \times I_e^2)_{\max} \leftrightarrow$ intermediate values of H_p) that is the foundation for keeping a condition of “open equilibrium” (see above). In such a way, the “free movement” of a given plot (i_p) from the left to the right edge across the H_p, m_e, I_e^2 space of phases implies that i_p gains eco-kinetic energy and information until reach an intermediate H_p value but, beyond this point, i_p begins to lose energy despite the increase of H_p due to a decreasing value of I_e^2 . Complementarily, the return of i_p from the right to the left edge across the H_p, m_e, I_e^2

Download English Version:

<https://daneshyari.com/en/article/6296797>

Download Persian Version:

<https://daneshyari.com/article/6296797>

[Daneshyari.com](https://daneshyari.com)