



## Concerns regarding the proposal for an ecological equation of state: an assessment starting from the organic biophysics of ecosystems (OBEC).

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### ABSTRACT

The goal of testing the theoretical fruitfulness and empirical utility of the links between ecology and thermodynamics has been elusive. This could explain the breakdown of ecology into multiple branches, some of them intended to develop models in agreement with the principles of physics. The maximum entropy algorithm (MaxEnt) is one of the most frequently mentioned topics in this field. Within the MaxEnt framework, a quantitative relationship between various ecological parameters has recently been proposed as a seeming ecological equation of state (EES<sub>H</sub>; Harte et al. 2022). An equation of state unifies diversity, productivity, abundance and biomass. Commun. Biol. 5: 874). We analyze the EES<sub>H</sub> from the interdisciplinary perspective of Organic Biophysics of Ecosystems (OBEC). Consistent with this analysis, the EES<sub>H</sub> neglects the analytical similarity between key ecological variables and statistical mechanical variables, it does not include any intensive variable useful to determine the distance of ecological systems from equilibrium, it does not involve any constant useful to define the statistical range within which the system can be considered out of danger despite widespread effects of anthropogenic impact, and its general structure bears no resemblance to previous equations of state because it is based on a subjective approach devoid of physical content that is only useful as a tool for statistical inference. So, our conclusions are: (i) the EES<sub>H</sub> does not withstand comparison with prior knowledge and empirical evidence from both ecology and physics, and (ii) it cannot be considered an ecological equation of state.

### 1. Introduction

The network of analytical connections and similarities between ecology and physics has remained a pervasive and all-encompassing background curtain since the dawn of modern ecology or even before (e.g., Fourier, 1824, 1827; Clausius, 1885; Lotka, 1925; Lindeman, 1942; Odum, 1968), until the current times (e.g., Svirezhev, 2000; Jørgensen et al., 2007; Tiezzi and Pulselli, 2008; Drossel, 2010; Azaele et al., 2016). However, developing models to explain ecosystem functioning in a way that is fully consistent with the principles of conventional physics has proven to be an elusive goal (Ulanowicz, 2004; Nielsen et al., 2020). At first sight, it seems unlikely that the current framework of theoretical physics is sufficient to adequately model the biological level of complexity, and further developments within physics itself are likely to be required (Katsnelson et al., 2018). Perhaps this situation could

explain the splitting of ecology into many branches during the last quarter of the 20<sup>th</sup> century, leaving the naturalistic point of view progressively devalued (Margalef, 1993). This intricate web of attempts, some of them fruitful at a given scale, and others totally unsuccessful in the long run, has been called by Riera et al. (2018) as a 'swarm of microparadigms'.

The application of the maximum entropy algorithm (MaxEnt) to explain a great variety of features of ecological systems is one of the most frequently mentioned attempts, sometimes very favorably (e.g., Renner and Warton, 2013; Harte and Newman, 2014; Brummer and Newman, 2019; Atzeni et al., 2020; Stuart et al., 2021; Golan and Harte, 2022), and others not so much (e.g., Syfert et al., 2013; Kramer-Schadt et al., 2013; Guillera-Arriota et al., 2014; Xiao et al., 2015; Shabani et al., 2018). Precisely within the MaxEnt framework, Harte et al. (2022) proposed an ecological equation of state (EES<sub>H</sub>). We analyze the EES<sub>H</sub>

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from the interdisciplinary perspective of Organic Biophysics of Ecosystems (OBEC; Rodríguez et al., 2017).

The purpose of this analysis is to address two significant epistemological distortions that must be carefully avoided. Firstly, neglecting previous references in the same field, whether intentionally or unintentionally, is a common reason for editorial rejection. This type of editorial screening is justifiable and reasonable since a scientific discipline built upon a fragmented chain of discoveries, leading to the reinvention of existing knowledge, is essentially void of any scientific progress. Secondly, conducting ecological investigations requires extensive fieldwork, data processing, and substantial financial investments in surveys and publications. Given that resources are inherently limited, it is essential to refrain from allocating time and resources towards research endeavors that are anticipated to be unsuccessful from the outset. Therefore, our objective is to examine whether the consistency of the ecological exploration and hypothesis system can mitigate these two epistemological distortions.

To achieve this, we present a brief section on the methods employed in our study, followed by a theoretical analysis supported by new empirical evidence. This contribution concludes with a concise section of conclusions, where we generalize our findings at an epistemological level. The aim is to provide insights into future research directions in this field.

## 2. Methods

### 2.1. Theoretical analysis

We performed a theoretical assessment by combining interdisciplinary knowledge with a comparison between previous publications in the field of OBEC and foundational publications by other authors to assess the reliability of the proposal of  $EES_H$ . Original publications in the field of physics underlying the application of MaxEnt to ecology were also reviewed, and more recent comments on the physical meaning of MaxEnt.

### 2.2. Data curation and processing

We combine data from our field work activity, previous publications, and data collected from several databases. All surveys included information that is essential to calculate Eq. (4), i.e.: species per plot, number of individuals per species per plot, biomass values per plot (either total value per plot or average value per individual per plot  $-m_{ep}$ , in kg), and central spatial coordinates per plot (in meters for relatively short average distances between plots, as well as in decimal degrees for larger average distances) regarding representative and well-defined areas (see Suppl. Table 1, and its footnote). The characteristics of the equations applied are explained in Suppl. Note 2, and the references included therein.

### 2.3. Statistics and reproducibility

All data sorting and statistical analyses were performed by means of Microsoft Excel (2016) and Statistica (StatSoft, Inc. STATISTICA –data analysis software system–, version 12. [www.statsoft.com](http://www.statsoft.com), 2014). As for the ergodic indicator of dispersal intensity ( $I_e$ , measured in dispersal units,  $\bar{d}$ ), there are freely available computer applications ('Bio-diversidad' and 'IeCalc-2.1') to calculate it at: <https://interdisciplinariosciencia.es/servicios>.  $H$  values were calculated by means of Primer 5 for Windows, version 5.2.9 (Primer-E, Plymouth Routines in Multivariate Ecological Research. PRIMER-E Ltd. 6 Hedingham Gardens, Roborough, Plymouth. PL6 7DX. United Kingdom, 2002).

### 2.4. Data availability

Raw data sources are detailed in Suppl. Table 1, footnote. The values

of the variables used to obtain Fig. 1, accompanied by several auxiliary variables, are also available in Suppl. Data. Other datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## 3. Results and discussion

Harte et al. (2022) is entitled "An equation of state unifies diversity...", and they comment on Shannon's  $H$ -measurement (Shannon, 1948), the most common diversity index (Magurran, 2004). Harte et al. (2022) used  $H$  in an underlying algorithm to get  $R$ , an 'ecosystem structure function'. Finally, richness (i.e., species number,  $S$ ) replaces  $H$  in the  $EES_H$ . The uncritical replacement of species diversity by richness neglecting the assessment of evenness ( $J = H/\ln S$ ) is frequent in ecology (e.g., Jiang et al., 2009; Mazón, 2016; Rapaccioulo, 2019). This habit follows an early recommendation about the measurement of species diversity at any hierarchical level of community organization (Whittaker, 1972). However, the drawbacks of this methodological habit has been analyzed by Spellerberg and Fedor (2003). In addition, there is empirical evidence indicating that  $S$  is an incomplete surrogate for species diversity (Wilsey et al., 2005). Furthermore, it is impossible to understand the trophodynamic meaning of species diversity without combining evenness and richness (Suppl. Note 1).

Several ecological parameters "are loosely analogous to state variables in thermodynamics" where "an equation of state, exists in the form of the ideal gas law:  $PV = nRT$ ... but in macroecological studies... such framing has been lacking" (Harte et al., 2022). However, the statistical mechanical equivalent of  $PV$  is (Aguilar, 2001):

$$Nmv^2 = 2N(1/2mv^2) = 2N(E_k) = 2E_{kT}, \quad (1)$$

where  $N$ : number of molecules;  $m$ : molecular mass;  $v$ : velocity;  $E_k$ : kinetic energy per molecule; and  $E_{kT}$ : total kinetic energy. It is well-known that from Eq. (1), the ideal gas law becomes:

$$2N(1/2mv^2) = Nk_B T, \quad (2)$$

where  $k_B$ : Boltzmann's constant =  $1.380649E-23 \text{ J}\cdot\text{K}^{-1}$ ; and  $T$ : absolute temperature. Hence, although  $PV$  seems disconnected from macroecology according to Harte et al. (2022), the ecological meaning of the product: abundance ( $N$ )  $\times$  mean biomass per individual ( $m_e$ )  $\times$  dispersal intensity squared ( $I_e^2$ ), should not be neglected (below). Furthermore, an ecological equation of state ( $EES_R$ ) was published by Rodríguez et al. (2012), and was used as a base model to obtain a sequence of innovative results (e.g., Rodríguez et al., 2013, 2015a,b,c, 2018; Riera et al., 2021). For a comparison, the structure of  $EES_H$  is (Harte et al., 2022):

$$B = c \frac{E^{4/3}}{S^{1/3} \ln\left(\frac{1}{\beta}\right)} = c \frac{E^{1.3333333}}{\sqrt[3]{S \ln\left(\frac{1}{\beta}\right)}}, \quad (3)$$

where  $c \approx 4.17$ ;  $\beta$  is estimated from the  $S/N$  ratio;  $E$ : total metabolic rate (an inadequate surrogate for productivity –trophic energy–; comments below);  $N$ : total number of individuals; and  $B$ : total biomass.

The structure of  $EES_R$  is (Rodríguez et al., 2012, 2013):

$$2N_p(1/2m_{ep}I_e^2) = \frac{N_p k_{er(e)}}{H_p}, \quad (4)$$

where ' $_p$ ' means 'per plot';  $k_{er(e)}$  is the expected value ( $_{(e)}$ ) of the ecological equivalent of Boltzmann's constant =  $1.380649E \pm \varphi \text{ J}_e \cdot \text{nat}/\text{individual}$ ; and  $\varphi$  is a reproducible integer per taxocene  $-\tau-$  (Rodríguez et al., 2013); (Suppl. Table 1, D-F columns). The meaning of the remaining variables of Eq. (4) has been described in previous sections. See above to graphs that  $k_B$  and  $k_{er(e)}$  share the same significant ( $1.380649$ ). Accordingly, Eq. (2) and Eq. (4) are analogous to each other.  $H_p$ , in Eq. (4), occupies a position opposite to that of  $T$  in Eq. (2) simply because of its cooling effect on biota. Suppl. Note 2 explains the

reasoning behind Eq. (4), including the cooling effect of  $H_p$ . From Eq. (4), in steady state (E.S.<sup>0</sup>):

$$k_{er(e)} = \frac{2N_p(1/2m_{ep}I_c^2) \cdot H_p}{N_p} = \frac{N_p m_{ep} I_c^2 H_p}{N_p} = m_{ep} \cdot I_c^2 \cdot H_p \quad (5)$$

Thus, the constant nature of  $k_{er(e)}$  depends on a biomass-dispersal trade-off along the gradient ( $\Delta H_p$ ) of species diversity values per plot (Rodríguez et al., 2013), (Suppl. Table 1, columns J and K):

$$m_{ep1} \cdot I_c^{\dagger} \cdot H_{p1} (r - \text{strategyedgeof} \Delta H_p) \Rightarrow (m_{ep} I_c^2)^{\dagger} \cdot (\Delta H_p' \text{smiddlesection}) \Rightarrow m_{ep}^{\dagger} \cdot I_c^{\dagger} \cdot H_p^{\dagger} (K - \text{strategyedgeof} \Delta H_p) \rightarrow \bar{k}_{er(e)} \rightarrow \text{constant} \quad (6)$$

So, Eq. (4) is based on  $r$ - $K$  selection theory, a foundational and well-known eco-evolutionary proposal (Bohn et al., 2014), whilst Eq. (3) is based on two recent hypotheses still under debate (see comments on MaxEnt, below). Eq. (4) was tested in 29 surveys belonging to 12 taxocenes (Rodríguez et al., 2013). We here include 25 additional surveys carried out in steady-state systems belonging to 2 unexplored and/or underexplored taxocenes (Suppl. Table 1). These new results coincide with what is theoretically expected according to Rodríguez et al. (2012, 2013).

There are no reliable methods to assess trophic energy (productivity) in mainstream ecology (Whittaker and Heegaard, 2003), and  $E \propto B^{0.75}$  in Eq. (3) is the rate of energy expenditure per unit time and unit biomass at full rest, excluding digestion, reproduction, and any kind of motion (McNab, 1997). But, in real ecosystems, individuals display motion, trophic activity, and reproduction, and all of this needs energy. Hence, the energy/richness ratio (Eq. (4) in Harte et al., 2022) cannot be evaluated based on the proposal of Eq. (3). It follows that the relationship between the energy/biomass ratio and diversity, discussed in Suppl. Note 1, cannot be assessed from the proposal of Harte et al. (2022) either.

However, from Eq. (4), the total value of eco-kinetic energy per survey ( $\zeta$ ) is  $E_{eTs} = N_s(E_{es}) = N_s(\frac{1}{2}m_{es}I_{es}^2)$ . This allows to explore the correlation between the energy/biomass ratio ( $E_{eTs}/m_{eTs}$ , the ecological analogue of specific energy in physics; Aguilar, 2001) and species diversity ( $H_s$ ); see Fig. 1.

According to the regression equation in Fig. 1, 1 kg of biomass at  $H_s = 0$  nat/individual ( $S = 1$ ) is 13.344 times more expensive in energy terms than at  $H_s = 5$  nat/individual (i.e.,  $2,705.135 \text{ J}_e \cdot \text{kg}^{-1} \div 202.726 \text{ J}_e \cdot \text{kg}^{-1} = 13.344$ ). This local anti-entropic increase in efficiency matches the ecological cooling effect of  $H$  and the Prigogine theorem (Shapovalov and Kasakov, 2018), but it does not match the hypothetical guiding role (Harte and Newman, 2014) of MaxEnt in ecology. Thus, either such a guiding role has been greatly overrated, and/or MaxEnt has no physical meaning (below). This does not contradict the

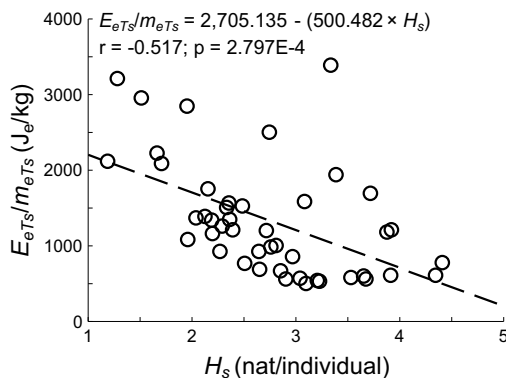


Fig. 1. Correlation between the amount of eco-kinetic energy per kg ( $E_{eTs}/m_{eTs}$ ), and species diversity per survey ( $H_s$ ) in a set of 45 steady-state systems (E.S.<sup>0</sup>). Data: Suppl. Table 1, columns L and M.

interdisciplinary use of MaxEnt beyond physical systems. It can serve as a general framework for statistical inference, even when the constraints do not have an immediate physical interpretation. In this context, MaxEnt is viewed as a method for assigning probabilities to different outcomes based on limited information or constraints. For instance, consider a scenario where you have a dataset representing the ages of individuals in a population, but you only have access to the mean and standard deviation of the ages. Without any further information, you can use MaxEnt to derive a probability distribution that maximizes entropy while being consistent with these constraints. This distribution would represent the "most likely" age distribution given the available information, even if there is no physical interpretation associated with it. This aspect makes MaxEnt a versatile tool for statistical inference, applicable beyond its traditional physical interpretation (Dewar, 2009).

Equations of state are relationships between state variables where at least one of them is extensive in nature, and the others are intensive (e.g.,  $v$  and  $T$  in Eq. (2), and  $I_e$  and  $H_p$  in Eq. (4)), since the thermodynamic imbalance necessary to carry out work depends on the inequality between the values of intensive variables (Halliday et al., 2011; Gould and Tobochnik, 2021). For example, the total amount of thermal energy (an extensive variable) in the ocean is enormous, but not useful for moving a ship through the use of a heat engine, because the gradient of temperature (an intensive variable) between the water and the air inside of the ship is not high enough. Extensive variables become very important to assess the total amount of work that can be done, but only after the necessary gradient exists between intensive variables. Accordingly, Eq. (3) is not an equation of state, because  $S$ ,  $E$ ,  $N$ , and  $B$  are all extensive variables.

The factor that most hinders the usefulness of Eq. (3) is the absence of a constant with a role at least similar to that of the Boltzmann constant ( $k_B$ ) in Eq. (2), unlike the presence of a constant ( $k_{er(e)}$ ) with such a function in Eq. (4). Thus, Eq. (2) and Eq. (4) are both comparisons between a given reality (left-hand side) and a theoretically expected framework (right-hand side) given the value of the respective constants. One of the effects of including these constants is that the results of both equations become quasi-binary. That is, in the ecological context, the system is or is not in open equilibrium conditions depending on whether or not there is statistical equality between the two sides of Eq. (4). Any extreme alternative (i.e.,  $k_{er(o)} < k_{er(e)} < k_{er(o)}$ , where  $(o)$  means 'observed value') for either edge beyond the statistically expected narrow range dependent on  $k_{er(e)}$  falls outside the spectrum of stationarity. So, it clearly qualifies as a non-stationary situation due to the deficit or excess of energy per individual compared to the expected value. This is crucial for biological conservation, because the human being has to intervene, or not, to save a certain species assemblage depending on such deficit or such excess.

Harte et al. (2022) conducted a study to explore the conditions under which Eq. (3) may not be valid, particularly when deviations from an ideal ecological behavior are present. They highlighted that it is challenging to compare ecological behavior to that of an ideal gas under steady state conditions. Due to the aforementioned absence of a constant equivalent to  $k_B$  in the  $EES_H$ , the analytically equivalent parameters that could define ideal ecological behavior are currently unavailable, making it statistically infeasible to identify what constitutes an ideal ecological behavior objectively, regardless of the researcher's perspective. Nevertheless, in Eq. (3) there is a parameter that can be considered a natural quasi-constant, significantly influencing the dynamics between biomass and energy: the exponent of  $E$ . However, Harte et al. (2022) acknowledge that determining the precise value of this exponent is uncertain. Previous studies, such as Cyr and Walker (2004) and Isaac and Carbone (2010), have demonstrated a wide range of values for this exponent, including,  $\frac{3}{4}$ , or even 1, emphasizing the lack of consensus. In tune with this lack of consensus, the research by Harte et al. (2022) brings attention to the complexities of understanding ideal ecological behavior and the challenges in determining the values of crucial parameters. It underscores the need for further investigation and a multidisciplinary

approach to gain deeper insights into ecological dynamics.

Actually, Harte et al. (2022), along their attempt of analogy to the ideal gas law at the level of classical thermodynamics ( $PV = nRT$ ; i.e., disregarding the analytical importance of Eq. (1) and Eq. (2)), have validated Eq. (3) by means of various datasets. However, this validation is associated with such a complicated set of mathematical transformations that it is almost inevitable to think that in the contrast between Eq. (3) and reality underlies a positivism forced by mathematical analysis. Contrastingly, Eq. (4) is based on replacing  $v$  and  $T$  in Eq. (2) by  $I_e$  and  $H_p$ , period.

In the study by Harte et al. (2022), the inclusion of MaxEnt as a tool for analysis raises some concerns about the validity of Eq. (3) as an equation of state. MaxEnt is recognized as a statistical inference tool without direct physical content, as pointed out by Dewar (2009). Moreover, the main corollary associated with MaxEnt, the maximum entropy production principle, lacks a definitive proof and relies on additional assumptions that are less evident than MaxEnt itself, as highlighted by Martyushev (2010). By employing MaxEnt in their analysis, Harte et al. (2022) introduce a statistical inference approach that may challenge the physical interpretation of Eq. (3) as a comprehensive representation of ecological dynamics. This raises questions about the suitability and robustness of using MaxEnt in this context. It is important to acknowledge the ongoing discussions and uncertainties surrounding the application of MaxEnt and its associated principles in the field of ecological dynamics, as pointed out by Dewar (2009) and Martyushev (2010). These considerations highlight the need for further investigation and careful examination of the assumptions and limitations associated with MaxEnt when applying it to ecological systems.

From its theoretical roots, MaxEnt results in a “‘subjective statistical mechanics’ [in which] the usual rules are justified independently of any physical argument, and in particular independently of experimental verification; whether or not the results agree with experiment, they still represent the best estimates that could have been made on the basis of the information available” (Jaynes, 1957). As a consequence, in the realm of MaxEnt, “entropy is an anthropomorphic concept, not only in the well-known statistical sense that it measures the extent of human ignorance as to the microstate. Even at the purely phenomenological level, entropy is an anthropomorphic concept. For it is a property, not of the physical system, but of the particular experiments you choose to perform on it” (Jaynes, 1965). Unlike the previous quotations, real statistical mechanics, and trophodynamics are experimental sciences based on objective physical principles.

#### 4. Conclusions

Modeling implies simplifying, but avoiding unrealistic crucial assumptions (Suppl. Note 2) in contradiction with well-established prior knowledge and empirical observations. This explains why “it is unclear why an apparently mechanism-free theory should work at all in ecology” (Harte et al., 2022), because Eq. (3) has no underlying explanation in connection with either physics or classical ecological theory. A new ecological equation of state is expected to solve the imperfections of the old one, but this only happens if the authors are aware that a previous equation of state and its derived models exist; however, it seems that this is not the case of Harte et al. (2022).

Plain and simple, if the term ‘equation of state’ is inextricably linked to physics, then it is futile to attempt an ‘ecological equation of state’ (Eq. (3)) detached from that science. Over the last few decades, it seems increasingly difficult to assume that science takes interest at the differences that emerges from generalities; hence the principle that the fewer and simpler the assumptions and the broader the results, the more valuable the model. It seems paradoxical, but sometimes the route towards simplicity in the essential understanding of natural processes is more difficult to travel than the other way around.

#### Author contributions

R.R., B.D.F., A.M.H., and R.A.R. performed the comparison between previous publications in the field of OBEC and publications by other authors to assess the reliability of the proposal of Harte et al. B.D.F. provided crucial analytical items in the interdisciplinary field, and remodeled the manuscript structure after a first version. A.M.H. participated in the collection of field data and its statistical processing, as well as in a detailed revision to obtain the final version of the manuscript following suggestions from B.D.F. R.A.R. initiated the theoretical assessment by combining interdisciplinary knowledge, field work data collected by himself and R.R., as well as freely available data from external sources that were gathered by R.R., and later updated, curated, and interpreted by R.A.R.

#### Declaration of Competing Interest

The authors declare no known competing financial interest or personal relationships to influence the work reported in this piece.

#### Data availability

Data will be made available on request.

#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2023.110462](https://doi.org/10.1016/j.ecolmodel.2023.110462).

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