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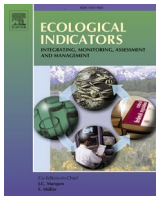

Perspective Article

Alpha species diversity measured by Shannon's *H*-index: Some misunderstandings and underexplored traits, and its key role in exploring the trophodynamic stability of dynamic multiscapes

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ABSTRACT

The spectrum of species diversity (SDi) can be broken down into αSDi (taxocene level), βSDi (community level), and γSDi (metacommunity level). Species richness (S) and Shannon's index (H) are well-known SDi measures. The use of S as a surrogate for SDi often neglects evenness (J). Additionally, there is a wide variety of indicators of SDi. However, there are no reliable theoretical criteria for selecting the most appropriate SDi index despite the undeniable empirical usefulness of this parameter. This situation is probably due to the analytical gap still existing between SDi and trophodynamics. This article contributes to closing that gap by analyzing why S as a single surrogate for SDi is inconsistent from the trophodynamic point of view, so that an index combining S and J, such as H or H_B (Brillouin's index), are the most appropriate choices in the context of a new theoretical framework (organic biophysics of ecosystems, OBEC) based on the well-known classical links between ecosystem ecology and thermodynamics. Exploration of data from reef fish surveys under stationary and non-stationary conditions corroborated the existence of the ecological equivalent of Boltzmann's constant ($k_{er(e)}$) at the worldwide scale. This result substantiates the usefulness of the ecological equivalent of the compressibility factor as an indicator of environmental impact. $k_{er(e)}$ stablishes an analytical linkage between ecology, information theory, and statistical mechanics that allowed us to propose a new measure of total negative entropy (a.k.a. syntropy) per survey (S_{erT}) that is easy to calculate and displayed a highly significant correlation with total standing biomass per survey (m_{eTs}). According to the slope of the regression equation S_{erT}, m_{eTs} there is a large portion of S_{erT} that leaks into the environment and/or is captured by numerous ecological degrees of freedom independent of standing biomass. According to the changing value of the exponent of $k_{er(e)}$, even among coexisting taxocenes, it would have been impossible to obtain the results discussed in this article if the analysis had been carried out at the βSDi or γSDi level. This establishes αSDi as the most appropriate level of analysis to obtain empirically useful results about the key functional connections on which trophodynamic stability depends in dynamic multispaces. The results summarized here are based on the careful selection and intertwining of a few key variables, which indicates the importance of developing models as simple as possible in order to achieve the reliability necessary for successful biological conservation.

1. Introduction

The concept of biodiversity has evolved from its initial form as 'biological diversity' (Harris, 1916) until the merger of both terms in the last decades of the 20th century (Wilson 1988). According to Whittaker (1960, 1972), species diversity (SDi) should be broken down into three levels: (1) A particular group of organisms in a community (αSDi). (2) The degree of community differentiation due to an environmental gradient (βSDi). (3) The SDi of a number of community samples which have been combined (γSDi). At any of these levels, *"the most generally*

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appropriate measure of diversity is simply S, the number of species per unit area as represented in some kind of standard sample" (Whittaker, 1972).

Agreeing with Whittaker (1972), Peet (1974) states that direct species counts (*S*), while lacking theoretical elegance, provide one of the simplest, most practical, and most objective measures of *species richness* (i.e., the author is not talking about SDi in *sensu lato*, but about the number of species in *sensu strictu*). Possibly as a consequence of the opinions of the aforementioned authors, the use of *S* as a surrogate for SDi neglecting the relative abundance of concurrent species (evenness) is common (e.g., Ricotta, 2000; Kahmen et al., 2005; Jiang et al., 2009; Mazón, 2016; Rapacciuolo et al., 2019), although richness seems to be an incomplete surrogate for biodiversity (Wilsey et al., 2005). However, this is an empirically derived assertion, without general theoretical foundation (additional arguments in sections 2 and 3).

In parallel, Margalef (1957; see also Sherwin and Prat i Fornells, 2019) proposed the *H*-measure of information amount (Eq. (1); Shannon, 1948) as an indicator of SDi:

$$H = k\left(-\sum_{i=1}^{S} (p_i \ln p_i) \right) = k\left(-\sum_{i=1}^{S} \left(\frac{n_i}{N} \ln \frac{n_i}{N}\right) \right) \quad (1)$$

where, in the ambit of mainstream ecology, $k = 1$; n_i: number of individuals of species i^{th}; and $N = \sum_{i=1}^{S} n_i$. *H* can be expressed in different measurement unit as bit/individual, dit/individual, or nat/individual. However, the use of natural logarithm is preferred in physics because it simplifies the calculations. Therefore, if interdisciplinary standardization is desired so as not to contribute to the existing methodological confusion (see below), nat/individual should also be preferred in ecology.

H combines the concept of *S* as such (a.k.a. richness), and the concept of evenness ($J = H / \ln(S)$, from Pielou, 1975; an alternative designation of the same parameter that was defined by Shannon –1948, pp. 398, 405– as "relative entropy"). As this combination goes beyond the proposal of Whittaker (1972), the term 'heterogeneity indices' (Krebs, 1989; Magurran, 2004) has been used to refer to *H* and other indices that combine richness and evenness (* in Box 1), since their values are proportional to the probability that two individuals chosen at random belong to different species (heterogeneity).

However, this is an interpretation that, although rationally valid, is purely statistical. From the point of view of the evolution of complex systems, it would perhaps be more fruitful to assume that the value of these indices (let us designate them collectively as $\boldsymbol{\xi}$, or "eco-information") is proportional to the capacity of each ecosystem to maintain an updated record of the environmental events that have taken place throughout its evolutionary history, and to store a certain amount of information about these events in the form of a set of species adapted to them, thus raising the probability of subsistence of the system as a whole.

Given that all species have their particular sensory systems to regulate their interaction with the environment, the only rational option is to assume that each organism is an "observer" of the environment, and life history adaptations allow each species to observe the environment on its own unique set of scales and time (Levin, 1992), thus achieving at the collective scale a situation in which the ecosystem (i.e., the biological community plus its internal inorganic environment) is a watchdog of itself. So, Eq. (1) indicates the average value of $\boldsymbol{\xi}$ per individual (i.e., the total amount of eco-information, or total SDi, per survey is: Eq. (1) × *N*), and has a specific unit of measurement, although these two attributes are often not taken into account.

Detailed studies have been published on the mathematical nuances of *H* (e.g., Washington, 1984; Botta-Dukát, 2018; Xu et al., 2020; Ricotta et al., 2021) and other indices that pursue similar objectives (Box 1). A review of the original sources of the equations in Box 1 allows us to arrive at some simple conclusions that are relevant to the context of this article:

i) Most of the equations in Box 1 involve some of the same variables included in Eq. (1). In fact, the only new parameter that has been necessary to explain is *q* in item 11.
ii) Some of the equations in Box 1 depend on precomputing the value of *H* (Eq. (1), in the main text) to calculate the value of the equation in question (e.g., items 7, 8, and 9), or the equations

Box 1
. Simplified summary of the variety of indices related to the measurement of SDi

1. ***S***: species richness; see main text.
2. ***H***: Shannon's index; see main text, Eq. (1). *
3. $\boldsymbol{H_B}$: Brillouin's index; see main text, Eq. (2) and related explanations. *
4. **1–*l***, with $\boldsymbol{l} = \frac{\sum_{i=1}^{S} n_1(n_i - 1)}{N(N-1)}$; Simpson (1949); (Margalef, 2021, p. 367). *
5. $\boldsymbol{d} = \frac{S-1}{\ln(N)}$; Margalef (1957). *
6. $\boldsymbol{H_\alpha} = (1/1-\alpha)\hat{A}\cdot\ln\left(\sum_{i=1}^{S} p_i^{\alpha}\right)$; Rényi (1961). H_α is a generalization of *H* (Liu and Xiao, 2021); when $\alpha \to 1$, $H_\alpha = H$ (Shannon's index, Eq. (1)). *
7. $\boldsymbol{E_{She}} = 2^H/S$; exponential evenness index of Sheldon (1969).
8. $\boldsymbol{N_1} = e^H$; Hill (1973); N_1 indicates the value of richness adjusted by their evenness. *
9. ***J***: evenness index (Pielou, 1975; see main text).
10. $\widetilde{\theta} = d + \left(n_1^2/2n_2\right)$; Chao (1984), where *d* is the total number of any type of statistical class observed, n_1 is the number of classes observed once, and n_2 is the number of classes observed twice. $\widetilde{\theta}$ is a non-parametric indicator of the minimum number of classes (or species, if that is what is being studied). $\widetilde{\theta}$ is preferably used for small samples biased in favor of low abundance species (i.e., this is not the case for most of the surveys used as examples in this paper). *
11. $\boldsymbol{^qD} = \left(\sum_{i=1}^{S} p_i^q\right)^{1/1-q}$; Tuomisto (2010), where $q = 0$ when the index is based on the weighted harmonic mean of species abundances ($1/S$) and so $^qD = S$; if $q \to 1$ then $^qD = N_1$, and if $q = 2$ the index is based on the arithmetic mean of species abundances. Thus, the value of *q* assigns a variable influence to the relative abundance of species in the final result of ^qD depending on the arbitrary analytical bias of the researcher in favor or not of very abundant species, or quite the opposite. *

simply reduce either directly (item 6) or indirectly (item 11) to the value of H in their most suitable calculation spectrum.

iii) One of the equations (item 3 in Box 1) approaches asymptotically to a value almost identical to that of H for large samples (see Eq. (2) and its associated explanations in section 3).

iv) Chao's (1984, item 10 in Box 1) proposal is not appropriate for processing the surveys used as empirical examples in this article. Furthermore, the non-parametric nature of $\widetilde{\theta}$ hinders the application of the more robust (parametric) tests of conventional statistics.

v) The references cited in Box 1 are more focused on the statistical-mathematical rigor of the proposal than on the analytical importance of such indices for understanding how and why ecological systems behave in a certain way and not in another. Mathematics can provide useful tools, but their analytical meaning is not the responsibility of mathematicians, but in this specific case of ecologists. For example, is there a non-arbitrary criterion derived from ecology instead of from mathematics to grant one or another value to the parameter q in the calculation of item 11 of Box 1? The most rational answer is no. In contrast, it took 68 years after Shannon (1948) to understand from the qualitative point of view that functional redundancy, the competitive exclusion principle, and species resilience in the performance of their ecological niche have their respective equivalent patterns in information theory (Rodríguez et al., 2016). In other words, mathematics needs company.

vi) Related to the previous point, there is a very precariously bridged analytical gap between the measurement of SDi and trophodynamics; perhaps because the fundamental principles of ecological science as they are commonly expressed do not reflect the central role of information processing (O'Connor et al., 2019). The most analyzed topic in this field is production-diversity patterns, which lack a single explanation fully integrated into orthodox theoretical ecology. One of the main reasons for such difficulty is linked to the variety of indices in Box 1. That is, if the index used to study the correlation between SDi and trophic production changes from one author to another, then it is practically impossible to find a relevant and non-contingent pattern. Amidst this controversy, a fact solidly contrasted with empirical evidence (see Fig. 2 in Rodríguez et al., 2013) is that, assuming those steady conditions early defined by MacArthur (1955; i.e., that the amount of energy going out of the food web is equal to the amount coming in) the relationship between *total* eco-kinetic energy per plot (Eq. (7) in section 3) and the value of H (Eq. (1)) follows an inverted U-pattern. That is, total production per plot is maximal at intermediate levels of SDi or, equivalently at a larger scale, at intermediate stages of ecological successions as established by Odum (1969). Nevertheless, paradoxically, such a pattern does not coincide with the relationship between SDi and average eco-kinetic energy per *individual* per plot (this issue is analyzed in section 3, below).

In summary, from items (i) to (vi), Eq. (1) seems the cornerstone in the issue of SDi measurement. Moreover, there are no reliable criteria based on eco-evolutionary theory for selecting the most appropriate SDi index in mainstream ecosystem ecology, despite the undeniable empirical utility of this parameter. After all, the abundance of SDi indices is not at all good news. That is, any monotonic function that is not very sensitive to sample size and sampling procedures, and that has a minimum value when all individuals belong to the same species and a maximum value when each individual belongs to a different species can be successfully used as a diversity index (Margalef, 2021). These requirements are not very restrictive. Thus, if we were to assemble a group of well-trained mathematicians, they could propose several dozen SDi indices in a few months. The key issue is to ascertain a relevant, non-contingent link between ξ and essential trophodynamic parameters.

Given that this key issue remains unresolved in orthodox ecology, the indices in Box 1 are used at the authors' discretion, producing confusion (Spellerberg and Fedor, 2003), as well as unconnected analytical trends (Moore et al., 2009) that weaken the link between theory and practice (Angilletta and Sears, 2011). Also, it might even hamper the effectiveness of wildlife conservation management (Joseph et al., 2013). After all, if the concept of biodiversity is demystified, it depends on a rule of thumb: ecosystems maximize the variety of internal options, as shown by old-field successions (Kelemen et al., 2017; Martínez-Ramos et al., 2021), and the rapid restoration of nature free of any human influence after a disaster (Matsala et al., 2021).

Thus, the methodological ambiguity discussed above reflects a problem pointed out by Hurlbert (1971), namely, that the study and management of SDi is not based on a concept as such, but on a set of calculation options in circumstances where there is a limited understanding of the theoretical meaning of SDi. So, this article is not addressed to improve any of the species diversity measures summarized in Box 1, but to figure out a pending question: What is the trophodynamic meaning of some of these measures and the empirical usefulness of this meaning for conservation biology?

As a result, this article is addressed, in the first instance, to provide an easily understandable argument as to why it is inconsistent to isolate richness and evenness when measuring SDi. Secondly, the paper explores the consequences and solutions to the paradoxical situation where $k = 1$ in Eq. (1); i.e., that reaching and maintaining a given amount of SDi is free in energy terms according to orthodox ecology. Finally, the article, based on abundant empirical data, demonstrates that the solution of the two previous problems allows the application of operational and relatively simple methods useful for the evaluation of the state of ecosystems and, therefore, of biological conservation. The article ends by analyzing a topic that encompasses and transcends the three aforementioned objectives, providing an epistemological point of view that the authors consider fundamental for a fruitful development of innovative ecological indicators.

2. Is it trophodynamically justified to use S as a surrogate for SDi?

Trophodynamics (Lindeman, 1942) refers to the production and movement of biochemical energy along trophic chains and food webs. The relationship between energy and SDi is clear, because in any type of system that can be categorized as sympoietic (from Greek *sún*, together, and *poíesis*, production; it means collective creation or organization of systems based on interconnected elements that are organizationally ajar, with vaguely defined boundaries; see Dempster, 2000; Haraway, 2018; Wells, 2018; Žukauskaitė, 2020; 2022), energy is the 'fuel' to increase information (Tribus and McIrvine, 1971). In fact, life may be defined operationally as an information processing system that has acquired through evolution the ability to store and process the information necessary for its own accurate reproductions, so the key word in the definition of life is information (Gatlin, 1972). The energy to support this information processing system comes primarily from the Sun. There is what is known as 'Solar Constant' (G_{SC}), with a value of 1360.8 ± 0.5 Joule/s/m^2 or Watt/m^2 (Kopp and Lean, 2011). That is, the maximum size of the 'energy pie' available to ecosystems is fixed. Simultaneously, it is well known that ecosystems tend to a state of increased number of species as ecological succession progresses (Margalef, 1963; Odum, 1969).

So, the only possible solution is to distribute the energy pie (G_{SC}) in a more equitable way (increase in J) as new species are added to the ecosystems, even if the graph based on a decreasing ranking of abundance per species maintains a negative exponential pattern. But it is a well-known fact that the slope of this pattern decreases with increasing SDi (Pielou, 1975; Krebs, 1989; Magurran, 2004; Margalef, 2021). Therefore, the average energy budget per species tends to decrease as

the ecosystem approaches the maximum limit of energy captured. As a consequence, the main way in which a given species can thrive in conditions of high H values is to become more efficient (i.e., lower value of the energy/biomass ratio; Margalef, 1963) to make the best use of an increasingly scarce energy share. The reduction of the energy/biomass ratio is an anti-entropic trend that implies an eco-evolutionary shift from *r*-strategists to *K*-strategists, which means a reduction in dispersal activity, reproductive turnover, and basal metabolic rate (Margalef, 1963; 2021; Odum, 1969; Brown et al., 2004). All this means that J is not a mere 'accompanying variable' of S that can be disregarded at will, but an inescapable requirement for the increase in SDi. Therefore, a combined index, such as Eq. (1), is the most appropriate option to measure SDi.

3. $k = 1$ in eq. (1)? A recent answer, and new supporting results

The mathematical structure of Eq. (1) is exactly the same as that of the Gibbs entropy in statistical mechanics (see Gibbs, 1928; Tolman, 1938). It is quantitatively satisfied that for a very large number of particles of which n_i particles are in the i^{th} microscopic condition (range) of position and linear momentum:

$$S_B = k \cdot (\ln\Omega) = k \cdot \left(\ln \frac{N!}{\prod_i n_i!}\right) = k \cdot (H_B \cdot N)$$
$$\simeq k \cdot \left(\left(-\sum_{i=1}^{S}(p_i \ln p_i)\right) \cdot N\right) \quad (2)$$

where k is a universal constant (below); S_B is Boltzmann's entropy; H_B (i.e., (ln Ω)/N) is the index of Brillouin (1956); and Ω is the number of microstates (a.k.a. 'complexions' or 'random permutations') which are different from each other as large assemblies of coordinates and linear momentum vectors of the set of molecules at the microscopic level, although macrostate variables (i.e., volume, pressure, temperature) *remains constant over time* (unique physical requirement to define equilibrium, a.k.a. stationary state; Aguilar, 2001; Callen 1985).

Each transition between microstates involves a small average amount of energy exchange per molecule. Thus, the constant k measures that energy in such a way that, through the product $k \times \ln \Omega$ in Eq. (2), the total entropy of the ensemble expressed in J/K is evaluated. In Eq. (2), the symbol $\simeq$ means that H_B and H are asymptotically equal or congruent to each other. That is, if the factorials in H_B are replaced by their approximate expression based on Stirling's formula, the values of H and H_B fully converge with each other when $\overline{n}_i \to \infty$ (e.g., from a sequence of values of $n_i = 1, 21, 5, 7, 14$; $H_B/H = 0.8976$; but if every value of this very sequence is multiplied by 7, then $H_B/H = 0.9768$, and so on). The physical relationship between microstates and macrostate is easily transferable to the analysis of ecosystems, where individuals of the same species are in constant movement and, in turn, each species oscillates around a set of mean values for each of the parameters that define its ecological niche (talandic temperature, below). However, this feverish activity on a small scale generally occurs without variation in the value of Eq. (1) at the total level as long as the system is in stationary conditions.

The role of Eq. (1) in Eq. (2) indicates that, in non-sympoietic physical systems, S_B increases with H. However, according to former authors (e.g., Brillouin, 1956; Odum, 1969; Tribus and McIrvine, 1971; Gallucci, 1973; Tiezzi and Pulselli, 2008; Margalef, 2021; Sethna, 2021), gaining information (H) at a given reference level means nothing more and nothing less than reducing entropy (a.k.a. uncertainty), and vice versa. The local decrease of entropy with the increase of information was explored even before the publication of Shannon (1948); see, e.g.: Maxwell (1872), Szilard (1929), Lewis (1930). Some of these publications include sharp, although dissimilar, reasoning intended to demonstrate what seems impossible at all: that two equations identical to each other (i.e., Eq. (1) and Gibbs entropy) mean opposite things.

The view that information and entropy are the same thing, but in different contexts (Guizzo, 2003), solves the above conundrum in the simplest way. That is, sympoietic systems, like ecosystems, are 'photographic negatives' of non-sympoietic systems in thermal equilibrium. For example, when a non-living physical system is in stationary state (thermal equilibrium) its entropy level is *maximum*, but living systems tend to stationary state because in it their level of entropy production is *minimum* (Prigogine's theorem; Aguilar, 2001; Shapovalov and Kasakov, 2018). Therefore, in addition to the anti-entropic influence of the decrease in the energy/biomass ratio discussed above, the calculation of Eq. (1) with reference to a single scale of hierarchical organization in ecology becomes information, rather than entropy.

This understanding is so fundamental that it deserves a brief anecdotal parenthesis that has profound significance for the understanding of a debate that, according to some authors (e.g., Bawden and Robinson, 2015; Shenker, 2020; Ben-Naim, 2022), has produced a great deal of confusion due to the "unfortunate mistake" of naming Eq. (1) as "entropy". According to an interview with C. E. Shannon narrated by Tribus and McIrvine (1971), the first name Shannon had in mind for Eq. (1) was "information". Later he thought of calling it "uncertainty". Shannon later discussed the issue with John von Neumann, who replied that *"you should call it entropy, for two reasons. In the first place your uncertainty function has been used in statistical mechanics under that name* [von Neumann was talking in this case about Gibb's entropy, whose well-known structure is exactly equal to that of Eq. (1)], *so it already has a name. In the second place, and more important, no one knows what entropy really is, so in a debate you will always have the advantage"*. The final result was that Shannon used both "information" (61 times) and "entropy" (153 times) seemingly indiscriminately in his 1948 publication. This apparent inaccuracy, unexpected in an author with a solid mathematical training, has a very rational explanation that seems to have been misinterpreted many times.

Shannon's article (1948) is a description, static due to purely grammar requirements, of an absolutely fluid process in real life: the encoding, emission, decoding and final reception of a message. The person expecting a message is ignorant of its content, and is not even sure that the content of the message, after being decoded, exactly reflects the information initially emitted because the message has traveled through a channel whose noise level is never zero. According to the 2nd and 3rd laws of thermodynamics, in any channel with a temperature above absolute zero, the physical entropy, and therefore the probability of message alteration, is always greater than 0; this potential defects are controlled in computing by inserting functions of redundancy commonly called "checksums". Therefore, the receiver's brain is invaded by uncertainty, proportional to the restlessness linked to waiting for the message, which causes extra and useless energy expenditure in his/her nervous system (entropy, wasted energy). But after the message is received in a coherent (readable) way, the aforementioned uncertainty/entropy is reduced, precisely because the information is already in the possession of the recipient of the message. As a result, entropy is ignored information (uncertainty) and, in a correlatively opposite way, information is reduced entropy. This explains the concurrent use of these two terms by Shannon (1948).

Thus, in sympoietic systems, entropy and information are two facets of the same phenomenon to the same extent that circumstances change. There is no contradiction in Shannon's manuscript, but rather in the hundreds of hasty interpretations that have been made of it. In a similar way to what was described above, ecosystems may be considered as channels which project information into the future (Margalef, 1961). Every day, each ecosystem "packages" the SDi (eco-information) that it has stored, transforming it into information encoded in the form of DNA contained in spermatozoa, unfertilized ova, zygotes, seeds, and eggs, sending that encoded information toward its own future (genetic channel of information flow in ecosystems; Margalef, 1968). Then, that information is decoded during the ontogenetic process (embryonic development and growth of the individual after birth), giving rise to more replicas of the original SDi that will be under the influence of a

process that modifies the information re-encoded in future messages to refine them according to changes in environmental circumstances: natural selection.

When we are faced with the study of high SDi ecosystems (which can last for months or even years, involving an enormous physical and mental effort not entirely fruitful on our part), the entropy involved in the study is not that of ecosystems, but our own, in order to aspire to understand the eco-information dynamics that those ecosystems have assembled throughout their successional development. This situation was wisely summarized by Margalef (2021, p. 368): *"From the point of view of the sampler, a greater diversity represents a greater uncertainty in the identification of a randomly collected individual* [but] *what for the external observer represents an uncertainty, corresponds to information, or to a measure of organization, if we consider the situation as the result of interactions in the ecosystem itself"*. Summarizing, when we include the term "entropy" as an indicator in our description of sympoietic systems this means, either implicitly or explicitly, that we lack information about our object of study. In turn, when we include the term "information" this means, either implicitly or explicitly, that what we are taking into account is the complexity of the sympoietic systems themselves. As a result, the term *"information entropy"*, so often used in the current literature, is an oxymoron.

After all, the increase of entropy in both classical thermodynamics and statistical mechanics is inversely proportional to the probability of existence of gradients useful for doing work by taking advantage of highly concentrated energy (Tolman, 1938; Callen, 1985; Aguilar, 2001; Gould and Tobochnik, 2021). Therefore, if we use the term "entropy" as an indicator of the development of sympoietic systems this means that either we are using an inverse indicator to the direction of development of such systems, or we are not fully understanding the true meaning of entropy. Even the simple statistical understanding of the heterogeneity indices in Box 1 (i.e., their values are proportional to the probability that two individuals chosen at random belong to *different species*; see section 1), indicates the likelihood of *inter-specific* relationships that are the basis of gradients and energy flows.

Perhaps as a result of a poor understanding of the paradoxical situation described above regarding the mirror-like relationship between entropy and information depending on the analytical parallax, there have been many attempts to "improve" the species diversity indices associated with different entropy concepts mainly through mathematical abstractions and hypothetical models unsupported by field work data (e.g., Rajaram et al., 2017; Gao and Li, 2019; Okamura, 2020; Roach, 2020), and their application to alternative analytical contexts (e.g., Papadimitriou, 2022). However, these or similar attempts could in turn be improved by adopting slight but significant terminological and methodological modifications, if the arguments set out in the preceding paragraphs were taken into account.

Shannon (1948) states about Eq. (1) that *"the constant k merely amounts to a choice of a unit of measure"*. In statistical mechanics, k is a universal constant called Boltzmann's constant (k_B; Aguilar, 2001). This constant means that in a physical thermodynamic system at an absolute temperature T, the average thermal energy is $½k_BT$ per degree of freedom (d.f., in physics, each of the dimensions or ways in which the atoms of a given molecule 'stores' kinetic energy input with increasing temperature: translation, vibration, rotation, and potential energy of vibration). So, there is an increase in total kinetic energy per molecule to the same extent as the number of d.f. increases from monoatomic to polyatomic substances. This is also an important issue to consider in the ecological context (below). The value of k_B is inferred from the statistical mechanical expression of the ideal gas law at the molecular level (being N: number of molecules; m: molecular mass, v: molecular velocity, and $½mv^2$: kinetic energy, E):

$$2N\left(½mv^2\right) = Nk_BT, \tag{3}$$

so:

$$k_B = \frac{2N(½mv^2)}{NT} = \frac{Nmv^2}{NT} = \frac{mv^2}{T}$$

$$= 1.380649\text{E} - 23 \text{ Joule}/\text{Kelvin per molecule} \tag{4}$$

So, Eq. (3) is a comparison between an observed value of total energy at the left-hand side of the equation ($2\ N½mv^2$), and a theoretically expected value given a universal constant (k_B) at the right-hand side of the equation. If the equality in Eq. (3) is satisfied, the observed value of k_B coincides with 1.380649E-23 J/K, and so the system is in stationary state. Given the difficulties in developing an ecosystem theory fully homomorphic with statistical mechanics (Svirezhev, 2000; Ulanowicz, 2004; Nielsen et al., 2020), mainstream ecology assumed that $k = 1$ in Eq. (1). However, according to Margalef (1972; 1993; 2021), the increase of H has an anti-kinetic effect on the 'oscillation' of organisms ('talandic temperature'; Goodwin, 1963; Margalef, 2021), by reducing their dispersal activity around a given reference functional position to perform their ecological niche in an equivalent manner either across space or over time (ergodicity; Hopf, 1932; Tolman, 1938; MacArthur, 1955; Kerner, 1957; Kikuzawa et al., 2009; Gould and Tobochnik, 2021). Therefore, since T increases with kinetic energy (see above), then H has an anti-thermic effect on flora and fauna. Thus, Eq. (4) was homeomorphically transformed from statistical mechanics to ecosystem ecology as follows (Rodríguez et al., 2012; 2013):

$$k_{e\tau(o)} = m_{ep} \cdot I_e^2 \cdot H_p \rightarrow 1.380649\text{E} \pm \varphi \text{ ecoJoule} \cdot \text{nat}/\text{individual}\ (k_{e\tau(e)}), \tag{5}$$

where $k_{e\tau(e)}$ is the expected value ($_{(e)}$) of the ecological equivalent of Boltzmann' constant per individual and taxocene ($_\tau$) under stationary and quasi-stationary conditions; m_{ep} is average body weight or standing biomass (fresh, as a general rule, except in the case of very watery organisms) per individual per plot expressed in kg; H_p is the value of Eq. (1) per plot; and I_e is an ergodic indicator of dispersal activity per individual per plot (Supplementary material) to replace v in Eq. (4) to obtain Eq. (5). Two apps to calculate I_e are freely available in: https://interdisciplinaryscience.es/servicios. The product $m_{ep}{\cdot}I_e{}^2$ expressed in kinetic energy units (i.e., $2(½m_{ep}I_e^2)$, given in kg·đ^2: ecoJoule –J$_e$–, ad hoc unit) indicates the average value of eco-kinetic energy *per individual per plot* (Eq. (6)) used as a proxy for trophic energy; and Eq. (7) assesses its *total value per plot*.

$$E_{ep} = ½m_{ep}I_e^2 \tag{6}$$

$$E_{eTp} = N_p\left(½m_{ep}I_e^2\right) \tag{7}$$

where N_p: N in Eq. (1), but at the plot level. Eq. (6) and Eq. (7) are feasible alternatives based on statistical mechanics to resolve the problem of measuring either productivity or trophic energy by means of variables assumed as direct surrogates, including biomass, rainfall, actual evapotranspiration, nutrients, and 'others' based on problematic assumptions (Whittaker and Heegaard, 2003). H_p is a multiplicative variable in Eq. (5), compared to the role of T as a divisor in Eq. (4), due to the aforementioned anti-thermic influence of H. φ is an integer value per taxocene, although the significand of $k_{e\tau(e)}$ (1.380649, equal to the significand of Boltzmann's constant –k_B– in statistical mechanics, see Eq. (4)) remains constant for all taxocenes. For example, $\varphi = -10$ in marine microalgae; $\varphi = +00$ in tropical rocky shore mollusks; and $\varphi = +03$ in Mediterranean scrub vegetation (Rodríguez et al., 2013). These three equations above ((5), (6), and (7)), has been the pillars for the development of a large set of non-contingent models based on a commonly shared theoretical framework, and brought together under the name Organic Biophysics of Ecosystems (OBEC, see its formal definition and a summary of models in Rodríguez et al., 2019).

Fig. 1 shows and example (see additional cases in Rodríguez et al., 2013) of the empirically proven origin of Eq. (5) based on field work data, all of them from the same survey. The statistical association

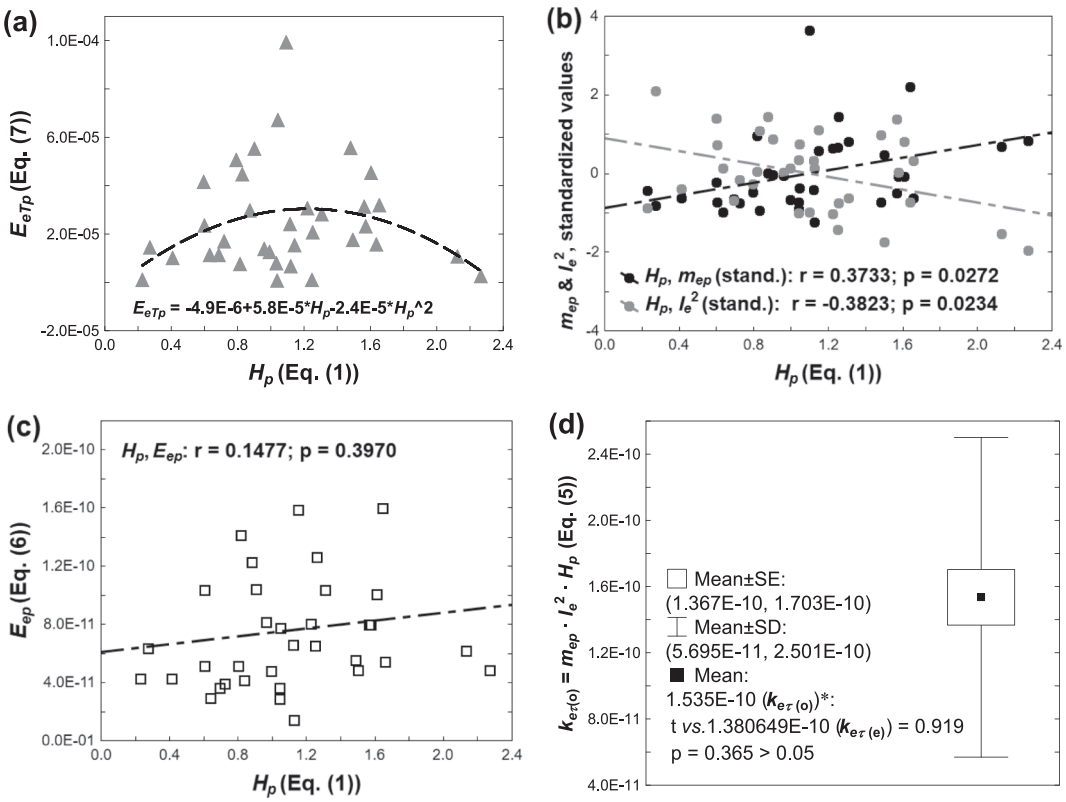

Fig. 1. Relationships between trophodynamic indicators and species diversity in a survey (brackish marsh microalgae) under steady conditions. (a) Inverted U-shaped arrangement of total eco-kinetic energy per plot along the species diversity gradient. (b) Biomass-dispersal trade-off along the species diversity gradient. (c) Correlation between mean eco-kinetic energy per individual per plot and species diversity. (d) Comparison of means between the observed and the expected value of the ecological equivalent of Boltzmann's constant under the conditions shown in (a), (b) and (c). *: two outliers were excluded to improve the result. However, the result remains approximately the same including the outliers: $k_{e\tau(o)} = 1.722196E\text{-}10$; t = 1.659, p = 0.106 > 0.05 *vs.* $k_{e\tau(e)} = 1.380649E\text{-}10$. The data to obtain this figure are available in "Supplementary Table.xlsx".

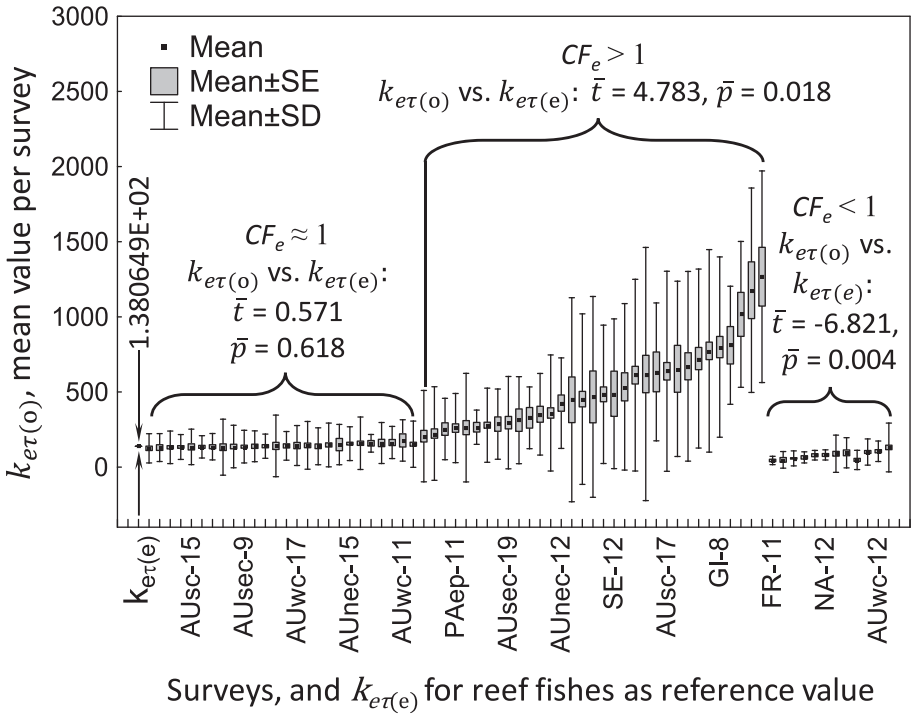

Fig. 2. Results of the calculation of Eq. (5) from 71 reef fish surveys conducted all over the world between 2006 and 2020 (data source: http://reeflifesurvey.com/survey-data/; sampling methodology in Edgar and Stuart-Smith 2014). E.g.: AU: Australia (different coastlines and years); PAep: Panama, eastern Pacific; SE: Seychelles Islands; GI: Galapagos Islands; FR: France; NA: Netherlands Antilles.

between total eco-kinetic energy per plot (Eq. (7)) and SDi per plot (Fig. 1a) follows an inverted U-pattern, just as it was commented in section 1, item (vi).

However, according to Fig. 1b, the average body weight per individual per plot (m_{ep}) *increases* significantly with SDi (Eq. (1)), at the same time that the average dispersal intensity per individual per plot (I_e^2) *decreases* significantly with SDi. That is to say, there is a biomass-dispersal trade-off that, given the structure of Eq. (6), hinders either the decrease or the increase of E_{ep} at any of the edges of the gradient of H_p values (see the lack of statistical association H_p, E_{ep} in Fig. 1c). As a result, since trophic energy (in this case its proxy: eco-kinetic energy) is the 'fuel' to increase information (in this case, eco-information or species diversity; see section 2, first paragraph), then the system remains under steady conditions (i.e., $CF_e \approx 1$, below), "imprisoned" by the situation in both edges of ΔH_p due to the aforementioned trade-off.

That is, H_p in Fig. 1b cannot decrease below a minimum of 0.227 nat/individual because, although there is a deficit of standing biomass per individual (m_{ep}), the dispersal capability per individual per plot (I_e^2) is high. At the opposite edge, H_p cannot grow above a maximum of 2.269 nat/individual because, although there is a high value of standing biomass per individual (m_{ep}), there is a deficit in dispersal capability (I_e^2). As a result, individuals tend to accumulate in the center of the H_p gradient, where the combination of conditions is most conducive to both biomass and dispersion, producing an inverted U-shaped pattern (Fig. 1a). Such accumulation increases the likelihood of competition, so some plots migrate cyclically toward extreme values of H_p.

In reality, Fig. 1b is a fixed picture of a set of interaction that is dynamic (comparative statics –Samuelson, 1941; Milgrom and Shannon, 1994–, similar to how we can acquire new insights by comparing the static situation of different surveys in Fig. 2, below). But Fig. 1b is easily interpretable from well-known physical principles (e.g., when total kinetic energy is added to a system with elements of different masses the heavier elements reach less velocity because they have more inertia, and the opposite is true for lighter elements). Complementarily on the ecological side, Rodríguez et al. (2013) provide a detailed exploration of the links between Fig. 1b and Cope's rule; Rappoport's rule, and *r-K* selection theory (see Eq. (8)).

In terms of analytical symbolism, the relationship commented above can be summarized in the following way (where ↑: increasing variable; ↓: decreasing variable; $\bar{}$: average value; compare Eq. (8) with Eq. (5)):

$$m_{ep}\downarrow I_e^2\uparrow H_p\downarrow\ (r-\text{edge sections}) \Rightarrow \overline{m}_{ep}\overline{I_e^2}\overline{H}_p\ \left(\text{continuum's middle section, net flow of } E_{ep} \text{ between plots tends to } 0\right) \Rightarrow m_{ep}\uparrow I_e^2\downarrow H_p\uparrow\ (K-\text{edge section});\ \text{so}\ \overline{k}_{e\tau(o)}\rightarrow\text{constant}\ \forall\Delta H_p\rightarrow k_{e\tau(e)}\ (\text{see Fig. 1d})\rightarrow CF_e \approx 1 \tag{8}$$

The discovery of $k_{e\tau(e)}$ is recent and unexpected, so its eco-evolutionary meaning is far from being fully understood. However, there are three issues arising from $k_{e\tau(e)}$ that should be emphasized:

i) The ratio between the mean observed value ($_{(o)}$) of $k_{e\tau}$ and the theoretically expected value ($k_{e\tau(o)}/k_{e\tau(e)} = CF_e$, i.e., the ecological equivalent of the compressibility factor in physics; see Aguilar, 2001) indicates the system position with respect to the stationary or quasi-stationary state that is ecologically dominant in the large scale, otherwise ecosystem classification would be impossible at all (see Keith et al., 2022). If $CF_e \approx 1$ the system is in stationary state (Fig. 2), and the total amount of eco-kinetic energy per plot (Eq. (7)) is just enough to sustain the observed value of SDi (stable successional state). If $CF_e > 1$ there is a transient 'excess' in the value of Eq. (7) that can fuel an increase in SDi (unstable and pro-successional state). If $CF_e < 1$ a transient 'deficit' in the value of Eq. (7), and the most plausible prospect is a reduction of SDi (unstable and anti-successional state). As a result, if $CF_e < 1$ the system is more in need of protection than in the other two cases. For instance, the surveys included under the right-hand bracket in Fig. 2 were conducted on the Mediterranean coast; the NW coast of Spain; the Red Sea; the SE and W coasts of Australia; and the Caribbean Sea. Most of these areas are close to large human settlements and/or farming areas that drain into basin-type seas with less capability to reduce waste concentration compared to oceanic areas. These areas are also more sensitive to overfishing, and are the target of intense tourist activity and maritime traffic. Therefore, the result that $k_{e\tau(o)}/k_{e\tau(e)} = CF_e < 1$, indicating degradation of the ichthyofauna in these areas, is plausible.

ii) The assumption that $k = 1$ in Eq. (1) is no longer consistent with reality. That is to say, the orthodox idea that species diversity or eco-information is free in terms of energy must be discarded, otherwise we would be treating the ecosystem as a perpetual motion machine even though we know perfectly well that it is not.

iii) From the fundamental understanding in this article (above), and combining Eq. (2) and Eq. (5), the aggregated value of negative entropy (Schrödinger 1944), a.k.a. negentropy (Brillouin, 1956) or syntropy (Fantappiè, 1942; 1993) can be assessed as:

$$Sn_{e\tau} = k_{e\tau(e)}\cdot(\ln\Omega) = k_{e\tau(e)}\cdot\left(\ln\frac{N!}{\prod_i n_i!}\right) = k_{e\tau(e)}\cdot\left(\left(-\sum_{i=1}^{S}(p_i\ln p_i)\right)\cdot N\right) \tag{9}$$

Eq. (9) is a proxy –within the theoretical framework of this study– for the total value of trophic energy dynamically involved in sustaining the total value of SDi during microstate oscillations in a given survey belonging to a given taxocene –τ–; its unit of measurement is $J_e{\cdot}nat/individual^2$. The negentropic sense of Eq. (9) is based on Eq. (5) as a homomorphic inversion of Eq. (4). That is to say, v^2 *increases* with T to calculate k_B in Eq. (4), while I_e^2 *decreases* with H_p to calculated $k_{e\tau(e)}$ in Eq. (5). The relation $N!/\prod_i n_i!$ in Eq. (9) implies a level of randomness in the combination of linear momentum and coordinates of transient assemblies of individuals/species on the ecosystem surface taken itself as phase space. This approach is not alien to conventional ecology, since there are other proposals essentially based on stochastic dynamics (e.g., Hubbell, 2001). The key difference relies on a minimum number of simple assumptions (e.g., replacing v^2 and T in Eq. (4) by I_e^2 and H_p in Eq. (5), respectively) to obtain a broad spectrum of results consistent with the principles and methods of conventional physics and classical eco-evolutionary theory (see above in the comments concerning Fig. 1), as well as valid for any type of taxocene.

As discussed above (section 2), the production of standing biomass linked to the reduction of the energy/biomass ratio is perhaps the most remarkable anti-entropic effect of eco-evolutionary processes. Therefore, if Eq. (9) is reliable, there should be a significant association between $Sn_{e\tau}$ and total standing biomass (m_{eTs}) per survey, both inter-taxocene and intra-taxocene (Fig. 3). This result indicates that the long eco-evolutionary process, summarized in Fig. 3, is highly biomass-dependent, thus, locally anti-entropic.

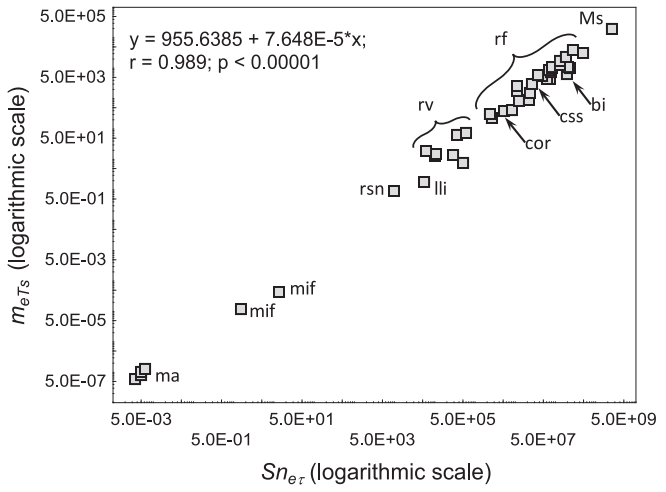

Fig. 3. Pearson correlation between total syntropy per survey ($Sn_{e\tau}$, Eq. (9)) and total standing biomass per survey (m_{eTs}) from 45 surveys from systems under stationary conditions (i.e., $CF_e \approx 1$) belonging to 10 taxocenes: marine microalgae (ma); sandy beach invertebrate meiofauna (mif); tropical rocky shore snails (rsn); litter invertebrates in laurel forests (lli); ruderal vegetation (rv); massive (non-branching) corals (cor); coastal succulent scrub (css); European birds (bi), reef fishes (rf), and Mediterranean scrub (Ms). Data sources: Rodríguez et al. (2013); Riera et al. (2021); and http://reeflifesurvey.com/survey-data/.

However, according to the low value of the slope (7.648E–5) of the regression equation in Fig. 3, for each unit of increase in $Sn_{e\tau}$ there is a high surplus of energy beyond the investment in standing biomass. Thus, in addition to leakage due to energy dissipation, there are additional ecological d.f. in which energy is invested during transitions from one microstate to another. Namely, fluctuations of active metabolic rate; alternation between competitive and symbiotic strategies; intraspecific and interspecific communication by sonic, chemical and electromagnetic signaling; selection of habitat; antibiosis; sleep and wake cycles; photo and chemotaxis; construction and deconstruction of functional guilds; learning; and even reasoning. This connects with the idea that large or large-brained and long-lived animals learn to learn and introduce reflection into nature (Margalef, 1992). Thus the key element in Fig. 3 is not the value of *r*, but the low value of the regression coefficient (i.e., 7.648E-5), which indicates the enormous amount of energy devoted to other purposes beyond standing biomass production. As previously argued, any ecosystem is a living physical system ruled by the interaction between energy and the amount of information. Therefore, the view that *all physical laws* become relationships between types of information, or information functions collected or constructed according to various procedures (Rothstein, 1951) is especially valid in the ecological context.

The idiosyncratic nature of $k_{e\tau(e)}$ (i.e., that φ changes depending on the taxocene) means that the pattern explored in this study would have been impossible to find by working with βSDi-level data, because the underlying pattern related to $k_{e\tau(e)}$ is hidden, completely blurred, by the coexistence of several taxocenes with different values of φ. A typical example is the concurrency of corals (cor) and reef fishes (rf) in the same range of the regression equation in Fig. 3. In fact, they coexist in real ecosystems, despite the fact that $\varphi_{cor} = -01$, and $\varphi_{rf} = +02$. The role of CF_e for monitoring and conservation biology (above) also is invalidated by working with γSDi-level data, as mixing data from several communities/ecosystems can result, for instance, in an overall classification of $CF_e \approx 1$, or the reverse, despite biological communities, isolated from each other, being in different trophodynamic states.

In addition, the net flow of trophic energy within and between ecosystem goes from low to high values of *H* or, conversely, as expected from physics, from high to low talandic temperature (Margalef, 1963). The key difference between non-sympoietic systems and ecosystems is that in the former case the energy flow ceases when equilibrium is reached spontaneously and the gradient is cancelled. However, in the second case, the system that receives the net flow of energy uses that flow to increase *H*, thus reaching a state of lower talandic temperature that maintains or even increases the gradient, and therefore the energy flow intensity. This makes αSDi the most important and understandable level to analyze trophodynamic flows. Furthermore, the equivalence of significand (1.380649) between k_B (Eq. (4)) and $k_{e\tau(e)}$ (Eq. (5)) would be impossible to achieve if the calculation of Eq. (5) is performed by using an index other than Eq. (1), with the exception of Brillouin's index (H_B, see Eq. (2)). Anyway, it is more practical to work with Eq. (1), because the direct calculation of factorials in H_B quickly exceeds the computational capacity of some standard software (e.g., 170! = 7.257E + 306). In a nutshell, it has been shown that αSDi is the key framework to understand ecosystem functioning and trophodynamic interactions in dynamic multiscapes.

The approach proposed in this article is based on a simplification of extremely complex systems (ecosystems) to only a few fundamental variables (species abundance, standing biomass, geographical coordinates, dispersal ability, and species diversity) at the taxocene scale. However, on the one hand, it has been very early established (see Margalef, 1968, p. 358) that the taxocene is the only truly operational unit for field work in ecology (see comments about the importance of this idea in the two preceding paragraphs).

On the other hand, the best science is usually done when a broad spectrum of theoretically and empirically relevant results is obtained from as simple a set of parameters and assumptions as possible. It is also true that this variant of Ockham's razor (a.k.a. principle of parsimony) is not universal, but it has been epistemologically very fruitful (Schaffer, 2015).

Simplicity is not synonymous neither with irrelevance nor lack of accuracy, but perhaps quite the opposite. For example, a review of articles based on economic forecasting models found no evidence that complexity improves forecast accuracy; on the contrary, increasing model complexity increases forecast error by 27 percent, and the 22 forecasting procedures whose validity was empirically verified were rated as simple (Green and Armstrong, 2015). In fact, it has been stated that papers in the fields of ecology and evolution receive 28 % fewer citations overall for each additional equation per page in the main text, although they tend to be more frequently cited by other theoretical papers; but this increase is outweighed by a sharp drop in citations from non-theoretical papers at a rate of 35 % fewer citations for each additional equation per page in the main text (Fawcett and Higginson, 2012).

Adding more and more variables and connections to a model to make it more and more "rigorous" leads us to the paradox of achieving a model as complex as reality itself, which we have not been able to understand precisely because it includes so many variables and connections. In this sense, like the biomass-dispersal trade-off around which this article revolves, there is also an epistemological trade-off between rigor and relevance. This is why Boddy (1999) describes this epistemological situation as *"rigour mortis"*. It seems paradoxical, but sometimes the road to simplicity in the essential understanding of natural processes is more difficult to travel than the other way around (Riera et al., 2023), and this has been the main epistemological axis to develop this article.

CRediT authorship contribution statement

Ada M. Herrera: Conceptualization, Resources, Validation, Visualization, Writing – original draft. **Rodrigo Riera:** Funding acquisition, Conceptualization, Investigation, Methodology, Resources, Validation, Writing – review & editing. **Ricardo A. Rodríguez:** Data curation, Formal analysis, Methodology, Project administration, Software, Supervision, Validation, Visualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.111118.

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