Short communication

Exploring the spontaneous contribution of Claude E. Shannon to eco-evolutionary theory

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A R T I C L E   I N F O

A B S T R A C T

This article performs an analysis of the article in which Claude E. Shannon proposed his now famous H measure of information amount, by finding that four crucial traits analyzed by Shannon in regard to the meaning of H in information theory (i.e.: (a) introduction of a constant ad hoc – k – in order to achieve a formal connection between the statistical dimension of H and a given system of measurement units; (b) redundancy measurement; (c) joint events; and (d) conditional information) have strong theoretical connections with several important and well-known ecological phenomena (i.e.: (a′) extensive measurement of ecological entropy in quasi-physical units; (b′) theoretical meaning and successional behavior of redundancy; (c′) competitive exclusion; and (d′) ecological niche resilience, respectively). This set of corresponding connections (a, b, c, d, vs. a′, b′, c′, d′) has not been reported in the literature ever before, and it is fully understandable from the ecological viewpoint, despite the fact that the proposal from Shannon is previous and fully independent in comparison with any posterior attempt to establish a connection between ecology, physics and information theory. So, in practice, Shannon was also investigating in ecology and evolutionary biology, despite he was neither an ecologist nor an evolutionary biologist. In summary, our set of results: (i) implies that Shannon was an spontaneous ecologist, or at least an unwitting founder of ecological science such that, after Shannon, every ecologist of ecosystems can thus be viewed as a sort of "computer technician of nature"; (ii) highlights the fruitfulness of thinking about natural history in interdisciplinary terms; and (iii) expands the theoretical justification for applying H as a key indicator to build reliable models that are coherent with the principles of ecology, evolutionary biology, information theory and physics.

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1. Introduction

There are scholars whose intellectual influence has had implications far beyond their original research field, many years or even decades after some of their seminal publication (1948, in this case), and in a way that could not have been foreseen by the scholar himself. This is precisely the case of Claude E. Shannon (1916–2001). This article is intended to explore the meaning of his unwitting scientific contribution, in the particular case of eco-evolutionary theory. Our goal is to enhance the theoretical foundation of a set of recent proposals (commented in sections below) to achieve an interdisciplinary understanding about the ecosystem functioning by using the measure of information amount (H) of Shannon as the main state variable in ecosystem ecology. With such a

goal, we analyze the eco-evolutionary meaning of four typical phenomena studied in the field of information theory. Firstly, we remark the interdisciplinary meaning of the introduction by Shannon of a constant – k – in his equation to measure the amount of entropy/information (H) in a message that is being sent by a channel with a variable level of noise. We then compare the ways of interpreting redundancy in information theory and in conventional ecology (A/N: the term "*conventional*", from now on in this article, refers to those branches and scholars of any science that are not devoted to interdisciplinary studies), and their opposite results to understand ecosystem functioning in comparison with very recent proposals in this field. In the remaining sections we deal with the eco-evolutionary significance of joint events and conditional information.

2. The transdisciplinary usefulness of *H*; its meaning and its meaninglessness to understand the ecosystem functioning, and the first contribution of Shannon to eco-evolutionary theory

The key point in this section, willfully neglecting some requisites for the emergence of life, as water availability and the appropriate range of temperature, is to understand the seemingly contradictory relationship between the emergence of life as a highly organized state of matter, and the influence of the second law of thermodynamics (SLT). The conventional viewpoint in this regard is that a flow of energy (i.e.: open nature of the system) is enough to dodge the pro-entropic influence from SLT that produces the spontaneous drift toward equilibrium in isolated systems.

However, two additional obstacles need to be surmounted to avoid the influence of SLT in living systems: (i) Light can be regarded as "physical rubbish" expelled by the Sun, i.e.: if the proton–proton chain reaction in the Sun would have an efficiency of 100% from the energy point of view for converting hydrogen to helium, the Sun would be absolutely black. Life on Earth as a whole is then supported by the consumption of energy of low quality (Sun's entropy) from the physical point of view, in a similar way in which bacteria are able to obtain energy from highly degraded organic wastes, or even from rocks. That is to say, the key problem of life is to be able to keep a state of high internal organization, sustained at low temperature conditions, by using low quality energy from the physical viewpoint. (ii) The *equilibrium* state in isolated systems and the *stationary* state in open systems are analytically equivalent to each other (see Montero and Morán, 1992), and Rodríguez et al. (2013a) have shown that the latter state is the most common in ecological systems and can be described by the physics of the former one. Escaping from the pro-entropic effect of SLT depends on a biomass-dispersal trade-off that is the *sine qua non* requisite to stably sustain a quantum ecological dynamics (see Rodríguez et al., 2013a, 2015b,c,d, 2016) in order to avoid the leak of energy in ecosystems under stationary conditions. In summary, a simple flow of energy is far to be enough to support life, some internal biological properties that depend on additional conditions are necessary in this regard. This explains why, from the point of view of conventional thermodynamics, life seems to be a very weird anomaly. So this issue is connected to one of the deepest questions of science: What is life? (Schrödinger, 1946).

The handiest argument from conventional physicists is that the anti-entropic trend of life is transient. This implies that it does not matter how young and strong we would be in a given moment of our lives, death is always the end, and entropy will win the fight. However, from the evolutionary point of view, a significant argument against the validity of this dismal statement seems to emerge when we connect the endurance of biological systems and the statistical factor linked to the internal increase of information amount in them. This seems to be the essence of life itself.

Mathematically speaking, if we assume that s_T is the total number of types of elements within a given system (i.e.: total species number or "richness" in ecosystem ecology); i is a particular type of these elements; n_i is the abundance of i; $N = \sum n_i$, and k is a positive constant (it is conventionally assumed that $k = 1$ in ecology) that merely amounts to a choice of a unit of measure (Shannon, 1948, p. 389) in order to perform the transference between the statistical dimension of H ($-\sum p_i \cdot \ln p_i$) and a given system of physical measurement units; then the measure of amount of information, choice, uncertainty and entropy of Shannon (1948) is:

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

Eq. (1) indicates the *mean amount of information per element* (nat/individual, if natural logarithms are used) within the system; and H does not stop to increase along the eco-evolutionary sequence of systems, from the diminutive bacterium until the biosphere as a whole. The whole epistemological trouble about the usage of H in sciences out of the theory of communication lies in two facts:

(a) H is an attractive formula because it has a relatively simple mathematical structure, and s_T can be almost anything: total of types of letters in a given message sent through a transmission channel affected by a variable degree of noise (this was the original analytical context in which Shannon worked); total of types of soils in an edaphological survey (e.g.: McBratney and Minasny, 2007); total of types of cells in a sample of tumor tissue (Park et al., 2010); total of types of employments in a city (e.g.: Attaran, 1986); and total of species in an ecological survey, a case in which an overwhelming number of articles could be cited. If the empirical usefulness of H in all of these fields due to its relevant correlations with other indicators is supported by an appropriate theoretical foundation, that is another matter.

(b) Shannon (1948) refers to H in a seemingly ambivalent way, either as *entropy* or as *information* or as *uncertainty*, in spite of the opposite relation between *information* and *entropy*, and the equivalence between *entropy*, *uncertainty*, and *information reduction* (e.g.: see Jaynes, 1957; Brillouin, 1956, pp. 159–161; Rothstein, 1952, p. 135; Gallucci, 1973; Brissaud, 2005; Tiezzi and Pulselli, 2008). This has produced a cascade of additional confusions in other sciences over the subsequent decades starting from "the bandwagon effect" (see Shannon, 1956) of his proposal. For example, the modeling of ecosystem structure based on the presumptive spontaneous trend of ecosystems to maximize entropy (maximum entropy formalism, MaxEnt) has supporters (e.g.: Harte, 2011; Harte and Newman, 2014) and critics (e.g.: Haegeman and Loreau, 2008; Yackulic et al., 2013). The main problems of MaxEnt from the theoretical point of view seem to be the following:

(b.1) "*The word 'entropy' refers here* [in regard to the ecosystem structure] to **information entropy** [H, Eq. (1)], rather than **thermodynamic entropy** [S, see Eq. (3), below]. *Information entropy is a quantitative measure of uncertainty about an outcome of a draw from a probability distribution.*" (Harte and Newman, 2014, p. 385). However, "*Shannon went on to define the information (I) in a message as the difference between two entropies, or uncertainties: one that is associated with knowledge X before a message and the other that is associated with knowledge X′ after a message*" (Tribus and McIrvine, 1971, p. 180). That is to say, entropy, in Shannonian terms, is nothing more than information that is ignored by a given system: a human observer that is waiting for a message that has been sent to him through a channel, in the original context of Shannon's studies. But,

what happen if the channel itself is another living system, like an ecosystem? It happens that the difference between entropy and information becomes a simple problem of the system of reference used to describe the message whose amount of information/entropy is given by H: "*Which to the outside observer represents an uncertainty corresponds to information or a measure of organization, considering the situation as a result of interactions within the ecosystem itself*" (Margalef, 1991, p. 368), given that "*every organism is an "observer" of the environment . . . each species observes the environment on its own unique suite of scales of space and time*" (Levin, 1992, pp. 1943, 1945). "*Von Neumann told me [Shannon said], 'you should call it [in reference to H] entropy, for two reasons. In the first place your uncertainty function has been used in statistical mechanics under that name, 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'*" (Tribus and McIrvine, 1971, p. 180). In addition: "*This expression [H], is equivalent to the one used by Brillouin [H_B, see Eq. (2)], that is the same used by Boltzmann [S, see Eq. (3)] divided by the number of N elements [of the system]*" (Margalef, 1991, p. 367). That is to say, $S = H_B \times \sum n_i = H_B \times N$; and if we have a highly representative sample in which $\forall n_i$: $1 \ll n_i \geq 100$; then $H \times \sum n_i = H \times N \approx H_B \times N = S$; with $H \times N = H_B \times N = S$ when $\forall n_i$: $1 \ll n_i \to \infty$:

$$H_B = \frac{1}{N} \ln \left(\frac{N!}{\prod_{i=1}^{s_T} n_i!} \right) \quad (2)$$

$$S = k_B \ln W = k_B \ln \left(\frac{N!}{\prod_{i=1}^{s_T} n_i!} \right) \quad (3)$$

where Π is the product of the sequence of values from $n_1!$ to $n_{sT}!$; and k_B is the Boltzmann constant (1.3806504E−23 J/K per molecule), which allows the conversion from a purely statistical expression ($\ln W$) to energy units. Since the following example is focused on the statistical dimension of H and S (i.e.: $-\sum p_i \cdot \ln p_i$ and $\ln W$, respectively, without constants as k and k_B), in this case it has been assumed, by the moment, that $k = k_B = 1$. This is the standard procedure in ecology given that the connection between the statistical side of H and the physical side, through k, has been systematically neglected until three years ago (Rodríguez et al., 2012). For example, let us suppose that we have a sample in which $n_1 = 389$, $n_2 = 299$, $n_3 = 240$, $n_4 = 550$, $n_5 = 225$, $n_6 = 441$, $n_7 = 503$, $n_8 = 565$, $n_9 = 627$, $n_{10} = 689$ and therefore $\sum n_i = N = 4528$. Consequently: $H_B = 2.23456$; $H_B \times N = 10118.07221 = S$; $H = 2.24213$; $H \times N = 10152.38241$; and $S/(H \times N) = 0.99662 \approx 1$. That is to say, it is superfluous to establish a differentiation between Eq. (1) as "**information entropy**" and "**thermodynamic entropy**" because H is the mean amount of entropy/information per individual in statistical thermodynamics. In other words, H is an intensive expression (i.e.: the mean amount of a given extensive indicator x per element of the system) of the well-known Boltzmannian entropy (S). The Second Law maintains its validity because any mean increase or gathering of additional information per individual implies a consumption (partial degradation) of energy taken from the outside (see, e.g.: Volkenshtein, 1985, p. 326), with a consequent dissipation of heat to the environment. But, simultaneously, the degree of internal self-control of ecosystems is higher and higher with the internal increase of H. This implies

a reduction of internal entropy in the same way in which the receptor of a message reduces its uncertainty (entropy) after the message has been received and read (see comment above).

(b.2) Thermostatistics is a description of classical thermodynamics by means of Newtonian mechanics. Thus, the explanation of ecosystem functioning by means of statistical mechanics by using either H (based on probability per species and therefore valid for surveys) or H_B (based on absolute total abundance per species and therefore valid for censuses) as a central state variable would imply a triple synthesis between information theory, Newtonian mechanics, and eco-evolutionary biology: "*None accepts the challenge of seeking a synthesis of the Newtonian and Darwinian traditions. I do not know how such a synthesis might come about, nor where it would lead. (. . .) A 'Fermi approach' based on models that capture the essence of the problem, but not all the details, might get us farther. We need to develop simple, mechanistic models*" (Harte, 2002, p. 31). However, it seems to be that Shannon himself laid the foundation stone for this synthesis when he included, 67 years ago, a positive constant (k, in Eq. (1)), in a similar way in which k_B is included in Eq. (3): Rodríguez et al. (2012, 2013a) calculated the product between the statistical fraction of H (i.e.: $-\sum p_i \cdot \ln p_i$) at the ecosystem plot ($_p$) level (H_p: H used as an indicator of species diversity per plot) and two crucial ecological indicators (mean biomass per individual per plot – m_{ep} – and a proxy of mean dispersal activity – I_e – per individual per plot that has equivalent statistical and physical traits to those of physical velocity – v; about the structure and meaning of I_e, see Appendix A, Sections 1) in the following way:

$$m_{ep} \times I_e^2 \times H; \quad (4)$$

with $k = 1$ in Eq. (1)

Eq. (4) yielded a constant (k_e) under stationary ecological conditions (SEC; i.e.: balance between energy gained and energy lost at the ecosystem scale) due to a biomass-dispersal trade-off in function of the gradient of H_p values (see Rodríguez et al., 2013a). In this way: $m_{ep\,min.} \leftrightarrow H_{p\,min.}$; $I_e^2{}_{min.} \leftrightarrow H_{p\,max.}$; $(m_e \cdot I_e^2)_{max.} \leftrightarrow$ intermediate values of H_p, close to the peak of the statistical density distribution of H_p values (i.e.: the mode of the distribution: M_{H_p}). In addition, the value of $k_e \to 1.3806504E\varphi J_e$ nat per individual (J_e: 1 ecoJoule = 0.5 kg ₫²; ₫: 1 dispersal unit, the unit of expression of I_e; about the necessity of introducing the unit J_e – ecoJoule, see Appendix A, Section 2); being $\varphi = -x_i, \ldots, -3, -2, -1, 0, +1, +2, +3, \ldots, +x_i$, with a typical recurrent value depending on the type of taxocenosis studied (e.g.: $\varphi = -10$ for marine microalgae, $\varphi = -04$ for marine interstitial meiofauna of sandy beaches, $\varphi = -01$ for massive – non-branching – corals and litter invertebrates in pine forest, $\varphi = +00$ for litter invertebrates in laurisilva and tropical rocky shore snails, $\varphi = +02$ for coral reef fish and ruderal vegetation, $\varphi = +03$ for Mediterranean shrub vegetation, etc., see Rodríguez et al., 2013a). In other words, Eq. (4) is equivalent to replace k in Eq. (1) by $m_{ep} \cdot I_e^2 = 2E_e$ (see Eq. (5)), assuming that $H = 1$. Regarding Eq. (4) there are two important points:

(b.2.i) The values of k_e and k_B (see Eq. (3)) are very similar to each other.

(b.2.ii) It is important to take into account that, on the contrary to k_B, which is a *quotient* constant (i.e.: its expression unit is J/K per molecule), k_e is a *multiplicative* constant (i.e.: its expression unit is J_e nat per individual). This means that if we take the

calculation of the mean value of eco-kinetic energy (from Rodríguez et al., 2012, 2013a,b, 2015a) per individual as a proxy for trophic energy calculated as

$$E_e = \frac{1}{2} m_{ep} \times I_e^2, \qquad (5)$$

in a similar way in which the kinetic energy in physics is (whit m: mass, and v: velocity)

$$E = \frac{1}{2} m \times v^2, \qquad (6)$$

then k_e indicates that the mean amount of eco-kinetic energy per individual *changes at a constant rate within the ecosystem* per every variation of 1 nat per individual either toward the left edge ($H_{p\,min.}$) or toward the right edge ($H_{p\,max.}$) of the gradient of species diversity starting from the peak or mode (M_{Hp}) of the distribution of H_p values taken as a reference point. This is in agreement with the anti-entropic influence of the increase of H (see references above), but in a very paradoxical and indirect way: at the local scale *under SEC*, on the one hand, the *reduction* of species diversity per plot from M_{Hp} to $H_{p\,min.}$ has a *pro-entropic* influence, because the amount of energy per unit of biomass (($N_p \cdot E_e$)/$m_{eTp} = E_{eTp}/m_{eTp} = x$ J$_e$/kg; where N_p: total abundance of individuals per plot, E_{eTp}: total eco-kinetic energy per plot, and m_{eTp}: total biomass per plot) *increases* with the decreasing value of H_p. On the other hand, the *increase* of species diversity per plot from M_{Hp} to $H_{p\,max.}$ has an *anti-entropic* influence, because E_{eTp}/m_{eTp} *decreases* with the increasing value of H_p. That is to say, from M_{Hp} to $H_{p\,min.}$, it is more and more expensive to sustain every unit of biomass in energy terms but, on the contrary, from M_{Hp} to $H_{p\,max.}$ it is cheaper and cheaper to sustain every unit of biomass in energy terms (see Fig. 1a). However, *under non-SEC* in favor of the successional process (i.e.: an increasing value of total species diversity: H_T), given the right skewed nature of gamma distribution of species diversity values (see Margalef, 1991, p. 367; Rodríguez et al., 2013b; Rodríguez et al., 2015b), the integral of the right tail (from M_{Hp} to $H_{p\,max.}$) of the distribution of H_p values is proportionally larger and larger ("*it has been shown that the more uniform – flat and smooth – a probability distribution is, the larger is its information*", Harte and Newman, 2014, p. 385) in comparison with those distributions with lower values of H_T. As a result, the anti-entropic effect of the increase of H_p (i.e.: lower values of E_{eTp}/m_{eTp}) prevails in the long run if the ecosystem moves in favor of the successional process, meanwhile entropy increases with the reduction of H_T when the ecosystem moves in the opposite direction (ecological degradation: movement toward narrower and more peaked distribution of H_p values with shorter right tails). Plainly, living creatures tend to use less energy per kg of biomass under high diversity conditions (see also Margalef, 1963, 1991; Odum, 1969). As a consequence, the adjustment of H_p values to gamma distribution creates a general differential selective pressure in favor of entropy reduction that explains why "*the right-skewed nature of H and I_e distributions can be seen as an evolutionary imperative instead*

of an accidental statistical peculiarity" (Rodríguez et al., 2013b, p. 4). Therefore, the relevant question in this case is: What would be the total amount of ecological entropy (S_e) expressed in quasi-physical terms (given that Eqs. (5) and (6) are analytically equivalent to each other) for the ecosystem as a whole? By replacing k_B by k_e in Eq. (3) in agreement with the above-mentioned meaning of k_e, S_e can be assessed as:

$$S_e = k_e \ln W = k_e \ln \left(\frac{N!}{\prod_{i=1}^{s_T} n_i!} \right) = k_e \times H_B \times N$$

$$\approx \left(-k_e \sum_{i=1}^{s_T} (p_i \cdot \ln p_i) \right) \cdot N \qquad (7)$$

In even simpler words, Eq. (7) responds to the following issue: If for 1 nat and 1 individual $k_e = 1.3806504$Eφ J$_e$; how much would be the amount of entropy expressed in quasi-physical measurement units for $x > 1$ nat and $N > 1$ individual? Answer: Eq. (7). This equation, as well as the simple analytical route that has been used to get it, has three advantages: (a) It is in agreement with one of the main traits to reach a Newtonian ↔ Darwinian synthesis in ecology according to Harte (2002, p. 31): "*They [the suitable synthetic models in ecology] will, perforce, be caricatures of the Earth system, but they must be falsifiable. Coupled with the development of such models, it is critical to identify appropriately lumped system variables that can substitute for subsets of the detailed variables in traditional complex models.*" (b) It overcomes the difficulties to apply conventional physics in order to understand the functioning of far-from-equilibrium systems because of the lack of a defined method to assess the physical entropy in living systems (see Aguilar, 2001, p. 180; Aoki, 2006, p. 56; Callender, 2004, p. 18). (c) It surpasses the underlying epistemological difficulty of MaxEnt, in comparison with the experimental nature of ecology, mainly if we take into account that MaxEnt was initially proposed to develop a "*subjective statistical mechanics . . . independently of any physical argument, and in particular independently of experimental verification*" (Jaynes, 1957, p. 620).

So, as it has been explained above (item (b.1)), an onion-like ecological structure is always sustained by a "game" between opposite trends (maximization vs. minimization) regarding the management of entropy values across a complex hierarchical sequence that embraces several ecological levels (i.e.: unit of biomass → individual → population → guild → stratum → taxocenosis, and so on). For example, the distribution of values of total eco-kinetic energy per plot ($E_{eTp} = N_p \times E_e$; see Eq. (5)) under stationary ecological conditions is fully equivalent to the classical pyramidal distribution of trophic energy, and can be described by means of a simple modification of the Boltzmann distribution of molecular energy in the equilibrium state, in the following way (Rodríguez et al., 2015a):

$$N_i = \left(\frac{N}{\sum_{\varepsilon_i=0}^{\varepsilon_{i\,max}} \cdot e^{-\varepsilon_i H_T / N_{mp} k_e}} \right) \times e^{-\varepsilon_i H_T / N_{mp} k_e} \qquad (8)$$

where N is the number of values of total eco-kinetic energy per plot (E_{eTp}) included in the observed distribution; e is the Euler's
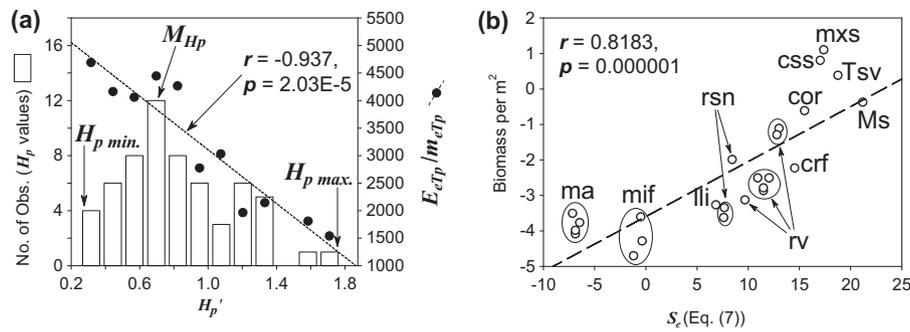
Fig. 1. Two key regularities about the physical effects of species diversity. (a) Behavior of E_{eTp}/m_{eTp} (in J$_e$/kg) across a statistical density distribution of species diversity values per plot (H_p). H_p': midpoint per category of H_p values. From data of ruderal vegetation (Rodríguez et al., 2015b, Appendix B, survey "rv9", rows 46–56); meaning of the remaining variables in the main text. (b) Statistical association between standing biomass per square meter and total ecological entropy (S_e, Eq. (7)) per survey for several taxocenes according to data from Rodríguez et al. (2013b, Table 1), and Rodríguez et al. (2015a, Appendix B, Table "Additional data"). ma: marine microalgae; mif: marine interstitial meiofauna of sandy beaches; lli: litter invertebrates in laurisilva; cor: massive (non-branching) corals; rsn: tropical rocky shore snails; rv: ruderal vegetation; crf: coral reef fish; Ms: Mediterranean shrub vegetation; mxs: mixed shrub vegetation; css: coastal succulent shrub vegetation; Tsv: succulent vegetation, Tenerife Island; Natural-log transformed values were used in both axes.

number; k_e is the ecological equivalent of the Boltzmann's constant (see above); N_i is the number of E_{eTp} values equivalent to the number of plots (n_p) per energy class associated to the energy level ε_i; ε_i are the lower limit of the class of E_{eTp} values for which the expected value of N_i is calculated; N_{mp} is the mean number of individuals per plot regarding the survey as a whole, and H_T is total species diversity at the survey level. The key point in Eq. (8) is the ecological equivalent ($\exp.-\varepsilon_i H_T/N_{mp}k_e$) of the physical Boltzmann factor ($\exp.-\varepsilon_i/k_B T$; where T is the absolute temperature), because the interaction between the elements of $\exp.-\varepsilon_i H_T/N_{mp}k_e$ determines the width, high and shape of the respective model of eco-kinetic energy pyramid. However, from Eq. (4), (5) and (7), $-\varepsilon_i H_T/N_{mp}k_e$ in Eq. (8) can also be expressed as (see Rodríguez et al., 2015a, p. 33, Eq. (10)):

$$-\frac{\varepsilon_i H_T}{N_{mp}k_e} = -\frac{\varepsilon_i \times S_T}{2N_T \times E_e \times S_p} \qquad (9)$$

where N_T is the total number of individuals at the survey level, S_T is entropy (calculated as $N_T \times (-\sum p_i \cdot \ln p_i)$) at a higher level (the ecosystem as a whole), S_p is entropy (calculated as $N_p \times (-\sum p_i \cdot \ln p_i)$) at a lower one (plot level, in this case), and E_e is the mean value of Eq. (5) at the ecosystem level. An increase of S_T in the numerator of Eq. (9) reduces the value of the ecological partition function ($Z_e = \sum \exp.-\varepsilon_i H_T/N_{mp}k_e$; in Eq. (8)) producing flatter and more acuminated pyramidal distributions of eco-kinetic energy, meanwhile an increase of S_p in the denominator of Eq. (9) produces just the opposite effect. So the size and shape of energy pyramids depend on the dynamic balance between entropy values at two different hierarchical levels.

For example, the evolutionary turning point between microscopic and macroscopic life seems to be linked to a transition border (from $S_T > 2 N_T \cdot E_e \cdot S_p$ to $S_T < 2 N_T \cdot E_e \cdot S_p$) between two opposite imbalances between the numerator and the denominator of Eq. (9) in function of the increase of maximum value of total eco-kinetic energy per plot ($E_{eTp\ max.}$) in the ecosystem (see Rodríguez et al., 2015a, Figure 5e). This trade-off between organization levels is a typical trait of complex systems. For example, an increase in the consumption rate of exosomatic energy from fossil fuels (increase of environmental abiotic entropy) to sustain a high-technology socioeconomic functioning allows a reduction in the consumption rate of somatic (metabolic) energy of individuals (reduction of biotic entropy per individual) as well as a socio-economic drift from work done with the body to work done with the mind (information gain) that it is commonly called as "well-being", and vice versa. For example, in nature, by using the results already exposed by

Rodríguez et al. (2013a, p. 13, Table 1), it is possible to obtain a direct and significant correlation between entropy at the survey level expressed in quasi-physical terms (S_e, Eq. (7)) and total standing biomass per unit of space (see Fig. 1b). Given that a higher capability for biomass production implies a more efficient conversion of solar energy to biological tissues, the conventional assumption that the internal entropy of an ecosystem rises with the increase of species diversity is not consistent with the empirical result in Fig. 1b.

In summary, this section shows that it is controversial to speak about "entropy" (in singular) at the ecosystem level given that every ecosystem is a combination of many taxocenes and hierarchical functional levels: a sort of "multi-layered cake" in which each taxocene has had its evolutionary opportunity to evolve from a minimum of $H_T = 0$ nat/individual to a maximum of $H_T \approx 5.64$ nat/individual (see Rodríguez et al., 2015c), but with different typical rates of exchange energy $\leftrightarrow$ information in agreement with the discrete (non-continuous) variations of k_e at the inter-taxocenosis level in any multi-hierarchical system: "...*it may come as a shock to realize that* (...) *thermodynamics knows of no such notion as the 'entropy of a physical system'. Thermodynamics does have the concept of thermodynamic system; but a given physical system corresponds to many different thermodynamic systems.* [hence] *Recognition that the 'entropy of a physical system' is not meaningful without further qualifications is important in clarifying many questions concerning irreversibility and the second law*" (Jaynes, 1965, pp. 397–398).

However, the meaning of the result exposed in this section is closely connected, from the point of view of physics and systems theory, with a tiny but crucial contribution of C. E. Shannon: the inclusion of k in Eq. (1). In other words, given the statistical nature of entropy in statistical mechanics, the calculation of statistical element involved in the calculation of entropy (i.e.: $\ln W$ in Eq. (3) and $-\sum p_i \cdot \ln p_i$ in Eq. (1)) can produce a value of, let us to say, 270.2 nat, or 1.961 nat/individual (in the expression units of Eqs. (3) and (1), respectively) in physics, information theory, edaphology, histology, economics, ecology, etc., and this produces a very untoward disarray between specific theoretical frameworks. So the inclusion of a value of k (e.g.: $k_B = 1.3806504E-23$ J/K per molecule in physics, and $k_e = 1.3806504E\varphi$ J$_e$ nat per individual in ecology), depending on every specific framework, produces a transference from an indiscriminate statistical approach, to a particular system of units compatible with each science; yielding at the same time a differential standardization between diverse specific models based on a single archetypal model of physics.

3. *H*, species coexistence and the measurement of redundancy in information theory, the second contribution of Shannon to eco-evolutionary theory

In this section we show why the conventional ecological understanding of redundancy would profit from the assumption of the meaning of redundancy as given by Shannon (1948). The integrity of biotic communities depends on mechanisms to maintain a stable concurrence of many species. Therefore, "coexistence" is the key word in ecosystem ecology. This subject has been treated in emblematic articles (e.g.: Hutchinson, 1959, 1961). In contrast with some conventional reviews in this regard (e.g.: Rosenfeld, 2002; Petchey and Gaston, 2006), the focus of the debate between the traditional competitive exclusion principle (CEP, one species ↔ one niche) and the hypothesis of functional redundancy (HFR, several species ↔ one niche) should be put in a more important underlying problem: the wave-like traits of the ecosystem functioning that determine a quantum uncertainty in the assessment of ecological niches (see Rodríguez et al., 2015c). The simplified version of the analysis performed by Rodríguez et al. (2015c) is the following: diversity and energy are essential and taxonomically all-encompassing for the performance of every ecological niche, but there is not statistical independence between the standard deviation of species diversity values (σ_{Hp}) and the standard deviation of eco-kinetic energy (σ_{Ee}). So, if we explore a wide spectrum of H_p statistical distributions from a given taxocenosis into a scalar space H_p, E_e, the increase of partition of H_p gradients (i.e.: decreasing σ_{Hp}) pushes certain species groups toward higher values of E_e (i.e.: increasing σ_{Ee}) in comparison with their ecological background. This relieves the competition pressure within any series of narrow intervals of species diversity values (i.e.: low σ_{Hp} value) when the number of coexisting species is significantly high. This means that species are capable to strongly coexist in regard to H_p values because they are capable to reduce their coexistence level in regard to E_e values (i.e.: high σ_{Ee} value), and vice versa. As a result, it is impossible to describe the ecological niche of a given species as exactly as we would like, because any increase of accuracy (σ reduction) in regard to H_p, means a simultaneous decrease in the accuracy of E_e, and vice versa, in a perfectly equivalent way to that of the Heisenberg's uncertainty principle in quantum mechanics (see Rodríguez et al., 2015c). Given that both CEP and HFR depend on an accurate description of the ecological niche that is unattainable under conditions of quantum ecological uncertainty, so the analytical debate between CEP and HFR is untenable. The only feasible solution is to assume that the presumed "redundancy" observed at the classical (macroscopic) scale in any ecosystem really informs us of an "uncertainty" at the quantum ("microscopic") scale in the empirical description of ecological niches, rather than of a full equivalence (redundancy) between ecological functions. The above-mentioned trade-off between σ_{Hp} and σ_{Ee} infiltrates eco-evolutionary dynamics as a whole (see Rodríguez et al., 2015c), proving that the conventional understanding and measurement of ecological redundancy is inadequate.

However, the approach explained in the previous paragraph does not imply that a conventional approach (i.e.: a classical or non-quantum version) to ecological redundancy is useless. But, even at the classical scale, the conventional approach misses the point in comparison with the original meaning of redundancy of Shannon's (1948). The standard understanding about ecological redundancy (see, e.g.: Walker, 1992; Naeem, 1998) is closely linked to the concept of species richness, and emphasizes on the seeming degree of equivalence between species functions that are taken as qualitatively distinguishable entities. Or, in other words, redundancy is conventionally regarded as an exclusive function of s_T in Eq. (1). Contrastingly, the measurement and therefore the meaning of redundancy (R) in information theory takes into account the two subsidiary variables involved in H: (a) species *richness* (i.e.: s_T in Eq. (1)) as well as (b) species *evenness* (J', see Eq. (10) according to Pielou, 1975) or *relative entropy* (according to Shannon, 1948, p. 392) understood as the ratio of the entropy (H) of an information source to the maximum value it could have while still restricted to the same set of types of elements (i.e.: with constant s_T, constant $N_T = \sum n_i$, and $n_1 = n_2 = n_3 = n_n$; see columns in pale gray in comparison with columns in dark gray in Fig. 2a, although the increase of J' under non-SEC is not independent of the increase of total species richness – s_T):

$$J' = \frac{H}{\ln s_T} \tag{10}$$

The range of J' goes from 0 to 1 and, in turn (Shannon, 1948), redundancy (R) is:

$$R = 1 - J', \quad \text{or} \quad R = (1 - J') \times 100 \tag{11}$$

As a result, since it is evident that Eq. (11) implies that $R = 1 - H/\ln s_T$, redundancy in information theory decreases with H (see Fig. 2b), instead of increasing, as it has been generally assumed in conventional ecology. Fig. 2b, despite its simplicity in the first glance, it is a clot of coincidences (whose nature is pending of further research) that is difficult to obtain by pure chance, mainly if we take into account that Fig. 2b is based on data not connected a priori with the calculation of Eq. (5): (a) There is a significant and opposite correlation ($r = -0.644994422$, $p = 0.00049$) between R and H_T; (b) the regression line starts at a level in y (intercept = 6.8271159E−01) of the order of the evolutionary equivalent of Planck's constant ($h_e^{ev} = 6.62606957\text{E}-01$ J$_e$ nat/individual; see Rodríguez et al., 2015d); (c) the absolute value of the mantissa (6.44994422) of the standardized covariance (i.e.: the correlation coefficient itself, r) between H_T and R also has a value quite similar to the mantissa of the ecological equivalent of Planck's constant ($h_e^{ec} = 6.62606957\text{E}\varphi$; see Rodríguez et al., 2015b); (d) the absolute value of the mantissa of the slope of the regression line H_T, R (regression coefficient = 1.3669689E−01) is quite similar to the mantissa of the ecological equivalent of Boltzmann constant ($k_e = 1.3806504\text{E}\varphi$, see references above); (e) the point in which the regression line ends ($H_T, R = 5, 0$) coincides pretty well with the maximum level of H_T per taxocenosis empirically measured in the most diverse ecosystems all over the world (i.e.: $H_p = 5.161 \pm \sigma = 0.415$; value calculated as the average from data in several peer-reviewed publications; see Rodríguez et al., 2015c, p. 95).

In summary, Fig. 2b seems to contain, implicitly within the information theory itself, all the basic information about constants and trends to develop a general model of ecosystem functioning based on physical principles. The value of the model shown in Fig. 2b partly lies in its concordance with the criteria of, for example, Derry (1999, p. 172: "*the role of science is not to provide certainty, but rather to provide coherence*") and Rothstein (1951, p. 173: "*...all physical laws become relationships between types of information, or information functions collected or constructed according to various procedures*").

The main difference between the original Shannonian approach and conventional ecology seems to be that redundancy, in information theory, depends on the combined influence of *richness* (a qualitative factor) and *evenness* (a quantitative factor). This is in agreement with field experience in ecology: ecological succession involves adding new species to ecosystems as well as a reduction of its predominance in order to promote coexistence. One result is that every new species, in average, is relatively scarcer that its predecessor species. But a decreasing level of relative abundance per each new species (increase of evenness, J') is one of the most important traits to describe an increasing differentiation between ecological niches. Besides, there is no quantitative way of measuring redundancy at the survey level in conventional ecology. In this
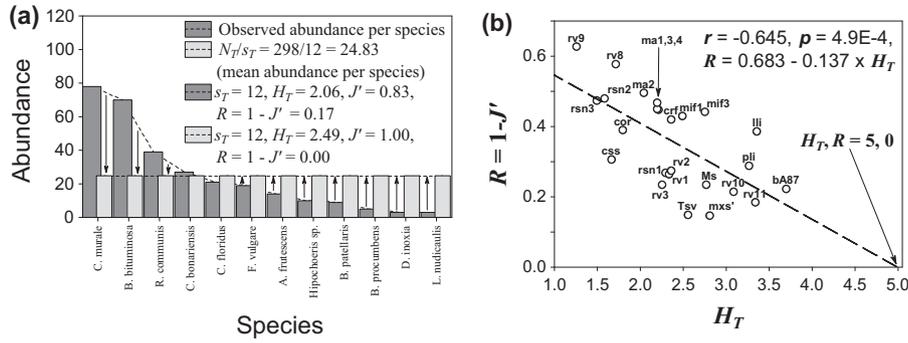
Fig. 2. Ecological meaning and effects of the calculation of Shannonian redundancy (R, see Eq. (11)). (a) Graphically exemplified summary of the structural effects (change indicated by the set of arrows) of the increase of evenness (J', see Eq. (10)) until its maximum value in a fraction (50% of the most abundant species from a total richness of 24 species) of a survey of ruderal vegetation ("rv1", data from Rodríguez et al., 2012). (b) Association between R and total species diversity per survey (H_T) starting from a set of 25 surveys. r: Pearson's correlation coefficient; p: significance level. Data from Rodríguez et al. (2013b, 2015a). The meaning of point labels coincide with those in Fig. 1b.

field it is a matter of contingent analysis that depends on the level of accuracy of the assessment of ecological niche in regard to pairs or small groups of species. However, such accuracy is limited by the ecological fulfillment of uncertainty principle, as it has been commented above (see Rodríguez et al., 2015c).

These differences in approach between ecology and information theory about redundancy explain why the HFR reaches analytical results completely opposite to those expected according to information theory. In addition, if the description of ecological niches is affected by quantum uncertainty (see comments at the beginning of this section), then it is not reliable asserting that the disappearance of a given species does not substantially affect ecosystem performance. Simply and plainly, we are not capable to exactly know in what a measure such a disappearance affects either the functioning of the ecosystem itself or the functioning of surrounding ecosystems. So the HFR is an excessively optimistic hypothesis about species extinction: as we are basically unable to know what really happens, we assume, optimistically, that nothing is happening. In summary this section, firstly, provides an additional reason by which it should be avoided to use richness as a reliable surrogate of species diversity (see, e.g.: Spellerberg and Fedor, 2003; Wilsey et al., 2005) and, secondly, it supports the idea that ecology has closer connections with information theory and physics than with any other science.

4. Joint events, species coexistence, and the third contribution of Shannon to eco-evolutionary theory

Independently of biology, information theory arrived at similar results to those of ecology in regard to the necessity of avoiding high levels of competition. One of these results is regarded to the topic known as "*joint events*" (Shannon, 1948, Brillouin, 1956). Suppose there are two events, x and y, with m possibilities for the first one and n possibilities for the second one. Let $p(i, j)$ be the probability that events occur together, with i for the first and j for the second. Information (species diversity in the case of the ecosystem) about the joint event is:

$$H(x, y) = -\sum_{i,j} p(i, j) \ln p(i, j) \tag{12}$$

while

$$H(x) = -\sum_{i,j} p(i, j) \ln \sum_{j} p(i, j), \tag{13}$$

$$H(y) = -\sum_{i,j} p(i, j) \ln \sum_{i} p(i, j) \tag{14}$$

It is fulfilled in this regard that:

$$H(x, y) \leq H(x) + H(y), \tag{15}$$

According to Eq. (15), the *information* of a joint event is less than or equal to the sum of the individual amount of information (here Shannon used the word "*entropy*" instead of "*information*" because he was describing the message from the outside, namely, from the point of view of an observer that waits for a message of ignored content, whereas we are speaking about already known information about the structure of ecosystems); with equality in Eq. (15) *if and only if the two events are independent from each other* in the statistical sense of the term (e.g.: if two coins are simultaneously flipped, the chance of both being heads is ½ × ½ = ¼), or, by using the previous symbols, if $p(i, j) = p(j) \times p(i)$.

Translating the previous arguments into ecological language: information of the joint event when there is not independence (complete overlap of ecological niches between two species, i.e.: a fully joint event) must always be less than the sum of individual information under conditions of complete independence (i.e.: either *existence in allopatry*, or *coexistence under the influence of character displacement* to avoid the increase of entropy due to high competition levels; e.g.: Brown and Wilson, 1956; Losos, 2000; Grant and Grant, 2006). Therefore, from Eqs. (12)–(15) and taking into account the above-mentioned opposite relationship between information and entropy, we can conclude that events of complete overlap between niches (joint events without statistical independence according to information theory, or complete functional redundancy according to HFR) should be negatively selected as unfavorable in evolution because they involve reducing the amount of information (species diversity) and increasing entropy. According to Section 3, first paragraph, quantum ecological uncertainty is the response of nature to avoid joint events. This is in agreement with the well-known bias against competition and in favor of facilitation through the progress of ecological succession (Odum, 1969; Odum, 1972; Margalef, 1963, 1991). In summary, this section shows that when C. E. Shannon was speaking about the reduction of the information amount due to joint events he also was speaking, unintentionally, about the negative effects of competition, as well as about the compensatory effect of character displacement in this regard.

5. Conditional information, species coexistence, and a fourth contribution of Shannon to eco-evolutionary theory

Conditional probability is the probability $p_i(j)$ that variable $y = j$ when it is known that another not necessarily independent variable $x = i$. Conditional information $I_x(y)$ is information about the variable or event y, when the event x is already known. Information theory has mathematically proved (Shannon, 1948;

Brillouin, 1956) that prior knowledge of x means a restriction or constraint which reduces the content of the information or probability about the selection of y, and equality of information for the selection of y only exists if x and y are completely independent from each other.

Translating the meaning of $I_x(y)$ into ecological language, this means that the previous performance of a niche (which depends on hereditarily conditioned information x) affects the individuals of a given species by imposing restrictions that reduce the likelihood of "*choosing*" to perform a different niche (y). The meaning of conditional information is consistent with the processes of extinction that occur when the habitat of a species is altered, or when species are confronted with new selective pressures caused by the introduction of a competitor.

In biology, the "restrictions" or "constraints" referred to by Shannon depend on fixation in the gene pool of the population of those traits that typify the ecological niche of each species and the subsequent preservation of such constraints by mechanisms of reproductive isolation. From the opposing relationship between information and entropy, previously commented, these genetic constraints that ensure low probability of joint events (complete overlap between niches) should be interpreted as one of the main evolutionary mechanisms to counter the effect of the second law of thermodynamics on ecosystems. Thus, the convergence of phylogenetically close species in conditions of allopatry and their divergence in sympatric conditions can be understood as "*character displacement*" (in evolutionary and ecological language) or as a process to avoid "*joint events*" by means of the occurrence of as many events of "*conditional information*" as species present (in the language of information theory).

6. Concluding remarks

This article, despite its mainly theoretical nature, has a deeper meaning than that we could suppose at the first glance due to a very simple reason: it provides the first group of theoretical evidences (starting from the pure information theory itself) in favor of the close connection between ecology, physics and information theory. This set of connections has an added appeal: it was unwittingly proposed by C. E. Shannon 64 years before the first one of the most recent proposals (Rodríguez et al., 2012) of unification between ecology and conventional physics, and in spite of the passive predominant position against establishing interdisciplinary approaches in order to achieve new solutions to very old problems, that was already active since the times of Shannon himself. In short, C. E. Shannon was also doing early crucial contributions to eco-evolutionary theory despite he was neither an ecologist nor an evolutionary biologist.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2015.12.021.

References

Aguilar, J., 2001. Curso de Termodinámica. Alambra Universidad, Madrid.
Aoki, I., 2006. Min–max principle of entropy production with time in aquatic communities. Ecol. Complex. 3, 56–63.
Attaran, M., 1986. Industrial diversity and economic performance in U.S. areas. Ann. Reg. Sci. 20, 44–54.
Brillouin, L., 1956. Science and Information Theory. Academic Press Inc., NY.
Brissaud, J-B., 2005. The meaning of entropy. Entropy 7, 68–96.
Brown Jr., W.L., Wilson, E.O., 1956. Character displacement. Syst. Zool. 5, 49–64.
Callender, C., 2004. A collision between dynamics and thermodynamics. Entropy 6, 11–20.
Derry, G.N., 1999. What Science is, and How it Works. Princeton University Press, Princeton, NJ.
Gallucci, V.F., 1973. On the principles of thermodynamics in ecology. Annu. Rev. Ecol. Syst. 4, 329–357.
Grant, P.R., Grant, B.R., 2006. Evolution of character displacement in Darwin's finches. Science 313, 224–226.
Haegeman, B., Loreau, M., 2008. Limitations of entropy maximization in ecology. Oikos 117, 1700–1710.
Harte, J., 2002. Toward a synthesis of the Newtonian and Darwinian worldviews. Phys. Today 55, 29–34.
Harte, J., 2011. Maximum Entropy and Ecology. A Theory of Abundance, Distribution and Energetics. Oxford University Press Inc., NY.
Harte, J., Newman, E.A., 2014. Maximum information entropy: a foundation for ecological theory. Trends Ecol. Evol. 29, 384–389.
Hutchinson, G.E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Am. Nat. 93, 145–159.
Hutchinson, G.E., 1961. The paradox of the plankton. Am. Nat. 95, 137–145.
Jaynes, E.T., 1957. Information theory and statistical mechanics, I. Phys. Rev. 106, 620–630.
Jaynes, E.T., 1965. Gibbs vs. Boltzmann entropies. Am. J. Phys. 33, 391–398.
Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943–1967.
Losos, J., 2000. Ecological character displacement and the study of adaptation. Proc. Natl. Acad. Sci. U. S. A. 97, 5693–5695.
Margalef, R., 1963. On certain unifying principles in ecology. Am. Nat. 97, 357–374.
Margalef, R., 1991. Ecología. Omega S.A., Barcelona.
McBratney, A.B., Minasny, B., 2007. On measuring pedodiversity. Geoderma 141, 149–154.
Montero, F., Morán, F., 1992. Biofísica, Procesos de Autoorganización en Biología. Madrid, Eudema, SA, pp. 48–49.
Naeem, S., 1998. Species redundancy and ecosystem reliability. Conserv. Biol. 2, 39–45.
Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.
Odum, E.P., 1972. Ecología. Nueva Editorial Interamericana S.A. de C.V., México D.F.
Park, S.Y., Gönen, M., Kim, H.J., Michor, F., Polyak, K., 2010. Cellular and genetic diversity in the progression of in situ human breast carcinomas to an invasive phenotype. J. Clin. Investig. 120, 636–644.
Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758.
Pielou, E.C., 1975. Ecological Diversity. Wiley InterScience, NY.
Rodríguez, R.A., Herrera, A.Mª, Otto, R., Delgado, J.D., Fernández-Palacios, J.Mª, Arévalo, J.R., 2012. Ecological state equation. Ecol. Model. 224, 18–24.
Rodríguez, R.A., Herrera, A.Mª, Delgado, J.D., Otto, R., Quirós, A., Santander, J., et al., 2013a. Biomass-dispersal trade-off and the functional meaning of species diversity. Ecol. Model. 261/262, 8–18.
Rodríguez, R.A., Delgado, J.D., Herrera, A.Mª, Riera, R., Navarro, R.Mª, Melián, C., et al., 2013b. Effects of two traits of the ecological state equation on our understanding of species coexistence and ecosystem services. Ecol. Model. 265, 1–13.
Rodríguez, R.A., Herrera, A.Mª, Riera, R., Delgado, J.D., Quirós, A., Perdomo, Mª.E., et al., 2015a. Thermostatistical distribution of a trophic energy proxy with analytical consequences for evolutionary ecology, species coexistence and the maximum entropy formalism. Ecol. Model. 296, 24–35.
Rodríguez, R.A., Herrera, A.Mª, Riera, R., Santander, J., Miranda, J.V., Quirós, A., et al., 2015b. Distribution of species diversity values: a link between classical and quantum mechanics in ecology. Ecol. Model. 313, 162–180.
Rodríguez, R.A., Herrera, A.Mª, Santander, J., Miranda, J.V., Fernández-Rodríguez, Mª.J., Quirós, A., et al., 2015c. Uncertainty principle in niche assessment: a solution to the dilemma redundancy vs. competitive exclusion, and some analytical consequences. Ecol. Model. 316, 87–110.
Rodríguez, R.A., Herrera, A.Mª, Riera, R., Escudero, C.G., Delgado, J.D., 2015d. Empirical clues about the fulfillment of quantum principles in ecology: potential meaning and theoretical challenges. Ecol. Model. 301, 90–97.
Rodríguez, R.A., Herrera, A.Mª, Santander, J., Miranda, J.V., Perdomo, Mª.E., Quirós, A., Riera, R., Fath, B.D., 2016. From a stationary to a non-stationary ecological state equation: adding a tool for ecological monitoring. Ecol. Model. 320, 44–51.
Rosenfeld, J.S., 2002. Logical fallacies in the assessment of functional redundancy. Conserv. Biol. 16, 837–839.
Rothstein, J., 1951. Information, measurement, and quantum mechanics. Science 114, 171–175.
Rothstein, J., 1952. Information and thermodynamics. Phys. Rev. 85, 135–136.
Schrödinger, E., 1946. What is Life?: The Physical Aspect of the Living Cell. The Macmillan Co, NY.
Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27, 623–656, 379–423.
Shannon, C.E., 1956. The bandwagon. IEEE Trans. Inf. Theory 2, 3.
Spellerberg, I.F., Fedor, P.J., 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' Index. Glob. Ecol. Biogeogr. 12, 177–179.
Tiezzi, E., Pulselli, R.M., 2008. An entropic approach to living systems. Ecol. Model. 216, 229–231.
Tribus, M., McIrvine, E.C., 1971. Energy and information. Sci. Am. 225, 179–188.
Volkenshtein, M.V., 1985. Biofísica. MIR, Moscú.
Walker, B.H., 1992. Biodiversity and ecological redundancy. Conserv. Biol. 6, 18–22.
Wilsey, B.J., Chalcraft, D.R., Bowles, C.M., Willig, M.R., 2005. Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. Ecology 86, 1178–1184.
Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, J.A., Nichols, J.D., Campbell Grant, E.H., et al., 2013. Presence-only modelling using MAXENT: when can we trust the inferences? Methods Ecol. Evol. 4, 236–243.