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Short communication

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

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ABSTRACT

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),

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http://dx.doi.org/10.1016/j.ecolmodel.2015.12.021 0304-3800/© 2016 Elsevier B.V. All rights reserved. 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:

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

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