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A strategic roadmap for interdisciplinary modeling in ecology: The result of reading *'Defining an ecological equation of state: Response to Riera et al. 2023'* (Newman et al., 2023)

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ABSTRACT

An interesting dialogue is developed between Newman et al. (2023) and Riera et al. (2023), in which proposals related to the development of equations of state in ecosystem ecology are discussed in depth. This debate is more important than it first appears, since the persistent gap between theoretical and empirical ecology is due, in part, to the absence of a comprehensive paradigm in this field. As it is exemplified in the first section of this article, a sequence of models derived from a reliable equation of state would help to bridge the aforementioned gap. Although this manuscript is analytically monolithic, five main thematic strands can be identified: (i) Examination of the objections of Newman et al. (2023), juxtaposing them with key concepts from ecology, information theory, physics and the MaxEnt algorithm. (ii) Validation of the criteria in (i) through theoretical and data-based examples. (iii) Interdisciplinary linkages between (i) and (ii). (iv) Epistemological generalizations from the previous strands to obtain a strategic roadmap for interdisciplinary modeling in ecology. (v) Conclusions referred to the general meaning of points (i) and (ii). On a general level, our objective is that this manuscript will go beyond a simple academic debate, being useful for colleagues interested in interdisciplinary modeling.

1. A description of the context and a statement of objectives by way of introduction

Numerous analytical links between ecology and physics have been claimed for decades (*e.g.*, Lotka, 1925; Lindeman, 1942; Margalef, 1963, 1972, 1974, 1993; Odum, 1969; Svirezhev, 2000; Jørgensen and Svirezhev, 2004; Jørgensen and Fath, 2004; Jørgensen et al., 2007; Ulanowicz, 2004, 2011a, 2011b) as one of the most potentially fruitful avenues for explaining some features of ecosystem functioning that have remained unanswered within mainstream contemporary ecology. In this sense, the development of an ecological equation of state (EES_R; Rodríguez et al., 2012; 2013) that acts as an emergent property unifying physics and ecosystem ecology (Eq. (4), below, Section 2.1) is a quite significant step. Rearranging the variables involved in such an equation, it has been possible obtaining a general model (Rodríguez et al., 2015a)

of the distribution of species diversity values (H_p, Eq. (2), below, Section 2.1), finding that each taxocene has a typical minimum acceptable amount of trophodynamic exchange (*i.e.*, the ecological equivalent $-h^{ec}-$ of Planck's constant); obtaining for the first time a fully quantifiable model of energy pyramids (Rodríguez et al., 2015b); measuring the trophodynamic power per taxocene (Rodríguez et al., 2017); and evaluating the extent to which many ecological systems inhabited by a massive number of fish species on a global scale are stable or unstable (Herrera et al., 2023); among other results published in several papers freely available at: https://interdisciplinaryscience.es/publications. This set of models has been grouped under the name Organic Biophysics of Ecosystems (OBEC; see the first comments on this term in Rodríguez et al., 2017).

In connection with the previous paragraph, Newman et al. (2023) evaluated the concerns of Riera et al. (2023) regarding a previous article

(Harte et al., 2022) based on an equation (E_H, Eq. (1)) purportedly considered an ecological equation of state.

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

Where B is total biomass (original physical unit of measurement undeclared, and resulting values normalized to: minimum value = 1); $c \approx 4.17$; E is total metabolic rate (original physical unit of measurement undeclared, and resulting values normalized to: minimum value = 1). $E \propto$ to $m^{3/4}$, where m is body weight per individual. This is a proxy for the basal rate of energy expenditure per unit time and unit biomass at full rest. This is, in turn, a limited reflection of trophic energy, because it excludes digestion, reproduction, and dispersal-related energy expenditure (McNab, 1997). β depends on the S/N ratio (*i.e.*, $1/\beta \propto 1/(S/N)$). S is the total number of species (a.k.a. richness); and N is the total number of individuals. Thus β indirectly represents the mean abundance of individuals per species given that $1/(S/N) = \boldsymbol{N/S}$.

Riera et al. (2023) concluded that Eq. (1) does not meet the minimum requirements to be considered an ecological equation of state. However, Newman et al. (2023) argue that our concerns are unfounded. This article thoroughly explores all facets of this debate to present an even more complete perspective on the objections of Newman et al. (2023).

Our main objective is to take advantage of this exchange of views to articulate ideas that go beyond the debate. Accordingly, this article has become a condensed roadmap of epistemological guidelines, supported by examples to highlight general procedures concerning interdisciplinary modeling in ecology. As a result, the particular context in which ecology, physics and information theory are intertwined should be considered circumstantial.

The model concept used here is: a simplification of reality to its most essential features based on a conciliation between standard conceptual frameworks whose main goal, instead of reaching a universal truth, is to generate good testable hypotheses relevant to important problems (Levins, 1966, p. 430). Reproducibility and compliance with Ockham's razor are also desirable features. For a fruitful outcome to close this debate definitively, all parties involved should recognize that this article is oriented to the advancement of science as the sole *raison d'être, techne* and *telos* of this exchange of perspectives. As a result, our aim is not to advocate for the primacy of the EES$_R$ proposed by Rodríguez et al. (2012) over any subsequent proposal.

In other words, all the sections and subsections in this article are nothing more and nothing less than a carefully developed 'epistemological Overton window' to obtain the generalizations (interdisciplinary modeling roadmap) summarized in Section 4.

2. Some paradoxes

2.1. The logic of some comments in Newman et al. (2023)

Accurately speaking, without a paradigm in ecosystem ecology due to the premature abandonment of the connection between 'classical ecology' and conventional physics (see Riera et al., 2018), it is not possible to *'define an ecological equation of state'* starting from the field of ecology itself, or any of its proto-paradigms with a tangential position with respect to physics. Additional elements are discussed below (Sections 2.2, 3.1, 3.2, and 3.3).

Eq. (1) proposes an interesting option to evaluate an ecological indicator that is particularly difficult to measure in practice (standing biomass) by combining, in an innovative way, metabolic and ecological indicators by using species richness (S) as an indicator of species diversity. The empirical utility of Eq. (1) is indisputable, and its reliability has been amply demonstrated by empirical data (see Harte et al., 2022). Eq. (1)) is theoretically based on a combination between the Metabolic Theory of Ecology (MTE; Brown et al., 2004), and the Maximum Entropy

Theory of Ecology (METE; Harte, 2011). In contrast to the theoretical foundation of EES$_R$, MTE and METE are more linked with the physiology of energy expending (*e.g.*, Kleiber, 1947) and a particular branch of statistics (*e.g.*, Jaynes, 2003) than with standard physics, although the latter link is an essential part of 'classical' ecology (see Section 1, first paragraph). The weak connection between a given proposal and solidly established prior knowledge has been recognized as a problematic issue in the development of contemporary ecology (see Spellerberg and Fedor, 2003; Belovsky et al., 2004; Scheiner, 2013).

In contrast, according to the list of reference in the first lines of Section 1, the path to developing the ESS$_R$ had previously been paved. Such development was based on the aforementioned background, and the anti-kinetic (and therefore biocenologically antithermic; *i.e.*, reduction of ecological oscillations around a multivariate center of functional coordinates, a.k.a 'talandic temperature') role of the increase in species diversity (see Margalef, previous references; based in turn on Goodwin, 1963; and Kerner, 1957). From these two premises, it was only necessary to replace T by H_p (Eq. (2), Shannon, 1948; at the plot level) and v by I_e in the equation of state of the ideal gas (Eq. (3)) to obtain the ESS$_R$ (Eq. (4)).

$$H_p = -k\sum_{i=1}^{S}(p_i\ln p_i) = -k\sum_{i=1}^{S}\left(\frac{n_i}{N}\ln\frac{n_i}{N}\right) \tag{2}$$

Where, in mainstream ecology, H_p: species diversity, a.k.a. 'ecological information' or heterogeneity (Magurran, 2004), of a given ecological unit (a plot, in this case); k: a positive constant that in mainstream ecology is assumed equal to 1, as it was done by Shannon (1948, p. 383); S: species number ('richness'); n_i: number of individuals of species i^{th}; N: $\sum_{i=1}^{S}n_i$; and $\sum_{i=1}^{S}p_i = 1$. That is to say, p_i is a probability. H_p is the average amount of information (*i.e.*, 'eco-information', in this context) per individual, and it is expressed in nat/individual when natural logarithms are used. Eq. (2) combines in itself richness, and level of homogeneity of abundance between species (evenness; J', below).

$$2N\left(\frac{1}{2}mv^2\right) = Nk_BT \Leftrightarrow Nmv^2 = Nk_BT \Leftrightarrow 2E_T = Nk_BT \tag{3}$$

Or, equivalently and interchangeably regarding the context of classical thermodynamics:

$$PV = nRT \tag{3a}$$

Where N: number of molecules; m: molecular mass (in kg); v^2: root mean square velocity of molecules (in m/s); k_B: Boltzmann's constant = $R \div N_A$ = 1.380649E−23 J·K^{-1} (Joule/Kelvin per molecule); N_A: Avogadro constant (number of molecules per mole: 6.022E+23 mol^{-1}); T: absolute temperature (in Kelvin); E_T: total kinetic energy (in Joule); P: absolute (not gauge) pressure; V: volume; R: molar gas constant (a.k.a. universal gas constant) = 8.3145 J·K^{-1}·mol^{-1}, R indicates the total increase of translational kinetic energy per mole with each temperature increase of 1 Kelvin; and n: number of moles.

$$2N_p\left(\frac{1}{2}m_{ep}I_e^2\right) = \frac{N_pk_{e\tau(e)}}{H_p} \Leftrightarrow m_{eTp}I_e^2 = \frac{N_pk_{e\tau(e)}}{H_p} \Leftrightarrow 2E_{eTp} = \frac{N_pk_{e\tau(e)}}{H_p} \tag{4}$$

Or, equivalently and interchangeably regarding the context of classical thermodynamics:

$$p_{e(s)}V_{e(s)}N_pm_{ep} = \frac{n_eR_e}{H_p} \Leftrightarrow P_eV_e = \frac{n_eR_e}{H_p} \tag{4a}$$

Where N_p: total number of individuals per plot; m_{ep}: average standing biomass (body weight in kg) per individual per plot; I_e: average value of the ergodic indicator of dispersal intensity per individual per plot (details in Rodríguez et al., 2013); $k_{e\tau(e)}$: ecological equivalent of Boltzmann constant (k_B, above) = 1.380649E±φ J$_e$·nat/individual, being φ and integer typical per taxocene ($_\tau$); H_p: value of Eq. (2) per plot; m_{eTp}: total

standing biomass per plot; $2E_{eTp}$ = twice the total amount of eco-kinetic energy per plot; J_e (ecoJoule) = kg·đ², đ = dispersal unit (the unit of measurement of I_e); $p_{e(s)}$ and $v_{e(s)}$: specific ecological pressure and volume, respectively (see Rodríguez et al., 2012, Table 1); n_e: number of ecological moles; and R_e: ecological equivalent of gas constant (the empirical assessment of these two parameters is in the making).

Equations from (2) to (4a) have been included here because without them readers would not understand the issues discussed in Sections 3.2 and 3.3. To close the circle of interdisciplinary connections, the assessment of $k_{e\tau(e)}$ in Eq. (4) showed that it depends on a universal ecological **constraint** (biomass-dispersion trade-off along species diversity gradients: ΔH_p) which is an emergent property from eco-evolutionary patterns known for decades ago (*i.e.*, Cope's rule, Rapoport's rule, and *r-K* selection theory; see Rodríguez et al., 2013).

Newman et al. (2023) cite Riera et al. (2023) in the following way: *'research endeavors anticipated to be unsuccessful [their words; Riera et al. (2023)], "where data are limited."'* It is important to note that the addition *"when data are limited"* changes the meaning of the original comment by Riera et al. (2023), because it did not refer to data availability at all, but to the theoretical underpinnings of the proposal by Harte et al. (2022).

Newman et al. (2023) also state that *'Riera et al. (2023) are confused about the Shannon index of diversity H, and the information entropy used in METE to derive the ecosystem structure function R. Both often appear as "H", and both are described by the form of Shannon entropy, but they are not the same thing'*. And then Newman et al. (2023) cite equations 27 to 30 in Brummer and Newman (2019) as an explanation. Nevertheless, in Harte et al. (2022) it is possible to read: *'At the core of METE is the "ecosystem structure function" R(n, ε|S, N, E) … The form of R is derived by maximizing its Shannon information entropy'; i.e.*, maximizing Eq. (2), just as it was explicitly stated in Harte et al. (2008) as well as in Harte and Newman (2014).

Paradoxically, a combined review of equations 27 to 30 in Brummer and Newman (2019) and the Supplementary Information in Harte et al. (2022) does not yield direct and clear results about how and why H (Eq. (2)) was used in these articles. The only indirect clue about the use of Eq. (2) is the use, in Fig. S1 (Harte et al., 2022, Supplementary Information), of ln(S); that is to say, *'the maximum value H could have while still restricted to the same symbols [species, in the ecological case]'* (Shannon, 1948, p. 398).

Obviously, the value of ln(S) is associated, in Eq. (2), with a distribution of probabilities in which $p_{i1} = p_{i2} = p_{i3} = p_{i4} = \ldots p_{iS}$ (*i.e., 'the uniform distribution maximizes the entropy; the uniform distribution contains the largest amount of uncertainty … when **no constraint** is imposed on the probability distribution'*; Guiasu and Shenitzer, 1985, p. 44; see also Jaynes, 2003, pp. 152, 563). In contrast, the only way to maintain a living system in a stable state without spontaneously drifting to a state of physical equilibrium (death) is to impose some type of physical **constraint** on the system (Callen, 1985, pp. 26–27; Montero and Morán, 1992, pp. 49–50). Constraints prevent falling into total stillness and degradation where nothing flows or varies over time (absence of evolution). In other words, uniform distribution and constraints are mutually exclusive factors, despite their attempted coexistence in some proposals (*e.g.*, Brummer and Newman, 2019, p. 1: *'information entropy is for the general case of a maximized* [uniform, p. 15] *distribution, which has empirical information that provides constraints on the overall predictions'*).

That is, the algorithms that support Eq. (1) is hypothetically connected to a statistical reference framework in conditions of data scarcity, in which all observed species tend to be equally abundant based on a total number *N* of individuals equally distributed among them (a very unlikely situation in nature according to Margalef, 1974, p. 365; additional comments below, Section 3.3). However, the trophodynamic role of evenness (*i.e., J'* = H/ln(S); Pielou, 1969; originally termed 'relative entropy' by Shannon, *ibid.*) in understanding ecosystem functioning remains absent in both Harte et al. (2022) and Newman et al. (2023) (see Section 2.2).
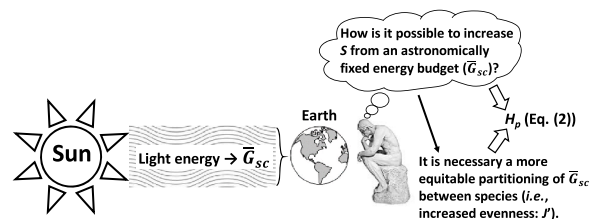
2.2. On the use of species richness (S) as a single indicator of species diversity

The persistent use of richness (*S*) as the sole indicator of species diversity is due to the convenience of least effort (*i.e.*, it is not necessary to assess species abundance) combined with an *ad verecundiam* fallacy. That is, the intellectual influence of a figure adopting a given stance is used as the sole proof that the stance is correct. It is likely that this influential figure was Whittaker (1972, p. 222: *'the most generally appropriate measure of diversity is simply S, the number of species per unit area'*).

The explanation in favor of using an index combining *S* and *J'* (*e.g.*, Eq. (2)) as the only option for measuring species diversity in connection with trophodynamics is so simple (Ockham's razor) that it becomes an axiom (ἀξίωμα: *'that which commends itself as evident'*); see Fig. 1.

3. The use of some physical concepts in connection with Eq. (1), broken down by subsections

A recurring criticism throughout the article by Newman et al. (2023) suggests that Riera et al. (2023) overly adhere to physics. We have already presented (Section 2.1) several reasons refuting this notion, emphasizing the equilibrium between ecological, physical, and

Table 1

Equations of state for various types of systems (Aguilar, 2001, pp. 8, 71; Landau and Lifshitz, 2008, p. 185, Eq. (55.15); Rodríguez et al., 2012, Table 1, Eq. (5); Al-Raeei, 2022, Eq. (37) and Eq. (38)).

Type of system	Equation of state	Intensive variable
Ideal gas	$PV = nRT$	P, T
Van der Waals gas	$\left(p + \dfrac{n^2 a}{V^2}\right)(V - nb) = nRT$	p, T
Berthelot gas	$\left(p + \dfrac{n^2 A}{TV^2}\right)(V - nb) = nRT$	p, T
Real gas, in general	$pV = A + \dfrac{B}{V} + \dfrac{C}{V^2} + \ldots$	p
Tight thread	$\dfrac{dl}{l} = \lambda dT + \dfrac{l}{AY}\, df$	T
Paramagnetic solid	$M = C \dfrac{\mathscr{H}}{T}$	T
Solids and liquids (approximate)	$\dfrac{V_2}{V_1} \simeq 1 + \alpha(T_2 - T_1) - k(p_2 - p_1)$	p, T
Fermi and Bose gases of elementary particles.	$PV = NT\left[1 + \dfrac{\pi^{3/2}}{2g}\dfrac{N\hbar^3}{V(mT)^{3/2}}\right]$	P, T
Taxocene (ecological assemblage)	$2N_p(1/2m_{ep}I_e^2) = \dfrac{N_p k_{e\tau(e)}}{H_p}$	I_e, H_p
Morse oscillator	$P_{tot}(\nu, T) = \Gamma_2 \nu^2 + \Gamma_1 \nu$; where:	P, T
	$\Gamma_1 = k_B \dfrac{6d^{-3}}{\pi} T$	

Fig. 1. Richness (*S*) and evenness (*J'*) are two trophodynamically inseparable facets in the process of increasing species diversity. Eq. (2) combines both indicators. $\overline{G}_{sc}$ (Solar Constant) = 1360.8 ± 0.5 J/s/m², or Watt/m² (Kopp and Lean, 2011): the total size of the 'energy pie' available for ecosystems is fixed. Additional explanations on the connection of this figure with other trophodynamic features in Riera et al. (2023), Suppl. Note 1; as well as in Herrera et al. (2023), pp. 3–4, section 2.

information theory aspects in deriving Eq. (4).

3.1. The concept of 'state variable' applied to Eq. (1)

The proponents of Eq. (1) appear to suggest that any ecological indicator can be regarded as a 'state variable.' To qualify as a state variable an indicator must meet certain criteria:

i) State variables should univocally characterize the state of a thermodynamic system. 'Univocally' means that, for instance, if the volume and pressure of a thermodynamic system remain constant, properties such as viscosity, refractive index, heat conductivity, or dielectric constant should also remain constant, regardless of who measures them or when and where (Dugdale, 1998, p. 11; see also Callen, 1985, p. 13, Postulate 1).

ii) It should be a macroscopic property that does not depend on the **rate** at which events occurs (Linder, 2004, p. 8).

iii) A state variable does not depend on the path that the system follows through the phase space to reach the coordinates defining its state (Resnick et al., 2001, p. 647). For example, work done by or on a system is not a state variable because it depends on the area under the curve indicating the system's path in a pressure-volume diagram (Tipler and Mosca, 2010, p. 604, Fig. 18.8). That is, state variables are not path-dependent quantities.

It is pertinent to ask whether any variable in Eq. (1) meets these requirements. The role of B in Eq. (1) is not univocal because two ecological systems, even belonging to the same taxocene, can reach different values of total biomass. The role of richness (S, in Eq. (1)) is also not univocal because its use as an indicator of species diversity ignores the crucial trophodynamic role of evenness (see Fig. 1). As for $1/\beta$, given that it has the meaning of N/S, it is not a macroscopic variable in the physical sense of the term (item (ii), above). Moreover, the mean number of individuals per species (N/S) is not a magnitude that univocally determines the functioning of ecosystems (item (i), above). The role of E in Eq. (1) is also not univocal because it neglects the expenditure of trophic energy in key ecological activities and crucial physiological process. Furthermore, E does not satisfy item (ii) because it depends on the basal **rate** of energy expenditure per unit time and unit biomass. Finally, E also fails to satisfy point (iii) because, even at full rest, any living body is doing physical work (W). For example, the movement of all internal organs and circulatory fluids (*i.e.*, blood, hemolymph, sap), since $W = F \times s \times \cos\theta$ (where F is force; s is displacement; and θ is the angle between the vector force and the vector of displacement), makes E a path-dependent quantity.

The first lines of Section 1, plus the origin and structure of Eq. (4), as well as the content of Fig. 1 show that ecology and physics, despite appearing to be different fields at first glance, are in fact nothing more than parts of the same machinery that moves the universe, only classified by humans as different in order to compartmentalize knowledge for the sake of facilitating our understanding of nature. Hence, the noticeable appearance of equations of states in various fields of science (Newman et al., 2023). However, no scholar in these fields minimizes the formal links with conventional physics.

An additional issue is that Newman et al. (2023) establish a parallelism on the plane of equality between Eq. (1) and other equations of state entirely based on physical principles in other fields of science. But, also according Newman et al. (2023) *'our **analogy** [Eq. (1)] extends an idea from the logic of physics to biodiversity science.'* However, the title of Harte et al. (2022) is emphatic: *'An equation of state unifies diversity, productivity, abundance and biomass.'*

This ambiguity brings to mind the Lakatosian concept of *'protective belt': 'It is this protective belt of auxiliary hypotheses which has to bear the brunt of the tests and get adjusted and re-adjusted, or even completely replaced, to defend the thus-hardened core of the theory'* (Lakatos, 1978. p.

48). The protective belt acts more strongly when a protoparadigm, such as the application of MaxEnt in ecology, is criticized (*e.g.*: Roxburgh and Mokany, 2007; Marks and Muller-Landau, 2007; Haegeman and Loreau, 2008; Royle et al., 2012; Yackulic et al., 2013; Guillera-Arroita et al., 2014; Xiao et al., 2015).

Although this section addresses the appropriateness of using the concept of *'state variable'*, this is not the concept that is at the thus-hardened core of the proposal defended by Newman et al. (2023). This place is occupied by the concepts of *'equation of state'*, and *'information entropy'*, as detailed in subsequent sections.

3.2. Concepts of 'equation of state' and 'intensive and extensive variables' in relation to Eq. (1)

Riera et al. (2023), starting from a summary of Halliday et al. (2011) and Gould and Tobochnik (2021) stated that *'equations of state [e.g.,* Eq. (3a)] *are relationships between state variables where at least one of them is extensive in nature, and the others are intensive, since the thermodynamic imbalance necessary to carry out work depends on the inequality between the values of intensive variables.'* Since this concept is an inference from two rather dense textbooks, it is normal for some colleagues (*e.g.*, Newman et al., 2023) to consider that such a concept is not accurate.

However, the point of view of the founder of axiomatic thermodynamics coincides with the concept inferred by Riera et al. (2023): *'such relationships, expressing intensive parameters in terms on the independent extensive parameters, are called equations of state'* (Callen, 1985, p. 37).

Callen's definition also clarifies that the counterargument by Newman et al. (2023) when they say that *'an extensive variable cannot be predicted by other variables that are all intensive'* it is just the other way around. In fact, it can be shown that this counterargument is not accurate given that it can be experimentally refuted, because it is possible to assess the ratio between the observed values of *two extensive variables* (left-hand side of the rightmost equation below) from the values of *two intensive variables* in combination with a universal *constant* (right-hand side of the rightmost equation below):

From Eq. (3):

$$\frac{Nmv^2}{N} = k_B T \;\Leftrightarrow\; \frac{m_T}{N} = \frac{k_B T}{v^2} \tag{5}$$

Where m_T: total mass of molecules, or total amount of substance, and N: total number of molecules (both extensive variables); T: absolute temperature, and v: molecular velocity (both intensive variables; see definition below).

Homeomorphically, from Eq. (4):

$$m_{eTp} I_e^2 = \frac{N_p k_{e\tau(e)}}{H_p} \;\Leftrightarrow\; \frac{m_{eTp}}{N_p} = \frac{k_{e\tau(e)}}{H_p I_e^2} \tag{6}$$

Where m_{eTp}: total standing biomass per plot, and N_p: total number of individuals per plot (both extensive variables –see definition below– and their ratio –m_{ep}– an extensive variable too; *e.g.*: large predators need larger hunting territories and larger and more numerous prey; *i.e.*, they depend on the number of elements and the size of the system); H_p: Eq. (2), and I_e: indicator of dispersal activity per individual per plot (both intensive variables). The satisfactory results of the comparison of means between the expected values from $k_{e\tau(e)}/(H_p I_e^2)$ and the empirically observed values from m_{eTp}/N_p for both three fish surveys under stationary trophodynamic conditions (taking stationarity as equivalent to equilibrium in living systems, see Montero and Morán, 1992, pp. 48–49), and four fish surveys under non-stationary conditions are shown in Fig. 2.

Variables, whether state variables or not, fall into two categories: extensive and intensive. This classification has been accepted in thermodynamics and actually in the whole field of physical sciences (Redlich, 1970). *Extensive variables* are those whose value depends on the dimensions of the system, and are often proportional to the amount of
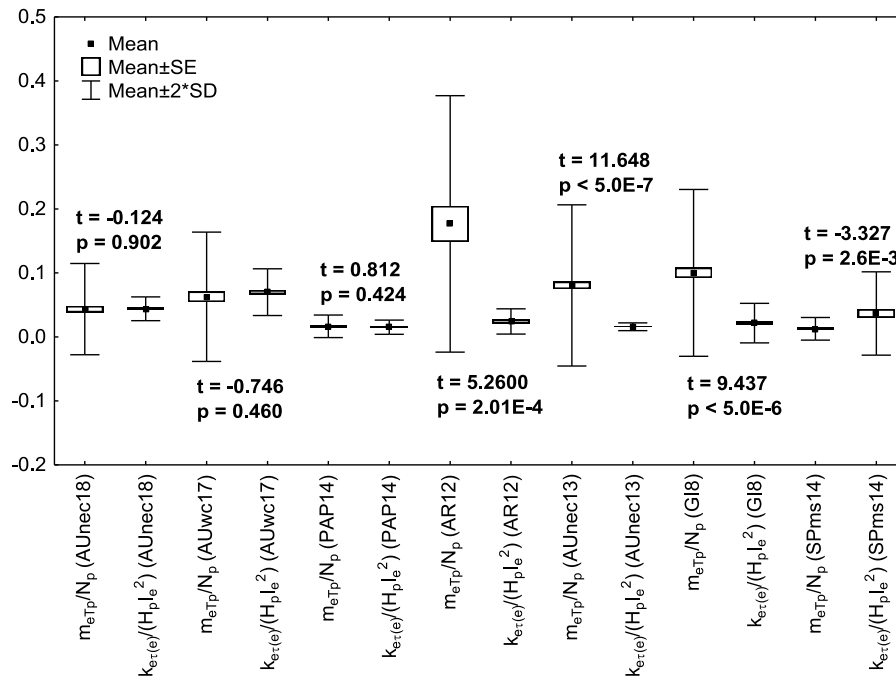
Fig. 2. Comparison of means between $m_{eTp}/N_p = m_{ep}$ (observed), and the expected value according to $k_{e\tau(e)}/(H_p I_e^2)$ (see Eq. (6), in turn, from Eq. (4)) in 7 surveys of reef fishes. Average size per plot in all surveys: 3640.00 m³. AUnec18: Australia, northeast coast, year 2018 (number of plots, $n_p = 58$); AUwc17: Australia, west coast, 2017 ($n_p = 41$); PAP14: Papua and New Guinea, 2014 ($n_p = 28$). The value of $p \gg 0.05$ indicates that these surveys are in stationary state. That is, the observed mean value of m_{eTp}/N_p does not differ from the theoretically expected value according to the EES$_R$ (Eq. (4)). AR12: Argentina, 2012 ($n_p = 13$); AUnec13: Australia, northeast coast, 2013 ($n_p = 134$); GI8: Galapagos Islands, 2008 ($n_p = 72$). The values of $t \gg 1$ and $p \ll 0.05$ indicate that these surveys are in non-stationary and hypertrophic state (*i.e.*, the observed value of m_{eTp}/N_p is higher than the theoretically expected value). SPms14: Spain, Mediterranean Sea, 2014 ($n_p = 27$). The values of $t \ll 1$ and $p \ll 0.05$ indicate that this survey is in a non-stationary and dystrophic state (*i.e.*, the observed value of m_{eTp}/N_p is lower than the theoretically expected value). In all these cases, $k_{e\tau(e)} = 1.380649E+02$ J$_e$·nat/individual, (according to Rodríguez et al., 2013; and Herrera et al., 2023). Raw data taken from Herrera et al. (2023). Values to obtain this figure in Supplementary Table 1.

substance considered. Such are, for example, mass (m); volume (V or v); number of moles (n, and therefore the number of elements in any system, N); electric charge (q or Q); total internal energy (U); enthalpy; and entropy (S; not species richness, also S) (Aguilar, 2001, p. 9).

In contrast, variables such as absolute temperature (T) (and therefore its microscopic expression, molecular speed: v); substance concentration (c); pressure (p or P); electric potential (φ; not the symbol φ from the explanation of $k_{e\tau(e)}$ in section 2.1); density (ρ or D); etc., which do not depend on the dimensions of the system (actually the number of particles) are called *intensive variables*. **The equilibrium between two systems is expressed by the equality of intensive variables**, such as mechanical balance depending on equal pressures, thermal balance depending on equal temperatures, and electrical balance depending on equal potentials (Aguilar, 2001, p. 9).

Consistent with the bolded sentence above, if we review some equations of state whose main objective is to detect whether systems are in equilibrium, we will see that all of them include some intensive variable (Table 1).

Simple examples are essential to illustrate the persistence of intensive variables in the equations listed in Table 1. Riera et al. (2023) also used a simple example about this subject. The examples below are even simpler. Suppose two narrow-mouthed spherical flasks containing the same gas at the same temperature and pressure, but one of the flasks has a size of 1 m³ and the other 0.25 m³. The flasks are connected to each other by a small pipe, in which there is a spigot (closed), and a small free-moving pinwheel. The thermodynamic condition of the system as a whole can be described (using the same symbols as in previous paragraphs) in a simple way as:

$$\Delta U > 0;\ \Delta m_T > 0;\ \Delta V\ [1\,\text{m}^3 - 0.25\,\text{m}^3 = 0.75\,\text{m}^3] > 0;\ \Delta P = 0;\ \Delta T = 0 \quad (7)$$

Now we open the spigot and the molecules of the two masses of gas, following the typical random walk, begin to move freely in both directions. However, what will happen with the small pinwheel? Nothing, it remains static because since there is no gradient of intensive variables the system is in equilibrium, and no work can be obtained from the gradient between extensive variables given that the net exchange of molecules between the two flasks is zero. That is, the value of ΔU in this case is only a consequence of the total mass $-\Delta m_T-$ and volume $-\Delta V-$ gradients, but there is no molecular velocity gradient (*i.e.*, $\Delta T = 0$). The application of Eq. (3) to this case would yield an equality before, during, and after the process. Now let's assume the behavior of a combined system similar to the previous one, but under the alternative conditions:

$$\Delta U > 0;\ \Delta m_T = 0;\ \Delta V\ [1\,\text{m}^3 - 1\,\text{m}^3] = 0;\ \Delta P > 0;\ \Delta T > 0 \quad (8)$$

When we open the spigot under the conditions described by Eq. (8), the molecules will preferentially pass in favor of ΔT and ΔP (elementary statement of the Second Law of Thermodynamics; ΔU in this case is a consequence of ΔT and ΔP), and the small pinwheel will be in motion until the exchange of molecules and energy reaches equilibrium between the two flasks ($\Delta T = 0$; $\Delta P = 0$; and $\Delta U = 0$). The application of Eq. (3) in this case would produce an inequality between both sides of the equation before and during the process (taking, hypothetically, infinitesimal static slides according to the context of statistical mechanics), and equality only after the process.

A situation analytically equivalent to the above was elucidated in ecosystem ecology six decades ago by Margalef (1963, p. 366), but considering the gradient of species diversity as the dominant intensive variable that replaces ΔT. The important disparity between two interconnected flasks and two connected ecosystems lies in the fact that, in the first case, equilibrium is reached due to the inert nature of the systems. In contrast, in the second case, the system with higher species

diversity uses the net energy input to further increase the value of (Eq. (2)), consequently reducing both its talandic temperature and its internal entropy (further explanation in Section 3.3). Therefore, a state of equilibrium between the two ecosystems is never reached.

Thus, contrary to Newman et al. (2023) argument, an equation of state lacking intensive variables would fail to capture the difference in behavior between systems described by Eq. (7) and Eq. (8).

Is there any intensive variable in Eq. (1)? No. According to the description of Eq. (1) in Section 1, B is ecologically equivalent to the total amount of substance in physics (extensive variable); $E^{4/3}$ is a limited ecological mimicry of total energy in physics (extensive variable). As for S, Newman et al. (2023) nullify the role of this parameter as an intensive variable in an ecological equation of state, asserting that *'species richness is **neither an intensive nor an extensive variable.'***

However, considering previous definitions in this section, S is an extensive variable because its variations are associated with fluctuations in the amount of substance (*i.e.*, N_p and m_{eTp} in Eq. (4)). Denying the extensive nature of S would be as unfounded as claiming that a tropical rainforest, with all its species and individuals, can fit inside our mouth (both are two types of ecosystems). Conversely, the value of Eq. (2) can reach the same magnitude in ecosystems that differ in size and number of individuals (*i.e.*, Eq. (2) behaves as an intensive variable). This feature of H_p should be recognized as a methodological advantage, in addition to other features explored above (Fig. 1).

3.3. The origin and misuse of the concept of 'information entropy' in ecology

The use of the term *'information entropy'* is frequent in contemporary ecology (*e.g.*, Harte, 2011; Singh et al., 2019; Mattos et al., 2022; Zhang et al., 2023; Pos et al., 2023; Xu, 2023). The equation of Josiah Willard Gibbs for entropy in statistical mechanics (Tolman, 1938, p. 539, Eq. (122.10)) is: Eq. (2). Gao et al. (2019) explored that this equality is particularly valid when the Boltzmann distribution of molecular energy values is also valid, a topic that is reliably plausible in ecology (see Rodríguez et al., 2015b). The equality between Eq. (2) and Gibbs' entropy raises a first point: **from a mathematical point of view**, the use of the term *'information entropy'* is a redundancy (*i.e.*, it is equivalent to say *'Eq. (2) Eq. (2)'*).

A good introduction to the solution of this confusion is provided by the first-person interview with C. E. Shannon narrated by Tribus and McIrvin (1971, p. 180): *'My greatest concern was what to call it* [this is Shannon talking about his deduction of Eq. (2)]. *I thought of calling it "information," but the word was overly used, so I decided to call it "uncertainty." When I discussed it with John von Neumann, he had a better idea. Von Neumann told me, "You should call it entropy, for two reasons. In the first place your uncertainty function has been used in statistical mechanics under that name* [obviously, here Von Neumann was talking about Gibbs entropy]*, 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."'*

From this advice, Shannon's decision followed two paths:

(i). He commented, with a certain degree of inaccuracy if we take into account subparagraphs v and vi of the previous section, that *'H is then, for example, the H in Boltzmann's famous H-theorem'* (Shannon, 1948, p. 393).

(ii). He used, apparently erratically, both the term *'entropy'* (56 times in the main text of Shannon, 1948) and the term *'information'* (53 times in the main text of Shannon, 1948) to refer to the same equation (Eq. (2)).

About item (i): The H (see Eq. (9)) of Boltzmann's H-theorem does not coincide either in magnitude or in sense of change with Eq. (2), Section 2.1, above. Boltzmann's H-theorem depends on the *'relaxation time'* at which an out-of-physical-equilibrium distribution of molecular

velocities evolves until it reaches the Maxwell-Boltzmann distribution of molecular velocities under equilibrium. The H-theorem expresses the *'speed'* with which an unbalanced system tends to seek the aforementioned distribution. Such a speed reduces over time (*i.e.*, the process 'decelerates' $–dH/dt \leq 0$– all the time); whereas in the sequential assessment of Eq. (2) dH_p/dt can reach negative, positive or null values in real ecosystems. Thus, this minor drafting inaccuracy of Shannon (1948) may have had a conceptually disturbing 'butterfly effect' on ecology.

$$H = \sum \left(N_i \cdot \ln N_i \right) \tag{9}$$

Where N_i represents the total number of molecules that exist in state i^{th}, instead of a probability like p_i in Eq. (2), and k_B does not intervene in the calculation of Eq. (9).

About item (ii): This behavior is unexpected according to Shannon's rigorous professional background. Tribus and McIrvine (1971, p. 180) provide the clearest explanation in this regard: *'For a given question (Q constant) it is of course possible to have different states of knowledge. Shannon defined the information in a message in the following way: A message produces a new X* [knowledge]. *A new X leads to a new assignment of probabilities and thus a new value of S* [entropy, a.k.a. uncertainty; Ayres, 1994, p. 36]. *To obtain a measure of the information Shannon proposed that the information (I) be defined by the difference between the two uncertainties: in symbols, I = S(Q | X) – S(Q | X'). The information content of a message, then, is a measure of the change in the observer's knowledge (from knowledge X before the message to knowledge X' after the message). A message that tells you what you already know produces no change either in knowledge (X remains the same) or in probability assignment and therefore conveys no information.'*

So, on the one hand, C. E. Shannon was not erratic at all. The entropy linked to the emission, transmission, and reception of a message (Eq. (2)) is equivalent to ignored information (mathematically equivalent to Boltzmann's entropy at the aggregate scale divided by the number of elements; see Eq. (10), below); and the amount of information (Eq. (2) also) is equivalent to the decreased entropy after the message has arrived and been accurately read. On the other hand, the relativity of both concepts depending on the frame of reference (in this case an individual waiting for a message), could lead to proposing that *'even at the purely phenomenological level, entropy is an anthropomorphic* [and so, subjective; Riera et al., 2023] *concept'* (Jaynes, 1965, p. 398).

$$S_B = k_B(\ln\Omega) = k_B\left(\ln\frac{N!}{\prod_i n_i!}\right) = k_B\cdot(H_B\cdot N) \simeq k_B\cdot(\text{Eq.}(2)\cdot N) \tag{10}$$

Where, in physics (there are some differences compared to ecosystem ecology; see Herrera et al., 2023), k_B: see above (Eq. (3)); S_B is Boltzmann's entropy; H_B (*i.e.*, $(\ln \Omega)/N$) is the index of Brillouin (Margalef, 1974, p. 367; Magurran, 2004, p. 113); and Ω is the number of microstates (a.k.a. 'complexions' or 'random permutations'). The distinction between complexions lies in the diverse configurations of coordinates and linear momentum vectors at the molecular level, while state variables (*e.g.*, volume, pressure, temperature) remain constant over time (*i.e.*, time-independence, the fundamental requirement to define equilibrium or a stationary state; Callen 1985, p. 13; Aguilar, 2001, p. 7). The symbol $\simeq$ means that H_B and Eq. (2) are asymptotically equal or congruent to each other.

In any case, there is an objective link between receiving new information through a message and saving energy dissipation on a metabolic scale, equating to a conservation of effort (*e.g.*, if we learn about a new discovery by reading a scientific publication, we are spared the effort of having to discover it ourselves). In a similar way, Margalef (1961; 1968, pp. 97–102) also analyzed ecosystems as living channels that decode (ontogenetic and phylogenetic development), select (natural selection), recode (gametogenesis) and send (fecundation and soil seed bank) information from their present to their own future.

Consequently, the increase of physical information is synonymous with the reduction of thermodynamic entropy, mirroring the effect of receiving a message by an individual (as discussed above). Herrera et al., 4) provide a list of 10 references supporting this approach, dating from 1872 to 2021. For instance, in a stationary state (thermal equilibrium), the entropy level of a non-living physical system is at its maximum. However, living systems tend toward stationarity, minimizing entropy production (Prigogine's theorem; see Prigogine, 1955; Jaynes, 1980; Aguilar, 2001, pp. 551–552; Shapovalov and Kasakov, 2018). Therefore, the calculation of Eq. (2) with reference to a single scale of hierarchical organization in ecology becomes a measure of information, rather than entropy. This explains why *'what for the external observer represents an uncertainty* [personal and metabolic entropy of the researcher during field work]*, corresponds to … a measure of organization* [Eq. (2)]*, if we consider the situation as the result of interactions in the ecosystem itself'* (Margalef, 1974, p. 368).

Taking into account the opposite relationship between information (in the form of species diversity) and physical entropy is crucial for understanding ecological phenomena, as recently discussed by Nielsen et al. (2020), and Nielsen and Müller (2023). As a consequence, **from a physical point of view**, the use of the term *'information entropy'* is also a contradiction in terms.

E. T. Jaynes (cited by Newman et al., 2023 in favor of the term *'information entropy'* applied to Eq. (1)) clarified this issue by stating, *'information entropy … is an unfortunate terminology, which now seems impossible to correct. We must warn at the outset that the major occupational disease of this field is a persistent failure to distinguish between the information entropy, which is a property of any probability distribution, and the experimental entropy of thermodynamics, which is instead a property of a thermodynamic state as defined, for example by such observed quantities as pressure, volume, temperature, magnetization, of some physical system. They should never have been called by the same name; the experimental entropy makes no reference to any probability distribution, and the information entropy makes no reference to thermodynamics. Many textbooks and research papers are flawed fatally by the author's failure to distinguish between these entirely different things, and in consequence proving nonsense theorems.'* (Jaynes, 2003, p. 351).

Therefore, according to E. T. Jaynes himself, mixing strictly physical terms (see previous sections) with terms from the field of the MaxEnt algorithm can only lead to confusions and analytical mismatches. E. T. Jaynes remained consistent with his own opinion until the end of his life, as none of the physical concepts discussed above was included in his posthumous work (Jaynes, 2003).

Harte et al. (2022, p. 4, right column, 1st paragraph) provide clues about the likely influence of these analytical mismatches when they say, referring to the METE, that *'it is unclear why an apparently mechanism-free theory should work at all in ecology.'* They also implicitly comment on the seemingly contingent nature of Eq. (1), because the results of Eq. (1) change not only due to fluctuations in observed natural systems but also because certain parameters of Eq. (1) can fluctuate at will within a wide range of values to adjust the equation to observed conditions (Harte et al., 2022, p. 5, left column, 2nd and 3rd paragraphs). Can the links between Eq. (1) and MTE (Brown et al., 2004) improve this situation? Apparently not, the MTE itself also needs improvements, either in isolation (*e.g.*, Duncan et al., 2007; Hawkins et al., 2007; Price et al., 2012; Lin et al., 2013; Giancarli et al., 2023), or in combination with the METE (Kendall, 2020).

References by Newman et al. (2023) to previous well-known successes of MaxEnt in many different scientific fields (see also examples in Harte, 2011; Harte et al., 2008, 2022; Harte and Newman, 2014; Brummer and Newman, 2019; and Cofré et al., 2019) do not strongly support Eq. (1) as an ecological equation of state. Many of these successes have been achieved in contexts in which physics and the laws of thermodynamics do not have any theoretical meaning. Therefore, the success of MaxEnt in these cases is attributable simply to a particular branch of statistics developed by E. T. Jaynes; it is pure statistical inference (see Favretti, 2018a, 2018b).

This means that, while Eq. (1) is an offshoot of an unconventional branch of statistical inference, Eq. (4) is the seed of what, according to Lakatos (1978), is a developing *scientific research program* (OBEC; see last sentence in section 1, first paragraph) coming in turn from the 'graft' between two solid trees: ecology and physics.

4. A strategic roadmap for interdisciplinary modeling in ecology developed from screening the previous sections

From the previous sections, it is possible to derive valuable guidelines for interdisciplinary modeling in ecology:

1) As with the spread of gossip in human populations, sequences of indirect quotes based on other indirect quotes on the same topic over time tend to distort the initial information. Therefore, in the case of interdisciplinary studies, it is especially advisable to consult the original source, which is usually a 'classical' publication ('classical' being understood as those publications that do not lose their value despite the passage of time). For example, Shannon (1948) is as much a classical in interdisciplinary studies as Symphony No. 5 in C Minor, Op. 67 of Ludwig van Beethoven in music.

2) A classical publication must be read in its entirety. Selective reading (*i.e.*, seeking out a specific topic and neglecting the rest) of a classical publication can result in missing interesting opportunities to make useful interdisciplinary connections that expand knowledge. For example, a relatively recent comprehensive analysis of Shannon's (1948) publication found that it had dealt, in the field of information theory, with phenomena completely equivalent to ecological phenomena such as: character displacement, the measurement of functional redundancy, the influence of the principle of competitive exclusion, and the origin of resilience in the performance of the ecological niche (see Rodríguez et al., 2016).

3) Two or more conceptual frameworks must participate in a given proposal on equal terms, and with a similar degree of accuracy.

4) Mere analogies count as premises to begin (*e.g.*, in quantum mechanics: *'an atom is like a tiny solar system'*), but not as final results.

5) There are relative concepts or 'hinge concepts'. These concepts, despite their full correspondence with real-world objects and measurable indicators, can change their meaning depending on the context (*e.g.*, the concept of 'entropy', in the framework of this article).

6) Homeotic genes regulate downstream gene networks involved in the modeling of large sections of the body. In a similar way, there are 'homeotic concepts'. When the context of application of certain conceptual frameworks change, these concepts either change the meaning of many other concepts, or determine whether it is epistemologically viable for these other concepts to be applicable to the model under development, or not (*e.g.*, the nonconcept of 'information entropy', and the concept of 'equation of state' in this article).

7) In interdisciplinary modeling, there is a particularly complex balance between the qualitative conceptual section and the mathematical section. Mathematics, seen at its most general level, is neither a theoretical nor an empirical science, but rather an abstract one (*'if the laws of mathematics referred to objects of our mere imagination, and not to objects of reality* [then] *As far as the laws of mathematics refer to reality, they are not certain; and as far as they are certain, they do not refer to reality'*; Einstein, 1922, pp. 27–28). Every reliable chain of mathematical deductions is based on certain conceptual assumptions, which are frequently lost in a cataract of equations. If those assumptions fail, the entire chain of deductions is wrong, even if all its intermediate steps are

rigorously correct. There are glaring examples of paradigms that have been in chronic danger of extinction for ignoring this rule (*e. g.*, see Leontief, 1982; López-Corredoira, 2017).

8) Ockham's razor is especially useful to obtain relevant results in this field. The most complex models, although they attract the attention of users more frequently, are not necessarily the most reliable (see Green and Armstrong, 2015). For instance, equation-laden papers in the fields of ecology and evolution tend to be less cited by those researchers who use the models in practice (Fawcett and Higginson, 2012).

9) Interdisciplinary models are generally the result of teamwork. In these cases, the main role of the team leader is not to be a know-it-all, but to diligently search for analytical contradictions and encourage criticism, the stronger the better.

10) An advisable question: Does this manuscript that we are developing, whatever it may be, belong to the core of a scientific research program (*sensu* Lakatos, 1978), or to its protective belt? If the answer is the second one, then the manuscript must be especially strong, because its main function will be to resist the attacks of critics. The core of a scientific research program is often a novel emerging idea. But the specialized work of science professionals on a given subject over many years makes it difficult to recognize such ideas quickly. So, when the scientific community becomes aware of the core-type manuscript, there is no longer time to criticize it, because it is a fait accompli. As a result, all the criticism will fall on belt-type manuscripts.

11) The current *zeitgeist* of science is strongly influenced by the drive for speed and novelty, which often results in publications older than five years being considered 'outdated'. Therefore, there will be a notable advantage if, in addition to the review of recent publications, a review of older publications is done, the older the better.

12) The previous point has two important effects: (i) Taking into account the state of the art in any science and the amount of information accumulated, it is difficult to find a really novel topic. (ii) Sometimes the solution to a current problem depends on a tiny detail that has been ignored as insignificant for decades (*e.g.*, the concept of *'talandic temperature'* related to the replacement of T by H_p to obtain Eq. (4) from Eq. (3)). That crucial detail usually lies buried under a mountain of 'outdated' information.

5. Conclusions

The question that ultimately arises is why it was necessary to try to amalgamate concepts of statistical inference with physical principles, thereby introducing more complexity and fostering debate. It might have been more prudent to refer to Eq. (1) just like *'An equation, based on the algorithm of maximum statistical entropy, allows the assessment of standing biomass by interrelating ecological and physiological indicators.'* However, our minds naturally seek connections, reminiscent of Simberloff (1980) age-old observation (1980, p. 49): '[in ecology, there is] *an unhealthy, often obsequious desire, termed "physics envy" by Cohen (1971), to gain the approval of physical scientists.'*

To distinguish a robust ecological equation of state proposal, it is imperative to illustrate that a specific approach, firmly aligned with the conceptual and methodological framework of physics, can be empirically beneficial in ecology and theoretically consistent with it. According to Newman et al. (2023), this demonstration is unnecessary, an error attributed to absolutism in favor of physics (see Section 2.1 and Section 3).

CRediT authorship contribution statement

Rodrigo Riera: Writing – review & editing, Visualization, Validation, Supervision, Project administration, Investigation, Conceptualization. **Brian D. Fath:** Writing – review & editing, Supervision,

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

Declaration of competing interest

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

Data availability

Data will be made available on request.

Supplementary materials

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