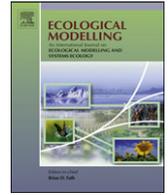




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Ecological state equation

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ABSTRACT

The direct equivalence between ecology and thermodynamics has not been attained despite accepted thermodynamic features of the ecosystem. This article explores the homeomorphism between ecology and statistical mechanics by analysis of ruderal vegetation. In conventional thermostistical algorithm, the pro-kinetic effect of temperature on molecules was replaced by the anti-kinetic effect of species diversity on biological individuals. The existence of an ecological equivalent of the thermodynamic Boltzmann constant was empirically verified. From the relationship of this constant with biocenological variables, we derived a probable ecological equation of state under stationary and quasi-stationary conditions. This equation of state is homeomorphic with regard to the ideal gas state equation, and it is useful to infer the value of some biocenological parameters whose direct measurement is difficult, as biomass, energy and dispersal. According to these results, ecosystem assessment from conventional thermostatics is plausible and empirically verifiable. This approach offers useful analytical tools for the conservation and restoration of ecosystems.

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1. Introduction

The background to the thermodynamic nature of ecosystems dates back to 1887, and particularly to 1925 (Odum, 1968). However, with some exceptions (e.g. MacArthur, 1955; Odum, 1969), references to the link between entropy and ecological information, or diversity, are generally scarce in the literature. Subsequent efforts to introduce thermodynamic approach into ecosystem ecology have given rise to wider dissemination of the topic (Messer, 1992; Jørgensen and Fath, 2004; Jørgensen and Svirezhev, 2004; Tiezzi, 2005; Ludovisi, 2006; Haegeman and Etienne, 2010), but the parallelism between the two disciplines has yet to be consolidated.

There is no standard procedure to measure entropy content of living systems (Aguilar, 2001; Aoki, 2006). This hinders the application of an interdisciplinary approach in this field. Thus, conventional physics seems, at the first sight, inadequate to describe ecosystem dynamics (Ulanowicz, 2004). In principle, there are no limits to the application of thermodynamic concepts to ecology and the problem is to achieve direct homeomorphism between thermodynamic and ecological models (Svirezhev, 2000).

This article explores such homeomorphism applying the laws of physics, as nearly as possible, to ruderal vegetation. In physical

terms, our main objective in this article is to explore whether the thermodynamic equation of state ($PV=Nk_B T$, whose variables are explained in Table 1) can be used as a precursor of an equivalent ecological equation of state. All our results indicate that an empirically verifiable ecological equation of state can be obtained directly from conventional thermodynamics.

2. Methods and theoretical foundations

Nine surveys (G1–G9) of 2-year-old bistratified ruderal vegetation were conducted in an approximately homogeneous area in terms of ecological conditions. Sixty fixed 4m² plots were established in accordance with a generally accepted criterion (Tilman, 1999). The spatial coordinates of the center point of each plot was specified in an *ad hoc* system of coordinates, in meters. The study area is located in the district “Guajara” (28°27'57.02"N; 16°18'05.98"W) in Tenerife, Canary Islands. The field work was performed from 07-25-2004 to 11-06-2005, with approximately monthly sampling. In all surveys, all the individuals were counted and systematically classified. In two surveys (G9 and replication in an equivalent geographic area adjacent to G4) all individuals were uprooted and grouped by species per plot to measure fresh weight in kg. In five of the remaining surveys, biomass per plot was estimated by uprooting as few plants as possible (3–5 individuals per species or specimens of another species of equivalent size in the case of rare species) in order to minimize the ecological impact.

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Table 1
Hypothetical homeomorphism between ecosystem ecology and thermodynamics.

Parameter	Thermodynamics	Ecology
Main state variable	T (K)	$H = - \sum_{i=1}^S \frac{n_i}{N} \cdot \ln \left(\frac{n_i}{N} \right)$ (nats/individual)
Structural element	Ideal gas molecule	Individual
Individual mass	m (kg) (constant for all the molecules of the same kind of gas, N_2 , H_2 , etc.)	Fresh biomass, m_e (kg) (variable even for individuals of the same species that live together)
Indicator of velocity	v (m/s) (independent of m for all the molecules of the same kind of gas, N_2 , H_2 , etc.)	I_e (\bar{D}) (Eq. (3)) (probably, inversely correlated with m_e even for individuals of the same species due to the multi-scale <i>trade-off</i> biomass (m_e) \leftrightarrow dispersal (I_e) that is an essential feature in the r - K life history theory) [•]
Individual energy	$E = 1/2m \cdot v^2 = 1/2k_B T^{\S}$	$E_e = 1/2m_e \cdot I_e^2 = 1/2k_e/H$ (4) [§]
Interactions between individuals for energy transmission	Intermolecular collisions	Interspecific interactions
Type of interaction for energy transmission	Non-elastic, conservative; without any tendency to establish intermolecular associations	Elastic, non-conservative; with a tendency to establish association (e.g. mutualism) as well as repulsion (e.g. competence) that can be mutually canceled at the aggregate scale (null net effect) under stationary conditions (see below)
Total energy	Constant, isolated system.	Constant due to replenishment from outside.
State of reference	Equilibrium state	Stationary state ("open equilibrium")
Specific _(s) volume	$V_{(s)} = 1/(m_T/s_T)$	$V_{e(s)} = 1/(m_e T/S_e)$
Specific _(s) pressure	$P_{(s)} = (1 \cdot v_s^2)/V_{(s)}$	$P_{e(s)} = (1 \cdot I_e^2)/V_{e(s)}$
Aggregate _(a) pressure–volumen product	$P \cdot V_{(a)} = P_{(s)} \cdot V_{(s)} \cdot N \cdot m = 2N(1/2m \cdot v^2)$	$P_e \cdot V_{e(a)} = P_{e(s)} \cdot V_{e(s)} \cdot N \cdot m_e = 2N(1/2m_e \cdot I_e^2)$
Boyle's law	(constant T): $P \cdot V_{(a)} = k^*$	(constant H): $P_e \cdot V_{e(a)} = k^{\dagger}$
Charles' law	(constant P): $V/T = k$	(constant P_e): $V_e \cdot H = k$
Gay–Lussac's law	(constant V): $P/T = k$	(constant V_e): $P_e \cdot H = k$
Coordinates to calculate Boltzmann constant	$k_B: P, [(P \cdot V_{(a)})/(N \cdot T)]$	$k_e: P_{e(s)}, [(P_e \cdot V_{e(a)})/H]/N^{\ddagger}$
Equation of state	$P \cdot V_{(a)} = N \cdot k_B \cdot T$ or, $2N(1/2m \cdot v^2) = N \cdot k_B \cdot T$	$P_e \cdot V_{e(a)} = (N \cdot k_e) \cdot H$ (5) ^{**} or, $2N(1/2m_e \cdot I_e^2) = (N \cdot k_e) \cdot H$ (5) ^{**}

Note: T : temperature. H : Shannon's diversity index, value per plot or class mark (midpoint) of the range of H values per plot per macrostate, the replacing of the midpoint by the mean yields equivalent results. S = number of species. k = a constant. N : total number of molecules or individuals. n_i = number of individuals of species i . $N = \sum n_i$. m_T : total physical mass ($N \cdot m$). $m_e T$: total ecological mass ($N \cdot m_e$) per plot (p), macrostate (m) or survey (s), depending on the studied scale. s_f : physical space occupied by the gas. s_e : mean space per plot or macrostate in the ecosystem. k_B : Boltzmann constant = $1.3806504 \times 10^{-23}$ J/K/molecule. k_e : ecological equivalent of Boltzmann constant. [•]This hypothetical correlation, given that $E_e = 1/2m_e \cdot I_e^2$, could be one of the fundamental conditions for stationarity because if there is a *trade-off* between m_e and I_e then $E_e \rightarrow$ constant at the aggregate scale (for the ecosystem as a whole); this subject only can be stated as a hypothesis in advance here because it is complex enough to deserve an independent analysis in a forthcoming article. [§]With 1 translational degree of freedom. ^{*} $P \cdot V_{(a)}$ increases with T . [†] $P_e \cdot V_{e(a)}$ decreases with H due to the anti-kinetic (therefore "ecologically antithermic") effect of diversity (Margalef, 1974; Odum, 1972). [‡]See Fig. 1 as well as Table 3. ^{**}From the antithermic transformation of the equation on the left, according to premise 2. In regard to [†]: the constant value of $P_e \cdot V_{e(a)}$ for a constant value of H expresses the well-known denso-dependence of many ecological phenomena in physical terms. That is to say, a same ecological assembling exerts a higher consumption pressure in a reduced space than in a wider one.

Biomass measurement for censuses G6 and G7 was impossible due to adverse weather conditions. From the diversity per plot values, we obtained 30 successive statistical distributions of density per survey with biomass data, and 1 distribution per survey without such data (212 distributions in total).

The division of ecosystem in many parcels of equivalent size is arbitrary. On the contrary, the grouping of parcels according to its diversity value can improve our description of ecosystem since any complex system develops inhomogeneities which enable us to recognize groups of elements that are more similar to one another than they are to the background (Levin, 1998). In fact, ecosystems have a recognizable structure because they are composed of different parts arranged in a definite pattern (Margalef, 1963).

Therefore, assuming a hierarchical functional structure of the ecosystem (Nielsen, 2000; Ulanowicz, 2004; Miller, 2008), the categories of H (diversity index of Shannon, 1948) of each distribution were interpreted as alternative internal thermostatical macrostates within potential functional fluctuations of the community, each including several species configurations (microstates) represented by their respective plots. For each microstate and macrostate, the value of the variables (Table 1) was calculated. Diversity calculations were performed using Primer-5.2.9 (Primer-E Ltd., 2002). For statistical tests, Statistica-6 (StatSoft Inc., 2001) was used.

According to Montero and Morán (1992), the stationary state is for the analysis of open systems what equilibrium is for the analysis of closed systems (premise 1); in both cases the mean values of state

variables are stable over time. The fundamental difference is that in the first case there are internal gradients that act as force fields and in the second there are not (Tschoegl, 2000). But if the gradients are constant, this difference should not affect the description of the ecosystem using the conventional thermodynamic algorithm.

In other words, the exchange of energy, substance and structural elements in an open system is not synonymous with change (non-stationarity) when the input of resources is exactly or approximately offset by the corresponding output (quasi-stationarity). In this situation the constancy of the state variables resembles that of a closed equilibrium state, and this stationary state can be interpreted as being in "open equilibrium" (gains \cong losses).

There have been several attempts to develop a theory of non-equilibrium stationary states as a direct analogy of the theory of states of equilibrium based on the Boltzmann approximation (Filyukov and Karpov, 1967; Jaynes, 1980; Oono and Paniconi, 1998) even in ecology (e.g. Shipley et al., 2006; He, 2010). According to Trepagnier et al. (2004) and Komatsu et al. (2009), the probabilistic distributions for non-equilibrium stationary states may possibly be obtained from a general principle that is analogous to that of equilibrium in statistical mechanics. This approach seems to be fruitful in physics (e.g. Hyeon-Deuk and Hayakawa, 2003) and should not be ignored because of its potential capacity to unify different disciplines, especially if we consider that there is still no consistent and generally accepted formalism to describe the behavior of complex systems away from equilibrium (Wei, 1966; Lin, 1999; Dewar, 2003).

Apparently, owing to the existence of inter-specific relationships, the ecosystem does not meet the requirement of physical independence between elements (resulting in a zero balance between intermolecular forces of attraction and repulsion) necessary for the ideal gases model of classical statistical mechanics, where molecular interactions take place at random. However, firstly, mutually negative and positive inter-specific relationships (e.g. competition and mutualism, respectively) may tend to cancel each other out, with a zero balance net result in a large-scale ecosystem. Secondly, since the publication of the unified neutral theory of diversity (Hubbell, 1997, 2001) there is a growing tendency to consider that diversity arises, at least in part, in a random manner, which downplays the evolutionary and ecological role of inter-specific relationships in ecology.

On the other hand, it is possible that the analytical importance of the debate between determinism and stochasticity has been historically overvalued in biology. For example, our conventional knowledge about biological evolution would not have any sense without a harmonious coexistence between the causality of the survival of the fittest and the randomness of mutation and Mendelian inheritance. Something similar to this could take place in the thermodynamic analysis of ecosystem; perhaps randomness is the norm within an analytical space enclosed by certain non-stochastic general conditions, as the competitive exclusion principle or the balance between trophic production and respiration, which can act as the ecological equivalents of thermodynamic constraints.

It is therefore possible to assume that the ergodicity or space-time transitivity (Birkhoff, 1931; Hopf, 1932; Aguilar, 2001) of the states of equilibrium is applicable to ecology (e.g. Kerner, 1957) in order to calculate an ergodic indicator (I_e) of species dispersal activity in stationary ecosystems (hypothesis 1). The empirical verification of I_e coherence with what would be expected from the physical point of view would allow extrapolating the rest of the analytical algorithm from conventional thermodynamics to the description of the ecosystem in a homeomorphic manner (hypothesis 2). The empirical confirmation of both hypotheses depends on the use of a biocenological variable to replace the role of temperature in the above-mentioned algorithm (see hypothesis 3, below). In physical terms, we explore whether, through this replacement, the thermodynamic equation of state ($PV = Nk_B T$, whose variables are explained in Table 1) can be used as a precursor of an equivalent ecological equation of state.

Shannon's (H) information measure (Shannon, 1948) has proved effective to estimate species diversity (Magurran, 2004). Lack of information (uncertainty) and entropy are identical in essence (Ayres, 1994). As a result, any increase of information has an anti-entropic effect at local level (Rothstein, 1951; Brillouin, 1953; Jaynes, 1957; Gallucci, 1973; Brissaud, 2005) generally linked to reduced population fluctuations, or the talandic temperature of the ecosystem (Margalef, 1974; Odum, 1972). These factors would involve a reduction of I_e with anti-kinetic effect. That is to say, an inverse correlation between H and I_e would indicate that diversity reduces individual dispersal in a similar way as low temperature reduces molecular movement (premise 2).

Therefore, the pro-kinetic role of temperature in the standard thermostatic algorithm could be replaced by the anti-kinetic effect of species diversity (H) in biocenosis, thereby enabling extrapolation of the algorithm to ecosystem modelling (hypothesis 3).

In order to calculate I_e (for a species i in a plot j), the value of the dispersal capacity (d) must be determined, as follows:

$$d_{i,j} = \frac{\sum_{k=1}^m \left[\sqrt{(x_j - x_k)^2 + (y_j - y_k)^2} \times 2i_{j,k}/(i_j + i_k) \right]}{m}, \quad (1)$$

where $d_{i,j}$ is the mean dispersal capacity of species i in plot j with central geographic coordinates (x, y) within an ecological space s_0 divided into m plots; i_j is the abundance of i in plot j ; i_k is the abundance of i in plot k ; and $i_{j,k}$ is the shared number of individuals of i in plots j and k . The element on the left (Pythagorean theorem) of the numerator in equation 1 for each plot is a measure of the physical distance of j from m according to the spatial distribution of species i in s_0 . According to the degree of homogeneity of the abundance of i for all the plots ($\forall m$), this element on the left is adjusted by the multiplier $(2i_{j,k})/(i_j + i_k)$, which is the Bray–Curtis similarity index (Washington, 1984), (range 0–1). Therefore, the magnitude of the ergodic indicator (I_e) of the ecological dispersal activity of i in plot j is:

$$I_{e,i,j} = \left(\frac{d_{i,j}}{\sigma_{i,j}} \right) \times 100, \quad (2)$$

where $\sigma_{i,j}$ is the standard deviation of $d_{i,j}$ (Eq. (1)).

Eq. (2) is the reciprocal of the coefficient of variation ($CV = \sigma/\mu \times 100$) or the signal-to-noise ratio of $d_{i,j}$. Therefore $I_{e,i,j}$ maintains the invariance to scale changes (spatial scale, in this case) of the variation coefficient. This allows comparing I_e values obtained from different-sized ecosystems; a desirable feature since, from the physical point of view, the same velocity can be measured in two trajectories of different lengths. The mean value of the ergodic indicator of dispersal capacity for all the species S in plot j is:

$$I_e = \frac{\sum_{i=1}^S (I_{e,i,j})}{S}, \quad (3)$$

Any species is represented by individuals in the ecological space, and the statistical influence of the number of individuals per species and plot on the value of I_e with respect to the entire ecological space s_0 is implicit in the overall distribution of values of $(2i_{j,k})/(i_j + i_k)$. Therefore, the value of I_e (Eq. (3)) can also be interpreted as an indicator of the mean dispersal capacity per individual for plot j . The parameter I_e only acquires operative utility for ecosystem modelling in Eq. (3) because this equation represents the minimum scale of aggregation necessary to calculate the main state variable (H). For the calculation of derived variables I_e is expressed in dispersal units (đ).

Eqs. (1)–(3) reflect two assumptions: (1) from conventional mechanics, any living being can also be interpreted as a physical object that invests a certain amount of trophic energy in movement, proportional to I_e . (2) It is not possible to estimate individual trajectories from a momentary observation of any ecosystem. This difficulty may be resolved by assuming the validity of hypothesis 1, i.e., a species with a wider and more homogeneous distribution in an observational time interval $\Delta t \rightarrow 0$ with regard to the successional process is also one represented by individuals with faster dispersal during an interval $\Delta t \gg 0$ just before the observation. The plausibility of both assumptions depends on the final empirical results being consistent with the laws of physics and ecology.

From our knowledge of standard physics (Roller and Blum, 1986; Aguilar, 2001) and combining hypotheses 2 and 3, we may infer the homeomorphism summarized in Table 1.

3. Results

The entire study included 49,009 individuals, belonging to 96 species, with a mean density of 22.731 ± 1.761 (SE) individuals/m² and a mean species diversity $H = 1.226 \pm 0.049$ (SE) nat/individual/plot. Mean fresh biomass was 0.541 ± 0.025 (SE) kg/plot (m_{eTp}) and 0.049 ± 0.002 (SE) kg/individual/plot (m_e). The mean value of I_e considering all the 520 plots with observable vegetation was 61.146 ± 0.851 (SE) đ /individual.

Table 2
Adjustment of I_e to gamma distribution (\dagger) and linear correlations (r) I_e vs. H (*).

Census	n	n_c^\dagger	χ^2^\dagger	p^\dagger	r^*	p^*
G1	59	9	0.740	0.864	-0.405	0.002
G2	59	6	0.699	0.403	-0.442	<0.001
G3	56	7	0.463	0.793	-0.251	0.063
G4	59	9	0.598	0.741	-0.446	<0.001
G5	54	9	1.295	0.730	-0.093	0.502
G6	60	9	2.036	0.565	-0.159	0.224
G7	60	6	0.202	0.653	0.087	0.507
G8	58	14	2.714	0.438	-0.619	<0.001
G9	59	9	1.586	0.662	-0.565	<0.001

Note: H : Shannon diversity per plot. I_e : ergodic indicator of dispersal per plot (Eq. (3)). n : number of plots. n_c : number of categories of the distribution. χ^2 : results of the chi-square test. p : significance level.

In conventional statistical mechanics the values of molecular velocity (v) fit the gamma distribution represented by the Maxwell–Boltzmann equation (Roller and Blum, 1986; Aguilar, 2001). In the present case, the distribution of I_e values per plot per survey fits the gamma distribution also (see \dagger in Table 2, left section). This supports the replacement of v by I_e to calculate E_e (see Eq. (4), Table 1). The correlation between H and I_e per set of plots and survey is generally inverse and significant (see * in Table 2, right section) except in the surveys G5, G6 and G7. This result confirms the anti-kinetic (therefore “ecologically anti-thermic”) effect of H under stationary conditions (premise 2). That is to say, biodiversity tends to reduce individual dispersal (movement) in a similar way as low temperature reduces molecular movement.

The linear fit of $(P_e \cdot V_{e(a)} \cdot H)/N$ with respect to $P_{e(s)}$ (Fig. 1) has in general a low slope ($n=7$; mean $b=0.124$; 0.027% of the range or 0.169% of the standard deviation of the ordinates as a whole), as expected according to ecological transformation of the laws of gases (Table 1). The whole set of regression equation intercepts ($n=7$) yielded a mean value of $k_e = 122.9543 \text{ J}_e/\text{nat}/\text{individual}/\text{individual}$, where J_e : 1 eco-Joule = 1 kg·d² (*ad hoc* unit), similar to $k_B \times 10^{25} = 138.06504$. If the surveys G4 and G5 (Fig. 1, panels d and e) are excluded from the analysis due to their deviation from the stationary state pattern (see Table 3), the mean value of k_e is 142.6260, which is also similar to $k_B \times 10^{25} = 138.06504$. According to these observed mean values, the value of k_e is approximately equivalent to a change in the mantissa of k_B of the order of 10^{25} , with k_e being the reduction of mean energy ($E_e = 1/2 m_e \cdot I_e^2 = 1/2 k_e/H$; see § in Table 1) per individual for each increment of H of one nat/individual (see \dagger in Table 1 note). The mean values of $(P_e \cdot V_{e(a)} \cdot H)/N$ per plot also coincided statistically with $k_e = 1.3806504 \times 10^2 \text{ J}_e/\text{nat}/\text{individual}/\text{individual}$ (Table 3), except in G4 and G5.

There are not significant differences between the means of $P_e V_{e(a)}$ and $(Nk_e)/H$ under stationary conditions (Fig. 2, censuses G1–G5 and G8–G9). In regard to these same censuses, there are not significant differences between the observed (m_{eTp}) and the expected ($m'_{eTp} = N \cdot k_e/I_e^2 \cdot H$) mean values of the total biomass per plot (Fig. 3a). There are not significant differences between the observed ($E_e = 1/2 m_e I_e^2$) and the expected ($E'_e = 1/2 k_e/H$) mean values of the eco-kinetic energy per individual per plot (Fig. 3b). Starting from these three results it does not seem rational to reject the plausibility of Eq. (5) (Table 1) as a probable state equation, at least in the first instance.

4. Discussion

In general, the scatter of internal macrostates (Fig. 1) in regard to $P_{e(s)}$, $(P_e \cdot V_{e(a)} \cdot H)/N$ resembles an isosceles triangle, much like the scatter plot corresponding to the concurrent analysis of several gases. However, in physical thermodynamics the apex of the

triangle is oriented to the left of P , while in ecological thermodynamics (Fig. 1) the apex is oriented to the right of $P_{e(s)}$ probably due to the anti-thermic effect of H .

It would be expected that, under conditions of perfect stationarity, $r \approx 0$, $b \approx 0$ and $p \gg 0.05$ for any estimation of k_e . The present case (Fig. 1) does not fulfill this combination of requirements in an exact way. Nevertheless, this expectation is neither observed exactly in regard to the empirical estimation of k_B in the real gases. The main conventional thermostatical factor in this regard is the adjustment of the scatterplot to a regular pattern, as well as the statistical tendency to a same value ($k_B = 1.3806504 \times 10^{-23} \text{ J/K/molecule}$) in any state of equilibrium. Fig. 1 and Table 3 indicate that these conditions are fulfilled in this case attending to k_e . In addition, the results of Figs. 2 and 3 reflect more general criteria in favor of the plausibility of the ecological state equation (Eq. (5)).

The estimation of k_e (Fig. 1) as well as the internal consistency of the state equation (Figs. 2 and 3) have been assessed through the statistical treatment of the same data. This could be seen as a case of analytical circularity. However, such a presumption is compensated if we take into account that applying a uniform methodology to all censuses we can obtain results as much in favor (G1–G3 and G8–G9) as against (G4–G5) stationarity. Additionally, it is important to take into account that there is also a certain level of analytical circularity in thermodynamics itself, without any significant damage to the prestige of this science: “in practice the criterion for equilibrium is circular. Operationally, a system is in equilibrium state if its properties are consistently described by thermodynamic theory” (Callen, 1985, p. 15).

The same criterion has been applied in this case. That is to say, ecosystem has been considered as stationary or quasi-stationary (it does not change or change very slowly) whenever $P_e V_{e(a)} \approx (Nk_e)/H$. Under these conditions, using variables that are relatively simple to measure empirically, such as diversity (H), species abundance (N) and spatial coordinates (x, y), it is possible to calculate the mean value per plot of other variables that are usually very difficult to measure, such as biomass (m_e) or energy (E_e), by means of the algebraic transformation of the equation of state (5), (Figs. 2 and 3).

The sequence of the total number of individuals per census (N_c) from G1 to G9 (G1: 308, G2: 319, G3 193, G4: 406, G5: 160, G6: 23,055, G7: 19,805, G8: 2618, G9: 1995) indicates that in G6 ($N_c = 23,055$) and G7 ($N_c = 19,805$) there must have been a substantial increase in biomass per plot (m_{eTp}). This indicates a probable absence of stationarity in G6 and G7. This can be a plausible explanation to the non-significant inverse correlation between I_e and H in G6 and G7 (Table 2), as well as in G5. That is to say, at the first sight, the opposite correlation between I_e and H (anti-kinetic or “anti-thermic” effect of H) could be used as a previous indicator of stationarity to decide the application of the state equation to estimate variables that are usually very difficult to measure directly in practice (e.g. biomass).

This article focuses on stationary or quasi-stationary ecosystems (with a minimum rate of change) and this can be seen as one limitation of this approach. However, assuming that stationary states of open systems produce minimal entropy (Prigogine’s theorem: Aguilar, 2001; Prigogine et al., 1972), these states should predominate naturally. As an example, in this study most surveys (5 of 7) with biomass values show stationarity. In fact, the predominance of stationary states in nature underlies all classification of ecosystems: if changes in biotic communities (non-stationarity) were too dynamic, we would be unable to identify any typical features of a given ecosystem, such as a rainforest, a coral reef, a ruderal community, a desert, and so on. Moreover, according to Schumpeter (1982), a non-stationary process can be described as a succession of relatively short stationary states (this procedure is known as comparative statics in economics). This can be also considered as a plausible alternative application of our proposal.

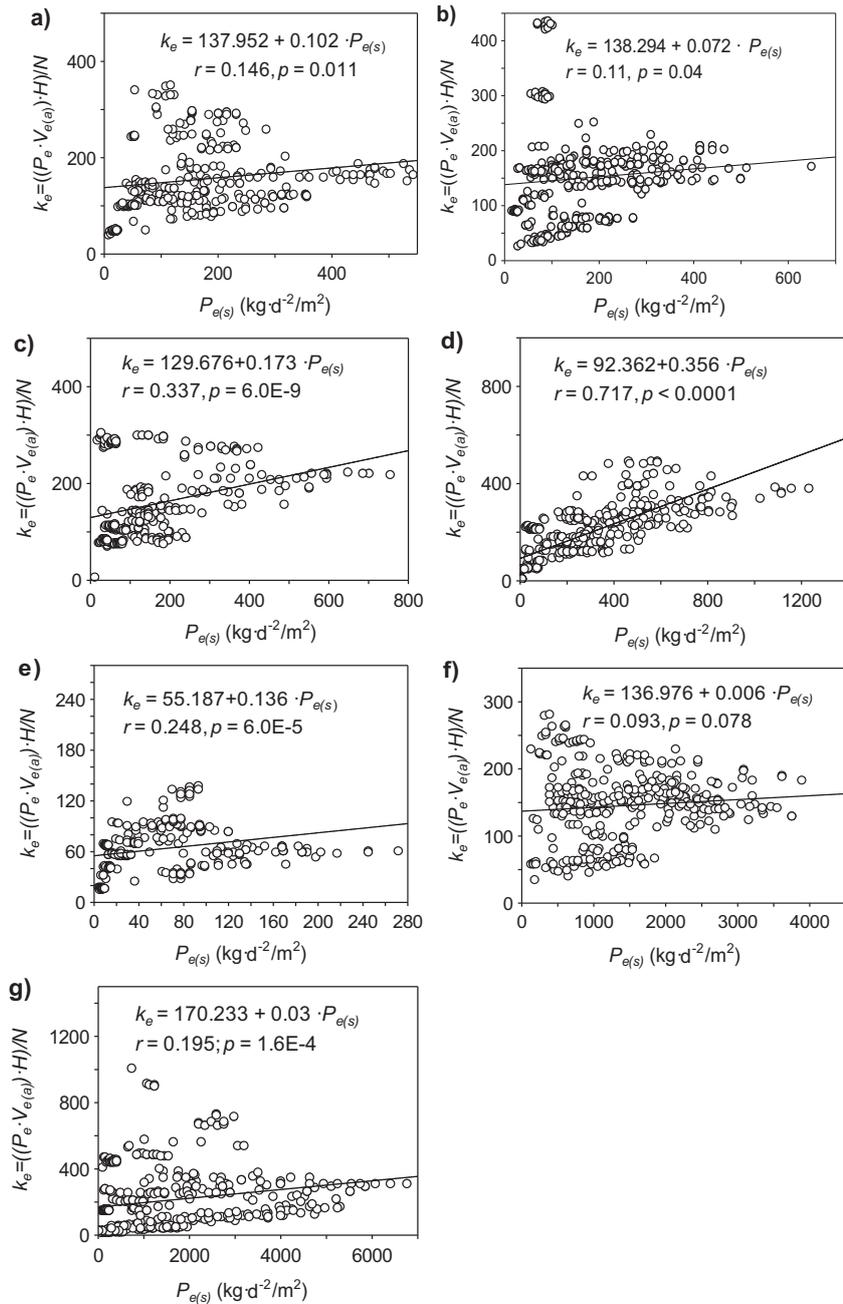


Fig. 1. Estimated value of k_e . (a–e) Censuses G1–G5. (f–g) Censuses G8–G9. The regression coefficients (b) of the regression equations tend to be low ($n = 7$; mean $b = 0.124$; 0.027% of the range or 0.169% of the standard deviation of the ordinates as a whole), as expected according to ecological transformation of the laws of gases (Table 1). The whole set of regression equation intercepts ($n = 7$) yielded a mean value of $k_e = 122.9543 \text{ J}_e/\text{nat}/\text{individual}/\text{individual}$, similar to $k_B \times 10^{25} = 138.06504$. If the surveys G4 and G5 (panels d and e) are excluded from the analysis due to their deviation from the stationary state pattern (see Fig. 2a and b), the mean value of k_e is 142.6260, which is also similar to $k_B \times 10^{25} = 138.06504$. Table 3 provides additional evidences of the lack of significant differences between the empirically determined mean value of k_e and 138.06504 as a reference value for the plots surveyed.

Table 3

Comparison between the mean values (μ) of $(P_e \cdot V_{e(a)} \cdot H)/N$ and $k_B \times 10^{25} = 138.06504$ as a reference value at the plot level.

Census	μ	s.d.	n	s.e.m.	Reference value	t	p
G1	145.597	84.150	55	12.021	138.06504	0.627	0.534
G2	138.555	94.058	57	12.458	138.06504	0.039	0.969
G3	148.542	85.693	46	12.635	138.06504	0.829	0.411
G4	272.703	341.160	59	44.415	138.06504	3.031	0.004*
G5	69.405	40.935	42	6.316	138.06504	-10.870	1.2E-13*
G8	154.593	79.630	60	10.280	138.06504	1.608	0.113
G9	200.007	347.910	60	44.915	138.06504	1.379	0.173

Note: The mean values of $(P_e \cdot V_{e(a)} \cdot H)/N$ were only statistically different from the reference value in surveys G4 and G5 (considered non-stationary states according to Fig. 2).

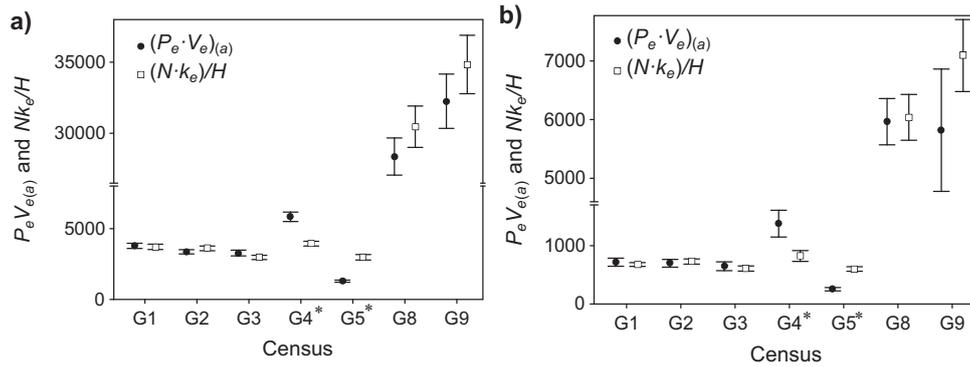


Fig. 2. (a) Means (± 1 SE) of $(P_e V_e)_{(a)}$ and $(Nk_e)/H$ at the macrostate level. (b) Means (± 1 SE) of $(P_e V_e)_{(a)}$ and $(Nk_e)/H$ at the plot level. * $p < 0.05$ between $(P_e V_e)_{(a)}$ and $(Nk_e)/H$ for the respective census. The non-significant differences in G1, G2, G3, G8 and G9 are consistent with the expected pattern for a state equation of the type $(P_e V_e)_{(a)} = (Nk_e)/H$ or $2N(1/2m_e I_e^2) = (Nk_e)/H$ (Eq. (5), Table 1) under stationary conditions.

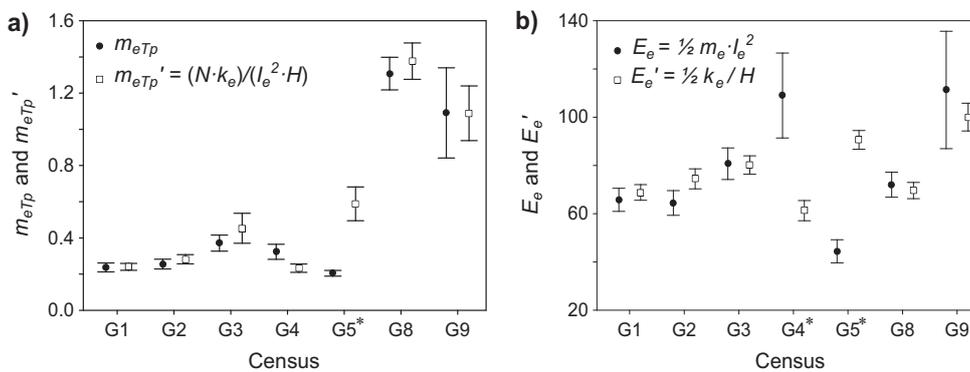


Fig. 3. (a) Means (± 1 SE) of the observed (m_{eTp}) and expected ($m'_{eTp} = Nk_e/I_e^2 H$) values of total biomass per plot. (b) Means (± 1 SE) of the observed ($E_e = 1/2 m_e I_e^2$) and expected ($E'_e = 1/2 k_e/H$) values of the individual eco-kinetic energy per plot. * $p < 0.05$ between $E_e = 1/2 m_e I_e^2$ and $E'_e = 1/2 k_e/H$ for the respective census. The non-significant differences in G1, G2, G3, G8 and G9 are consistent with the expected pattern for a state equation of the type $(P_e V_e)_{(a)} = (Nk_e)/H$ or $2N(1/2m_e I_e^2) = (Nk_e)/H$ (Eq. (5), Table 1) under stationary conditions.

The fact that an ecosystem is not a totally random entity (albeit being a very complex system) but a deterministic one does not change significantly the main scheme from Table 2 and Eq. (5): that, under stationary conditions, diversity (or information) has an “anti-kinetic” effect (reduction of I_e).

Certain doubts about the application of this approach to more complex systems in which the movement of individuals could be a dominant feature are completely expectable. Obviously, the analytical treatment of these doubts completely depends on the chosen definition of “complexity”. By general norm, complexity in ecology is implicitly identified with ecosystems of high diversity. In addition, as we can see in Table 2, dispersal (I_e , Eq. (3)) is correlated with diversity (H) in an inverse fashion. That is to say, if we subordinate the validity of this model to movement intensity, then the model has been tested, with apparent good results, in a ruderal ecosystem with relatively low diversity and high dispersal activity at the first trophic level. In other words, complexity does not seem to be associated with high dispersal, but just the opposite. Entropy is to be thought of as ‘spread’ because high entropy means that the elements of an assembly are spread over a wide range of energy levels (Guggenheim, 1967; Dugdale, 1998). Therefore, if diversity (H) has an anti-entropic effect (see references with regard to premise number 2 in Section 2) on an environment with gradients that mean different energy levels, then the reduction of dispersal activity with the increment of diversity is the expected.

On the other hand, if our model is valid for the first trophic level, then there is a plausible possibility that it could be also valid for the remaining levels, because the consumers depend on the producers: “we are forced to compute our diversity through samples of the

community (...). Nevertheless, there is evidence that the more inclusive structure is reflected in the composition of these selected parts” (Margalef, 1963, p. 358). It is possible that the main methodological change in this regard would have to be an increment of the spatio-temporal scale of sampling to compensate the individual mobility of the consumers.

Certainly, the great animal migrations are the major exhibitions of dispersal in nature. But a migratory system is, by definition, in a non-stationary state since it is in movement through a non-constant gradient between two zones with different environmental characteristics. Therefore, given the boundary conditions sketched in this article, our model is clearly not applicable to this last situation.

5. Conclusions

According to our results, ecosystems can be modelled starting directly from conventional statistical mechanics. The advantages of this approach are: (a) simplicity, (b) interdisciplinary consistency, (c) low level of algebraic complexity, (d) extensive possibilities for empirical testing.

This approach offers some potential answers to several important questions for the restoration and conservation of ecosystems, e.g. What is the preliminary indicator of stationarity under natural conditions? (Answer: an inverse and significant correlation between I_e and H); Is there any standard quantitative interaction indicative of ecological change? (Answer: a breakdown of the equivalence $P_e V_e(g) = Nk_e/H$ towards lower stable diversity indicates ecological deterioration); What is the

elemental trophodynamic impact of diversity loss? (Answer: 138.06504 J_e/nat/individual/individual). The potential ecological importance of these answers should not be underestimated.

Taking into account the relative simplicity of the studied subsystem (only one taxocene) the presented approach would seem too simple with regard to ecosystems of high complexity, e.g. a tropical forest. However, Eq. (5) can be considered a description of a simple ecological structure which, replicated thousands of times and interconnected at many hierarchical levels, can be the elemental functional unit of very complex ecosystems.

The authors of this article have a residual uncertainty about the application of this analytical procedure to any kind of stationary ecosystem. Nevertheless, this is precisely one of the main aims of the present article: to offer this idea to a wider empirical scrutiny with the goal of fixing the validity limits of our results in consistency with the boundary conditions sketched in this article.

This approach can probably be improved, but the important factor is that the application of a well known algorithm provides a pattern that can be quantified and empirically verified; these could be useful as benchmarks for evaluating radical or gradual environmental change. According to Brown et al. (2002), a theory of diversity that explains the variety of living things and ecological systems in terms of relatively simple principles is one of the greatest challenges to modern science. The approach exposed here could be, perhaps, an additional step to reach such an ambitious goal, whit the added benefit of its coherence with the thermodynamic foundation of the conventional ecosystem ecology.

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