

Additional empirical evidence on the intrinsic trend to stationarity in the long run and the nested relationship between abiotic, biotic and anthropogenic factors starting from the organic biophysics of ecosystems (OBEC)



Ricardo A. Rodríguez^{a,*}, Janelle M. Duncan^b, Juan D. Delgado^c, Michael J. Vanni^b, Rodrigo Riera^{d,e}, María J. González^b

^a Calle Cartero Casiano Díaz, n°19. Bajo B. La Gallega., Tenerife, Canary Islands, Sta Cruz de Tenerife, 38107, Spain

^b Department of Biology, Miami University, Oxford, OH, 45056, USA

^c Department of Physical, Chemical and Natural Systems, Faculty of Experimental Sciences, University Pablo de Olavide, Sevilla, E-41013, Spain

^d Center for Research on Biodiversity and Sustainable Environments (CIBAS), Catholic University of the Most Holy Conception, Concepción, Chile

^e Department of Ecology, Faculty of Sciences, Catholic University of the Most Holy Conception, Mailbox 297, Concepción, Chile

ARTICLE INFO

Keywords:

Eco-kinetic energy
Ecological state equation
Ecosystem dynamics
Interdisciplinary models
Holistic ecological indicators
Hierarchical ecological setup

ABSTRACT

Conventional ecology lacks a non-contingent theory on the relationship between abiotic, biotic and anthropogenic factors under natural or quasi-natural conditions. As a result, since ecology is the science that studies the interaction between ecological factors in nested complex systems, we should recognize that ecology needs significant enhancements to understand the functioning of ecosystems. This article combines the ecological state equation (ESE, one of the earliest models derived from the Organic Biophysics of Ecosystem –OBEC), with abundant field data of abiotic factors, biotic factors and human factors from inland water rotifers and crustaceans (1022 samples taken over 21 years), litter invertebrates in laurel forest and pine forest (308 samples), and marine interstitial meiofauna of sandy beaches (90 samples). This has been done in order to obtain additional empirical evidence on the intrinsic trend to stationarity in the long run, even in perturbed ecosystems (man-made eutrophic water reservoirs, forest vegetation affected by traffic, and coastal ecosystems close to disposal points of sewage that are fully or partially treated, respectively to the above-mentioned taxocenes), and the relationship between the above-mentioned ecological factors. Our results indicate that there is a complex natural arrangement that intertwines the trend to stationarity and the resilience capability of ecosystems with a clear pattern of hierarchical setup between ecological factors. This is reflected by the role of ESE as a trophodynamic interface in hierarchical statistical models (cluster analysis) because they involve, in the following order of increasing rank: lower level abiotic factors (a.f.), biotic factors (b.f.), the holistic combination of state variables included in the ESE and, finally, higher level human factors (h.f.). In such a way, there is a clear trend to a hierarchical assemblage in agreement with the evolutionary origin of ecological factors in the deep time, as well as in regard to the net direction (\leftarrow) of ecological homeostasis: a.f. \leftarrow b.f. \leftarrow h.f. In this setup, the ESE accomplishes a key liaison role, because it reflects a long run trend to stationarity which allows an essential degree of ecological stability, as well as our capability to classify ecosystems, in spite of the random influence of ecological perturbations in the short run. The above-mentioned set of additional evidence can be regarded as a step to develop a non-contingent theory about the relationship between abiotic, biotic and anthropogenic factors. Furthermore, since the OBEC, in its origin, deals with only the dynamics of biotic variables, this is the first time that the interaction between one of its main models and other kind of ecological factors is studied yielding reliable results in the process.

* Corresponding author.

E-mail address: arodveg@gmail.com (R.A. Rodríguez).

1. Introduction

There have been several definitions and detail additions in regard to the concept of “ecology” (see, e.g.: Haeckel, 1866, p. 8; King and Russell, 1909; Elton, 1927, pp. 1–4; Eggleton, 1939; Friederichs, 1958; Kormandy, 1978; Margalef, 1991). However, whatever the concept we select, the original cornerstone idea is that there are **biotic factors** (b.f.) in constant eco-evolutionary interactions with each other as well as with pre-biosphere **abiotic factors** (a.f.). A.f. have been gradually modified by biological activity and human influence over a very large span of time. Finally, the ecosystem is the structural and functional unit in this “ecological realm” (Margalef, 1963, 1991, 1993).

In a macro-interpretation of life evolution, each one of the above-mentioned successively added layers is named by Knoll and Bambach (2000) as a “megatrayjectory”. Every new megatrayjectory is characterized by a process of diversification or information accumulation. In general, the main trend is that every new added layer modifies and regulates all the previous ones in an irreversible way, but keeping an inextricably connection with them (Knoll and Bambach, 2000). The above-mentioned arrangement leads to the well-known nested nature (like the layers of an onion, see Valentine and May, 1996; Wu, 1999; Holling, 2001; Wu and David, 2002; Sachs and Simms, 2006; Miller, 2008; Riera et al., 2018) of planetary functioning as a whole. From the evolutionary point of view, the relationship a.f. ↔ b.f. is just in the middle of a much more complex hierarchical evolutionary arrangement that embraces from the prebiotic environment of our planet in its very beginning, to the ambit of anthropogenic or human factors (h.f.: *anthroposphere*, see Kuhn and Heckelei, 2010) placed on its opposite limit nowadays. Thus, the interaction a.f. ↔ b.f. is a sort of hinge or pivot that plays a crucial role in the stability of this complex system by linking two functional edges with each other.

In general, if we ask about the interaction between a.f., b.f., and h.f. to a significant sample of ecologists, the majority of them would response that this relationship is *contingent*. That is to say, it is very variable and requires *ad hoc* studies because there is no general pattern in this regard. This is the expected situation in a science so young that we could say, after consulting abundant literature (see, e.g.: Watt, 1971, p. 569; Hurlbert, 1971; Simberloff, 1981; Hall and DeAngelis, 1985; Fagerström, 1987; Weiner, 1995; Lawton, 1999; Spellerberg and Fedor, 2003; Belovsky et al., 2004; Pilkey and Pilkey-Jarvis, 2006; Ginzburg et al., 2007; Campbell, 2008; Rossberg, 2008; Moore et al., 2009; Angilletta and Sears, 2011; Joseph et al., 2013; Scheiner, 2013; Rodríguez et al., 2017a; Riera et al., 2018), that ecology has all the typical traits of a science with a chronic and long-lasting lack of a truly reliable paradigm, in the Kuhn (1962) sense of the term.

The situation in regard to the relationship between a.f. and b.f. is described by Hall (1988 pp 8–9), in the following terms: “*What is the relative importance of biotic vs. abiotic factors in determining the basic properties of species and of ecosystems, and their dynamics over time?...For example, a common starting point in many analytic models is that the distribution and abundance of a species is a function only of other species.*” About the second part of this statement, let us suppose we are studying the ecological dynamics of a single plant species x living in an ecosystem that includes 400 species. The list of a.f. impinging on x is relatively short in comparison with the list of potential b.f. (399 species). So, at first glance, b.f. seem to be more important than a.f., and it is well known that large species sets are more reliable as ecological indicators than isolated species or a singular a.f. (Odum, 1972). Furthermore, the ecological role a.f. is in many cases under the influence of b.f. (hence the term “bio-geo-chemical cycles”), a mechanism that fails mainly due to the disturbing influence of h.f.

However, the first part of the previous statement (i.e.: “*What is the relative importance of...*”) has no definitive answer so far, mainly at the

ecosystem or taxocene scale. Thus, this article is addressed to two main goals: (i) Providing a plausible answer to this subject and its nested nature starting from the combination of theoretical principles and methods stated by the organic biophysics of ecosystems (OBEC; see Rodríguez et al., 2017a, p. 45; Riera et al., 2018, pp. 2, 11–12), and large sets of abiotic, biotic and anthropogenic field data. (ii) Verifying if the pattern derived from the previous item is stable in connection with the general trend of ecosystems to stationarity (either in the long run or in the large scale) even in perturbed ecosystems (e.g.: man-made eutrophic water reservoirs, forest vegetation affected by the influence of traffic, and coastal ecosystems close to disposal points of sewage that are fully or partially treated). Thus, a key question to achieve these goals is to show the influence of those intrinsic factors that produce a spontaneous drift toward stationarity in ecological systems in comparison with those “extrinsic” or non-biological factors that produce noticeable oscillations around stationarity (stationarity traits from the point of view of OBEC are defined in Section 2.1).

Our hypothesis (h) in order to reach the above-mentioned goals is that, together with gradients that promote energy flows depending on combinations of a.f. and h.f. acting at the short run, there is a single and all-pervasive gradient based on b.f. intertwined with each by the ecological state equation (ESE; Eq. (3), below), with a key influence in favor of stationarity in any kind of ecosystem in the long run. This very gradient allows identifying and classifying an ecosystem of a certain particular kind in comparison with other types of ecosystems. The plausibility of this hypothesis requires, at least, three empirically tested results: **h_i**) That the mean value of the quotient between the left and the right side (LS_{ese}/RS_{ese}) of ESE would be statistically equivalent to 1 in the long run without producing the typical linear regression elliptical scatterplot between dependent and independent variables. The second result (**h_{ii}**) is based on the fact that gradients unfolded either across space or over time become sequences of oscillations. These oscillation sequences including different variables can be statistically processed by means of multiple association statistical techniques¹ based on coefficient of variation values:

$$c_v = \left(\frac{\sigma}{\mu} \right) \times 100 \quad (1)$$

where σ : standard deviation and μ : mean. This use of c_v is justified given that it is a dimensionless indicator of dispersion, in such a way that it can be used to compare variables expressed in different measurement units. So, if there is a clear hierarchical pattern of homeostatic influence between ecological factors, the clustering of c_v of LS_{ese}/RS_{ese} and a.f. will tend to include LS_{ese}/RS_{ese} in a group apart from a.f., indicating that LS_{ese}/RS_{ese} has an oscillation dynamics at a higher hierarchical level than a.f. **h_{iii}**) The very statistical techniques mentioned in **h_{ii}**, but by involving b.f., would also include LS_{ese}/RS_{ese} in a group apart from the rest of b.f., and it would be connected with them at a higher hierarchical association level in combination with h.f.

The expected results according to **h_i**, **h_{ii}** and **h_{iii}**, would support the idea that LS_{ese}/RS_{ese} is a suitable integral reflection of more particular sets of ecological factors with a lower level of specific influence on the ecosystem functioning. In addition, the verification of these results would support the existence of a pattern of nested connection between a.f., b.f. and h.f. which can be evaluated even at the small scale (taxocene level).

¹ I.e.: Techniques without a clear distinction between a dependent or “passive” variable and independent or “active” variables which are not hierarchically arranged (e.g.: multiple linear regressions). However, this is not the case in most of the ecological systems in which “passive variables” are often scarce. Thus, cluster analysis seems to be the most appropriate statistical tool in this case.

2. Materials and methods

2.1. Theoretical foundation about the biophysical intrinsic gradient that supports ecological stationarity

It is well-known that the flow of trophic energy plays an essential role in ecosystem functioning (Lindeman, 1942; Margalef, 1963; Odum, 1968; 1972; Fretwell, 1987; Fenchel, 1988; Hall et al., 1992; Higashi et al., 1993; Kemp and Boynton, 2004). The key issue in this regard is that energy flows are impossible without some kind of gradient (i.e.: a Δx about a given variable x). Several examples in favor of the key influence of gradients of b.f. on trophic energy flows in comparison with the influence of a.f. can be cited: 1) They are fully functional ecosystems in areas which, from the geophysical point of view, seem to be very isotropic. So, some kind of underlying Δx of b.f. should be acting in these cases. 2) Margalef (1992) establishes an equivalence between the decreasing light gradient from canopy to soil in rainforests, and the same gradient between surface and depths in the open sea. However, the former one of these two cases mainly depends on b.f. (canopy filtering action), meanwhile the latter one mainly depends on a.f. (water depth). 3) It would be impossible to identify and classify ecosystems if their typical traits only depend on stochastic fluctuations of a.f. These set of examples indicates that there should be a general underlying influence, based on intrinsic b.f., which gets back ecosystems even from extreme random oscillations to a basic stationary state.

Given the above-mentioned connection between gradients and energy flow, it is easier and more relevant to use the flow of trophic energy as an indirect indicator of underlying gradients than the direct measurement of gradients themselves. Thus, the key issue is applying a suitable proxy for measuring trophic energy. By applying the universal fulfillment of first law of thermodynamics (i.e., that energy never disappears, but only changes from one form to another), the OBEC assumes that eco-kinetic energy per individual (Eq. (2)) is the most appropriate proxy to assess trophic energy in practice, in a similar way in which kinetic energy is calculated in classical mechanics ($E = \frac{1}{2}mv^2$; where m : physical mass, and v : physical velocity), but replacing physical variables by their ecological equivalents.

$$E_{ep} = \frac{1}{2}m_{ep} \times I_e^2, \quad (2)$$

where m_{ep} : mean biomass per individual per plot (p), and I_e : an aggregate indicator of dispersal activity (either passive or active) per individual per plot, with physical and statistical traits similar to those of v in order to replace v by I_e without producing significant failures in the extrapolation of principles of classical mechanics and statistical physics to ecosystem ecology. For additional details about I_e , see Rodríguez et al. (2013a, pp. 9–10).

The analytical equivalence between trophic energy, E_{ep} and E is, in the first instance, only a plausible assumption. The key point is that there are fifteen previous articles (Rodríguez et al., 2012, 2013a,b, 2015a,b,c,d, 2016a,b,c, 2017a,b,c,d; Riera et al., 2018) that support the reliability of Eq. (2) as a proxy for trophic energy due to its clear connections with well-known eco-evolutionary subjects. Eq. (2) means the operative assessment in practice of a largely misunderstood magnitude (trophic energy, normally replaced by incomplete indicators –dry biomass, wet biomass, carbon dioxide fixation, J/kg measured by calorimetry –because none of them includes the particular investment of energy in realized dispersion). Furthermore, Eq. (2) is a comfortable solution from the field work point of view, because it also means that trophic energy can be assessed starting from field data samplings themselves, without using any kind of technical device.

The empirically observed mean values of Eq. (2) can be combined with the respective theoretically expected mean values (right side of Eq. (3), below) in order to obtain an ecological state equation (ESE: Eq. (3); according to Rodríguez et al., 2012; 2013a,b) that is valid for any kind of taxocene, with the single requirement of using the appropriate

typical value of $k_{e(e)}$ per taxocene:

$$2N_p \left(\frac{1}{2} m_{ep} I_e^2 \right) = \frac{N_p k_{e(e)}}{H_p} \vee 2N_p (E_{ep}) = \frac{N_p k_{e(e)}}{H_p} \vee 2E_{eTp} = \frac{N_p k_{e(e)}}{H_p}, \quad (3)$$

where N_p : total number of individuals per plot; H_p : species diversity per plot according to the Shannon (1948) information index ($H = -\sum_{i=1}^{S_p} \frac{n_i}{N_p} \ln \frac{n_i}{N_p}$, where S_p : total species number per plot, n_i : number of individuals of species i per plot, and $N_p = \sum n_i$); $k_{e(e)} = m_{ep} \times I_e^2 \times H_p$, is the theoretically expected value (\cdot) of ecological equivalent of Boltzmann constant (k_B). $k_{e(e)}$ emerges due to a typical gradient of b.f. on a 2D scalar space H_p , $m_{ep} \leftrightarrow I_e^2$. This scalar space is partitioned in three main contiguous functional sectors with alternative increments (\uparrow) or decrements (\downarrow) of b.f. in every ecosystem under stationary conditions: **Sector 1:** ($m_{ep}\downarrow, I_e^2\uparrow, H_p\downarrow$). **Sector 2:** ($\bar{m}_{ep}, \bar{I}_e^2, \bar{H}_p$). **Sector 3:** ($m_{ep}\uparrow, I_e^2\downarrow, H_p\uparrow$). Therefore, $m_{ep} \times I_e^2 \times H_p \rightarrow \text{constant} = 1.3806504E \pm \varphi \text{ ecoJoules} \times \text{nat/individual}$, with $\varphi = \dots, -3, -2, -1, 0, 1, 2, 3, \dots$; always an integer number typical, although not exclusive, of a given taxocene.

So, $k_{e(e)}$ emerges due to a trade-off between biomass and dispersal activity in function of ΔH_p in the ecosystem space. This gradient of b.f. has one main effect: 1) It keeps the ecosystem trapped inside a pro-stationary ecological potential well despite the random disturbing influence of a.f. and h.f., because the net variations of eco-kinetic energy (Eq. (2)) that are necessary to allow fluctuations of species diversity (i.e., either backward or forward ecosystem evolution) are impossible in any of the two edges of ΔH_p . That is to say, $I_e^2\uparrow$ but $m_{ep}\downarrow$ when $H_p\downarrow$; and $m_{ep}\uparrow$ but $I_e^2\downarrow$ when $H_p\uparrow$; in contrast with the fact that m_{ep} and I_e^2 must change in the same sense to promote a net variation of Eq. (2). Such a variation, in turn, is an essential requirement to allow species diversity fluctuations in the large scale given that getting new information requires net energy consumption from the outside (Tribus and McIrvine, 1971). Consequently, the key point is to use an operative way to assess the above-mentioned gradient in order to distinguish between pro-stationary influences due to b.f. and anti-stationary influences due to a.f. and h.f. (see our hypothesis and its presumptive supporting results – h_i to h_{iii} – in Section 1). According to Rodríguez et al. (2016a), this goal can be achieved by means of the quotient between the left side (LS) and the right side (RS) of ESE (Eq. (3)):

- i) If $2N_p \left(\frac{1}{2} m_{ep} I_e^2 \right) = \frac{N_p k_{e(e)}}{H_p}$ (quotient $LS_{ese}/RS_{ese} = 1$): the observed mean value of total eco-kinetic energy per plot coincides with the expected one according to the calculation of $k_{e(e)}$ due to the above-mentioned trade-off, and the ecosystem is under **stationary conditions**.
- ii) If $2N_p \left(\frac{1}{2} m_{ep} I_e^2 \right) > \frac{N_p k_{e(e)}}{H_p}$ (quotient $LS_{ese}/RS_{ese} > 1$): the observed mean value of total eco-kinetic energy per plot is higher than the expected one according to the calculation of $k_{e(e)}$, and the ecosystem is under pro-successional non-stationary **eutrophic conditions** given that the increase of species diversity needs a net increase of energy input.
- iii) If $2N_p \left(\frac{1}{2} m_{ep} I_e^2 \right) < \frac{N_p k_{e(e)}}{H_p}$ (quotient $LS_{ese}/RS_{ese} < 1$): the observed mean value of total eco-kinetic energy per plot is lower than the expected one according to the calculation of $k_{e(e)}$, and the ecosystem is under anti-successional non-stationary **oligotrophic conditions** given that a net decrement of energy input reduces species diversity.

It is well-known that, in general, sun-light energy by itself is not a limiting factor to ecosystem development. On the contrary, anthropic influences, the availability of some chemical elements, as well as some limiting physical non-living factors, interfere with the physical-chemical combination of light and substances during the photosynthetic process that sustains ecosystem metabolism. Thus, conditions (ii) and (iii) should act mainly due to the indirect incidence of a.f. and h.f. But,

if our hypothesis is valid, condition (i) should rule in the large scale (i.e.: approximately constant mean value of $LS_{ese}/RS_{ese} \approx 1$ either over time or across space, without deploying the typical linear regression elliptical scatterplot between dependent and independent variables), as long as ecosystems are not impinged by sudden overwhelming disturbances.

2.2. Sampling of taxocenes and assessment of environmental factor values

See Appendix A in Supplementary material.

2.3. Statistical procedures

2.3.1. Exploring the intrinsic trend to stationarity despite the random influence of a.f., b.f. and h.f.

The respective values of $k_{e(c)}$ for every taxocene included in this study have been evaluated in previous publications (Rodríguez et al., 2013a, 2016c, 2017c). So, the quotient LS_{ese}/RS_{ese} per plot (according to items i–iii in Section 2.1), was calculated by using field data from: marine interstitial meiofauna of sandy beaches from Tenerife Island (“mif”: 90 plots); litter invertebrates in laurisilva and pine forest from Tenerife Island (“lli” & “pli”: 170 plots and 80 plots, respectively, throughout a sampling stage of 2 years); and inland water rotifers and crustaceans from Acton Lake, Ohio, U.S.A. (“rot” & “crust”: 511 plots each one, throughout a sampling stage of 21 years). See additional details in Appendix A.

LS_{ese}/RS_{ese} values per plot were ordered following either a time progression (i.e., date sequences for rot and crust) or a combined progression of ordinal spatial criteria and date in the cases of mif, lli and pli, with the goal of obtaining the respective sequences of trophodynamic oscillations. The average values of LS_{ese}/RS_{ese} for the oscillation sequences of these 5 taxocenes were compared with 1 (single sample t-test; Dell Inc, 2015) in order to know if trophodynamic stationarity predominates in the large scale in spite of the direction and amplitude of LS_{ese}/RS_{ese} fluctuations due to the random influence of a.f., b.f. and h.f. in the small scale.

2.3.2. Exploring the nested nature of functional arrangements of ecological factors

The coefficients of variation (c_v) of oscillation sequences of LS_{ese}/RS_{ese} either per transect or per time lapse (month or year) of every taxocene (mif, lli, pli, rot, and crust) were calculated and included in the respective cluster analyses (amalgamation rule: unweighted pair-group average; distance measure: $1 - \text{Pearson } r$; Dell Inc, 2015) together with the c_v values of: (a) nitrogen (N), carbonates (Cb), organic matter (Om), gravel (Gr), very coarse sand (VCS), coarse sands (Cs), medium sand (Ms), fine sand (Fs), very fine sand (VFs), and silt and clay (SC) in the sampling of mif; (b) percentage of tree cover per plot (Tc%), height of the tree canopy per plot (Th, in meter), percentage of leaf litter cover per plot (Lc%), depth of the leaf litter layer per plot (Ld), and the adjusted value per plot of the annual average daily frequency of vehicles that pass through each road (Vdf_a) in the samplings of lli and pli; (c) outside average temperature (OAT), chlorophyll content in water (Chlo), non-volatile suspended solids (NVSS), and total phosphorus (P) in the samplings of rot and crust.

3. Results

3.1. Exploring the intrinsic trend to stationarity despite the random influence of a.f., b.f. and h.f.

The values of a.f., b.f., h.f., as well as the calculations in regard to Eq. (3) and items from (i) to (iii) in Section 2.1 per taxocene are included in Appendix B. This appendix also includes the descriptive statistical parameters as well as the results of Eq. (1) for every ecological factor per taxocene. The values of LS_{ese}/RS_{ese} per taxocene, as it is

explained in Sections 2.1 and 2.3.1, are included in the panels (from (a) to (e)) of Fig. 1. A first remarkable point is that the scatterplots of these panels do not have the elliptical shape typically expected from any consistent statistical correlation. Second, in all the cases the mean value of LS_{ese}/RS_{ese} per taxocene is statistically equivalent to 1 (stationary conditions) in the large scale in spite of large fluctuations either > 1 (eutrophic conditions) or < 1 (oligotrophic conditions) in the small one. Only panel 1d (rotifers) shows an exception in a lapse of 4 years (1994–1998: 71 plots), of a total of 21 years (71 plots/511 plots \times 100 = 13.89% of the total sampling period). In this lapse, LS_{ese}/RS_{ese} mean = 14.689 J_e , a situation in agreement with item (ii) in Section 2.1. However, in the remaining 86.11% of the sampling period for rotifers LS_{ese}/RS_{ese} mean = 1.070 J_e ($p = 0.396 > > 0.05$ vs. 1), in agreement with item i in Section 2.1. These set of results is in agreement with the expected empirical result h_i (general trend to stationarity in the large scale) in connection with our central hypothesis of work (h) in Section 1. However, the above-mentioned exception from 1994 to 1997 in panel 1.d deserves additional analysis (see Section 4).

3.2. Exploring the nested nature of functional arrangements of ecological factors

The results shown in the panels of Fig. 2 support the nested functional arrangements of ecological factors by following the above-mentioned hierarchical order: a.f. \leftarrow b.f. \leftarrow h.f. (see Section 1) under the general stabilizing influence of the relationship between both sides of the ESE (see Section 2.1, items i to iii) acting as a “trophodynamic interface” between a.f. and h.f.

4. Discussion

There is a plausible explanation for the span from 1994 to 1997 of panel 1d (rotifers) in which LS_{ese}/RS_{ese} mean = 14.695 $> > 1$. A multiple regression analysis ($N = 71$ plots) between LS_{ese}/RS_{ese} as a dependent variable and OAT, Chlo, NVSS and P as independent variables yields the regression equation: $LS_{ese}/RS_{ese} = -10.15 + (0.68 \cdot \text{OAT}) - (0.05 \cdot \text{Chlo}) - (0.84 \cdot \text{NVSS}) + (0.23 \cdot \text{P})$; with $p < 0.05$ for NVSS and P. That is to say, a combination of low levels of non-volatile suspended solids (NVSS) and high levels of phosphorus (P) can produce more transparent waters allowing a deeper penetration of light as well as a higher availability of a limiting nutrient (P) for photosynthesis: Acton Lake, in which our long-term sampling of rotifers and crustaceans was performed, is the typical case of a highly eutrophic human-made water reservoir which receives large subsidies of water rich in nutrients from extensive surrounding tillage areas, often in a very episodic manner depending on the timing and intensity of storms (Winner et al., 1962). The significant combination of a.f. (low NVSS and high P) in the previous regression equation can increase the abundance of phytoplankton per m^3 with the corresponding stimulus to rotifer development ($LS_{ese}/RS_{ese} > > 1$), given that many rotifers are active predators of phytoplankton species. Obviously, this is only a plausible inference, because we did not record direct data of phytoplankton species abundance.

Fig. 2a is a typical case of the above-mentioned nested order of homeostatic influences in regard to the relationships between a.f., b.f., and ESE: a wide spectrum of a.f. linked to substratum granulometry (i.e., the continuum from c_v , VFs to c_v , Cb) are clustered at a relatively compact mean hierarchy level of $32.43 \pm 12.9\sigma$ (i.e., clustering levels from left to right: $(38.22 + 15.79 + 43.00 + 20.25 + 49.11 + 38.71 + 21.91)/7 = 32.43$). This average hierarchy level is, in turn, under the association level between byproducts linked to the disposal of sewage that are fully or partially treated (organic matter $-c_v$, OM- and nitrogen $-c_v$, N-; average hierarchy level = $63.39 \pm 11.46\sigma$). Finally, this arrangement as a whole is encompassed by the combined influence of pure trophodynamic factors (biomass, dispersal activity, abundance and species diversity, see Eq. (3)) intertwined with each other by the balance between observed and

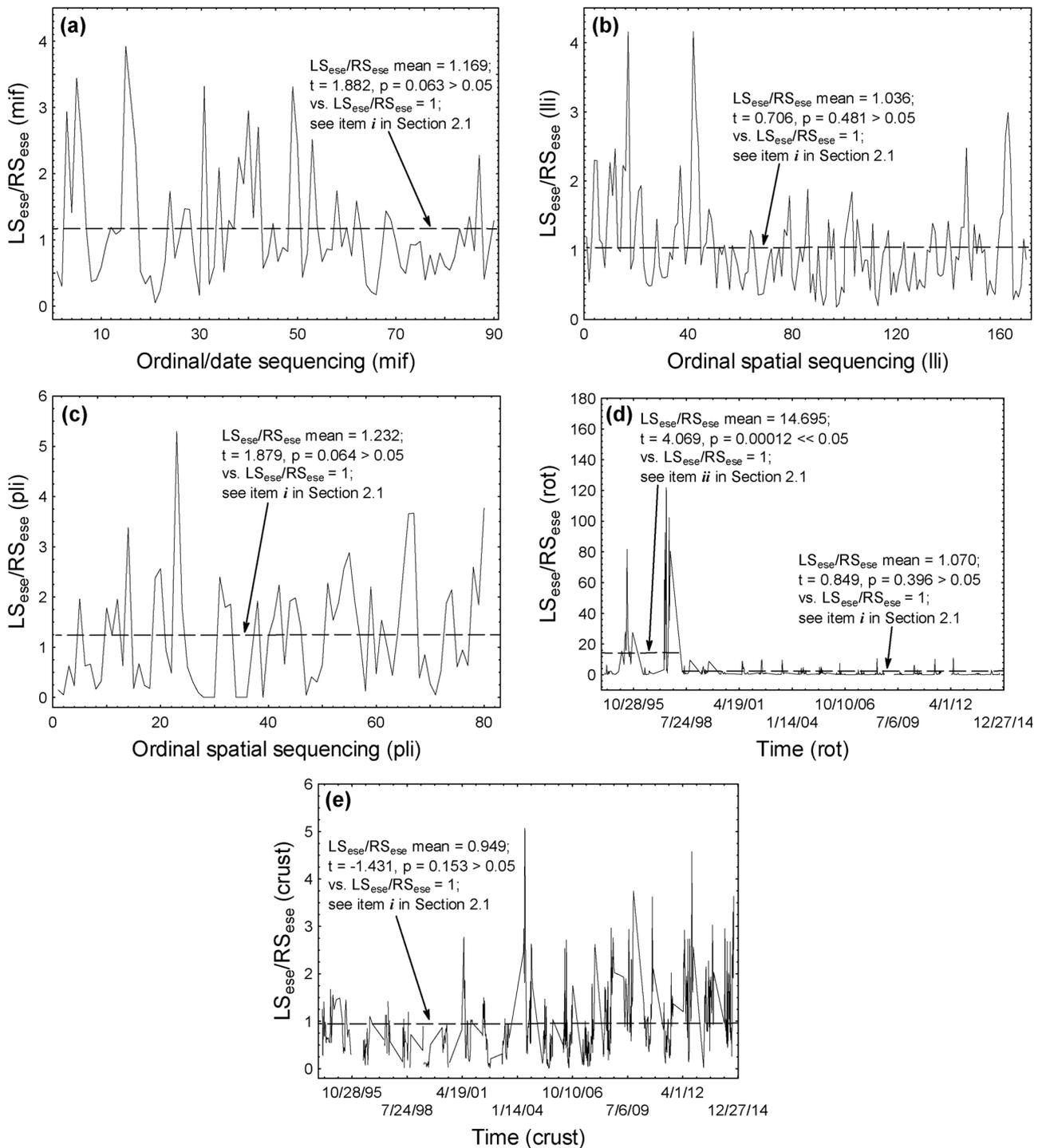


Fig. 1. General trend to stationarity in ecosystems assessed by means of the quotient between the left (LS) and the right (RS) side of Eq. (3). (a) Marine interstitial meiofauna of sandy beaches (mif), 90 samples. (b) and (c) Litter invertebrates in laurisilva and pine forest (lli and pli, 170 and 80 samples, respectively). (d) and (e) Inland water zooplankton (rotifers and crustaceans: rot and crust, respectively; long-term study –21 years–; 511 samples in both cases).

theoretically expected values of the ESE ($c_v, LS_{ese}/RS_{ese}$; hierarchical association level = 100.0).

The above-described nested arrangement is, in general, also valid in the cases of panels (b), (d) and (e), Fig. 2. The main difference takes place when some h.f. (e.g., c_v, Vdf_a : the adjusted value of the mean daily frequency of vehicle traffic per year) is included, because in such a case (e.g.: panel (b) in Fig. 2) h.f. takes up a clustering level higher than that of $c_v, LS_{ese}/RS_{ese}$, by fully encompassing the expected increasing influence order a.f. ← b.f. ← h.f.

Nevertheless, it is clear that there could be exceptions to the pattern

commented in the previous paragraph. For example (in panel 2c) c_v, Vdf_a has an intermediate association level between a lower level of b.f. and a higher level of $c_v, LS_{ese}/RS_{ese}$; exactly the opposite pattern to panel 2b. However, this result has a plausible explanation: pine forest vegetation is significantly less compact than laurel forest vegetation; thus, its level of “shielding” either in front of traffic influence (c_v, Vdf_a), or in front of the influence of any other kind of ecological factor, should be lower in comparison with laurel forest vegetation. This combination of factors allows that the influence of c_v, Vdf_a penetrates deeper into the cluster arrangement in panel 2c, until an association level below

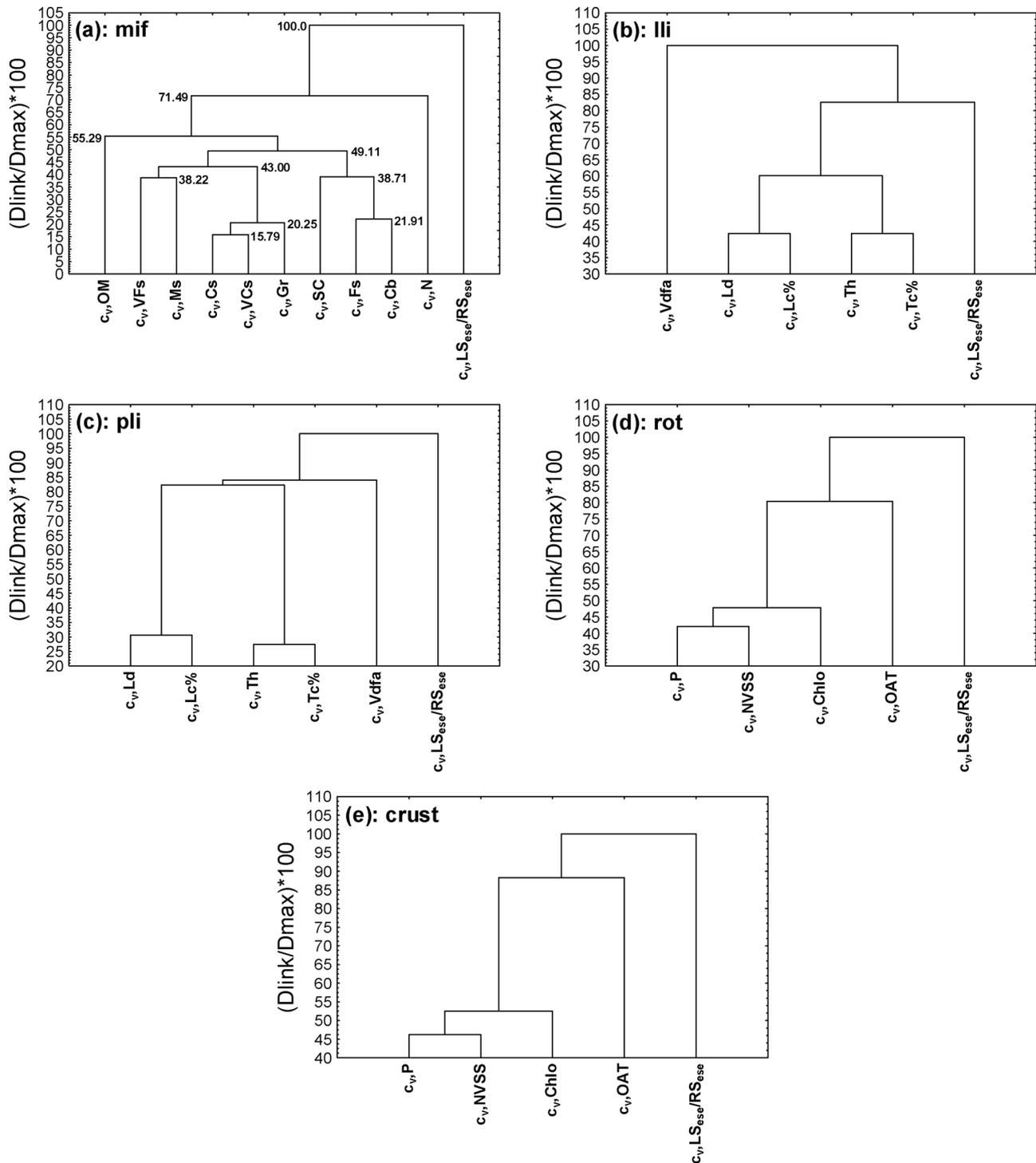


Fig. 2. Trend to a general nested setup of abiotic, biotic and anthropogenic gradients (in that increasing order of hierarchical level), starting from the values of environmental indicators corresponding to the same taxocenes included in Fig. 1. *c_v*: coefficient of variation, see Eq. (1) and its meaning in regard to the goals of this manuscript in Section 1. Meaning of the variables per cluster in Section 2.3.2.

$c_{v,LS_{ese}/RS_{ese}}$, indicating a stronger anthropogenic impact on the development of litter invertebrates of pine forest (pli). In fact, according to the calculations in Appendix B, spreadsheet “pli”, columns W, X and Y; the total value of eco-kinetic energy per plot ($\Sigma E_{eTP} = \Sigma \text{columnW}$) **below** (oligotrophic conditions) the mean value of $c_{v,LS_{ese}/RS_{ese}} = 1.232$ (Fig. 1c) for litter invertebrates of pine forest is 22.259% (see calculation in cell Y43) of the total value of eco-kinetic energy per plot **above** (eutrophic conditions) the mean value of $c_{v,LS_{ese}/RS_{ese}} = 1.232$. Meanwhile, in the case of lli (see Appendix B,

spreadsheet “lli”, columns W, X and Y), the total value of eco-kinetic energy per plot **below** the mean value of $c_{v,LS_{ese}/RS_{ese}} = 1.036$ is 51.239% (see calculation in cell Y78) of the total value of eco-kinetic energy per plot **above** the mean value of $c_{v,LS_{ese}/RS_{ese}} = 1.036$ (Fig. 1b). According to this comparison, litter invertebrates in pine forest perform their trophodynamics with a deficit of eco-kinetic energy, in the average, of -28.98% ($22.259\% - 51.239\% = -28.98\%$) in comparison with litter invertebrates in laurel forest, despite both taxocenes are under similar stationary conditions in the large scale (Fig. 1b

and c). This trophodynamic deficit can be a reflection of the higher impact of traffic (Vdf_a) on litter invertebrates of pine forest due to the lower shielding effect of vegetation because of its less compact structure.

In addition to the previous considerations in this section, the essential point is grasping more insights about: the trend to ecological stationarity (i), and the nested relationship between a.f., b.f. and h.f. (ii). In regard to point i, a comparative analysis between Figs. 1 and 2 indicates that the nested relationship between different ecological factors may not have a significant influence on stationarity in the long run. A concrete value of H_p (a key variable in Eq. (3)) under natural or quasi-natural conditions is nothing more than ecological information transmitted in an irreversible way in the form of species diversity throughout the ecosystem development process in space and time. Therefore, if a combination of ecological factors acting at random would have a strong disturbing influence on such an “ecological message” without an intrinsic counterbalance based on the trend of LS_{ese}/RS_{ese} to 1, nature would be so unstable that life evolution would be very difficult. This highlights the importance of the general trend to stationarity shown in Fig. 1. This insight is in agreement with an old statement by Margalef (1963, p. 363) about the capability of ecosystems to neutralize or dampen the random oscillations of ecological factors: “The properties associated with the structure of the ecosystem define the operations to do with the random inputs, and give more or less regular output patterns. Analogously, a crystalline body converts a random x-ray input into a regular diffraction pattern”.

In regard to point ii (i.e.: the hierarchical arrangement of ecological gradients that support energy flow), a nested structure acts in a similar way to the filtering action of a sieving column in regard to sand: a system with many hierarchical levels is able to catch each quantum of energy in a more efficient way than a simple system with a small number of hierarchical levels. For example, despite we have analyzed rotifers and crustaceans as taxocenes isolated from each other due to methodological reasons, both groups coexist in nature and are trophodynamically contiguous to each other (Rodríguez et al., 2016c). That is to say, the value of ecological equivalent of Boltzmann constant for crustaceans is $k_{e(c)} = 1.3806504E-04 J_e \text{ nat}/\text{individual}$ (Rodríguez et al., 2016c, 2017c) and, from the comparison between the results of Rodríguez et al. (2013a) and the results of Rodríguez et al. (2015c), the constant of conversion between $k_{e(c)}$ and the minimum discrete variation of eco-kinetic energy allowed per individual (i.e., the ecological equivalent of Planck constant: h_e^{ec}) is $1/208.366420758845 = 4.79923778677064E-03$. As a result, $h_{ecrust}^{ec} = 1.3806504E-04 \times 4.79923778677064E-03 = 6.62606957E-07 J_e$. In turn, the respective values for rotifers are $k_{e(r)} = 1.3806504E-05 J_e \text{ nat}/\text{individual}$, and $h_{erot}^{ec} = 6.62606957E-08 J_e$.

In such a way, at the same time that rotifers (due to its lower value of $k_{e(r)}$) are in disadvantage in comparison with crustaceans in regard to the conversion rate between energy and information, they are able to take advantage of aliquots of energy 10 times below the minimum energy value usable by crustaceans, since $h_{erot}^{ec} \div h_{ecrust}^{ec} = 0.1$. Thus, in the opposite direction of the interspecific relationship between both taxocenes, the rate $h_{erot}^{ec} \div h_{ecrust}^{ec}$ means that the turnover ratio of rotifers, whose value is 10 fold that of crustaceans, is able to successfully sustain the trophic exploitation of the latter ones, which are very frequent predators of the former ones. This insight is in agreement with the well-known conventional principle about that the net transference of energy between contiguous trophic levels in trophic pyramids is, in the average, a decreasing multiple of ten in comparison with the available energy in the previous trophic level (see, e.g.: Pauly and Christensen, 1995).

5. Concluding remarks

In summary, our results are in agreement with our initial hypothesis: there is an intrinsic stabilizing biotic gradient (Eq. (3)) that gets

back ecosystems even from strong oscillations to a basic stationary state. Besides, our results are also in agreement with the nested arrangement of increasing homeostatic ranking a.f. ← b.f. ← h.f. which emerges in connection with the above-mentioned pro-resilient biotic gradient.

This article should also be regarded as an “acid test” applied to one of the main models included in OBEC; in the first place, because the OBEC is based on only four biotic primary variables (fresh biomass or body weight, dispersal activity, abundance, and species diversity), and this is the first time that an OBEC model (Eq. (3)) is correlated with abiotic factors, anthropogenic factors and other biotic factors, yielding reliable results in the process. In the second place, because the above-mentioned model had not been tested so far with data from a long-term study (21 years) performed in an artificial ecosystem (Acton Lake) under strong anthropic influences from extensive peripheral areas of tillage.

Acknowledgements

Funding for this research was provided by the Federal Aid in Sport Fish Restoration Program (F-69-P, Fish Management in Ohio) administered jointly by the US Fish and Wildlife Service and the Ohio Department of Natural Resources Division of Wildlife to M.J. González and M.J. Vanni; National Science Foundation DEB-LTREC: 0743192 to M.J. Vanni, M.J. González. The authors declare no actual or potential conflict of interest in relation to this manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ecolmodel.2018.05.014>.

References

- Angilletta, M.J., Sears, M.W., 2011. Coordinating theoretical and empirical efforts to understand the linkages between organisms and environments. *Integr. Comp. Biol.* 51, 653–661.
- Belovsky, G.E., Botkin, D.B., Crowl, T.A., Cummins, K.W., Franklin, J.F., Hunter, M.L., Joern, A., Lindennayer, D.B., MacMahon, J.A., Margules, C.R., Scott, J.M., 2004. Ten suggestions to strengthen the science of ecology. *BioScience* 54, 345–351.
- Campbell, R., 2008. How ecological should epistemology be? *Hypatia* 23, 161–169.
- Dell Inc, 2015. Dell Statistica (Data Analysis Software System), Version 13. [software.dell.com](http://www.dell.com).
- Eggleton, F.E., 1939. Fresh-water communities. *Am. Midl. Nat.* 21, 56–74.
- Elton, C., 1927. *Animal Ecology*. The MacMillan Co., N.Y.
- Fagerström, T., 1987. On theory, data and mathematics in ecology. *Oikos* 50, 258–261.
- Fenchel, T., 1988. Marine plankton food chains. *Ann. Rev. Ecol. Syst.* 19, 19–38.
- Fretwell, S.D., 1987. Food chain dynamics: the central theory of ecology? *Oikos* 50, 291–301.
- Friederichs, K., 1958. A definition of ecology and some thoughts about basic concepts. *Ecology* 39, 154–159.
- Ginzburg, L.R., Jensen, C.X.J., Yule, J.V., 2007. Aiming the ‘unreasonable effectiveness of mathematics’ at ecological theory. *Ecol. Modell.* 207, 356–362.
- Haeckel, E., 1866. *Generelle Morphologie der Organismen*. Georg Reimer, Berlin.
- Hall, C.A.S., 1988. An assessment of several of the historically most influential theoretical models used in ecology and of the data provided in their support. *Ecol. Modell.* 43, 5–31.
- Hall, C.A.S., DeAngelis, D.L., 1985. Models in ecology: paradigms found or paradigms lost? *Bull. Ecol. Soc. Am.* 66, 339–346.
- Hall, C.A.S., Stanford, J.A., Hauer, F.R., 1992. The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. *Oikos* 3, 377–390.
- Higashi, M., Burns, T.P., Patten, B.C., 1993. Network trophic dynamics: the tempo of energy movement and availability in ecosystems. *Ecol. Modell.* 1/2, 43–64.
- Holling, C.S., 2001. Understanding the complexity of economics, ecological and social systems. *Ecosystems* 4, 390–405.
- Hurlbert, S.H., 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology* 52, 577–586.
- Joseph, M.B., Mihaljevic, J.R., Arellano, A.L., Kueneman, J.G., Preston, D.L., Cross, P.C., Johnson, P.T.J., 2013. Taming wildlife disease: bridging the gap between science and management. *J. Appl. Ecol.* 50, 702–712.
- Kemp, W.M., Boynton, W.R., 2004. Productivity, trophic structure, and energy flow in the steady-state ecosystems of silver Springs, Florida. *Ecol. Modell.* 178, 43–49.
- King, L.A.L., Russell, E.S., 1909. A method for the study of the animal ecology of the

- shore. *Proc. R. Phys. Soc. Edinb.* 17, 225–253.
- Knoll, A.H., Bambach, R.K., 2000. Directionality in the history of life: diffusion from the left wall or repeated scaling of the right. *Paleobiology* 26, 1–14.
- Kormandy, E.J., 1978. Ecology/economy of nature-synonyms? *Ecology* 6, 1292–1294.
- Kuhn, T.S., 1962. *The Structure of Scientific Revolutions*. University of Chicago Press, Chicago.
- Kuhn, A., Heckelei, T., 2010. Anthroposphere. In: Speth, P., Christoph, M., Deikkrüger, B. (Eds.), *Impacts of Global Change on the Hydrological Cycle in West and Northwest Africa*. Springer-Berlag, Berlin Heidelberg p. 284.
- Lindeman, R.L., 1942. The trophic-dynamic aspects of ecology. *Ecology* 23, 399–417.
- Lawton, J.H., 1999. Are there general laws in ecology? *Oikos* 84, 177–192.
- Margalef, R., 1963. On certain unifying principles in ecology. *Am. Nat.* 97, 357–374.
- Margalef, R., 1991. *Ecología*. Omega S.A., Barcelona.
- Margalef, R., 1992. *Planeta Azul, Planeta Verde [Blue Planet, Green Planet]*. Biblioteca Científica. Prensa Científica, S.A., Barcelona.
- Miller III, W., 2008. The hierarchical structure of ecosystems: connections to evolution. *Evol. Edu. Outreach* 1, 16–24.
- Moore, S.A., Wallington, T.J., Hobbs, R.J., Ehrlich, P.R., Holling, C.S., Levin, S., Lindemayer, D., Pahl-Wostl, C., Possingham, H., Turner, M.G., Westoby, M., 2009. Diversity in current ecological thinking: implications for environmental management. *Environ. Manage.* 43, 17–27.
- Odum, E.P., 1968. Energy flow in ecosystems: a historical review. *Am. Zool.* 8, 11–18.
- Odum, E.P., 1972. *Ecología*. Nueva Editorial Interamericana, México, D.F.
- Pauly, D., Christensen, V., 1995. Primary production required to sustain global fisheries. *Nature* 374, 255–257.
- Pilkey, O.H., Pilkey-Jarvis, L., 2006. *Useless arithmetic: Why Environmental Scientists can't Predict the Future*. Columbia University Press, N.Y.
- Riera, R., Rodríguez, R.A., Delgado, J.D., Herrera, A.M., Fath, B.D., 2018. Endorheic currents in ecology: an example of the effects from scientific specialization and interdisciplinary isolation. *Interdiscip. Sci. Rev.* 43, 175–191.
- Rodríguez, R.A., Herrera, A.M., Otto, R., Delgado, J.D., Fernández-Palacio, J.M., Arévalo, J.R., 2012. Ecological state equation. *Ecol. Modell.* 224, 18–24.
- Rodríguez, R.A., Herrera, A.M., Delgado, J.D., Otto, R., Quirós, Á., Santander, J., et al., 2013a. Biomass-dispersal trade-off and the functional meaning of species diversity. *Ecol. Modell.* 262, 8–18.
- Rodríguez, R.A., Delgado, J.D., Herrera, A.M., Riera, R., Navarro, R.M., Melián, C., et al., 2013b. Effects of two traits of the ecological state equation on our understanding of species coexistence and ecosystem services. *Ecol. Modell.* 265, 1–13.
- Rodríguez, R.A., Herrera, A.M., Riera, R., Delgado, J.D., Quirós, Á., Perdomo, M.E., et al., 2015a. Thermostatistical distribution of a trophic energy proxy with analytical consequences for evolutionary ecology, species coexistence and the maximum entropy formalism. *Ecol. Modell.* 296, 24–35.
- Rodríguez, R.A., Herrera, A.M., Riera, R., Escudero, C.G., Delgado, J.D., 2015b. Empirical clues about the fulfilment of quantum principles in ecology: potential meaning and theoretical challenges. *Ecol. Modell.* 301, 90–97.
- Rodríguez, R.A., Herrera, A.M., Riera, R., Santander, J., Miranda, J.V., Quirós, A., et al., 2015c. Distribution of species diversity values: a link between classical and quantum mechanics in ecology. *Ecol. Modell.* 313, 162–180.
- Rodríguez, R.A., Herrera, A.M., Santander, J., Miranda, J.V., Fdez.-Rguez, M.J., Quirós, A., et al., 2015d. Uncertainty principle in niche assessment: a solution to the dilemma redundancy vs. competitive exclusion, and some analytical consequences. *Ecol. Modell.* 316, 87–110.
- Rodríguez, R.A., Herrera, A.M., Santander, J., Miranda, J.V., Perdomo, M.E., Quirós, A., et al., 2016a. From a stationary to a non-stationary ecological state equation: adding a tool for ecological monitoring. *Ecol. Modell.* 320, 44–51.
- Rodríguez, R.A., Herrera, A.M., Quirós, A., Fernández-Rodríguez, M.J., Delgado, J.D., Jiménez-Rodríguez, A., 2016b. Exploring the spontaneous contribution of Claude E. Shannon to eco-evolutionary theory. *Ecol. Modell.* 327, 57–64.
- Rodríguez, R.A., Herrera, A.M., Duncan, J.M., Riera, R., Quirós, A., Perdomo, M.E., et al., 2016c. Response to comments on 'Uncertainty principle in niche assessment: a solution to the dilemma redundancy vs. competitive exclusion, and some analytical consequences. *Ecol. Modell.* 341, 1–4.
- Rodríguez, R.A., Riera, R., Delgado, J.D., 2017a. Ecology: science or philately? An interdisciplinary analysis of sustainability by exploring if it is possible to get more and more information by reducing collateral environmental damages. *Sci. Total Environ.* 596/597, 43–52.
- Rodríguez, R.A., Duncan, J.M., Vanni, M.J., Melkikh, A.V., Delgado, J.D., Riera, R., et al., 2017b. Exploring the analytical consequences of ecological subjects unwittingly neglected by the mainstream of evolutionary thought. *Ecol. Modell.* 355, 70–83.
- Rodríguez, R.A., Duncan, J.M., Riera, R., Delgado, J.D., Quirós, A., Vanni, M.J., et al., 2017c. Thermostatistical distribution of a trophic energy proxy: extension for modelling energy pyramids at the inter-taxocene scale and under non-stationary conditions. *Ecol. Modell.* 361, 113–121.
- Rodríguez, R.A., Duncan, J.M., Delgado, J.D., Vanni, M.J., Riera, R., Herrera, A.M., González, M.J., 2017d. Assessment of ecosystem trophodynamic power: a model based on the power equation for an oscillating string. *Ecol. Modell.* 362, 80–86.
- Rossberg, A.G., 2008. The problem of biodiversity. In: Hokkaido Univ. Tech. Rep. Ser. Math. JST Presto Symposium on Mathematical Sciences Towards Environmental Problems 136. pp. 20–30.
- Sachs, J.L., Simms, E., 2006. Pathways to mutualism breakdown. *Trends Ecol. Evol.* 21, 585–592.
- Scheiner, S.M., 2013. The ecological literature, an idea-free distribution. *Ecol. Lett.* 16, 1421–1423.
- Shannon, C.E., 1948. A mathematical theory of communication. *Bell. Syst. Technol. J.* 27, 623–656.
- Simberloff, D., 1981. The sick science of ecology: symptoms, diagnosis, and prescription. *Eidema* 1, 49–54.
- Spellerberg, I.F., Fedor, P.J., 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon-Wiener' index. *Global Ecol. Biogeogr.* 12, 177–179.
- Tribus, M., McIrvine, E.C., 1971. Energy and information. *Sci. Am.* 225, 179–188.
- Valentine, J.W., May, C.L., 1996. Hierarchies in biology and paleontology. *Paleobiology* 22, 23–33.
- Watt, K., 1971. Dynamics of populations: a synthesis. In: den Boer, P.J., Gradwell, G.R. (Eds.), *Dynamics of Populations: A Synthesis*. Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands, pp. 568–580.
- Weiner, J., 1995. On the practice of ecology. *J. Ecol.* 83, 153–158.
- Winner, R.W., Strecker, R.L., Ingersoll, E.M., 1962. Some physical and chemical characteristics of Acton Lake, Ohio. *Ohio J. Sci.* 62, 55–61.
- Wu, J., 1999. Hierarchy and scaling: extrapolating information along a scaling ladder. *Can. J. Remote Sens.* 25, 367–380.
- Wu, J., David, J.L., 2002. A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. *Ecol. Modell.* 153, 7–26.