Short communication

From a stationary to a non-stationary ecological state equation: Adding a tool for ecological monitoring

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ABSTRACT

How complex systems are able to self-organize away from equilibrium and maintain their internal functional gradients over time, by adapting themselves and changing their own environment? This is one of the most interesting questions for contemporary ecology because of its potential usefulness to assess the ecological health of our natural environment by means of ecological monitoring. This article shows how a replacement and complementation of variables, that is very simple from the mathematical point of view, can be useful to transform the state equation previously developed to describe stationary ecological conditions into a state equation for non-stationary ecological conditions. The method applied was (a) empirically tested starting from field data collected from five surveys belonging to four different kinds of taxocenosis and (b) explained in a very brief and didactic way that can be easily understandable to everybody with a standard undergraduate training in ecological studies. The main result of this article is a simple mathematical equation that can be useful to perform an instantaneous assessment of the state and trend of ecosystem development in the short run starting from a single survey, that is to say, without the availability of long time series of data that allows the conventional studies of comparative ecology in order to assess the course of ecological succession. This proposal adds an innovative diagnostic tool empirically useful for ecological monitoring.

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1. Introduction

Getting reliable information about the ecosystem *state* and its *trends* is crucial to keep a healthy environment, as well as to handle the economic exploitation of natural resources in a sustainable way. Ecological monitoring (EM) generates a large part of the information required to respond to these challenges. EM has repercussions in three main ambits, at least: (a) at the applied scale, because EM allows a better assessment and management of our socio-economic impact on nature; (b) at the pure informative scale, because scientists are able to get new basic knowledge about nature by gathering the appropriate data to assess the ecosystem status (i.e., surveillance: the systematic measurement of variables and processes at

regular intervals over time in order to establish a series of comparable data, see Spellerberg, 2005); and (c) at the theoretical adjustment scale, because EM in itself is a fruitful scenario to obtain an essential degree of adjustment between theoretical and empirical ecology which is suitable to maintain a healthy state in every science (*"a theory which cannot be confronted with the facts or which has not been verified quantitatively by observed data, is, in fact, devoid of any scientific value"*; Allais, 1990, p. 5).

Although these three scales are connected with each other in an indivisible whole, the latter of them is a sort of "epistemological glue" that confers, or should confer, an all-encompassing coherence in ecology as a science. For example, according to Lindenmayer and Likens (2010, p. 1322), an appropriate conceptual model for EM becomes a focal point for discussions among partners about how an ecosystem might be managed and monitored. If the conceptual model fails, the respective program of EM fails as a whole also, either by excess (*"snowed by a blizzard of ecological details"*, see

Lindenmayer and Likens, 2010, Section 5.3) or by defect of information, or because there is a lack of coherence between information gathered and EM's goals. Correspondingly, given the limited conservation funding and the almost unlimited conservation needs, an additional key point in connection with item (c) is that every program of EM should be useful to perform a selective comparison aimed to discriminate among competing conceptual models in order to enhance the general efficiency level of ecological research (see Nichols and Williams, 2006).

Unfortunately, the general state of conventional ecology does not seem to have been in favor of the above-mentioned points in regard to item (c) given that, during the last four decades ecology (i) has shown a significant degree of theoretical turmoil and contingency (e.g., Watt, 1971, p. 569; Lewin, 1983; Lawton, 1999, p. 178; Woodward, 2001; Simberloff, 2004; Roughgarden, 2009; Palma, 2010); (ii) it has been affected by a chronic lack of appreciation of past literature and theoretical fickleness (see Belovsky et al., 2004); (iii) and the linkage between theoretical and empirical ecology seems to have been systematically, although unwittingly, weakened (see, e.g., Belovsky et al., 2004; Loreau, 2010; Angilletta and Sears, 2011; Joseph et al., 2013; Scheiner, 2013). The main negative effect of this situation in regard to the usefulness of EM has been implicitly summarized in the following way: *"today, the needs of conservation biology for metrics of 'ecological health' that can be applied across types of communities prompts a renewed interest in the possibility of general theory for community ecology"* (Roughgarden, 2009, p. 521). This statement exactly reflects the main problem that gives rise to this paper.

Given the above-mentioned problem (i.e., to set up the elementary principles for a basic metric of ecological health valid for a wide spectrum of ecosystems), the main goal of this article is aimed to answer the following set of interrelated questions in order to add a diagnostic tool to EM: (1) is it possible to know in what a measure an ecosystem is stable, or not, by means of a single survey? Assuming that a given ecosystem is under non-stationary ecological conditions (non-SEC); (2) is it possible to assess the direction of ecological change (either in favor or against the spontaneous pro-diversity trend of ecological succession) in the short run by means of a single survey? Assuming positive responses to these previous questions; (3) is it possible to express such a metric of "ecological health" under non-SEC by means of an obviously simple mathematical formulation in agreement with the ecological state equation (ESE, see Eq. (1) in Table 1, cell A3) previously developed by Rodríguez et al. (2012) under stationary ecological conditions (SEC)? In general, these questions are related to a more general question: How complex systems are able to self-organize away from equilibrium and maintain their internal functional gradients over time, by adapting themselves and changing their own environment?

As commented above, the first section of this manuscript describes a scientific problem of significant importance for conservation and sustainability, and establishes our goals in order to contribute to an operative solution in this regard. The second section is aimed to assess the state of the ecosystem (SEC vs. non-SEC), in order to respond to question number (1). This response was implicitly proposed before by Rodríguez et al. (2012, 2013), but it needs to be retaken in this context with the goal of supporting a chain of reasoning connected with later publications that expand its meaning. The third section is aimed to answer to questions (2) and (3), being the core of this article. Finally, the fourth section of the article performs a straightforward exploration of the meaning of these results for ecology, in general, as well as for EM, in particular.

Table 1
Summary of the main indicators connected with the alternative states of ecosystems.[a]

Raw	Criterion of comparison	Column (alternative states of the ecosystem)	
		A — SEC	B — Non-SEC
1	B–D$_{TO-H}$: biomass (m_{ep} or m_{eTp}) $\leftrightarrow$ dispersal (I_e) trade-off in function of H_p values	*Yes*; significant *negative correlation* H_p, I_e; and significant *positive correlation* H_p, m_{ep} or H_p, m_{eTp} (Rodríguez et al., 2013). So $m_{ep\ min.} \leftrightarrow H_{p\ min.}$; $I_e^2{}_{min.} \leftrightarrow H_{p\ max.}$; $(m_e \cdot I_e^2)_{max.} \leftrightarrow$ intermediate values of H_p, close to the peak of H_p distribution (see Fig. 2a)	*No*; statistically *non-significant negative correlation* H_p, I_e; and statistically significant *positive correlation* H_p, m_{ep}
2	Ecological equivalent (k_e) of Boltzmann constant (k_B)	*Yes*; *non–significant* difference between the mantissa of observed value ($k_{e(o)}$) and the mantissa of k_B. k_e emerges from B–D$_{TO-H}$ given that k_e is the average value of the product $I_e^2 \times H_p \times m_{ep}$	*No*; *Significant* difference between the mantissa of observed value ($k_{e(o)}$) and the mantissa of expected value ($k_{e(e)} \approx 1.3806504E\varphi$ J$_e$·nat/individual). $k_{e(o)} \neq k_{e(e)}$ precisely because of B–D$_{TO-H}$ is broken
3	ESE: ecological state equation	$2E_{eTp} = N_p k_{e(e)}/H_p$; (Eq. (1); see explanations in the footnote, as well as in Rodríguez et al., 2012)	$2E_{eTp} \neq N_p k_{e(e)}/H_p$ (see examples starting from four surveys under non-SEC in Fig. 1a)
4	Adjustment of H_p values to gamma distribution	Statistically *non-significant* difference either with standard gamma distribution or with Eq. (2). See, e.g., Fig. 2a	Statistically *non-significant* difference with standard gamma distribution, but statistically *significant* difference with Eq. (2). See, e.g., Fig. 2b
5	Ecological inertia and elasticity	*Undetectable* because the system is not moving through the species diversity gradient because of the influence of B–D$_{TO-H}$	*Detectable* at the intra-survey scale. See Fig. 2b,c in comparison with each other and with Fig. 2a. Additional comments below (Section 3)
6	h_e^{ev}: eco-evolutionary equivalent of Planck's constant	$h_e^{ev} = 6.62606957E - 1$ J$_e$ per unit of ∇k_e). *Undetectable* at the intra-survey scale	*Detectable* at the inter-survey scale as the regression coefficient of E_e vs. $k_{e(e)}$; intercept = 0. So the regression equation: $E_e = k_{e(e)} \times h_e^{ev}$. i.e., h_e^{ev} indicates the non-continuous variation of E_e per each unit of $\nabla k_e = 1$ J$_e$·nat/individual (Rodríguez et al., 2015a)

[a] SEC: stationary ecological conditions. m_{ep}: mean value of biomass per individual per plot. m_{eTp}: total biomass per plot. I_e: indicator of dispersal activity (see Eq. (1A), Appendix A). H_p: species diversity per plot $= -\Sigma[(n_i/N) \cdot \ln(n_i/N)]$, where n_i: number of individuals of species i, $N = \Sigma n_i$, and ln: natural logarithm (see Shannon, 1948; Magurran, 2004). $k_{e(o)} = I_e^2 \times H_p \times m_{ep}$. $k_{e(o)}$ becomes $k_{e(e)}$ (i.e., the typical expected value for a given kind of taxocenosis) if the mantissa of its mean value in regard to the set of plots of the survey as a whole (excluding plots in which $H_p = 0$, these cases indicate that the plot size should be larger) is not significantly different from the mantissa of physical Boltzmann constant (k_B). $k_B = 1.3806504E-23$ J/K per molecule. ESE: ecological state equation (Eq. (1)). E_{eTp}: total eco-kinetic energy per plot $= N_p \times E_e$. N_p: total number of individuals per plot. E_e: mean eco-kinetic energy per individual per plot $_{(p)}$ or survey $_{(s)}$ expressed in ecoJoules (J$_e$; see Appendix A, Section 2) as a proxy for trophic energy $= \frac{1}{2}m_e p I_e^2$; in a similar way in which the kinetic energy in physics is $E = \frac{1}{2}m \cdot v^2$; where m: mass and v: velocity. h_e^{ev}: equivalent of Planck's constant at the evolutionary (ev) scale. $\varphi = -x_i, \ldots -3, -2, -1, 0, +1, +2, +3, \ldots, +x_i$, with a typical recurrent value depending on the type of taxocenosis studied.

2. Assessing the alternative *states* (SEC vs. non-SEC) of ecosystems: ecological, thermostatistical, and quantum traits

It is a truism to say that a healthy ecosystem will be kept well-conserved if it does not change with time. The underlying problem is to assess, as soon as possible, if the ecosystem is changing in the short run, or not. Rodríguez et al. (2012) implicitly proved that, under SEC, the equality that supports the ESE (Eq. (1) in Table 1, cell A3) is fulfilled, meanwhile under non-SEC it is not. However, additional important traits were added in this regard by Rodríguez et al. (2013, 2015a,b) in order to improve our understanding of the physical principles that rule the ecosystem functioning. In general, the ESE was applied by Rodríguez et al. (2013) by showing its capability to discriminate between surveys under SEC and surveys under non-SEC across a wide spectrum of ecological assemblages (e.g., marine microalgae, marine interstitial meiofauna of sandy beaches, massive – non-branching – corals, litter invertebrates in laurisilva, tropical rocky shore snails, coral reef fish, litter invertebrates in pine forest, ruderal vegetation, Mediterranean shrub vegetation, mixed shrub vegetation, pine forest vegetation, and coastal succulent shrub vegetation). Table 1 summarizes the most essential traits of this difference in a simple way. The general pattern from Table 1 embraces three central axes:

(a) It is easy to establish a general opposition SEC ↔ non-SEC starting from a single list of parameters; this implies a clear underlying connection between both states of the ecosystem.

(b) Biomass–dispersal trade-off in function of species diversity values (B–D$_{TO-H}$) plays a key role in this connection because it is associated with the most of the cells in Table 1 (from A1 to B5), and the expected value ($k_{e(e)}$) of the ecological equivalent (k_e) of Boltzmann constant (k_B) is the biophysical expression of B–D$_{TO-H}$.

(c) Despite the dissimilarity SEC vs. non-SEC, these alternative patterns are connected to each other: in both cases there is a good adjustment of the observed distribution of H_p values with standard gamma distribution, as well as with Eq. (2) only under SEC. In fact, according to Margalef (1991, p. 367, Fig. 11–7), *any series enough representative of H values* with regard to time or space (i.e., ergodicity, or statistical equivalence between measurements taken in space and measurements taken over time; see additional comments in regard to Eq. (1A), Appendix A) fits a quasi-normal statistical distribution skewed to the right, this pattern being very similar to gamma distribution.

$$dN_{Hp} = 4\pi N \left[\sqrt{\frac{k_{e(e)}H_T}{2\pi(E_e)}} \right]^3 H_p^2 \cdot e^{(-0.5k_{e(e)}H_T H_p^2/E_e)} dH_p \qquad (2)$$

where dN_{Hp}: expected number of H_p values (species diversity per plot) from H_{pi} to $H_{pi}+dH_p$; π: 3.14159; N: total number of H_p values included in the distribution (plots with $S=1$ and $H_p=0$ should be excluded from N, but all species should be included in the calculation of H_T); $k_{e(e)}$: expected value of the ecological equivalent of Boltzmann constant (1.3806504Eφ J$_e$·nat/individual; J$_e$: 1 eco-Joule = 0.5 kg đ^2; đ: 1 dispersal unit, the unit of expression of I_e; see Eq. (1A) and Section 2, Appendix A); H_T: Shannon index calculated for the survey as a whole (see footnote of Table 1); E_e: mean value of individual eco-kinetic energy at the survey level (see footnote of Table 1); $H_p=H_{pi}$: minimum of the category of H_p for which the expected value of dN_{Hp} is estimated; e: Euler's number (2.71828); dH_p: amplitude of the categories of H_p values of the distribution (see Rodríguez et al., 2015b).

3. Assessing the alternative trends (in favor of ecological succession vs. against ecological succession) of the ecosystem under non-SEC: theoretical foundation, testing, and a simple mathematical formalization

According to Rodríguez et al. (2015b) the degree of statistical adjustment between the observed distributions of H_p values and Eq. (2) tangibly shows traits of *stability* and *inertia* (see the pros and cons of the use of this concepts in Orians, 1975; Grimm and Wissel, 1997, respectively). This is the expected behavior from B–D$_{TO-H}$ (see cell A1 in Table 1): On the one hand, those macrostates on the right edge of H_p distribution are heavier and slower. Hence they react more slowly (with higher inertia) to net energy inputs, jamming the translation of the distribution as a whole by obstructing the movement of those macrostates with the opposite set of features toward higher diversity values. This produces distributions of H_p values *compressed toward the left* under non-SEC (see Fig. 2b) in comparison with the stationary expected pattern according to Eq. (2). On the other hand, those macrostates on the left edge of H_p distributions are lighter and faster. Thence they react more rapidly (with lower inertia) to net energy leaks, pulling the distribution as a whole toward lower diversity values. But this movement is also obstructed by those macrostates of higher inertia that react with delay in the opposite edge of H_p gradient. This produces distributions of H_p values *decompressed or lengthened from the right* under non-SEC (see Fig. 2c,d) in comparison with the stationary expected pattern according to Eq. (2). Coherently, the perfect coincidence between the observed pattern and the expected one according to Eq. (2) indicates that the distribution is stopped (*neither compressed nor decompressed*) from the successional point of view (i.e., it is under SEC; see Fig. 2a). Hence, those plots of high diversity values have a crucial conservative influence in favor of ecological stability, either when H_T increases or when it decreases, because they act as a ballast system that avoids abrupt variations of H_T.

The key point to respond to question (2) in Section 1 is that the above-explained statistical relationship can be useful for EM as an indicator of trends in the short run: The maximum value of total eco-kinetic energy per plot (E_{eTp}, see footnote of Table 1) is always placed at the peak (mode) of H_p distribution (see Rodríguez et al., 2013, 2015b). Additionally, those observed distributions *compressed toward the left* under non-SEC (e.g., Fig. 2b) tend to have a higher number of H_p values (i.e., a larger set of plots that embraces a higher total number of individuals: N_p) staked at a modal value placed in a distribution section of high I_e^2 (this indicator exponentially increases toward the left) and low m_{ep} (this indicator linearly increases toward the right) in comparison with the expected pattern under stationary conditions. As a result, $2E_{eTp} = 2 N_p \times E_e = 2 N_p \times (½m_{ep}I_e^2)$ tends to be higher than the expected theoretical value of $N_p k_{e(e)}/H_p$ according to Eq. (1). That is to say, if the survey is under non-SEC and moving in favor of ecological succession (toward higher future values of total energy and species diversity), then the ESE (Eq. (1)) should show the following pattern:

$$2E_{eTp} > \frac{N_p k_{e(e)}}{H_p} \qquad (3)$$

Complementarily, those observed distributions *decompressed or lengthened from the right* under non-SEC (e.g., Fig. 2c,d) tend to have a lower number of H_p values (i.e., a smaller set of plots that embraces a lower total number of individuals: N_p) staked at a modal value placed in a distribution section of low I_e^2 (this indicator exponentially increases toward the left) and high m_{ep} (this indicator linearly increases toward the right) in comparison with the expected pattern under stationary conditions. As a result, $2E_{eTp} = 2N_p \times E_e = 2N_p \times (½m_{ep}I_e^2)$ tends to be lower than the expected theoretical value of $N_p k_{e(e)}/H_p$ according to Eq. (1).

That is to say, if the survey is under non-SEC and moving in an opposite direction in comparison with a healthy ecological succession (i.e., toward lower future values of total energy and species diversity), then the ESE (Eq. (1)) should show the following pattern:

$$2E_{eTp} < \frac{N_p k_{e(e)}}{H_p} \qquad (4)$$

The relationship reflected by this pair of equations (Eqs. (3) and (4)) can be formalized in a quite simple mathematical way in order to respond to question (3) in Section 1. According to cell B6 in Table 1, h_e^{ev} indicates the constant and discrete (non-continuous) variation rate of E_e per each value of $\nabla k_e = 1$ J$_e$·nat/individual under non-SEC in which $k_{e(o)} \neq k_{e(e)}$. Given that the ESE under SEC (Eq. (1)) can be expressed as a value of $2E_{eTp}$ (where $2E_{eTp}$ is twice the total amount of eco-kinetic energy per plot, or $2E_e \times N_p$) proportional to $N_p \times k_{e(e)}$, with a factor of proportionality equal to $1/H_p$:

$$2E_{eTp} = \left(\frac{1}{H_p}\right) \times (N_p k_{e(e)}), \qquad (5)$$

then it is obvious that inequalities in Eq. (5) under non-SEC (i.e., when $k_{e(o)} \neq k_{e(e)}$ and $2E_{eTp} \neq N_p k_{e(e)}/H_p$) could be balanced by compensating the right side of Eq. (1) replacing $k_{e(e)}$ by the product of h_e^{ev} (see cells A6 and B6, Table 1) and the number of times in which $k_{e(o)}$ is higher, or lower, than $k_{e(e)}$ (i.e., the $k_{e(o)}/k_{e(e)}$ ratio). By means of this simple procedure, Eq. (1) becomes:

$$2E_{eTp} = \frac{N_p k_{e(e)}(h_e^{ev}(k_{e(o)}/k_{e(e)}))}{H_p}$$

Simplifying:

$$2E_{eTp} = \frac{N_p k_{e(o)} h_e^{ev}}{H_p} \qquad (6)$$

If Eq. (6) is a reliable result, then it should produce statistical equality ($p \geq 0.05$) between the left and the right side of equation when it is applied to surveys under non-SEC, compensating in such a way the inequality detected by (Eq. (1), see Fig. 1a) for those cases of surveys under non-SEC (see Fig. 1b in comparison with Fig. 1a).

Correspondingly, when the same transformation applied from Eq. (1) to Eq. (6) (i.e., the replacement of $k_{e(e)}$ by $k_{e(o)} \times h_e^{ev}$) it is applied to transform Eq. (2) into Eq. (7), then there is an improvement 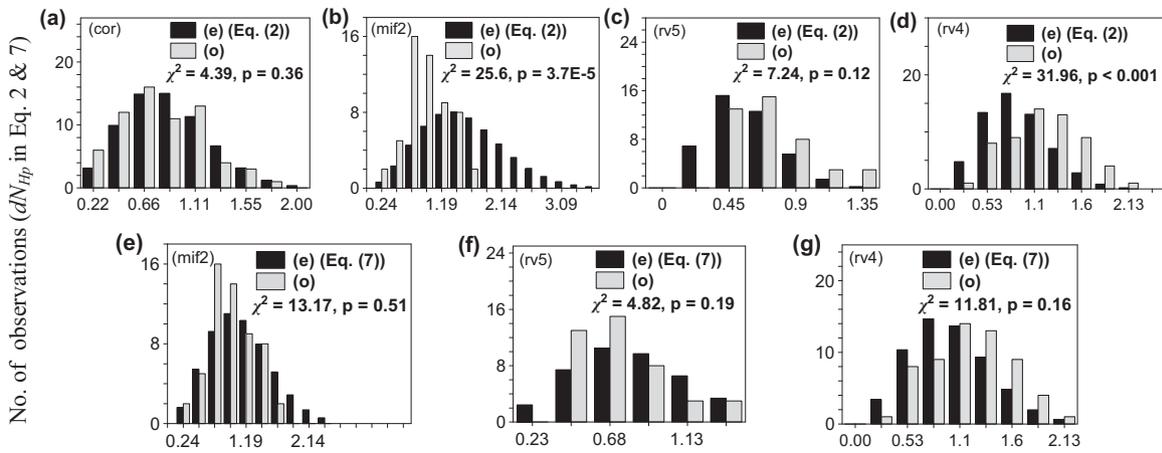in the degree of statistical adjustment between observed and expected distributions of H_p values under non-SEC (see Fig. 2e–g, in comparison with Fig. 2b–d, respectively).

$$dN_{Hp} = 4\pi N \left[\sqrt{\frac{k_{e(o)} h_e^{ev} H_T}{2\pi(E_e)}} \right]^3 H_p^2 \cdot e^{(-0.5 k_{e(o)} h_e^{ev} H_T H_p^2 / E_e)} dH_p \qquad (7)$$

Fig. 3 summarizes the analytical sequence that we followed in order to highlight the meaning of the equations included in this article for EM. Qualitatively speaking, the steps to apply this analytical sequence are the following: (1) collection of basic data about: (a) abundance of individuals per species per plot (n_{ip}) and total abundance per plot ($N_p = \Sigma n_{ip}$); (b) central spatial coordinates per plot either in UTM or in regard to an ad hoc system of coordinates in which the first plot sampled is the origin (0,0) of coordinates; (c) mean individual biomass per species (m_{ei}) at the survey level assessed by means of sampling: dry weight in some cases (mainly in species in which water is a highly significant fraction of body weight, e.g.: microalgae, corals, succulent vegetation), and fresh weight in the most of cases; (d) the size and number of plots (either an area or a volume) must be adjusted in such a way that the set of plots should embrace the whole possible spectrum of H_p values of the taxocenosis studied in the respective area, but avoiding those cases in which $H_p = 0$ ($0 < H_p < 5.64$ nat/individual; see Rodríguez et al., 2015c, Fig. 3b); consistent previous results have been obtained from surveys with a total number of plots as low as 15, but a higher number is suitable; plots should be contiguous with each other, but this is not an inescapable requisite. (2) Calculation of $m_{ep} = \Sigma(n_{ip} \times m_{ei}) = m_{eTp}/N_p$; see footnote of Table 1. (3) Calculation of I_e (see Eqs. (1A)–(3A) in Appendix A; or Rodríguez et al., 2012, 2013, 2015b,c), this requires either an ad hoc calculation table in Excel or ad hoc software (e.g., software IeCalc-2.1 can be provided, free, by the main author of this article). (4) Calculation of $k_{e(o)} = I_e^2 \times H_p \times m_{ep}$ per plot. (5) Exclusion of noticeable outliers within the set of values of $k_{e(o)}$. (6) Comparison of the mean value of the mantissa (mt) of $k_{e(o)}$ (i.e.: if $k_{e(o)} = 0.00012726199 = 1.2726199 \times 10^{-4} = 1.2726199$E-4; so $k_{e(o),mt} = 1.2726199$) with 1.3806504 by using the Student's t-test for single sample; if $p \geq 0.05$ $k_{e(o)}$ becomes $k_{e(e)} = 1.3806504$Eφ J$_e$·nat/individual; by taking $k_{e(e)}$ as the value of 1.3806504Eφ closest to $k_{e(o)}$. This result should be associated with a biomass–dispersal trade-off in function of species diversity values (see Table 1, cell A1). (7) Calculation of $2E_{eTp} = 2(\frac{1}{2}N_p \times$
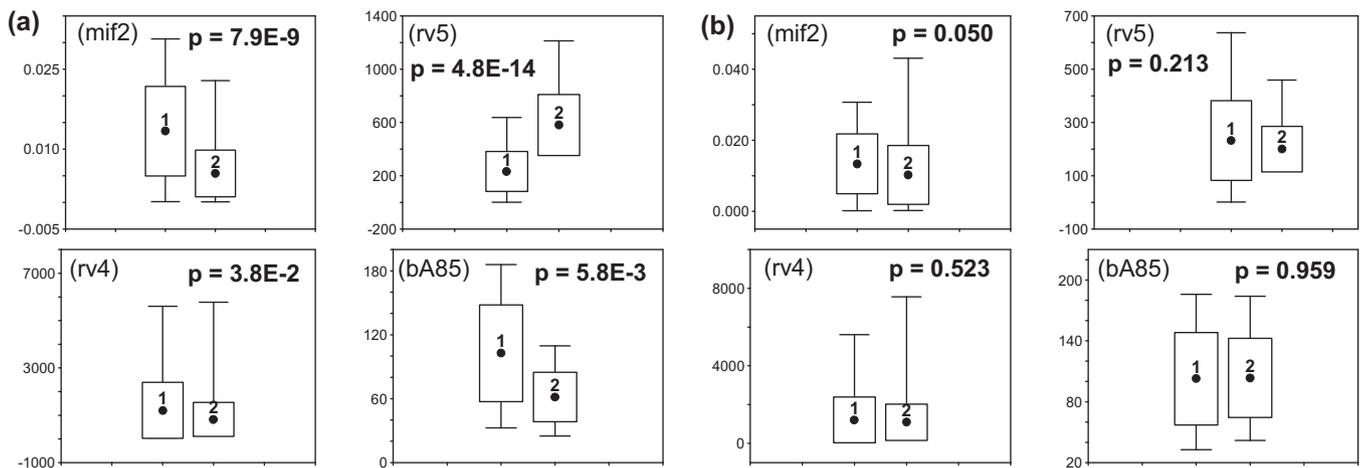
Fig. 1. (a) Results of the statistical comparison of mean values (t-Student test, independent, by variables) between the left (1) and the right (2) side of Eq. (1) (see Table 1) for four surveys (mif2, rv4, rv5 and bA85; sampling methods and additional calculation details in Appendix A, Section 3) under non-stationary ecological conditions (non-SEC). (b) Results of the statistical comparison of mean values (t-Student test, independent, by variables) between the left (1) and the right (2) side of Eq. (6) for the same surveys and original data used to obtain (a). mif: marine interstitial meiofauna of sandy beaches in Tenerife Island, Spain; rv: ruderal vegetation in Tenerife Island, Spain; bA85: benthic fauna in Port Valdez, Alaska (1985); ●: mean value; ‖: ± standard deviation; ⊥: minimum and maximum values.

Fig. 2. (a) Statistical adjustment between observed ((o), gray color) and expected ((e), black color) distributions (Eq. (2)) of species diversity values per plot (H_p) in a survey under SEC. (b)–(d) Statistical adjustment between observed and expected distributions (Eq. (2)) of H_p in three surveys under non-SEC. (e)–(g) Statistical adjustment between observed and expected distributions (Eq. (7)) of H_p in three surveys under non-SEC. cor: massive (non-branching) coral reefs in Veracruz, Mexico. χ^2: Chi-square test.

$m_{ep} \times I_e^2$) and $(N_p k_{e(e)})/H_p$, and comparison of means between $2E_{eTp}$ and $(N_p k_{e(e)})/H_p$ by means of the Student's t-test (t), independent, by variables. (8) If $p_t \geq 0.05$ in item (7) the survey is under SEC (left branch in Fig. 3) → (8.1) a set of observed statistical density distributions of H_p values (the most advisable number of H_p categories per distribution is $k = (\sqrt{n_p}) \pm 2$, where n_p: total number of plots per survey) is calculated, and an observed distribution arbitrary chosen is compared with the expected distribution according to Eq. (2) by means of the chi-square (χ^2) test; it is expectable that $p_{\chi2} \geq 0.05$. (9) If $p < 0.05$ in item (7) the survey is under non-SEC (right branch in Fig. 3) → (9.1) if $2E_{eTp} > (N_p k_{e(e)})/H_p$ (by taking $k_{e(e)}$ as the value of $1.3806504E\varphi$ closest to $k_{e(o)} \neq k_{e(e)} = 1.3806504E\varphi$ J$_e$·nat/individual) the survey is "moving" *in favor of* ("E.S.+" in Fig. 3) the natural direction of successional process under favorable eco-evolutionary conditions → (9.2) if $2E_{eTp} < (N_p k_{e(e)})/H_p$ the survey is "moving" *against* ("E.S.−" in Fig. 3) the natural direction of successional process under

favorable eco-evolutionary conditions. (10) Eq. (6) is applied, and the inequalities commented in items (9.1) and (9.2) should disappear → (11) Item (8.1) is repeated taking the same observed distribution previously chosen as reference but, in this case, by using Eq. (7) as expected distribution: it is expectable that $p_{\chi2} \geq 0.05$ from the comparison between the observed distribution and the expected one (Eq. (7)).

4. Concluding remarks, and some epistemological considerations

Twenty nine surveys have been explored in total from Rodríguez et al. (2012) to Rodríguez et al. (2015b) in order to test different equations and hypotheses, all of them connected to a common developing analytical framework linked to the proposals in this article. Only four of these surveys (mif2, rv4, rv5 and bA85, all of them included in this work) resulted to be under non-SEC. So, there are two main methodological insights in this regard: (a) non-SEC surveys are not the most frequent and perdurable alternative under natural conditions. (b) It is desirable to expand the future number of surveys under non-SEC in order to test the results of this article in a stronger way. However, despite these "natural" drawbacks, the results of this article are supported by their coherence with several previous publications, and they seem statistically reliable and clear enough as to deserve a publication that is able to offer useful information by itself.

The most of the equations used in this article are quite simple (mainly Eqs. (1), (3)–(6)). So an obvious question arises: How is this possible if we take into account the overall complexity of open systems far from equilibrium that it is often alleged in the literature? (e.g., Rescher, 1998; Page, 2011). A fairly widespread opinion is that complex systems cannot be managed because they are self-organized and too complex. For example, according to Rzevski and Skobelev (2014, p. 7), the seven criteria of complexity are the following: (1) *non-equilibrium*, (2) *connectivity*, (3) *autonomy*, (4) *emergence*, (5) *non-linearity*, (6) *self-organization*, and (7) *co-evolution*; plus two additional secondary traits: *non-determinism*, and *uncertainty*. Hence a high level of theoretical connectivity should exist between these 9 traits also, because connectivity is a trait included within the set itself in order to define complexity. That is to say, there should have a strong association between the fulfillment of any one of these criteria and the rest of them. A note, included below in this very section, explains why non-equilibrium is not an obstacle in order to describe the ecosystem by using the simplest principles of conventional physics; in fact,
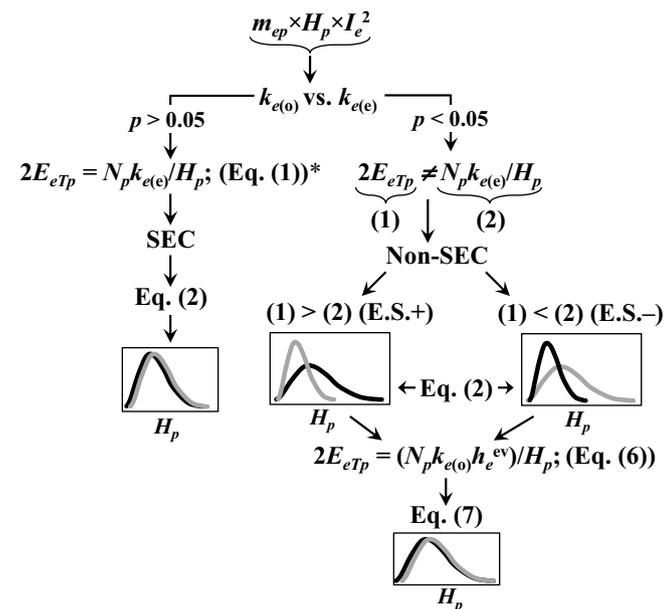
Fig. 3. Summary of the analytical sequence followed in this article. E.S.+: the survey is moving in favor of ecological succession. E.S.−: the survey is moving against ecological succession. *: Ecological state equation (ESE) under stationary ecological conditions (SEC); see Eq. (1) in Table 1, cell A3. All of the remaining symbols and colors (black: expected distributions; gray: observed distributions) coincide with those in the main text and the rest of the figures.

this article itself supports this point of view. In addition, there must be certain degree of trade-off between properties (2) and (3), because the higher the internal connectivity between the elements of a given system, the lower the autonomy of any of these elements. Rodríguez et al. (2015c; see Figs. 4–7 and their respective comments) offer a detailed analysis about the eco-evolutionary meaning of this trade-off. In addition, Rodríguez et al. (2015a,b,c), have developed a suitable theoretical framework that offers empirical evidence in favor of the fulfillment of quantum principles, including the quantum uncertainty principle itself, in ecosystem ecology. Finally, these results are determined (by understanding the concept of "*determinism*" as the philosophical position in which for every event or set of events there is a given set of conditions that cannot cause other event or set of events) by a biomass–dispersal trade-off in function of species diversity values (see Rodríguez et al., 2013, and Table 1, cell A1, in this article) that is coherent with the analytical meaning of cavity resonators in quantum mechanics which, by the way, it is a typically case of science based on linear relationships between observable variables. In summary, this previous set of characteristics indicates that a fruitful option to understand key traits of ecosystem functioning can combine *mathematical simplicity* + analytical *equivalence between stationarity and equilibrium* (see below) + mutual *restrictions between connectivity and autonomy* + *linearity* + *determinism* + *uncertainty* in order to explain the emergence of a *statistically-organized* set of degenerate ecological states (see Rodríguez et al., 2015c) that involves a significant degree of functional isolation (i.e., *without co-evolution* in comparison with the ecological background under sympatric conditions) that is in favor of evolutionary leaps. As a result of the noticeable dissimilarity between this latter set of traits and the former one, conventional definitions of complexity are quite debatable.

Goldenfeld and Kadanoff (1999, p. 87) established the key question about complexity in the following way: "*So why, if the laws* [of nature] *are so simple, is the world so complicated?*" Our understanding of the meaning of complexity in ecology lies in two factors, one of them *objective* and the other one *subjective*. The *objective* one depends on the level of our analytical cut off: in a similar way to a tree, a transversal slice at the central root level shows a very simple structure (tissues to transport nutrients and sustain all the system). On the contrary, a cut off at the branches level shows a more complex structure full of anastomoses and divergences in many directions. Hence, complexity firstly depends on the degree of generalization of the model sought: a single root and a trunk with only one or few branches it is still a tree; meanwhile, a very complex system of branches in the air, without a trunk, is not a tree.

The *subjective* side of complexity can depend, paradoxically, on our inability for thinking in a simple enough way. In other words, sometimes a system that is not well understood appears complex and our natural response is to increase the complexity of our models instead of the opposite. In such a sense, complexity is a subjective effect that emerges from the distance between our epistemology (i.e., the branch of philosophy concerned with the nature and scope of knowledge) and the phenomenology of the system rather than from the real complexity of the system itself. As a result, one frequent failure to build a model is that in our desire to obtain a complete description of the system we add more and more variables and dimensions to our model at the expense of generality, predictability, and understanding (Rosindell et al., 2012). There is a general epistemological trade-off in this regard: the most exact models are completely irrelevant in the same measure in which an approximated model that only reflects the essential features of the system has an insurmountable analytical value; in fact, without this general trait the word "*model*" loses all its meaning. After all, every equation is a sort of concept expressed in mathematical terms, and it is well-known that there is an opposite relationship

between the *content* of a concept (its definition itself) and its *volume* (the spectrum of examples for which the concept is valid). If we add more and more requirements (items) to the concept's definition its volume diminishes in consequence, and vice versa: the concept of "*house*" defined as "*a place in which a family lives isolated from outside influences*" includes from a Paleolithic cave to a modern skyscraper, and reflects the important socio-ecological fact that our species is a strongly gregarious one, and that outdoor weathering conditions are not healthy for humans all the time. In the same measure in which we add more and more items to the concept of "*house*" (i.e.: country and city in which the house is located, neighborhood, size, color, number of rooms and baths, number of inhabitants, etc.), it is possible to arrive even until the particular case of *the house of a particular person*, but this case is only relevant for that person instead of for science as a whole. Equations are similar to this case sometimes: the addition of more and more complexity could lead to more accurate results whose theoretical relevance could be negligible. In this very article, Eq. (1) is significantly simpler, but more relevant, than Eq. (7). This way of building a model reflects one of the most essential traits of life: biological adaptation, as the supreme expression of life, precisely implies the capability of every living system to modify some of its non-essential traits without sacrificing its essential features. Thus, the key question about modeling complexity is to include the essential traits that rule the functioning of the system, neither more nor less. If the main laws of science are quite simple, then it is because the essential functioning of nature it is also simple rather than complex because systems that are too complex tend to have a high frequency of failures. Darwinian theory is precisely based on the selective elimination of those biological units that tend to fail.

Sagoff (2003) establishes a dichotomy between two alternative ways to research in ecology; (1) the contingent or idiosyncratic way (each particular system requires a particular model) and (2) the generalist way (there are very general patterns or principles valid for a wide spectrum of ecological circumstance). The main problem with option (1) is that it disagrees with the epistemological experience of any other science as well as with the epistemological experience of biology itself. That is to say, (a) any proposal in physics must alternatively fit with the general principles of Newtonian mechanics, relativity theory or quantum mechanics; in a similar way, (b) any proposal in chemistry is in agreement with the atomic theory initially proposed by Dalton as well as with the periodic table of Mendeleev; (c) any proposal in geology lies after all in the plate tectonic theory proposed by Wegener, and (d) any proposal about the origin of species diversity should coincide with natural selection and the structure and function of DNA. Without general patterns, there is not science at all. The existence of many complex models to describe a single reality precisely indicates that we do not have any pattern at all and therefore we should not rely on any of those models. But this does not mean that the simple and general pattern we are looking for does not exist, simply it has still not been found. If we would have to accept a "*dogma of faith*" in science, then it would be that, beneath the external complexity of nature, there are always underlying simple patterns that are the main goal of any scientific search.

Additionally, the novelty of this approach precisely lies in its heterodox manner of adding a small step toward the ambitious goal of describing the dynamics of systems far away from equilibrium (natural ecosystems are a central target in this research activity) in a simple manner. Thousands of papers and books have been published about this topic; however, it is possible to find astonishing statements as this one: "*after more than 20 years, first 10 years of theoretical investigation, then, several years of diverse experimental practice in chemistry laboratories, I have a clear opinion regarding this entropy theory* [Prigogine's theory]. *Its main problem is that it*

does not conform with the second law of thermodynamics. Therefore, it is not a surprise that an honest chemist (among any other educated chemists, physicists, biologists, etc.) will tell you that he has never found an application of this entropy theory in chemistry (or in biology, physics, engineering,. . .)" (Lin, 1999, pp. 2 and 3). So any additional approach, mainly if it is simple enough and coherent with physics and ecology as for being widely used, should be welcomed.

On the one hand, it is undeniable (see, e.g., Callen, 1985, pp. 6, 13–15; Lin, 1991, p. 70) that classical thermodynamics is a time-independent science characterized by the study of static states (SEC) rather than dynamic processes. However, the laws of thermodynamics and the principles of quantum mechanics had not been combined as in Rodríguez et al. (2015a,b,c) ever before, either in ecology or in physics itself. Since, according to Rodríguez et al. (2015a), the evolutionary equivalent of Planck's constant emerges as a discrete rate of variation of eco-kinetic energy values per individual (E_e) along a succession of $k_{e(e)}$ values under SEC, then h_e^{ev} acts as a constant rate of dynamic variation (under non-SEC) between successive static states (SEC). This explains why it is possible to combine, in Eq. (6), a value that is not expected to be a constant anymore (since $k_{e(o)} \neq k_{e(e)}$) with an evolutionary constant (h_e^{ev}) in order to describe non-SEC.

On the other hand, very probably, there have been two issues, which are related with epistemology rather than with pure ecology, that have hindered the development of a reliable solution in this field so far: (a) the frequent misunderstandings about the physical meaning of the term "equilibrium" in biology; and (b) neglecting the importance of reaching an appropriate degree of analytical equivalence between analogous variables in those proposals aimed to attain interdisciplinary solutions in this field.

About (a): The understanding of equilibrium that is normally used in colloquial ecology suggests the absence of *tangible boundaries* between the system (commonly the ecosystem, in the particular scientific field of this article) and its surrounding, and therefore a sort of general equalization or "dilution" of the internal properties of the system of reference that ends with the disappearing (death) of the system itself. But this concept is quite debatable: firstly, the most of the surrounding functional boundaries are not tangible at all, and secondly, even non-living systems are able to maintain a distinctive structure in comparison with its surroundings, providing that they can count with a stable energy flow (e.g., the stars are able to keep a well-defined and classifiable structure for billions of years despite they cannot be regarded as "living systems" in the conventional sense of this term). If the temperature of a glass of water = indoor environmental temperature, then we would said that the glass is "in equilibrium". But the indoor environmental temperature ≠ outdoor temperature; and the outdoor local temperature ≠ the mean value of temperature of regional weather conditions, and so on. Then, where is the validity of our concept of equilibrium based on the absence of tangible differences between a given ecosystem and its environment? If these physical differences exist everywhere in the large scale, then the equilibrium state based on the presence of differences does not exist anywhere. The physical concept of equilibrium is simpler than the former one: time-independence is the only solid requirement for equilibrium (see Callen, 1985, p. 13); and the values of state variables (temperature, pressure volume, entropy, etc.) do not change with time either under equilibrium or under stationarity in far-from-equilibrium open systems. This implies that stationarity in open systems is analytically equivalent to equilibrium in isolated systems (Montero and Morán, 1992) given that, under stationarity, energy gains ≈ energy losses even in the absence of tangible physical walls. So, contrarily to the conventional viewpoint, there has never been any obstacle of scientific principle to describe the essential features of the ecosystem functioning by means of conventional physics.

About (b): Something is wrong when we are doing the same thing over and over again, expecting different results. Equivalently, something is also wrong when we are doing a different thing expecting the same result. If we are really interested in successfully applying physics to understand the functioning of ecological systems, then it is necessary to find in the functioning of these systems certain indicators that need to be equivalent to those variables normally used by physics. However, if we are aprioristically convinced that there are insurmountable differences between physical and ecological systems, then we are underestimating similarities (i.e., we would be seeking models based on non-equivalent variables) because we have been overestimating differences from the very beginning. As a result, our work itself becomes a very effective way of being farther and farther from our initially stated goal. But this obstacle is a result of a widespread epistemological bias in favor of scientific specialization and interdisciplinary isolation, rather than a reflection of the underlying structural complexity of the natural world itself.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2015.08.030.

References

Allais, M., 1990. My conception of economic science. Methodus 2, 2–5.
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., et al., 2004. Ten suggestions to strengthen the science of ecology. BioScience 54, 345–351.
Callen, H.B., 1985. Thermodynamics and an Introduction to Thermostatistics. John Wiley & Sons, Inc., Singapore.
Goldenfeld, N., Kadanoff, L.P., 1999. Simple lessons from complexity. Science 284, 87–89.
Grimm, V., Wissel, C., 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109, 323–334.
Joseph, M.B., Mihaljevic, J.R., Arellano, A.L., Kueneman, J.G., Preston, D.L., Cross, P.C., et al., 2013. Taming wildlife disease: bridging the gap between science and management. J. Appl. Ecol. 50, 702–712.
Lawton, J.H., 1999. Are there general laws in ecology? Oikos 84, 177–192.
Lewin, R., 1983. Santa Rosalia was a goat. Science 221, 636–639.
Lin, S.-K., 1991. Time symmetry and thermodynamics. Comput. Math. Appl. Int. J. 22, 67–76.
Lin, S.-K., 1999. Diversity and entropy. Entropy 1, 1–3.
Lindenmayer, D.B., Likens, G.E., 2010. The science and application of ecological monitoring. Biol. Conserv. 143, 1317–1328.
Loreau, M., 2010. Linking biodiversity and ecosystems: towards a unifying ecological theory. Philos. Trans. R. Soc. B 365, 49–60.
Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, Inc., Malden.
Margalef, R., 1991. Ecología. Omega, Barcelona.
Montero, F., Morán, F., 1992. Biofísica, Procesos de Autoorganización en Biología (Biophysics, Processes of Self-Organization in Biology). Eudema, S.A., Madrid, pp. 48–49.
Nichols, J.D., Williams, B.K., 2006. Monitoring for conservation. Trends Ecol. Evol. 21, 668–673.
Orians, G.H., 1974. Diversity, stability and maturity in natural ecosystems. In: van Dobben, W.H., Lowe-McConnell, R.H. (Eds.), Unifying Concepts in Ecology. Report of the Plenary Sessions of the First International Congress of Ecology. September 8–14, Dr W. Junk B. V. Publishers, The Hague, the Netherlands, pp. 139–150.
Page, S.E., 2011. Diversity and Complexity. Princeton University Press, New Jersey.
Palma, A., 2010. Nicho, teoría neutral, o una alternativa emergente? (Niche, neutral theory, or an emergent alternative?). Ecol. Aust. 20, 63–69.
Rescher, N., 1998. Complexity: A Philosophical Overview. Transaction Publishers, New Brunswick, NJ.
Rodríguez, R.A., Herrera, A.M., Delgado, J.D., Otto, R., Quirós, A., Santander, J., et al., 2013. Biomass–dispersal trade-off and the functional meaning of species diversity. Ecol. Model. 261/262, 8–18.
Rodríguez, R.A., Herrera, A.M., Otto, R., Delgado, J.D., Fernández-Palacio, J.M., Arévalo, J.R., 2012. Ecological state equation. Ecol. Model. 224, 18–24.

Rodríguez, R.A., Herrera, A.Mª., Riera, R., Escudero, C.G., Delgado, J.D., 2015a. Empirical clues about the fulfillment of quantum principles in ecology: potential meaning and theoretical challenges. Ecol. Model. 301, 90–97.

Rodríguez, R.A., Herrera, A.Mª., Riera, R., Santander, J., Miranda, J.V., Quirós, A., et al., 2015b. Distribution of species diversity values: a link between classical and quantum mechanics in ecology. Ecol. Model. 313, 162–180.

Rodríguez, R.A., Herrera, A.Mª., Santander, J., Miranda, J.V., Fernández-Rodríguez, Mª.J., Quirós, A., et al., 2015c. Uncertainty principle in niche assessment: a solution to the dilemma redundancy vs. competitive exclusion, and some analytical consequences. Ecol. Model. 316, 87–110.

Rosindell, J., Hubbell, S.P., He, F., Harmon, L.J., Etienne, R.S., 2012. The case for ecological neutral theory. Trends Ecol. Evol. 27, 203–208.

Roughgarden, J., 2009. Is there a general theory of community ecology? Biol. Philos. 24, 521–529.

Rzevski, G., Skobelev, P., 2014. Managing Complexity. WIT Press, Southampton, UK.

Sagoff, M., 2003. The plaza and the pendulum: two concepts of ecological science. Biol. Philos. 18, 529–552.

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. Tech. J. 27, 379–423.

Simberloff, D., 2004. Community ecology: is it time to move on? Am. Nat. 163, 787–799.

Spellerberg, I.F., 2005. Monitoring Ecological Change. Cambridge University Press, New York.

Watt, K.E.F., 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, the Netherlands, pp. 568–580.

Woodward, J., 2001. Law and explanation in biology: invariance is the kind of stability that matters. Philos. Sci. 68, 1–20.