



Response to comments on “Uncertainty principle in niche assessment: A solution to the dilemma redundancy vs. competitive exclusion, and some analytical consequences”



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ABSTRACT

The influence of quantum ecological uncertainty (QEU: a discrete statistical trade-off between the standard deviations of species diversity and energy, two indicators that are essential to define the ecological niche of every species), has been proposed as a plausible explanation to the debate between the competitive exclusion principle (CEP) and the hypothesis of functional redundancy (HFR). The debate CEP ↔ HFR is a manifestation of the wide spectrum of issues connected with a very important problem in ecology: the so-called “biodiversity paradox” (i.e.: How is it possible that so many species can coexist despite the underlying influence of interspecific competition?). Any testable theoretical alternative to explain species coexistence depends on an accurate assessment of the ecological niche in practice. However, under QEU, the assessment of ecological niche cannot be as accurate as we want due to an objective limitation of nature: the above-mentioned trade-off. Consequently, it is nonsense following the debate about this topic in the conventional way; it is necessary to change our traditional point of view about this issue in order to develop a non-conventional interpretation of ecosystem functioning. However, QEU has been strongly criticized in a recently published article. This article is devoted to clarify certain misunderstandings whose nature is evident by reading the above-mentioned criticism and its precursory publications in comparison with the spectrum of articles that supports QEU. The general fulfillment of QEU has also been questioned by the above-mentioned criticism, so it is additionally supported in this article by a noticeably abbreviated inclusion of results from field data, surveyed under different circumstances in comparison with previous data, from two inland water taxocenoses (zooplankton rotifers and crustaceans, Acton Lake, Ohio, U.S.A.) to which this model has not been applied so far. Our general conclusion is that the criticism to QEU has been groundlessly proposed due to epistemological inaccuracies; fragmentary understanding about the principles connected with QEU; as well as an incomplete literature review.

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1. Introduction

Rodríguez et al. (2015a), starting from large sequences of statistical frequency distributions of species diversity values, have shown that in the same measure in which the spectrum of species diversity per plot (H_p : diversity index of Shannon at the plot level; see

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Rodríguez et al., 2015a; Eq. (1)) in which species live is assessed with higher accuracy (lower standard deviation: σ) there is an increment of σ in the measurement of the spectrum of eco-kinetic energy values per plot (E_{ep} : a proxy for trophic energy; additional explanations in Section 2), and vice versa. So there is an insurmountable level of inaccuracy in our description of the ecological niche. Rodríguez et al. (2015a) named this trade-off as quantum ecological uncertainty (QEU, hereafter; additional explanations in Section 2). Under these circumstances, it is impossible to increase the accuracy of our knowledge about the nature and intensity of competition as much as we want by means of conventional methods. So, it is necessary to apply a wave-like interpretation of ecosystem functioning; an option that has also been proposed by the very authors that have proposed the QEU (see Rodríguez et al., 2015b). Thus, a debate that has endured for decades (see Lewin, 1983), has arrived to a win-win solution: species coexistence is possible only because when the hypothesis of functional redundancy (HFR) is true in one dimension (either low values of σ_{Hp} or σ_{Eep}) the competitive exclusion principle (CEP) is influencing in the opposite one (either high values of σ_{Eep} or σ_{Hp}), and vice versa. After all ecologists, willy nilly, have been forced to accept the coexistence of CEP and HFR in the collective academic mind, perhaps as an unwitting reflection that species coexistence depends on a combination of both alternatives in the real world.

The main goal of this article is to perform a comparative analysis in order to elucidate in what a measure the proposal of the authors of QEU, or the proposal of their critics (Kalmykov and Kalmykov, 2016), matches with the traits of any scientific model defined as an incomplete reflection of reality whose main goal, instead of reaching a “universal truth”, is obtaining good testable hypotheses relevant to understand important problems (see Levins, 1966, p. 430) in practice. The general fulfillment of QEU is additionally supported in this article by a very condensed inclusion (Appendix A, and a few lines at the end of the first paragraph in Section 3) of additional results from field data, surveyed under different circumstances in comparison with previous data, from two inland water taxocenoses (rotifers and crustaceans, Acton Lake, Ohio, U.S.A.) to which this model has not been applied so far.

2. Epistemological inaccuracies in the criticism from Kalmykov and Kalmykov (2016)

Kalmykov and Kalmykov (2016, p. 1) start with a rhetorical resource or “*argumentum ad verecundiam*” (appeal to authority) that pervades their article as a whole: “*I can never satisfy myself until I can make a mechanical model of a thing. If I can make a mechanical model, I can understand it. As long as I cannot make a mechanical model all the way through I cannot understand*” (Lord Kelvin). A preliminary conceptual clarification is necessary here: What is the most probable meaning of the term “*mechanical*” in this statement? William Thomson (Lord Kelvin, 1824–1907) was an outstanding physicist that surely had to be used to speaking in rigorous scientific terms. In addition, Lord Kelvin lived between the heyday of classic industrial revolution and just before the emergence of “modern physics” (relativity and quantum mechanics). As a consequence, the only possible meaning of the word “*mechanical*” in this statement is in reference to classical or Newtonian mechanics, because it was the only type of mechanics that Lord Kelvin knew. So, if a chain of reasoning about an allegedly mechanical model begins with the above-mentioned statement, it is supposed that the model should be based on Newtonian mechanics.

The statement of Lord Kelvin is brandished by Kalmykov and Kalmykov (2016; see, e.g.: p. 2, Table 1, third column) to classify models along a gradient of black → grey → white boxes. A model is more “white” (clearly understandable) if it is more related to

mechanics. Since Kalmykov and Kalmykov (2016) consider that the proposal of QEU is not connected with mechanics at all, then they classify QEU as a black-box model.

A first problem is that of conceptualization. The terms “*mechanical*”, “*mechanistic*”, “*mechanistically*”, “*mechanicalness*” and “*mechanistic mechanism*” are used, as a whole, 53 times by Kalmykov and Kalmykov (2013, 2015, 2016). However, it is not clarified, even once, what is the kind of “*mechanics*” they are talking about. They simply assume that the analysis of cause-effect and part-whole relationships (see Kalmykov and Kalmykov, 2013, p. 125), is enough to consider that a model is based on “*mechanistic mechanisms*”. In addition, we are unable to know if some equations similar to those of mechanics are used to develop their analysis, because not even one physical or ecological equation is included in any of these three articles.

A second problem is that Kalmykov and Kalmykov (2016) are not aware about the reasoning chain to arrive to QEU, which it is summarized below from a total of 96084 words from original printed publications condensed in 512 words: (a) The state variable values remain constant with time under equilibrium (Callen, 1985, p. 13). So there is equivalence between closed systems in equilibrium and stationary open systems, like steady ecosystems whose net balance input ↔ output tends to 0. Besides, the increase of H_p per plot has an “anti-thermic” and therefore anti-kinetic effect, by reducing the investment of metabolic energy in dispersal activity. So the ideal gas state equation (IGSE: $2N[\frac{1}{2}m \cdot v^2] = Nk_B T$, or $2NE = Nk_B T$) can be transformed, every physical variable matched with its respective ecological equivalent, into an ecological state equation (ESE: $2N_p[\frac{1}{2}m_{ep} \cdot I_e^2] = (N_p k_e) H_p$, or $2N_p E_{ep} = (N_p k_e) H_p$; where N_p : total number of individuals per plot; E_{ep} : average individual value of the classical eco-kinetic energy per plot (p) as a proxy for trophic energy; m_{ep} : mean fresh biomass per individual per plot in kg; I_e : dispersal indicator with equivalent traits to those of physical velocity $-v$ in IGSE–; k_e : ecological equivalent of Boltzmann constant; see Rodríguez et al., 2012). →(b) $E_{ep} = \frac{1}{2} m_{ep} \cdot I_e^2$ tends to reach an insurmountable limit at minimum H_p values because of a deficit of m_{ep} , despite the maximum value of I_e^2 (i.e.: $m_{ep} \downarrow$, $I_e^2 \uparrow$, $H_p \downarrow$). On the opposite edge of ΔH_p , E_{ep} also reaches an insurmountable limit at maximum H_p values because of a deficit of I_e^2 , despite the maximum value of m_{ep} (i.e.: $m_{ep} \uparrow$, $I_e^2 \downarrow$, $H_p \uparrow$). So $m_e \times I_e^2 \times H_p = \text{constant} = k_e = 1.3806504E\varphi$ ecoJoule-nat/individual; in which φ has a typical integer value ($-x_i, \dots, -2, -1, 0, +1, +2, \dots, +x_i$) depending on the type of taxocenosis studied (see Rodríguez et al., 2013). →(c) This biomass-dispersal trade-off in function of H_p is perfectly consistent with the well-known r - K selection theory in ecology. As a result, E_{ep} in stationary ecosystems (the most common state in nature, on the contrary, the conventional classification of ecosystems would be impossible at all) is confined within a sort of “**ecological box**” (ΔH_p). →(d) Within an “**ecological box**” any fluctuation of E_{ep} becomes a stationary wave that bounces forward and backward along ΔH_p , in a similar way to the waves in all kinds of musical instruments, or in the electron orbits in an atom. →(e) Given this scenario, it has been empirically proven (Rodríguez et al., 2015b) that there is a local compensation (i.e., at the level of plot or small groups of plots) between ecological wavelength (λ_e), m_{ep} and I_e along the inhomogeneous internal environment of ecosystem. The average of the product of these variables (i.e.: $\lambda_e \times m_{ep} \times I_e$) yields a constant (h_e) whose mantissa is equal to the Plank constant (h). So, the most general principles of quantum mechanics, including the quantum uncertainty principle itself (that has become QEU in this new approach; see Rodríguez et al., 2015a), are valid to explain the most general functional traits of an ecosystem: when a species set has a high risk of intense competition (low σ) along the spectrum of H_p values, this risk is relieved by an increase of σ_{Eep} into the H_p , E_{ep} functional scalar 2D field, and vice versa.

From this reasoning chain, our proposal is perfectly understandable and it is deeply rooted in Newtonian mechanics. So, applying the criterion of Kalmykov and Kalmykov (2016), QEU must be regarded a white-box model instead of a black-box model. Additionally, QEU is empirically supported by a large set of field data (29 surveys, 1438 plots, 1586 species and 88737312 individuals from 12 different taxocenes).

In a sharp contrast with the previous paragraphs: (a) The main hypothesis that sustains the proposal from Kalmykov and Kalmykov (2013, p. 125, Section 1.3) is based on the existence of solitons (non-stationary and self-reinforcing solitary traveling waves that maintain their amplitude and wavelength constant while they propagate at a constant velocity across a non-confined –open– and homogeneous or quasi-homogeneous environment) at the population level. (b) Kalmykov and Kalmykov (2015) proposed an approach, with similarities in regard to methods and results in comparison with their article of 2013, in order to analyze the topic again but, in an unexpected discontinuity, the words “soliton” and “waves” were omitted from this article. (c) The amount of field data that support the proposal from Kalmykov and Kalmykov (2013, 2015, 2016) is zero (0). Their proposal is based on pure mathematical simulations. Firstly, it is not clear how a soliton dynamics would match with a stationary wave dynamics within a non-homogeneous environment. Secondly, given the absence of field data; it has not been tested so far if the proposal of Kalmykov and Kalmykov is empirically reliable, or not.

In addition, the criterion of Kalmykov and Kalmykov (2016) to establish their scale of black-grey-white models is weak: “What is gravity? But is this such a simple law? What about the machinery of it? All we have done is to describe how the earth moves around the sun, but we have not said what makes it go. Newton . . . was satisfied to find what it did without getting into the machinery of it. No one has since given any machinery. . . the great laws of mechanics are quantitative mathematical laws for which no machinery is available.” (Feynman et al., 1963, p. 7–9). So, even mechanics itself is a black-box-like model. Contrastingly, there is no connection between the formal concept of black box and mechanics: a black box is a system which can be viewed in terms of its inputs and outputs, without any knowledge of its internal workings (Glanville, 2009). But, in the case of QEU, we clearly understand how and why it emerges, as well as its internal influence on the ecosystem functioning.

According to Kalmykov and Kalmykov (2016, p. 3): (a) Rodríguez et al. (2015a) have mistakenly replaced the thesis “CEP vs. natural biodiversity” by the thesis “CEP vs. HFR”. (b) Rodríguez et al. (2015a) do not mention that the “biodiversity paradox” was completely solved earlier by Kalmykov and Kalmykov (2013, 2015). However, item (a) leads Kalmykov and Kalmykov to a blind alley: On the one hand, a classical article about the general academic situation in this matter (we refer to Lewin, 1983; additional information in Palma, 2010) clearly shows that the debate “CEP vs. HFR” has been one of the main expressions of the so-called “biodiversity paradox” during many decades. So Rodríguez et al. (2015a) did not perform any “substitution of thesis”. On the other hand, suppose that Kalmykov and Kalmykov (2016) are right because Rodríguez et al. (2015a) analyzed a problem **that is not similar to. . . or it is completely disconnected from. . .** the “biodiversity paradox”. In this case there would be no motive of criticism by Kalmykov and Kalmykov (2016) because we would have been studying two different topics that should not be mixed. About item (b): the traits commented above, and below, in regard to Kalmykov and Kalmykov (2013, 2015, 2016) establish reasonable doubt about if the “biodiversity paradox” has been really resolved by these authors.

We could guess that, perhaps, the win-win solution via QEU renders meaningless to all of the subsequent arguments about the “biodiversity paradox”. But this is good news instead of bad: the goal of science is resolving problems once and for all instead of

keeping never-ending running arguments; unless one is interested in maintaining the controversy in order to artificially keep alive a hackneyed topic for the sake of keeping open its publication window forever and ever.

3. Fragmentary understanding about the principles that support QEU, and incomplete review of the literature that sustains the proposal criticized by Kalmykov and Kalmykov (2016)

The “gedankenexperiment” proposed by Kalmykov and Kalmykov (2016, p. 3) to refute QEU is unrealistically restrictive due to several reasons: (a) A beetle that is in hibernation is transiently “offline” from its ecological network, so it has no “ecological behavior” at all because its participation in the flow of energy tends to 0. (b) “One person as an observer vs. one beetle as a target of observation” is an observation without the statistical nature of any scientific observation in ecology or in statistical mechanics and quantum mechanics. (c) A valid quantum observation always implies the interaction between two different scales of nature (i.e.: a classical observer vs. a quantum system that is observed). The observation produces a collapse (quantum decoherence) of the superposition state of the wave packet of the quantum system, by randomly displaying only one of the many possible simultaneous states in which the quantum system exists when it is not under observation. A suitable and very general example involving the whole of these traits is analyzed by Rodríguez et al. (2015a, Section 4.3.3), but Kalmykov and Kalmykov (2016) do not issue any comment in this regard. (d) QEU cannot be based on the complementarity between coordinates and momentum because the concept of ecological niche is functional instead of structural. So we applied the well-known approach to the ecological niche concept like an n -dimensional functional hypervolume (see Hutchinson, 1957) in the particular case in which $n=2$ = a 2D scalar field that depends on absolutely universal ecological indicators (H_p and E_{ep}) because no any species can live either completely isolated or without a flow of energy. So the fulfillment of QEU is very general. For example, the data analyzed by Rodríguez et al. (2015a,b) were obtained from surveys distributed in space in a lapse of time t that is negligible at the ecological scale. Contrastingly, Appendix A is based on data from a sequence of 25 surveys performed in the same area from April to October 2010. From Tables B.1 and C.1, Appendix A, the observed (\circ) value of k_e is not different in comparison with the expected one ($p=0.559$ for rotifers, and $p=0.153$ for crustaceans). From Tables B.2 and C.2, Appendix A, the left side of the ESE is not different to the right side ($p=0.865$ for rotifers, and $p=0.319$ for crustaceans). From Tables D.1 and E.1, Appendix A, QEU is fulfilled even under these new circumstances ($r \sigma_{Hp}, \sigma_{Eep} = -0.769, p = 1.836E-12$ for rotifers; and $r \sigma_{Hp}, \sigma_{Eep} = -0.651, p = 3.202E-08$ for crustaceans), consistently with the assumption of ergodicity (Rodríguez et al., 2012).

A recurrent main condition in the proposal from Kalmykov and Kalmykov (2013, p. 210); Kalmykov and Kalmykov (2015, pp. 218, 220); Kalmykov and Kalmykov (2016, p. 3) is the assumption of “ceteris paribus” (“all other things being equal”). But it is well-known that the seemingly stationary condition of multitudinous complex systems at the macrostate level is sustained only because internally, at the microstate level, there are thousands of unremitting fluctuations to keep macro-stationarity, even when no any external or internal perturbation is acting on the system (see Schramski et al., 2007; as well as a detailed ad hoc analysis in Rodríguez et al. (2015b), pp. 172–174, an article indissolubly connected to the proposal criticized by Kalmykov and Kalmykov (2016) – but that it was not cited by these authors at all. It is a similar situation to that of

the hovering flight of a hummingbird: the bird has a fix position in the air, like a floating stone (a seemingly “*ceteris paribus*” condition if we look at the bird from afar), but it is only because the wing-flapping rate of the hummingbird is 50/s, and its heart frequency is 1260/min. The physical reason of this behavior is clearly understandable: in a similar way to the hummingbird, which is caught in the gravity field of Earth, any living system is constantly fighting against the pro-entropic influence of the second law that pushes it toward coordinates of information and energy in which there is not life at all. So, the system is trapped in a sort of “trophodynamic well” (like a ball within a basin). The only way to sustain a position far away from the bottom of the well is to keep a perennial oscillating orbital movement on the walls of the well.

The assumption of “*ceteris paribus*” is inextricably connected to the assumption about that “*the individual-based approaches are more appropriate for modelling mechanisms of interspecific competition*” (Kalmykov and Kalmykov, 2016, p. 3). However, this option was attempted in the dawn of modern physics to describe a system so simple (in comparison with ecosystems) as a small amount of gas starting from the values of mass, velocity and spatial coordinates of every molecule. But, due to the extremely high complexity of this approach and its infeasibility in practice, this option was discarded in favor of the statistical approach based on the concepts of macrostate and microstate or “complexions” that unremittingly fluctuate on the phase space of the system (see, e.g.: Brillouin, 1962; pp. 119–120; Callen, 1985; pp. 5–8). In such a sense, Kalmykov and Kalmykov (2015, p. 205) state that they use the individual-based approach “to solve the biodiversity paradox using our model of two-species competition in relatively small ecosystems”. However, the increase of species diversity (H_p , see above) is the most conspicuous spontaneous trend of ecological successions, and the case in which there are only two species is the closest situation to the condition in which $H_p = 0$ (i.e., when there is only one species and the concept of ecosystem is not valid). So, firstly, the phrase “relatively small” is not exact; it should be replaced by the word “elementary”. Secondly, what would happen if we pass from this constrained theoretical context to a real system in which tens, hundreds or even thousands of species coevolve by involving large groups of organisms per species under natural circumstance that fluctuate in space and time? The most plausible response is that, by using the individual-based approach, it would be very difficult to obtain a reliable pattern of the whole spectrum of probable trophodynamic microstates of a large set of species.

The final reformulation of CEP, transformed into “principle of competitive coexistence” by Kalmykov and Kalmykov (2016, p. 3), states that “if competitors always have access to all necessary

resources and all have the ability to use them, then, all other things being equal and without a global catastrophe, they will coexist indefinitely”. This statement is a tautological truism: *competitors do not compete with each other when there is no reason to compete*; fortunately (because, on the contrary, evolutionary changes would be quite unlikely since competition is one of the main biotic selection pressures in ecosystems), this special circumstance is quite uncommon in nature.

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.2016.09.014>.

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