Exploring the analytical consequences of ecological subjects unwittingly neglected by the mainstream of evolutionary thought

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A B S T R A C T

The Darwinian interpretation (Di) of evolutionary process, and its subsequent development in the form of modern evolutionary synthesis (MES), plays a paradigmatic role in the mainstream biological thought. However, the main role in the improvement from Di to MES has depended on population genetics. Conventional ecosystem ecology has added relatively few specific insights to this endeavor in spite of the well-known combined selective influence from environment. This article integrates i) recent findings in genetics (i.e.: evolutionary capacitance); ii) orthodox topics as well as recent results from a large set of models in ecosystem ecology which have recently been encompassed under the term “organic biophysics of ecosystem”; and iii) an epistemological analysis of the origin of On the Origin of Species. … by reaching four main particular conclusions: (a) Despite the contemporary recognition that any kind of interspecific relationship has an evolutionary influence, the analytical emphasis of Di and MES on competition has been unwittingly oversized because of the paradoxical manner in which mutualism can emerge as an essential evolutionary force starting from competition, being this an unquestionable topic that is analyzed in this manuscript by the first time. This link between two interspecific relationships that seem opposite to each other at the first glance is based on quantum effects that are totally unknown in conventional evolutionary theory due to its bias in favor of genetics, neglecting ecological considerations by contrast. (b) A holistic combination of ecological, genetic and evolutionary insights at the ecosystem level additionally confirms that the analytical role of evolutionary gradualism has also been oversized. (c) The main criterion of evolutionary success conventionally applied by Di and MES should be modified given that: (d) the preferential direction of evolutionary process theoretically proposed by Di and MES does not match with the direction of spontaneous development of natural ecosystems. The final section of this manuscript explains that these four critical outcomes in regard to Di and MES seem to have their root in epistemological inaccuracies involved in the origin of On the Origin of Species…that have been passed from generation to generation without being subjected to interdisciplinary scrutiny. This article showcases the need to review some of the foundational principles of Di and MES before building a “new floor” (i.e.: the extended evolutionary synthesis) supported on our current perspective about the evolutionary process. So, contrasting this with the genocentric nature of conventional evolutionary theory.

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1. Introduction

Every science oscillates around a paradigm that stabilizes its theoretical framework at the same time that favors a variable degree of conservatism (Kuhn, 1962). Darwinism (1859), and its subsequent improvement by the modern evolutionary synthesis (MES; Huxley, 1942; Mayr and Provine, 1998), plays this role in biology. However, there is a general bias in favor of considering the most of our current knowledge as immutable (De Broglie, 1962, p. 30). Hence, it is essential to select the most appropriate moment and direction to adjust every paradigm. “Extended evolutionary synthesis” (EES; see Pigliucci and Müller, 2010; Danchin et al., 2011; Laland et al., 2015) is the latest attempt of MES readjustment which incorporates recent findings in this field. The most of these findings are phenomena connected with extra-DNA inheritance (i.e.: ecological inheritance – niche construction-, epigenetic inheritance, heritable parental effects, and the inheritance of cultural traits) also known as “soft inheritance” (Dickins and Rahman, 2012). EES is not in contradiction with the main principles that support MES. EES only harmonizes some recent genetic discoveries with a well-known paradigm, neglecting (once again) some ecological phenomena (both old and new) with a strong potential influence to modify our traditional point of view about the evolutionary process.

Di and MES can be compared with an unbalanced table with three legs: i) That the habits, morphology and physiology of species change over time. This is a very old idea from the times of some pre-Socratic Greek philosophers (Kirk et al., 1983). ii) That the above-mentioned variations have a hereditary origin at the population level which has been deeply investigated for many decades after Darwin, because its nature was completely unknown in 1859. This second leg has absorbed the main effort of the most gifted minds in this field to the detriment of the third leg, iii) That, due to a chronic scarcity of environmental resources in a relative manner to the biotic potential of species, there is a constant struggle for existence (i.e., biological competition). So, the environment selects those individuals that are the most appropriate to survive because they produce more abundant offspring that is the fittest one because it has a higher probability to survive. The latter one is an essentially tautological analytical borrow from Malthus to Darwin (see item (b), Section 5.2) that was performed in times when ecology did not even exist as a science. As a result, this third leg has remained atrophied from the very beginning because, on the one hand, there is a general tacit opinion about the meaning of natural selection (NS): It simply means that environment selects, period. On the other hand, most of the ecologists seem to be so focused on developing a specialized ecology, that they have been paying relatively little attention to the evolutionary meaning of some old as well as new results from the research in ecosystem ecology.

Consequently, there is still a wide gap between evolutionary and ecological disciplines, despite progresses in eco-evolutionary dynamics (see Pelletier et al., 2009). Indeed, ecological and evolutionary phenomena share a similar time scale in some processes. As a result, a neat distinction between macroevolution, speciation and microevolution is difficult to set in practice. However, there is a consensus about that macroevolution embraces everything above the species level. Thus, the epistemological usefulness of species concept (the most objective taxonomic category) is relegated to somewhere in between micro and macroevolution. If evolution never ceases to occur in natural systems which embrace abiotic selection pressures as well as biotic selection pressures (many concurrent species), then there is no reason to segregate ecological factors from evolutionary factors (Matthews et al., 2011).

This article explores a tortuous and branching interdisciplinary path starting from two main issues which, in the first instance, are only used as starting points: evolutionary gradualism (EG) and the conventional criterion of evolutionary success (CCES). EG and CCES are analytically compared with recent results of a set of interdisciplinary models of ecosystem functioning (i.e.: organic biophysics of ecosystems; additional explanations in Section 2), whose meaning is synthetically exposed in order to facilitate the understanding of their evolutionary implications. The aim of the above-mentioned comparison is to assess if some intermediate modifications between MES and EES could be suitable, or not. These intermediate modifications suggest a change of our current point of view of the concept of transitional form, by introducing a novel cause-effect relationship between competition and mutualism. In addition, it is analyzed how this cause-effect relationship is linked to non-gradual mechanisms of evolutionary change based on quantum ecological effects that allow species coexistence, understood in this case as the main evolutionary force. Several empirical examples that support the above-mentioned ideas are included. We also perform a plausible theoretical exploration of an eco-evolutionary mechanism equivalent to quantum tunneling in order to explain the non-gradual transition between successive taxocenes, mainly at the macroevolutinal scale. The article also explores the historical origin of some pending problems in evolutionary theory in order to achieve a more integrative eco-evolutionary synthesis. This synthesis is based on an interdisciplinary framework that has been theoretically exposed and empirically proven in ten previous articles. Finally, we summarize the meaning of our most general outcomes.

As a result, our proposal is a sort of “reverse engineering” of evolutionary theory through ecosystem ecology. This is a parallel path which, from our point of view, has been undervalued so far. In summary, this article indicates that important items of our current evolutionary thought can be improved if we take into account some results from the investigation in ecosystem ecology.

2. To leap or not to leap. conventional doubts about EG, and the combined meaning of two relatively recent findings

Dekkers (2005, p. 170) makes a list of 11 theses that support Darwinism and, therefore, MES itself. Gradualism is, perhaps, the most contentious issue within this complex set of theses (i.e.: “...the process of modification must be extremely slow. The variability of each species is quite independent of that of all others —Darwin, 1859, p. 314—...” As natural selection acts solely by accumulating slight, successive, favourable variations, it can produce no great or sudden modifications; it can act only by very short and slow steps. Hence the
canon of *Natura non facit saltum*, which every fresh addition to our knowledge tends to make more strictly correct, is on this theory simply intelligible. . . . But why this should be a law of nature if *each species has been independently created, no man can explain*” —Darwin, 1859, p. 471).

EG has been regarded as controversial from the very beginning, even on the part of an unquestionable follower of Darwinism: “the only objections [in regard to ‘On the Origin of Species. . . .] that have occurred to me are 1st that you have loaded yourself with an unnecessary difficulty in adapting *Natura non facit saltum* so unreservedly. I believe she does make small jumps — and 2nd it is not clear to me why if external physical conditions are of so little moment as you suppose variation should occur at all” (Huxley, 1859). Such reserves have lasted till present time (e.g., Levit et al., 2008, pp. 74–75; Theisen, 2009; Gamberele-Stille et al., 2011).

The comment from Thomas H. Huxley (1825–1895) can be considered the starting point for the emergence of a plethora of non-gradualist evolutionary approaches: (i) Macromutation theory (Willis, 1923). (ii) The sudden emergence of “hopeful monsters” (Goldschmidt, 1940; Dietrich, 2003). (iii) The conventional view of “quantum evolution” as a drastic all-or-none shift (tachytely) in the adaptive zones by including unstable transitional forms that perish rapidly to be replaced by new taxonomic units of a higher rank (Simpson, 1953). (iv) The more gradual than the former ones, but also more sudden than the MES, “punctuated equilibrium theory” (Gould and Eldredge, 1977). (v) The observation, under conditions of high environmental stress, of non-random directed mutations or “adaptive mutations” (AM). (vi) AM was quickly followed by the proposal of quantum effects that could produce sudden variations by switching the genome from a situation of coherence (quantum superposition of underlying alternative states) to a situation of decoherence in which only one of the states is the favored one to promote an AM (Oryzko, 1997; McDafden and Al-Khalili, 1999; Davies, 2004). Finally, in a sort of intermediate position, (vii) the concept of partially-directed evolution (PDE) has been proposed (Melikikh, 2005, 2008, 2014a,b, 2015; Melikikh and Khrennikov, 2015). According to PDE, the exponential emergence of genomic variants is only possible if a priori information about the system future state is available just in the moment of an evolutionary leap. With a priori information (it is not completely clear by the moment how this apriority could emerge) evolution would be partially-directed, reaching a more balanced interaction between genetic and environmental factors in comparison with MES.

Starting from these synthetic explorations of conventional trends either in favor of EG (MES) or against it (from item (i) to (vii)), it is clear that ecology has very little or even nothing to “cook” at the first instance, since the environment only selects from the genetic menu (aka “genetic determinism” or “genocentric nature of MES”; see Balari and Lorenzo, 2009; Depew and Weber, 2011; Krimsky and Gruber, 2013). NS is thus strictly contingent; it has neither goals nor a preferable direction. As a result, NS is not striving to produce any kind of progress or any sort of functional balance between concurrent species within an ecosystem, since this goal would directly clash with the Darwinian assumption that “each species has been independently created” (see above). Contrastingly, Sections 4, 5.1 and 5.2 in this manuscript include evidence indicating this lack of a goal is not exact from an interdisciplinary point of view.

The factor that hinders a reliable alternative to EG is the following one: MES is the fusion between external evolutionary forces (i.e., Darwinian NS) and internal evolutionary forces (i.e., Mendelian inheritance extrapolated to the level of population genetics starting from the statistical contribution of Fisher, 1930). This fusion results in an inextricable connection between the genetic material and its environment. So, if an evolutionary approach implies some kind of quantum or discontinuous behavior in regard to genetic material, then the same discontinuous or quantum nature should be observed regarding some traits of environment itself. Any of these two sides is weak without the other one given that “organism and environment are both causes and effects in a coevolutionary process” (Lewontin, 2000, p. 126). However, conventional eco-evolutionary theory has not found evidence about the discontinuous or quantum nature of biotic environmental changes as yet.

Nevertheless, the combination of these two recent findings can shed certain clarity over the darkness that rules in this corner of theoretical biology. Evolutionary capacitance (Bergman and Siegal, 2003; Kim, 2007; Masel and Siegal, 2009; Masel, 2006, 2013) is the first finding. Evolutionary capacitance means the storage and massive sudden release of variations (as a dam wall that retains more and more water behind it until reaching a breaking point) that have remained “hidden” due to the capability of living systems for accumulating genetic modifications without obvious phenotypic effects (i.e.: genetic robustness). However, when the system is disturbed by stress (e.g.: starvation, irregular abiotic environmental changes, sudden increment or decrement of biotic selective pressures), genetic robustness breaks down and variations have phenotypic effects being subject to the full force of NS. A molecular switching mechanism can act like an evolutionary capacitor that “toggles” genetic variation between hidden and revealed states, in a similar way to the process of quantum decoherence commented above in regard to AM. If some subset of newly revealed variation is adaptive, it becomes fixed by genetic assimilation. After that, the rest of variations, most of which is presumably deleterious, can be switched off, leaving the population with a newly evolved advantageous trait, but no handicap in the long term. This mechanism allows rapid adaptations to new environmental conditions by helping to cross “gullies” in the fitness landscape, where a combination of two mutations would be beneficial, even though each is deleterious on its own. Obviously, the influence of evolutionary capacitance is difficult to insert into the theoretical landscape of MES if we are strict followers of EG.

The second finding is the granular or discontinuous nature of ecosystem functioning, either at the non-stationary evolutionary time scale (see h from below) or at the ecological (see h from below) stationary scale (Note: every horizontal arrow inserted between successive items below indicates that this is a cause-effect deductive sequence instead of a mere item list, and those vertical arrows associated to a given variable indicate either increase or decrease): (a) The ideal gas state equation (*IGSE*: $2N\frac{\sqrt{8mT}}{\pi} = N_k g_T$, or $2NE = N_k g_T$; where $N$: number of molecules, $m$: molecular mass, $v$: molecular velocity, $k$: Boltzmann constant, $T$: absolute temperature, and $E$: molecular kinetic energy) can be homeomorphically transformed into an ecological state equation (*ESE*: $2N_p \frac{\sqrt{m_{ep}l^2}}{\pi} = (N_p k) H_p$, or $2N_p E_{ep} = (N_p k) H_p$, where $N_p$: total number of individuals per plot ($n_p$); $H_p$: measure of information amount of Shannon – 1948—commonly used as species diversity index in ecology; $E_{ep}$: average individual value of the classical eco-kinetic energy per plot as a proxy for trophic energy; $m_{ep}$: mean fresh biomass per individual per plot per survey in kg; $l$: dispersal indicator with equivalent statistical traits to those of physical velocity $v$ in *IGSE*; $k$: ecological equivalent of Boltzmann constant; see Rodriguez et al., 2012). (b) $E_{ep} = \frac{1}{2} m_{ep} l^2$ reaches an insurmountable limit at minimum $H_p$ values because of a deficit of $m_{ep}$ (i.e.: $m_{ep} l^2 \cdot H_p$: see the left edge of $H_p$ distribution in Fig. 1a). On the opposite edge of the gradient, $E_{ep}$ also reaches an insurmountable limit at maximum $H_p$ values because of a deficit of $l^2$ (i.e.: $m_{ep} l^2 \cdot H_p$: see the right edge of $H_p$ distribution in Fig. 1a). Meanwhile, in the intermediate zone of $\Delta H_p$: $(m_{ep} l^2 \cdot H_p)$, $H_p$. Thus, $m_{ep} \cdot l^2 \cdot H_p = \text{constant} = k = 1.3806540 E\psi$ eJoule · nat/individual; in which $\psi$ has a typical integer value ($-x$, . . . −2, −1, 0, +1, +2, . . .,+x) depending on $k$ implies the mean rate in which an individual exchanges $E_{ep}$ by $H_p$ throughout its dif-
different permutations within the functional space of a stationary ecosystem. 

(c) This biomass-dispersal trade-off in function of $H_p$ is consistent with the well know r-K selection theory in ecology (see MacArthur and Wilson, 1967; Pianka, 1970; Reznick et al., 2002): small-body organisms with high dispersal capability and high biotic potential ($r$) accumulates at low $H_p$ values, at the same time that the contrary phenomenon (K-strategists accumulation) takes place in the opposite edge of $H_p$ gradient (see Fig. 1a). As a result, $E_{ep}$ in stationary ecosystems is confined within a sort of “ecological box” ($\Delta H_p$). 

(d) Within this box, any fluctuation of $E_{ep}$ becomes a stationary wave, with a measurable value of ecological wavelength ($\lambda_e$) in practice (see example in Fig. 11 and 12, book I, Appendix A), that bounces forward and backward along $\Delta H_p$, similarly to 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., 2015a) that the increase of $E_{ep}$ is discontinuous or quantized at the microscale across the non-stationary evolutionary transitions between contiguous taxocenes at a rate of $h_{ke}^{ev} = 6.626069571 \times 10^{-1} \text{J} \text{ s}$ per every unit of $k_e$; being $h = 6.626069571 \times 10^{-34} \text{Js}$ the constant of Planck in quantum mechanics. According to this finding, any genetic variation with a successful phenotypic expression, in addition to its non-lethality due to morphofunctional issues, should have a trophodynamic effect higher than $h_{ke}^{ev}$ and approximately proportional to $h_{ke}^{ev} \times n$; being $n$ an integer number. 

(f) According to Rodríguez et al. (2015b) there is a local compensation (i.e., at the level of plot or small groups of plots) between $\lambda_e$, $m_{ep}$ and $l_e$ along the inhomogeneous internal environment of ecosystem. The observed $\langle \sigma $ mean value of the product of these variables (i.e.: $\lambda_e \times m_{ep} \times l_e$) yields a constant ($h_{ke}^{ev}$) whose mantissa, in a similar way to $h_{ke}^{ev}$, is statistically equivalent to Planck’s constant (see Fig. 1a), but with changing integer exponents in an equivalent way to $k_e$ (see the meaning of $\psi$, above) depending on the specific type of taxocene. In general, there is a trend to a constant coefficient $k_e/h_{ke}^{ev} = 208.366$ for any typical class of taxocene (e.g.: for marine microalgae: $\psi_{me} = -10$ and $\psi_{ske} = -13$; for corals: $\psi_{me} = -01$ and $\psi_{ske} = -04$; for marine tropical snails of rocky shore: $\psi_{me} = +00$ and $\psi_{ske} = -03$; for ruderal vegetation: $\psi_{me} = +02$ and $\psi_{ske} = -01$; and so on...). In such a way, the stable position of any taxocene is kept in a sort of evolutionary homeostatic plateau by the compensation between variables given by $m_{be} \times H_p = \text{constant} \times k_e$. 

(g) So, most of the principles of quantum mechanics, including the Heisenberg’s uncertainty principle itself (which has become quantum ecological uncertainty – QEU – in this new approach; see Rodríguez et al., 2015c), are valid to explain the most general functional traits of an ecosystem: when a species set have a high risk of intense competition (low standard deviation, $\sigma$) along the spectrum of a density distribution of $H_p$ values into a 2D scalar field $H_p$, $E_{ep}$ this risk is relieved by a simultaneous increase of $\sigma_{tep}$, and vice versa. In other words, if we have a 2D scalar field $H_p$, $E_{ep}$, when species are highly aggregated or “compressed” on the spectrum of $E_{ep}$ values (low $\sigma_{tep}$) they migrate to an expanded set of values of $H_p$ (high $\sigma_{tep}$) and, correspondingly, when species are highly aggregated or “compressed” on the spectrum of $H_p$ values (low $\sigma_{tep}$) they migrate to an expanded set of values of $E_{ep}$ (high $\sigma_{tep}$). This allows very high levels of species coexistence in high diversity ecosystems despite the underlying influence of interspecific competition, because the two main competition dimensions (species diversity and energy) are compartmentalized, and their respective levels of dispersion ($\sigma$) around the mean are alternative to each other instead of simultaneous. 

(h) QEU has an interesting collateral evolutionary effect due to the emergence of degenerate ecological states (DES; see Fig. 1b): a group of plots that combines individuals of different species which emerges in association with a noticeable peak of $E_{ep}$ when $\sigma_{tep} \to 0$ and $\sigma_{tep} \to 0$, avoiding in such a manner the negative effects of interspecific competition. That is to say, they differentiate their niches toward extremely high levels of $E_{ep}$, for the sake of avoiding negative effects of their close coexistence with other species in regard to the spectrum of $H_p$ values. The name of the set of proposals from item (a) to (h) is “organic biophysics of ecosystems” (OBEC). Conventional ecosystem biophysics deals with the influence of inanimate or lifeless physical factors on ecological systems. Contrasting, OBEC only deals with the dynamics of living creatures (hence the introduction of the term “organic”) analyzed as indivisible physical particles in a constant movement at the population scale within the ecosystem space.

According to Appendix B in Rodríguez et al. (2015c), the results explained in items (g) and (h) in the previous paragraph, as well...
as in items (i) and (ii) in the following one, are supported by a set of empirical field data that embraces 22 surveys belonging to 11 different taxacenes with a total of 1257 species and 88 653 611 individuals. 400 density distributions of $H_p$ values were calculated by Rodríguez et al. (2015c) starting from these original data. The total set of $H_p$ distributions included 5948 macrostates (categories or statistical classes of $H_p$ values), and 1577 of these macrostates deployed the emergence of peaks or extreme values (e.v. $\times \mathcal{X}_p: \{x(x+75\text{th percentile}) + (2 \times \mathcal{O}_c) \times ((x+75\text{th percentile}) - (x-25\text{th percentile}))\}$; where $\mathcal{O}_c$ is the outlier coefficient $= 1.5$ by default according to Dell Inc., 2015) of $E_{ep}$ (DESs). So, the random probability of DES's emergence was of approximately 26.513% (i.e.: $(1577/5948) \times 100 = 26.513\%$); with a mean number of 3.943 DESs per distribution of $H_p$ values (i.e.: $1577/400 = 3.943$). This summary means that, if we would consider items (g), (h), (i) and (ii) as “extraordinary claims” (by using the well-known statement from Carl Sagan), then these claims are supported by empirical evidence in a suitable proportion. In addition, these “extraordinary claims” have been issued under a new epistemological situation in which more complete and harmonic knowledge is used in comparison with the “unbalanced table with three legs” outlined in Section 1.

According to Rodríguez et al. (2015c, Fig. 7 and analysis in connection with it), DES emergence has two interesting traits: (i) The level of interspecific coexistence within a DES is so tight (i.e., several abundant species can coexist with each other in a DES within a narrow interval of species diversity – $\Delta H_p$: see caption of Fig. 1b), and the mean value of eco-kinetic energy is so high, that mutualism is the most likely interspecific relationship at the intra-DES level. In the opposite case, DES would be so unstable that they would literally explode in the case in which competition would be their typical internal interspecific relationship. So, competition is an underlying influence mainly useful to be avoided by species that are concurrent and/or collaborate with each other in order to get advantages in comparison with their ecological background. In such a way, mutualism would be, paradoxically, the main pro-evolutionary effect from competition, and evolution in clusters (additional comments in item 4, Section 5.1) would be a more reliable option than species evolution in isolation or independent from each other. This result is connected with the respective comment in the fourth paragraph of Section 1. (ii) The emergence of DESs is stimulated by the combination of high diversity levels and relatively low levels of total availability of eco-kinetic energy ($E_{tp} = N_p \times E_{ep}$, see variable meaning above). That is to say, the emergence of DESs does not depend on an additional input of energy given that the ecosystem is stationary, but it is a quantum response to stress situations, in a similar way to the factors that trigger AM and the phenotypic expression of evolutionary capacitance.

Human evolution itself can be regarded as suitable paleontological evidence in favor of item (i) and (ii) in the previous paragraph. About (i), Haile-Selassie et al. (2016, p. 6365, Fig. 1) offer reliable evidence of the coexistence of at least three and six early species of hominids 6 and 3.5 million years ago, respectively. About (ii), according to the savanna-based theory, early hominids were forced (directional selection) to adapt to an open savanna by walking erect on two feet by the stress derived from a climate change after they left forest areas that were in a process of retrogression (Dart, 1925; DeSalle and Tattersall, 2008, p. 113: “It was out of this climatic stress that the hominid family was born”). This is one of the most plausible explanations of human bipedalism and our subsequent evolution (Kortlandt et al., 1974; Curry, 2008; Ko, 2015). According to these authors, it is very probable that the replacement of forest by grassland went on by an intermediate fluctuating stage of intense ecological patchiness that mixed savanna areas with scrublands and forest plots, with the consequent increase of species diversity by edge effect. At the same time, the energy supply for our pre-bipedal ancestors starting from the consumption of their conventional resources began to dwindle. If we compare these circumstances with the above-mentioned combination of high $H_p$ and low $E_{tp}$ in favor of the emergence of DESs, it is easy to grasp that the hypothesis about that the emergence of our ancestors could have been linked with the emergence of DESs should not be regarded as a totally far-fetched assumption.

If we seek a simple mechanical simile in the quotidian world to grasp the emergence of DESs, the emerging lump of ice from the open mouth of a bottle where the water has frozen, would be a good model. So a certain group of mutualistic species “bounces”, leaping toward higher values of $E_{tp}$, for the sake of avoiding the negative effects of interspecifc interference that takes place at low levels of $E_{tp}$ and intermediate values of the spectrum of $H_p$ (see Fig. 1b). If this “excited” subgroup of species surpasses that transition limit in which $h_{kEp}^\text{E} \Rightarrow h_{kEp}^\text{Es}\Delta N$, and $k_{Ep}^\text{E} \geq k_{Ep}^\text{Es}+1$ it can stay irreversibly caught in a new adaptive zone to begin a forthcoming adaptive radiation. This effect of invasion/creation of new adaptive zones can be genetically supported by evolutionary capacitance. In this way, a new macro-evolutionary leap is triggered even without the necessity of geographic isolation and allopatry, because any DES tends to a state of functional isolation from its ecological background, even under sympatric conditions (see the space between dashed lines $-\Delta H_p = 827.505 - 87.303 = 740.202\text{Ja}$ in Fig. 1b, as well as additional comments in Rodríguez et al., 2015c, p. 100).

3. DESs’ emergence vs. the conventional criterion of evolutionary success (CCES)

At first glance, it seems that the emergence of DESs is not connected to either $r$-$K$ selection theory or to biotic potential magnitude (i.e.: reproductive success or “evolutionary fitness” of species) at all, because the trophodynamic direction in which a given DES emerges (vector $T_{DES}$ in Fig. 1b) is vertical and more probable at intermediate $H_p$ values. In other words, the highest DES emerges neither at the $r$ nor at the $K$ edge of the distribution of $H_p$ values (see coincidence between DES and $H_p$ in Fig. 1a and b). So, the only role of $\Delta H_p$ would seem to be to promote an ecological potential difference to stimulate the emergence of DESs. However, this is an illusion from our static study (from a quasi-stationary state to the next one) of a dynamic process. Conversely, it is well-known (Margalef, 1963; Odum, 1969) that ecological successions slowly advance from low to high species diversity values (see vector $E_{sp}$ in Fig. 1b). As a consequence, the resulting direction of emergence of DESs is vector $E_{tnv}$ in Fig. 1b. In other words, under conditions undisturbed by man nature spontaneously selects, either at the interspecific level or at the population level (Note: all the individuals of the same species included in Fig. 1a and b belong to the same population), in favor of $K$-strategists. That is to say, in favor of species with larger bodies (rule of Cope, 1896), lower metabolic rates (i.e., lower values of $E_{tp} = (N_p \times m_{Ep})$=caloule per kg), higher energy budget ($E_{tp}$) per individual, and less investment in reproductive activity (see Fig. 1a). As a result, variations in favor of $r$-strategists are not favored by natural ecological successions at the large scale.

This evolutionary choice is easily understandable: $K$-strategists are more savers of energy per unit of biomass than $r$-strategists. Thus, this selection direction facilitates coexistence (higher species diversity values, i.e., a higher accumulation of ecological information in order to reach a better control on the internal environment of ecosystems) in comparison with a selection in favor of $r$-strategists. Simply and plainly, it would be thermodynamically unsustainable, due to the expensive metabolism of $r$-strategists, to reach high levels of species coexistence without a net evolutionary drift from
543; Dekker, 2005, p. 111; Barker, 2009, p. 4) and the connection between biomass-dispersal trade-off (an ecological phenomenon) and r-K selection theory (an evolutionary phenomenon), it seems to be a little contradictory to state that the whole evolutionary process is a progression toward less successful evolutionary positions (from r to K) only because almost any species of recent evolution has a lower biotic potential than species of bacteria that are at the root of evolutionary tree. So, according to the general trend of ecological successions, natural evolution goes in one direction (r → K), whilst according to the CCES it should go in the opposite one (K → r).

This paradoxical relationship seems to be mirrored in the problem about the eco-evolutionary balance between competition and mutualism; the former one (a relationship ←→ at any scale, either at the intra- or inter-population level) was enshrined by Darwin via Malthus as the key evolutionary influence in thesis (3) outlined by Dekkers (2005, p. 170). But the empirical observation of ecosystem evolution indicates that there is a net drift in favor of mutualism and protocooperation (both relationships of type +, +) across the successional process (see Odum, 1969, 1972) by favoring a survival strategy more based on commensalism than on struggle for existence (the cause ← effect relationship between competition and mutualism is analyzed in connection with the emergence of DESs in Section 2). If competition is the main promoter of evolution, then it would be expected that mutualistic species would have the lowest rate of molecular evolution; but the result of Rubin and Moreau (2016) does not support this analytical consequence. This result reinforces the result from Sachs and Simms (2006) about that parasites, as well as many non-mutualist taxa, are nested within ancestrally mutualistic clades. In addition, the strongest evidence in favor of granting a more prominent role to mutualism in our evolutionary thought is the emergence of eukaryotic cell starting from the association of microorganisms which previously lived in isolation from each other (Sagan, 1967); as well as the successful emergence of symbiotic organisms like lichens, corals, termites, leguminous plants, mycorrhizae, and the whole of superior animals with their respective normal microbial flora.

In addition, how is it possible to conciliate thesis number (6) of Darwinism outlined in Dekker (2005, p. 170: biogeographic distribution; i.e., that species occur close by related species) with the comment of Darwin himself about that “the variability of each species is quite independent of that of all others” (see original reference above) as well as with a theory predominantly focused on genetics at the population level. Contrastingly, the emergence of DESs used as carriers for evolutionary leaps is always the result of large groups of interacting species in their constant quest to avoid lethal levels of interspecific competition. This contrast has been regarded as a controversial point by many authors (e.g., Labandeira, 2002, p. 26; Margulis and Sagan, 2003, pp. 82–83; Teeling et al., 2005; Lanfear et al., 2010).

The concept of transitional form, due to its qualitative morphological nature, reduces its analytical importance in the eco-evolutionary context analyzed in this article. That is to say, a given organism could be conventionally regarded as a transitional form (e.g., Ichthyostega sp.; Acanthostega gunnari; Aurornis xui; Archosauromorpha: Archaeopteryx lithographica) because it is a mosaic of anatomical traits that belong to two border taxa. In contrast, let us suppose that any species regarded as a transitional form performs its ecological niche within an adaptive zone in which \( k_e = 1.3806504 \times 0.01 \times \text{natural/individual} \) and \( h_{\text{EC}} = 6.62606957 \times 01 \times \text{natural/individual} \), whilst its ancestral species occupy a more primitive but contiguous adaptive zone in which \( k_e = 1.3806504 \times 01 \times \text{natural/individual} \) and \( h_{\text{EC}} = 6.62606957 \times 02 \times \text{natural/individual} \). If this would be the case, then this species cannot be regarded as a transitional form from the point of view of OBEC. That is to say, the discontinuous increase of \( k_e \) and \( h_{\text{EC}} \) implies per se that the new species really belongs to...
a totally new adaptive zone, despite its anatomical intermediate traits in comparison with its ancestors and its further evolutionary
descendants. After all, the approach in this paragraph can be
empirically tested given that the ESE (see item (a) in Section 2), due
to its ergodic nature, results in a statistical equivalence of meaning-
between space and time (i.e.: that average values calculated from
data taken over time are equivalent to average values cal-
culated from data taken from space). Hence, the ESE can also be
applied to the ecological study of fossil record if we have data of
abundance and spatial position of fossils, in conjunction with
approximate values of body weight starting from paleontological
anatomical measurements.

4. Why is it so difficult to grasp remarkable signals of
evolutionary discontinuity starting from the observation of
current ecosystems? A plausible explanation based on field
data and very simple tests

Tables in books B, C, E and F (see Appendix A; sampling methods
and data origin explained in book A of the same Appendix) show
that the four taxocenes (planktonic rotifers and crustaceans from
inland water —rot” and “crust”, respectively--; and non-branching
corals and coral reef fishes of the Gulf of Mexico —“cor” and “cfr”,
respectively) involved in the analysis in this section are stationary
in themselves. That is to say, there are not significant differ-
ences either between the observed ($k_{a(c)}$) an the expected ($k_{e(c)}$)
value of the ecological equivalent of Boltzmann constant ($p_{ae}$,
rot = 0.559; $p_{ae}$, crust = 0.153; $p_{ae}$, cor = 0.242; $p_{ae}$, cfr = 0.345), or
between both sides of the ESE ($p_{ESE}$, rot = 0.865; $p_{ESE}$, crust = 0.318;
$p_{ESE}$, cor = 0.702; $p_{ESE}$, cfr = 0.434).

Fig. 2a shows the result of mean comparison between the
east and the right side of ESE, by combining data from two of the
above-mentioned concurrent taxocenes that are tropodynamically
contiguous to each other (rotifers —$k_{a}$ rot = 1.3806504E−05--; and
crustaceans —$k_{a}$ crust = 1.3806504E−04, i.e., $\Delta p = 1$ in $k_{a}$; see
results from the calculation of combined ESE in Appendix A, book D).
Fig. 2a indicates that a consistent equivalence ($p = 0.821 > 0.05$)
between both sides of the ESE can be attained by using a median
($\mu_{m}$) inter-taxocene value of $k_{em} = (1.3806504E−05 + 1.3806504E−04)/2 = 7.5935772E−05$.

Contrastingly, Fig. 2b shows the result of mean comparison
between the right and the left side of ESE, by combining data from
two concurrent taxocenes that are not tropodynamically contiguous to each other (corals —$k_{a}$ cor = 1.3806504E−01--; and
coral reef fishes —$k_{a}$ cfr = 1.3806504E−02, i.e., $\Delta p = +03$ in $k_{a}$; see
results from the calculation of combined ESE in Appendix A, book G).
Fig. 2b indicates that the calculation of ESE based on
$k_{em} = (1.3806504E−01 + 1.3806504E−02)/2 = 6.1015525E−01$
also yields an equivalence between both sides of the ESE in regard to
mean values ($p = 0.319 > 0.05$), but the difference between variances
is high and significant ($p < 0.00000001$). That is to say, the expected
mean value starting from ($N_{p} = 6.9101553E−01$)/$H_{p}$ “gobbles” the
observed one starting from $2N_{p}(\frac{1}{N_{p}}L_{p})$.

But this inclusion only takes place because the latter mean value is widely encompassed
by the variance of the former one. Even the two mantissas of mean values are very similar
to each other in Table G of Appendix A (i.e.: $2N_{p}(\frac{1}{N_{p}}L_{p}) = 7.269979$, and
$N_{p} = 6.9101553E−01$)/$H_{p} = 7.6320202$, only the exponent changes from +03 to +09.

This confirms that there is an eco-evolutionary “connection”
between both taxocenes (cor & cfr): the ecological coordinates in
terms of $E$ and $H$ of the set of plots of the taxocene with
the highest $k_{a}$ value (cfr) is a sort of “trophicdynamic expansion”
from the taxocene with the lowest $k_{a}$ value (cor). This “trophicdy-
namic expansion” takes place along a commonly shared axis that
keeps both taxocenes trapped in a same “eco-evolutionary poten-
tial well”, despite their non-contiguity from the trophodynamic point of view ($\Delta p = +03$ in $k_{a}$). This result explains why, despite
the ergodic nature of current stationary or quasi-stationary ecosys-
tems, it is so difficult to infer the “granularity” (non-continuous
nature) of evolutionary path of life from ecological observations.

Simply put, when we observe an ecosystem we are observing a full
spectrum of taxocenes supporting each other in a process of tropho-
dynamic expansion toward higher and wider adaptive zones along
the above-mentioned axis.

So, the trophodynamic continuum of any ecological observation
in the large scale (e.g.: the set of observations that Darwin
performed in his now famous expedition around the world) hides
the discontinuity and non-graduality of evolutionary processes.
The influence of top-down and bottom-up trophic cascades (e.g.,
Preiser 2003: Ripple and Beschta, 2012) is perhaps the main oppor-
tunity in which this eco-evolutionary continuity is clearly evident.
Trophic cascades show that by suppressing a single ecosystem ele-
ment a catastrophic or discontinuous change may occur.

5. Eco-evolutionary potential wells in connection with EG,
and the influence from the origin of On the Origin of Species
. . . on our current perspective about evolutionary processes

5.1. Eco-evolutionary potential wells, EG, and evolutionary
tunneling

This section offers additional insights about: (a) the meaning
of the concept of “eco-evolutionary potential well” and (b) the
influence of the above-commented eco-evolutionary overlapping
of taxocenes on the dominant paradigm regarding evolutionary
biology.

The top and ultimate scientific question is: why? Very fre-
quently, many scientific discoveries respond to how much, when or
how a set of phenomena and parameters behaves. The question of
why, due to its great epistemological difficulty, frequently remains
without an exact quantitative solution. In these cases, the best alter-
native is achieving a plausible explanation in the form of a simple
and engaging image. For example, in the atomic model of
Bohr (1913), the combination between the stability of electron orbits at
discrete distance from the nucleus and the exchange of energy (E) in
proportion to $\Delta E = \hbar \nu$ only when an electron jumps between orbits is
an instrumental axiom in order to gaining additional insights.
Given that quantum mechanics is a positivist approach, an explana-
tion about why nature is discontinuous or “granular” at the atomic
scale is not an indispensable requirement. However, the introduc-
tion of any sort of “granularity” in evolutionary theory by means
of pure postulates would be a little uncomfortable from the episte-
ological point of view. So, at least an appealing image is desirable.

Shelford’s law of tolerance (1931: that the success of any species
depends on certain minimum, maximum, and optimum values of an
environmental factor or combination of factors) is perhaps the
most conventional and well-known evidence about that species
are trapped in a sort of “ecological bowl” or “metabolic valley”.
That is to say, any species has a variable capability to live far away
from its most suitable surrounding conditions. But, sooner or later,
this “exploration” far away from its optimum has a high cost in
survival rate reduction. So the probability of survival is always a
maximum near to the optimum environment; as if a sort of “hidden
force” has been perpetually attracting organisms toward a given
eco-evolutionary position. In fact, if we invert (by calculating the
reciprocal of observed values) the typically unimodal curve of sur-
vival obtained from an environmental stress test performed on
any species, the result looks like a basin whose relative depth is
inversely correlated with the species’ tolerance. This law is so evi-
dent and pervasive that a theoretical generalization in this regard could have important analytical consequences.

For example, the biomass-dispersal trade-off in function of species diversity values commented in items (b) and (c) of Section 2 (i.e.: $m_{qp}^1$, $I_e^2$, $H_p$; $m_{qp}^1$, $I_e^2$, $H_p$; $[m_{qp}^1 \times I_e^2]$, $H_p$; and so $m_{e} \times I_e^2 \times H_p \rightarrow constant = k_p = 1.3806504e(\psi)$) indicates that a position near to $H_p$ under stationary conditions is highly suitable for the living creatures, because the value of eco-kinetic energy per plot ($E_{kp} = m_{qp}^1 \times I_e^2$) tends to a maximum at $H_p$ (see Fig. 1a and b). This has two main effects: (i) The living creatures of most species with an individual abundance equal to $N_p$ tend to $H_p$ (e.g.: the highest bar–maximum number of plots and individuals– in Fig. 1a coincides with $H_p$), producing an increment of total eco-kinetic energy per plot ($E_{kp} = N_p \times E_{kp}$) at intermediate values of species diversity. This explains the well-known unimodal or hump-backed curve or trophic energy in function of species diversity values (see polynomial fit in Fig. 3a, as well as additional comments in Rodriguez et al., 2013). (ii) The effect explained in item (i) increases the probability of high competition levels at $H_p$. The main response to relieve the mutually negative effects of competition is the emergence of DESS (Fig. 1b) that functionally isolates a group of individuals from their ecological background. As a result, a stationary ecosystem is externally constant in the large scale, at the same time that it is internally fluctuating and dynamic in the small one.

In other words, the species set of any ecosystem needs to keep a bubble of biological order that is held open by a mutual complementarity between $H_p$ and $E_{kp}$. This complementarity yields QEU ($\sigma_{H_p}$, $\sigma_{E_{kp}}$, and vice versa; see items (b), (d), (f), (g) and (h) in Section 2) within a surrounding cosmic ocean of entropy for the sake of avoiding high competition levels. This bubble keeps the organisms far away from a dangerous position at $H_p$ on the vertical and horizontal axis of the 2D scalar space $H_p$, $E_{kp}$. But, simultaneously and paradoxically, organisms also need to recurrently pass as close as possible to $H_p$ in order to obtain a “recharge” of energy that is essential to stay alive.

In such a way, organisms are trapped in a bidimensional potential well (like a moving ball within a bowl) in which a global reduction of $H_p$ under non-stationary conditions is associated to a global reduction of $E_{kp}$ or $E_{kp}$, and vice versa. QEU indicates that there is no notion of dependent and independent variable in this case. So, an orthogonal fit (dashed straight line in Fig. 3a) is a better option than a linear fit to get the most parsimonious view about the relationship between species diversity and eco-kinetic energy. The orthogonal fit is a linear regression that allows for measurement error in the independent $–x$– variables as well as the dependent $–y$– variables by assuming a feedback causal relationship $x \rightarrow y$; meanwhile the linear fit only allows for measurement error in $y$ by assuming a causal relationship $x \rightarrow y$ (for a graphical example see Appendix A, book H). This means that either the scalar space $H_p$, $E_{kp}$ (in Fig. 3a) or its transposition ($E_{kp}$, $H_p$; in Fig. 3b) yields an eco-evolutionary potential well with the shape of a remarkably sloped funnel with one of its corners pointing toward the origin of coordinates in which $H_p$, $E_{kp} = 0, 0$ (absence of life).

Let us combine the above-described scenario with the inter-taxocenes connection around a common trophodynamic axis (see comments about Fig. 2 in Section 4). As a result, a sequence of several adjacent taxocenes (i.e., a continuum from $\psi_{ke} = +02$ to $\psi_{ke} = +04$; data directly taken from Rodriguez et al., 2015b; Appendix B) represented into a trophodynamic scalar space $E_{kp}$, $H_p$ is a suitable example of the general trend of evolutionary process (see Fig. 3c). The dashed gray line with an arrowhead in Fig. 3c has been obtained by means of the logarithmic fit of minimum values of $H_{pM}$ and the respective values of $E_{xM}$ for every taxocene. It is easy to grasp that there is a direct correlation between $H_{pM}$ and $E_{xM}$ values, in such a manner that, when species diversity decreases, there is a general process of inter-taxocenes shrinking toward the area where the most primitive forms of life are dominant or, in the last instance, toward the point in which $E_{xM}$, $H_{pM} = 0, 0$.

That is to say, the wide end of the funnel in Fig. 3c is pointing in favor of the spontaneous net direction of evolutionary development, meanwhile the narrow end of the funnel indicates in the opposite direction: toward a pro-entropic attractor at very low levels of eco-kinetic energy and species diversity, placed just in the origin of life. Now we can think about biological evolution as myriads of organisms that laboriously climb the slopes of a valley (the funnel walls in Fig. 3c) in a constant struggle “against the force of gravity” (i.e.: the pro-entropic influence from the second law of thermodynamic that pushes toward $E_{xM}$, $H_{pM} = 0, 0$). At the same time that they are climbing, they are also trying to keep the position that have attained around a given value of $H_p$ without falling back down toward the attractor at the funnel bottom. That is to say, $H_p$ in Fig. 1 is only a local metastable attractor, sustained in its place by a particular intensity of energy exchange and QEU in the small scale, but with a net trend to drift toward $E_{xM}$, $H_{pM} = 0, 0$. 

![Fig. 2. Mean comparison between both sides of the ecological state equation (see “ESE” in the main text). (a) Comparison by combining data from two concurrent taxocenes (planktonic rotifers and crustaceans of inland waters) which are contiguous to each other from the trophodynamic point of view. Sampling methods in Appendix A, book (A), and data in books (B), (C) and (D). (b) Comparison by combining data from two concurrent taxocenes (corals and coral reef fishes) which are not contiguous to each other from the trophodynamic point of view. Sampling methods in Appendix A, book (A), and data in books (E), (F) and (G).](image-url)
Starting from the scenario described in the previous paragraphs, there are only 2 alternatives ways to evolve: (i) The walls of the eco-evolutionary potential well, in perfect agreement with our conventional thought about evolution (EG), are completely smooth, without any system of rungs or terraces to facilitate evolutionary escalation, as in Fig. 3c. This alternative would imply unstable orbits round the attractor at $H_p$, as well as a constant expenditure of large amounts of energy to sustain those orbits. But this option does not match with the principle that stationary states of open systems produce minimal entropy (Prigogine’s theorem; see Aguilar, 2001; Prigogine et al., 1972); (ii) The walls of the eco-evolutionary potential well, in agreement with the quantum or granular dynamics of ecosystems, are staggered (see Fig. 3d) in the small scale (in proportion to $h_{ee}^{ev}$) as well as in the large scale (in proportion to $k_e$ and $h_{ee}^{ev}$). This alternative does not have the drawbacks of option (i). In other words, the existence of large eco-evolutionary landings (depending on $k_e$ and $h_{ee}^{ev}$), with several intermediate small leaps (depending on $h_{ee}^{ev}$) inserted between them, facilitates a more stable evolutionary climbing with a lower consumption of energy. In terms of conventional evolutionary language, the most probable option is that the “evolutionary landscape” proposed by Wright (1932) should be more similar to the rice terrace cultivations in China than to the fields of drumlins with smooth slopes that are so common in Michigan, Minnesota and Wisconsin.

The dotted line in Fig. 3d has been drawn in a staggered fashion with didactical goals, but the most probable non-gradual progression from an eco-evolutionary landing to the next one is in diagonal (see vector Eco-ev $h_{ee}^{ev}$) in Fig. 1b, as well as for Fig. 1c, 3b and 4 in Rodriguez et al., 2015a). This would imply to cut across the wall that there is on the right side of every eco-evolutionary landing, instead of jumping on it. This imposes several challenges: (i) It is difficult to overcome the wall if it is too wide. (ii) It is difficult to overcome...
the wall if it is too high. (iii) Regardless the quantum energy push in favor of DES emergence for the sake of avoiding competition it is very probable that this push is not strong enough by itself to easily overcome the trophodynamic wall between two contiguous eco-evolutionary landings or adaptive zones. After all, the individuals of any proto-species still are within its primitive adaptive zone, instead of within the following new potential adaptive zone with higher energy values.

That is to say, it is necessary a particularly high value of eco-kINETIC energy to sustain an eco-evolutionary leap originally triggered by QEU, but this energy is available in the future adaptive zone instead of in the current one. So any proto-species is trapped in a sort of trophodynamic negative feedback: like the movement of a ball within a bowl, which transfers kinetic energy to potential energy in the same measure in which it is closer and closer to the bowl rim. This transference keeps the ball within the bowl forever and ever, because the ball can leave the bowl only with the help of an external input of kinetic energy received from outside. In the evolutionary case, this external input is in an adaptive zone that has not been invaded yet, and so on. . . So nature should have some additional “tricks” to drill the wall on the right of eco-evolutionary landings, breaking in such a way the above-mentioned negative feedback. A ball cannot “drill” the walls of a bowl (potential well) in the realm of classical physics; but in the realm of quantum mechanics a quantum particle can go across the wall of a potential well by tunneling effect (see, e.g., Razavy, 2014). The influence of tunneling effect is more and more important when the wall is thinner and thinner in a value closer to the wavelength of the particle, because the crossing probability tends to decrease exponentially with increasing barrier width for a classical wave-particle association (Eddi et al., 2009). The following paragraphs perform a semi-quantitative interdisciplinary exploration of the spectrum of potential “tricks” of nature in favor of evolutionary tunneling from an adaptive zone to the next one.

1) The ecosystem as an ecological wave packet: The species set of every ecosystem can be understood as a wave packet due to the superposition of several trophodynamic waves, each of them for every concurrent species (see, e.g., Rodríguez et al., 2015b; Fig. 6 f and g; as well as Rodríguez et al., 2015c, Fig. 9b to 9f). But it is well-known in physics that the segment of maximum probability of any wave packet becomes increasingly localized (narrower and with a higher peak; like the peak of DES in Fig. 1b) with the addition of more and more waves. So this physical effect is in favor of ecological tunneling, because it contributes to increase the module of vector Eco-evol$_{E}$ in Fig. 1b by simply adding more and more species to a single ecosystem. According to this insight, it is impossible at all that the variability of each species is quite independent of that of all others, just as Darwin thought. Thus, population genetics offers an oversimplified view of species evolution.

2) The ecological “phase problem”: It is well-known that, due to feedback processes in oscillatory systems, speakers output can become microphone input. This event produces a wave superposition, and the resulting sound is more and more loud -wave amplitude increase- and acute -wavelength decrease- until that the correlative spatial orientation of speakers and microphones is modified. The resulting sound from acoustic feedback is always shifted towards acute tones (a sort of chirp), because bass tones, due to their larger wavelength, have a higher probability of destructive interference with each other. Contrastingly, a perfect superposition state of 180° out of phase in space and time in regard to wave amplitude and wavelength in the case of acute tones is very improbable, precisely due to their shorter wavelength. So, acute and loud tones are the dominant output in feedback processes. Fig 11, Appendix A, shows that the emergence of resulting trophodynamic waves in Fig. 12 is due to wave superposition between oscillations of species richness and oscillations of species evenness (see also Rodríguez et al., 2015b; Fig. 1b). Thus, a destructive interference in this case would mean species disappearance. Nature seems to have resolved this problem by means of non-perfectly periodic waves similar to Maass forms (Maass, 1949), whose exact superposition is very unusual (as in Fig. 11, Appendix A; and Fig. 1b in Rodríguez et al., 2015b). However, this is not a mystery at all, but an obligatory consequence of the fulfillment of above-mentioned equalities (i.e., $m_{E} \times k_{E} \times H_{E} = \text{constant} = k_{E}$, and $m_{E} \times k_{E} \times \lambda_{E} = \text{constant} = h_{E} \text{c}$) within a non-isotropic ecological environment. That is to say, if $m_{E}$ and $k_{E}$ are not constant in space and time, then $\lambda_{E}$ must also be non-constant to achieve that $k_{E}$ and $h_{E} \text{c}$ are constant. However, the higher probability of destructive interference between bass tones remains as an underlying influence that is in favor of narrower trophic antinodes (lower values of $\sigma_{ep}$; see Rodríguez et al., 2015c, Fig. 1e2; as well as Fig. 11 in Appendix A of this article) and, therefore, in favor of higher local values of $\sigma_{ep}$ (DES emergence) at $H_{E}$ which are in favor to surpass the walls of eco-evolutionary potential wells.

3) Expectation as a trophodynamic factor in favor of ecological tunneling between contiguous adaptive zones: Expectation is the emergence of anatomical, functional and behavioral traits that evolve because they served one particular function, but subsequently they may come to serve another. For instance, temperature regulation was the initial function of bird feathers, but later on they were adapted for flight; arthropods were suitably pre-adapted to colonize land because their exoskeletons, pre-existing in water environment, provided support against gravity on land (for a deeper analysis, see Gould and Vrba, 1982). So, expectation is perhaps the most conspicuous manifestation of eco-evolutionary tunneling from an adaptive zone or eco-evolutionary landing $I_{2}$ to another adjacent landing $I_{2}+1$. That is to say, if a given organism A uses a trait evolutionary developed within $I_{2}$ to increase its access to additional resources available at $I_{2}+1$, then this is equivalent to an input of energy “stolen” by A from $I_{2}+1$ to $I_{2}$, previously to the definitive evolutionary leap of A from $I_{2}$ to $I_{2}+1$. This extra energy, “surreptitiously smuggled” by A “below the wall of the potential well” can promote a successful evolutionary transition via DES between adjacent eco-evolutionary landings.

4) Quantum ecological tunneling and cluster evolution: The main theoretical principle of quantum tunneling in physics can be extrapolated to eco-evolutionary tunneling. According to Razavy (2014, p. 10), quantum tunneling in the realm of physics is a consequence of the fulfillment of Heisenberg’s uncertainty principle in regard to energy ($E \leftrightarrow t$) complementarity:

$$\sigma_{E} \times \sigma_{t} \geq \frac{h}{2}$$

(1)

where $\sigma$: standard deviation, and $h$: Dirac constant or reduced Planck constant ($h/2\pi$). Let us denote the background kinetic energy of a given quantum particle incident on the wall of the potential wall by $E$ (i.e. $\sqrt{m_{p} v_{m}}^{2}$; similar to $E_{\text{ep}}(\text{back}) = \sqrt{m_{p} V^{2}}$ in Fig. 1b). For a very short time $\sigma_{t}$, the corresponding uncertainty in $E$ is $\sigma_{E}$. Starting from Eq. (1), for sufficiently small $\sigma_{t}$ the energy of the particle $E + \sigma_{E}$ (similar to $E_{\text{ep}}(\text{back}) + [E_{\text{DES}} - E_{\text{ep}}(\text{back})]$ in Fig. 1b) is greater than the height of the potential well wall $V$, and tunneling takes place if in $\sigma_{E}$ the particle can traverse the wall. That is to say, a sufficiently-low value of $\sigma_{t}$ pushes the particle to overcome the wall of the potential well. Starting from previous comments about QEU, Eq. (1) in ecology becomes (see Eq. (14) and comments about it in Rodríguez et al., 2015c):

$$\sigma_{E_{\text{DES}}} \times \sigma_{E_{\text{ep}}} \geq \frac{h \text{c}}{2}$$

(2)

So, the very principle commented above starting from Razavy (2014) is valid in ecosystem ecology: the “evolutionary momentum” of a given individual or group of individuals to invade a new
adaptive zone depends on the successive alternation of sufficiently-low values of \( \sigma_{\text{HMP}} \) (i.e., high values of \( \sigma_{\text{EEP}} \)) and sufficiently-low values of \( \sigma_{\text{EEP}} \) (i.e., high values of \( \sigma_{\text{HMP}} \)). Taxocenes constantly oscillate along its harmonic spectrum as a whole (i.e., along the total sequence of density distributions of \( H_P \) values; Fig. 1a and b show only one of the possible results from a wide gamut of distributions). This constant oscillation is a strategy to avoid falling down toward the pro-entropic attractor at the bottom of the eco-evolutionary potential well, because the only way to sustain a position far away from the bottom of a basin is to keep a perennial oscillating orbital movement on the walls of the basin (see Rodríguez et al., 2016b, pp. 3–4). From Eq. (2), this strategy is based on a trade-off \( \sigma_{\text{HMP}} \) vs. \( \sigma_{\text{EEP}} \), and vice versa, that changes the module of vectors \( T_{\text{DfEP}} \) and \( E_{\text{S2}} \) in Fig. 1b. As a consequence, the resulting vector Eco–Evo1 đổi performs constant movements of battering ram (see \( T_{\text{R}} \) in Fig. 1b) in a sort of “drilling” of the potential well wall, as well as nodding movements (see \( n_{\text{R}} \) in Fig. 1b) in a sort of “exploration” by trial and error of the most suitable combination of coordinates, or the weakest point, to drill the potential well wall. This scenario matches with a vivid description on the part of Margulis and Sagan (2003, pp. 82–83) about the theory of punctuated equilibrium: “The small variations within species [of Cambrian trilobites] indicative of changing gene frequencies would oscillate back and forth . . . The appearance of new species and genera and the loss of old ones by extinction was always discontinuous.” The \( \sigma_{\text{HMP}} \leftarrow \sigma_{\text{EEP}} \) trade-off starting from Eq. (2) has two main additional outcomes: (I) QEU can be, besides an inescapable requisite for species coexistence under stationarity (see Rodríguez et al., 2015c), an essential tool to promote the evolution of species toward new adaptive zones under non-stationary conditions. (II) Since QEU lacks meaning in the absence of a large set of species (see the collinearity between \( H_{\text{DfEP}} \) and \( E_{\text{S2}} \) in Fig. 1b), then the evolutionary change of an isolated species should be a very unlikely event under natural conditions; being the simultaneous evolution of several species (i.e., cluster evolution) the most plausible alternative. As a consequence, it is plausible that species coexistence by itself should be regarded as the main evolutionary force.

5.2. The primordial influence from the origin of On the Origin of Species . . . on our current perspective about the evolutionary process

The previous sections indicate that there is an underlying bias in favor of gradualism, competition and reproduction in our evolutionary thought. This bias became even more complex and tortuous with the development of Darwinism toward MES. When Mendelian laws were added to Darwinism in an epoch in which ecology was in diapers, genetics “stole the show” at the population level (i.e., if there is a genetic at the ecosystem level, then it is still waiting to be discovered) by leaving all of the additional considerations regarding the evolutionary role of environment thrown into a dark corner of evolutionary theory. The majority of biologists would respond with a simple tautology to the question about “how does the natural environment ‘select’ an organism?” by stating that the environment selects “by selecting”, or that environment simply kills all the misfit individuals, period. However, some authors believe this is a too simplistic view of the facts (e.g.: “It is doubtful, however, whether even the most statistically minded geneticists are entirely satisfied that nothing more is involved [in the evolutionary process] than the sorting out of random mutations by the natural selective filter”; Waddington, 1942, p. 563).

All of the previous sections indicate that, if the environment is under the influence of physical constraints, then some issues could change in evolutionary biology. The probability of this eventuality is not null because some theoretical principles in this field are supported by experimental evidence which has been gathered far away from those real conditions in which DESs emerge. For example, experiments in which two species are forced to compete isolated from their interspecific ecological background (Gause, 1934a,b), experiments in which the tails of white mice were cut off in a lab along many generations in order to debunk the inheritance of acquired characteristics (Weissman, 1899), as well as observations at the population level performed under very particular natural conditions at the small and fragmented spatial scale (e.g., Grant and Grant, 2003; Podos and Nowicki, 2004; Kubel et al., 2007) whose conclusions are difficult to extrapolate to successfully explain the evolution of life at the continental and planetary scale.

The key point in this section is to perform a plausible epistemological exploration about why the origin of On the Origin of Species . . . could produce the above-mentioned primordial biases:

a) Regardless of the unquestionable talent of Darwin, even someone with an untrained eye can clearly see that species do not evolve rapidly, so gradualism seems to be the most rational option. Consequently, gradualism could have also been a solution of epistemological compromise chosen by Darwin in order to avoid analytical conflicts between his theoretical framework and natural reality. But evolutionary slowness in the large scale is not equivalent to gradualism, even if leaps are very small or variable in “length”. In a similar manner, previously to quantum mechanics, energy exchange was regarded as a continuous phenomenon until the discovery of Planck’s constant (\( h \), see above). But, despite its so tiny value (of the order of E–34), \( h \) radically changed the landscape of physics as a whole forever.

b) Darwin borrowed important cornerstones of his approach from social sciences: “Here then I had at last got a theory by which to work” (Charles Darwin by commenting about the idea of “struggle for existence” from the socio-economic approach of Malthus, 1803; cited in Darwin, 1888, p. 68); “as clear as daylight. I fully agree with all that you say on the advantages of H. Spencer’s excellent expression of ‘the survival of the fittest’. This however had not occurred to me till reading your letter” (Darwin, 1866; by commenting about a phrase proposed by the philosopher, anthropologist, sociologist, and prominent classical liberal political theorist Herbert Spencer). First, these are back-extrapolations just in the opposite direction of an evolutionary process in which Homo sapiens sapiens is one of the youngest species. Secondly, Homo sapiens sapiens is a very particular species. It is capable of handling large amounts of substance, energy and information at the exosomatic scale, at the same time that it is prone to amass prejudices of many kinds (intelligence also has a dark side). We are also capable of killing other human beings due to some differences of prejudices. So, Homo sapiens sapiens is perhaps one of the most bellicose species on Earth, in comparison with other species that are more “pragmatic” and free of intellectual prejudices in regard to satisfy their biological necessities. As a result, many monospecific genera in nature include scarce species in danger of extinction. On the contrary, Homo sapiens sapiens is a notorious exception: it is the single species that has prevailed in its genus at the same time that it is notoriously abundant. The above-mentioned epistemological back-extrapolations explain the bias of Darwinism in favor of conflictive interspecific relationships (competition, predation, parasitism), in detriment of the evolutionary role of neutral or positive symbiotic relationships, as mutualism and protocooperation. So, this “anthropomorphization of natural species” that underlies in Darwinism only can account for a fraction of the evolutionary landscape. Contrarily, as it has been commented in Section 2, it seems to be that the main role of biological competition is to be avoided, instead of to be reinforced: “I treat competitive exclusion as a central organizing concept in community ecology, though the relaxation, disruption, or prevention of interspe-
cific competition is probably the status quo in most communities” (Palmer, 1994, p. 552).

c) The terms “man's selection”, “artificial selection”, and “domestication” were used, as a whole, 48 times by Darwin (1859). The title of the first chapter of On the Origin of Species (1859, pp. 7–43) is “Variation under domestication”. The book that Darwin published after On the Origin of Species was “The Variation of Animals and Plants under Domestication” (Darwin, 1868). Darwin had a remarkable interest in domestication techniques. Artificial selection, as practiced by plant and animal breeders in the times of Darwin, seemed to offer a model about how speciation under NS may have taken place. Therefore, Darwin studied the work of cattle, sheep, and dog breeders; and many observations about the artificial selection of pigeons and plants were performed by Darwin himself. According to Campbell (1985, p. 150), one of the central themes of Darwin's Origin of Species is that changes in domesticated species are ultimately evolutionary in nature. The fact that artificial selection was an important background model for Darwinism has been commented by many authors (e.g.: Mayr, 1982; Bartley, 1992; Bidaux, 2009; Bowler, 2009; Driscoll et al., 2009; Gregory, 2009; Purugganan and Fuller, 2009; Abeles, 2016). Starting from this solid historical background we must think about an issue that, although simple, it is not so evident. Any successful attempt of breeding with commercial goals needs to include as its main asset a species of plant or animal with the following traits: (i) tolerance to overcrowding; (ii) fast ontogenetic development; (iii) resistance to diseases derived from living in isolation from the rest of species; (iv) great plasticity to adapt to a wide diversity of potential environmental conditions in the large scale, as well as to seasonal variations in the small one and, chiefly; (v) abundant and very frequent offspring. So, most of the species domesticated by man are, in the first instance, r-strategists which have been genetically improved by artificial selection later on by adding only one trait typical of K-strategists: larger body size. In hyperbolic terms, the ideal breeding species should have all of the ecological traits of a fly and the body size of an elephant. In such a manner, domesticated species are “evolutionary monsters” whose self-sufficient existence is very unlikely in the wilderness, because any attempt of breeding is an effort to establish a trophodynamic loop by unifying the two opposite edges of $H_p$ distribution in Fig. 1a. But such a loop is impossible at all under natural conditions, because this would mean to close the eco-evolutionary potential well in Fig. 3c and d. In addition, the existence of domesticated species needs to be subsidized by man from the energy point of view. Besides, any breeding attempt requires isolation from other species to avoid economic yield reductions due to the infiltration of selection pressures from nature, and this means impossibility of DESs emergence. Finally, the above-mentioned combination of energy subsidiation + population isolation + productive yield expansion leads to the settlement of non-indigenous species, simultaneously to the eviction of wild species from their natural environment and, ultimately, to its massive extinction with the consequent lack of sense of the term “natural selection”. In summary, Darwin embraced a remarkably anti-evolutionary framework as the paradigmatic model to try to understand natural evolution, and this explains his bias in favor of reproductive success of species as the essential criterion of evolutionary success. As a result, a different criterion of evolutionary success probably based on the combined capability of species to handle larger amounts of energy (see Peacock, 2011) and information per individual is urgently needed. Margalef (1992, pp. 221–223) was a precursor in this regard. According to him, species should be classified along a spectrum from species of immediate response to species of deferred response. Species of immediate response are those whose adaptive response depends on massive reproduction at the population level; extreme examples: the bacterium Escherichia coli, with a generation time of 20 min; or the bacterium Pseudomonas putrefaciens with a generation time of 8.9 min (Eagon, 1962). On the contrary, species of deferred response are those whose adaptive response depends on individuals with a large energy budget and a long life cycle that allows gathering a significant amount of information about the way of functioning of their environment; extreme examples: whales, elephants, and human beings. For a well-trained ecologist, it is evident that evolution has a spontaneous drift in favor of species with deferred response, instead of the opposite (CCES).

6. Concluding remarks

According to this article, there are several topics with a pervasive influence on the principles of conventional evolutionary biology which should be rescanned: (a) the relationship between EG and complementary options based on evolutionary capacitance and the quantum nature of ecosystem dynamics; (b) CCES and its relationship with r-K selection theory in ecosystem ecology; (c) the eco-evolutionary role and meaning of the concept of transitional form; (d) whether species evolve in sets (cluster evolution) or isolatedly from each other; (e) if evolutionary theory can remain centered in population genetics or not; (f) the influence of interdisciplinary links of evolutionary theory either with other branches of biology (i.e., with ecosystem ecology) or with other disciplines (i.e., with physics); (g) the cause→effect relationship competition→mutualism; (h) the parallelism between four well-known events that take place during evolutionary transitions and the respective number of processes typical of quantum tunneling; and (i) if the selection by Charles Darwin of breeding practices as an analytical background model to develop his model of natural evolution was a suitable choice, or a ballast, for the future development of evolutionary theory.

However, the issue that acts as the analytical axis of this conundrum is of epistemological nature rather than of biological nature: it is probable that our current evolutionary paradigm has been infiltrated by inaccurate theoretical interpretations from the very beginning. It is appropriate adding to this situation the seemingly passive or isolated behavior of conventional ecosystem ecology in regard to the analytical structure of evolutionary theory. In addition, the birth of evolutionary theory in an epoch in which ecology was not regarded as a science at all (despite NS has been an essential element of evolutionary biology from the very beginning) did not contribute to develop a more solid proposal. Thus, we have there the hidden root of a fragmentary model which, paradoxically, has been passed from generation to generation without being subjected to a deep interdisciplinary scrutiny.

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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.2017.03.029.