



## Uncertainty principle in niche assessment: A solution to the dilemma redundancy vs. competitive exclusion, and some analytical consequences



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### ABSTRACT

There has been a categorically unresolved crucial question in ecology and evolutionary theory for many decades; perhaps from the times of Charles Darwin himself: Is it possible, under natural conditions, that two species can perform a commonly shared ecological niche? There are two extreme conventional responses that have kept divided the scientific community in this regard for almost forty years: (a) No; that is to say, the well-known competitive exclusion principle (CEP). (b) Yes; that is to say, the well-known hypothesis of full functional redundancy (HFR). Obviously, the reliability of both responses depends on an underlying and even more essential requisite: that the ecological niche of a given species can be assessed with such accuracy as we could want in order to detect the degree in which it is shared between coexisting species. This article is the seventh in a continuous series of interconnected recent publications that promotes an alternative understanding of ecology and evolutionary biology which is in favor of strong and mutually fruitful analytical links between biology and physics. This article analyzes the statistical behavior of ecological niches by taking into account two indicators that are essential to perform the ecological niche of all species: species diversity per plot ( $H_p$ ) and eco-kinetic energy ( $E_e$ ) as a proxy for trophic energy in a scalar field  $H_p, E_e$  in which an oscillating performance of ecological niches is deployed. According to our results, in the same measurement in which the accuracy of  $H_p$  assessments increases (reduction of  $H_p$ 's standard deviation:  $\sigma_{H_p}$ ) the accuracy of  $E_e$  assessment decreases (increment of  $\sigma_{E_e}$ ), and vice versa, in agreement with a pattern that is completely equivalent to that of the Heisenberg's uncertainty principle in quantum mechanics (i.e.:  $\sigma_{H_p} \cdot \sigma_{E_e} \gg 1/2h_e^{ec}/2\pi$ ; where  $h_e^{ec}$ : ecological equivalent of Planck's constant found in previous publications). As a result, the ecological niche is, even in principle in addition to in practice, indeterminable with enough exactness to arrive to a categorical response to the above-stated question. This means that CEP and HFR are simultaneously true and false in the same measure, because the only feasible option to keep the functional stability of ecosystems is a wave-like combination of both options: when species are pushed to a high degree of coexistence (increase of partition of the gradient)

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in regard to  $H_p$  values (a trend in favor of HFR), their degree of coexistence in regard to  $E_e$  values diminishes (decrease of partition of the  $E_e$  gradient, a trend in favor of CEP), and vice versa. The final sections of the article highlight the eco-evolutionary, biogeographical and socio-economic meaning of this result, by offering plausible alternative explanations to a wide spectrum of phenomena that appear to be only partially understood so far, e.g.: the contradictory results about the relationship between body size, species diversity and macroevolutionary rates; the general environmental scenario in favor of macroevolutionary leaps with a low probability to leave footprints in the fossil record; the unnecessary, although stimulant, influence of geographic isolation to promote evolutionary changes; the island rule; and the general meaning of the interaction between nature and society.

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## 1. Introduction

The conventional statement of competitive exclusion principle (CEP) holds that perfect competitors (complete niche overlap) cannot coexist (Hardin, 1960). CEP, or Gause's principle (Volterra, 1926, 1931; Gause, 1934a,b), dates back to The Origin of Species (Darwin, 1859), where it was already implicit (Hardin, 1960). The first explicit statement of CEP is attributed to Grinnell (1904). According to some authors, CEP is one of the most important laws in ecology and evolution (e.g., Hardin, 1960; Whittaker, 1965; Darlington, 1972; Gordon, 2000; Wang et al., 2005). In contrast, others believe that CEP is an oversimplification that contradicts observed reality, and its contribution to our understanding of nature is not commensurate with its degree of widespread acceptance (e.g., Savile, 1960; Ayala, 1969; den Boer, 1986; Stanley, 2008).

Certainly, close coexistence of similar species of plants (e.g., Shmida and Ellner, 1984; Hubbell, 1979, 2006; Silvertown, 2004) is, at least, paradoxical. One would expect such coexistence to be rapidly dissolved under the influence of CEP. If this dissolution does not occur in practice, then there is a hard argument against CEP. The need to explain this paradox has led to the hypothesis of functional redundancy (HFR or FR, hereafter). This hypothesis, as well as other approaches derived from it, such as the unified neutral theory of biodiversity and biogeography (Hubbell, 2001), offers alternative interpretations to CEP in an attempt to compensate for its apparent limitations. According to HFR, many species in the ecosystem act as spare parts for each other, providing information that is repeated and exceeds the amount needed to maintain the viability of the system (see, e.g.: Naeem, 1998; Rosenfeld, 2002a, p. 156). What really matters, from the point of view of HFR, it is the existence of functional groups: a group of species that are interlinked due to the equivalent exploitation of the same resource, the consumption of which is optional in other species, or humans. Thus the function of a given species that disappears is easily offset by another species of the same functional group (Naeem, 1998; Clarke and Warwick, 1998; Mistri et al., 2001). Functional groups with few species are more susceptible to extinction due to their low capability of internal replacement (Holling, 1986). Therefore, conservation of these functional groups must be a priority (Walker, 1992). As a result, FR has been equated to surplus of resources (see Lawton and Brown, 1993). FR could explain why changes in species diversity, within certain broad limits, do not change the essential functioning of the ecosystem; because there could be a total functional equivalence between species.

Despite the current influence of this debate (see Palma, 2010) its point of origin is very old, very important, as well as rooted in the deepest foundations of contemporary ecology (see Lewin, 1983). It is probable that several wide reviews (e.g., Rosenfeld, 2002a,b; Petchey and Gaston, 2006) and additional explanations based on inter-branches links in ecology (e.g., Mayfield and Levine, 2010) have drained the conventional viewpoint about this subject. However, since the debate continues, it seems to be that a more comprehensive alternative explanation could be suitable.

From time to time, an old scientific debate needs to be updated due to some recent findings that pose the same old question in a new perspective. This is the first objective of this article. From our point of view, the cornerstone of the debate HFR vs. CEP lies in a wider and deeper question. Since both trends (either HFR or CEP) have a common origin in responding if a given ecological niche can be performed in a shared way or not, respectively (this is one of the oldest questions in ecology), then the essential question that reflects the main objective of this article is the following: Is it possible to define in practice a given ecological niche in a way exact enough as to know if it is being performed in a shared way, or not? Besides, since an explanation based on physics could be little attractive to some biologists, the second objective of this article is to establish links, as abundant as possible, between our main results and well-known eco-evolutionary issues in order to support the usefulness of this approach for conventional ecological thinking.

Section 2.1 offers a theoretical panorama of recent findings that are used in Section 2.2 to expose the methodology applied. Section 3 exposes our main results in this regard. Sections 4.1 and 4.2 analyze the meaning of our results in order to answer the central question posed in the previous paragraph. If this response is *positive* (i.e., there is not uncertainty in niche assessment) the debate HFR vs. CEP will remain as so far, without a clear solution. On the contrary, if this response is *negative* (i.e., there is uncertainty in niche assessment), then the main conclusion is that this old and acrimonious debate is nonsense either because (a): the common-root concept (ecological niche) for CEP and HFR is, even in principle in addition to in practice, indeterminable with enough exactness to arrive to a categorical response; or because (b): the functional coupling between CEP and FR is the unique feasible solution to keep the stability of ecosystem functioning. Finally, Section 4.3 explores the consequences of our results by means of empirical examples and alternative explanations to well-known eco-evolutionary problems, in order to achieve the second objective mentioned in the previous paragraph. Albeit the core content of this article is exposed in Sections 2–4.2, Section 4.3 is perhaps the most interesting of all of them for the readers of this journal due to its strong connections with the classical point of view about ecology, evolution, biogeography and biological conservation.

## 2. Theoretical foundation and methods

### 2.1. An analytically evolving theoretical framework, including all the essential physical principles for ecologists

A branch of ecological analysis based on a greening of an old foundational proposal has grown in the last 3 years (2012–2015). That is to say, ecology can be understood, in the last instance, as a set of emergent properties starting from physics (see, e.g., Lindeman, 1942; Odum, 1968, 1969; Gallucci, 1973; Bugmann and Martin, 1995). So the essential traits of ecosystem functioning could be backward-assembled until reaching their primordial contact points

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