



Short communication

Effects of two traits of the ecological state equation on our understanding of species coexistence and ecosystem services



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ABSTRACT

Species coexistence has been a fundamental issue to understand ecosystem functioning since the beginnings of ecology as a science. The search of a reliable and all-encompassing explanation for this issue has become a complex goal with several apparently opposing trends. On the other side, seemingly unconnected with species coexistence, an ecological state equation based on the inverse correlation between an indicator of dispersal that fits gamma distribution and species diversity has been recently developed. This article explores two factors, whose effects are inconspicuous in such an equation at the first sight, that are used to develop an alternative general theoretical background in order to provide a better understanding of species coexistence. Our main outcomes are: (i) the fit of dispersal and diversity values to gamma distribution is an important factor that promotes species coexistence mainly due to the right-skewed character of gamma distribution; (ii) the opposite correlation between species diversity and dispersal implies that any increase of diversity is equivalent to a route of “ecological cooling” whose maximum limit should be constrained by the influence of the third law of thermodynamics; this is in agreement with the well-known asymptotic trend of diversity values in space and time; (iii) there are plausible empirical and theoretical ways to apply physical principles to explain important ecological processes; (iv) the gap between theoretical and empirical ecology in those cases where species diversity is paradoxically high could be narrowed by a wave model of species coexistence based on the concurrency of local equilibrium states. In such a model, competitive exclusion has a limited but indispensable role in harmonious coexistence with functional redundancy. We analyze several literature references as well as ecological and evolutionary examples that support our approach, reinforcing the meaning equivalence between important physical and ecological principles.

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1. Introduction

Species coexistence is a pivotal concept in ecosystem ecology since the late 1950s (see Hutchinson, 1959, 1961; Lewin, 1983; Palma, 2010). According to Tilman (1982, p. 3) “in his ‘Homage to Santa Rosalia’ G. E. Hutchinson posed what I believe is the most

fundamental question that an ecologist can address”. How can species coexistence and diversity be explained? Why is it so difficult to obtain a satisfactory solution to this issue? Without reliable answers to these questions the understanding of the forces that allow multiple species to coexist remains a central focus of community ecology (Lankau, 2011). The empiricism in this regard, which was early analyzed by Hurlbert (1971), is still partially unresolved (Rossberg, 2008).

The search for a definitive answer has led to a debate between the competitive exclusion principle (CEP, one species ↔ one niche: those species that perform the same ecological function cannot coexist; see Hardin, 1960; Darlington, 1972; Gordon, 2000; Wang

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et al., 2005) and the hypothesis of functional redundancy (HFR, several species ↔ one niche). For some authors the CEP is, either explicitly or implicitly, an over simplistic description of reality with an unjustified degree of widespread acceptance (Savile, 1960; Ayala, 1969; Walter, 1988; Mayfield and Levine, 2010).

Within the theoretical framework of CEP, the close coexistence of similar species of plants in high-diversity communities (e.g. Goldberg and Werner, 1983; Shmida and Ellner, 1984; Hubbell, 1979, 2006) is paradoxical, to say the least. The need to explain this paradox has led to the HFR and other approaches derived from it, such as the unified neutral theory of biodiversity (Hubbell, 2001).

Alternative interpretations of redundancy (Lawton and Brown, 1993) are presented as a dichotomy between: (a) the “rivet hypothesis” (Ehrlich and Ehrlich, 1981), i.e. gradual losses of species progressively weaken the whole until catastrophe ensues and (b) the HFR itself, i.e. many species in the ecosystem provide repeated information; what really matters is a proper ratio of producers–consumers–decomposers which allows the integrity of the main ecosystem functions (Walker, 1992).

Several extensive reviews (e.g. Rosenfeld, 2002; Petchey and Gaston, 2006) have drained the most conventional aspects of this topic. On the contrary, this article is deliberately biased toward elements that have not been included in an interrelated analysis so far.

These elements come from the ecological state equation (ESE, Eq. (6)), very similar to the ideal gas state equation (Eq. (7)), whose structure and connections with the conventional theoretical ecology has recently been exposed (Rodríguez et al., 2012, 2013). This article explores several non-evident traits of the ESE that are used to develop an alternative theoretical background in order to provide a better understanding of species coexistence that is simultaneously consistent with conventional ecology and physics.

The first part of this article includes a brief summary of the conventional knowledge about species coexistence. The second part begins with a concise preface about the traditional importance of interdisciplinarity in ecosystem ecology followed by two subsections embracing interdisciplinary elements, inferred from the ESE, that are linked to the facilitation of species coexistence. The third part of this paper exposes the main limitation of ESE to explore species coexistence in scales beyond the ecological models based on classical mechanics. From this, a first qualitative draft of a wave solution that harmonically combines the CEP and the HFR within a more general theoretical framework is exposed. Finally, this paper ends with a set of concluding remarks that generalize our main results and their epistemological meaning.

2. The interdisciplinary nature of species coexistence and biodiversity

Ecosystem ecology has a long tradition of direct and indirect exchange of ideas and techniques with many other fields, including (a) social sciences (e.g. Malthus–Darwin epistemological connection: Bowler, 1976; parallelism between the supply–demand equilibrium model in economics and the insular equilibrium model proposed by MacArthur and Wilson, 1967; socio-economic application of species diversity indicators: Marcuzzi and Camuffo, 1968; Attaran, 1986; Xu et al., 2002; bio-economics: Dragan and Demetrescu, 1986; *r*–*K* strategies in human populations: Alfonso-Sánchez et al., 2003); (b) information theory (e.g. early extrapolations of Shannon’s *H* measure: MacArthur, 1955; Margalef, 1957) and (c) physics (e.g. thermodynamics – Odum, 1968; Svirezhev, 2000; Jørgensen and Fath, 2004; Tiezzi, 2005 – as well as statistical mechanics – Shipley et al., 2006; Dewar and Porté, 2008; Kelly et al.,

2011 – applied to ecology). Nekola and Brown (2007) cite additional examples in this regard. Given the connections between all these topics and species diversity, the analysis of species coexistence should also be treated from the interdisciplinary point of view.

2.1. Effects of the gamma distribution of inter-plot dispersal values on species coexistence

The understanding of the ecological meaning of gamma distribution requires a preliminary description of the distributed indicators. Due to some of its particular features (see below), we will take the index of dispersal (I_e ; Eq. (1)), proposed by Rodríguez et al. (2012), as one of our indicators of reference in this subsection.

$$I_e = \frac{\sum_{i=1}^S (I_{ei,j})}{S}, \quad (1)$$

$$I_{ei,j} = \left(\frac{d_{i,j}}{\sigma_{i,j}} \right) \times 100, \quad (2)$$

$$d_{i,j} = \frac{\sum_{k=1}^m (\sqrt{(x_j - x_k)^2 + (y_j - y_k)^2} \times 2i_{j,k}/(i_j + i_k))}{m}, \quad (3)$$

where $d_{i,j}$ is the mean dispersal activity of a species i in plot j with central geographic coordinates (x, y) within a given ecological space divided into m plots; i_j is the abundance of i in plot j ; i_k is the abundance of i in plot k ; and $i_{j,k}$ is the shared number of individuals of i in plots j and k (for example, if $j=9$ and $k=22$, then $i_{j,k}=9$); $(2i_{j,k})/(i_j + i_k)$ is the Bray–Curtis similarity index (Washington, 1984) (range 0–1); $\sigma_{i,j}$ is the standard deviation of $d_{i,j}$; $I_{ei,j}$ is the ergodic indicator of dispersal intensity of a species i in plot j ; I_e is the ergodic indicator of dispersal intensity of the species group in plot j ; and S is the species number in plot j . If $(2i_{j,k})/(i_j + i_k) = 1$ the Euclidian distance

estimated by $\sqrt{(x_j - x_k)^2 + (y_j - y_k)^2}$ remains unchanged, but it is proportionally shorter as $(2i_{j,k})/(i_j + i_k) < 1$. Eq. (2) is the reciprocal of the coefficient of variation of Eq. (3). So, I_e is an intensive variable (independent of the system size in a similar way to physical velocity) without correlation with the population density. For the calculation of derived variables I_e is expressed in dispersal units (đ). Eq. (3) assumes that a species with a wider spatial distribution in a time interval $\Delta t \rightarrow 0$ with regard to the successional process is also one represented by individuals with faster dispersal during a $\Delta t \gg 0$ just before the observation. Precisely, according to Hopf (1932, p. 205), ergodicity means that “the time average is equal to the space average”; as a result, there is a transitivity or meaning equivalence between space and time in a similar way as it has been proposed in ecology (e.g. Kerner, 1957; Kikuzawa et al., 2009). Rodríguez et al. (2013) includes additional remarks in regard to the calculation and meaning of Eqs. (1)–(3).

The adjustment of I_e to gamma distribution (Rodríguez et al., 2012) is essential in this context since the Maxwell–Boltzmann distribution for molecular velocity (v) values is a particular case of a generalized standard gamma distribution (Chakraborti and Patriarca, 2008; Khodabin and Ahmadabadi, 2010; Lallouache et al., 2010; Lienhard and Meyer, 1967; Melker et al., 2010; Patriarca et al., 2004; Stacy, 1962). The epistemological sequence applied in this case to derive this inference is the following: Point 1: the adjustment of dispersal values to gamma distribution under stationary conditions is an empirically proven fact (Rodríguez et al., 2012). Point 2: the ecosystem has been recognized as a thermodynamic system from the beginning of modern ecosystem ecology. Point 3: the ecological state equation, very similar to the ideal gas state equation, proposed by Rodríguez et al. (2012) seems to be valid for any stationary ecological system, independently of scale

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