A Contextual Quantum-Based Formalism for Population Dynamics

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Abstract

Population ecology is mainly based on nonlinear equations of the Lotka-Volterra type, which provide mathematical models for describing the dynamics of interacting species. However, for many interacting populations, these equations entail complex dynamical behavior and unpredictability, generating such difficulties and problematical situations as illustrated by the "paradox of the plankton" and the "paradox of enrichment", for instance. A careful analysis shows that an ecosystem is a fundamentally contextual system, hence any formalism describing such systems should incorporate contextuality from the very beginning. But existing approaches are based on classical physics and probability theory, and introduce contextuality as an external effect, so that they cannot generally explain the main peculiarities of ecosystems. Basing ourselves on a contextual formalism elaborated to study microscopic systems in quantum mechanics and including appropriate nonlinear equations, we construct a generalization of the Lotka-Volterra equations for contextual systems, apply these equations to discuss some paradoxical situations encountered in ecology, and propound alternative solutions to those currently existing in the literature.

Keywords. Population dynamics; contextuality; quantum mechanics.

1 Ecological modeling

In modern times two approaches have been followed to deal with complex systems, such as living organisms or ecosystems. The first, the *thermodynamic approach*, looks at the system as a whole and extracts from its behavior in space and time a global principle that characterizes its dynamics. It seeks to identify the most relevant factors governing the system evolution from the very beginning, *e.g.* biodiversity in ecosystems, behavioral patterns of animals, organic codes in biochemistry, etc. (*holistic approach*). The second is the *dynamical approach*, which instead aims to reconstruct the complexity observed from its elementary components and to grasp the law of formation of the phenomenon (*reductionist approach*). In particular, inspired by classical mechanics one can model the dynamics of interacting populations

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by using deterministic differential equations, based on the Lotka-Volterra equations (Lotka 1925, Volterra 1928), and several (analytical and numerical) studies have been conducted producing remarkable results in describing the behavior of aquatic and terrestrial ecosystems. However, in general, the dynamics of many interacting populations is a problem with several coupled variables and, consequently, complex dynamical behavior results, so that it is difficult in such cases to provide "stable" mathematical models yielding long-term predictions. Moreover, ecosystems present peculiarities (autocatalysis, centripetality, ascendency, etc.) that cannot be explained only in terms of either the thermodynamic or the dynamical approach, but mixed approaches are useful in some cases (Del Giudice et al. 2009). As a consequence, classical ecology is still facing the problem of answering the question of "what has made it possible for ecosystems to develop a complex, self-organizing, coherent, hierarchical structure with a non-linear self-consistent dvnamics?" (Jørgensen et al. 2009). In this regard some authors have observed that existing simulation techniques are far from achieving a satisfactory understanding of ecosystem dynamics, suggesting that some metaphysical assumptions underlying existing models could be flawed at a deeper level, and hence calling for new sets of formal assumptions about ecosystem functioning (see e.g. Jørgensen et al. 2007, Ulanowicz 2009). In particular, M. Colyvan and L. R. Ginzburg (2003) maintained that, although ecology and physics have different subject matters and use different methods, they are similar in several respects and have proved to be mutually productive over time. Other scholars have suggested that the developments in our understanding of microscopic physics obtained through quantum mechanics in the last century could supply valuable techniques to deal with ecological systems. They have propounded quantumbased frameworks and methodologies for describing the behavior of special ecological systems by using both the formalism of quantum mechanics for a single particle (see e.g. Leme de Mattos et al. 2007) and the formalism of quantum mechanics for many interacting particles (see e.g. Kirwan Jr. 2008, Del Giudice et al. 2009).

2 The paradox of the plankton

Connected with the deep difficulties expounded in Sec. 1, the paradoxical situation raised by the plankton biodiversity has been puzzling ecologists for more than forty years. This problem can be roughly stated as follows.

Freshwater streams, lakes and oceans are habitats for complex ecosystems, of which phyto- (and zoo-) plankton are important components. Marine ecosystems including their plankton have a major ecological and economic significance. In particular, the study of plankton has played a crucial role in our understanding of ecological processes, phytoplankton being the basis of most aquatic food chains. Most of the species of phytoplankton are phototrophs, i.e., they carry out photosynthesis to produce energy. These phototrophic phytoplankton species "... reproduce and build up populations in inorganic media containing a source of CO₂, inorganic nitrogen, sulphur and phosphorous and a considerable number of other elements (Na, K, Mg, Ca, Si, Fe, Mn, Cl, Zn, Mo, Co and V) most of which are required in small concentrations and not all of which are required by all groups" (Hutchinson 1961). However, in many natural waters, only nitrate, phosphate, light and carbon are limiting resources regulating phytoplankton growth. The *competitive* exclusion principle (Gause 1935), which can be explained in terms of classical deterministic Lotka-Volterra competition models, suggests that in homogeneous, well-mixed environments, species that compete for the same resource cannot co-exist, and that in such competitions one species should win over the others so that in a final equilibrium, the cluster of the competing species should turn into a population consisting of a single species. Indeed, simple competition models and laboratory experiments also suggest that the number of species that can co-exist in equilibrium cannot be greater than the number of limiting factors, unless additional mechanisms are involved. It is well known, however, that in most aquatic ecosystems hundreds of species of phytoplankton are found to co-exist throughout the year. Even in summer, when the natural waters suffer from a striking nutrient deficiency and the resource competition becomes extremely severe, in situ measurements show prolonged co-existence of a large number of phytoplankton species. Antithetical to the competitive exclusion principle, the co-existence of a large number of phytoplankton species on a seemingly limited variety of resources in aquatic ecosystems was first recognized by (Hutchinson 1961), and is usually known as the paradox of the plankton, being one of the most classical problems in plankton ecology. An extensive literature exists related to this paradox, and a number of mechanisms have been proposed, most of them inclined to non-equilibrium explanations (see e.g. Hutchinson 1961, Tilman 1977, Huisman 1999), that is, suggesting that equilibrium is never reached in interacting phytoplankton communities. But, although these "ad hoc" mechanisms seem to offer an explanation for the diversity of certain systems, an investigation of a universally accepted theory is still an unachieved goal (see e.g. Schippers et al. 2001, Shovonlal and Chattopadhyay 2007, Shoresh et al. 2008).

3 A contextual formalism for ecosystems

Ecological research has shown that living systems organize themselves into correlated entities, each comprising many individuals belonging to many species (*ecosystems*), and that

ecosystems themselves play a driving role in the behavior and dynamics of each individual. The dynamics of the individuals of the same species follows different paths inside different ecosystems, while, of course, keeping the same fundamental structure. The dynamics of the ecosystems, then, affects the dynamics of the constituent individuals, but is in turn affected by their dynamics, so that the change of state of the whole is simultaneously a cause and a consequence of the dynamics of its constituents. This means that ecosystems are highly contextual and nonlinear systems and, in fact, all models trying to provide an explanation for the "plankton paradox" more or less implicitly introduce contextuality as a possible cause of the phytoplankton biodiversity. It has now become relevant that the same problem arose in physics in the last century. Classical mechanics could describe situations where the effect of the measurement was negligible, or at least controllable, but not situations where the measurement intrinsically influenced the properties and the dynamics of a system. This is because classical theory does not provide for a means of coping with contextuality (except in the initial conditions or in an ad hoc way, by introducing an additional model of perturbation to unstable equilibriums). Modern classical theories, such as chaos and complexity, although they still have this limitation, provide for a means of transcending reductionism. The shortcomings of classical mechanics were revealed most explicitly when it came to explaining what happens when many systems become entangled. These situations could be accounted for by quantum mechanics, which contains an elaborate mathematical framework for describing the change and actualization of potentiality that results from contextual interaction. However, in quantum mechanics this is limited to the extreme case, when the response of the system is maximally contextual. For this reason, the Brussels group has for many years researched the mathematical description of contextual interactions between systems. Continuing the work started in Geneva (Piron 1976) with the aim of providing a physical justification for the mathematical apparatus of quantum mechanics by establishing an operational foundation of this theory, a general formalism has been elaborated in which every system is described by the set of its states, the set of its contexts, the set of its properties, and the connections between these sets (SCoP formalism) (Aerts 1983, Aerts 1986, Aerts et al. 2000, Aerts 2002). The SCoP formalism unifies the representation of classical systems (systems in which context effects can be considered negligible) and quantum systems (systems with maximum context effects, e.g. the effects of a measuring apparatus on a microscopic physical system), while allowing rigorous representation of systems with any degree of contextuality. In recent years, the SCoP formalism has been applied to various disciplines, such as cognition theory (Aerts and Gabora 2005, Aerts 2009, Aerts and D'Hooghe 2009), economics (Aerts and D'Hooghe 2009, Aerts and D'Hooghe 2010), biology (Aerts et al. 2003, Aerts and Czachor 2006, Aerts et al. 2006), etc., where context effects cannot be ignored because of their usually predominant role in the behavior and dynamics of such systems (a similar approach which applies contextual quantum-based structures to cognitive science and psychology can be found in Khrennikov 2010). In addition, a general theory of evolution has been propounded within the SCoP formalism. In this perspective, evolution is considered as a context-driven actualization of potential (CAP), in which every system evolves through a reiterated and continuous interaction with its relevant context which modifies and actualizes the system's properties. If evolution is conceived of as a change of state induced by a context, then the CAP formalism supplies a general framework that makes it possible to recover evolutions within different disciplines, including but not limited to physics, biology and culture (Gabora and Aerts 2007, Gabora and Aerts 2009). This approach can also account for the occurrence of such phenomena as selfconsistency, coherence, emergence, etc. which are typical of complex systems and can hardly be explained in classical terms but appear as natural effects of contextual interactions between systems in the SCoP formalism. It is this mathematical formalism generalizing quantum mechanics that can be used to describe contextual interactions and dynamics of ecosystems. This assertion has been corroborated by studies of nonlinear integrable systems occurring in nonlinear generalizations of quantum mechanics, which have led to a discovery of a class of kinetic equations whose exact solutions exhibit features analogous to those known from the plankton paradox. In particular, a large number of species have been shown to survive the dynamics in spite of formal similarity to Lotka-Volterra models. This asymptotic behavior is a consequence of soliton dynamics and the non-Kolmogorovian probabilistic structure of the resulting nonlinear kinetics (Leble and Czachor 1998, Aerts and Czachor 2006, Aerts et al. 2006, Doktorov and Leble 2007).

4 The contextual Lotka-Volterra equations

Our analysis in Sec. 3 shows that ecosystems are intrinsically contextual systems and that the Geneva-Brussels approach constitutes a natural basis to construct such a contextual formalism and to provide predictive models for interactions between species, populations and communities. We thus associate each ecosystem $\mathcal E$ with a set Σ of states, a set $\mathcal L$ of properties, a set $\mathcal M$ of contexts and two mappings, $\mu:\Sigma\times\mathcal M\times\Sigma\times\mathcal M\longrightarrow[0,1]$ and $\nu:\Sigma\times\mathcal L\longrightarrow[0,1]$, where μ describes the structure of the contextual interaction of the ecosystem, that is, the degree to which a change of state of a context (ecosystem) provokes a change of state of the ecosystem (context), and ν describes how properties depend on the different states of the ecosystem.

Let us now consider two interacting species S_1 and S_2 in \mathcal{E} . Mapping μ can be made explicit to derive a set of context-dependent Lotka-Volterra equations (*contextual Lotka-Volterra equations*) that rule the dynamics of the two species in the presence of a (possibly variable) context. These equations admit the Lotka-Volterra equations as limiting cases when context plays a negligible role. Moreover, it can be shown that the contextual Lotka-Volterra equations

are particular cases of the nonlinear soliton kinetic equations introduced to generalize the von Neumann equations in the framework of nonlinear quantum mechanics. This result is relevant from our point of view, because soliton kinetic equations have already been proved to admit analytic solutions which occur in chemical and biological dynamics (Aerts and Czachor 2006, Aerts *et al.* 2006).

The contextual Lotka-Volterra equations can be extended to N interacting species S_1, S_2, \dots, S_N and particularized to the various forms of contextual interactions (predation, competition, mutualism, disease). More specifically, by considering a community of competing phytoplankton species and following the strategy known from soliton kinetic equations, we show that solutions of the contextual Lotka-Volterra equations exist such that they admit the competitive exclusion principle as a possible solution (when context effects are weak) but also different solutions (when context effects are predominant). This result allows us to evaluate the distribution of phytoplankton species in a given phytoplankton community and to compare our theoretical predictions with experimental data existing in the literature. Hence, an alternative solution of the "paradox of the plankton" can be provided and analyzed in the light of existing models. We finally suggest the existence of genuine quantum (Hilbert space) structures that model the patterns observed.

We conclude this section by considering two further paradoxes of population ecology involving the Lotka-Volterra models, namely, the "paradox of enrichment" (Rosenzweig 1971) and the "enrichment response" (Oksanen et al. 1981). The "paradox of enrichment" was introduced by (Rosenzweig 1971). He proposed a generalization of the Lotka-Volterra equations to show that in a stable predator-prey system, as the prey carrying capacity increases, the system will become more and more destabilized, potentially resulting in extreme situations in which one of the species goes extinct. This counterintuitive effect, together with the "enrichment response", which concerns higher trophic levels, are usually accepted as ecological axioms in population ecology, even though they have received little empirical evidence as yet. According to (Jensen and Ginzburg 2005), these paradoxes follow from an implicit assumption on the prey-predator interaction, which seems to be intuitive from the point of view of a classical Lotka-Volterra model, but is problematical when analyzed in detail. From our perspective, the enrichment paradox must be faced by taking into account the contextual interactions between prey and predator. These paradoxes can therefore be examined in our mathematical framework, and we can prove that the contextual Lotka-Volterra equations, when applied to predator-prey interactions, yield different predictions with respect to the "paradoxical" situations envisaged by existing models.

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¹The mathematical derivation of the results presented in this section has been omitted, for the sake of brevity. We intend to provide a more formal treatment, including explicit calculations, in a forthcoming paper.

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