Comment

Can a mathematical model of mass extinctions do without environmental noise? Comment on "Knowledge gaps and missing links in understanding mass extinctions: Can mathematical modeling help?" by Ivan Sudakow et al.

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One of the most fundamental questions in ecology concerns the extinction of species with respect to their persistence and the understanding of how it depends on biotic and abiotic factors [1-3]. In this regard, Sudakow et al., after revisiting and clarifying the fundamental difference between mass extinction triggers and killing mechanisms, provide an overview of modeling approaches and population dynamics models useful for describing the triggering and occurrence of mass extinctions, with a view to building a solid bridge between real datasets and mathematical models.

However, the overview of mathematical models provided by Sudakow et al. considers stochastic models as one of the framework among all others, while they should have a prime position. In fact, population dynamics always occurs in time-varying noisy environments, and understanding the impact of environmental noise on the mean extinction time of a population is still today a fundamental and challenging open question. We will give some arguments in this respect and briefly mention recent stochastic models relevant to mass extinction.

Any physical, biological and ecological system is not an isolated system because it is naturally immersed and surrounded by the environment, which generally includes the entire universe. All the individual parts of the environment interact with the system in a random and independent, often uncorrelated way, giving rise to a highly random action whose intensity varies over time. This is the environmental noise always present in natural systems, which are indeed open systems. Also, ecological complex systems are strongly nonlinear due to the nonlinear interactions between constituent parts. The interplay between the nonlinearity of living systems and the environmental noise can give rise to new counterintuitive phenomena such as noise enhanced stability, pattern formation, quasiperiodic oscillations, and noise delayed extinction [4-10]. These phenomena cannot be explained by deterministic approaches, which treat noise as a mere nuisance. The characterization of the resulting spatiotemporal patterns is a key element for the analysis of ecological time series and the modeling of ecosystem dynamics. Moreover, the characteristic timescales of environmental variations play a fundamental role in how living systems adapt to the variability of environmental parameters. Relevant questions include the stationary population density and the role of the multiplicative noise on the extinction dynamics within an ecosystem [4]. Indeed, the presence of noise can change in a fundamental way the physics of the system. Thus, it is not surprising that the study of noise in ecological systems has emerged as a "hot" research topic in the last few years. Population fluctuations typically result from the interplay between demographic stochasticity, caused by random variations in survival and reproduction events in a finite population, and environmental stochasticity. Whilst demographic stochasticity tends to average out with the population size and remains important only in small populations, environmental stochasticity affects populations regardless of their sizes. Extinction of a long-lived self-regulating population can occur as a large fluctuation resulting from the intrinsic discreteness of individuals and stochastic nature of birth-death processes.

Of particular interest is the remarkable general study of Kamenev et al. [11], who analyzed a logistic model in which birth and death rates fluctuate in time. Specifically, they showed that, depending on the interplay between the system size and the temporal scale of the environment, the

model exhibits qualitatively different functional dependencies of the mean extinction time with the system size [11]. These authors performed a path-integral formulation, including both demographic and environmental stochasticity, and found diverse regimes depending on the ratio between system size and noise correlation time. In particular, the dependence on the system size of the mean extinction time changes from exponential in the absence of environmental noise to a power law for a short-correlated noise, up to no dependence whatsoever for noise with very large correlation times. This last regime implies that, when there are extremely long periods of adverse external conditions, the system reaches deterministically the absorbing state regardless its size. Furthermore, Assaf et al. [12], using a variant of the stochastic Verhulst model, investigated how a catastrophic event exponentially increases the extinction probability of an isolated self-regulated population. This was achieved by combining the probability generating function technique with an eikonal approximation to evaluate the exponentially large increase, caused by a catastrophic event, in the extinction probability [12]. A predictive theory for the temporal statistics of spatially extended systems approaching extinction, which accounts for environmental stochasticity and coupling, has been proposed by O'Regan [2]. The author developed spatially implicit two-patch models with environmental stochasticity, which are slowly forced through population collapse by changing environmental conditions, and derived patch-specific expressions for the indicators of extinction. Finally, Plata et al. [13] proposed a model for catastrophic events based on asymmetric stochastic resetting, which can account for abrupt changes in some state variable. In particular, the effects of catastrophic events are modelled by introducing random resetting events to a nonvanishing fixed value of the population density within a diffusive stochastic process. The authors obtained the exact nonequilibrium steady state and the mean first passage time to reach the absorbing barrier corresponding to the mass extinction. In particular, they showed how asymmetric stochastic resetting is an appealing tool to understand the fundamental features of the natural disaster dynamics in different contexts, including ecosystems [13]. These are just a few examples of theoretical techniques useful for a better and more realistic description of mass extinction in ecosystems.

Overall, as briefly argued here, deterministic approaches neglect the effect of random environmental fluctuations, which are now recognized as inherent and essential to ecosystems and have important consequences on their stability, species coexistence and mass extinction [4]. This scenario can be neither reproduced nor explained by purely deterministic models.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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