

Randomness in Ecological evolution: the role of complexity on the Allee effect

Marcelo A. Pires^{1,*}, Nuno Crokidakis^{2,†} and Silvio M. Duarte Queirós^{1,3,‡}

¹*Centro Brasileiro de Pesquisas Físicas, Rio de Janeiro/RJ, Brazil*

²*Instituto de Física, Universidade Federal Fluminense, Niterói/RJ, Brazil*

³*National Institute of Science and Technology for Complex Systems, Brazil*

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Considering an ecological Allee-like dynamics under linearly uncorrelated perturbations with random and nonrandom temporal arrangements we show that a complexity measure, rather than the standard autocorrelation function, is able to properly explain the fate of extinction and to what extent the threshold establishing the risk of extinction. Accordingly, these results allows comprehending *how* randomness jeopardises the long-run proliferation of organisms.

I. INTRODUCTION

The study of Ecological problems – namely, population dynamics – can be easily placed at the spotlight of Complexity. Besides the hard-core interaction between the biotic and abiotic elements, it is possible to find several layers of further interactions and dependencies that impact in the evolution of the system. With that respect, extinction is still the subject of great academic debate and in the spotlight of opinion public and mass media because of the rising interest in environmental preservation and conservation. Several ecological mechanisms of extinction were discussed in Ref. [1], like distinct rates of population increase (e.g., fecundity, survival rates, generation times), differential vulnerability of lineages to habitat loss, introduction of predators, mobility among other features. Those mechanisms often influence one another and can also affect and be affected by macroscopic measures of the ecosystem like the population size/density. One of those cases is the Allee effect that describes the relation between population measures and the fitness of a species [2]. Moreover, mechanisms as those we have listed are usually translated into parameters when we establish quantitative descriptions of Ecology. However, quantities like survival, fecundity, etc., are not fixed in time and generically subjected to randomness.

Mathematically, randomness can assume alternative origins implying in different dynamical and statistical features, namely correlation and dependence. In this manuscript, we aim at shedding light on the effects created by different non-linear proprieties of the randomness of the ‘parameters’ of a standard Allee effect dynamical model.

II. LITERATURE REVIEW

From molecular biology [3, 4] (eg, cell mitosis, morphogenesis) to collective behaviour [5], passing by evolution

[6, 7], randomness – including disorder – has shown to be a key ingredient in Biology [8, 9]. Actually, it is well established several of the most important milestones in biology reached during the last two centuries were achieved by acknowledging the importance of random dynamics [10], namely adaptive Brownian motion processes.

For instance, in respect of flocking it is known that one of the main functions of the collective behavior of a bird is protection against predators. It is known that randomness – in the form of bird reshuffling in the flock – contributes to the alignment order of the flock [11].

Understanding the ecological mechanisms that lead to the extinction of a species is thus fundamental to conserve it. The impact of the different sources of ecological evolution – particularly those we have made mention to – have been consistently surveyed in the literature. Considering the ancestry issue it was observed different lineages are threatened by distinct mechanisms of extinction, and unrelated ecological factors predispose taxa to different sources of extinction risk [12]. In Ref. [13], its authors pointed that population size and trend in population size were clearly the best predictors of extinction risk. Mathematical and computational models were widely proposed to explain the phenomenon of extinction [14–16].

At the level of the resources in ecological systems, it is possible to find randomness and stochasticity as well. Namely, simple models incorporating the key features of time-dependent resources and specific descriptions of survivorship for consumer species show the importance of the time dependence of available resources and the role that allochthonous inputs play on the temporal and spatial abundances of species [17, 18].

Extinction is a major ecological event. Because it corresponds to the termination of a species, extinction can be understood within a Physics framework as a phase transition event with the emergence of an absorbing state. The Contact Process (CP) is the paradigmatic model for phase transitions into absorbing states [19]. In the CP, temporal disorder can be introduced by allowing the control parameter to be time dependent. For example, the authors in [20] showed that in contrast to spatial disorder, uncorrelated temporal disorder does not forbid the existence of discontinuous absorbing phase transitions, and it can also turn a discontinuous transition into a continuous one when disorder is sufficiently strong,

* piresma@cbpf.br

† nuno@mail.iff.uff.br

‡ sdqueiro@cbpf.br

even for low-dimensional systems [21]. Also considering the CP, the authors in [22, 23] considered the temporal disorder as an external environmental noise. The results suggest that the temporal disorder gives rise to an exotic critical point, where the average density and survival probability decay only logarithmically with time. In nonequilibrium magnetic models, temporal disorder acting as a time-dependent magnetic field leads to rich critical phenomena, with the occurrence of dynamical tricritical points [24, 25].

Ecosystems have been regarded as the quintessential complex system since the interactions between its components can feed back to impact such interactions by means of the macroscopic state that gets established [26]. Accordingly, considering tools like agent-based or cellular automata models, a new understanding arises of ecosystems as wholes that emerge in novel ways from possibly simple, mechanical rules governing interactions among their parts [27].

Finding robust methods for quantifying spatio-temporal signals in the presence of noise, nonstationarity and short data series is an active area of research in many disciplines. For ecosystem applications, we would expect these methods to detect pattern transitions (i.e., sequences of stable, periodic, quasi-periodic, chaotic, or random trends) as well as where and when they occur [28].

III. MODEL

A. Extinction dynamics

We consider an ecological dynamics for the proportion of individuals in a given population, $p(t)$, that takes into account the Allee effect by means of the minimal ODE [29]

$$\frac{dp(t)}{dt} = \lambda [1 - p(t)] p^2(t) - \alpha(t) p(t). \quad (1)$$

The first term on the right hand side is related to reproduction occurring at rate λ and the second term is related to death rate $\alpha(t)$. While in Ref. [29] the death rate is a constant, here we consider that it is time-dependent.

The reproduction-death dynamics described by Eq. (III B) also includes the Allee effect [30, 31] that is an important class of density-dependent phenomenon which has been widely observed in nature [32]. Apart from Ecology, the Allee effect is also important in several research areas such as conservation biology [2], invasion biology [33] as well as biofilm formation [34, 35], epidemiology [36–38] and cancer biology [39–42]. Such variety of domains wherein the Allee effect plays a role highlights the significance and broad interest of our work.

An initial insight into Eq. (III B) is obtained from the steady-state solution for the case with constant death

rate $\alpha(t) = a$

$$P^\infty = \begin{cases} \frac{1}{2} + \frac{1}{2} \sqrt{1 - 4\frac{a}{\lambda}} & P_o \geq P_c^o \text{ and } a \geq \frac{\lambda}{4} \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

where P_c^o is the initial density required for the long-run survival

$$P_c^o = \frac{1}{2} \left(1 - \sqrt{1 - 4\frac{a}{\lambda}} \right). \quad (3)$$

From Eq. (2), we see that the time-independent model with $\alpha(t) = a$ presents a discontinuous absorbing transition [19, 43, 44]. Equation (3) yields the Allee threshold, ie, the population fraction below which extinction is the eventual scenario. Thus, the bistable nature incorporated in Eq. (III B) is the mechanism responsible for the Allee effect. Frameworks more general than Eq. (III B) could be considered [45], but we are interested in a fundamental question: What makes the pure randomness increase the vulnerability of populations?

B. Protocol for $\alpha(t)$

As we aim at studying the possible effects of randomness on the dynamics of we assume the simplest of the instances where α alternates between α_0 and α_1 . In order to assess the role of non-linearities in that process we assume that $\alpha(t)$ sequences are given by either purely or Rudin-Shapiro protocols. In such binary arrays we map $0 \rightarrow \alpha_0$ and $1 \rightarrow \alpha_1$. In all the cases, we start from 0, subsequently we apply one of the following rules:

- Rudin-Shapiro: first, we generate a sequence with four letters by means of the substitution rule $A \rightarrow AB$, $B \rightarrow AC$, $C \rightarrow DB$ and $D \rightarrow DC$. Then we set $A = B \rightarrow 0$ and $C = D \rightarrow 1$;
- Random: we first generate a sequence with the Rudin-Shapiro protocol until t_{\max} , then we shuffle it. This procedure is done to make a fair comparison between such sequences.

For further details on the Rudin-Shapiro (RS) sequences we point the reader to Refs. [46, 47]. From such references, we see that aperiodic series have been used for a long time in Physics, but these sequences remain underemployed in Ecology. Here, we show that the pure RS and the randomly rearranged RS sequences work as an insightful platform that enables setting a new perspective on the subject of how extinction is molded by correlation versus complexity.

IV. RESULTS AND DISCUSSION

In this section, we show our results obtained by solving the ODE in Eq. III B, where we employ the *solveivp* of

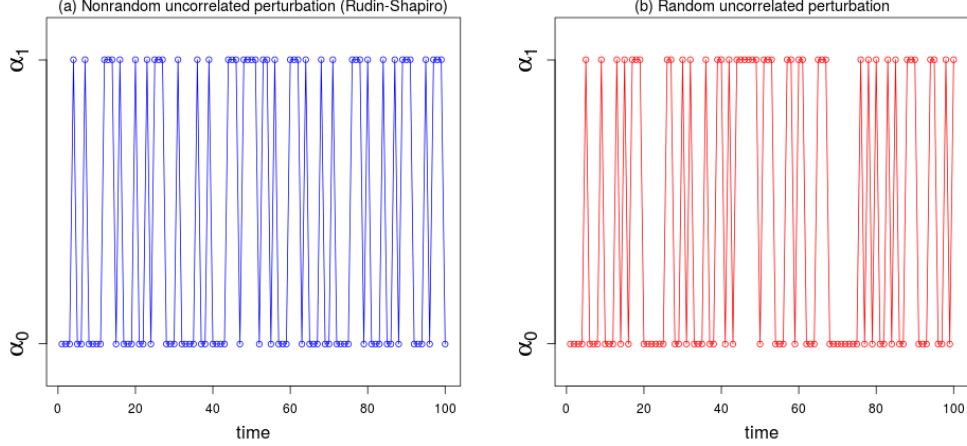


FIG. 1. Time-dependent death rate $\alpha(t) = \{\alpha_0, \alpha_1\}$ considering the protocols: (a) nonrandom and (b) random. Both time series have the same mean value $\bar{\alpha}$, since the case (b) is just a shuffle of the case (a).

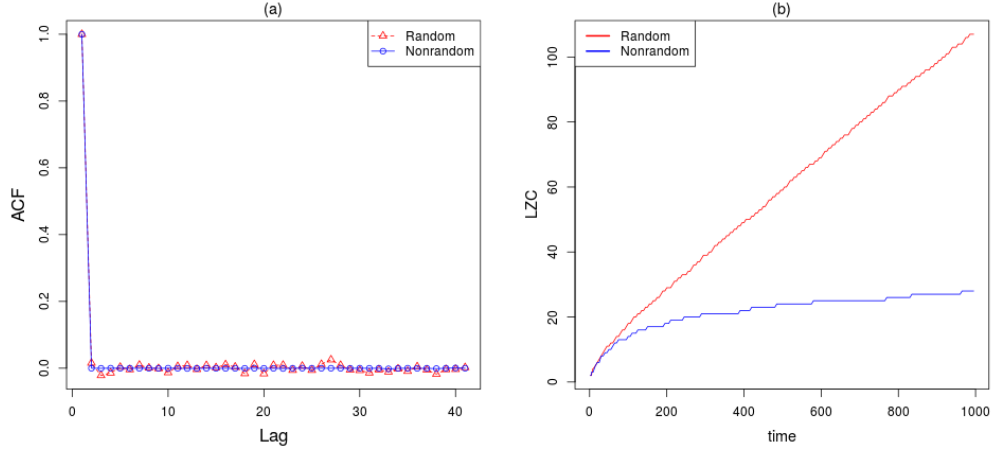


FIG. 2. Main properties of the time-dependent binary sequences used for $\alpha(t) = \{\alpha_0, \alpha_1\}$. (a) Autocorrelation (ACF) versus lags. (b) Lempel-Ziv complexity (LZC) over time. The LZC is able to detect hidden patterns that are not recognized by the ACF.

python. Concretely, we apply the *RK45* routine that performs the Runge-Kutta method of order 5(4). Thus, the time evolution takes place with a 4-order accurate control of errors and 5-order accurate formula for steps. In such procedure, we set the increment with maximum value $dt_{max} = 0.1$ and between each interval $[i, i + 1[$ we keep the same $\alpha(i)$, where $i = 0, 1, 2, \dots, t_{max}$.

Before delving into the analysis of the population dynamics per se, let us discuss the properties of $\alpha(t)$. In Fig.1 we illustrate the setups for $\alpha(t)$ and in Fig.2 we evaluate the architectural characteristics of the sequences we use for each protocol. Firstly, we compute the autocorrelation function (ACF) considering several lags. In Fig.2(a) we see that the overall behavior of the nonrandom RS array presents values for the ACF that resem-

bles the ACF values for the random series, although with weak fluctuations.

Additionally, we quantify the Lempel-Ziv complexity (LZC) of the sequences we use. The LZC is a nonlinear measure that provides information about the abundance of nonidentical patterns in an array when examined from t_0 to t_{max} [48, 49]. In this sense, the minimum and maximum values for the LZC are obtained for the periodic and random sequences, respectively. Although the Rudin-Shapiro chain has a correlation pattern comparable to random series [Fig.2(a)], its LZC presents considerable differences [Fig.2(b)].

In Fig. 3, we observe how the bistability embedded in Eq.III B is impacted by the presence or not of randomness in $\alpha(t)$. On the one hand, if the initial density P_0

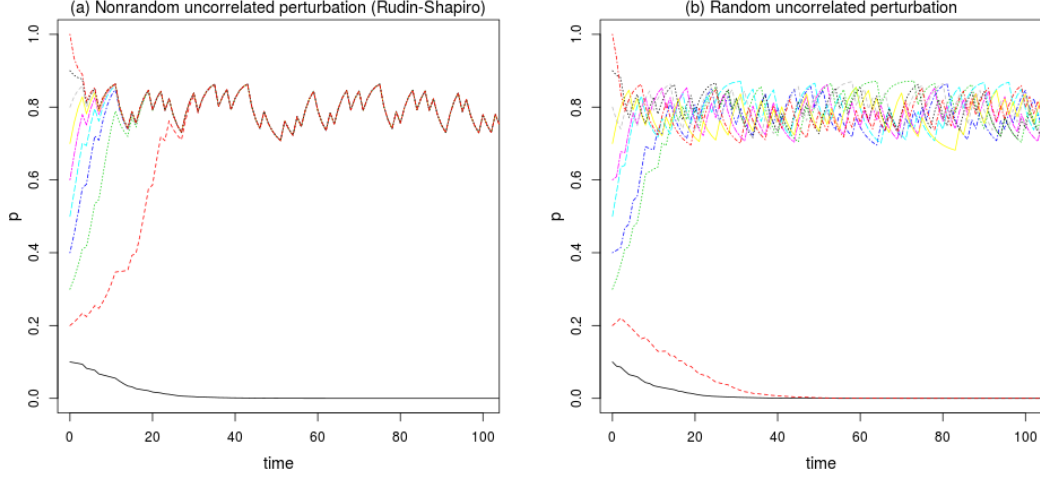


FIG. 3. Time series for the population fraction considering (a) nonrandom and (b) random perturbations. Each curve is obtained with increasing initial population densities $P_0 = \{0.1, 0.2, \dots, 1\}$. Parameters: $\lambda = 0.9$ and $\alpha_0 = 0.2$.

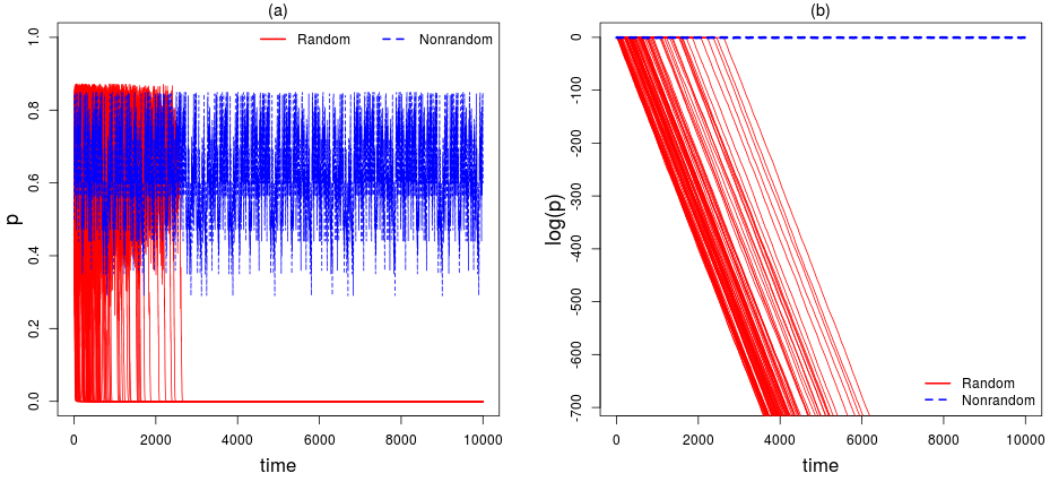


FIG. 4. Time series for the population fraction considering nonrandom and random perturbations. (a) Linear scale and (b) Semi-log scale. We use 100 samples for the protocol with randomness. Parameters: $P_0 = 0.5$, $\lambda = 0.9$, $\alpha_0 = 0.1$ and $\alpha_1 = 0.3$.

is high enough, the population survives regardless of the type of perturbation. On the other hand, if the initial density P_0 is too low, the extinction takes place independently of the kind of perturbation. Between both cases, it is clear the ecological outcome depends on how the perturbation is temporally arranged. In such setting ($P_0 = 0.2$) the time evolution leads to extinct state for the random protocol, whereas it leads to a survival state for the nonrandom protocol. If $\alpha(t)$ exhibits the same autocorrelation pattern and the same mean $\bar{\alpha}$, why do the random and nonrandom protocols lead to different outcomes? The answer in our controlled computational experiment relies on the complexity pattern incorporated in $\alpha(t)$, as shown in Fig.2(b). Thus, the dynamics of a

species on the verge of extinction is strongly influenced by the complexity of time-dependent perturbation. This is an important finding because at present there several species at risk of extinction [50, 51].

In Fig.4, we see the long-run scenarios arising from the random and nonrandom setups considering a fixed initial condition $P_0 = 0.5$. Both time evolutions are marked by fluctuations that are driven by the switches between $\{\alpha_0, \alpha_1\}$. We emphasize that all the curves (blue or red) are obtained considering sequences that display null Pearson's correlation and have the same mean $\bar{\alpha}$. Despite that the nonrandom perturbation promotes a long-run survival of the population, however the presence of randomness compromise the population persistence. That

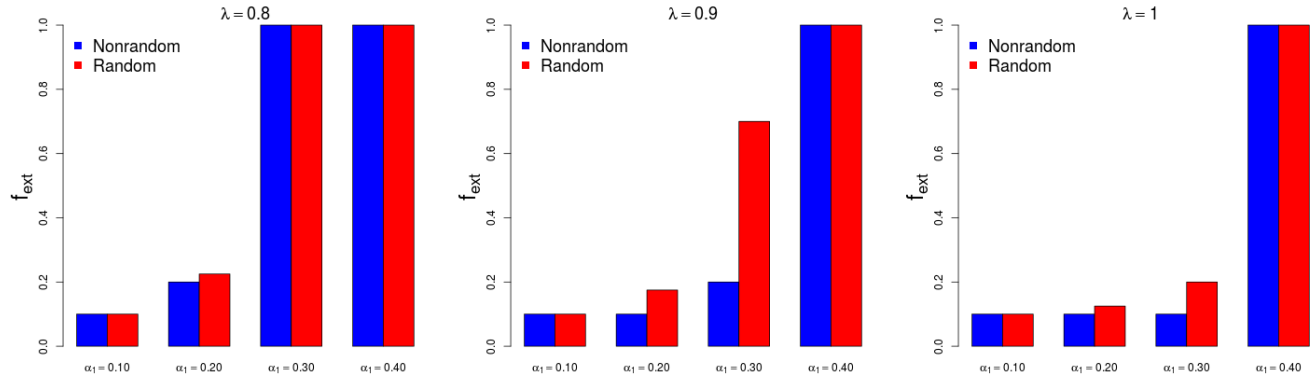


FIG. 5. Barplot with the fraction of populations undergoing extinction, f_{ext} , among the total of time series obtained with $P_0 = \{0.1, 0.2, \dots, 1\}$. Parameters: $\alpha_0 = 0.1$.

is, the Rudin-Shapiro protocol for time-dependent perturbations in $\alpha(t)$ is less prone to induce a transition to an absorbing state. This adds new understanding of the field of nonequilibrium absorbing-state phase transitions [19, 43, 44].

In Fig. 5, we see how the outcomes regarding fraction of extinction f_{ext} are affected by different values for the reproduction rate as well as the death rate α_1 . We note an agreement between the long-run scenarios for some combinations of parameters meaning that in such cases the underlying birth-death dynamics is more important than the type of patterns in $\alpha(t)$. For other cases, we see a disagreement between f_{ext} , meaning that for such settings the temporal arrangement of the patterns in the perturbation $\alpha(t)$ plays an important role on the final ecological outcome. Thus, it is clear a competition between dynamics (reproduction and death) and structure of $\alpha(t)$.

Taking a broad view of the information conveyed in Figs. 1-5, we note that the random and nonrandom perturbations can lead to different scenarios depending on the balance between the birth-death dynamics and the disposition of the patterns in $\alpha(t)$. When the imbalance between structure and dynamics sets the arrangement of patterns as a relevant feature, we see that the ACF fails to provide an explanation for the fate of extinction in the random perturbation, whereas the LZC allows us to explain the distinct emergent phenomenon observed in the time evolution of the population. In such cases, the mass extinction events are triggered by cumulative effects arising from hidden patterns in $\alpha(t)$ that are detected by a complexity quantifier. Mathematically, this can be traced back to the fact that the time series can be embedded with nonlinear dependencies that are not recognized by a single measure (see e.g. Ref. [52]).

While we could have employed an agent-based simulation [53–55], in this work we have used a mean-field approach because we avoid the presence of multiple sources of randomness. With a single source of randomness we

can make controlled computational experiments. Equation III B – valid in the limit of infinitely large population size – enables us to understand how large populations respond to random and nonrandom perturbations. In relation to that, we note in Figs. 3-5 that uncorrelated sequences do not necessarily endanger the sustainability of a population, but non-trivial and hidden patterns – produced by randomness – are the great villain of population survival in our controlled setup.

The relation between correlation and complexity is subtle. For instance, consider an ordinary situation of a coin with probability q for head. After many tosses, we observe correlated results if $q \neq 0.5$, thus we say the outcome has some predictability. The unbiased case ($q = 0.5$), produces the minimal absolute value for the correlation that coincides with the maximum complexity. This is an intuitive notion. The proposal we have worked is rather different since correlation and complexity are not strictly related. In this sense, our results point out that what makes the pure randomness increase the vulnerability of populations is not strictly its lack of linear self-dependence but its high-level complexity though. Thus, our results contribute with fresh perspectives about the underlying foundations that lead to extinction.

Previously, it was shown [21] that temporal randomly distributed disorder does not destroy the bistable nature of dynamics described by models similar to Eq. III B. Our results exhibited in Fig. 3 and in Fig. 5 expand such claim regarding the robustness of the bistability for the realm of nonrandom aperiodic disorder incorporated as a time-dependent perturbation.

V. FINAL REMARKS

The minimal and universal set of ingredients embedded in Eq. III B puts us in a position to provide fundamental comprehension on how the notion of chance shapes the

ecology of extinctions [1, 56, 57]. Specifically, we show that a complexity measure, rather than the standard autocorrelation function, is able to properly explain the fate of extinction for Allee-like dynamics under linearly uncorrelated perturbations with random and nonrandom temporal arrangements. Thus, our work opens the door for the possibility of new bridges between the theory of complexity and ecological dynamics beyond the already existing connections [58–63].

While our work is not designed to address practical puzzles related to species loss, our results provide us with the evidence that complexity measures [64] can be an ally in combating species extinction by monitoring and detecting hidden patterns that are not detected by usual measures.

As previously mentioned, the Allee effect has been considered as an important phenomenon in several fields including cancer research [39–42]. For instance, in Ref. [39] it was proposed that the presence of the Allee effect in the tumor growth dynamics may offer a window for therapeutics. In that sense, the results shown herein can provide insights into this kind of dynamics since they show *how* randomness becomes a threat for the long-run proliferation of organisms. Effects of diffusion were analyzed in the context of models similar to Eq.III B with temporal disorder [65]. Such temporal disorder was considered as a time-dependent diffusion rate $D(t)$. The results suggest a strong effect of such time dependence on the phase diagrams of the CP. It can be interesting to also consider diffusion in our model with a time-dependent rate $D(t)$, and analyze the impact of such disorder in the extinction patterns.

From an experimental point of view, the few number

of parameters in our proposal – basically related to reproduction and death – is an advantage in terms of the build-to-understand approach in Synthetic Biology [66–69]. For instance, we mention that in such a new field bacteria can be engineered to display the Allee effect [66] as well other new behaviors [67–69]. In other words, our take-home message that complexity jeopardizes population survival can be biologically programmed within the current technology. Still taking into account that Synthetic Biology [66–69] is a fastly-growing field, we suggest that bacteria can possibly be programmed to perform pattern detection algorithms in a way that the long-run survival or not is a sign of the character of the complexity embedded in a natural time-dependent perturbation. The feasibility of such proposal will require controlled setups. If this challenge is surpassed, biologically engineered devices may provide a compelling opportunity to develop natural complexity recognition sensors.

Complexity plays a major role across science and technology [70]. Therefore, we have adopted a widespread and practical measure of complexity that is based on the number of unlike patterns [48, 49]. By using the paradigmatic Rudin-Shapiro sequence and its shuffled version we have disentangled how correlation and complexity impact extinction dynamics. In future works, it would be interesting to engineer new sequences for $\alpha(t)$ that capture further nuances of complexity [71].

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