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# Fluctuations-induced coexistence in public goods dynamics

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**Abstract** – Cooperative interactions between individuals in a population and their stability properties are central to population dynamics and evolution. We introduce a generic class of dynamical systems describing such interactions between producers and non-producers of a rapidly equilibrating common resource. In the mean field, fast-growing non-producers drive the entire population to extinction. However, the presence of arbitrarily small perturbations destabilizes this fixed point into a stochastic attractor where both phenotypes survive. Phase space arguments and moment closure are used to characterize the attractor. Spatial Monte Carlo simulations with demographic fluctuations and diffusion illustrate the same effect, establishing the validity of the stochastic two dimensional model as an approximation. The functional distribution of the noise emerges as the main factor determining the dynamics outcome, noise resulting from diffusion between different regions, or additive noise induce coexistence, while multiplicative or local demographic noise do not alter the outcome of the dynamics. These results are presented in the context of public goods, but similar conclusion may apply to large number of other systems.

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**Introduction.** – The evolution and stability of cooperative interactions between individuals has been a topic of interest in many areas of research. Growth and reproduction typically depend on a limited supply of resources that are shared, to some degree, by many individuals in the population; the production and consumption of these resources can mediate indirect interactions between them. One type of cooperative interaction is induced by the production of public goods: in a population inhabiting a shared environment, growth may depend on resources produced or actively extracted from the environment, typically at a cost. Once produced, these resources can be shared by other individuals and can thus benefit the population as a whole. Cooperative public goods interactions are particularly important in microbial populations [1–5].

The problem of public goods can be viewed in a general theoretical context. In the extreme case where they are essential for survival, a simple argument can be made for the selective advantage of "cheater" phenotypes that utilize the goods without investing the cost of producing it [6,7]. Evolutionary consequences of this argument were

investigated theoretically by different approaches, including extending two-player game theory [8,9], general evolutionary dynamics [10] and more specific microbial dynamics [11,12]. These studies have shown that the apparent paradox of extinction is easily solved with the addition of realistic effects such as privileged share, time-varying strategy, spatial structure and segregation, and more [13,14].

Less investigated is the ecological approach which considers physical interactions mediated by the environment [15–18]. We have recently developed such an approach, especially suited for the context of microbial public goods dynamics, and showed that both temporal [19] and spatial [20] fluctuations induce coexistence in nontrivial ways. In particular, simulations show that demographic noise and diffusion in space can induce long lasting spatio-temporal patterns [20], for intermediate diffusion coefficients, This fluctuation-driven coexistence was explained by a directed percolation argument which relies on organism discreteness and cycles of local extinction. However, the discreteness of this model limits the scope of this approach.

In this letter, we revisit the effect of noise and diffu-

sion in common-goods ecological models by a more fundamental and generic approach. We consider a simplified two-dimensional nonlinear dynamical system valid in the regime of rapid resource turnover and investigate its sensitivity to different noise regimes. We find that for a large class of such models the extinction state, transforms upon introduction of infinitesimal noise to a stochastic attractor. This instability is not sensitive to the noise amplitude, but to the noise functional shape. These results are then demonstrated using numerical simulations in a realistic spatial model with diffusion and demographic noise, indicating the natural emergence of an effective noise inducing the emergence of a stochastic attractor over a broad parameter regime.

**Model.** – Consider two populations with concentrations  $A$  and  $B$ , sharing resource  $C$ . This resource is extracted from the environment by  $B$ , which pays the price of a slightly lower net growth rate, and is therefore the cooperative sub-population. Once available, the resource is consumed by both producers and non-producers. In the mean-field approximation [19, 20]:

$$\begin{cases} \dot{A} = [\mu_A(C) - 1] A \\ \dot{B} = [\mu_B(C) - \alpha] B \\ \dot{C} = h(B) - \left[ \frac{\mu_A(C)}{Y_A} A + \frac{\mu_B(C)}{Y_B} B \right], \end{cases} \quad (1)$$

Here time is measured in dimensionless units  $\delta_A t$  - the death rate of  $A$ . Production of the resource by  $B$  follows an increasing non-linear saturating function  $h(B)$ , consistent with a finite environment. The resource is consumed by both  $A$  and  $B$ . For simplicity, we assume that both populations have the same growth rate,  $\mu_A(C) = \mu_B(C)$  a non-decreasing function of  $C$ , and the same yield coefficient  $Y_A = Y_B$ . The cost of production is modelled as a higher death rate for  $B$ ,  $\alpha > 1$ . Relaxing these assumptions leads to qualitatively similar results. An isolated producer population ( $A = 0, B > 0$ ) undergoes a bifurcation as a function of parameters from an extinction phase to a growth phase where it can sustain a stable equilibrium with the extracted resource [19]; we assume the conditions for such equilibrium are met.

The key approximation employed here is that resource extraction and consumption are significantly faster than organism reproduction. For example, bacterial secretion of enzymes occurs on a time scale of seconds, while division typically takes 20 minutes or more. Assuming mixing of resources with no privileged share leads to a Quasi Steady-State (QSS) approximation:

$$\begin{cases} \mu(C) = f(A, B) = \frac{h(B)}{A+B} \\ \dot{A} = [f(A, B) - 1] A \\ \dot{B} = [f(A, B) - \alpha] B \end{cases} \quad (2)$$

The environmentally mediated indirect interaction between the two sub-populations is now described by their

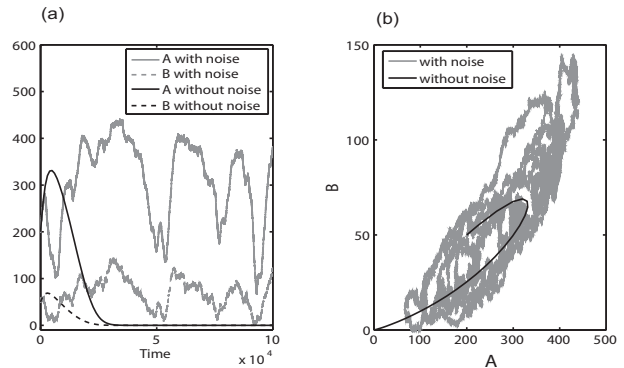


Fig. 1: Solutions of Eq. (2) and Eq. (3) (without and with fluctuations), as a function of time for the initial condition  $A = 200, B = 50$ . (a) Concentrations of  $A$  (solid lines) and  $B$  (dashed lines) without noise (black lines) and adding additive noise with amplitude  $\varepsilon = 3.16 \cdot 10^{-2}$  (gray lines). (b) The same trajectories plotted in the  $(A, B)$  plane. In order to maintain consistency with the discrete numerical simulations, we used in all figures a scaling of  $\delta_A = 10^{-3}$ .

common growth rate:  $f(A, B)$ , instantaneously determined by the population composition.

The growth rate function, common to both phenotypes has an increasing saturating term,  $h(B)$ , representing the production of resource by one sub-population; and a denominator  $1/(A+B)$  describing a density-dependent decrease of the growth rate. It therefore decreases with  $A$  for fixed  $B$  and is non-monotonous with  $B$  for fixed  $A$ , with a maximum at some intermediate value. All theoretical conclusions below depend only on these general features and are not sensitive to the exact functions. Computations will be shown for a hyperbolic production function  $h(B) = B/(B+V)$ .

**Results.** – System (2) has two saddle fixed points: (i) An empty state  $(A_1^*, B_1^*) = (0, 0)$  corresponding to extinction. (ii) A saddle-point corresponding to the equilibrium of  $B$  in the absence of  $A$ , given by  $f(0, B_2^*) = \alpha$ . This saddle point is stable along the line  $A = 0$  and unstable to perturbations with a nonzero  $A$  component ("invasion" of a small  $A$  population), see Supp.-Mat. A for details. Following such an invasion, the system will be driven to extinction. In a typical solution, the non-producer population  $A$  grows to a high concentration and subsequently drives both sub-populations to zero (Black lines in Fig. 1).

To incorporate the effect of random fluctuations, still assuming a well-mixed environment, we rewrite Eq. (2) as a Stochastic Differential Equation (SDE):

$$\begin{cases} dA = [f(A, B) - 1] A dt + g_A(A, B) dw_t^{(A)} \\ dB = [f(A, B) - \alpha] B dt + g_B(A, B) dw_t^{(B)} \end{cases} \quad (3)$$

where  $dw_t^{(i)}$ ,  $i = A, B$  are independent, zero mean Gaussian random variables and  $g_A, g_B$  are sufficiently smooth

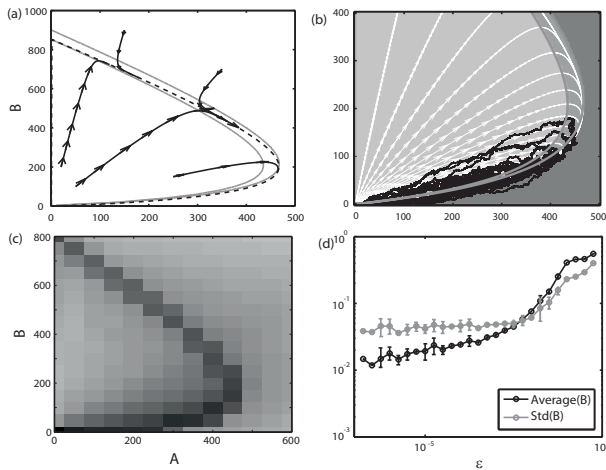


Fig. 2: (a) Nullclines (gray lines) and exemplary trajectories (black lines) show their rapid convergence to the invariant manifold and the subsequent flow along that manifold to the origin. (b) The nullclines divide space into regions with different signs of the dynamic variables derivatives. Light gray: both populations increase; medium gray:  $A$  increases, while  $B$  decreases; dark gray: both decrease. Deterministic trajectories are depicted in white arrows. A trajectory of the system with additive noise ( $\varepsilon = 3.16 \cdot 10^{-2}$ ) is shown in black on top of this picture, which cycles around the lower portion of the invariant manifold, comes close to the origin but is repeatedly kicked away by fluctuations. (c) Numerical estimate of the invariant measure. Eq. (3) was solved with 40 initial conditions on a uniform grid. A histogram representing the underlying invariant measure of the stochastic dynamics ( $\varepsilon = 10^{-1}$ ), was constructed using the number of time-steps visited by the trajectories in each bin. (d) The average and standard deviation of  $B$  over a trajectories as a function of the rescaled noise amplitude  $\varepsilon$ .

noise amplitude functions. Such noise can be, for example, the result of fluctuations in the environment, causing stochastic birth and death rates; suggesting multiplicative amplitudes,  $g_A = \varepsilon A$ ,  $g_B = \varepsilon B$ . Alternatively, noise can originate from demographic fluctuations, in which  $g_A = \varepsilon \sqrt{A}$ ,  $g_B = \varepsilon \sqrt{B}$ . Finally, noise could result from the migration of individuals from neighboring regions. Such a noise can be roughly approximated by an additive noise  $g_A = g_B = \varepsilon$ . We will later show that discrete spatial simulation produce a similar behavior to the one obtained with additive noise. These three types of noise result in qualitatively different dynamics.

Figures 1a,b (gray lines) show that with additive noise, both populations continue to fluctuate for the entire time presented and do not collapse to zero, in contrast with the deterministic trajectory. Surprisingly, the introduction of arbitrarily small noise levels induces a qualitative change in the dynamics and leads to the emergence of a stochastic attractor, keeping the trajectories away from the origin inside the coexistence regime ( $A, B > 0$ ).

The emergence of this stochastic attractor can be understood using a geometric analysis of Eq. (2). Fig. 2a

shows the nullclines, which include the entire  $A = 0$  axis and two curves defined by  $f(A, B) = 1$  and  $f(A, B) = \alpha$ . The dynamical system presented by Eq. (2) has an unstable manifold  $\Gamma$  originating from  $(A_2^*, B_2^*) = (0, B_2^*)$ , which terminates at the origin becoming the stable manifold of  $(A_1^*, B_1^*) = (0, 0)$ . For any initial condition  $A, B > 0$ , trajectories approach  $\Gamma$  exponentially, and then follow it closely towards the origin (See Fig. 2a. for examples of trajectories).

Now, consider the effect of small additive noise. Any trajectory will initially follow a noisy approximation of the fast relaxation towards the invariant manifold of the deterministic solution and follow it closely as it approaches the origin (black line Fig. 2b). However, the invariant manifold is below the two nullclines, forming a narrowing "channel" as they approach the origin; therefore it becomes increasingly improbable that the trajectory remains below the nullclines and not enter the growth region (light gray in Fig. 2b). Once a random fluctuation causes a shift in the trajectory above the nullclines into this region, it will shoot up as the two populations grow exponentially to relax rapidly again towards the invariant manifold and then follow slowly along this route back towards the origin. Thus, in the small noise limit, the structure of phase space (the nullclines and the deterministic invariant manifold) suggest a typical picture of cycling trajectories, which can get close to the origin, but have an exceedingly small probability to actually reach it. In this region the noise amplitude does not strongly affect the dynamics (see small  $\varepsilon$  values in Fig. 2d).

For larger noise values the attractor is broader and can be characterized using a self-consistent moment closure argument. Assuming a unique invariant measure with finite averages  $A_0, B_0$  and standard deviations  $\sigma_A, \sigma_B$ , the differential changes in dynamical variables weighted by the invariant measure should average to zero. These differential changes  $dA, dB$  can be computed over the ensemble of trajectories, averaged over noise realizations and initial conditions. Expanding them in moments, yields a formal hierarchy of equations. Truncating at the second moment, i.e. neglecting all moments of  $(A - A_0)$  and  $(B - B_0)$  higher than 2, yields the following equations for the first moments (Supp.-Mat. B)

$$\begin{cases} dA_0/dt = [f(A_0, B_0) - 1]A_0 + \\ + \frac{1}{2}[2\frac{\partial f}{\partial A} + A\frac{\partial^2 f}{\partial A^2}]_{A_0, B_0}\sigma_A^2 + \frac{1}{2}[A\frac{\partial^2 f}{\partial B^2}]\sigma_B^2 \\ dB_0/dt = [f(A_0, B_0) - \alpha]B_0 + \\ + \frac{1}{2}[2\frac{\partial f}{\partial B} + B\frac{\partial^2 f}{\partial B^2}]_{A_0, B_0}\sigma_B^2 + \frac{1}{2}[B\frac{\partial^2 f}{\partial A^2}]\sigma_A^2 \end{cases} \quad (4)$$

For the parameters of Fig. 2, we find that the conditions  $\langle dA_0 \rangle = \langle dB_0 \rangle = 0$  are met with the following signs

$$\begin{cases} [f(A_0, B_0) - 1]A_0 > 0 \\ [f(A_0, B_0) - \alpha]B_0 < 0 \end{cases} \quad (5)$$

Therefore  $1 < f(A_0, B_0) < \alpha$ , i.e. in this case the

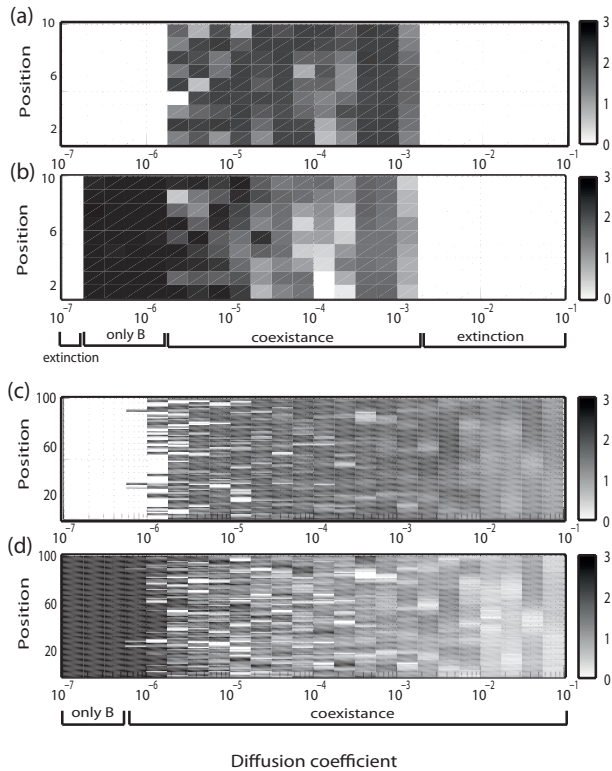


Fig. 3: **Snapshots of simulations with a discrete number of individuals in an extended one-dimensional environment.** Dynamics of the stochastic interaction producing a mean field equation as in Eq. (2) with diffusion were simulated for extended time and a snapshot of the concentrations in space is displayed. Diffusion coefficients (the same for both phenotypes; x-axis) and grid size (y-axis) were varied in different simulations. The initial conditions are uniform over all space. The grayscale represent log concentrations. (a) Log of  $A$  and (b) log of  $B$  concentrations on  $10 \times 1$  grid size; (c) Log of  $A$  and (d) log of  $B$  concentration on  $100 \times 1$  grid size. Regions of total or partial extinction are explicitly marked. One can clearly see an intermediate range of diffusion coefficients where both populations survive, which grows with increasing grid size.

average of the stochastic attractor ( $A_0, B_0$ ) lies between the two nullclines.

A similar calculation for the second moment (Supp.-Mat. B), with additive noise and hyperbolic production shows a strictly positive variance, which is consistent with simulations showing that both populations undergo fluctuating trajectories, and *neither become extinct*. Fig. 2c depicts a numerical computation of the invariant density. Fig. 2d shows the computed averages and standard deviations of  $B$  as a function of the noise amplitude. At low noise value, trajectories follow the manifold, and changing noise amplitude by four orders of magnitudes leads to a very small effect on the first moments of  $B$ . As expected, both moments increase with sufficiently large noise.

For multiplicative fluctuations, the qualitative argument described above fails. As trajectories follow the in-

variant manifold to the origin, the amplitude of the fluctuations decreases and may not be large enough to push it back into the growth regime (Supp.-Mat. Fig. C1). Indeed, applying the moment-closure approximation, the equations for the first moments ( $A_0, B_0$ ) are the same as Eq. (4). However, the second moment equations differ, with no solution other than zero ( $A_0 = B_0 = \sigma_A = \sigma_B = 0$ ; Supp.-Mat. C). Demographic fluctuations present an intermediate case where, for small population sizes, fluctuations are sub-linear but still vanish at the origin. Monte-Carlo simulations using discrete individuals, in which the probability of division/birth is determined by the environment in the same way as the growth rate in Eq. (2), show that in this case the system is again driven to extinction (Supp.-Mat. D).

Adding noise to the mean-field equations may be considered as a phenomenological approximation. However, additive noise is not required for the emergence of a noise induced attractor. The only requirement is that the probability to cross the null-clines approaches one as one approaches the origin. Such a behavior is observed in natural systems. As different types of noise gives rise to qualitatively different dynamics, it is of interest to return to a fully stochastic model and investigate its behavior directly. Therefore, we constructed a Monte Carlo simulation of two populations of discrete individuals interacting as in Eq. (2) with diffusion in a one-dimensional lattice. Each lattice site had an unlimited carrying capacity, and the number of  $A$  and  $B$  agents added/removed to each lattice site in each time interval  $\Delta t$  was computed using a binomial probability distribution (e.g. if 3.7  $B$  individual were expected to diffuse from a lattice site with population  $N$  to the neighboring lattice site in a given time interval, a binomial generator was used to estimate the number of  $B$  individual actually moving). Diffusion and reactions were performed using asynchronous updating of the lattice sites. The order at which lattice sites were updated was randomized in each time interval. Diffusion was only to neighboring lattice sites. A detailed description of the simulation platform was previously reported [20–23]. A synchronous simulation led to similar results (data not shown). Fig. 3 shows the distribution of both sub-populations in space at a given point in time, for two different lattice sizes (number of lattice sites) and for a broad range of diffusion coefficients. Coexistence by spatio-temporal fluctuations persists if the system is large enough as compared with the typical diffusion scales to allow for the existence of weakly coupled regions. This observation supports the mean field equation with additive noise as a simplified model for the fully stochastic system: even if the environment itself is homogeneous, diffusion in extended space induces an effective additive noise between neighboring regions. Note that the noise induced by the diffusion term in the simulation above has indeed no correlation in time and a standard deviation weakly affected by the amplitude (Supp.-Mat E). However, it does not have a zero mean. Instead it has a positive contribution

leading to a net movement across the nullclines, reproducing the scenario described above (Supp.-Mat. E). Interestingly, the corresponding reaction-diffusion equations do not exhibit Turing instability (Supp.-Mat. F); instead, coexistence is induced by the combination of the intrinsic demographic noise and the sensitivity of the local solution to infinitesimal additive noise.

**Conclusions.** – In summary, starting from a model with explicit description of the environment as a dynamical variable and assuming timescale separation, we derived an ecological framework for cooperative public-goods interactions. The resulting two-dimensional, nonlinear equations reflect the non-symmetric role of subpopulations with respect to the environment and their indirect mutual effect on growth. Analyzing the geometry of nullclines, we found that in the continuous mean-field limit (no noise), invasion by a cheater population results in extinction of the entire population. However, this point is dynamically unstable and is sensitive to additive noise due to the appearance of a stable stochastic attractor. These results are insensitive a wide range of model details and parameters, such as the noise amplitude, the functional dependence of growth rate on the environment, the resource extraction rate and the fitness advantage for the non-producers (e.g., lower growth instead of higher death; Supp.-Mat. D). However, different types of noise, such as multiplicative noise, do not destabilize the extinction fixed point. These results highlight the important effect of fluctuations and their nature on the basic properties of ecological systems and the possible failure of mean-field approximations [21, 24–27].

To support the realistic role of additive noise, we have shown in numerical simulations that a stochastic attractor naturally emerges by coupling diffusion with a demographic noise in an extended system. This supports a picture where the out-of-phase dynamics of different spatial regions introduces a random flow that is weakly affected by the local concentration of individuals. It provides justification for adding noise phenomenologically to the mean-field equations and shows that our simplified model captures the behavior of more complex and realistic models.

Our results represent, to the best of our knowledge, the first example of a purely stochastic emergence of a new attractor in a system with a single attractor at the absorbing state. A similar argument may hold in a variety of other systems, where extinction is the only expected outcome of the mean field system.

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