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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 nonlinear dynamical systems describing such interactions between producers and non-producers of a rapidly equilibrating common resource extracted from a finite environment. In the deterministic mean field approximation, 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 can survive. Phase space arguments and moment closure are used to characterize the attractor and show that its properties are not determined by the noise amplitude or boundary conditions, but rather it is stabilized by the stochastic nonlinear dynamics. Spatial Monte Carlo simulations with demographic fluctuations and diffusion illustrate a similar effect, supporting the validity of the two-dimensional stochastic differential equation as an approximation. The functional distribution of the noise emerges as the main factor determining the dynamical 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 deterministic dynamics. The results are discussed in a general context of the effect of noise on phase space structure.

1. 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, with many examples including extracellular enzymes [1–3] and iron chelators [4–8]. For reviews see [9–11].

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 [12, 13]. Evolutionary consequences of this argument were extensively investigated within the framework of game theory [14–16]. In this approach, individuals directly interact with one another in pairs; in well-mixed systems the probability of interaction is uniform, whereas in spatial extensions assumptions about the mode of interaction needs to be made, for example nearest neighbors. More specific to microbial dynamics, models have been developed that extend game theory to include physical aspects of the particular problem [2, 17-19]. These studies have shown

that the apparent paradox of extinction is readily solved with the addition of realistic effects such as privileged share, time-varying strategy, spatial structure and segregation, and more [20, 21].

Here, we take an ecological approach which considers physical interactions mediated by the environment [18, 22-24]. The environment is a dynamical variable which is shaped by the populations' behavior; in turn, this environment affects the growth and fitness of the same populations. We have recently developed such an approach, especially suited for the context of microbial public goods dynamics, and showed that both temporal [25] and spatial [26] fluctuations induce coexistence in nontrivial ways. In particular, simulations show that demographic noise and diffusion in space can induce long lasting spatio-temporal patterns for a broad range of intermediate diffusion coefficients [26]. This fluctuation-driven coexistence was explained by an absorbing state transition argument which relies on organism discreteness and cycles of local extinction.

In many cases, the public goods are small molecules that turn-over much more rapidly than the timescales typical of cell division. This time scale separation provides the opportunity to reduce the problem by one variable and describe the environmental dynamics through the indirect effect of the populations on themselves. This approach is widespread in ecology but has not been extensively studied in the context of public goods. We develop a general two-dimensional nonlinear dynamical system valid in this regime and investigate its sensitivity to different noise types. For a large class of such models the extinction state transforms upon introduction of infinitesimal noise to a stochastic attractor. This instability is non-perturbative, namely the attractor dimensions are not proportional to the noise amplitude. Extinction is destabilized by noise, meaning that a single progenitor (e.g. added by migration) can restore a macroscopic population, even though the deterministic equations predict that it should go back to extinction.

We find that the effect strongly depends on the noise functional shape. In particular, only additive noise destabilizes the extinction fixed point and gives rise to a stochastic attractor. 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 a stochastic attractor over a broad parameter regime.

2. Deterministic 2D ecological model

Consider two populations with concentrations A and B, sharing a 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 considered the cooperative sub-population. Once available, the resource is consumed by both producers and non-producers. In the mean-field

approximation [25, 26]:

$$\begin{cases} \dot{A} = [\mu_{A}(C) - 1]A \\ \dot{B} = [\mu_{B}(C) - \alpha]B \\ \dot{C} = h(B) - \left[\frac{\mu_{A}(C)}{Y_{A}}A + \frac{\mu_{B}(C)}{Y_{B}}B\right]. \end{cases}$$
(1)

Here time is measured in dimensionless units, where the death rate of *A* is taken to be unity. Production of the resource by *B* follows an increasing nonlinear 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 nondecreasing function of *C*, and the same yield coefficient $Y_A = Y_B = 1$. The cost of production is modeled as a higher death rate for *B*, $\alpha > 1$.

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 [25]; intuitively, it needs to consume the resource not faster than it extracts it. In what follows we assume parameters of the producer population are in the region allowing such equilibrium.

The key approximation employed here is that resource extraction and consumption are significantly faster than organism reproduction. This approximation is relevant in many biological cases, since often the public goods are small molecules that diffuse rapidly. Bacterial production and secretion of enzymes occurs on a time scale of seconds to minutes, while division typically takes 20 min to an hour. Assuming mixing of resources with no privileged share leads to a Quasi Steady-State (QSS) approximation:

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

The environmentally mediated indirect interaction between the two sub-populations is now described by their common growth rate: f(A, B), instantaneously determined by the population composition.

This growth rate function, common to both phenotypes, has an increasing saturating numerator, 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*, showing that *A* is always a burden on the shared environment; and is non-monotonous with *B* for fixed *A*, with a maximum at some intermediate value, because of the saturating benefit and linear cost of increasing the producer population (figure 1). These features represent general qualitative properties of microbial growth and resource extraction and have a crucial effect on the dynamics. All theoretical conclusions below depend on these general features and are not sensitive to the



Figure 1. Lines of constant growth function f(A, B) as a function in the (A, B) plane. Bottom: f(A, B) as a function of A for fixed B ($f_B(A)$). Right: f(A, B) as a function of B for fixed A ($f_A(B)$).



exact functions. Computations will be presented for the specific case of a hyperbolic production function h(B) = B/(B + V).

3. Results

The dynamical 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 the producing *B* population with the resource in the absence of *A*; this point occurs at $f(0, B_2^*) = \alpha$. 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 appendix 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 figure 2).

These saddles points are the intersections of the two nullclines in phase space. Given the general properties of f(A, B) described above, these nullclines create a typical

geometric structure in phase space, as can be seen in figure 4(a). The generality of this structure is illustrated in the two bottom lines of figure 3; compare left column displaying the equations of motion, to right column showing the phase space. In what follows it will be shown that the effect of noise on the nonlinear dynamical system is strongly affected by this nullcline structure, which in turn reflects the properties of the growth function.

4. Effect of stochastic fluctuations

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

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

where $dw_t^{(i)}$, i = A, B are independent, zero mean Gaussian random variables and g_A, g_B are sufficiently smooth noise amplitude functions. Such noise can be, for example, the result of fluctuations in the



Figure 3. Groups of dynamical systems determined by growth function f(A, B) properties. The first column describes the equations studied in each case. All systems converge to the origin in the mean field. The second column is the results of integrating these equations, with additive fluctuation, as a function of time. While some systems exhibit dynamics similar to the one obtained in the mean field (first three rows), others have oscillating solutions around a non-zero stochastic attractor. The third column represents the same trajectories plotted in the (*A*, *B*) plane. The last column describes the lines of constant growth function f(A, B) as in figure 1. When the functional shape of f(A, B) is similar to figure 1, a stochastic attractor emerges (last two rows). When it is different, even if the noise and the boundary and initial condition are the same, a stochastic attractor does not emerge.

environment, causing stochastic birth and death rates, suggesting multiplicative amplitudes, $g_A = \varepsilon A$, $g_B = \varepsilon B$. It can also be the result of additive noise in C in the original three variable system (1), that would translate after the QSS approximation into a multiplicative noise in A and B. Alternatively, noise can originate from demographic fluctuations, leading to: $g_A = \varepsilon \sqrt{A}$, $g_B = \varepsilon \sqrt{B}$. Finally, noise could result from the migration of individuals from neighboring regions. This can be roughly approximated by an additive noise $g_A = g_B = \varepsilon$. We will later show that discrete spatial simulation produce a behavior similar to the one obtained with additive noise. A more complex nonlinear noise can emerge from the effect of additive noise in A and B on the noise level in C in the original equations. This nonlinear noise is shown to have an effect to the linear noise in appendix B.

Figures 2(a), (b) (gray lines) show solutions of equation (3) for the case of additive noise. It is seen 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 equation (2). Figure 4(a) shows the nullclines, which include the

entire A = 0 axis and two curves defined by f(A, B) = 1 and $f(A, B) = \alpha$ (depicted by gray solid lines). The dynamical system presented by equation (2) has an invariant manifold connecting the two fixed points, namely, a manifold with the property that initial conditions starting in it will give rise to trajectories that remain inside the same manifold (in this case, a line). This manifold Γ originates from $(A_2^*, B_2^*) = (0, B_2^*)$; trajectories move away from this point, and terminate at the origin along the stable manifold of $(A_1^*, B_1^*) = (0, 0)$. This manifold is depicted by a dashed black line in figure 4(a). For any initial condition A, B > 0, trajectories will approach Γ exponentially fast and then follow it closely towards the origin. (See figure 4(a), black lines with arrows, for examples of trajectories).

Now, consider the effect of small additive noise on this phase space structure. Any trajectory will initially follow a noisy approximation of the fast relaxation towards the invariant manifold and then proceed close to that manifold as it approaches the origin (black line figure 4(b)). However, the invariant manifold crosses between the two nullclines, which form a narrowing 'channel' as they approach the origin; therefore it becomes increasingly improbable that the noise trajectory remains below the nullclines and does not enter the growth region (light gray in figure 4(b)).



Figure 4. (a) Deterministic dynamics: 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 single long trajectory of the system with additive noise ($\varepsilon = 3.16 \times 10^{-2}$) 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. Equation (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 by counting 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 ε .

While the noise can in principle lead to negative values, these are avoided throught reflecting boundary conditions. Once a random fluctuation causes shifts in the trajectory above the nullclines into the growth 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. Accordingly, the moments of the stochastic attractor in this region, are insensitive to the noise amplitude, as seen in figure 4(d) in the regions of small ε .

These geometric considerations hold also for the nonlinear systems described in figure 3, two bottom rows, since they depend on qualitative features of the nullclines.

For larger noise values, the attractor is broader and can be characterized using a self-consistent moment closure argument. We assume a unique point density, namely, a probability density for a trajectory to visit that point in phase space. It is computed by initiating a large sample of trajectories at different parts of phase space and following them over time. If this point density has finite averages A_0 , B_0 and standard deviations σ_A , σ_B , the differential changes in dynamical variables weighted by the point density 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 (see appendix C for the justification of truncating beyond the second moment):

$$dA_0/dt = [f(A_0, B_0) - 1]A_0$$

$$+ \frac{1}{2} \left[2\frac{\partial f}{\partial A} + A\frac{\partial^2 f}{\partial A^2} \right]_{A_0, B_0} \sigma_A^2 + \frac{1}{2} \left[A\frac{\partial^2 f}{\partial B^2} \right] \sigma_B^2$$

$$dB_0/dt = [f(A_0, B_0) - \alpha]B_0$$

$$+ \frac{1}{2} \left[2\frac{\partial f}{\partial B} + B\frac{\partial^2 f}{\partial B^2} \right]_{A_0, B_0} \sigma_B^2 + \frac{1}{2} \left[B\frac{\partial^2 f}{\partial A^2} \right] \sigma_A^2.$$
(4)

For the parameters of figure 4, we find that the conditions $\langle dA_0 \rangle = \langle dB_0 \rangle = 0$ are met with the following signs

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

Therefore $1 < f(A_0, B_0) < \alpha$ (i.e. in this case the average of the stochastic attractor (A_0, B_0) lies between the two nullclines).

A similar calculation for the second moment (appendix D), 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*. Figure 4(c) depicts a numerical computation of the density point. Figure 4(d) shows the computed averages and standard deviations of the producing population *B* as a function of the noise amplitude. As discussed above, at low noise trajectories follow the nullclines 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.

While we have here studied a specific realization, the failure of the mean field approximation and the emergence of a stochastic attractor as described, result from general properties of the growth function f(A, B). Different growth functions with similar shapes yield similar results (figure 3, two bottom rows). Moreover, growth functions with different shapes in equation (3), with similar boundary conditions and noise levels, converge to the extinction state as predicted by deterministic dynamics (figure 3, three top rows). This shows that the results presented above are a consequence of intrinsic properties of the dynamics (e.g. phase space structure), rather than being a trivial consequence of noise or boundary conditions.

As mentioned, reflecting boundary conditions prevent negative values. However, these events of reflection from the walls are rare and they do not provide the mechanism for population maintenance (see appendix E for evidence of long times between reflections from the walls).

For multiplicative fluctuations, the qualitative argument described above fails. As trajectories follow the invariant manifold to the origin, the amplitude of the fluctuations decreases and may not be large enough to push them back into the growth regime (appendix F, figure 11). Indeed, applying the moment-closure approximation, the equations for the first moments (A_0, B_0) are the same as equation (4). However, the second moment equations differ, with no solution other than zero $(A_0 = B_0 = \sigma_A = \sigma_B = 0; \text{ appendix F}).$ Demographic fluctuations present an intermediate case where, for small population sizes, fluctuations are sub-linear but still vanish at the origin. Numerical integration with demographic noise shows that this vanishing induces a collapse of the stochastic system to the extinction fixed point, similar to multiplicative noise (appendix F, figure 11). 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 equation (2), show that in this case the system is indeed driven to extinction (data not shown).

5. Realization of additive noise

Adding noise to the mean-field equations may be considered as a phenomenological approximation. However, strictly additive noise is not required for the emergence of a stochastic attractor; the only requirement is that the probability to cross the null-clines approaches one near the origin. As different types of noise gives rise to qualitatively different dynamics, it is of interest to return to a full two-variable stochastic model and investigate its behavior directly. Therefore, we constructed a Monte Carlo simulation of two populations of discrete individuals interacting as in equation (2) with diffusion in a one-dimensional lattice. Each lattice can contain many individuals; the population composition places constraints on the possible growth rate. The number of A and B individuals added/removed to each lattice site in each time interval Δt was computed using a binomial probability distribution. 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 took place between neighboring lattice sites. A detailed description of the simulation platform was previously reported [26-29]. Figure 5 shows the distribution of both sub-populations in space at a given time, for two different lattice sizes (10 for a, b, 100 for c, d) and for a broad range of diffusion coefficients. Coexistence by spatio-temporal fluctuations persists for a large intermediate range 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. Gillespie simulations produce similar results (appendix G). The noise induced by the diffusion term in the simulation has, to a good approximation, no correlation in time, a zero average and a standard deviation weakly affected by the amplitude. Figure 6 show the means and standard deviations of the diffusion terms in the simulation of figure 5. Specifically, for each lattice site and each time step the contribution of diffusion was measured from its neighbors. A diffusion coefficient that leads to coexistence in the spatial simulation was used. The diffusion term produces an effective noise with an average close to 0 (figure 6(a)). One can see that large changes in the local concentration has a weak effect on the noise standard deviation (figure 6(b)). The absence of correlation can be observed in figure 6(c). We conclude that the similar effect of spatial, explicitly discrete models and of non-spatial models with additive noise suggests that these two types of realizations are similar, one providing a good approximation of the other. Further study is required to determine whether this similarity can be generalized to a large class of systems.

6. Discussion

Starting from a model with explicit description of the environment as a dynamical variable, relying on the approximation of rapid equilibration of resource and assuming timescale separation, we derived an



Figure 5. Snapshots of simulations with discrete numbers of individuals in an extended one-dimensional environment. Dynamics of the stochastic interaction producing a mean field equation as in equation (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 (top two versus bottom two panels) were varied in different simulations. The *y*-axis denotes position along the one-dimensional lattice. The initial conditions are uniform over all space. The grayscale represent log concentrations. (a) log of *A* and (b) log of *B* concentrations on 10×1 grid size; (c) log of *A* and (d) log of *B* concentration on 100×1 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 increases with increasing grid size.



Figure 6. (a) Mean of the diffusion terms of *A* (black line) and *B* (gray line) as a function of the values of *A* and *B*, respectively. (b) Standard deviations of the diffusion terms of *A* (black line) and *B* (gray line) as a function of the values of *A* and *B*, respectively. (c) Autocorrelation of the diffusion terms of *A* (black line) and *B* (gray line) as a function of time. The simulation runs on 100x1 one dimensional lattice, with the same parameters as figure 5, with a diffusion coefficient of 0.1.

ecological model for cooperative public-goods interactions. The resulting two-dimensional nonlinear dynamical system reflects the non-symmetric role of subpopulations with respect to the environment and their indirect mutual effect on growth. The model retains the total population size as a dynamical variable in addition to the fractions of the two competing-cooperating sub-populations. The importance of maintaining this ecological factor in the model can be appreciated by comparing our results to recent models that have addressed explicitly the diffusivity of public goods in cooperative population models [24, 30]. In these spatial models, each lattice site could contain only one cell. The results showed no coexistence in a rapidly equilibrating resource limit [24], or a coexistence that depended on privileged share overcoming the diffusion [30]. This is in contrast to the results presented here and in [26].

The role of population size was highlighted also in [31]. Here the formalism of the Wright–Fisher model was extended to a varying population size that depends on its composition. This work illustrated clearly that the invasion probability in finite mixed population reflects not only the relative fitness but also the population size, and indeed can result in coexistence. In our model the population size reflects its structure without explicitly assuming a form for the carrying capacity, as discussed in the model presentation. A carrying capacity effect thus emerges naturally from our model without the need to postulate it as an additional assumption.

Analyzing the geometry of nullclines in the two dimensional model, we found that in the continuous mean-field approximation (no noise), invasion by a non-producing population results in extinction of the entire population. Introducing noise to the differential equations, we found that this point is dynamically unstable and is sensitive to additive noise; this instability results in the appearance of a stable stochastic attractor. These results are insensitive to a wide range of model details and parameters, such as the noise amplitude, the functional dependence of growth rate on the environment, the exact form of resource extraction rate and the fitness advantage for the non-producers (e.g., lower growth instead of higher death; data not shown). However, other types of noise, such as multiplicative noise, do not destabilize the extinction fixed point.

To support the realistic role of additive noise in the differential equations, we have shown in numerical simulations that coupling of diffusion with a demographic noise in an extended system may be indeed approximated by an effective additive noise in a well mixed system. This supports a picture where the outof-phase dynamics of different spatial regions introduces a random flow that is weakly affected by the local concentration of individuals. However, additional investigation is required to fully justify this approximation of adding noise phemonenologically to the mean-field equations and show that our simplified model with additive noise 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 absorbing state attractor. A similar argument may hold in a variety of other systems, where extinction is the only expected outcome of the mean field system. While in most dynamical system with a single absorbing state at the origin, the introduction of additive noise and reflecting boundary condition would keep the system close to the origin, there may be a wide category of models with long trajectories, where such perturbations could have a drastic effect. More generally these results highlight, as seen many times before, the important effect of fluctuations and their nature on the basic properties of ecological systems and the possible failure of mean-field approximations [27, 32–35].

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Appendix A

The dynamical system (2) with hyperbolic production has a fixed point $(A^*, B^*) = (0, 1/\alpha - V)$. Since *A* and *B* are non-negative densities, this fixed point exists if and only if $V < 1/\alpha$. This state is stable in the *B* direction, and unstable in the *A* direction. Therefore, this fixed point is only stable in the system with no *A*.

System (2) also has a fixed point at the origin. Note that the dynamics at the zero point itself are not defined, since B/[(A + B)(B + V)] is not defined for A = B = 0. Only deviations that are on the *B*-axis are attracted to the $(A^*, B^*) = (0, 1/\alpha - V)$ fixed point. All deviations with a positive *A* value are attracted to the zero state.

Appendix **B**

Additional noise that can affect the results of the system is additive noise in the full model. The three variables model is:

$$\begin{cases} \frac{dA}{dt} = [C - \delta_1]A\\ \frac{dB}{dt} = [C - \delta_2]B\\ \frac{dC}{dt} = \frac{B}{B+V} - C(A + B). \end{cases}$$
(6)

Additive noise in this model creates another indirect noise resulting from the effect of *A* and *B* on *C*. Assume that we have additive noise in *A* and *B*, the dynamic of *C* changes to be $\frac{dC}{dt} = \frac{B+\varepsilon_2}{B+\varepsilon_2+V} - C(A + \varepsilon_1 + B + \varepsilon_2)$ while ε_1 and ε_2 are the fluctuations in *A* and *B* Respectively. In QSS $C = \frac{B+\varepsilon_2}{(B+\varepsilon_2+V)(A+\varepsilon_1+B+\varepsilon_2)} = f(\varepsilon_1, \varepsilon_2)$. The Tailor Series of *C* at $(\varepsilon_1, \varepsilon_2) = (0, 0)$ is C = $f(0, 0) + f_{\varepsilon_1}(0, 0)\varepsilon_1 + f_{\varepsilon_2}(0, 0)\varepsilon_2$ while f(0, 0) = $\frac{B}{(B+V)(A+B)}$; $f_{\varepsilon_1}(0, 0) = -\frac{B(B+V)}{[(B+V)(A+B)]^2}$; and $f_{\varepsilon_2}(0, 0) = \frac{AV-B^2}{[(B+V)(A+B)]^2}$. Thus, $C = \frac{B}{(B+V)(A+B)} - \frac{B(B+V)}{[(B+V)(A+B)]^2}\varepsilon_1 + \frac{AV-B^2}{[(B+V)(A+B)]^2}\varepsilon_2$ and the matching







two variables model is:

$$\begin{cases} \frac{\mathrm{d}A}{\mathrm{d}t} &= \left[\frac{B}{(B+V)(A+B)} - \delta_{1}\right]A \\ &- \frac{B(B+V)A}{\left[(B+V)(A+B)\right]^{2}}\varepsilon_{1} \\ &+ \frac{(AV-B^{2})A}{\left[(B+V)(A+B)\right]^{2}}\varepsilon_{2} \end{cases} \\ \frac{\mathrm{d}B}{\mathrm{d}t} &= \left[\frac{B}{(B+V)(A+B)} - \delta_{2}\right]B \\ &- \frac{B^{2}(B+V)}{\left[(B+V)(A+B)\right]^{2}}\varepsilon_{1} \\ &+ \frac{(AV-B^{2})B}{\left[(B+V)(A+B)\right]^{2}}\varepsilon_{2}. \end{cases}$$

In this model both populations survive (figure 7).

Appendix C

We have estimated the moments of the distribution of A and B as a function of the noise level. As discussed in the main text, the effect of the noise level on the moment is limited. The more important point is that for all noise levels, the third and fourth moments are much smaller than the first and second moment and can thus be ignored in the moment closure approach (figure 8).

Appendix D

Denote the averages of A(t) and B(t) over all possible realization with a fixed initial condition, at fixed time t by $A_0(t)$ and $B_0(t)$, respectively. Similarly, denote the variances as $\sigma_A^2(t)$ and $\sigma_B^2(t)$. The expected change in A(t) can be computed to be:

(7)

$$E(\Delta A) = E[([f(A(t), B(t)) - 1])) \times ((A(t))dt + \varepsilon dw_t^A] \qquad (8)$$

$$= E([f(A(t), B(t)) - 1]A(t))dt.$$

Since the added noise is assumed to be of zero mean; and similarly for the *B* derivative. If *A* and *B* sample an invariant measure, i.e. assuming the dynamics are ergodic, we can estimate equation (8) to be

$$E(\Delta A) = \int \Delta A \ p(A, B) \ dAdB$$

=
$$\int dAdB \ p(A, B) [f(A, B) - 1]Adt$$
(9)

$$E(\Delta B) = \int \Delta B \ p(A, B) \ dAdB$$

= $\int dAdB \ p(A, B)[f(A, B) - \alpha]Bdt,$
(10)

where p(A, B) is the probability density of trajectories passing in a given position infinitesimal rectangle in phase space $[A, A + dA] \times [B, B + dB]$. This can be approximated to first order by

$$E(\Delta A) = [f(A_0, B_0) - 1]A_0 dt + \frac{1}{2} \Big[2\frac{\partial f}{\partial A} + A\frac{\partial^2 f}{\partial A^2} \Big]_{A_0, B_0} \sigma_A^2 dt + \frac{1}{2} \Big[A\frac{\partial^2 f}{\partial B^2} \Big]_{A_0, B_0} \sigma_B^2 dt = \Big[\frac{B_0}{(B_0 + V)(A_0 + B_0)} - 1 \Big] A_0 dt \frac{B_0^2 (B_0 + V)^2 \sigma_A^2 + A_0 (3 V A_0 B_0 + V A_0^2 + V^2 A_0 - B_0^3) \sigma_B^2}{(B_0 + V)^3 (A_0 + B_0)^3} dt,$$
(11)

where odd terms cancel the last line is specifically for hyperbolic production. Similarly for *B*

$$\begin{split} E(\Delta B) &= [f(A_0, B_0) - \alpha] B_0 dt \\ &+ \frac{1}{2} \bigg[2 \frac{\partial f}{\partial B} + B \frac{\partial^2 f}{\partial B^2} \bigg]_{A_0, B_0} \sigma_B^2 dt + \frac{1}{2} \bigg[B \frac{\partial^2 f}{\partial A^2} \bigg]_{A_0, B_0} \sigma_A^2 dt \\ &= \bigg[\frac{B_0}{(B_0 + V)(A_0 + B_0)} - \alpha \bigg] B_0 dt \\ &+ \frac{B_0^2 (B_0 + V)^2 \sigma_A^2 + (V^2 A_0^2 - V B_0^3 - 3V A_0 B_0^2 - A_0 B_0^3) \sigma_B^2}{(B_0 + V)^3 (A_0 + B_0)^3} dt. \end{split}$$

$$(12)$$

We can write the average of ΔA and ΔB :

$$\begin{cases} E(\Delta A) = [f(A_0, B_0) - 1]A_0 dt \\ + r_A(A_0, B_0, \sigma_A, \sigma_B) dt \\ E(\Delta B) = [f(A_0, B_0) - \alpha]B_0 dt \\ + r_B(A_0, B_0, \sigma_A, \sigma_B) dt, \end{cases}$$

where

$$\begin{cases} r_A (A_0, B_0, \sigma_A, \sigma_B) = \\ - \frac{B_0^2 (B_0 + V)^2 \sigma_A^2 + A_0 (3 V A_0 B_0 + V A_0^2 + V^2 A_0 - B_0^3) \sigma_B^2}{(B_0 + V)^3 (A_0 + B_0)^3} \\ r_B (A_0, B_0, \sigma_A, \sigma_B) \\ = \frac{B_0^2 (B_0 + V)^2 \sigma_A^2 + (V^2 A_0^2 - V B_0^3 - 3V A_0 B_0^2 - A_0 B_0^3) \sigma_B^2}{(B_0 + V)^3 (A_0 + B_0)^3}. \end{cases}$$

For most parameters studied here, the function r_A is negative and the function r_B is positive. A sufficient condition for this is $\sigma_B \ll \sigma_A$. Similar equations can be computed for the second moment in the case of additive noise, where we ignore higher moments

$$E(\Delta \sigma_A^2) = 2 \left[\frac{B_0^2}{(B_0 + V)(A_0 + B_0)^2} - 1 \right] \sigma_A^2 \mathrm{d}t + \varepsilon^2 \mathrm{d}t$$

and similar for the second moment of B

$$E(\Delta \sigma_B^2) = 2 \left[\frac{2A_0 B_0 V + B_0^2 (A_0 + V)}{(B_0 + V)^2 (A_0 + B_0)^2} - \alpha \right] \sigma_B^2 dt + \varepsilon^2 dt.$$

If there is a stochastic attractor, the averages should vanish, and one obtains the following four equations for

hyperbolic production:

$$\begin{cases} (a) \left[\frac{2B_0A_0V + B_0^2(A_0 + V)}{(B_0 + V)^2(A_0 + B_0)^2} - \alpha \right] \sigma_B^2 \\ + \varepsilon^2 = 0 \\ (b) 2 \left[\frac{B_0^2}{(B_0 + V)(A_0 + B_0)^2} - 1 \right] \sigma_A^2 \\ + \varepsilon^2 = 0 \\ (c) [f(A_0, B_0) - 1] \cdot A_0 - \frac{B_0^2(B_0 + V)^2\sigma_A^2}{(B_0 + V)^3(A_0 + B_0)^3} \quad (13) \\ - \frac{A_0(3VA_0B_0 + VA_0^2 + V^2A_0 - B_0^3)\sigma_B^2}{(B_0 + V)^3(A_0 + B_0)^3} = 0 \\ (d) [f(A_0, B_0) - \alpha] \cdot B_0 \\ + \frac{B_0^2(B_0 + V)^2\sigma_A^2}{(B_0 + V)^3(A_0 + B_0)^3} \\ + \frac{(V^2A_0^2 - VB_0^3 - 3VA_0B_0^2 - A_0B_0^3)\sigma_B^2}{(B_0 + V)^3(A_0 + B_0)^3} = 0. \end{cases}$$

Therefore, the steady state values for the second moment (from equations (13)-(a)-(b)):

$$\begin{cases} \sigma_A = \frac{1}{\sqrt{2}} \left[1 - \frac{(B_0)^2}{(B_0 + V)(A_0 + B_0)^2} \right]^{-1/2} \varepsilon \\ \sigma_B = \frac{1}{\sqrt{2}} \left[\alpha - \frac{2B_0A_0V + (B_0)^2(A_0 + V)}{(B_0 + V)^2(A_0 + B_0)^2} \right]^{-1/2} \varepsilon \end{cases}$$
(14)

showing that it attains a nonzero value. Figure (9) depicts the solution of (13).

Appendix E

Adding noise to the system in equation (2) has the potential to bring the populations below 0. In order to prevent negative values, the stochastic simulation has reflecting boundary conditions for all noise types preventing any negative values. Note that a wall boundary condition would do the same, since the additive noise would remove us from the wall. Note, importantly that a stochastic attractor is obtained that rarely encounter the boundary. This attractor is the result of the positive feedback of the producers on themselves and is expressed by a net contribution to the growth term of the second order noise term. In order to show that this is indeed the case, we set a threshold near B = 0 ($B = 10^{-4}$), and computed the distribution of time periods spent above the threshold, and the same distribution below the threshold. While the distribution of times above the threshold spans many orders, the distribution of times below threshold is limited to short interval. Thus, once the trajectory escapes the absorbing state, it passes through a long trajectory far from the boundaries. The typical time between encounters with the wall is not a function of the production saturation level, but is decreasing linearly with the noise level, since as the noise level increase so does the random probability of making a random jump beyond to negative values (figure 10).

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Figure 10. Histogram of the time periods spent above the threshold (solid black line with circles), and below the threshold (gray bar). The threshold $B = 10^{-4}$.

Appendix F

If the fluctuations in the population growth rates are multiplicative:

$$\begin{cases} (a) dA = \left[\frac{B}{(B+V)(A+B)} - 1\right] A dt + \varepsilon A dw \\ (b) dB = \left[\frac{B}{(B+V)(A+B)} - \alpha\right] B dt + \varepsilon B dw. \end{cases}$$
(15)

The dynamics of the first moment are equal to the ones obtained for the additive noise (equations (11) and (12) in appendix D and figure 9). However, the equations for the second moment are different. For

hyperbolic production, they are:

$$E(\Delta \sigma_A^2) = \left(2 \left[\frac{B_0^2}{(B_0 + V)(A_0 + B_0)^2} - 1 \right] \sigma_A^2 \right) dt + (\varepsilon^2 (A_0^2 + \sigma_A^2)) dt.$$
(16)

Similarly for *B*:

$$E(\Delta \sigma_B^2) = \left(2 \left[\frac{2B_0 A_0 V + B_0^2 (A_0 + V)}{(B_0 + V)^2 (A_0 + B_0)^2} - \alpha \right] \sigma_B^2 \right) dt \qquad (17)$$

+ $(\varepsilon^2 (B_0^2 + \sigma_B^2)) dt.$

Therefore the steady-state conditions for the stochastic attractor are











$$\begin{cases} (a) 2 \left[\frac{2B_0 A_0 V + B_0^2 (A_0 + V)}{(B_0 + V)^2 (A_0 + B_0)^2} - \alpha \right] \sigma_B^2 \\ + \varepsilon^2 (B_0^2 + \sigma_B^2) = 0 \\ (b) 2 \left[\frac{B_0^2}{(B_0 + V) (A_0 + B_0)^2} - 1 \right] \sigma_A^2 \\ + \varepsilon^2 (B_0^2 + \sigma_B^2) = 0 \\ (c) [f (A_0, B_0) - 1] \cdot A_0 \\ - \frac{B_0^2 (B_0 + V)^2 \sigma_A^2}{(B_0 + V)^3 + (A_0 + B_0)^3} \\ - \frac{A_0 (3VA_0 B_0 + VA_0^2 + V^2 A_0 - B_0^3) \sigma_B^2}{(B_0 + V)^3 (A_0 + B_0)^3} = 0 \\ (d) [f (A_0, B_0) - \alpha] \cdot B_0 \\ + \frac{B_0^2 (B_0 + V)^2 \sigma_A^2}{(B_0 + V)^3 + (A_0 + B_0)^3} \\ + \frac{(V^2 A_0^2 - V B_0^3 - 3VA_0 B_0^2 - A_0 B_0^3) \sigma_B^2}{(B_0 + V)^3 (A_0 + B_0)^3} = 0. \end{cases}$$

The only solution of equation (18) is $A_0 = B_0 = \sigma_A = \sigma_B = 0$, as can be seen in figure 12.

Appendix G

Two types of simulations were used: Synchroneous Monte Carlo simulation, and a Gillespie model. Monte Carlo simulations of the systems studied have been performed on one dimensional lattice. This stochastic simulation includes a discrete number in each lattice point, and is run in discrete space. The population size in each lattice point was initiated in a Poisson distribution around the initial value. At each lattice point the probability of each reaction was computed, and the reactions were performed according to the prescribed probabilities. At high reaction rates, we used a Poisson approximation. The simulation was described in detail in previous publications [26–29, 32, 36]. In parallel, Gillespie simulations of the systems studied have been performed on one dimensional lattice. This simulation includes discrete number in each lattice point, and is run in discrete space. The population size in each lattice point was initiated in a Poisson distribution around the initial value. At each time step, the probability of each reaction was computed, and the time to the next reaction was drawn from the corresponding exponential distribution. The reaction with the lowest time was performed according to the prescribed probability. The simulation updating was asynchronous. The results of both Gillespie and synchronous simulations are similar (figure 13).

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