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Bounding the quality of stochastic oscillations in population models

S. Risau-Gusman[1,a] and G. Abramson[1,2,b]

[1] Centro Atómico Bariloche and CONICET, 8400 S.C. de Bariloche, Argentina
[2] Instituto Balseiro, 8400 S.C. de Bariloche, Argentina

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Abstract. We analyze general two-species stochastic models, of the kind generally used for the study of population dynamics. Although usually defined *a priori*, the deterministic version of these models can be obtained as the infinite volume limit of many stochastic models (which are necessarily defined by more parameters than the deterministic one). It is known that damped oscillations in a deterministic model usually correspond to oscillatory-like fluctuations in their deterministic counterparts. The quality of these "oscillations" depends on details of each stochastic model. We show, however, that the parameters of the deterministic system are generally enough to obtain very good bounds for the quality of "oscillations" in *any* of its stochastic counterparts. These bounds are shown to depend on only one dimensionless parameter.

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It is well known that the dynamics of many systems of two species can display an oscillatory behavior in the populations of both agents. This happens in predator-prey systems [1], in models of measles epidemics [2], in chemical systems such as those exemplified by the Brusselator [3], etc. These systems are usually modelled by a set of two coupled ordinary differential equations, which are assumed to represent a macroscopic level of description of the system. Oscillations can appear in these models as limit-cycle solutions to the equations. However, it frequently happens that the macroscopic model only has *damped* oscillatory solutions, even though the modelled system displays sustained oscillations in the same region of parameter values. Examples of this are not uncommon in population dynamics (see, e.g., the discussion in [4] with regard to predator-prey and measles problems).

It has often been noted that the stochastic counterpart of these models — assumed to represent a more microscopic description of the same system — usually do display a kind of *sustained* oscillatory behavior, with a frequency very similar to the one of the damped solutions of the differential equations [5–7] (see Fig. 1 for an example based on a susceptible-infected epidemic model). These oscillations are said to be generated by environmental [8] or demographic noise [9]. The problem is that stochasticity precludes a clear-cut definition of "oscillations" for such systems.

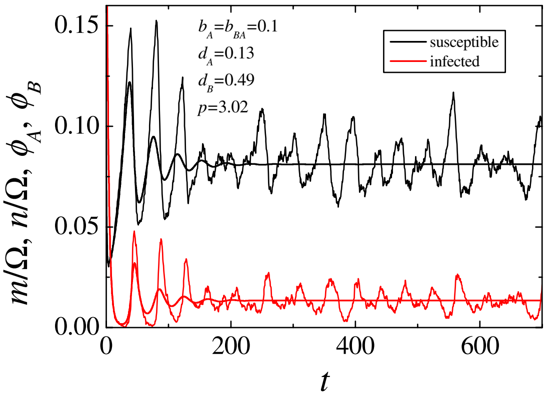

Fig. 1. Deterministic dynamics (smooth lines) and one stochastic realization (fluctuating lines) of an SI epidemic model (susceptible and infected, respectively A and B, with populations m and n and densities ϕ_A and ϕ_B). The dynamics includes birth and death processes in both populations, and contagion. A self-limiting intraspecific competition mechanism is implemented as in [9,12], with a total system size $\Omega = 5 \times 10^5$. See the text for details of the model.

The usual approach is to use a quality factor for the stochastic fluctuations. This factor is defined as some relative measure of the width of a peak of the power spectrum of the fluctuations [10]. The narrower this peak is, the more oscillatory the fluctuations will look. Of course, this quality factor depends on the parameters defining the

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[a] e-mail: `srisau@cab.cnea.gov.ar`
[b] e-mail: `abramson@cab.cnea.gov.ar`

corresponding model. It is natural to hope that different stochastic counterparts of the same deterministic model could display very different quality factors. But, how different could they be? This is the question we address in this article, for systems of two populations.

We define a dimensionless quantity, ϵ, that depends solely on the parameters of the deterministic model, and show that both the quality factor and the position of the peak are bounded by functions of only this quantity. For a wide range of values of ϵ, the upper and lower bounds are very close, showing that the parameters defining the deterministic system give a very good characterization of the oscillatory quality of the fluctuations in any of its stochastic counterparts. In other words, we show that the quality of the oscillations is only weakly dependent on the details of the underlying demographic noise.

Let us consider systems of two populations, A and B, described by stochastic variables $m(t)$ and $n(t)$. The state of the system is defined by the joint probability $P(m, n; t)$ that the system has m individuals of species A, and n individuals of species B. The transition from a state with (m, n) individuals to a state with $(m+i, n+j)$ individuals takes place at a rate:

$$T(m+i, n+j|m, n) = f(\Omega) T_{ij} \left(\frac{m}{\Omega}, \frac{n}{\Omega} \right), \qquad (1)$$

where $-k < i < k$ and $-k < j < k$. Ω is a scale parameter that governs the fluctuations of the stochastic evolution. Its precise definition depends on the system, but one chooses it in such a way that for large Ω the fluctuations are small. It usually represents the volume containing the reactants in chemical systems [11], or the available resources in biological ones [9]. The constant k gives the maximal number of elements that can appear, or disappear, from a given population at each step of the dynamics. The most common choice are one-step processes, with $k = 1$.

For the purpose of illustrating the kind of systems just defined, it is worth introducing a simple susceptible-infected epidemic system (SI). The total population of a biological species is divided into two classes: susceptible individuals (S) and infected ones (I), corresponding to the species A and B just discussed. The discrete populations of S and I are m and n. The total possible population is demographically limited by a system volume Ω, measured in units of individuals. Reproduction takes place only if space is available, thus representing indirect intra-specific competition. This available space (or any other resource) is modeled by a fictitious population E: $\Omega = m + n + E$ (see [12] for details). Each one of the three distinct (one-step) processes at the individual level: reproduction, death and contagion, involves one or more possible transitions in the microscopic state of the system. Each one of these, in turn, is characterized by a transition probability T_{ij}. Let us consider that individuals reproduce asexually, with both S and I giving birth to new susceptible members. In addition, let us say that there is no vertical transmission of the infection, so that no infected are born. The usual representation of birth in the form of chemical reactions reads:

$$\begin{aligned} \text{birth to susceptibles: } & S + E \xrightarrow{b_A} S + S, \\ \text{birth to infected: } & I + E \xrightarrow{b_{BA}} I + S, \end{aligned} \qquad (2)$$

where the parameters above the arrows represent the rates at which each of the processes occur. The transitions represented by equations (2), incrementing in 1 the population of susceptibles, take place in the system with a probability:

$$T_{10} = 2b_A \frac{m}{\Omega} \frac{E}{\Omega - 1} + 2b_{BA} \frac{n}{\Omega} \frac{E}{\Omega - 1}. \qquad (3)$$

The factor 2 represents the two distinct ways of choosing the pairs $\{S, E\}$ and $\{I, E\}$ for interaction in equations (2).

Death of individuals of both classes, in a similar way, can be found to occur with probabilities $T_{-10} = d_S m/\Omega$ and $T_{0-1} = d_I n/\Omega$ respectively (with appropriate death rates). Contagion, finally, involves steps in the two population classes, with: $T_{-11} = 2pmn/[\Omega(\Omega - 1)]$, where p is the rate of contagion in pair interactions of a susceptible and an infected individuals. All the specific examples shown in this work correspond to implementations of this SI model, either in analytical calculations or in numerical simulations of the stochastic model.

We return now to the general treatment of two-species models. The evolution of the probability $P(m, n; t)$ is given by the master equation [11]:

$$\begin{aligned} \frac{\partial P(m, n; t)}{\partial t} = & \sum_{ij} P(m-i, n-j; t)\, T_{ij} \left(\frac{m-i}{\Omega}, \frac{n-j}{\Omega} \right) \\ & - P(m, n; t) \sum_{ij} T_{ij} \left(\frac{m}{\Omega}, \frac{n}{\Omega} \right), \end{aligned} \qquad (4)$$

where, as in the rest of this article, the summation indices run from $-k$ to k.

Except for a few simple cases, this equation is extremely difficult to solve exactly. For this reason many methods have been devised to look for approximate solutions. One such method is van Kampen's expansion [11], which is a systematic expansion in terms of Ω^{-1}, the first order of which reproduces the macroscopic equation. In the following we sketch the main steps leading to the series solution (a detailed account can be found in van Kampen's book [11]).

If one assumes that, at time zero, the system is in a state where both populations have well defined macroscopical values, $P(m, n) = \delta(m - m_0)\delta(n - n_0)$, with the initial values of order $O(\Omega)$, it is reasonable to expect that at later times $P(m, n)$ will have a sharp peak at some position of order $O(\Omega)$ (in both populations), and a width of order $O(\Omega^{1/2})$. That is, the fluctuating variables will satisfy $m = \Omega\phi_A + \sqrt{\Omega}\xi_A$ and $n = \Omega\phi_B + \sqrt{\Omega}\xi_B$, where the variables ϕ represent the "macroscopic" evolution, while the stochastic variables ξ represent fluctuations around them. Observe that this ansatz implies that the fluctuations vanish with the system size in a prescribed fashion.

Replacing this in equation (4), equating terms of the same order in Ω and adequately rescaling the time, one obtains, for the leading order:

$$\begin{aligned} \dot{\phi}_A &= \sum_{ij} i\, T_{ij}(\phi_A,\phi_B) \equiv C_A(\phi_A,\phi_B), \\ \dot{\phi}_B &= \sum_{ij} j\, T_{ij}(\phi_A,\phi_B) \equiv C_B(\phi_A,\phi_B). \end{aligned} \quad (5)$$

These equations, called *deterministic* or *macroscopic*, are usually the starting point of many models of chemical and biological systems. They are generally written down from macroscopic considerations of the population dynamics, disregarding its individual level origin. To analyze the differences between the stochastic (individual level) and the deterministic (population level) approaches one usually chooses a stochastic model that gives the right deterministic equations.

Let us first analyze briefly the dynamics of the macroscopic system. Its equilibria are obtained by solving the system $C_A(\phi_A,\phi_B) = C_B(\phi_A,\phi_B) = 0$, and their stability is studied by means of a linear stability analysis. When the system is close to equilibrium, its behavior is determined by the determinant Δ and the trace T of the Jacobian matrix $C_{i,j} = \frac{\partial C_i}{\partial \phi_j}$ at the fixed point:

$$\begin{aligned} \Delta &= C_{A,A}C_{B,B} - C_{A,B}C_{B,A}, \\ T &= C_{A,A} + C_{B,B}. \end{aligned} \quad (6)$$

In the region of parameter space where the equilibrium is a focus, the system performs damped oscillations characterized by a damping factor and a frequency of oscillation given by, respectively:

$$\begin{aligned} \gamma &= |T|/2, \\ \omega_d^2 &= \Delta(1-\epsilon^2/4), \end{aligned} \quad (7)$$

with

$$\epsilon = |T|/\sqrt{\Delta}. \quad (8)$$

The underdamped regime is therefore given by the condition $\epsilon < 2$. When $\epsilon > 2$ the equilibrium is a node, and the solutions of the macroscopic system do not oscillate. We show below that this parameter, which depends only on the parameters of the macroscopic equation (5), plays a fundamental role in the characterization of the oscillations of stochastic origin. Notice also that the number of oscillations observed in the characteristic time γ^{-1} depends only on ϵ (for small ϵ, it is just $1/\pi\epsilon$).

The following order in the van Kampen expansion gives the evolution of $\Pi(\xi_A,\xi_B,t)$, the joint probability function of the fluctuations around the macroscopic variables ϕ, in the form of a Fokker-Planck equation. To look for oscillations in the fluctuations it is easier to work with the equivalent Langevin equations, as shown in [9]:

$$\begin{aligned} \dot{\xi}_A &= C_{A,A}\xi_A + C_{A,B}\xi_B + L_A(t) \\ \dot{\xi}_B &= C_{B,A}\xi_A + C_{B,B}\xi_B + L_B(t) \end{aligned} \quad (9)$$

where $L_A(t)$ and $L_B(t)$ are delta-correlated Gaussian noises of zero mean, satisfying $\langle L_A(t)L_A(t')\rangle = D_A\delta(t-t')$, $\langle L_B(t)L_B(t')\rangle = D_B\delta(t-t')$, and $\langle L_A(t)L_B(t')\rangle = D_{AB}\delta(t-t')$. The noise intensities are given by:

$$\begin{aligned} D_A(\phi_A^*,\phi_B^*) &= \sum_{i,j} i^2\, T_{ij}(\phi_A^*,\phi_B^*), \\ D_B(\phi_A^*,\phi_B^*) &= \sum_{i,j} j^2\, T_{ij}(\phi_A^*,\phi_B^*), \\ D_{AB}(\phi_A^*,\phi_B^*) &= \sum_{i,j} ij\, T_{ij}(\phi_A^*,\phi_B^*), \end{aligned} \quad (10)$$

where the stars denote the equilibrium values. The noises L_A and L_B are often called *demographic* because they stem from the discrete nature of the components of the system.

These equations, however, can be considered from a different point of view: they can result from a linearization of a deterministic model with small *environmental* (i.e. external) noise [13,14]. In such a case, the parameters D_A, D_B, D_{AB} are independent from the parameters C_A and C_B. Therefore, all the results given below apply both to environmental and demographic noise.

By Fourier transforming equations (9) it is straightforward to obtain the power spectrum of the fluctuations around the deterministic equilibrium [9]. In the following we concentrate on population A. The corresponding expressions for population B are obtained by exchanging A and B in all the subindices. The average power spectrum of ξ_A is

$$\langle S_A(\omega)\rangle = \left[\frac{F_A + \hat{\omega}^2}{(1-\hat{\omega}^2)^2 + \hat{\omega}^2\epsilon^2}\right]\frac{D_A}{\Delta}, \quad (11)$$

where

$$\begin{aligned} \hat{\omega}^2 &= \omega^2/\Delta, \\ F_A &= \frac{C_{A,B}^2 D_B + C_{B,B}^2 D_A - 2C_{A,B}C_{B,B}D_{AB}}{\Delta D_A}. \end{aligned} \quad (12)$$

We stress that F_A (and correspondingly F_B), through its dependence on C_A, C_B, D_A and D_B, depends ultimately on the transition probabilities that define the model. Notice also that in the case of external noise, F_A (and F_B) and ϵ are independent parameters.

It is straightforward to see that $\langle S_A(\omega)\rangle$ is either monotonically decreasing or it has a single maximum at

$$\hat{\omega}_A^2 = -F_A + \sqrt{(F_A+1)^2 - \epsilon^2 F_A}. \quad (13)$$

The condition of positivity for the argument of the square root gives the region in phase space where the power spectrum has a single maximum. Notice that for $\epsilon < \sqrt{2}$ this condition is fulfilled *regardless of the exact dependence of* F_A *on the parameters of the model.* On the other hand, if $\epsilon > \sqrt{2}$, the power spectrum has a peak only if $F_A < (\epsilon^2 - 2)^{-1}$.

If we consider $\hat{\omega}_A$ as a function of F_A, with ϵ fixed (i.e. we only vary the noise), it is straightforward to see that it is a positive decreasing function. Therefore, it is bounded:

$$(1-\epsilon^2/2)\Theta(\epsilon-\sqrt{2}) < \hat{\omega}_A^2 < 1, \quad (14)$$

where Θ is the Heaviside step function.

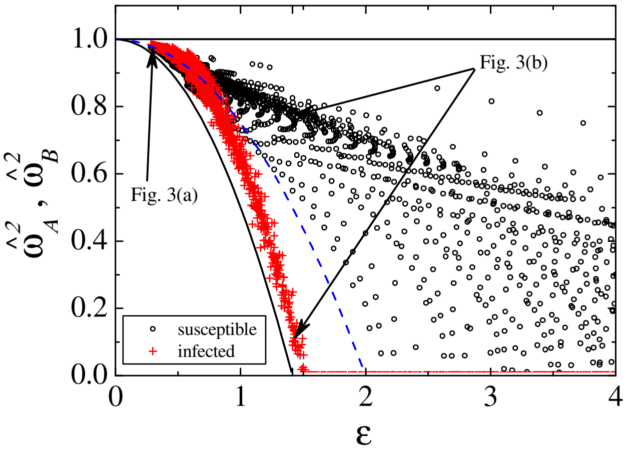

Fig. 2. $\hat{\omega}_A^2$ and $\hat{\omega}_B^2$ for the same SI model as in Figure 1. The points correspond to a uniform scanning of a portion of phase space: $b_A = b_{BA} = 0.1$, $d_A \in (0, 0.2)$, $d_B \in (0, 0.5)$, $p \in (2d_B, 3.2)$. The full lines show the bounds of equation (14), while the dashed one corresponds to $\hat{\omega}_d = \omega_d/\Delta$. The arrows point to the values corresponding to the parameters used in Figure 3.

In particular, this implies that in *all* the possible stochastic models that lead to the same deterministic equations (same C's, different D's) the position of the maximum can only vary within a finite range, that shrinks with ϵ.

For small ϵ, $\hat{\omega}_A^2$ approaches the value 1, which means that not only the frequencies of possible oscillations for both populations become close, but also that they become close to the frequency of the damped oscillations of the deterministic model (which tends to Δ as $\epsilon \to 0$). It is in this regime that the populations show the coherent dynamics characteristic of stochastic oscillations. This motion will be further characterized below by the quality of the spectrum peak. Figure 2 shows $\hat{\omega}_A^2$ and $\hat{\omega}_B^2$ as functions of ϵ for the epidemic model presented in Figure 1, for a wide range of system parameters. The bounds given by equation (14) are shown by continuous lines. Each point represents the normalized squared frequency for one set of parameters, for both populations. The deterministic frequency, $\hat{\omega}_d = \omega_d/\Delta$, is also shown, to emphasize the difference between the three frequencies present in the system.

When $\sqrt{2} < \epsilon < 2$ there can be some stochastic models for which no peak is present in $S(\omega_A)$ or $S(\omega_B)$. And, for some values of F_A or F_B, it can happen that the power spectrum of either ϕ_A or ϕ_B has a maximum even if $\epsilon > 2$, i.e. even when the deterministic system does not display damped oscillations (see Fig. 2: all the points to the right of $\epsilon = 2$ correspond to systems with a peak in the spectrum of the susceptible (A) population, no peak in the infected (B) one, and no damped oscillations in the deterministic model). These two features show that the peaks of the stochastic power spectrum on the one hand, and the deterministic damped oscillations on the other, are not necessarily closely related.

The above discussion establishes the conditions for the existence of a peak in the power spectrum of one or both populations. That is, for the existence of a preferred frequency in their dynamics. But, should all peaks in the power spectrum be regarded as “oscillations”? The answer to this question is certainly negative, and leads to the definition of the quality factor of the fluctuations. It is natural to expect that the narrower the peak, the more closely the fluctuations will resemble an oscillatory movement. The quality factor is therefore defined as a measure of the relative width of the power spectrum peak. A usual measure is the ratio between the height of the peak and its width: $Q_{st} \sim \frac{\Delta f}{f}$ [10]. Even though this definition is very natural in the analysis of time series, it usually leads to very complicated formulas in analytical treatments. Besides, it can only be defined when the spectrum reaches a value equal to half the height of the peak, both to the right and to the left of the peak. Unfortunately there are some cases when this does not happen. For these reasons, we use a slightly different definition of quality. In principle, it should be possible to translate the bounds we find to related bounds for any quality factor.

Given a power spectrum of the form (11) we define the quality of a peak at ω_{peak} as

$$Q_A(\omega_{peak}) = \frac{\omega_{peak}\langle S_A(\omega_{peak})\rangle}{\int\langle S_A(\omega)\rangle d\omega}. \tag{15}$$

This quantity is dimensionless and scale invariant. It is related to Fisher's kappa, which measures the non-stationarity of a signal, given its periodogram [15]. For functions with only one peak, Q_A increases as the peak sharpens. This definition of quality is very simply related to the more usual one in many cases: $Q_A = Q_{st}$ for a triangular and rectangular peak, $Q_A = 2\sqrt{\ln 2/\pi} Q_{st}$ for a Gaussian, $Q_A = \frac{2}{\pi} Q_{st}$ for a Lorentzian, etc. Furthermore, it is easy to see that $Q_{st} > Q_A/2$ for any power spectrum. Thus any lower bound for Q_A will also be a lower bound for Q_{st}.

For power spectra of the form (11), Q_A can be readily calculated (using that $\int\langle S_A(\omega)\rangle d\omega = \langle \xi_A^2\rangle$, see [11]):

$$Q_A(\omega_A) = \frac{2\hat{\omega}_A\epsilon}{(\hat{\omega}_A^2 - 1)^2 + \hat{\omega}_A^2\epsilon^2}\left(\frac{F_A + \hat{\omega}_A^2}{F_A + 1}\right). \tag{16}$$

The quality Q_A diverges as ϵ vanishes, regardless of the exact dependence of F_A on the parameters of the model. Therefore, one can assure that the corresponding time series will look oscillatory when ϵ is small enough (see Fig. 3 for an example of this). In such a case we have already shown that the frequencies of both populations are very close, and also very close to the frequency of the deterministic damped oscillations. Note that the limit $\epsilon \to 0$ is not the regime of interest in applications, since this situation is structurally unstable (it gives a center in the linearized deterministic system). On the contrary, one would be interested in the regime of small but positive ϵ, for which the quality can be large enough to ensure the observation of stochastic oscillations.

But, could it also happen that, for large values of ϵ, when the frequencies of populations A and B can be rather

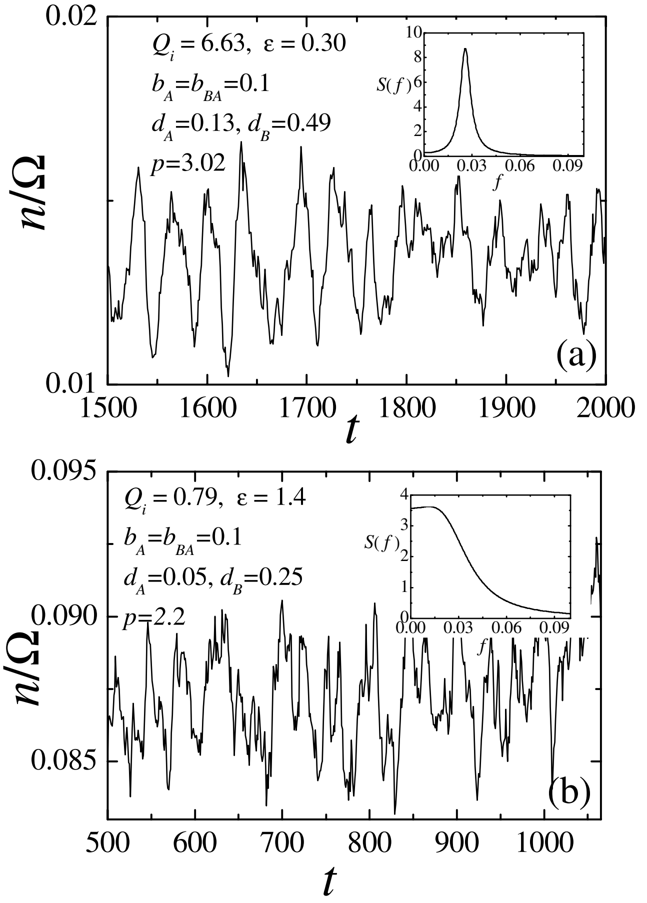

Fig. 3. Two stochastic realizations of the SI model, with different qualities. The insets show the corresponding analytical average power spectra. Only the infected population is shown. The arrows in Figure 2 point to the corresponding frequencies: $\omega_A \sim \omega_B \sim \omega_d$ for the good quality case shown in (a), and $\omega_A \gg \omega_B$ for the bad quality one shown in (b). $\Omega = 10^5$.

different, one gets very sharp peaks? It can be shown that this is not the case by giving bounds to Q_A that depend solely on ϵ.

To calculate these bounds, let us consider Q_A as a function of F_A, for ϵ fixed. It is not difficult to see that if $\epsilon < \sqrt{4/3}$ this function has only a single minimum at $F = (1 + (4 - 3\epsilon^2)^{-1/4})/3$, whereas if $\sqrt{4/3} < \epsilon < \sqrt{2}$, Q_A is monotonically decreasing. This leads to the bounds

$$f(\epsilon) < Q_A(\omega) < \frac{2}{\epsilon}. \qquad (17)$$

with

$$f(\epsilon) = \begin{cases} \frac{2}{\epsilon}\frac{2+\sqrt{4-3\epsilon^2}}{4}\sqrt{\frac{3}{1+\sqrt{4-3\epsilon^2}}} & \text{if } \epsilon < \sqrt{4/3} \\ \frac{2}{\epsilon}\frac{\sqrt{1-\epsilon^2/2}}{1-\epsilon^2/4} & \text{if } \sqrt{4/3} < \epsilon < \sqrt{2} \\ 0 & \text{otherwise.} \end{cases} \qquad (18)$$

These two bounds are very close when $\epsilon < 1$: the relative distance between the two is smaller than 9% (see the inset of Fig. 4). This bounds the relative error made when approximating the quality by one of the bounds.

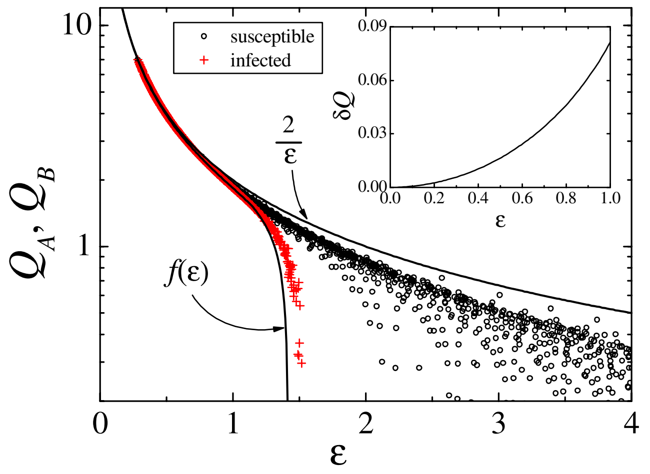

Fig. 4. Q_A and Q_B as functions of ϵ for the SI model of Figure 1. The points correspond to the same portion of phase space as in Figure 2. The lines show the upper and lower bounds of equation (17). The inset shows the relative difference between the bounds ($\delta Q = [2/\epsilon - f(\epsilon)]/2/\epsilon$).

The upper bound shows that, when ϵ is not small, the peak cannot be arbitrarily sharp. On the other hand, the lower bound shows that, when ϵ is small the peak is sharp for *all* the stochastic counterparts of a deterministic model. In Figure 4 we illustrate this by showing several values of Q_A and Q_B for the epidemic model, along with the corresponding bounds.

One practical question remains: what is the critical quality value above which one can be sure that the time series will indeed "look" oscillatory? As it is to be expected, the continuous nature of Q precludes a conclusive answer. From exhaustive observations of different models we find that when $Q(\omega_{peak}) > 4$, the oscillations are well defined and notably different from a noisy evolution (see Fig. 4). An evaluation of the values of ϵ corresponding to published oscillating systems also suggest that $\epsilon < 0.5$ is a good rule of thumb for the search of stochastic oscillations. Our bounds (Eqs. (14) and (17)) imply that in this range the quality of these oscillations will be always larger than 4, and that the relative difference between their ω (both between models and between populations) will be smaller than 5%.

In summary, we have shown, by defining and bounding a quality measure, that the parameters that define a deterministic model are enough to characterize, to a surprising degree of accuracy, how oscillatory the time series of any of its stochastic counterparts looks like. We find that good stochastic oscillations are clearly present only when ϵ is small. Although this behavior was to be expected, and it is often loosely alluded to in the literature [13], our bounds provide a *quantitative* (and accurate) measure of this effect. For increasing values of ϵ, there is a smooth transition to a behavior that is indistinguishable from noise. This means that, given a deterministic model, one can know, using the bounds (17), whether the time series given by *any* stochastic counterpart of the model will look oscillatory or not. In addition, we have shown that, when oscillations are clear, the corresponding frequencies of both populations will be close to each other and to the frequency of the damped oscillation of the deterministic system.

Although our results have been obtained for a particular measure of the quality of stochastic oscillations, we believe that other measures should behave in much the same way, but probably with more complicated bounds.

Given that our conclusions are based on the analysis of the first two terms of the systematic van Kampen's expansion of the master equation, they are exact only in the limit $\Omega \to \infty$. These analytical results, nevertheless, compare well with the numerical observations made on finite systems. More details about the validity of the expansion for finite systems will be given elsewhere.

It must be stressed that two-species models as the ones studied here provide only the roughest of approximations to real systems, because they do not take into consideration the space where these species move (full mixing hypothesis). But at this level of description non-spatial models with more species have also proven to be useful. An example of these are the three-species systems studied in [16,17], in which the three species succeed each other cyclically (as in an SIRS model). It would therefore be interesting to extend our results to systems of more than two species and to spatial models (where every patch of landscape plays the role of a species, as it is shown in [12]). Unfortunately, the calculations in this case are much more complicated because of the large number of parameters of these models, thus precluding the derivation of simple expressions like equations (14) and (17). But numerical bounds could certainly be very useful, provided it can be shown that they are close enough.

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