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A Markov Embedding Approximation for a Stochastic Population Model with Exogenous Disturbances

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Abstract. We present and study an approximation scheme for the mean of a stochastic simulation that models a population subject to nonlinear birth and exogenous disturbances. We use the information from the probability distribution for the disturbance times to construct a method that improves upon the mean-field approximation. We show through two example systems the effectiveness of the Markov embedding approximation and discuss the contexts in which it is an appropriate method.

Keywords: exogenous disturbance, Markov embedding, mean-field

AMS 1991 Subject Classification: 60-04, 60G99, 60J99, 92-08, 92D25, 92D40

1. Introduction

We present and study an approximation scheme for the mean of a stochastic simulation that models a population subject to nonlinear birth and exogenous disturbances. We call the method a Markov embedding since we embed aspects of the original Markov process in the approximation; namely, we use the information from the probability distribution for the disturbance times to construct a method that improves upon the mean-field approximation. Such approximate methods are needed because stochastic simulations of this nature are computationally expensive and difficult to analyze. The immense computational cost is vividly illustrated by the examples considered in this paper where the stochastic simulations take several hours to several weeks on a modern personal computer for each parameter set, whereas the Markov embedding approximations take on the order of one second.

Exogenous disturbances play important roles in ecological systems such as benthic populations and forests. In benthic systems, the birth rate is often treated as a constant, whereas disturbances may be density dependent. Methods for such systems were treated by Pascual and Levin (1999). In forest systems, the disturbance rate is often treated as density independent, which is reasonable in the context of processes such as windfall; the birth rates may be density dependent and nonlinear due to resource competition

(Kohyama, 1991, 1993; Pacala *et al*., 1996). It is the case of forest systems that motivates the methods in this paper.

The system considered in this paper is a stochastic patch model with an infinite number of patches. In each patch, one of two events may occur. A patch may create a new individual, which then may stay with probability $1 - m$ or migrate with probability m, or a patch may be struck by an exogenous disturbance, which results in all individuals being removed from that patch. We assume that migrants are distributed according to a Poisson distribution with mean equal to the average number of migrating offspring per patch (''Poisson Rain''.) This corresponds to a uniform distribution of migrants to other sites when the number of patches is finite. This assumption on the migration yields a spatially implicit model. For simplicity, a given disturbance affects only one patch.

We study the effectiveness of the Markov embedding approximation in the context of two example systems with competition. The first is motivated by a forest system with competition for light (Kohyama, 1991, 1993; Pacala *et al*., 1996). Fecundity takes the form of a negative exponential. In the second system, the fecundity is a rational function (DeWit, 1960; Pacala and Silander, 1987). These example systems have two-dimensional parameter spaces that illustrate some of the contexts in which the Markov embedding gives a more accurate prediction of the mean population than a mean-field prediction.

The systems considered are ones for which a moment method does not apply (Bolker and Pacala, 1997; Levin and Pacala, 1997). The nonlinearities involved have Taylor expansions with an infinite number of terms. The moment method requires the nonlinearity to be polynomial at worst so that we can truncate the higher moments.

2. The Stochastic Process

We have a random p-vector $X(t) = (X_1(t), X_2(t), \ldots, X_p(t))$ where $X_i(t)$ is the population size at patch $i(1 \le i \le p)$ at time $t(t \ge 0)$. The number of patches is taken to be sufficiently large to mimic the behavior of an infinite patch model (the results presented in this paper use $p = 100$). The population size in each patch is determined by a stochastic birth process with exogenous disturbances and migration between patches. The model parameters will be chosen so that the corresponding infinite patch model has a nontrivial stationary distribution. Of interest is then to determine the long-term average population size in a randomly chosen patch.

We formulate the dynamics as a continuous time Markov process, where at time $t = 0$ the number of individuals at all patches is initialized to $X(0) = 1$. To formulate such a process, it is most convenient to separate the event times from the actual events; that is, we simulate the events as a discrete time Markov process separate from the times at which these events occur. To keep with the standard formulation of Markovian patch models, all events occur at exponential rates. The dynamics can then be described by the following algorithm:

Determine in which patch the event occurs. At rate $\beta(X_i)$, patch i gives birth to one new individual. At rate δ, the patch is struck by an exogenous disturbance. We define

$\lambda_i = \beta(X_i) + \delta$ and $\lambda = \sum_{i=1}^{p} \lambda_i$. An event occurs in patch i with probability λ_i/λ.

Determine the event time. The event occurs a length of time from the last event that is chosen randomly from an exponential distribution with parameter λ.

Determine if the patch is disturbed or gives birth and offspring migrates. Let i denote the index where the event occurs. An exogenous disturbance occurs with probability $\delta/\big(\beta(X_i) + \delta\big)$. In this case we set $X_i = 0$. With probability $\beta(X_i)/\big(\beta(X_i) + \delta\big)$, a new individual is created which either stays with probability $1 - m$, so that X_i is incremented (denoted by $X_i \to X_i + 1$), or migrates with probability m to patch j, chosen uniformly from the p patches, so that $X_j \to X_j + 1$.

3. Deterministic Predictions

We discuss approximation schemes for the mean of the stochastic simulation at large time. We show that the problem is one of approximating the expected value of a nonlinear function. We describe the mean-field approximation and present the Markov embedding method that is an improvement over the mean-field prediction.

For the ''next'' event time, we have the following equation for the mean of one patch:

$$\langle X_{t+\Delta t}\rangle = \langle X_t\rangle + \Delta t(\langle \beta(X_t)\rangle - \langle \delta X_t\rangle)$$

or

$$\frac{\langle X_{t+\Delta t}\rangle - \langle X_t\rangle}{\Delta t} = \langle \beta(X_t)\rangle - \langle \delta X_t\rangle.$$

Set $u = \langle X\rangle$ and let $\Delta t \to 0$ to get

$$\frac{du}{dt} = \langle \beta(X)\rangle - \delta u.$$

The problem is to approximate $\langle \beta(X)\rangle$.

3.1. Mean-field Approximation

In the mean-field prediction we approximate the function of the continuous time random variable X, $\langle \beta(X) \rangle$, by $\beta(u)$ where $u(t) = \langle X(t) \rangle$. The resulting mean-field ordinary differential equation is

$$\frac{du}{dt} = \beta(u) - \delta u, \quad t > 0, \tag{1}$$

with initial condition $u(0) = u_0$. The long-time prediction given by the mean-field model is obtained by solving for the equilibrium solution of Equation (1).

We will consider cases of the fecundity β that are nonlinear and more complicated than polynomials; specifically, the nonlinearities involved will have Taylor expansions with an infinite number of terms. Applying the moment method (Bolker and Pacala, 1997; Levin and Pacala, 1997) would either require truncation of the Taylor expansion after finitely many terms, thus reducing the nonlinearity to a polynomial, or to approximate all higher order moments appropriately to achieve closure of the moment equations, a rather daunting if not impossible task.

3.2. Markov Embedding Approximation

We can build a better approximation scheme than mean-field by taking into account that the disturbance times are exponentially distributed with parameter δ.

For the Markov embedding prediction, we approximate $\langle\, \beta(X(t))\, \rangle$ by

$$\int_0^t \beta(v(\tau))\; dP(t+w(t);\tau+w(\tau)),$$

where $dP(t;\tau) = \delta\exp(-\,\delta\tau)/\big(1-\exp(-\,\delta t)\big)\; d\tau$ is the probability density function at time t for the time since the last exogenous disturbance, $w(t)$ is the mean wait-time from disturbance to recolonization at time t and v is the population from a ''birth-only'' process,

$$\frac{dv(t)}{dt} = \beta(v(t)), \quad t>0, \tag{2}$$

with initial condition $v(0)=1$. The Markov embedding approximation of the mean of β is thus an integration over probabilities since the last disturbance and subsequent recolonization.

We approximate $w(t) = 1/\langle\beta(X)\rangle$ by replacing the mean of the birth function, β, with the birth function applied to the approximate mean, $w(t)\approx 1/\beta(u(t))$. The resulting system for the Markov embedding in integro-differential form is

$$\frac{du(t)}{dt} = \int_0^t \beta(v(\tau))\; dP(t+w(t);\tau+w(\tau)) - \delta u(t), \tag{3}$$

$$\frac{dv(t)}{dt} = \beta(v(t)), \tag{4}$$

for $t>0$, and with initial conditions $u(0)=u_0$ and $v(0)=1$.

Equations (3) and (4) can be rewritten as a system of ordinary differential equations,

$$\frac{du(t)}{dt} = \frac{I(t)}{\big(1-\exp(-\,\delta(t+w(t)))\big)} - \delta u(t), \tag{5}$$

$$\frac{dI(t)}{dt} = \beta(v(t))\delta\exp(-\,\delta(t+w(t))), \tag{6}$$

$$\frac{dv(t)}{dt} = \beta(v(t)), \tag{7}$$

for $t>0$, and with initial conditions $u(0)=u_0$, $I(0)=0$, and $v(0)=1$.

4. Example Systems

We present examples of the utility of the Markov embedding for two forms of β representing competition. The first case is exponential fecundity, in which we take $\beta(x) = x\exp(-\gamma x)$, where γ is a measure of the effects of competition (Kohyama, 1991, 1993; Pacala *et al.*, 1996). The second example is fecundity modeled by a rational function, $\beta(x) = 1/(1 + \gamma x)$, where γ is again a measure of the effects of competition (DeWit, 1960; Pacala and Silander, 1987).

The full set of parameters involved in each case consists of γ, δ, p, m and the number of iterations of the stochastic simulation. In both examples, we take the number of patches to be $p = 100$ and set the migration parameter to $m = 1$. We examine the mean at large time of 100 iterations of the stochastic simulation. We vary γ and δ. We will see below that the results are stable because the perturbations are continuous in their parameters.

For both examples of β, we find that the mean increases at least exponentially as both γ and δ decrease. In examining the effectiveness of the mean-field and Markov embedding approximations, we will use the notion of relative error given by $(u - \mu)/\mu$, where μ is the mean of the stochastic simulation. Thus a positive relative error indicates overprediction of the mean, whereas a negative relative error indicates underprediction of the mean.

We study the effect of reduced migration in the stochastic model on the accuracy of the Markov embedding approximation. We note that both the Markov embedding scheme and the mean-field approximation are not dependent on the migration parameter. The Markov embedding approximation and the mean-field approximation are only valid for m close to one. In our simulations, the mean of the stochastic simulation decreased with a decrease in m; this is most likely caused by a delayed colonization of empty patches with decreased m. A large change in the mean population for small deviations of m from unity will most likely result in a degradation of the Markov embedding approximation.

For the case of negative exponential fecundity, $\beta(x) = x\exp(-\gamma x)$, we consider the parameter set $\gamma = \delta = 0.2$ and take $m = 1, 0.95, 0.9, 0.85, 0.8$. In this case, the Markov embedding approximation overapproximates the mean of the stochastic simulation, which in turn decreases as m decreases. The degradation in accuracy of the Markov embedding is tied to the decrease in the mean of the simulation for decreased migration. The Markov embedding approximation overpredicts the mean of the stochastic simulation by 2.56% for the case of $m = 1$, by 4.98% for the case of $m = 0.95$, by 5.49% for the case of $m = 0.9$, by 6.53% for the case of $m = 0.85$ and 9.37% for the case of $m = 0.8$. Because the population size seems to be a decreasing function of m, for situations where the Markov embedding approximation underpredicts the mean of the stochastic simulation, we expect for some range of the change in m an improvement in the approximation.

Regardless, the Markov embedding either overpredicts or underpredicts the mean of the stochastic simulation. We will expand on this below. For small deviations of m from unity, we expect acceptable degradation in the accuracy of the Markov embedding approximation provided recovery after a disturbance is quick so that the recovery process is well approximated by its deterministic analogue.

4.1. Exponential Fecundity

We assume that birth is affected by competition for some resource, such as trees competing for light (Kohyama, 1991, 1993; Pacala *et al*., 1996). In this case the birth term has the form $\beta(x) = x\exp(-\gamma x)$, which represents density dependent birth with fecundity $\exp(-\gamma x)$.

The long-time prediction given by the mean-field model for $\beta(x) = x\exp(-\gamma x)$ is $\bar{u} = -\ln(\delta)/\gamma$. Comparison of the mean-field prediction and the stochastic simulation is exhibited in Figure 1. The mean-field does not do very well and does exceptionally poorly when the mean of the simulation is small or when δ is small. Moreover, the region where the mean-field approximation does well corresponds to the region where it goes from overpredicting the mean (large δ), to underpredicting the mean (small δ). The location of this area is dictated by Jensen's inequality which says that $\beta(u) \geq \langle\beta(X)\rangle$ if β is concave down and vice versa if β is concave up. In the case of negative exponential fecundity, β is initially concave down and then becomes concave up. For δ small, the population is sufficiently large so that β is mostly concave up. For δ large, the population is kept low in each patch so that β is mostly concave down. This accounts for the transitions from underprediction to overprediction as δ increases.

Comparison of the Markov embedding prediction and the stochastic simulation, as a function of the parameters γ and δ, is exhibited in Figure 2.

One parameter range where the Markov embedding does poorly in the case of negative exponential fecundity is for δ small. The loss of accuracy in the Markov embedding is

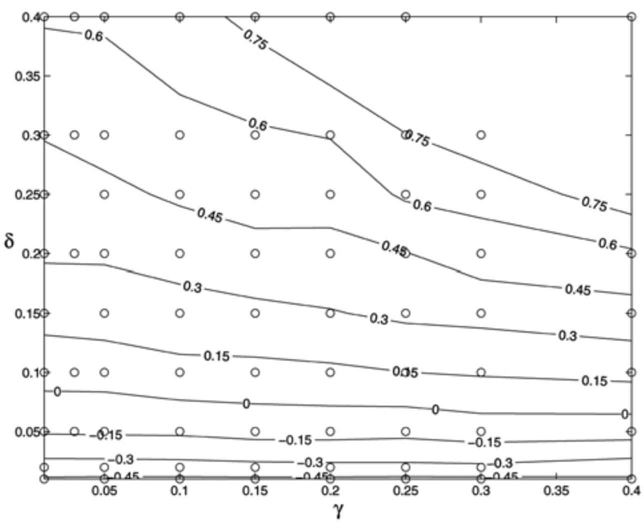

Figure 1. Contour plot of the relative error for the mean-field approximation to the multi-patch simulation as a function of the parameters δ and γ for the case of $\beta(x) = x\exp(-\gamma x)$. The circles show the location of data points. A positive relative error indicates overprediction of the mean, whereas a negative relative error indicates underprediction of the mean.

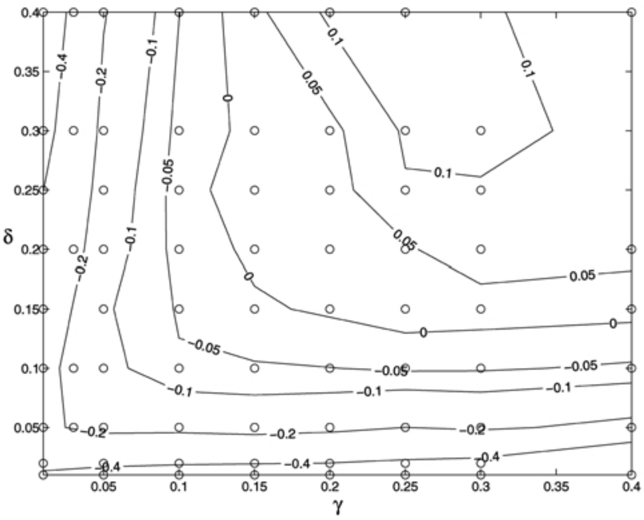

Figure 2. Contour plot of the relative error for the Markov embedding approximation to the multi-patch simulation as a function of the parameters δ and γ for the case of $\beta(x) = x\exp(-\gamma x)$. The circles show the location of data points. A positive relative error indicates overprediction of the mean, whereas a negative relative error indicates underprediction of the mean.

similar in nature to that of the mean-field approximation. If δ is small, then the Markov embedding approximation will behave much like the mean-field approximation. This is because the mean-field approximation will be close to a birth-only process, Equation (2). The Markov embedding will be close to an integration of the birth-only process without weighting by the probability density, hence the correlation in behavior. The weighting by the exponential probability density in the integral is diminished because for δ small, the weight is close to unity for small time, whereas for large time, the negative exponential birth term is close to zero.

For the other regions where the Markov embedding does not perform as well as we would like, we examine in Section (5) the growth dynamics of a single colony after disturbance and recolonization to determine the cause. We will see that in this region of the parameter space, the simulation is kept near the start of the birth curve, raising the variance over mean of the population in a single patch.

4.2. Rational Fecundity

We consider the case when the birth term has the form $\beta(x) = x/(1+\gamma x)$ (DeWit, 1960; Pacala and Silander, 1987), which represents density dependent birth with fecundity $1/(1+\gamma x)$. While the fecundity in this case can be viewed as a fatter-tailed version of the negative exponential, the birth term as a whole has a substantially different form. For the negative exponential, birth goes to zero as population size increases, whereas for the birth term considered in this section, birth goes to a nonzero constant as population size increases.

The long-time prediction given by the mean-field model for $\beta(x) = x/(1 + \gamma x)$ is $\bar{u} = (1 - \delta)/(\gamma\delta)$. Comparison of the mean-field prediction and the stochastic simulation is exhibited in Figure 3. The mean-field approximation does not do very well. By Jensen's inequality, the fact that β is concave down indicates that the mean-field approximation will overpredict the mean of the stochastic simulation everywhere.

Comparison of the Markov embedding prediction and the stochastic simulation, as a function of the parameters γ and δ, is exhibited in Figure 4. We see that the Markov embedding approximation is a marked improvement over the mean-field approximation. Again, the areas where the Markov embedding method does poorly corresponds to a region where δ is large and γ is small.

4.2.1. One Colony Birth-only Process

To understand the poor performance of the Markov embedding approximation for large δ and small γ, we study the dynamics of one colony. We ignore the effects of colonization and disturbance.

We have a random variable, $X(t)$, which represents the population in one patch at time t. We initialize $X(0) = 1$. The system at each discrete event time is determined by the following algorithm:

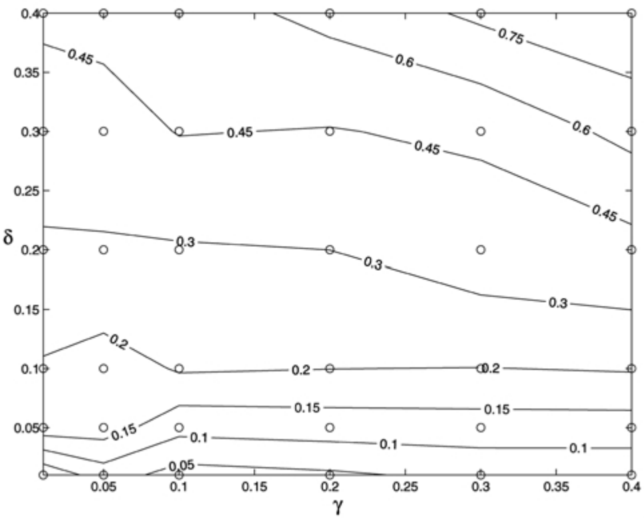

Figure 3. Contour plot of the relative error for the mean-field approximation to the multi-patch simulation as a function of the parameters δ and γ for the case of $\beta(x) = x/(1 + \gamma x)$. The circles show the location of data points. A positive relative error indicates overprediction of the mean, whereas a negative relative error indicates underprediction of the mean.

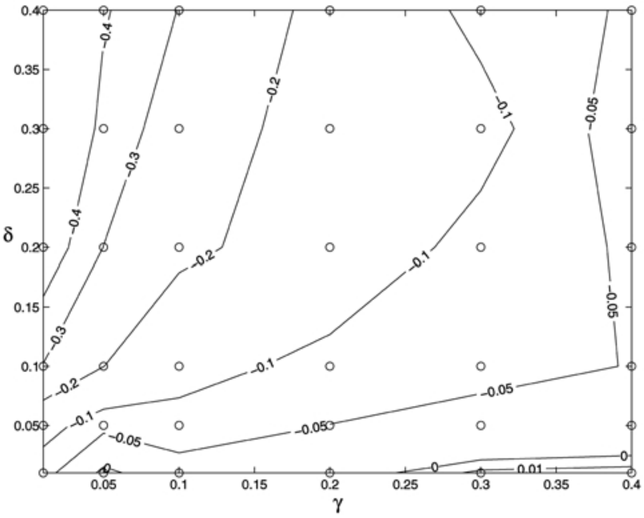

Figure 4. Contour plot of the relative error for the Markov embedding approximation to the multi-patch simulation as a function of the parameters δ and γ for the case of $\beta(x) = x/(1 + \gamma x)$. The circles show the location of data points. A positive relative error indicates overprediction of the mean, whereas a negative relative error indicates underprediction of the mean.

Give Birth. At rate $\beta(X)$, give birth to one new individual, $X \to X + 1$.

Determine the event time. The event occurs a length of time from the last event that is chosen randomly from an exponential distribution with parameter $\lambda = b$.

We study the variance of $X(1/\delta)$ over its mean, σ^2/μ, for 1,000 runs of the simulation, using various values of δ and γ. The results are shown in Figure 5 for the case of $\beta(x) = x\exp(-\gamma x)$ and in Figure 6 for the case of $\beta(x) = x/(1 + \gamma x)$. We see that σ^2/μ becomes very large for large δ and small γ. This corresponds to an area of the parameter space where the Markov embedding does poorly. In this area, the high disturbance rate keeps the population in a patch near a slower (small γ) initial birth phase.

5. Conclusions

In the two examples considered in this paper, we see that the Markov embedding method provides a significant improvement over the mean-field approximation for most parameter ranges. Moreover, the Markov embedding gives a ''good'' approximation most everywhere. Where it does not do as well as hoped, the reasons are reasonable and fairly well understood.

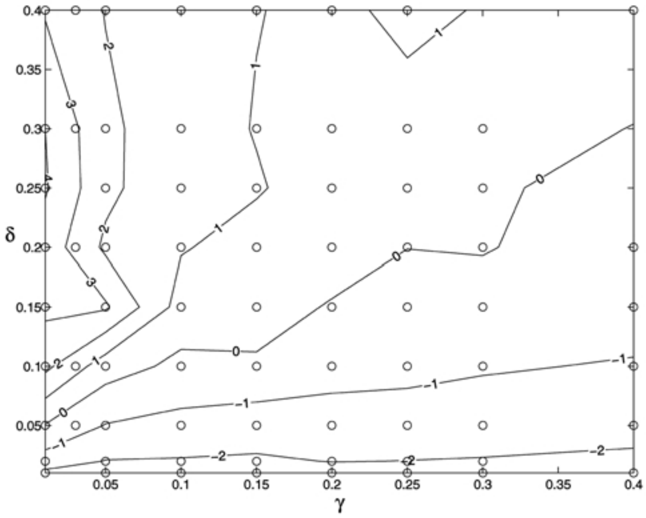

Figure 5. Contour plot of the log of the variance over mean, $\ln(\sigma^2/\mu)$, of the population for the single patch stochastic simulation as a function of the parameters δ and γ, for the case of $\beta(x) = x\exp(-\gamma x)$. Note that the areas where σ^2/μ is large (large δ and small γ) correspond to one parameter range where the Markov embedding does poorly. The circles show the location of data points.

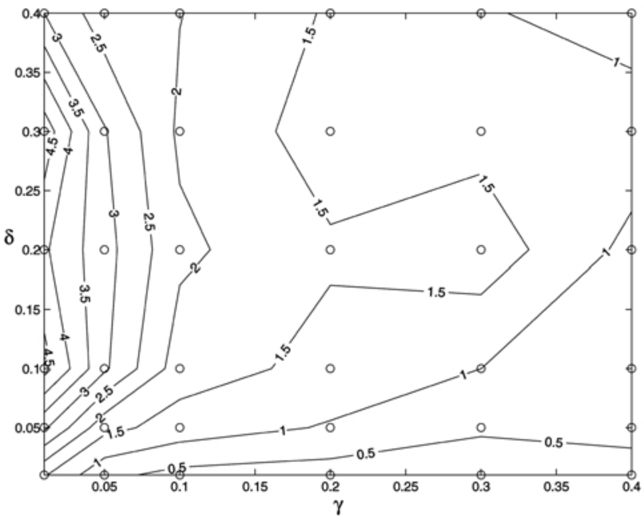

Figure 6. Contour plot of the log of the variance over mean, $\ln(\sigma^2/\mu)$, of the population for the single patch stochastic simulation as a function of the parameters δ and γ, for the case of $\beta(x) = x/(1 + \gamma x)$. Note that the areas where σ^2/μ is large (large δ and small γ) correspond to one parameter range where the Markov embedding does poorly. The circles show the location of data points.

The Markov embedding results in a system of ordinary differential equations whose computational cost is on the same order as moment methods. The Markov embedding approximation is an effective and efficient alternative to mean-field and moment method approximations for certain situations with exogenous disturbances where these methods do not work well or not at all.

In the case of exogenous disturbances, we speculate that the Markov embedding will generalize to multiple species better than moment methods since the critical information the Markov embedding uses, the disturbance rate, is the same for all species. This means that we will need only one set of Markov embedding equation for each of the n species, giving a work estimate of $\mathcal{O}(n)$. In the moment method, we would need to incorporate the moments of all the species in the equations for each individual species, giving a work estimate of $\mathcal{O}(n^2)$.

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