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Deterministic stability analysis can predict the dynamics of some stochastic population models

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Summary

1. Some workers (e.g. Morrison & Barbosa 1987) have suggested that the conclusions from standard deterministic population dynamics models do not hold for stochastic versions of the same models.
2. Stochastic versions of two standard models — Hassell’s (1975) single-species model and May’s (1978) host—parasitoid model — were simulated, for a range of parameter values giving different deterministic dynamics.
3. In several cases there was a qualitative difference in stochastic dynamics between systems which were deterministically stable and unstable: for the host—parasitoid model and the single-species model with weak regulation, the variability in densities was much greater for unstable systems than stable ones.
4. In all cases the stability eigenvalue \( \lambda \) obtained from deterministic analysis was clearly related to the variability of the stochastic simulations: populations varied less when \( |\lambda| \) was small.
5. Increasing the magnitude of the external stochastic variability produced greater variability in densities.

Key-words: dynamics, theory, density dependence, parasitoid—host, variability.


Introduction

Most current theory on population dynamics and interactions is based on stability analyses of simple deterministic models. In these models, population densities are determined entirely by a few explicitly modelled endogenous factors, whose relevant parameters do not vary. Stability analysis is a further abstraction, ignoring dynamics other than close to equilibrium. Most real populations, in contrast, are affected by numerous, often unpredictable, factors, and fluctuate over a substantial range, far from any ‘equilibrium.’

This discrepancy between models and reality has led some workers to doubt the relevance of conclusions derived from deterministic theory. A recent statement of this position was by Morrison & Barbosa (1987). They simulated a stochastic version (from Hassell 1985) of May’s (1978) ‘negative-binomial’ host—parasitoid model, with a set of parameter values which give strong stability in the deterministic analogue of the model. In the stochastic simulations populations often went below an arbitrarily defined ‘extinction’ threshold within a few (<50) generations. Morrison & Barbosa (1987, p. 612) then concluded that deterministic stability analysis did not accurately predict the behaviour of the stochastic simulations: ‘the high rates of parasitoid extinction that occurred . . . make it difficult to classify the interactions as “well-regulated” in the classical sense.’

Given the extreme simplicity and arbitrariness of the models being used, however, it does not seem appropriate to draw specific quantitative conclusions from them, such as extinction rates for a particular system. Rather, the models should be used to obtain relative, qualitative conclusions: predictions of how the general nature of the dynamics will differ between systems with different parameter values.

In the following, therefore, I address the question raised by Morrison & Barbosa (1987): does the behaviour of stochastic simulations agree with expectations from deterministic stability analysis. I do so, however, by comparing simulations having differing deterministic predictions, looking for correspondence in the general pattern of changes in dynamics as parameters change. In part, I follow Morrison & Barbosa (1987) by using a model based on May’s (1978) host-parasitoid model. As will be seen, though, this model could not be properly simulated with parameter values giving deterministic
instability. Most of the following therefore concerns a simpler single-species model (based on Hassell 1975), which was better behaved and therefore could be studied more thoroughly.

Methods

MODELS

Single species

The deterministic component of the single-species model was that of Hassell (1975; also Bleasdale & Nelder 1960):

\[ N_{t+1} = fN_t(1 + aN_t)^{-b} \]

where \( N_t \) is the population density in generation \( t \), \( f \) is the per capita finite rate of increase, \( a \) scales the density, and \( b \) determines the form of density dependence (scramble-like for large \( b \) and contest-like for small \( b \)). Deterministic stability in this model depends on \( f \) and \( b \), but not on \( a \); \( a \) therefore was kept equal to 1 in all simulations.

Stochastic variability was modelled by having each of the parameters, \( a, b \) and \( f \) as independent, log-normally distributed pseudorandom variates in each generation. Specifically, each parameter was multiplied by \( e^{\epsilon_i} \), where \( \epsilon_i \) is a normally distributed pseudorandom variate with mean 0 and standard deviation \( \sigma_i \) (\( i \) represents the generation and \( i \) the parameter, i.e. \( i = a, b, \) or \( f \)).

The resulting model was log-transformed for simulation, giving:

\[ n_{t+1} = n_t + r + \epsilon_{r,t} - b e^{\epsilon_0} \ln \left( 1 + e^{(n_t + \epsilon_n)} \right) \]

where \( n_t = \ln(N_t) \) and \( r = \ln(f) \). Deterministic simulations, when needed, used the same model without the \( \epsilon \).

**Parasitoid-host**

The deterministic component of the host-parasitoid model was:

\[ H_{t+1} = fH_t(1 + \frac{aP_t}{k})^{-k} \]

\[ P_{t+1} = cH_t \left[ 1 - \left( 1 + \frac{aP_t}{k} \right)^{-k} \right] \]

(May 1978), where \( H_t \) and \( P_t \) are, respectively, host and parasitoid densities in generation \( t \), \( f \) is the finite per capita rate of increase of the host, \( c \) is the number of parasitoid progeny produced per parasitized host, \( a \) is the ‘area of discovery’ of the parasitoid, and \( k \) describes the degree of aggregation over hosts of encounters with parasitoids (smaller \( k \) giving greater aggregation). Stability depends on \( f \) and \( k \); the scaling parameters \( a \) and \( c \) do not affect stability, and were kept equal to 1 in all simulations.

Stochastic variability was introduced similarly to the single-species model: the parameters \( f, a, \) and \( c \) were multiplied by independent log-normal random variates, \( e^{\epsilon_i} \). The aggregation parameter, \( k \), was treated as constant. The resulting model, after log transformation, was:

\[ h_{t+1} = h_t + r + \epsilon_{r,t} - k \ln \left( 1 + \frac{e^{(n_t + \epsilon_n)}}{k} \right) \]

\[ p_{t+1} = h_t + \epsilon_{r,t} + \ln \left( 1 - \left( 1 + \frac{e^{(n_t + \epsilon_n)}}{k} \right)^{-k} \right) \]

where \( h_t = \ln(H_t) \), \( p_t = \ln(P_t) \), and \( r = \ln(f) \).

**DETERMINISTIC STABILITY ANALYSIS**

The index of deterministic stability to which the stochastic dynamics were related was the leading eigenvalue, \( \lambda \), of the Jacobian for the deterministic component of the model, obtained by standard methods. This eigenvalue measures the rate of contraction (if \( |\lambda| < 1 \)) or expansion (if \( |\lambda| > 1 \)) of small deviations of the population from equilibrium: smaller \( |\lambda| \) implies stronger regulation of the deterministic system.

**STOCHASTIC SIMULATIONS**

**Design**

The single-species model was simulated for each of three combinations of \( r \) and the level of stochastic variability:

- \( r = 3, \ \sigma_r = \sigma_a = 0.3, \ \sigma_b = 0.1; \)
- \( r = 3, \ \sigma_r = \sigma_a = 0.6, \ \sigma_b = 0.2; \) and
- \( r = 6, \ \sigma_r = \sigma_a = 0.3, \ \sigma_b = 0.1; \)

For each of these combinations a range of values of \( b \) was selected to give values of \( \lambda \) (see above) from 0.98 to 1.95. The model also was simulated for \( r = 4, 5, 6 \) and 7, \( b \) chosen to give \( \lambda = 1 \) for each \( r \), and with \( \sigma_a = \sigma_r = 0.3 \) and \( \sigma_b = 0.1 \). For each combination of \( r \) and \( b \) giving deterministic instability (\( \lambda < 1 \)), the deterministic version of the model was also simulated. Finally, the model was simulated for each combination of \( r \) and \( b \) in a factorial design with \( r \) ranging from 0 to 7 in steps of 0.1, and \( b \) ranging from 0 to 10 in steps of 0.2.

The parasitoid-host model was simulated only with \( r = 3 \) and \( \sigma_r = \sigma_a = \sigma_b = 0.1 \). The stability eigenvalues for this model can be either real, positive and <1 for small \( k \), or complex for larger \( k \). Simulations were run with values of \( k \) giving real \( \lambda \) from 0.5064 (the minimum possible with \( r = 3 \)) to 0.95, and complex \( \lambda \) with \( |\lambda| \) from 0.5064 to 1.1 (the largest that could be sensibly simulated; see below).

One simulation was run for each set of parameter values for each model. For the stochastic models,
densities were started at equilibrium and usually run for 10,500 generations, the first 500 of which were discarded. When deterministic simulations were needed, they were started at the densities occurring at generation 250 (i.e. the middle of the discarded transient) of the corresponding stochastic model, and usually run for 10,250 generations, of which the first 250 were discarded.

The exception to these procedures was for the host-parasitoid model with parameter values giving deterministic instability (i.e. \( k > 1 \)). These simulations rapidly reached densities so extreme they caused numerical under- or overflow. The transient therefore was reduced to 25 or even 10 generations, and the simulation was run only until the proportion of hosts parasitized was smaller than the computer could handle (the log parasitoid density was \(< -50 \) or so). With \( |\lambda| = 1.1 \), this occurred after only 66 generations (including a 10-generation transient); it did not seem worthwhile to push \( \lambda \) to more extreme values.

Rather than impose arbitrary thresholds for 'extinction', I simply observed the distributions of densities (on the log scale), after subtracting the equilibrium density. These distributions often were quite skewed, so I summarized them by quartiles, ranges and interquartile ranges (IQRs) rather than means and standard deviations.

Programming

Simulations were programmed in Turbo Pascal 5.0 (Borland International, 1987, 1988) using extended precision (10 byte) floating-point arithmetic. Normal random variates were generated by the Box-Muller method (function GASDEV of Press et al. 1989) applied to uniform random variates generated by function RAN1 of Press et al. (1989). Source code is available upon request.

Results

SINGLE-SPECIES MODEL

Effect of varying \( b \) only

The behaviour of the stochastic simulations clearly was related to the corresponding deterministic \( \lambda \). The variability of the simulated densities (as measured by both the range and the IQR) was least when \( \lambda \) was near 0, corresponding to the greatest deterministic stability, and increased as \( |\lambda| \) increased (Fig. 1). The minimum densities were most strikingly related to \( \lambda \), but the maximum and both quartiles were also affected. The median density also dropped slightly below the deterministic equilibrium at the extreme values of \( \lambda \) (Fig. 1).

The relationship between the dynamics of these simulations and the value of \( \lambda \) was not so simple, however, as suggested by standard stability analyses. Most importantly, there was no abrupt change as the stability boundary \( (\lambda = -1) \) was crossed. Instead, the increase in variability was continuous, so that a barely 'stable' model (e.g. \( \lambda = -0.95 \)) behaved more like a barely 'unstable' one (e.g. \( \lambda = -1.05 \)) than like a strongly stable one (\( \lambda = 0 \)).

The behaviour of the simulations depended on the sign as well as the absolute value of \( \lambda \). For positive \( \lambda \), the distribution of log densities was roughly symmetrical, and the upper and lower ends of the distribution were affected similarly by increasing \( \lambda \) (Figs 1 & 2). For negative \( \lambda \), however, the distribution was skewed toward negative values, and the increase in variability as \( |\lambda| \) increased was primarily in the lower end of the distribution (Figs 1–3).

In the unstable region \( (\lambda < -1) \), the deterministic simulations showed a similar skewness, which increased as \( |\lambda| \) increased (and dynamics progressed from two-point cycles through higher-order cycles to chaos) (Fig. 3).

The temporal nature of the variability also differed between positive and negative \( \lambda \), in ways which again reflected the different dynamics of the deterministic simulations (Fig. 4). Positive \( \lambda \) indicates undercompensating density dependence and exponential damping towards equilibrium, with large \( \lambda \) (e.g. \( \lambda = 0.98 \)) approaching density independence. The stochastic simulation for \( \lambda = 0.98 \) indeed somewhat resembled a random walk, the density showing rapid small fluctuations around a larger, much slower drifting up and down, reflecting the very weak regulation in the deterministic system. With \( \lambda = 0.5 \) the trajectory was much more constrained, but still had a drifting quality, with often several generations being spent on the same side of equilibrium.

(The random-walk-like appearance of the simulation with \( \lambda = 0.98 \), however, should not be inter-
Fig. 2. Frequency distributions of densities for selected stable values of $\lambda$ from Fig. 1. Note that plots on each side have the same $|\lambda|$.

Fig. 3. Frequency distributions of densities for selected unstable values of $\lambda$ from Fig. 1. For $\lambda = \pm 1.2$ and $\pm 1.5$ the deterministic dynamics are two-point limit cycles, at the densities indicated by X above the frequency plot. For $\lambda = \pm 1.7$ the deterministic dynamics are an eight-point limit cycle, and for $\lambda = \pm 1.9$ they are apparently chaotic; frequency distributions for these ($\#$) are shown above the distributions for the stochastic simulations (O).

Interpreted as evidence that the regulation present in this model is unimportant. A completely unregulated model — a random walk, equivalent to setting both $r$ and $b$ to 0, giving $\lambda = 1$ — was simulated in the same way with the same degree of stochastic variability. The variation in log density over 10000 generations was much greater than with $\lambda = 0.98$; the range was almost 45, and the IQR range almost 16. More importantly, the median over 10000 generations was $-7.11$, far from the starting point of 0, while all the regulated systems remained centred very close to the deterministic equilibrium.

Negative $\lambda$, in contrast, indicates overcompensating density dependence and oscillatory dynamics. Accordingly, the stochastic simulations were oscillatory, the populations bouncing up and down rapidly rather than drifting slowly. As $|\lambda|$ increased, these oscillations became more rapid, larger and more asymmetric, in both stochastic and deterministic simulations (Fig. 4).

**Effect of varying $\sigma$**

Not surprisingly, when the magnitude of the stochastic variation in parameters was increased, the variability in the population densities also increased for given $\lambda$. 
Fig. 4. Simulation trajectories for the same stable values of $\lambda$ as in Fig. 2. For each $\lambda$, a deterministic simulation is shown above a stochastic simulation.

(compare Fig. 5 with Fig. 1). This increased stochastic variation somewhat amplified the effect of $\lambda$ in highly unstable systems: for $\lambda < -1.5$, the minimum, first quartile, and median all dropped off more rapidly with decreasing $\lambda$ when $\alpha$ was larger. Overall, however, the relationship between $\lambda$ and stochastic dynamics remained roughly the same when $\alpha$ were changed.

Effect of varying $r$

Population densities generally were somewhat more variable with $r = 6$ than with $r = 3$ for given $\lambda$, but the relationship between $\lambda$ and the distribution of densities was largely the same (compare Fig. 6 with Fig. 1). Interestingly, however, for given $\lambda$ in the unstable range ($\lambda < -1$), the interquartile range was larger with larger $r$, but the total range was similar or (for extreme $\lambda$) even smaller. Comparing the distributions of densities for $r = 3, 4, 5, 6$ and 7 (Figs 3 & 7), it can be seen that the amplitude of the deterministic limit cycle for each $r$ is responsible for the increase in interquartile range as $r$ increases: as $r$ increases, the limit cycle widens, pulling the stochastic distribution wider until eventually it becomes bimodal. The attraction of the system towards the limit cycle, however, if anything is stronger at large $r$, so that the tails of the distribution do not spread out as $r$ increases.

The results in Figs 6 & 7 show that $\lambda$ does not fully
Fig. 7. Frequency distributions of densities for various r, with λ = −1.5. Xs above distribution indicate the corresponding deterministic two-point cycle.

capture the combined effects of r and b on the variability of the stochastic system. Figure 8, however, indicates that this discrepancy is fairly subtle. The least variability occurs with 0 < λ < 0.75 (and r small) rather than in the region centred around λ = 0, as might have been expected. In addition, λ appears to underestimate the destabilizing effect of larger r combined with small b. For example, the λ = 1 contour coincides with IQR = 1.5 at the top centre of Fig. 8, but with IQR = 3 at the bottom right. Qualitatively, however, the patterns shown by the variability of the simulations and by λ, as functions of r and b, are much the same: both increase (stability decreases) as r or b increase, except at very low values of either parameter, where the effect is reversed.

**HOST–PARASITOID MODEL**

Within the range of parameters giving deterministic stability, the behaviour of the host–parasitoid model (Fig. 9) was much like that of the single-species model (Fig. 1). Variability was least when |λ| was smallest, and increased fairly rapidly as |λ| exceeded 0.9. This increase in variability was greater for complex λ than real λ, just as in the single-species model it was greater with negative than positive λ; in both cases the greater variability corresponds with oscillatory rather than monotonically damped deterministic dynamics.

In the host–parasitoid model, however, there was an extreme change in dynamics when the stability boundary (|λ| = 1, at k = 1) was crossed (Fig. 10). At |λ| = 0.99, the simulation presumably could have run indefinitely; in 10000 generations the ranges in log density were only 7–04 for hosts and 7–54 for parasitoids. For all |λ| ≥ 1, however, extreme densities required the simulations to be stopped prematurely.

Even in the neutrally stable case of |λ| = 1, the log parasitoid density went below −47, and had a range of almost 63, in less than 2300 generations. These explosive oscillations were even more rapid as |λ| increased. The extreme densities were not infrequent, either, since the IQR also increased abruptly at |λ| = 1 (Fig. 10).

**Discussion**

Stability analysis of the deterministic component of these models clearly was quite predictive of the behaviour, specifically, the degree of variability, of the stochastic simulations. This suggests that conclusions concerning the effects of various parameters

Fig. 8. Comparison of deterministic stability (λ) and stochastic variability (IQR) as functions of r and b. Solid lines are contours of λ, at levels of 0.5 (closest to origin), 0, 0.5, 1, 2 and 3 (furthest from origin). Shading represents the average IQR for the corners of each 0.1 × 0.2 cell of the r × b grid. Levels of transitions in shading are 0.75 (white to light shading), 1.5, 3, 6 and 12 (to darkest shading).
on the stability of deterministic models can be extended to address the ‘stability’ (in a more general sense) of analogous stochastic systems.

Even the simplest form of stability analysis, a dichotomous classification of systems as stable or unstable, was meaningful in some situations. For both the host—parasitoid model and the single-species model with positive \( \lambda \), there was an explosive increase in variability as the deterministic system became unstable (taking the random walk as the unstable equivalent of the single-species model).

For the single-species model with negative \( \lambda \), the stable—unstable dichotomy was not useful: there was no qualitative change in dynamics when the stability boundary was crossed. However, in every instance more-detailed information from stability analysis — the magnitude and nature (sign, if one-dimensional, or real vs. complex if two-dimensional) of \( \lambda \) — was closely correlated with the variability of the stochastic simulations. For a given level of stochastic perturbation, systems with small \( |\lambda| \) varied less than related systems with larger \( |\lambda| \) (apart from minor variations when more than one parameter was varied, e.g. Fig. 8), and systems with monotonic deterministic dynamics (\( \lambda \) real and positive) varied less than oscillatory systems (\( \lambda \) negative or complex) with the same \( |\lambda| \).

The two models explored here represent only a small portion of population dynamics theory. It is possible that for other models there would be less correspondence between deterministic analysis and stochastic dynamics. However, preliminary studies of several other models gave results similar to those presented above. The form of the stochastic component does not appear to be important: the same two deterministic models as above, but with additive stochastic terms, gave results almost identical to those presented above. For the host—parasitoid model, neither host self-damping (as in Beddington, Free & Lawton 1978) or more complex parasitoid competition (as in Taylor 1988), or both, made any essential difference; in particular, explosive oscillations occurred for unstable cases of all these models. Finally, a model of interspecific competition similar to the single-species model presented above (based on the model of Ives & May 1985) again showed a continuous, monotonic increase in variability as \( |\lambda| \) increased.

These correspondences between the behaviours of simple deterministic and simple stochastic models of course do not prove that either sort of model is relevant to natural populations. They do, though, refute the suggestion that introducing a stochastic component fundamentally alters the nature of the dynamics, producing behaviour which is ‘difficult to describe and understand using the classical approach alone’ (Morrison & Barbosa 1987, p. 612). To the contrary, stability analysis was very able to predict — in the relative, qualitative terms appropriate for such simple models — the effects of model parameters on simulated dynamics. There does not seem to be any need to throw out the vast body of deterministic theory simply because it is deterministic.

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