How I learned to stop worrying about chaos and love the Gompertz

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INTRODUCTION

Robert May published a manuscript in 1974 showing that a simple deterministic density-dependent population model – the logistic equation - could exhibit complex dynamics. More specifically, chaotic dynamics (May, 1974). For many ecologists, the take-home message of Robert May's work was that medium and long-term natural population fluctuations may be very difficult if not impossible to predict because natural population dynamics, like the weather, may often be chaotic. And chaotic dynamics are very sensitive to initial conditions and thus, tiny errors in initial population estimates would lead to large prediction errors. Interest in chaotic dynamics has remained high in five decades since the May paper was published though an analysis of publication rates suggests that interest in chaos in ecology peaked in 1996 (Munch et al 2022).

The debate about the ubiquity of chaotic dynamics in natural systems began shortly after the publication of the May paper and continues to today (Beddington et al. 1975, Gilpin 1979, Hastings 1993, Munch et al. 2022, Rogers et al. 2022). May and Oster (1976) made the explicit argument that ecologists should not be quick to attribute lack of predictability of population fluctuations to measurement, sampling or model error. That, in fact, natural populations may be commonly exhibiting chaotic dynamics and be subject to extreme sensitivity to initial conditions.

"*Nevertheless, there is still a tendency on the part of most ecologists to interpret apparently erratic data as either stochastic "noise" or random experimental error. There is, however, a third alternative, namely, that wide classes of deterministic models can give rise to apparently chaotic dynamical behavior*."

Hastings et al (1993) made an enthusiastic case that chaos has important and substantive concerns for ecologists.

"*We strongly believe that the study of chaos will yield important insights for ecologists.* "

"*We argue that chaotic dynamics are likely to be common rather than the exception in ecological systems by looking for chaos in ecological models, focusing only on biologically reasonable interactions and parameter values."*

For the first several decades, meta-analyses of natural population dynamics found little evidence that chaotic dynamics are common in nature (Turchin and Taylor, 1992, Ellner and Turchin 1995, Jaggi and Joshi 2001). More recently, Munch et al 2022, and Rogers et al have made the case that chaotic dynamics are common in nature. Both meta-analyses concluded that chaotic dynamics could be found in up to 30% of populations if (1) the underlying population model is multi-species rather than a one-dimensional discrete time model, (2) more sensitive detection methods, and (3) longer time series are used. However, the concerns raised by those early papers were that simple deterministic density-dependent models could lead to chaotic dynamics. I suspect that few ecologists would have been surprised that populations controlled by many drivers interacting in nonlinear ways could lead to complex dynamics that would be indistinguishable from chaos. What was surprising was that the 'default' population dynamics model that is routinely taught in introductory ecology courses could have chaotic dynamics.

One example of how embedded the concept of chaotic dynamics in scientific thought is that Cohen (1995) even referenced May's work when discussing human carrying capacity despite no evidence that the logistic model captured human population dynamics better than other models and clear understanding that the intrinsic growth rather of human populations almost certainly didn't fall above the r-thresholds of the logistic model.

Logistic population models were what May simulated in his early papers and are routinely taught as foundational ecological models in introductory ecology courses, but recently, Gebreyohannes and Houlahan (2024) have shown that another simple model – a Gompertz model – makes better predictions for natural populations than the logistic model. However, the underlying dynamics and the effects of r and K have not been explored in the literature.

The objectives of this paper are to (1) examine the simulated population dynamics of three simple population models - the differential logistic, the difference logistic and a Gompertz model – with particular emphasis on chaotic dynamics and (2) make recommendations about future population research.

METHODS

Equations

The logistic equations used in May's 1974 paper were the continuous population dynamics and the difference logistic equation for discrete populations.

$$N_{t+1} = N_t * \exp\,(r * \left(1 - \frac{N_t}{K}\right))$$ Differential logistic

$$N_{t+1} = N_t + (r * N_t * \left(1 - \frac{N_t}{K}\right))$$ Difference logistic

$$N_{t+1} = e^r * {N_t}^{1-\frac{r}{LN(K)}}$$ Gompertz

The difference logistic equation and the Gompertz equation can be linearized and r and K parameters estimated using linear regression. The estimated intercept equals the intrinsic growth rate (i.e. r) for both the logistic and Gompertz models and the estimated slope is -r/K for the logistic difference model and -r/log(K) for the Gompertz model.

$$Log\left(\frac{N_{t+1}}{N_t}\right) = r + -\frac{r}{K} * N_t \quad \text{linearized Difference logistic}$$

$$Log\left(\frac{N_{t+1}}{N_t}\right) = r + -\frac{r}{logK} * \log\left(N_t\right) \quad \text{Linearised Gompertz}$$

The linearized difference logistic equation was used to estimate the intrinsic growth rate for each time series across the 14 datasets.

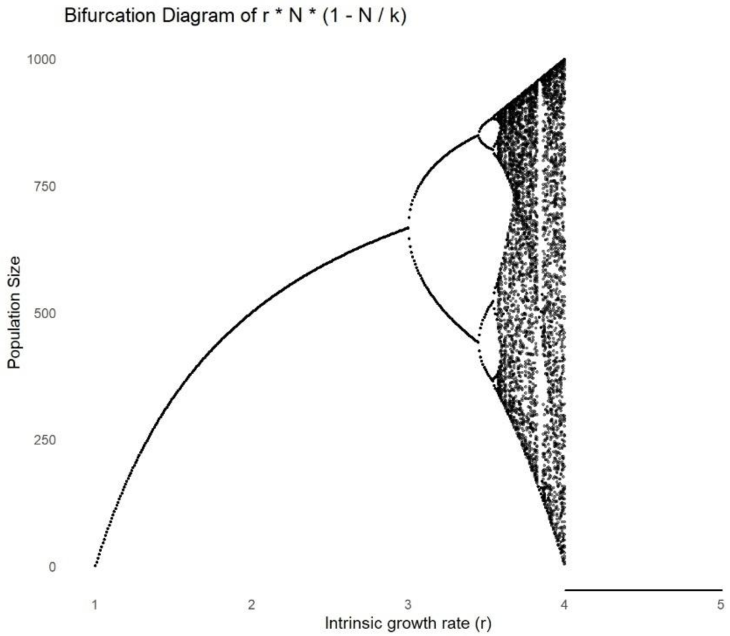
Simulations

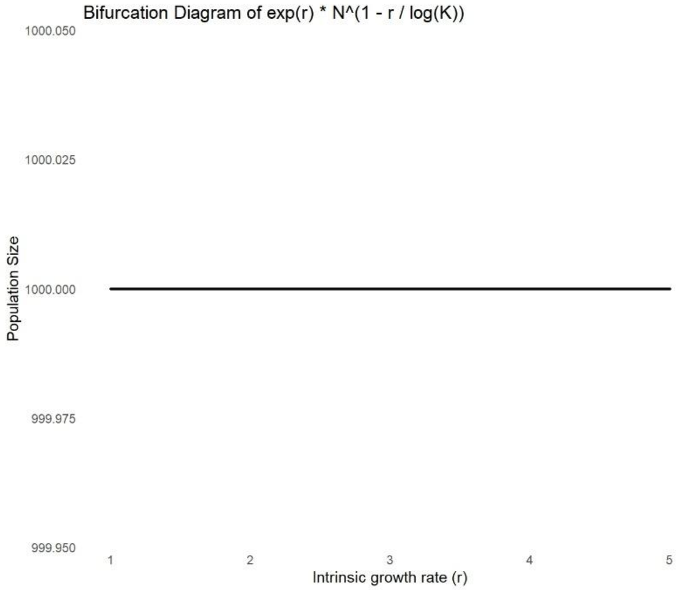
For each of equations 1, 2 and 3, I set K =1000, Nt=0 = a range of values from 0.01 * K to 1.01 * K and r to a range of values from 0.5 to 6.0. I ran each simulation for 1000000 time steps and identified the break points between convergence to a single value, 2-point cycles, 4-point cycles, 8-points cycles, and cycles of longer than 8 points or chaotic dynamics.

Initial simulation used r values of 0.1, 0.5, 1.0, 2.0, 3.0, 4.0, 5.0, and 6.0. When break points were observed the range of r values was changed iteratively to identify more precisely the breakpoint. The breakpoints were identified to 4 significant digits.

RESULTS

Both the differential and difference deterministic logistic equations lead to chaotic dynamics above an intrinsic growth rate threshold (i.e. 3.57 and 2.57, respectively) (Figures 1a and 1b and Table 1). In addition, differential and difference logistic models have intrinsic growth rate thresholds that result in extinction (i.e. 4 and 3, respectively) (Figures 1a and 1b and Table 1). The deterministic Gompertz model always reaches a single stable equilibrium regardless of the intrinsic growth rate and there is no intrinsic growth rate that inevitably leads to extinction (Figures 1c and Table 1).


Bifurcation Diagram of r * N * (1 - N / k)


Bifurcation Diagram of exp(r) * N^(1 - r / log(K))

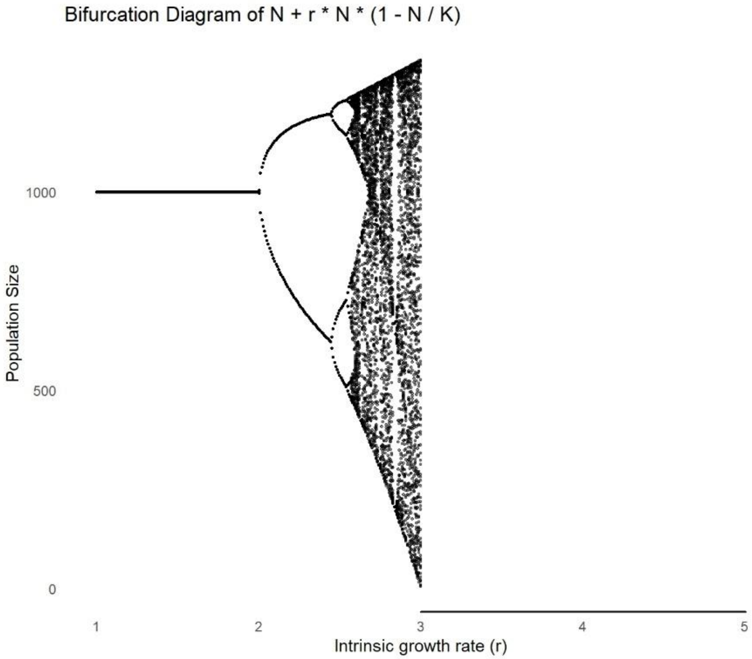

Bifurcation Diagram of N + r * N * (1 - N / K)

Figure 1. Bifurcation plots of the logistic differential equation (top left panel), the logistic difference equation (top right panel) and a Gompertz equation (bottom panel).

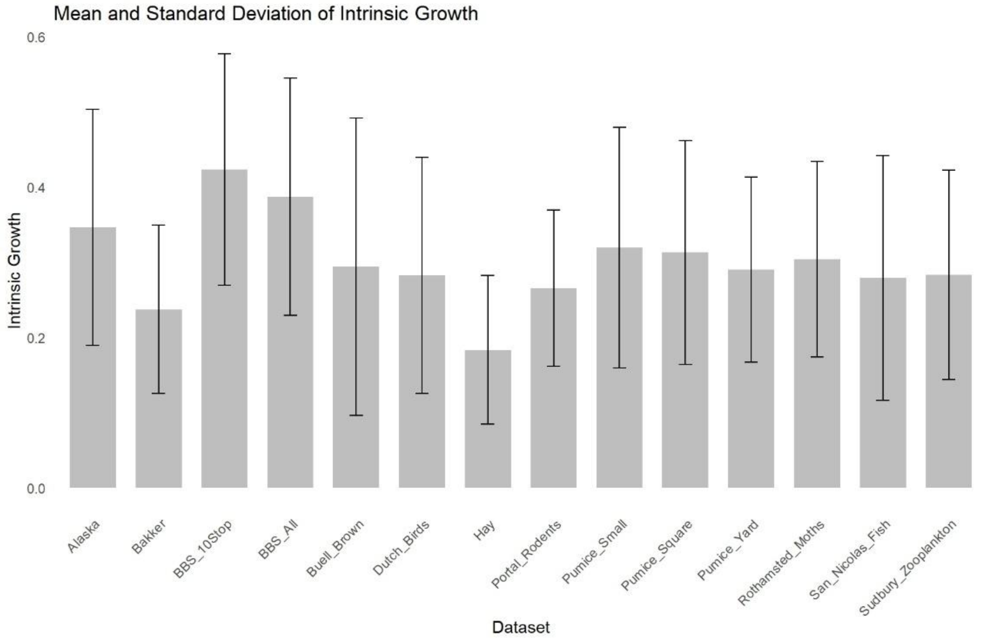


Figure 2. The means and standard deviations of r-values across 14 datasets.

Population Dynamics	Differential logistic r-threshold	Difference logistic r-threshold	Gompertz r-threshold
Stable point	3	2	All
2 – phase	> 3.0	> 2.0	None
4 – phase	> 3.545	> 2.4494	None
8 - phase	> 3.565	> 2.544	None
16 - phase	> 3.5688	> 2.5644	None
32 - phase	> 3.5697	> 2.5687	None
64 - phase	> 3.5699	> 2.5696	None
128 – phase and greater	>3.57	> 2.5699	None
Extinction	> 4.0	> 3.0	None

Table 1: Stable, cycle and chaos thresholds for the logistic differential, logistic difference and Gompertz equations.

The mean intrinsic growth rates over more than 25000 time series across 14 datasets never exceeded 0.5, far below the threshold required for chaotic dynamics in the logistic models. Further, not a single time series had am estimated intrinsic growth rate above the threshold required for chaotic dynamics

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DISCUSSION

Gebreyohannes and Houlahan (2024) showed that, on average, a linearised Gompertz model made better predictions to new data than the linearised logistic differential model. Here, I've shown that the Gompertz equation most commonly used to model population dynamics does not lead to chaotic dynamics even as the simulated intrinsic growth rate values grow implausibly large. The difference logistic model did make better predictions than the Gompertz model from some time series (Gebreyohannes and Houlahan 2024), but none of the more than 25000 estimated intrinsic growth rates was above the threshold for chaotic dynamics.

Early claims were made that chaotic dynamics may be common in natural systems. Initial reviews searching for chaotic dynamics in natural systems concluded they were rare, but two recent reviews have concluded they are common. Both recent reviews concluded that observed chaotic dynamics likely aren't emerging from simple one-dimensional causal models. The methods for detecting chaos in simulated and natural systems examine time series for exponential short-term divergence (i.e. predictive ability beyond the short term). Munch et al. acknowledge that these methods can often not distinguish between chaotic dynamics and noise. Rogers et al (2022) simulated chaotic and non-chaotic dynamics to evaluate six different methods for detecting chaos and chose the three approaches that made the fewest combined false positives and false negatives. They concluded that > 30% of natural populations exhibited chaotic dynamics. The simulations showed that five of the six methods made more false negatives than false positives, which, on the surface, is reassuring, suggesting that if their estimates of > 30% is wrong it is likely biased low rather than high. However, the model used to simulate non-chaotic dynamics will decide the frequency of false positives. The non-chaotic models used in Rogers et al, were simple ecological models, parameterized to produce either periodic cycles or chaotic dynamics and a set of purely stochastic models (e.g. random walk or various shades of noise). And Rogers et al. (2022) set the ceiling on observation error and process error at 0.3 x standard deviation. Those were taken from published estimates , but I believe published estimates are optimistic. Because ecologists don't publish estimates of observation error that imply we should have little confidence in their findings. Underestimating observation and process error will make the 'true' dynamics easier to detect and reduce both Type I and Tye II errors.

But I have little doubt that I could simulate complex population dynamics that were non-chaotic but would appear chaotic if I included enough causal variables with interacting nonlinear effects and propagation of observation error. I haven't tested this assumption and would be happy to be proven wrong.

In addition, Rogers et al (2022) move the goalposts on the chaos discussion. What was startling about Mays' 1974 paper was not the assertion that chaotic dynamics might be common in nature, but that chaotic dynamics could arise from a simple, deterministic non-linear logistic model. The same model that was taught in first year ecology.

Rogers et al (2022) explicitly state that their motivation for re-assessing the prevalence of chaotic dynamics in nature is that population are complex systems embedded in complex systems.

"*But, the apparent rarity of chaos in natural populations is a mystery. Nonlinear dynamics are common in ecological time series, and abiotic drivers of population dynamics are themselves chaotic. Moreover, ecosystems involve tens to thousands of species, and large complex systems are prone to chaos. In light of this, we hypothesize that the dearth of evidence for ecological chaos reflects methodological and data limitations, rather than genuine rarity."*

Given that, I think the true test is to see if the diagnostic techniques used in Rogers et al (2022) can distinguish between chaotic and complex dynamics. I don't believe they have provided a severe test of that question.

Further, Rogers et al. conclude that more flexible models like empirical dynamic modelling should be used in population status assessments and…

"*…new frontiers are open for characterizing the complex, non-equilibrium, and high-dimensional dynamics of ecology…"*

and

"…management should avoid defining objectives in terms of equilibrium conditions.

But these conclusions have little to do with whether chaotic dynamics are common in nature. They are conclusions we would draw if populations are driven by complex (not necessarily chaotic) dynamics and are hard to measure.

Why should we care if chaos is common or not in natural systems? Because chaotic dynamics make medium and long-term prediction an insoluble problem. And why would we waste time and money on insoluble problems. But it seems very unlikely to me that our inability to predict natural population dynamics is due to chaotic dynamics (i.e. sensitivity to initial conditions) and ecologists should be committed to making progress on what is a hard but soluble problem – predicting population fluctuations.

Ecological models are made up of four pieces. First, the phenomenon of interest (i.e. dependent variable), second, the causal driver(s) (i.e. independent variable(s)), third, the functional relationship(s) between independent and dependent variable(s) and fourth, the strength of the relationship(s) among dependent and independent variable(s). There are four reasons that ecological models make bad predictions. First, we get the causal drivers wrong. That is, we include variables that aren't true drivers, or we exclude variables that are true drivers. Second, we get the functional relationships wrong. For example, we assume linear relationships when they are nonlinear or assume the wrong form of non-linear relationship. Third, we make poor estimates of the strength of relationships. For example, get slope estimates in regressions wrong or make poor estimates of interactions (i.e. how the strength of relationships vary depending on other causal variables). Fourth, measurement error. That is, we don't measure the variables accurately, which will lead to less-than-perfect predictions even if we have the 'true' model. This is especially important if model predictions are very sensitive to initial conditions. However, measurement error probably has its most important effect during model selection. That is, when we are trying to identify the correct causal drivers, correct functional relationships and correct strength of relationships. Because measurement error will prevent us from selecting the exact right model and/or getting the parameter estimates right. So, the problem that chaotic dynamics cause is a narrow subset of the concerns associated with one of the four ways (i.e. measurement error) we get predictions wrong.

But as I have demonstrated, there are two very good reasons why we should not expect chaotic dynamics in natural populations. First, the density-dependent model - the Gompertz - for which there is the most empirical support does not exhibit chaotic dynamics for any values of r. Second, values of r that fall within the range that results in chaotic dynamics are rare in natural systems.

Further, propagation of error implies that there will be exponential divergence if the 'true' model is complicated enough, and our estimated model is 'wrong' enough. Lastly, there is little evidence that we are able to make good population predictions even on very short time horizons (Gebreyohannes and Houlahan 2024) and poor predictions over short time horizons are not caused by sensitivity to initial conditions. The study of chaotic dynamics, while interesting, has been a blind alley for ecologists.

Ecology is a wide-ranging discipline, but I suspect most ecologists would agree that understanding the causes of spatial and temporal variability in population size is one of the core ecological questions. And we have made relatively little progress. Ultimately, Hasting et al. (1993) make a case for population dynamics being complex rather than chaotic. That is, hard to understand rather than sensitive to initial conditions. By 'complex and hard to understand' we mean – generally have many causal drivers, that impact populations in nonlinear ways and interact with each other. Population fluctuations are going to be very hard to understand and therefore hard to predict, but not because they are chaotic; it is because they are complex. We have shown that there are datasets where simple density dependent models like the Gompertz allow us to make better predictions than the random walk. Why is this true for some datasets and not others?

The job of ecologists is to begin building the list of causal drivers, identifying the true functional relationships and accurately estimating the strength of relationships. Then assessing the transferability of models over time, space and taxonomy. Studying chao dynamics has likely been an interesting waste of time.

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