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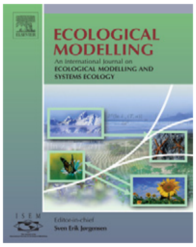

The Time Invariance Principle, the absence of ecological chaos, and a fundamental pitfall of discrete modeling

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ABSTRACT

This paper is to show that most discrete models used for population dynamics in ecology are inherently pathological that their predications cannot be independently verified by experiments because they violate a fundamental principle of physics. The result is used to tackle an on-going controversy regarding ecological chaos. Another implication of the result is that all dynamical systems must be modeled by differential equations. As a result it suggests that researches based on discrete modeling must be closely scrutinized and the teaching of calculus and differential equations must be emphasized for students of biology.

1. Introduction

No models in ecology are better known than the Logistic Map, or have played a greater role in the development of the chaos theory (May, 1974; Hassel, 1975; Hassel et al., 1975; Berryman and Millstein, 1989; Logan and Allen, 1992). Surprisingly, however, there is not a greater controversy than what was generated by the model's prediction that one-species populations are inherently chaotic.

The key prediction of the Logistic Map, $x_{n+1} = Q(x_n, r) := r x_n (1 - x_n)$, says that increasing the intrinsic reproductive rate r leads to chaotic oscillations in population. However, contradicting evidence existed even before the chaos theory was popularized in ecology. One noticeable example was given by McAllister and LeBrasseur (1971) who showed that enriching an aquatic system led to stable equilibrium. Ensuing extensive search for field chaos came up empty-handed. For example, well-established geographic patterns on microtine species (Hanski et al., 1991; Falck et al., 1995) showed that ecological systems tend to stabilize down the north-to-south latitude gradient, correlating well with the ultimate resource abundance in liquid water and sunlight towards the equator. A comprehensive hunt for ecological chaos was down by Ellner and Turchin (1995) who used three

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different Lyapunove exponent estimators to analyze a large collection of empirical data and showed rather conclusively that ecological chaos is not to be expected in the wild.

The glaring irreconcilability between the theory and reality can only lead to one logical conclusion: the theory is wrong. Concluding it otherwise would have to imply that logic imperatives do not apply to ecology. However, a definitive explanation to the theory's failure is lacking while efforts to justify it continue (e.g. Eskola and Geritz, 2007). The purpose of this paper is to make a case that the Logistic Map and most discrete maps used in ecology and life sciences cannot be models for *any* physical process, population dynamics in particular because their predictions cannot be *independently* verified by experiments.

2. The result

This conclusion rests on a fundamental principle of physics held since the time of Copernicus in the 15th century that a physical law should be the same anywhere and anytime in the universe. In other words, a law must take the same mathematical form, derivable from experiments carried out at independently chosen times and spaces. As a result, the mathematical formulation of a law must be endowed with such time invariance property. Taken to be self-evident, we state the principle in the following formulation more suited for the issues under consideration:

> *Time Invariance Principle* (*TIP*): A physical law has the same mathematical form to every independent choice of observation time.

This principle has an important implication to dynamical systems as laws of physical processes. To be precise, let y be the set of state variables and p be the set of parameters of a physical process. As a dynamical system, y changes in time t. Suppose an observation is made at t_0 and the state is y_0, where t_0 is the time passage since the start of the process. Another observation is made $t>0$ time after t_0 and the state is y_t. Then, as a physical law, y_t is governed by a function, denoted by $y_t=\psi_t(y_0,t_0,p)$, depending on the passage of time t beyond t_0, the state y_0 at t_0, and the system parameter p. As a default requirement, it must satisfy the unitary condition

$$\psi_0(y_0,t_0,p)=y_0,$$

that is, with time increment 0, the law ψ_0 leaves every state fixed. Now by the Time Invariance Principle, if another observation is made $s>0$ unit time later, the same functional form $(y_t)_s=\psi_s(y_t,t+t_0,p)$ must hold. Most importantly, the function ψ_t must satisfy the following group property and the unitary condition

$$(y_t)_s=\psi_s(\psi_t(y_0,t_0,p),t+t_0,p)=\psi_{s+t}(y_0,t_0,p)=y_{s+t},$$
$$\text{and}\quad \psi_0(y_0,t_0,p)=y_0, \tag{1}$$

which together is referred to being *TIP-conforming*. That is, if an observation is made t time after the initial observation, and another is made s time later, then the result must be the same if only one observation is made $s+t$ time after the initial observation. More generally, the state at $s+t$ after the state y_0 at t_0 is the same state at s after an intermediate state y_t which is the state at t after the same initial y_0 at t_0. A violation of this property that $\psi_{s+t}(y_0,t_0,p)\neq\psi_s(\psi_t(y_0,t_0,p),t+t_0,p)$ implies that either such an "experiment" is not reproducible, i.e., using independent observing times lead to irreconcilable conclusions, or such a functional form ψ does not govern the laws that the experiment is to establish or to verify.

A physical process is called *autonomous* if its dynamical law $\psi_t(y_0,t_0,p)$ is independent of t_0. In fact, every process can be considered as autonomous by augmenting the state only one-dimension higher. More specifically, let $x=(y,\tau)$ and denote $x=(y_0,\tau_0)=(y_0,t_0)$, $x_t=(y_t,\tau_t)$ with

$$\tau_t=t+\tau_0=t+t_0,$$

Then the augmented state x is autonomous even if y is not. More specifically, let

$$\phi_t(x_0,p)=(\psi_t(y_0,\tau_0,p),t+\tau_0),$$

then it is straightforward to check the following

Lemma 1. *The functional form ψ satisfies the TIP-conforming property (1) if and only if the augmented functional form ϕ satisfies the autonomous TIP-conforming property*

$$(x_t)_s=\phi_s(x_t,p)=\phi_s(\phi_t(x_0,p),p)=\phi_{s+t}(x_0,p),$$
$$\text{and}\quad \phi_0(x_0,p)=x_0, \tag{2}$$

Thus, from now on we will assume all TIP-conforming functional forms are autonomous, and both properties (1) and (2) are interchangeably referred to as the *TIP-conforming group property*.

As a result, an immediate consequence to the Time Invariance Principle is the following.

Lemma 2. *If a TIP-conforming dynamical system $\phi_t(x,p)$ is continuously differentiable at $t=0$ and any x in its domain of definition, then $x(t)=\phi_t(x_0,p)$ must be the unique solution to an initial value problem of a differential equation:*

$$\frac{dx(t)}{dt}=F_\phi(x(t),p),\quad x(0)=x_0,$$

where

$$F_\phi(x,p)=\frac{\partial\phi_h}{\partial h}(x,p)|_{h=0}$$

is the generating vector field of ϕ_t. Conversely, if the vector field F is continuous differentiable, then the solution to the initial value problem satisfies the TIP-conforming group property (2).

Proof. Because ϕ is differentiable and is TIP-conforming (2), we have the following derivative

$$\begin{aligned}\frac{dx(t)}{dt}&=\lim_{h\to0}\frac{\phi_{t+h}(x_0,p)-\phi_t(x_0,p)}{h}\\&=\lim_{h\to0}\frac{\phi_h(\phi_t(x_0,p),p)-\phi_0(\phi_t(x_0,p),p)}{h}\\&=\frac{\partial\phi_h}{\partial h}(\phi_t(x_0,p),p)|_{h=0}=F_\phi(x(t),p),\end{aligned}$$

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Table 1 – TIP-nonconforming and possible TIP-nonconforming maps

Generalized Beverton–Holt (Maynard-Smith and Slatkin, 1973; Hassel, 1976; Hassel et al., 1975)	$N_{t+1} = \frac{bN_t}{1+(hN_t)^\gamma}, \gamma \neq 1$
Bernoulli	$N_{t+1} = aN_t \pmod 1$
Logistic	$N_{t+1} = N_t[1 + r(1 - N_t/K)]$
Richard (Richards, 1959)	$N_{t+1} = N_t[1 + r(1 - (N_t/K)^m)], m \neq 1$
Ricker (Ricker, 1954)	$N_{t+1} = N_t \exp(r(1-N_t/K))$
Nicholson–Bailey (Nicholson and Bailey, 1935)	$\begin{cases} N_{t+1} = N_t \exp(-aP_t) \\ P_{t+1} = N_t(1 - \exp(-aP_t)) \end{cases}$
LPA (Denis et al., 1995)	$\begin{cases} L_{t+1} = bA_t \exp(-c_{el}L_t - c_{ea}A_t) \\ P_{t+1} = L_t(1 - \mu_1) \\ A_{t+1} = P_t \exp(-c_{pa}A_t) + A_t(1 - \mu_a) \end{cases}$
Leslie (Leslie, 1945)	$\vec{N}_{n+1} = \begin{bmatrix} 0 & f_1 & \cdots & f_{k-1} & f_k \\ s_1 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_k & 0 \end{bmatrix} \vec{N}_n$

showing $x(t)$ is a solution of the equation. Since $F_\phi(x, p)$ is continuous differentiable in x because $\phi_t(x, p)$ is, the solution to the initial value problem is unique. The converse follows from a well-known result on the existence and uniqueness of the solution to the initial value problem. □

We now conclude that the Logistic Map does not model any population dynamics subject to time-independent observations. More precisely, we have the following result.

Theorem. *Let $x_{n+1} = Q(x_n, r)$ be the Logistic Map with $x \in [0, 1]$. Then, there does not exist a continuously differentiable, TIP-conforming, 1-dimensional autonomous or nonautonomous dynamical system so that $\phi_{t_0}(x, r) = Q(x, r)$ at any time t_0 and for all x from any interval containing [0, 1] or $\psi_{t_1}(x, t_0, r) = Q(x, r)$ at any time t_0 and for all x from any interval containing [0, 1] and any passage of time t_1 after t_0.*

Proof. By the preceding lemmas, we can assume without loss of generality that $x(t) = \phi_t(x_0, r)$ and that $x(t)$ is the solution of an autonomous differential equation $x' = F_\phi(x)$ generated by ϕ. As such, $Q(x, r) = \phi_{t_0}(x, r)$ (or $Q(x, r) = \psi_{t_1}(x, t_0, r)$) would be the time-fixed Poincaré map of the continuous flow. We know by an elementary property of differential equations that this is impossible since such time-fixed Poincaré maps are invertible but Q is not in the interval [0,1]. □

This conclusion not only applies to the Logistic Map, but also to most discrete maps in ecology. Table 1 lists some popular discrete models in ecology. To be more precise, the same argument can be used to show that the generalized Beverton–Holt map, the Bernoulli model, the Richard map, and the Ricker map are not TIP-conforming.

Applying the same argument for any dimensional, TIP-conforming functionals shows that such functionals must be solutions to higher dimensional differential equations for which the time-fixed Poincaré maps must be invertible. Thus, for invertible maps, the argument above does not apply, and their TIP-conformity needs be established by some other ways based on the group property (1) or (2). If short of definitiveness, here is a diagnostic test for probable TIP-nonconformity. More specifically, we certainly assume that all biological processes are governed by physical laws that are TIP-conforming, allowing time-independent observation and verification on their states. Assume observation is made every unit of time and x_n is the state at time $t = n$. Because the state is TIP-conforming, we must have

$$x_n = \phi_1(x_{n-1}, r) = \phi_1(\phi_1(x_{n-1}, r), r) = \cdots = \phi_1^n(x_0, r)$$

where the exponent stands for iterative composition. Therefore,

$$\phi_n(x_0, r) = \phi_1^n(x_0, r)$$

that is, the nth iterative composition of ϕ_1 must have the *same* functional form as itself since both ϕ_1 and ϕ_n have the same functional form. This property can be used as a diagnostic test for *probable* TIP-nonconformity. For example, the nth iterate of the Logistic Map is a 2^n-degree polynomial with evolving coefficients for each n. This implies that the map is very unlikely to be TIP-conforming because of the ever-changing functional forms of its iterates or its TIP-conforming functional would be extremely complex, in which case it is unlikely that such a complex functional happens to satisfy a stringent condition that is of the TIP-conformity and at the same time arises from a relatively simplistic modeling exercise that is typical of most discrete modeling. This diagnostic test can be used to cast serious doubts on the TIP-conformity of a model if the test fails to be conclusive. For example, we can conjecture based on the preliminary diagnostic test that the remaining maps from Table 1, the Nicholson–Bailey map, the LPA map, and the Leslie matrix map, are unlikely to be TIP-conforming. The same can be said for all nonlinear models in cell-automata in games of life that they are very unlikely to model any physical processes subject to TIP-conformity. Without TIP-conformity, time-independent observations can neither verify nor establish such maps as models, theories, or laws.

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3. Discussions

A plausible model for a physical process needs to pass two types of objective scrutiny: the internal conceptual consistency in the model's structure and the external empirical verification of its prediction. The Logistic Map and its variants from Table 1 have failed both. They are theoretically pathological for not being TIP-conforming. They make the wrong chaos prediction for one-species system that empirical observations do not support as pointed out in Section 1. In the view of their TIP-nonconformity, these fundamental defects are inextricably intertwined: TIP-nonconforming functional forms cannot be established by independent observations to model any underlying physical law.

While the conventional TIP-nonconforming models predict diametrically the opposite, their TIP-conforming counterparts are consistent with a variety of converging observations that enrichment and reproductive efficiency promote ecological stability. To make this point, we comment below from two mechanistically constructed models: a one-species model and a three-trophic food chain model.

The one-species model can be derived in two ways. The first derivation is based on the following postulate:

> *One-Life Rule*: Every individual organism dies at most once in any fixed time span and exactly once in any fixed time span at an infinite density of its species.

More specifically, fix any time interval and use it as the unit of time. Denote x_0 the initial population of a species and x_n the population at the nth unit of time. Then we consider the *per-capita growth* functional $(x_{n+1}-x_n)/x_n$. Translate the One-Life Rule in terms of the per-capita growth, the latter must be greater than -1 and approach -1 as $x_n \to \infty$. The simplest functional form satisfying this property is the following

$$\frac{x_{n+1}-x_n}{x_n} = \frac{b-mx_n}{1+mx_n},$$

where b is the maximum per-capita growth parameter and m is the intra-competition-induced mortality parameter because of the One-Life Rule. Solving for x_{n+1} leads to

$$x_{n+1} = \frac{(b+1)x_n}{1+mx_n} := \frac{rx_n}{1+mx_n} := B_1(x_n, r, m)$$

where $r = b+1 > 1$, resulting in the Beverton–Holt model which was first used by Beverton and Holt in 1956 for fishery studies (Beverton and Holt, 1956). The second derivation is based on a mass balance law or stoichiometry. More specifically, an organism is recognized to be a package of elemental atoms, obeying the law of mass conservation. For example, let us use carbon (C) as a basic unit to measure an individual organism's biomass for a one-species system. Arbitrarily fix a time increment, again say $t = 1$ for definitiveness. Let x_n and x_{n+1} be the numbers of individuals for the current generation and the "next" generation, respectively. Let N be the amount of C available in the time interval, i.e., a nutrient flux rate in C. Let c be the amount of C that is needed during the period for each individual which is to make to the next generation, i.e., the per-capita maintenance cost rate in C. Let a be the efficiency ratio, which measures the proportionality of the new generation that each individual of the current generation gives rise to for each unit of resource in C. It is the per-capita growth-to-consumption ratio. Then $N - cx_{n+1}$ is the amount available for the transition to the next generation, and the product of $N - cx_{n+1}$, a, and x_n gives the next generation's population:

$$x_{n+1} = (N - cx_{n+1}) \times a \times x_n.$$

Solve for x_{n+1} to have

$$x_{n+1} = \frac{rx_n}{1+mx_n} \quad \text{with} \quad r = Na, \quad m = ac,$$

the same Beverton–Holt model obtained above.

Basic properties of the Beverton–Holt model include the following. First, it is straightforward to check that the model is TIP-conforming:

$$B_1^k(x_n, r, m) = B_1\left(x_n, r^k, m\frac{r^k-1}{r-1}\right) = B_k(x_n, r, m)$$

that is, its kth iterate has the same functional form as itself, which then can be extended to all continuous time t:

$$B_t(x_0, r, m) := B_1\left(x_0, r^t, m\frac{r^t-1}{r-1}\right) = \frac{r^t x_0}{1+m[(r^t-1)/(r-1)]x_0},$$

which in turn satisfies the defining Eq. (2) for TIP-conformity for time-independent observations. In fact, the discrete Beverton–Holt map is simply the time-1 Poincaré map of the continuous counterpart. Also, the generating differential equation to which x_t is a solution is obtained as

$$\frac{dx_t}{dt} = \frac{d}{dh}B_{t+h}(x_0, r, m)|_{h=0} = \frac{d}{dh}B_h(x_t, r, m)|_{h=0} = \left(\ln r - m\frac{\ln r}{r-1}x_t\right)x_t,$$

the Logistic Equation. In contrast to the per-capita growth in any fixed time interval, the instantaneous per-capita growth *rate* is linear which can be arbitrarily negative at high-population density. More importantly, any non-zero initial population converges to an equilibrium, the carrying capacity of the Logistic Equation:

$$\lim_{t\to\infty} x_t = \lim_{t\to\infty} B_t(x_0, r, m) = \lim_{t\to\infty} \frac{r^t x_0}{1+m[(r^t-1)/(r-1)]x_0} = \frac{r-1}{m},$$

for which $r > 1$ as a default assumption. In the context of our stoichiometric modeling for which $r = Na$, $m = ca$ we see that the greater the nutrient influx N, the greater the stable equilibrium, and the same holds for smaller per-capita maintenance cost c as well. The model predicts that prosperity or efficiency or both promote stability, not chaos, consistent with experimental findings cited in Odum, 1971; McAllister and LeBrasseur, 1971; Ellner and Turchin, 1995.

The same *enrichment and efficiency stabilization principles* hold for a mechanistically constructed three-trophic food chain model as well. More precisely, consider this system of differential equations for a prey, X, a predator, Y, and a top-predator, Z, of the predator:

$$\begin{cases} \dot{X} = X(b_1 - d_1 - m_1 X) - \dfrac{a_1 X}{1+h_1 a_1 X}Y \\ \dot{Y} = Y\left(\dfrac{b_2 a_1 X}{1+h_1 a_1 X} - d_2 - m_2 Y\right) - \dfrac{a_2 Y}{1+h_2 a_2 Y}Z \\ \dot{Z} = Z\left(\dfrac{b_3 a_2 Y}{1+h_2 a_2 Y} - d_3 - m_3 Z\right) \end{cases} \tag{3}$$

Mechanistic justification of this model is threefold. First, being a unique solution to this autonomous ordinary differential equation, $x_t = \phi_t(x_0)$ with $x_0 = (X_0, Y_0, Z_0)$ is automatically

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TIP-conforming by Lemma 2. Second, each species obeys the Logistic Equation because of the incorporation of the intra-specific mortality rates m_i. It in turn implies that each species obeys the One-Life Rule even if the other two species are fixed at a constant density, respectively. Third, the per-predator predation rates, $(a_1X)/(1+h_1a_1X)$, $(a_2Y)/(1+h_2a_2Y)$, are mechanistically TIP-conforming in their own right. To see this, let h_d be the average time a predator needs to discover a prey starting from a search and let h_k be the average time the predator needs to kill the prey after its discovery. Then $h=h_k+h_d$ is the total handling time from the start of searching for a prey to the end of killing it. The reciprocal $r_d=1/h_d$ is the number of prey discovered per unit time that results in kills, i.e., the discovery rate, and $r=1/h$ is the number of prey discovered and then killed per unit time, i.e., the predation rate. Assuming the discovery rate r_d is proportional to the prey density, $r_d=aX$ with a being the discovery probability rate, then the predation rate is

$$r=\frac{1}{h}=\frac{1}{h_d+h_k}=\frac{1/h_d}{1+h_k(1/h_d)}=\frac{aX}{1+ah_kX},$$

with the last functional form being the Holling Type II disc function (Holling, 1959). Because of the *Time Conservation Law*, $h=h_k+h_d$, one can check that the rate function is TIP-conforming. That is, it has the same functional form $r=(aX)/(1+ah_kX)$ regardless of the temporal cut-off defining the killing time h_k—which can end at the moment of killing the prey, or the moment of consuming the prey, or digesting the prey, or all the above before starting a new search again. More importantly, the model predicts the enrichment and efficiency stabilization principles. In fact, the result of (Deng, 2006) shows that any oscillation, periodic or chaotic, of the model must bifurcate into a steady state as the efficiency parameters b_1, b_2 increase for the top-predator and the predator, respectively. In fact, one can show that all oscillations, chaotic or otherwise, must bifurcate into a steady state by increasing any two of the three reproductive efficiency parameters in b_1, b_2 and b_3. Moreover, it is shown in (Deng, 2001, 2004, 2006; Deng and Hines, 2002, 2003) that when b_3 and b_2 are small relative to b_1 the model can exhibit a variety of distinct chaotic attractors. In other words, reproductive inefficiency fosters chaos whereas efficiency promotes ecological stability, consistent with not only empirical findings but also the hypothesis that evolution by natural selection promotes species efficiency in survival fitness.

Empirical data are almost always collected at discrete times. Discrete modeling is an instinctive reaction to that reality to use discrete models to fit discrete data. However, a discrete model has little to say about data collected at different discrete times of the same process if the process permits. If it is not TIP-conforming, it does not model the underlying process subject to time independent observation. This may underlie many attempts via stochastic inclusion to discrete modeling, attributing noise as the chief cause of the irreconcilability between a theory and the reality when in fact TIP-nonconformity of the theory may have been the problem. This paper advocates the approach to use time-continuous models (i.e., differential equations) to fit discrete data because all differential equations (ODE, PDE, delayed DE, stochastic DE) with independent time evolution are automatically and necessarily TIP-conforming. Unlike their TIP-nonconforming counterparts, such models permit the scrutiny by all time-independent, continuous or discrete, observations. This approach makes sure that its models are theoretically consistent in their internal structure, allowing their refinement within the framework of TIP-conformity.

Our TIP-equivalence result for fixed time-step Poincaré maps and differential equations implies that autonomous one- and two-dimensional TIP-conforming maps cannot be chaotic because one- and two-dimensional autonomous differential equations of continuously differentiable vector fields cannot be chaotic. Equivalently, chaotic one- and two-dimensional maps must not be TIP-conforming. (One-dimensional, noninvertible, chaotic maps do arise as *singular limits* of two-dimensional, invertible, but time-varying Poincaré maps of 3 or higher dimensional differential equations (Deng, 1999, 2001, 2004; Deng and Hines, 2002, 2003; Deng et al., 2007). However, such maps alone do not model the physical processes in any *time-independent* fashion.) As a result, an ecological conclusion can be made unequivocally that single- and two-species population dynamics cannot be chaotic. The fact that the controversy has lasted this long was due to the combination of a few understandable factors. To name a few obvious ones: first, the derivations of all popular discrete ecological models seemed logical, but TIP-nonconforming nevertheless. Secondly, because of their TIP-nonconformity, all predictions could not be independently and objectively reproduced, leading to the inevitably confusing state between a seemingly reasonable theory and an uncompromising reality. Thirdly, the empirical irreproducibility against all low dimensional chaos theory was conveniently masked by the inherent unpredictability of all chaotic systems. And fourthly, the irreconcilability was also conveniently masked by a noisy reality that is for most biological experiments and observations.

Comparing to differential equations, discrete maps are easier to teach, easier to do research with. But we should not compromise the Time Invariance Principle just for their simplicity. TIP-conformity is the minimal necessary condition a conceptually consistent model must satisfy. More importantly, the requirement is fundamental to all branches of science, governing the reproducibility of experiments. Because of these reasons, the usage of stand-alone TIP-nonconforming maps is difficult to justify in most circumstances. This conclusion has some important implications to both research and training: both past and future researches based on discrete models must be scrutinized against their TIP-conformity and be justified for their TIP-nonconformity. The subject of discrete maps may have to be de-emphasized in the classrooms and be viewed through the lens of TIP-conformity. On the other hand, training in calculus and differential equations must be further enhanced and greatly emphasized for future generations of theoretical biologists.

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