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3-2007

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The Time Invariance Principle, Ecological (Non)Chaos, and A Fundamental Pitfall of Discrete Modeling

Bo Deng[1]

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 continuous 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 ([29, 19, 20, 3, 27]). 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, $x_{n+1} = Q(x_n, r) := rx_n(1 - x_n)$, says that increase in the intrinsic reproduction rate r leads to chaotic dynamics for the population x_n. Contradicting evidence existed before the chaos theory was popularized in ecology. For example, in a 1971 study of an aquatic system, McAllister and LeBrasseur ([31]) showed that enrichment led to stable equilibrium. Extensive search for field chaos came up equally empty-handed. For example, well-established geographic patterns on microtine species ([18, 16]) showed that ecological systems tend to stabilize down the north-to-south latitude gradient, correlating well with the ultimate energy abundance from the Sun towards the equator. The most comprehensive hunt for ecological chaos was down by Ellner and Turchin ([15]). They used 3 different Lyapunove exponent estimators on a large collection of empirical data. Out of their 21 field data sets, not a single set scored a positive Lyapunove exponent by two of the 3 estimators. Out of their 20 lab data sets, only two scored a positive Lyapunove exponent by two estimators. The inescapable conclusion is overwhelming — ecological chaos is not to be expected in the wild. (Although laboratory chaos is possible with stringent setups, such systems are never simple. In fact, the dimension required is 3 or higher, c.f. [14, 6].)

The glaring irreconcilability between the theory and reality can only lead to one logical conclusion: the theory is wrong. Otherwise, ecology would be the definitive branch of science that logic imperative would have failed. The purpose of this paper is to make a case that the Logistic Map and most discrete models used in ecology and life sciences cannot be models for *any* physical process, population dynamics in particular, and their predictions cannot be *independently* verified by experiments.

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2. Time Invariance Principle. 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 x be the set of state variables and p be the set of parameters of a physical process. As a dynamical system, x changes in time t. Suppose an observation is made at $t = 0$ and the state is x_0. Another observation is made at time $t > 0$ and the state is x_t. Then, as a physical law, x_t is governed by a function, denoted by $x_t = \phi_t(x_0, p)$, depending on the observation time t, the initial state x_0, and the system parameter p. As a default requirement, it must satisfy the unitary condition

$$\phi_0(x_0, p) = x_0,$$

that is, with time increment 0, the law ϕ_0 leaves every state fixed. Now by the Time Invariance Principle, if another observation is made $s > 0$ unit time later, the same function form $(x_t)_s = \phi_s(x_t, p)$ must hold. Most importantly, the function ϕ_t must satisfy the following group property and the unitary condition

$$(x_t)_s = \phi_s(x_t, p) = \phi_s(\phi_t(x_0, p), p) = \phi_{s+t}(x_0, p) = x_{s+t}, \text{ and } \phi_0(x_0, p) = x_0, \tag{1}$$

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 an initial x_0 is the same state at s after an intermediate state x_t which is the state at t after the same initial x_0. A violation of this property that $\phi_{s+t}(x_0, p) \neq \phi_s(\phi_t(x_0, p), p)$ implies that either such an "experiment" is not reproducible, i.e., independent observation times inevitably lead to irreconcilable conclusions, or such a functional form ϕ does not govern the laws that the experiment is about to establish.

An immediate consequence to the Time Invariance Principle is the following result.

Lemma 1. *If 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:*

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

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where

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

is called the generating vector field of ϕ_t.

Proof. Because ϕ is differentiable and is TIP-conforming (1), we have the following derivative

$$\frac{dx(t)}{dt} = \lim_{h \to 0} \frac{\phi_{t+h}(x_0, p) - \phi_t(x_0, p)}{h} = \lim_{h \to 0} \frac{\phi_h(\phi_t(x_0, p), p) - \phi_0(\phi_t(x_0, p))}{h}$$
$$= \left.\frac{\partial \phi_h}{\partial h}(\phi_t(x_0, p), p)\right|_{h=0} = F_\phi(x(t), p),$$

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. $\qquad\square$

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

Theorem 1. *There does not exist a continuously differentiable, TIP-conforming, 1-dimensional dynamical system $\phi_t(x, r)$ so that $\phi_{t_0}(x, r) = Q(x, r)$ at any time t_0 and for all x from any interval containing $[0, 1]$ for which Q is the Logistic Map and r is the intrinsic growth rate with $r > 3$.*

Proof. By the preceding lemma, $x(t) = \phi_t(x_0, r)$ is the solution of an autonomous differential equation $x' = F_\phi(x)$ generated by ϕ. Since the system is 1-dimensional, it does not allow periodic solutions. However, the Logistic Map has a period-2 orbit for $r > 3$ which would correspond to a periodic solution to the TIP-conforming flow if it were true that $\phi_{t_0}(x, r) = Q(x, r)$ for some t_0. A contradiction. $\qquad\square$

This conclusion not only applies to the Logistic Map, but also to most other 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 the following. The generalized Beverton-Holt map is not TIP-conforming for $\gamma > 1$ and large b. The same for the Bernoulli model for $a > 1$, the Richard map, the Ricker map for large r. Applying the same argument for 2-dimensional TIP-conforming functionals shows they are solutions to 2-dimensional autonomous differential equations which do not allow orientation reversing periodic orbits which occur to the Nicholson-Bailey map.

For 3-dimensional or higher systems, the argument above for lower dimensional systems do not apply. However, here is a diagnostic test for possible 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

$$x_n = \phi_1(x_{n-1}, r) = \phi_1(\phi_1(x_{n-2}, r), r) = \cdots = \phi_1^n(x_0, r)$$

where the exponent stands for iterative composition. Therefore,

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

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Table 1: TIP-nonconforming Maps

Generalized Beverton-Holt ([30, 19, 20])	$N_{t+1} = \frac{bN_t}{1+(hN_t)^\gamma}$, $\gamma \neq 1$
Bernoulli	$N_{t+1} = aN_t(\mathrm{mod}\ 1)$
Logistic	$N_{t+1} = N_t[1 + r(1 - N_t/K)]$
Richard ([36])	$N_{t+1} = N_t\left[1 + r(1 - (N_t/K)^m)\right]$, $m \neq 1$
Ricker ([37])	$N_{t+1} = N_t\exp(r(1 - N_t/K))$
Nicholson-Bailey ([33])	$\begin{cases} N_{t+1} = N_t\exp(-aP_t) \\ P_{t+1} = N_t(1 - \exp(-aP_t)) \end{cases}$
LPA ([14])	$\begin{cases} L_{t+1} = bA_t\exp(-c_{\mathrm{el}}L_t - c_{\mathrm{ea}}A_t) \\ P_{t+1} = L_t(1 - \mu_{\mathrm{l}}) \\ A_{t+1} = P_t\exp(-c_{\mathrm{pa}}A_t) + A_t(1 - \mu_{\mathrm{a}}) \end{cases}$
Leslie ([25])	$\vec{N}_{t+1} = \begin{bmatrix} 0 & f_1 & \cdots & f_{k-1} & f_k \\ s_0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & \cdots & 0 & 0 \\ & & \cdots & & \\ 0 & 0 & \cdots & s_{k-1} & 0 \end{bmatrix} \vec{N}_t$

that is, the nth iterative composition of ϕ_1 must have the *same functional form* as itself. 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 such as 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 a serious doubt on the TIP-conformity of the model under consideration. Unlike the 1- and 2-dimensional maps discussed above, for which the preceding theorem provides a definitive means to determine their TIP-nonconformity, we can only conjecture based on the preliminary diagnostic test that the LPA map and the Leslie matrix are very 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, independent observations cannot verify nor establish such maps as models, theories, or laws.

3. Discussions. The suggestion that biological research based on discrete maps is build on a shaky scientific ground inevitably leads to a few questions: One, is the Time Invariance Principle consistent with other known physical principles? Two, what are the TIP-conforming alternatives to discrete modeling in ecology? Three, can TIP-nonconforming maps be justified and under what

circumstances? Four, contradicting to predictions by all discrete, chaotic maps in theoretical ecology, why chaos is rare in the wild? We will exam these issues for the remainder of the discussion.

Consistency With The Principles of Relativity. The Copernican idea that physical laws must be universal in space and time has guided many great theories in physics. Einstein's theories of special and general relativity are two of the most celebrated examples. The Time Invariance Principle is simply a corollary of the same idea that governs dynamical processes.

One consequence of Einstein's theory of special relativity is that there is no absolute time. TIP captures this time-relativity aspect of his theory for the convenience of our discussion. As an example to make the point, consider two inertial frames with Frame 2 moving at a constant velocity v with respect to Frame 1. Assume at the origin of Frame 1 there is an on-going dynamical process. Let $f_t(x)$ be the law deducted by observers of Frame 1 over a time interval t with initial state x. Due to the time dilation effect of special relativity for Frame 2, observers in Frame 2 will not see the same output $f_t(x)$ even though or precisely because they use the same clock time interval t. Instead, they will see $f_\tau(x)$ for $\tau = t/\gamma > t, \gamma = \sqrt{1 - v^2/c^2}$ with c being the speed of light. That is, both will see the same law but at two different observation times because of their best intention to use synchronized clocks at rest. This effect is equivalent to two observers in the same inertial frame using independent sampling times.

At the center of the special relativity lies the Lorentz Transformation, relating space-time coordinates between two inertial frames. Let $X = (t, x, y, z)$ be the space-time coordinate of Frame 1 and $X_v = (t_v, x_v, y_v, z_v)$ be the space-time coordinate of Frame 2 moving at a constant velocity v with respect to Frame 1, say along the same x-axis. Let $X_v = L_v(X)$ be the Lorentz Transformation between the two coordinates. It is well-known that it satisfies this self-consistent Compositional Invariance Property that $L_u(X_v) = L_u(L_v(X)) = L_w(X)$ where $w = (u + v)/(1 + uv/c^2)$ with c being the speed of light. That is, a third frame, Frame 3, moving at a velocity u relative to Frame 2 along the x-axis is a frame moving at a velocity w relative to Frame 1. The operation $(u, v) \to w$ defines the so-called Lorentz group. The Lorentz Transformation is one of the most well-known nontrivial and linear maps in physics that is compositionally invariant. The TIP-conforming group property is just a simpler kind of this more generalized *Compositional Invariance Property*. Stochastic matrixes (those which have non-negative entries and whose columns each sums to 1) form another well-known class of compositionally invariant linear maps.

Most Dynamical Systems Should Be Modeled By Differential Equations. It is a well-known simple fact that if $\varphi(t, x_0, p)$ is the solution of a differential equation $x' = F(x, p)$ with t the time, x_0 the initial state at $t = 0$, and p the parameter, then it always satisfies the TIP-conforming group property

$$\varphi(t + s, x_0, p) = \varphi(t, \varphi(s, x_0, p), p),$$

for continuously differentiable right-hand side F. Continuous-time and probabilistic processes can be modeled by stochastic differential equations which also satisfy the TIP-conforming group property (1), c.f. [26]. In additions, the same group property is satisfied for hyperbolic PDE for age-structured populations, for parabolic PDE for reaction-diffusion and traveling wave phenom-

ena, and for delayed differential equations. In such cases, the states lie in some functional spaces which are infinitely dimensional. (Hence, by differential equations for the remainder of the discussion we also mean to include such infinite dimensional equations with or without stochasticity, and as an extension by deterministic dynamical systems we also mean to include probabilistic processes modeled by stochastic differential equations for which it is the statistics in the means, variances, distributions, etc. of some state variables that become TIP-conforming, evolving deterministically.)

TIP-conforming processes are not restricted to deterministic continuous-time processes only. In fact, true discrete probabilistic processes can be TIP-conforming. For example, the process of coin tossing has the same probability distribution satisfying $\phi_n = \phi_1$ with ϕ_n representing the distribution at the nth tossing, i.e., the same probabilistic law at any iterate of the process. Also, stochastic processes modeled by Markov chains are in general TIP-conforming because their transition matrixes have the same functional form for all iterates.

The conclusion is that all (sufficiently differentiable, continuous-time) TIP-conforming laws are governed by differential equations. Hence, it is advisable to model all biological systems whose states are subject to independent time observation by differential equations in order to avoid the TIP-nonconforming trap that discrete maps can easily fall into. For true discrete probabilistic processes not modeled by differential equations, one must check the models TIP-conformity, for which stochastic matrixes represent one class of TIP-conforming, discrete, probabilistic models.

The practitioner-dependent subjectiveness and arbitrariness of picking time increments in discrete modeling cannot be more apparent than modeling systems of various time scales. For example, when modeling a system of two species, such as an algae-zooplankton system or a plant-herbivore system, of which one operates at a faster time scale and the other operates at a slower time scale, what time step a discrete modeler should choose? If she picks the fast time scale to be her discrete time increment, she will end up fixing the slower species population as a parameter rather than an evolving variable, and missing out the population's temporal booms and busts. If she picks the slow time scale, she will end up aggregating the dynamics of multiple generations of the faster species, missing out its temporal booms and busts as well. Whatever choice she makes, it is very likely that her choice will not be honored by any independent modeler. Worse still, if her model is not TIP-conforming, which is extremely likely, her model is doomed. On the other hand, differential equation modeling does not have this time-scale misalignment problem of discrete modeling, which is easily dealt with by singularly perturbed differential equations, which will be discussed further later.

TIP-Conformal Model — Derivation by One-Life Rule. Any textbook derivation of the Logistic Map as an one-species population model seems logically sound, yet it cannot be substantiated by independent time observation. The inescapable conclusion is that TIP must have been violated in all derivations. Two alternative fixes are proposed below.

The first proposed fix follows the standard derivation of the Logistic Map with modification to the functional form of the *per-capita growth* of the species. The Logistic Map is the result of

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assuming a linear functional for the per-capita growth as follows

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

where b is the maximal per-capita growth rate, and m is the mortality rate due to intraspecific competition. All empirical data (c.f. [34]), collected independently for different systems, with uncoordinated time increments, point to a density-dependent decreasing per-capita growth. That is, the decreasing monotonicity is *qualitatively* TIP-conforming for one-species per-capita growth. Although the linear functional is qualitatively TIP-conforming, it must have failed quantitatively, in particular at high population density. For example, if the density is $x_n = (9+b)/m$, then the per-capita growth is $b - m(9 + b)/m = -9$, implying paradoxically that each individual dies 9 times during the given interval of time, possible only for mythological cat. Furthermore, the per-capita growth any kth generation into the future, $(x_{n+k} - x_n)/x_n$, fails to be strictly decreasing in x_n at hight growth rate r for any $k \geq 2$. This implies that the per-capita growth measured at a unit time interval $t = 1$ decreases in the population density, but does not when measured at, say, two units of time interval with $t = 2$. In other words, independent experiments would give contradicting outcomes in the per-capita growth functionals if the Logistic Map were right, a not-so-surprising paradoxical effect of the map's TIP-nonconformity. Such inconsistencies are not limited to the Logistic Maps alone. In fact, they plague all one-dimensional maps from Table 1, most of which are failed attempts to correct the Logistic Map.

Our proposed fix assumes instead

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

Like the linear growth functional, it also decreases in x_n, qualitatively TIP-conforming. More importantly, the per-capita growth is bounded below from -1, and approaches -1 only as $x_n \rightarrow \infty$. That is, *individuals die, but each dies at most once in any fixed period of time* — a self-evident but both fundamental and universal principle for all organisms which is referred to as the *One-Life Rule*. As a result, the model is

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

where $r = b + 1 > 1$. This results in the Beverton-Holt model which was first used by Beverton and Holt in 1956 for fishery studies ([2]), but not derived from the One-Life Rule as we did here.

It is simple to check that the Beverton-Holt model is TIP-conforming — the composition of two B maps is another B map:

$$B_2(x_n, r, m) := B_1^2(x_n, r, m) = B_1(x_n, r^2, m(1 + r)).$$

In fact, one can demonstrate in general,

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

whose definition then can be extended to any continuous time t:

$$x_t = B_t(x_0, r, m) := B_1(x_0, r^t, m\frac{r^t - 1}{r - 1}) = \frac{r^t x_0}{1 + m\frac{r^t - 1}{r - 1}x_0}.$$

That is, any choice of fixed time increments leads to the same functional form. More importantly, the discrete Beverton-Holt map is simply the time-1 Poincaré map of the continuous counterpart, and in this sense it cannot be regarded as a *true* discrete map.

Also, as a consistency check, one can easily show that the per-capita growth over any time interval t is always a decreasing function of the initial population x_0 because

$$\frac{x_t - x_0}{x_0} = \frac{r^t - 1 - m\frac{r^t - 1}{r - 1}x_0}{1 + m\frac{r^t - 1}{r - 1}x_0}.$$

and that the One-life Rule is always satisfied since

$$\lim_{x_0 \to \infty} \frac{x_t - x_0}{x_0} = -1.$$

The Ricker model is an improvement over the Logistic Map in that it does obey the One-Life Rule. But it is not TIP-conforming and produces the same pathological chaos prediction for one-species population.

TIP-Conformal Model — Derivation by Mass Balance Law. The second derivation can be best argued in terms of stoichiometry. It recognizes that an organism is a package of elemental elements, 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, 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 interval, i.e., a constant flux 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 in C. Let a be the efficiency rate, 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 transition to the next generation, and the product of $N - cx_{n+1}$, a, and x_n gives the next generation's population:

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

Simplify to obtain

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

the same Beverton-Holt model obtained above.

The Beverton-Holt model for one-species population is qualitatively consistent with all empirical studies cited in [34, 31, 15]. In particular, any initial non-zero population converges to an

equilibrium:

$$\lim_{n\to\infty} x_n = \lim_{n\to\infty} B_n(x_0, r, m) = \lim_{n\to\infty} B_1(x_0, r_n, m_n)$$
$$= \lim_{n\to\infty} \frac{r^n x_0}{1 + m\frac{r^n-1}{r-1}x_0} = \frac{r-1}{m},$$

for which $r > 1$ as a default assumption. In the context of the stoichiometry for which $r = Na$, $m = ca$, we see that the greater the nutrient influx N, the greater the stable equilibrium. 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 such as [31].

TIP-Equivalence Example — The Logistic Equation. As an illustration, consider the continuous-time Beverton-Holt model

$$x_t = B_t(x_0, r, m) = \frac{r^t x_0}{1 + m\frac{r^t-1}{r-1}x_0}.$$

Identical to the discrete case, it is also straightforward to check the TIP-conforming group property

$$B_{s+t}(x_0, r, m) = B_s(B_t(x_0, r, m), r, m).$$

Thus, 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 Differential Equation! The per-capital growth *rate* is linear which can be arbitrarily negative at high population density. This does not violate the One-Life Rule which is for the per-capital growth in a fixed time interval rather than the instantaneous rate. The analysis above reaffirms a view that the Logistic Differential Equation is a good population model. By our argument it is because it is TIP-equivalent to the Beverton-Holt model.

Justifications of TIP-nonconforming Maps in Theoretical Ecology. Continuous models of food chains of three species or more can exhibit chaotic dynamics, which has been known since the earlier days of the chaos theory, see for examples, [22, 17, 21, 32, 39, 24]. One particularly effective method to establish the existence of chaos in such models is the method of singular perturbation, see for examples, [7, 8, 9, 10, 11]. At the so-called singular limit, some Poincaré return maps are one-dimensional, nonlinear, and chaotic. However, such maps are not obtained by fixed time interval samplings. Instead, they are event return maps. For example, such a map may be defined when one of the predators reaches local maximums in population density, for which to occur the moments in time cannot be independently chosen. Such event Poincaré maps are different from fixed time-step Poincaré maps in 3 critical ways: First, the sampling time for the former covers a continuum range of interval, conditioned on the occurrence of the event. Second, the event Poincaré maps are not TIP-conforming, but the fixed time-step Poincaré maps are like their continuous time flows. Third, the fixed time-step Poincaré maps are always at least 1-dimensional higher than their

event counterparts. One-dimensional event return maps are of many types, including the unimodal type of which the Logistic Map is prototypical as demonstrated in the cited references. In conclusion, discrete event Poincaré maps are used as auxiliary means to understand continuous models which generate them. They alone do not model the underlining process in any time *independent* fashion.

Discrete maps also play an irreplaceable role in numerical approximations. In fact, the Logistic Map is a discretization of the Logistic Differential Equation. It is not TIP-conforming for any r but it is a good approximation of the TIP-conforming continuous model when r is near 1. Similarly, TIP-nonconforming maps generated as numerical schemes to approximate continuous models do serve useful and important purposes in theoretical and practical applications. But they are relevant only within their realistic ranges. For example, it has always been an unjustifiable extrapolation to large r of the Logistic Map that it becomes artificial and problematic. More *ad hoc* still than the Logistic Map, the Ricker Map is not a discretization of any known differential equation, further removed from TIP-conformity. Similarly, a Leslie matrix should have been derived as a discretization of the linearization of its PDE counterpart of the age-structured population intended by the matrix, which unfortunately was not always the case. Such a discretization of the linear PDE should impose constraints on the time step and the age increment. Outside such constraints, the Leslie model may become problematic as is the case for the Logistic Map. With the above rather thorough analysis of the Logistic Map, one implication seems hard to miss that discrete models without underlining TIP-conforming origins only have limited if not all questionable scientific values.

Enrichment and Efficiency Stabilization Principles. As pointed out in the introduction that empirical studies do not support the hypothesis of chaotic one-species population at high reproductive per-capita rate, or high efficiency rate. In fact, the Beverton-Holt model implies diametrically the opposite. For higher dimensional systems, the same opposing dichotomy existed, and it can also be reconciled by TIP-conforming models.

On one hand, chaotic dynamics do occur in models for three species or more in food chains and webs ([22, 17, 21, 32, 24, 35, 8, 9, 10, 11, 4, 5, 13]), as well as in laboratory models of 3-dimensional systems ([6]). Also, almost all models exhibit the same paradoxical effect that high reproductive efficiency leads to chaotic population dynamics. Recent analysis from [12, 13] concluded that this "Chaos Paradox" is an artifact of the Malthusian exponential growth model for populations. In addition to its projected unbounded growth fallacy, the Malthusian model, $P' = rP$, also violates the One-Life Rule: $(P(t) - P_0)/P_0 = e^{rt} - 1$, not going to -1 as $P_0 \to \infty$. As pointed out in [12, 13], this Malthusian pathology hides in almost all continuous models in the literature, and paradoxical results are inevitable. The Enrichment Paradox ([38]), the Biological Control Paradox ([28]), the Competition Exclusion Principle ([1]), and the Chaos Paradox are of the most notorious.

On the other hand, however, assuming logistic growth for all species provides a sufficient remedy to all these paradoxes, the Chaos Paradox in particular. For example, consider the following

food chain equations

$$
\begin{cases}
\dot{X} = X\left(b_1 - d_1 - m_1 X\right) - \dfrac{a_1 X}{1 + h_1 a_1 X} Y \\[2mm]
\dot{Y} = Y\left(\dfrac{b_2 a_1 X}{1 + h_1 a_1 X} - d_2 - m_2 Y\right) - \dfrac{a_2 Y}{1 + h_2 a_2 Y} Z \\[2mm]
\dot{Z} = Z\left(\dfrac{b_3 a_2 Y}{1 + h_2 a_2 Y} - d_3 - m_3 Z\right)
\end{cases}
\tag{2}
$$

The result of [13] shows that all chaotic attractors bifurcate into either limit cycles or steady states as the top-predator's reproductive efficiency parameter b_3 increases, and that the limit cycles further bifurcate into steady states if the predator's reproductive efficiency parameter b_2 also increases. In fact, one can show that all chaos attractors must bifurcate into a steady state by increasing any two of the three reproductive efficiency parameters in b_1, b_2, b_3. In other words, efficiency promotes ecological stability, a result of evolution if the hypothesis holds that evolution promotes species efficiency as a survival fitness.

TIP-conformity is a necessary but not a sufficient requirement for physical laws. Comparing to most studied in the literature, the food chain model (2) above is significantly better because of two features incorporated into the model. First, with the inclusion of parameters m_1, m_2, m_3, intraspecific competitions are taken into consideration for all species which leads to the logistic growth rate for individual species ([40]) which in turn conforms to the One-Life Rule. Second, the Holling Type II predation functional form ([23]) is used for all predators. The importance of this particular form lies in the fact that it is TIP-conforming from its own derivation, and more generally it satisfies the Composition Invariance Principle. To see this, we recall from Holling's original mechanistic derivation that $r_e = aX$ is the number of prey, X, encountered in a unit time by one predator, Y, or the encounter rate, and h is the handling time per kill of the prey, and $r = \frac{r_e}{1 + h r_e} = \frac{aX}{1 + ha X}$ is the number of handled kills in one unit time by one predator, or the predation rate. This functional form is TIP-conforming for the following reasons. If one breaks the handling time down to, say, per-killing time h_k, and per-consuming time h_c with $h = h_k + h_c$, then Holling's derivation will give rise to the kill rate $r_k = \frac{r_e}{1 + h_k r_e}$ as a function of killing time and encounter rate, and the consumption rate $r_c = \frac{r_k}{1 + h_c r_k}$ as a function of consuming time and kill rate. It is straightforward to check that

$$
r_c = \frac{r_k}{1 + h_c r_k} = \frac{\frac{r_e}{1 + h_k r_e}}{1 + h_c \frac{r_e}{1 + h_k r_e}} = \frac{r_e}{1 + (h_k + h_c) r_e}.
$$

That is, the rate function has the same mathematical form regardless the temporal cut-off or definition of handling time, the essence of TIP-conformity and compositional invariance.

In conclusion, theoretical and qualitative predictions of the food chain model (2) are consistent with those of the Beverton-Holt model as well as relevant empirical findings that enrichment and efficiency promote ecological stability. The consistency may not be coincidental, because all compartmental constituents of the model are mechanistically TIP-conforming.

Concluding Remarks. Empirical data almost always are collected at discrete times. Discrete modeling is an intuitive response to that reality to fit discrete data by discrete models. 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 or stochasticity as the chief cause of the irreconcilability between a theory and reality when in fact TIP-nonconformity of the theory may have been the problem. TIP-nonconforming event maps are secondary structures of inherently higher dimensional TIP-conforming differential equations. They rarely have a closed-form formula with system parameters in plain sight for meaningful manipulations because of the aggregating procedures that produce them. Even in such cases, they are not closer in capturing the underlying physical laws for the processes than the TIP-conforming differential equations that model the processes. Given all these considerations, this paper advocates a typical approach to use continuous models to fit discrete data. Such models are open to the scrutiny of all observations carried out at any discrete times. This approach makes sure the models are necessarily consistent in its internal and conceptual construct, allowing the modelers to modify and to refine them within the realm of TIP-conformity.

Our TIP-equivalence result for fixed time-step Poincaré maps and differential equations implies that 1 and 2 dimensional TIP-conforming maps cannot be chaotic because 1 and 2 dimensional differential equations of continuously differentiable vector fields cannot be chaotic. Equivalently, chaotic 1 and 2 dimensional maps must be TIP-nonconforming, and at the best arise as event Poincaré maps of 3 or higher dimensional differential equations. As a result such maps do not model any physical processes at a time-independent fashion. Hence an ecological conclusion can be made unequivocally that single- and two-species population dynamics cannot be chaotic. That the controversy has lasted this long was due to the combination of a few understandable factors. To name a few obvious: 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 inevitable confusing state between a seeming reasonable theory and an uncompromising reality. Thirdly, the field irreproducibility of all low dimensional chaos theory was conveniently masked by the inherited 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 the simplicity appeal of discrete modeling. 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, usage of 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 modeling 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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