

A Fundamental Principle Governing Populations

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Abstract Proposed here is that an overriding principle of nature governs *all* population behavior; that a single tenet drives the many regimes observed in nature—exponential-like growth, saturated growth, population decline, population extinction, and oscillatory behavior. The signature of such an all embracing principle is a differential equation which, in a single statement, embraces the entire panoply of observations. In current orthodox theory, this diverse range of population behaviors is described by many different equations—each with its own specific justification. Here, a single equation governing all the regimes is proposed together with the principle from which it derives. The principle is: *The effect on the environment of a population's success is to alter that environment in a way that opposes the success.* Experiments are suggested which could validate or refute the theory. Predictions are made about population behaviors.

Keywords Population dynamics · Evolution · Ecology · Biology

1 Traditional Perspective

The acknowledged source of theories about population is the monograph by the venerable Malthus (1798). His place in history rests largely on these two sentences from Chapter I,

Population, when unchecked, increases in a geometrical ratio. Subsistence increases only in an arithmetical ratio.

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The archaic terms ‘geometric ratio’ increase and ‘arithmetic ratio’ increase are today called ‘exponential growth’ and ‘linear growth’. In this quote he takes pains to distinguish between these because his thesis is based on the distinction. Malthus was thinking only of human population. Darwin (1859) took the idea to apply to populations in “the whole animal and vegetable kingdoms.”

The rationale for exponential growth is this: In living systems growth is proportional to the population because each member (or pair of members) once produced, begin, themselves, to reproduce. There are more reproducers in a larger population. So the greater the number in the population, the greater is the growth. The same for deaths. The rate is proportional to the number available to die. However, as will be demonstrated in the next section, this analysis is fallacious.

Malthus didn’t offer equations to express his thoughts but writing them down reveals the fallacy. Call the number of members in the population, n . At each moment of time, t , there exist n individuals in the population. So we expect that $n = n(t)$ is a continuous function of time.

The rate of growth of the population is dn/dt ; the increase in the number of members per unit time. That this is proportional to population number, n , is the substance of the idea. Call the constant of proportionality, R . Then the differential equation that embodies the idea of ‘increase by geometrical ratio’ is:

$$dn/dt = Rn \quad (1)$$

when R is constant, its solution yields the archetypical equation of exponential growth.

$$n(t) = n_0 e^{Rt} \quad (2)$$

The n_0 is simply the starting population, $n_0 = n(0)$; the number of its members at $t = 0$. Again with R a constant and n_0 as defined above, linear growth—not a solution to (1)—is expressed by this equation:

$$n(t) = n_0(1 + Rt) \quad (3)$$

These formulas for $n(t)$ exhibit starkly different behaviors. That is why they were contrasted by Malthus.

Now, common experience tells us that exponential growth cannot proceed indefinitely. No population grows without end. Suppose the birth rate declines. Maybe, instead, the death rate increases. Perhaps because the weather gets cold or food becomes scarce. Conventionally this is accounted for by a new exponent, say R' ; a smaller one. So R is really not a constant. It may vary with time. $R = R(t)$.

In describing living systems the traditional idea has been to retain that appealing exponential-like form and seek to explain events by variations in R . “The problem of explaining and predicting the dynamics of any particular population boils down to defining how R deviates from the expectation of uniform growth” (Berryman 2003). The concept is that exponential growth is always taking place but at a rate that varies with time. Put mathematically:

$$\frac{1}{n} \frac{dn}{dt} = R(t) \tag{4}$$

Fisher endows R with its own name, the Malthusian Parameter (Fisher 1930). Equation (4) is called Darwinian Dynamics by Michod (1999). In connection with his writing on genotype fitness Michod’s “Fisherian Fitness” is exactly of this form. Equation (4) is the standard analytical tool for describing population data.

Of course, any theory on how R might depend on n —rather than on t —produces a theoretical $R(t)$. This is because the differential equation:

$$\frac{dn}{dt} = nR(n) \tag{5}$$

is completely solvable for n as a function of t . Once we have $n(t)$ we can deduce $R(t)$ via it’s definition in Eq. (4). This theoretical $R(t)$ may be compared to measurements of $(1/n)dn/dt$ to assess the match of theory to observations. Equations (4) and (5) or their discrete-time equivalents are ubiquitous in textbooks (Britton 2003; Murray 1989; Turchin 2003).

An object example of this process is provided by the celebrated Verhulst equation.

$$\frac{dn}{dt} = nR(n) = nr \left(1 - \frac{n}{K}\right) \tag{6}$$

A population history, n versus t , resulting from this equation is the black one of Fig. 1.

What motivated Verhulst (1838) is the common observation that nothing grows indefinitely. Here the constant, r , is the exponential growth factor and K is the limiting value that n can have—“the carrying capacity of the environment” (Vainstein et al. 2007). The equation insures that n never gets larger than $n_{max} = K$. Because n is understood to be the number in a *given physical space* it represents, in fact, a population density (number/space). That this density has a limit is the reason

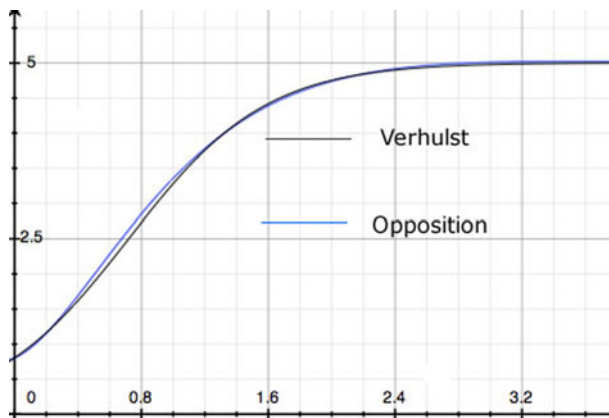


Fig. 1 Two population histories: number versus time. The *black curve* is the Verhulst (Logistic) Equation. The *blue curve* is one of the solutions to the Opposition Principle differential Eq. (12). (Color figure online)

for the association of K with crowding. The name, r/K Selection Theory, derives from the competing dynamics of exponential growth and of crowding—the r and the K . The Verhulst equation—often cited as the Logistic Equation—is regularly embedded in research studies (Nowak 2006; Torres et al. 2009; Jones 1976; Ruokolainen et al. 2009; Okada et al. 2005; Ma 2010).

2 Shortcomings of the Traditional Perspective

The textbook mathematical structure outlined in the last section has acquired the weight of tradition. It is certainly appealing. But it has some serious failings.

Assigning all behavior to variations in R seems to preserve the pristine Malthusian exponential growth idea. But, in fact, allowing R to vary with time severs the connection to exponential growth.

The idea is dramatized in this example. Malthus makes it clear that if a population is growing exponentially with time then it is certainly *not growing linearly* with time. Linear growth is the antithesis of exponential growth. Equations (2) and (3) display the difference. But suppose R varies as $R(n) = H/n$. Using this in solving the Malthusian Eq. (5), produces exactly linear growth! The constant H is n_0R . Linear growth *is* variable-rate exponential growth! *Any growth at all is variable-rate exponential growth.*

There is no more content in conjectures about $R(t)$ than there is in direct conjecture about how n might depend on t ; $n = n(t)$. Except for the tenacity of tradition there is no reason to focus on R as the basic parameter of population dynamics. Because $R(t)$ can be anything so, too, can $n(t)$ be anything. An equation expressing a true principle of population dynamics would yield only those behaviors biologically and ecologically possible for $n(t)$. Equation (4) doesn't do this. It does no more than substitute one variable for another.

A good reason *not* to use R concerns extinction. A phenomenon well known to exist in nature is the extinction of a species. "... over 99 % of all species that ever existed are extinct" (Carroll 2006). But there exists no finite value of R —positive or negative—that yields extinction. There is no mechanism for portraying extinction. It cannot be represented by R except for the value negative infinity; $-\infty$. So, in fact there is good reason to avoid R as the key parameter of population dynamics.

In the continuous- n perspective the mathematical conditions for extinction are these: $n = 0$ and $dn/dt < 0$. No infinities enter computations founded on these statements. Hence embracing $n(t)$ directly allows one to explore the dynamics of extinction.

The eponymous Verhulst Equation (the Logistic Equation) doesn't derive from some fundamental biological constraint. It's motivated only by the observation that populations never grow to infinity. They are bounded. But there are other ways—not described by Verhulst's equation—in which a population may be bounded! For example, $n(t)$ may oscillate. Or, as in Fig. 1, a curve essentially the same as Verhulst's may arise from an entirely different theory where no $K = n_{\max}$ limit exists. One of the possible population histories resulting from the alternative theory offered below—which contains no n_{\max} —is shown in blue. Data fit by one curve

will be fit equally well by the other. The limited validity of r/K Selection Theory has been noted by researchers over the years (Parry 1981; Kuno 1991).

The most significant failing of the accepted Malthusian Structure of population dynamics is its limited domain of validity. Many population histories cannot be fit by exponential growth nor by the Logistic Equation. Oscillatory behavior demands that a new paradigm be requisitioned; the Lotka-Volterra equations (Lotka 1956; Volterra 1926) or, because their solutions are not structurally stable, their later modifications (Murray 1989; Vainstein et al. 2007).

Thus, in current orthodox population theory, to describe the entire range of population behaviors requires many different equations—each with its own specific justification. Exponential growth has a limited range of validity, as does the Logistic Equation, and any other equation of first order. And none of these describe population oscillations, nor population decline, nor extinction.

No structure exists that embraces—in *one single statement*—all possible behaviors. Contemporary theory offers no overriding principle that governs the gamut of population behaviors. To produce such a structure is the aim of what follows.

Why is such an undertaking important? The essential virtue of an overriding structure is that it expresses a principle of nature. The wider the range of applicability the more valuable the principle. A single mathematical statement that describes a multitude of phenomena is the signal of such a principle and to achieve that is the goal here.

The proposed mathematical statement is a second order differential equation. As long ago as 1972, in a challenge to orthodox convention, Ginzburg (1972) took the bold step of proposing that population dynamics is best represented by a second order differential equation. All accepted formulations relied on first order differential equations as they still do today. He developed his thesis over the years (Ginzburg 1986, 1992; Ginzburg and Taneyhill 1995; Ginzburg and Inchausti 1997) culminating in the pithy and persuasive book, “Ecological Orbits” (Ginzburg and Colyvan 2004).

In the following we take a route different from Ginzburg’s and arrive at a substantially different equation—albeit a second order differential one. We proceed from a guess at what may be the underlying principle and then derive the second order differential equation that expresses that principle. If empirical reality is well fit by the progeny of that equation then we may conclude that the principle is true.

3 Conceptual Foundations for an Overriding Structure

The key equation is built on some foundational axioms. Empirical verification of the equation they produce is what will measure the validity of these axioms. The axioms are:

First: Variations in population number, n , are due entirely to environment.

Conceptually we partition the universe into two: the population under consideration and its environment. We assume that the environment drives

population dynamics; that the environment is entirely responsible for time variations in population number—whether within a single lifetime or over many generations.

The survival and reproductive success of any individual is influenced by heredity *as well as* the environment it encounters. This statement doesn't contradict the axiom. The individual comes equipped with heredity to face the environment. Both the environment and the population come to the present moment equipped with their capacities to influence each other; capacities derived from their past histories.

That the environment molds the population within a lifetime is clear; think of a tornado, a disease outbreak, or a meteor impact. That the environment governs population dynamics over generations is precisely the substance of 'natural selection' in Darwinian evolution.

That principle may be summarized as follows: "... the small selective advantage a trait confers on individuals that have it..." (Carroll 2006) increases the population of those individuals. But what does 'selective advantage' mean? It means that the favored population is 'selected' by the environment to thrive. Ultimately it is the environment that governs a population's history. Findings in epigenetics that the environment can produce changes transmitted across generations (Gilbert and Epel 2009; Jablonka and Raz 2009) adds further support to this notion.

Much productive research looks at traits in the phenotype that correlate with fitness or LRS (Lifetime Reproductive Success) (Clutton-Brock 1990; Coulson et al. 2006). The focus is on how the organism fits into its environment. So something called 'fitness' is attributed to the organism; the property of an organism that favors survival success. But environmental selection from among the available phenotypes is what determines evolutionary success. The environment is always changing so whatever genetic attributes were favorable earlier may become unfavorable later. Hence there is an alternative perspective: fitness, being a matter of selection by the environment, is induced by it and may, thus, be seen as a property of the environment.

Although, fitness, in some sense, is 'carried' by the genome, it is 'decided' by the environment. Assigning a fitness to an organism rests on the supposition of a static environment; one into which an organism fits or into which it doesn't fit. A dynamic environment incessantly alters the 'fitness' of an organism.

This is the perspective underlying the axiom that *variations in population number, n , are due entirely to environment*.

In this view, although birth rates minus death rates yield population growth they are *not the cause* of population dynamics; rather birth and death rates register *the effect* of the environment on the population.

Second: An increasing growth rate is what measures a population's success.

The 'success' of a population is an assertion about a population's time development; it concerns the size and growth of the population. A reasonable notion of success is that the population is *flourishing*. We want to give quantitative voice to the notion that flourishing growth reveals a population's success.

Neither population number, n , nor population growth, dn/dt , are adequate to represent 'flourishing'. Population number may be large but it may be falling. Such a population cannot be said to be flourishing. So we can't use population number as

the measure of success. Growth seems a better candidate. But, again, suppose growth is large but falling. Only a rising growth rate would indicate ‘flourishing’. This is exactly the quantity we propose to take as a measure of success; the growth in the growth rate. By flourishing is meant growing faster each year.

A corollary of these two foundational hypotheses is that *change is perpetual*. Equilibrium is a temporary condition. What we call equilibrium is a stretch of time during which $dn/dt = 0$; an interval during which the population neither increases nor decreases. Hence ‘returning to equilibrium’ is not a feature of analysis in this model.

Another corollary is this: The environment of one population is other populations. It’s through this mechanism that interactions among populations occur: via reciprocity—if A is in the environment of B, then B is in the environment of A. So the structure offers a natural setting for ‘feedback’ via the coupling between populations (Pelletier et al. 2009). It provides a framework for the analysis of co-evolution or cooperation, of competition and of predator–prey relations among populations. All of these obey the same equation differing only in the signs of interaction coefficients relating any pair of populations.

4 The Opposition Principle: Quantitative Formulation

Based on the understandings outlined above we propose that an overriding principle governs the population dynamics of living things. It is this: *The effect on the environment of a population’s success is to alter that environment in a way that opposes the success*. In order to refer to it, I call it the Opposition Principle. It is a *functional* principle (McNamara and Houston 2009) operating irrespective of the *mechanisms* by which it’s accomplished. In the way that increasing entropy governs processes irrespective of the way in which that is accomplished.

Examples of the Principle abound. We, humans, produce toxins that we breath and drink. We deplete resources. We fish in order to multiply and, when multiplied, exhaust the fish. Aphid populations are limited by their own excrement (Matis et al. 2009). Does not every creature pollute and feed on it’s environment?

In wine making, the yeast *Saccharomyces cerevisiae* is added to grapes and water. The organism ingests sugar and water and excretes alcohol. Finding itself amidst plenty in a bath of sugary grapes the fungus—the yeast—multiplies and rejoices in its prosperity. Finally it produces enough waste to kill itself by alcohol poisoning. The process is called fermentation. We celebrate our prosperity by drinking what killed the yeast—they who had, but recently, rejoiced in their prosperity.

These examples are extreme ones but the postulate here is that such phenomena exemplify a principle of nature. The principle is not one of doom. That would be a misunderstanding. Populations can thrive even under this principle. The Opposition Principle does not say that populations destroy themselves but only that success never makes the environment more favorable to further success. ‘Success’ has been carefully defined in the previous section.

The Principle applies to a society of living organisms that share an environment. The key feature of that society is that it consists of a number, n , of members which

have an inherent drive to survive and to produce offspring with genetic variation. Their number varies with time: $n = n(t)$.

Because we don't know whether n , itself, or some monotonically increasing function of n is the relevant parameter, we define a population strength, $N(n)$. Any population exhibits a certain strength in influencing its environment. This population strength, $N(n)$, expresses the potency of the population in affecting the environment—its environmental impact. Perhaps this strength, N , is just the number n , itself. The greater n is, the more the environmental impact. But it takes a lot of fleas to have the same environmental impact as one elephant. So we would expect that the population strength is some function of n that depends upon the population under consideration.

Two things about the population potency, N , are clear. First, $N(n)$ must be a monotonically increasing function of n ; $dN/dn > 0$. This is because when the population increases then its impact also increases. Albeit, perhaps not linearly. Second, when $n = 0$ so, too, is $N = 0$. If the population is zero then certainly its impact is zero. One candidate for $N(n)$ might be n raised to some positive power, p . If $p = 1$ then N and n are the same thing. Another candidate is the logarithm of $(n + 1)$.

We need not specify the precise relationship, $N(n)$, in what follows. Via experiment it can be coaxed from nature. The only way that N depends upon time is parametrically through its dependence on n . In what follows we shall mean by $N(t)$ the dependence $N(n(t))$. We may think of N as a surrogate for the number of members in the population.

The population strength growth rate, $g = g(t)$, is defined by

$$g := \frac{dN}{dt} \quad (7)$$

Like N , g too acquires its time dependence parametrically through $n(t)$.

$$g = (dN/dn)(dn/dt)$$

To quantify how the environment affects the population we introduce the notion of 'environmental favorability'. We'll designate it by the symbol, f . It represents the effect of the environment on the population.

A population flourishes when the environment is favorable. Environmental favorability is what drives a population's success. We may be sure that food abundance is an element of environmental favorability so f increases monotonically with nutrient amount. It decreases with predator presence and f decreases with any malignancy in the environment—pollution, toxicity.

But in the last section we arrived at a quantitative measure of success. The rate of growth of the population strength—'the growth of growth' or dg/dt —measures success. Hence, that a population's success is generated entirely by the environment can be expressed mathematically as:

$$\frac{dg}{dt} = f \quad (8)$$

By omitting any proportionality constant we are declaring that f may be measured in units $(\text{time})^{-2}$. Since Eq. (8) says that success equals the favorability of the environment, it follows that f measures not only environmental favorability but also

population success. One can gauge the strength of the favorability of the environment—the value of f —by measuring population success.

We're now prepared to cast the Opposition Principle as a mathematical statement. The Principle has two parts. 1. Any *increase* in population strength *decreases* favorability; the more the population's presence is felt the less favorable becomes the environment. 2. Any *increase* in the growth of that strength also *decreases* favorability.

Put formally: That part of the change in f due to an increase in N is negative. Likewise the change in f due to an increase in g is negative. Here is the direct mathematical rendering of these two statements:

$$\frac{\partial f}{\partial N} < 0 \quad \text{and} \quad \frac{\partial f}{\partial g} < 0 \tag{9}$$

We can implement these statements by introducing two parameters. Both w and α are non-negative real numbers and they have the dimensions of reciprocal time. (Negative w values are permitted but are redundant.)

$$\frac{\partial f}{\partial N} = -w^2 \quad \text{and} \quad \frac{\partial f}{\partial g} = -\alpha \tag{10}$$

These partial differential equations can be integrated. The result is:

$$f = -w^2N - \alpha g + F(t) \tag{11}$$

The 'constant' (with respect to N and g) of integration, $F(t)$, has an evident interpretation. It is the gratuitous favorability provided by nature; the gift of nature. Equation (11) says that environmental favorability consists of two parts.

One part depends on the number and growth of the population being favored: the N and its time derivative, g . This part has two terms both of which always act to decrease favorability. These terms express the Opposition Principle.

The other part— $F(t)$ —is the gift of nature. There must be something in the environment that is favorable to population success but external to that population else the population would not exist in the first place. This gift of nature may depend cyclically on time. For example, seasonal variations are cyclical changes in favorability. Or it may remain relatively constant like the presence of air to breathe. It may also exhibit random and sometimes violent fluctuations like a volcanic eruption or unexpected rains on a parched earth. So it has a stochastic component. All of these are independent of the population under consideration. However, dF/dt may depend on population number since this is the rate of consumption of a limited food supply.

Inserting Eqs. (7) and (8) into (11) we arrive at the promised differential equation governing population dynamics under the Opposition Principle. It is this.

$$\frac{d^2N}{dt^2} + \alpha \frac{dN}{dt} + w^2N = F(t) \tag{12}$$

In the world of physical phenomena this equation is ubiquitous. Depending upon the meaning assigned to N it describes electrical circuits, mechanical systems, the

production of sound in musical instruments and a host of other phenomena. So it is very well studied. The exact analytical solution to (12), yielding $N(t)$ for any given $F(t)$, is accessible (Marion 1970).

5 Some Consequences

To explore some of the solutions to this differential equation we consider the easiest case; that the gift favorability is simply constant over an extended period of time. Assume $F(t) = C$ independent of time. Non-periodic solutions arise if $\alpha \geq 2w$. One of these, displayed in Fig. 1, produces results mimicking the Verhulst equation. If $\alpha < 2w$ the solutions to (12) are periodic and are given by:

$$N(t) = \frac{C}{w^2} + Ae^{-\alpha t/2} \sin(\omega t + a) \quad (13)$$

where the amplitude, A , and the phase, a , depend upon the conditions of the population at a designated time, say $t = 0$. And the oscillation frequency, ω , is given by:

$$\omega := w \sqrt{1 - \left(\frac{\alpha}{2w}\right)^2} \quad (14)$$

In Fig. 2, Eq. (13) is compared to empirical data. The figure shows the population fluctuations of larch budmoth density (Turchin et al. 2003) assembled from records gathered over a period of 40 years. The data points and lines connecting them are shown in black. The smooth blue curve in the background is a graph of Eq. (13) for particular values of the parameters.

We assumed α is negligibly small so it can be set equal to zero. The frequency, ω , is taken to be $2\pi/(9 \text{ years}) = 0.7$ per year. The vertical axis represents N . In the units chosen for N , the amplitude, A , is taken to be 0.6 and C is taken to be 0.6 per year². The phase, a , is chosen so as to insure a peak in the population in the year 1963; $a = 3.49$ radians.

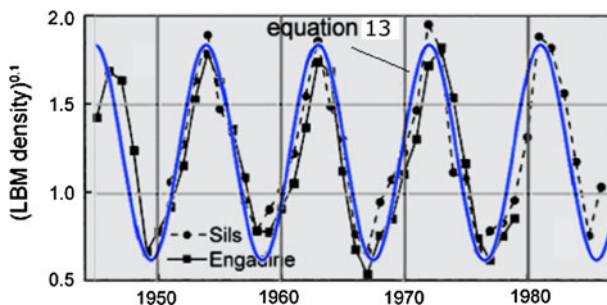


Fig. 2 Observational data on the population fluctuations of larch budmoth density is shown as *black circles* and *squares*. The smooth *blue curve* is a solution of Eq. (13). (Color figure online)

Because the fluctuations are so large the authors plotted $n^{0.1}$ as the ordinate for their data presentation. The ordinate for the smooth blue theoretical curve is N . Looking at the fit in Fig. 2, suggests how population potency may be deduced from empirical data. One might be led to conclude that the population strength, $N(n)$, for the budmoth varies as the 0.1 power of n . But the precision of fit may not warrant this conclusion.

The conclusions that may be warranted are these:

Considering that no information about the details of budmoth life have gone into the computation the graphical correspondence is noteworthy. It suggests that those details of budmoth life are nature's way of implementing an overriding principle. The graphical correspondence means that, under a constant external environmental favorability, a population could behave not unlike that of the budmoth.

Equation (13) admits of circumstances in which population extinction can occur. If $A > c/w^2$ then N can drop to zero. Societies with zero population are extinct ones. (On attaining zero, N remains zero. The governing differential Eq. (12), doesn't apply when $N < 0$.)

But the value of A derives from initial conditions; from $N(t = 0)$ and $g(t = 0)$. So depending upon the seed population and its initial growth rate the population may thrive or become extinct even in the presence of gift favorability, C . This result offers an explanation for the existence of the phenomenon of 'extinction debt' (Kuussaari et al. 2009) and a way to compute the relaxation time for delayed extinction.

The case explored reveals that periodic population oscillations can occur without a periodic driving force. Even a steady favorability can produce population oscillations.

Among the plethora of solutions to the governing differential Eq. (12), is this one: Upon a step increase in environmental favorability—say, in nutrient abundance—the population may overshoot what the new environment can accommodate and then settle down after a few cycles. Figure 3 illustrates this behavior. That there are such solutions amounts to a prediction that population histories like that of Fig. 3 will be found in nature. In fact, already found, is precisely this behavior in observations on *Escherichia coli* (Blount et al. 2008).

Experiments to validate or refute the Opposition Eq. (12) are possible. Prepare a population—say *Drosophila melanogaster*—in a controlled environment. In such an environment one may manipulate 'environmental favorability', say nutrient level or

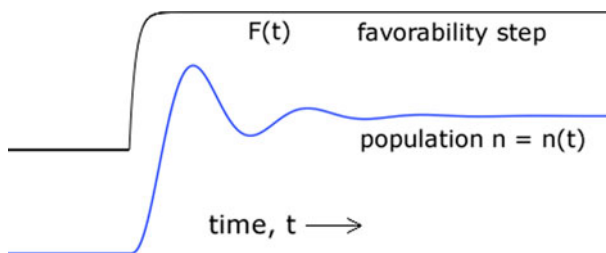


Fig. 3 A theoretical population history that can result from the Opposition Principle differential equation

toxicity level. A controlled step in environmental favorability produces a response in population numbers. The Opposition equation says that the down-step response curve is governed by the same parameters as is the rise curve of growth upon a favorability up-step. Measure the population's time development following a *step decrease* in nutrients. From this, the response curve to a *step increase* in nutrients can be deduced and compared with measurement results! Population rise dynamics and population fall dynamics are predicted to be related. If the relationship found empirically fails to match predictions the theory will be refuted.

The theory also makes predictions regarding interacting populations. Their numbers may oscillate—albeit not indefinitely. These oscillations have a relaxation time—a disappearance time. It's determined by how strongly the populations interact. Depending upon whether their co-evolution is cooperative (symbiosis, altruism), competitive or predator–prey there is a phase relationship between their oscillations. Theory predicts that predator and prey populations oscillate 90° out of phase with each other. Competing populations oscillate 180° out of phase. Two symbiotic populations have 0° phase difference; they grow or decline together as if they were a single population. Experiments with interacting organisms can test these predictions.

Opposition theory indicates that there are measurable critical parameters leading to extinction or survival under adverse conditions. These were mentioned in Sect. 5 above. They can be measured in controlled experiments.

6 Conclusion

We noted at least five disparate regimes of population history—each with its own individual and disjoint descriptive equation: exponential-like growth, saturated growth, population decline, population extinction, oscillatory behavior. It's argued here that these regimes can be brought under the embrace of a single differential equation describing them all.

That equation is the mathematical expression of general concepts about how nature governs population behavior. Being quantitative it offers us a framework with which to validate or refute these concepts. The concepts are itemized as axioms and principles. Some of them run counter to accepted convention thus making empirical refutation a substantive matter; something worthy of investigation in experimental ecology. Experiments have been proposed. The author stands ready to collaborate on any of these.

In short: a refutable proposition about the nature of populations is offered for assessment by the scientific community. Verification of the proposed equation would establish a basic understanding about the nature of living organisms.

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