Differential Equations (Ordinary)

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Since their Newtonian inception, differential equations have been a fundamental tool for modeling the natural world. As the name suggests, these equations involve the derivatives of dependent variables (e.g. viral load, species densities, genotypic frequencies) with respect to independent variables (e.g. time, space). When the independent variable is scalar, the differential equation is called ordinary. Far from ordinary, these equations have provided key insights into catastrophic shifts in ecosystems, dynamics of disease outbreaks, mechanisms maintaining biodiversity, and stabilizing forces in food webs.

I. Basic definitions and notation

Before getting caught up in definitions, let’s consider two classical ecological examples of ordinary differential equations. The Logistic equation describes population growth rate of a species with density \( x \) with respect to time \( t \)

\[
\frac{dx}{dt} = r x (1 - x/K) \tag{1}
\]

where \( r \) is the intrinsic rate of growth of the population and \( K \) is its carrying capacity. The left hand side of this equation is the derivative of \( x \) with respect to time \( t \) and corresponds to the population growth rate. The right hand side describes how the population growth rate depends on the current population density. For this equation, one might be interested in understanding how the species’ density changes in time and how these temporal changes depend on its initial density. Often, ecological systems involve many “moving parts” with multiple types of interacting individuals in which case describing their dynamics involves systems of ordinary differential equations. A classical example of this type is the Lotka-Volterra predator-prey equations that describe the dynamics between a prey with density \( x_1 \) and its predator with density \( x_2 \)

\[
\begin{align*}
\frac{dx_1}{dt} &= r x_1 - a x_1 x_2 \\
\frac{dx_2}{dt} &= c a x_1 x_2 - m x_2
\end{align*} \tag{2}
\]

where \( a, c, \) and \( d \) are the predator’s attack rate, conversion efficiency, and per-capita mortality rate. For these more complicated equations, one might ask “do these equations have well-defined dynamical behaviors?” and “how complicated can these behaviors be?” This entry addresses the answers to these and many more questions.
A system of ordinary differential equations involves a finite number of state variables, say \( x_1, x_2, \ldots, x_n \), possibly representing densities of interacting species, abundances of different age or size classes, frequencies of behavioral strategies, or availability of abiotic factors such as light, water, or temperature. These equations assume the state variables vary smoothly in time. If the instantaneous rates of change of the state variables are given by functions \( f_1(x_1, \ldots, x_n), \ldots, f_n(x_1, \ldots, x_n) \) of the dependent variables, then one arrives at a system of autonomous, first-order ordinary differential equations:

\[
\begin{align*}
\frac{dx_1}{dt} &= f_1(x_1, \ldots, x_n) \\
\frac{dx_2}{dt} &= f_2(x_1, \ldots, x_n) \\
\vdots \\
\frac{dx_n}{dt} &= f_n(x_1, \ldots, x_n)
\end{align*}
\]  

where \( t \) denotes time. Here, *first-order* refers to the fact that only first-order derivatives appear in the equations. *Autonomous* refers to the fact that the rates of change \( f_1, \ldots, f_n \) do not depend on \( t \). Equation (3) can account for higher-order time derivatives or time dependence by introducing extra state variables as discussed later.

A simple example of this type of differential equation is the Logistic equation

Equation (3) can be written more succinctly in vector notation. Let \( \mathbf{x} = (x_1, x_2, \ldots, x_n) \) be the vector of state variables and \( \mathbf{f}(\mathbf{x}) = (f_1(x), f_2(x), \ldots, f_n(x)) \) be the vector of their corresponding rates of change. Then (3) simplifies to the vector-valued differential equation:

\[
\frac{d\mathbf{x}}{dt} = \mathbf{f}(\mathbf{x}).
\]  

II. Existence, uniqueness, and geometry of solutions

After writing down a differential equation model of an ecological system, a modeler wants to know how do the variables of interest change in time. For instance, how are densities of the prey and predator changing relative to one another? Moreover, how does this dynamic depend on the initial densities of both populations? To answer these types of questions, one needs to find solutions to the differential equation. A *solution* to (4) is a (vector-valued) function of time \( \mathbf{x}(t) \) such that when \( \mathbf{x}(t) \) is plugged into both sides of the equation, both sides are equal to one another i.e. \( \mathbf{x}'(t) = \mathbf{f}(\mathbf{x}(t)) \) where ' denotes a derivative with respect to time. If \( \mathbf{x}(t) \) is a solution and the initial state of the system is given by \( \mathbf{x}(0) = \mathbf{x}_0 \), then \( \mathbf{x}(t) \) is a solution to the *initial value problem*:

\[
\frac{d\mathbf{x}}{dt} = \mathbf{f}(\mathbf{x}) \quad \mathbf{x}(0) = \mathbf{x}_0.
\]
Verifying a function $x(t)$ is a solution is straight-forward: plug $x(t)$ in both parts of the equation and verify both sides are equal.

Consider, for example, the simplest model of population growth in which the per-capita growth rate $r$ of the population is constant in time. If $x = x$ is the population density, then

$$\frac{dx}{dt} = r x \quad x(0) = x_0.$$  

The solution of this initial value problem is $x(t) = x_0 e^{rt}$. Indeed, $x'(t) = r x_0 e^{rt} = r x(t)$, and $x(0) = x_0$. Intuitively, when the per-capita rate $r$ is positive and $x_0$ is positive, the population exhibits unbounded exponential growth. When $r$ is negative, the population declines exponentially to extinction. However, extinction is only achieved in the infinite time horizon. When the per-capita growth rate or the initial population density is zero, the population density remains constant for all time. This latter type of solution is known as an equilibrium or steady-state solution.

In general, an *equilibrium* for (4) is a state $x = x^*$ such that the rates of change are zero at this state: $f(x^*) = 0$. The solution corresponding to an equilibrium $x = x^*$ is the constant solution $x(t) = x^*$ for all $t$. Indeed, plugging $x(t) = x^*$ into the left and right side of equation (3) yields $x'(t) = 0$ and $f(x^*) = 0$. For example, for the Logistic equation (1) $x = 0$ is the “no-cats,
no-kittens” equilibrium and \( x = K \) is the equilibrium corresponding to the carrying capacity of the population.

A fundamental question is “when do solutions to the initial value problem (5) exist?” After all, if there is no solution, there is no point in looking for one. In 1890, the Italian mathematician Giuseppe Peano proved that solutions to (5) exist whenever \( f(x) \) is continuous. This continuity assumption is met for many models (in particular, the Logistic equation and the Lotka-Volterra equations), but not all. For example, population models including optimal behavior can exhibit discontinuities at population states where multiple behaviors are optimal. When these discontinuities occur, what constitutes the dynamic of the equations needs to be defined by the modeler.

Given a solution to the initial value problem (5) exists, one has to wonder whether it is unique. After all, if it is not unique, one may never know if all solutions have been uncovered and which, if any, are biologically relevant. Provided that \( f(x) \) is differentiable, French mathematician Émile Picard proved that solutions are unique. When \( f(x) \) is not differentiable, biologically plausible things can still happen. For example, if \( x = x \) is the density of a declining population whose growth rate is \( \frac{dx}{dt} = -\sqrt{x} \), then the growth rate is not differentiable at \( x = 0 \). This equation yields an infinite number of solutions in which the population has gone extinct by some specified time (Fig. 1a). Despite the model being deterministic, knowing the population is extinct now doesn’t tell you when it went extinct. This biologically realistic feature does not occur in models where \( f(x) \) is differentiable. While \( f(x) \) is differentiable for most ecological models, there are important exceptions such as predator-prey models with a ratio-dependent functional response (e.g., \( a(x_1/x_2)/(1+ahx_1/x_2) \) where \( x_1/x_2 \) is the ratio of prey density to predator density), epidemiological models with frequency dependent transmission rates, or models incorporating optimal behavior.

Even if solutions to the initial value problem (5) exist and are unique, they might not be defined for all time. An important example is super-exponential population growth where the rate of change of the population density \( x \) is \( \frac{dx}{dt} = r x^{1+b} \) where \( b > 0 \) and \( r > 0 \). This model with \( b \approx 1 \) was the basis for the 1960s prediction of “Doomsday: Friday, 13 November A.D. 2026.” Indeed, for \( b = 1 \), this equation can be solved by separating variables and integrating which yields \( x(t) = 1/(1/x_0 - rt) \) where \( x_0 \) is the initial population density. Amazingly this solution approaches infinity as \( t \) approaches \( t = 1/(x_0r) \). This phenomena is called blow-up and occurs in models of combustion and other runaway processes. In this ecological context, the time of blow up \( t = 1/(x_0r) \) corresponds to doomsday. In the words of a Pogo cartoon, at this time “everyone gets squeezed to death” (Fig. 1b).

Provided \( f(x) \) is differentiable, solutions to (5) exist for all time if the system is dissipative: there is a bounded region that all solutions eventually enter and remain in for all time. Since the world is finite and can only sustain a finite density of individuals, all ecologically realistic models should be dissipative i.e. there populations densities eventually are bounded by a constant independent of initial conditions. Verifying dissipativeness can be challenging, and may be violated in unexpected ways. For example, in Lotka-Volterra type models of mutualistic interactions, pop-
Fig. 2.— A solution \( x(t) \) of a differential equation plotted in its state space. At each point along the solution, it’s tangent vector is given by \( f(x(t)) \).

Population densities can blow up in finite time despite each species being self-limited. In the words of Robert May, “for mutualisms that are sufficiently strong, these simple models lead to both populations undergoing unbounded exponential growth, in an orgy of reciprocal benefaction.”

Geometrically, solutions trace out curves in the state space, the set of all possible states. For example, for models of \( n \) interacting species, the state space consists of all vectors \( x = (x_1, \ldots, x_n) \) whose components are non-negative. Alternatively, in metacommunity models where each patch can be in one of \( n \) different states (e.g. a particular community of species is occupying the patch), the state space consists of all distributions on the \( n \) states: non-negative \( x = (x_1, \ldots, x_n) \) such that \( x_1 + \cdots + x_n = 1 \). Solutions \( x(t) \) are characterized by being curves whose tangent vectors are given by the right hand side \( f(x(t)) \) of the differential equation (Fig. 2). This geometric interpretation of solutions is extremely useful for understanding their qualitative behavior as discussed further below.

III. Linear equations

In the absence of density-dependent or frequency-dependent feedbacks, ecological dynamics can be described by systems of linear differential equations. These linear models, just like their discrete-
Fig. 3.— Different dynamical behaviors in the phase plane for two dimensional linear equations.

Time Matrix model counterparts, are particularly useful for describing populations structured in space, size, or age. For these models, the rates of change are linear functions of the state variables:

\[ f_i(x) = a_{i1} x_1 + a_{i2} x_2 + \cdots + a_{in} x_n. \]

If \( A \) is the matrix whose \( i-j \)-th entry is \( a_{ij} \), then these linear differential equations can be written more simply as

\[ \frac{d\mathbf{x}}{dt} = A\mathbf{x} \]

where \( A\mathbf{x} \) denotes matrix multiplication of \( A \) and \( \mathbf{x} \).

Remarkably, as in the scalar case, the general solution for these equations can be written down explicitly as \( \mathbf{x}(t) = \exp(A t) \mathbf{x}(0) \) where \( \exp(A) \) denotes matrix exponentiation of \( A \) and \( \mathbf{x}(0) \) is the initial state of the system. As in the case of the exponential function, matrix exponentiation is given by an infinite power series, \( \exp(A) = I + A + A^2/2! + A^3/3! + \cdots \), and can be carried out easily in most numerical software packages and program languages.

For the “typical” matrix \( A \) (i.e. the eigenvalues all have non-zero real part), the behavior of the matrix equation (4) can be classified into two types (for \( n = 2 \) see Fig. 3). Analogous to the exponential growth model with a negative per-capita growth rate, all solutions of (4) decay exponentially to zero if all eigenvalues of \( A \) have negative real part. In this case, the origin is stable: solutions starting near the origin asymptotically approach the origin. For structured populations, this behavior corresponds to a deterministic asymptotic decline to extinction. Alternatively, all (or
almost all) non-zero solutions of (4) grow exponentially when one the eigenvalues of $A$ has a positive real part. In particular, in this case, the origin is unstable: small perturbations away from the origin result in solutions moving further away from the origin. For structured populations, this behavior corresponds to unbounded exponential growth of the entire population. When the eigenvalues of $A$ have imaginary parts, the dynamics can exhibit dampened oscillations if the corresponding real parts of the eigenvalues are negative or undampened oscillations if the corresponding real parts are positive.

IV. Nonlinear equations

All natural populations exhibit some degree of density-dependence or frequency-dependence. Therefore, more realistic models are necessarily nonlinear e.g. the per-capita growth rates are no-longer constant. While it is possible to solve special nonlinear equations (e.g., the Logistic equation or the doomsday equation), in general it is impossible to find explicit solutions. In the words of Henri Poincaré, a French mathematician and the founder of modern dynamical systems theory, “Formerly an equation was not considered solved except when the solution was expressed by means of a finite number of known functions; but that is possible scarcely once in a hundred times. What we can always do, or rather what we may always try to do, is to solve the problem qualitatively, so to speak—that is, to find the general shape of the curve which the unknown function represents.” Poincaré’s suggestion to find “the general shape of the curve” is the genesis of the qualitative theory of differential equations. Instead of finding or approximating the elusive solutions of nonlinear differential equations, this theory examines whether solutions tend to increase or decrease, oscillate or not, or exhibit more complicated long-term behaviors. To achieve these goals, a diversity of techniques have been developed including linearization to understand qualitative behavior of solutions near a well-understood solution such as an equilibrium, bifurcation theory to understand how long-term behaviors change (i.e. “bifurcate”) as one varies parameters of the system, and ergodic theory to understand the long-term statistical behavior of solutions.

The number possible asymptotic behaviors exhibited by nonlinear differential equations increases with the dimensional of the system. Some of the highlights of this increasing complexity are as follows.

One dimensional systems. When there is only one state variable, say population density, the solutions of (3) are monotonic: either the population density remains constant for all time (i.e. the population is at equilibrium), the population density constantly increases, or the population density constantly decreases. If the population dynamics are bounded in time, then increasing or decreasing solutions always asymptotically approach an equilibrium state. All three of these behaviors can be observed in the Logistic model of population growth (Fig. 4a). For solutions initiated below the carrying capacity, the population density increases and asymptotically approaches the carrying capacity. For populations starting at the carrying capacity, their density remains constant for all
Fig. 4.— Asymptotic behaviors of nonlinear differential equations. For 1-dimensional equations such as the Logistic equation (a), solutions plotted against time are monotonic and asymptotically approach an equilibrium. For 2-dimensional systems, two new asymptotic behaviors are introduced in the phase-plane: periodic motions as in predator-prey models (b) and heteroclinic cycles as in rock-paper-scissor population games (c). For 3-dimensional systems, the dynamics become infinitely enriched. This enrichment includes quasi-periodic motions of periodically forced predator-prey interactions (d), and chaotic motions (e) and chaotic transients (f) of tritrophic interactions.

For population starting above the carrying capacity, overcrowding results in the population density decreasing to the carrying capacity.
Despite the simplicity of the short-term and long-term behaviors of one-dimensional models, they can produce surprising predictions due to the appearance and disappearance of equilibria as parameters vary. For example, consider the Logistic model with constant harvesting at rate \( h \),
\[
\frac{dx}{dt} = rx(1-x/K) - h.
\]
For harvesting rates below a critical threshold \( h = rK/2 \), the population can persist at an equilibrium supporting a density greater than half of the carrying capacity \( K \). For harvesting rates above this threshold, the population goes deterministically extinct in finite time. Hence, increasing harvesting rates above this critical threshold cause sudden population disappearances as population crash from densities greater than \( K/2 \) to extinction.

**Two dimensional systems.** Nonlinear feedbacks between two state variables introduces two new asymptotic behaviors for solutions: periodicity and heteroclinic cycles.

Periodicity occurs when the system supports a periodic solution: there exists a period \( T > 0 \) such that \( x(t + T) = x(t) \) for all time \( t \). The classic ecological example of periodic behavior is Logistic-Holling model of predator-prey interactions. For this model, the prey exhibit Logistic growth in the absence of the predator and the predator has a saturating functional response. If \( x_1 \) and \( x_2 \) denote the prey and predator densities, respectively, then their dynamics are given by
\[
\begin{align*}
\frac{dx_1}{dt} &= r x_1(1 - x_1/K) - \frac{a x_1}{1 + a h x_1} \\
\frac{dx_2}{dt} &= \frac{c a x_1}{1 + a h x_1} - m x_2
\end{align*}
\]
where and \( a, h, c, m \) denote the predator’s searching efficiency, handling time, conversion efficiency, and per-capita mortality rate. When prey’s carrying capacity is sufficiently large, the equilibrium supporting the predator and prey becomes unstable and there is a periodic solution supporting both species (Fig. 4b). For this model, this periodic solution is globally stable (almost all solutions approach it asymptotically) and unique. However, for other forms of functional responses, there can be multiple periodic solutions. Determining the multiplicity of periodic solutions is a tricky affair. Unlike equilibria, there is no simple algebraic procedure to solve for periodic solution. In fact, one of the most difficult open problems in mathematics, Hilbert’s 16th problem, involves finding upper bounds to the number of possible periodic solutions to two-dimensional differential equations.

The other new asymptotic behavior introduced by the 2nd dimension corresponds to solutions approaching a heteroclinic cycle: equilibria connected in a cyclic fashion by other solutions of the differential equations. A classic example of this behavior occurs for three competing strategies playing an evolutionary game of rock-paper-scissors (Fig. 4c). If \( x_1, x_2, x_3 \) denote the frequencies of the rock, paper, and scissor strategies, respectively, then this dynamic can be described by a
replicator equation of the form:

\[
\begin{align*}
\frac{dx_1}{dt} &= x_1(bx_3 - cx_2 - W(x)), \\
\frac{dx_2}{dt} &= x_2(bx_1 - cx_3 - W(x)), \\
x_3 &= 1 - x_1 - x_2
\end{align*}
\]  

(6)

where \(b\) is the benefit a dominant strategy receives in a pair-wise interaction, \(c\) is the cost the subordinate strategy plays, and \(W(x) = (b - c)(x_1x_2 + x_1x_3 + x_2x_3)\) is the population average fitness. For this evolutionary game, pair-wise interactions always result in the dominant strategy (e.g. rock) displacing the subordinate strategy (e.g. scissor). These pair-wise displacements create the heteroclinic cycle between the pure strategy equilibria: rock beats scissors, paper beats rock, and scissor beats paper. If costs are greater than benefits \((c > b)\), then most solutions initially supporting all strategies asymptotically approach this heteroclinic cycle (Fig. 4c). As the solutions wrap around this heteroclinic cycle, they spend a longer and longer time near each of the pure strategy equilibria. Moreover, as they spend longer times near pure strategy equilibria, the frequencies of the remaining strategies get lower and lower. Biologically, this dynamic implies that all but one of the strategies is lost in the long run. These heteroclinic cycles arise quite naturally in a variety of ecological models in higher dimensions.

**Three dimensions and higher.** In three dimensions or higher, many new dynamical phenomena arise and, unlike planar systems, there is no simple classification of all these phenomena. Three new behaviors that can not occur in lower dimensions are quasi-periodic motions, chaos, and chaotic transients.

*Quasi-periodic motions* (Fig. 4d), roughly, correspond to solutions that exhibit multiple, incommensurable frequencies i.e. the ratio of frequencies is irrational. When there are two frequencies, one can visualize quasi-periodic motions as a curve on a torus (i.e. the surface of a donut) that wraps around the torus without ever returning to the same point. These quasi-periodic motions arise quite naturally when there is periodic forcing of a system with biotically-generated periodic behavior or when there are periodic subsystems that interact with one another as discussed below.

One of the most astonishing behaviors exhibited by ordinary differential equations with three or more state variables is *chaotic behavior*: complex dynamics that make long-term predictions about the state of the system difficult by exponentially amplifying the smallest uncertainty about the current state of the system. This chaotic behavior is exhibited in models of tritrophic interactions. If \(x_1\), \(x_2\), and \(x_3\) are the densities of the prey, predator, and top-predator, the prey exhibit Logistic growth, and the predators have saturating functional responses, then a classical model of these
interactions is

\[
\begin{align*}
\frac{dx_1}{dt} &= r x_1(1 - x_1/K) - \frac{a_2 x_1 x_2}{1 + a_2 h_2 x_1} \\
\frac{dx_2}{dt} &= \frac{c_2 a_2 x_1 x_2}{1 + a_2 h_2 x_1} - m_2 x_2 - \frac{a_3 x_2 x_3}{1 + a_3 h_3 x_2} \\
\frac{dx_3}{dt} &= \frac{c_3 a_3 x_2 x_3}{1 + a_3 h_3 x_2} - m_3 x_3
\end{align*}
\]

where \(a_i, h_i, c_i, m_i\) are searching efficiencies, handling times, conversion efficiencies, and per-capita mortality rates of the predator and top-predator. Alan Hastings and Thomas Powell showed that this deceptively simple system exhibits chaotic motions (Fig. 4e) for biologically plausible parameter values. These chaotic motions trace out a tea-cup in the three dimensional state space: the predator and prey exhibit oscillatory dynamics that dampen as they wind up the tea cup, a reduction in the predator’s density causes top-predator’s density to crash down the handle of the tea cup, and the oscillatory path up the tea cup reinitiates.

Chaotic motions may be unstable i.e. population trajectories initiated near a chaotic motion ultimately move away from this chaotic motion. However, unstable chaotic motions can “trap” nearby solutions in their topologically complex maze for exceptionally long-periods of time. When this occurs, the system exhibits chaotic transients before switching to its final asymptotic behavior. For example, Kevin McCann and Peter Yodzis showed that the tri-trophic model (7) can exhibit long-term chaotic transients supporting all three species, but ultimately the top-predator is lost as the dynamics simplify to a predator-prey oscillation (Fig. 4f). This outcome is somewhat shocking as it implies that even without any additional disturbances, a population that appears to persisting heartily today may be deterministically doomed to extinction in the near future.

One startling way to generate chaotic dynamics and quasi-periodic motions is to increase dimensions by spatially extending models. For ordinary differential equations, this extension can be achieved by modelling space as a finite number of discrete patches and coupling local interactions.
by dispersal. These spatial extended models can generate chaos even when the local interactions do not. Fig. 5 illustrates this phenomena for a spatially extended version of the rock-paper-scissor model (6).

**Competitive and cooperative systems.** While there is no complete qualitative theory for higher dimensional systems, there are two important classes of systems for which there is an exception. The first class are *cooperative systems* which are characterized by all direct feedbacks between pairs of state variables being positive: \( \frac{\partial f_i(x)}{\partial x_j} > 0 \) for all \( i \neq j \). As the name suggests, this assumption is meet for some models of mutualistic interactions. For these models, the American mathematician Morris Hirsch has shown that “most” solutions converge to one (of possibly several) equilibria. Hence, the long-term dynamics are “typically” quite simple. The second class are *competitive systems* which are characterized by all direct feedbacks between pairs of state variables being negative: \( \frac{\partial f_i(x)}{\partial x_j} < 0 \) for all \( i \neq j \). As their name suggests, this assumption is meet for many models of competing species. Remarkably, Hirsch has shown that the dynamics of an \( n \)-dimensional competitive system can be “projected” onto a \( n-1 \) dimensional system. Hence, while models of three competing species can exhibit periodic motions and heteroclinic cycles, they cannot exhibit chaotic or quasi-periodic motions.

**V. Non-autonomous equations**

In the natural world, environmental conditions rarely remain static over time. Consequently, it is valuable to consider models where the rates of change \( f(x,t) \) depend on time \( t \). A trick to doing this and retaining the sheep’s clothing of autonomy of (4) is to introduce \( t \) as an extra state variable, say \( x_{n+1} = t \), that satisfies the trivial equation \( dx_{n+1}/dt = 1 \). Thus, a non-autonomous systems can be viewed as an autonomous system with an extra dimension. An important special case is *periodically forced systems*: the rates of change \( f(x,t) \) are periodic in \( t \). Intuitively, one dimensional periodically forced systems can exhibit periodic solutions. For example, periodically varying the carrying capacity \( K(t) \) in the Logistic equation results in all non-zero solutions approaching a unique periodic motion. Due to intrinsic lags of population growth, this periodic motion does not perfectly track \( K(t) \). In contrast, two-dimensional periodically forced systems can exhibit the dynamic complexity of three-dimensional autonomous systems. For example, periodically forcing the carrying capacity of the prey in a predator-prey system can generate quasi-periodic motions (Fig. 3d) and chaos.

**VI. Numerical considerations**

When the chips are down and analysis isn’t possible, one can close one’s door, turn one’s computer on, and compute with a fury. Over the past 50 or so years, numerical analysts developed
methods to accurately and efficiently approximate solutions of ordinary differential equations. The simplest method is *Euler’s method* in which you approximate $dx/dt$ with the difference quotient $(x(t + h) - x(t))/h$ where $h$ is a “time step.” This approximation yields the difference equation (see Difference Equations)

$$x(t + h) = x(t) + hf(x(t))$$

that can be applied iteratively to approximation solutions to (4). While this method has been used by many theoreticians due to its simple and intuitive appeal, it is generally inefficient for two reasons: errors are of order $h^2$, and time steps do not dynamically adjust to the magnitude of $f(x)$ e.g. one can take larger time steps when $f(x)$ is small. Higher order methods (e.g. fourth-order Runge-Kutta) with adaptive time steps are available in standard libraries for computing languages like C or Fortran, and computational software like MatLab, R, Maple, and Mathematica. When using these advanced libraries, however, it is important to find implementations that preserve basic structural aspects of the models e.g. preserve non-negativity of population densities.
V. Philosophical considerations.

When is it appropriate to model ecological dynamics with differential equations? This question can be answered indirectly by examining two defining features of differential equations.

First, and foremost, differential equations are deterministic. In the words of Henri Poincaré, “If we knew exactly the laws of nature and the situation of the universe at the initial moment, we could predict exactly the situation of the same universe at a succeeding moment.” Differential equations cannot account for populations being finite collections of interacting individuals and the associated uncertainty of the individual demography. However, when population abundances are sufficiently large, the American mathematician Thomas Kurtz showed that differential equations provide good approximations (over finite time horizons) to individual based stochastic models. For instance, consider the Levins’ metapopulation model for which the fraction of occupied patches $p$ is modeled by $\frac{dp}{dt} = cp(1-p) - ep$ with per-capita extinction and colonization rates $e$ and $c$. Implicit in Levins’ model formulation is that there are an infinite number of patches. This idealization does a good job approximating stochastic models with a finite number of patches whenever the number of patches is sufficiently large (Fig. 6).

A second defining feature of differential equations is that they assume all demographic processes occur continuously in time. For autonomous differential equations, this assumption is quite strong and implies that the populations exhibit overlapping generations. However, by adding time-dependence into differential equations, one can account for temporally concentrated demographic events such as synchronized reproductive or migratory events. Classically, populations with these concentrated demographic events have been modeled by difference equations. For populations exhibiting a combination of discrete and continuous demographic processes, there exist impulsive differential equations that lie at the crossroads of difference and differential equations. Despite having a long mathematical history, the impulsive differential equation models have only recently entered the theoretical ecology literature. Whether these hybrid models will overtake the literature remains to be seen.

See Also the Following Articles:

- Bifurcations
- Birth and Death Models
- Chaos
- Difference Equations
- Matrix Models
- Non-dimensionalization
- Phase-Plane Analysis
- Predator-Prey Models
- Single-Species Metapopulation Models
Glossary

continuous a function $f(x)$ is continuous, roughly, if small changes in $x$ result in small changes in $f(x)$. Equivalently, the graph of $f$ exhibits no breaks or jumps.

derivative the derivative of a function $f(x)$ is given by its instantaneous rate of change: the value of $(f(x+h) - f(x))/h$ as $h$ gets infinitesimally small. A function for which this limit is defined at $x$ is called differentiable at $x$.

dissipative the state of the system asymptotically entering and remaining in a bounded set.

equilibrium the state of system remaining constant over time. For a differential equation $dx/dt = f(x)$, equilibria correspond to states $x^*$ such that $f(x^*) = 0$.

ergodic theory a branch of mathematics that examines the long-term behavior of dynamical systems from a statistical or probabilistic viewpoint. This view is particularly useful for systems exhibiting complex behavior such as quasi-periodic or chaotic motions.

quasi-periodic curves in state space that exhibit multiple, incommensurable frequencies i.e. the ratio of frequencies is irrational. When there are two frequencies, one can visualize quasi-periodic motions as a curve on a torus (i.e. the surface of a donut) that wraps around the torus without ever returning to the same point

periodic a pattern that repeats itself at regular intervals. A function $x(t)$ is periodic if there exists $T > 0$ such that $x(t + T) = x(t)$ for all $t$.

rate of change the change in a quantity per unit of time. For example, speed is rate of change corresponding to distance traveled per unit time. For a function $x(t)$ of time $t$, the rate of change over an interval of length $h$ is given by $(x(t+h) - x(t))/t$.

state space a set corresponds to all possible states of the system being modeled. For example, the state space for models of planetary motion is the position and velocity of all the planets.

Further Reading


