

Does population ecology have general laws?

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There is a widespread opinion among ecologists that ecology lacks general laws. In this paper I argue that this opinion is mistaken. Taking the case of population dynamics, I point out that there are several very general law-like propositions that provide the theoretical basis for most population dynamics models that were developed to address specific issues. Some of these foundational principles, like the law of exponential growth, are logically very similar to certain laws of physics (Newton's law of inertia, for example, is almost a direct analogue of exponential growth). I discuss two other principles (population self-limitation and resource-consumer oscillations), as well as the more elementary postulates that underlie them. None of the "laws" that I propose for population ecology are new. Collectively ecologists have been using these general principles in guiding development of their models and experiments since the days of Lotka, Volterra, and Gause.

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Like many scientists who are not physicists, ecologists have been unable to resist unfavorable comparisons between their science and physics. Some argue that ecologists do not think like physicists, and that is why there is little progress in ecology (Murray 1992). Others reply that biologists should not think like physicists because of the nature of biological science (Quenette and Gerard 1993, Aarssen 1997). On both sides of the debate, there is a widespread belief that ecology is different from physics because (1) it lacks general laws, and (2) it is not a predictive (and, therefore, not a "hard") science. For example, Cherrett (1988) commented that "there is unease that we still do not have an equivalent to the Newtonian Laws of Physics, or even a generally accepted classificatory framework" (see Kingsland 1995: 222–223 for a commentary). "Parts of science, areas of physics in particular, have deep universal laws, and ecology is deeply envious because it does not" (Lawton 1999). Even eminent theoretical ecologists appear to subscribe to this view: ecology, apparently, is different from physics because one of its distinguishing features is the near absence of universal facts and theories (Roughgarden 1998: xi). As to ecology's ability to generate testable theories, Aarssen (1997:

177) thinks that "On this scale, ecology admittedly has a weak record" (see also Weiner 1995). "Ecology was not and is not a predictive science" (McIntosh 1985).

Much can be said to counter these arguments. First, physics is not a monolithic science. In certain highly respectable subfields, like astrophysics, it is not possible to test theoretical predictions with manipulative experiments. Does it mean that there is no progress in astrophysics? No, because astrophysicists can still make predictions about yet unobserved phenomena. A true experiment can be conducted without actively messing with nature. Second, it is a gross exaggeration to claim that physics is a predictive science in all its aspects. Physicists assure us, on one hand, that they have a complete understanding of the laws of fluid dynamics that govern atmospheric movements. On the other hand, neither they nor anybody else can accurately predict weather more than 5–7 days in advance. I could go on, but I do not think that trying to counter each charge of the critics is what is needed. A more productive approach is to simply do ecology and eventually show that it is a vigorous, theoretical, and, yes, predictive science. In fact, we may not need to wait very long to demonstrate this, because, in my opinion, at least the

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population dynamics branch of ecology is on the verge of a major synthesis (Turchin unpubl.).

Furthermore, I think that population ecology has general laws resembling laws characterizing certain fields of physics (e.g., classical mechanics, or thermodynamics). In particular, population dynamics appears to have a set of foundational principles which are very similar, in spirit and in logic, to Newton's laws (Ginzburg 1972, 1986). In the rest of this paper, I will sketch out what I think these foundational principles are, and discuss the similarities between the logical foundations of population dynamics and Newtonian mechanics. I should warn you right away, however, not to expect any deep and novel insights. My main argument will essentially be that we had, and used these principles all along (at least since the 1920s), but simply did not call them "laws".

Exponential growth – the first law of population dynamics

Practically all ecological textbooks start exposition of population ecology with the exponential law of population growth (Malthus 1798). There is a reasonable consensus among ecologists that the exponential law is a good candidate for the first principle of population dynamics (e.g., Ginzburg 1986, Brown 1997, Berryman 1999). My formulation of this principle is as follows: "a population will grow (or decline) exponentially as long as the environment experienced by all individuals in the population remains constant". Environment here refers to all environmental influences affecting vital rates of individuals, including abiotic factors, the degree of intraspecific crowding, and density of all species in the community that could interact with the focal species.

Most elementary textbooks give the derivation of the exponential law for the case when all individuals in the population are absolutely identical (in particular, there is no age, sex, size, or genetic structure) and reproduce continuously. We start by writing the law of conservation (the number of individuals can only change as a result of birth, death, emigration, and immigration), and then change to per capita rates:

$$\frac{dN}{dt} = B - D = bN - dN = (b - d)N = rN \quad (1)$$

where B and D are the total birth and death rates, b and d are the per capita rates, N is the total number of individuals in the population, and r is the per capita rate of population change. There are no immigration/emigration terms because I assumed that the population is closed. This elementary derivation readily generalizes to more realistic settings:

- For semelparous organisms (such as annual grasses or insects) we obtain the discrete form of the exponential law: $N_{t+1} = \lambda N_t$
- Adding age or stage structure is also relatively straightforward. However, we now have to wait for the population to achieve a stable age distribution, after which all age classes (as well as total number of individuals) begin to grow according to the exponential law.
- The general pattern of growth is still exponential when we consider finite populations and add demographic stochasticity. For example, Bartlett (1966) shows that the expected population size in a stochastic birth process is the same as in the deterministic model.
- The environment does not have to be constant. If the environment varies in such a way that the per capita rates b and d have stationary probability distributions, then we obtain a model of stochastic exponential growth/decline (Maynard Smith 1974: 14–15). The expected population density is again described by the exponential equation (but see e.g. Lande 1998 for a caveat).
- Finally, adding space and diffusive movements leads to a simple partial differential equation model, analyzed by Fisher (1937) and Skellam (1951). In this model, the total number of individuals continues to grow exponentially, even as they diffuse out from the initial center.

In short, as long as the environmental influences do not change in a systematic manner, we end up with one or another version of the exponential law. In fact, we can formulate it even more generally by substituting "constant environment" with "stationary environment" (environmental influences on vital rates fluctuate with a constant mean and variance) in the definition given above. The exponential law is a very robust statement.

But is it a *law*? Let us compare it to something about which there is no argument that it is a law – Newton's First Law, or the law of inertia. The similarity between the exponential law and the law of inertia is striking. First, both statements specify the state of the system *in the absence of any "influences" acting on it*. The law of inertia says how a body will move in the absence of forces exerted on it; exponential law specifies how a population will grow/decline in the absence of systematic changes in the environmental factors influencing reproduction and mortality.

Second, the action of both laws in real life is obscured by complexities characterizing real-life motions of bodies, or population fluctuations. As a result, neither statement can be subjected to a direct empirical test. Just as we cannot observe a body on which no forces are acting, we cannot observe a population growing exponentially (at least, not for long), because we cannot indefinitely keep its environment stationary. In-

evitably, as a result of population growth, individuals will eventually experience higher degree of crowding, start running out of food, and suffer greater predation or begin succumbing to epidemics. Thus, both laws have to be arrived at by speculative thinking, and only their consequences can be empirically tested. This point is forcefully made by Murray (1992: 594) in his discussion of Newton's laws, although Murray does not appear to agree with the proposal that the exponential law is the equivalent of the law of inertia (see Murray 2000).

Third, both statements are in some sense self-evident (at least, in retrospect!), so there is a suspicion that they are trivial, or tautological in some sense. However, we can imagine an alternate universe in which different versions of first laws of population dynamics or classical mechanics would hold. The alternative to the law of inertia is Aristotle's concept that bodies come to a rest in the absence of forces, discussed by Murray (1992: 594). In fact, in the pre-Galileo and Newton's days, Aristotle's "First Law" was widely believed. Similarly, recollect that the exponential law is based on the notion that organisms can come only from other organisms (this principle underlies the law of conservation to which I alluded to above). Interestingly, it so happens that as late as in the 19th century many scientists believed that life could spontaneously generate from nonliving matter. During the Middle Ages it was thought that dirty laundry and refuse bred mice and flies, and that frogs fell from the skies with rain. It took Louis Pasteur and his famous experiments to finally lay that theory to rest.

Note that if spontaneous generation were possible, then population dynamics theory would be completely different (just as classical dynamics based on Aristotle's First Law would be a completely different science). In particular, the equivalent of Eq. (1) would be

$$\frac{dN}{dt} = S + B - D = S + bN - dN = S + rN \quad (2)$$

All notation is as in Eq. (1) except S , which is a constant rate at which organisms spontaneously generate themselves. Note that there is no per capita equivalent to S because, unlike in the case of birth and death processes, per capita spontaneous generation rate does not make sense. By definition, spontaneous generation depends on the properties of the environment (e.g., on how dirty the laundry is), rather than on the number or density of organisms.

For N near 0, Eq. (2) can be approximated as

$$\frac{dN}{dt} \approx S \text{ which solves to: } N(t) = N(0) + St \quad (3)$$

In other words, when population density is small, population will grow linearly with time. In contrast, popu-

lation growing according to the exponential law exhibits a nonlinear, accelerating pattern of growth. Actually, Eq. (2) is not quite as ridiculous as it sounds. It can be used to model population dynamics in a sink habitat, dominated by immigration from some source habitat (S , then, would represent a constant flow of immigrants). Incidentally, if the biological universe was based on the law of spontaneous generation, then we would have many fewer examples of population oscillations (see Turchin unpubl.).

The fourth way in which the two "First Laws" are similar is that they provide the basis for building predictive theories for population dynamics and for classical mechanics, respectively. Just as Newton was able to predict how far an apple would fall by using the law of inertia (plus several other laws, to be sure), population ecologists use the exponential law as the basis for modeling populations. This can be seen by rewriting Eq. (1) by dividing both sides by N , and making the per capita rate of population change, r , a function of "all sorts of things" that may affect the population change:

$$r \equiv \frac{dN}{N dt} = f(\dots) \quad (4)$$

Practically all population dynamics models have this form (or an equivalent if we use some other mathematical framework than ordinary differential equations). In fact, the exponential law is most profitably thought of as the null state in which any population would be if no forces (= environmental changes) were acting on it. It is a direct equivalent of the law of inertia, and is used in the same way, as a starting point to which all kinds of complications are added. Thus, the starting point in the analysis of time-series data is the discrete version of (4):

$$r_t \equiv \ln \frac{N_t}{N_{t-1}} = f(N_{t-1}, X_{t-1}, Y_{t-1}, Z_{t-1}, \dots) \quad (5)$$

where r_t is the realized per capita rate of change and N_t is the density at time t . X_t , Y_t etc. are various environmental factors that affect growth of the target population (other species, climatic factors, and so on). If we have data on how these factors change, we can investigate their effect by regression methods. If we only have data on N_t , then we can employ Takens theorem (Schaffer 1985), and represent the action of unknown interacting species with lagged population densities:

$$r_t = \ln \frac{N_t}{N_{t-1}} = f(N_{t-1}, N_{t-2}, \dots, \varepsilon_t) \quad (6)$$

where ε_t represents the action of exogenous (non-inter-active) variables (Royama 1981, 1992, Turchin 1990, Turchin and Taylor 1992, Berryman 1999).

Population self-limitation

One cannot predict the motion of planets with just the law of inertia. Similarly, we need more principles in addition to the exponential law to predict population dynamics, so that we can eventually subject the complete framework to empirical tests. The second foundational principle that I would like to propose is a formalization of the notion that population growth cannot go forever: there has to be some upper bound beyond which population density cannot increase. I think that self-limitation should be elevated to the status of a foundational principle because (1) it is logically necessary at the level of population mechanisms, and (2) because it is a very important ingredient in models of population dynamics, at the level of population dynamics. I acknowledge that the application of this principle to practical investigations of population dynamics has been very controversial in the past; however, a certain degree of consensus is also emerging (for reviews, see Turchin 1995, 1999).

How can we formalize the notion of self-limitation? One possible approach is to require that population density would always decrease when density is above some threshold. That is,

$$\frac{dN}{N dt} \equiv r < 0 \text{ if } N > N^* \quad (7)$$

where N^* is the upper threshold density. Note that r is not a constant in this equation (as it was in the exponential model, Eq. 1), but a function of environmental influences, including population density (as in Eq. 4). The problem with this approach is that the value of N^* is likely to change with time depending on environmental conditions, such as resource or natural enemy abundances. For example, individuals may defend smaller territories when food is abundant, and larger territories when it is scarce. It is desirable to separate the effects of self-limitation, understood as direct, or undelayed density dependence, from population feedbacks involving time lags, such as depletion of food (when food is a slow dynamical variable), or increase in specialist natural enemies.

The alternative approach, thus, is to require that the partial derivative of r with respect to N is negative:

$$\frac{\partial r}{\partial N} < 0 \text{ for } N > N^* \quad (8)$$

The biological meaning of this statement is that as we vary N , while keeping all other variables that affect r constant, increasing N leads to a decrease in r , and vice versa. In the example of territories varying with food availability, we fix food availability and then consider how increasing population density will affect the per capita growth rate. Clearly, as N becomes large enough

so that there are not enough territories for all individuals, r will decrease, and so (8) holds. We now also see why we have to hedge (8) with a condition that it should only hold for high enough densities. It is conceivable that r will not change with N when N is low (or even increase if we have an Allee effect). What is important for self-limitation is that there is a negative relationship between r and N at high population densities.

Having a mathematical statement of the principle of self-limitation allows us to easily find out whether any particular ecological model includes self-limitation or not. We simply rewrite the equation for the focal species in per capita form, differentiate the right-hand side with respect to N , and check whether it is negative for any values of N , especially those greater than some average level of fluctuations (for example, the equilibrium density, if the model has an equilibrium). For example, the Lotka-Volterra predation model fails this test (the partial derivative of r with respect to N is zero for all N). This makes sense because the Lotka-Volterra predation model does not involve any self-regulation terms in either prey or predator equations.

As I pointed out in the previous section, all ecological textbooks discuss the law of exponential growth. Another “standard” ecological model that is often discussed right after the exponential one is the logistic. The relationship between the principle of self-limitation and the logistic model is obvious. Can the logistic curve, however, serve as a general law of population growth? Raymond Pearl thought so (e.g., Pearl and Reed 1920), and during the 1920s vigorously advocated the logistic curve as such a general law of population biology (see Kingsland 1995 for the history of the ensuing debate). Pearl failed to establish his point. The logistic equation is a much maligned model in the ecological literature, and it is certainly not my intention to add to the abuse here (in fact I consider it an extremely useful building block in modeling population interactions). However, I agree with the currently prevailing opinion among ecologists that the logistic model is not a general law of population growth, and it is worth discussing why not.

The main reason why the logistic model falls short of a general law is that it is too much of a special case: it assumes a linear relationship between the realized per capita rate of population change and density, there is no explicit consideration of effects of noise, and, most importantly, no lags. Each of these assumptions, when relaxed, leads to a rather substantial change in the qualitative type of the predicted behavior. Nonlinearities in density dependence result in an asymmetric pattern of growth, noise changes the nature of equilibrium from a stable point to a stationary distribution, and lags allow density to overshoot the equilibrium, potentially leading to cycles and chaos (for example, in the discrete versions, such as the Ricker model). Con-

trast this with the exponential model, which generalizes very nicely, as I pointed out in the previous section. No matter what complications we throw at it, as long as there is no density dependence in any form or shape, the pattern of growth remains essentially the same (especially, if we sample the population once each generation, to get away from any effects of fluctuating age structure).

My conclusion, therefore, is that the logistic lacks generality to qualify as a central organizing principle for population dynamics. It is rather the simplest possible model embodying this principle (Berryman 1999). Nevertheless, it is worth repeating that the logistic model remains an extremely useful tool for modeling fluctuating populations. In fact, the diagnosis of its failures in the previous paragraph can be turned around as a prescription of how it could be modified in any specific case study.

Consumer-resource oscillations

Ecologists distinguish five general classes of pairwise species interactions, classified by the positive (+), negative (-), or no (0) effect of species on each other: interference competition (-, -), mutualism (+, +), commensalism (+, 0), amensalism (-, 0), and trophic interaction (+, -). Although resource-consumer or trophic interaction is only one of the five types, population ecologists have devoted a massive share of their attention to studying trophic interactions. This is not to say that other interactions, like mutualisms, are unimportant. But there is something very fundamental and universal about consumption. Certainly, we cannot hope to understand one important class of ecological dynamics, population oscillations, without a thorough grounding in resource-consumer theory.

Arguably, the simplest possible model for the dynamics of a resource-consumer system is the Lotka-Volterra model (Lotka 1925, Volterra 1926):

$$\begin{aligned}\frac{dN}{dt} &= rN - aNP \\ \frac{dP}{dt} &= -dP + caNP\end{aligned}\tag{9}$$

where N and P are population densities of resources and consumers, r is the per capita rate of population growth of resources in the absence of consumers, d is the per capita rate of population decline of consumers in the absence of resources, a is the consumer searching rate, and c is the constant of proportionality relating the number of consumed resources to the number of new consumers produced per unit of time.

The Lotka-Volterra equations are a horribly unrealistic model for real resource-consumer systems. It is, in fact, so bad that, to my knowledge, there has been no successful application of it to any actual population system, whether in the field or laboratory. But this is all beside the point, because the Lotka-Volterra model seems to get at some extremely basic feature of trophic interactions: their inherent proneness to oscillations (May 1974). In fact, the Lotka-Volterra model predicts a rather special kind of oscillations that have no fixed amplitude. Such dynamics, in which the amplitude of oscillations depends on initial conditions, and does not either decrease or increase with time (unless perturbed by an external force), are called neutral oscillations.

Let us rewrite Model (9) using per capita growth rates (remember, this is the right thing to do, because it is what the first law of population dynamics tells us):

$$\begin{aligned}\frac{dN}{N dt} &= r - aP \\ \frac{dP}{P dt} &= -d + caN\end{aligned}\tag{10}$$

Model (10) has one extremely interesting feature: the per capita rate of each species depends only on the density of the other species. For example, N does not appear on the right-hand side of the resource equation. Thus, there is no direct population feedback to resource density, although there is, of course, an indirect connection (since increase in prey density will eventually cause the predator to increase, which will in turn have a negative effect on prey per capita rate of change). Similarly, consumer dynamics depend directly only on resource density. I will call a system in which per capita rates of change of both resource and consumer do not depend on their own density a *pure resource-consumer system*. Also note that the right-hand sides in Model (10) are linear functions. Thus, the Lotka-Volterra model is, indeed, the simplest possible formulation of a pure resource-consumer system (because a line is the simplest function).

Two features of Model (10), that it is a pure resource-consumer system, and that its dynamics are oscillatory, are clearly connected. This observation suggests that the Lotka-Volterra model may have identified an important general principle, which may deserve the status of a law of population dynamics. Let us first see how this law might be stated based on the observation made above, and then we will consider whether it is a general result, or depends sensitively on particular assumptions of the Lotka-Volterra model. Here is my statement of the law of consumer-resource oscillations: a pure resource-consumer system will inevitably exhibit unstable oscillations. By “unstable oscillations” I understand population oscillations that do not converge to a point equilibrium. They can be either neutral, as in

the Lotka-Volterra model, or they may actually diverge, getting away from the point equilibrium with each cycle, as in the Nicholson-Bailey model.

Does this statement depend on details of the Lotka-Volterra model? In particular, what about the linear form of right-hand sides in Model (10)? Actually, we can make an argument that this is not a problem. The stability of nonlinear generalizations of the Lotka-Volterra model will be determined by the stability of the linearized version in the vicinity of an equilibrium. As long as the linearized version has the same signs in front of its coefficients (and lacks direct population feedbacks in both equations), we should obtain neutrally stable oscillations. (Of course, what happens when the oscillation gets away from the equilibrium will depend on the nonlinearities.) Interestingly, this is the argument by which Lotka accomplished his derivation of the Lotka-Volterra model. Unlike Volterra, who started by considering specific mechanisms of predators chasing prey, Lotka first wrote the predator-prey equations in general form. He then considered the linearization of the general equations that leads to Model (10).

We also need to check on how the general insight from Model (10) depends on its mathematical formulation as a system of ordinary differential equations. One alternative framework is discrete difference equations. May (1973) considered a discrete version of the Lotka-Volterra model, and showed that it is characterized by diverging oscillations for all values of parameters. The oscillations are not neutral, as in the continuous variant, because discretization introduces a lag in the responses of predators and prey to each others' densities, and lags are an inherently destabilizing feature in any model. By making time step increasingly smaller, we can make the oscillations diverge very slowly, and in the limit, when the time step is 0, we recover the neutral stability of the Lotka-Volterra model. May (1973) further showed that the Nicholson-Bailey parasitoid-host model is equivalent in its stability properties to the discrete Lotka-Volterra model (despite different functional forms used by Nicholson and Bailey). In summary, it appears that the tendency of pure consumer-resource systems to show unstable oscillations does not depend sensitively on the specific assumptions of the Lotka-Volterra model.

There may be two objections to my proposal of consumer-resource oscillations as a general law of population dynamics. First, we know very well from experience that not all (actually, a minority) of real-life consumer-resource systems show persistent oscillations. This objection, however, misunderstands the nature of a general law. Like the law of exponential growth, the law of consumer-resource oscillations is not meant to be tested directly. In real life, we never expect to encounter pure resource-consumer systems. Necessarily, the per capita growth rate of both resource and consumer populations would be affected by their densities

(as formulated by the population self-limitation principle). Furthermore, there will be other species in the community. Consumers may be generalists. Resources may not be killed during the process of consumption, but only lose a part. There are refuges, spatial and temporal heterogeneity, and many other potentially stabilizing (as well as destabilizing) mechanisms known to ecologists. What the law says, however, is that there is an inherent tendency for specialist consumer-resource systems to oscillate. This "signal" may or may not come through the "noise" of real-life complications.

The second point (raised by Joel Brown in his review of an earlier version of this paper) is that consumer-resource oscillations are a consequence of certain assumptions about how these two types of organisms interact, and thus it has the logical status of *theorem*. This is in contrast to, for example, relation (8), which has the status of *postulate* (assumption) because we do not derive it from more elementary principles. I agree that this is a very important consideration, and is worth discussing in some greater detail.

“Laws”: postulates or theorems?

Note that up to now I have avoided defining just what exactly I mean by “law”. I did this on purpose, because I wanted to avoid definitional wrangles. Instead, I adopted the approach of arguing by analogy with the laws of classical dynamics. At this point, however, it is becoming clear that we have to think more carefully about the logical status of various “law-like” statements. In particular, perhaps we should distinguish between elementary propositions that are taken without proof (postulates) and statements derived from a set of these postulates (theorems). Note, however, that this distinction is not absolute. For example, we can take exponential growth as a postulate. On the other hand, we can also derive it from more elementary principles (namely, the law of conservation and the assumption that births and deaths are proportional to the number of organisms in the population). In the second approach (which I favor) exponential growth is a theorem.

Population self-limitation, relation (8), as pointed out above, is a postulate. If we use another postulate, that the expected per capita population growth rate is positive at low densities, then we can derive another theorem, stating that population density will stay within certain limits, or undergo bounded fluctuations (see Chesson 1982 for a rigorous treatment of this proposition).

Resource-consumer oscillations is a theorem that clearly follows from some more elementary principles. Analyzing the structure of a typical resource-consumer model we observe that in addition to exponential

growth and self-limitation terms (although the Lotka-Volterra model does not have the latter term), there are two other components. The first one, in the resource equation, reflects the impact of predators on prey numbers or biomass. It is typically written as a product of predator density and “killing rate” per predator, known as the functional response. The second term, in the predator equation, typically specifies how consumed prey biomass is translated into enhanced predator survival and reproduction. This process, “numerical response”, is clearly based on some principle related to conservation of energy. Thus, it appears that we need at least two postulates, in addition to those underlying exponential growth and bounded fluctuations.

The preceding discussion, thus, suggests that we may have several kinds of law-like statements in population ecology. The postulates may include (1) conservation of numbers, (2) per capita rates, (3) self-limitation, (4) positive rate of change, (5) functional response, and (6) numerical response. The theorems are (1) exponential growth, (2) bounded fluctuations, and (3) consumer-resource oscillations. Incidentally, the exponential, logistic, and Lotka-Volterra equations are the simplest possible ways to model these three “laws” in the ODE (ordinary differential equations) framework.

I want to emphasize that what I propose here is no more than a bare sketch. I have only focused on two ecological “forces”: the self-limitation and the trophic interaction. Other interactions such as mutualisms could also be included. Population structure is important. Spatial considerations is another huge area.

Furthermore, I do not insist on this particular set of six postulates and three theorems as foundational principles even of temporal dynamics of unstructured populations. In fact, I am following Joel Brown’s prescription (Brown 2001) to be both opinionated and open-minded. On one hand, I insist that we need a set of general principles to place population dynamics on a firm logical foundation. On the other hand, if somebody can come up with a better set than the one in this paper, I will be happy to switch to it.

Comparison to other proposals

Once again, I wish to make a disclaimer: there are no novel theoretical proposals in this paper. The elementary ecological models that I have discussed have been the foundations of theoretical ecology since the times of Lotka and Volterra. All I tried to do here was to point out that these fundamental concepts that are presented in all ecological texts, and we routinely use in constructing ecological theory (without thinking much about it), are very similar to general laws, as they are used in some areas of physics. I am, similarly, not the first to propose that ecology has general laws, and it

would therefore be useful to say a few words about other proposals.

Going back to the origins, Alfred Lotka (1925: 64–65) proposed his Law of Population Growth in the following form:

$$\frac{dN}{dt} = F(N) \quad (11)$$

Lotka expanded the function F in a Taylor series, and noted that the minimum number of terms that need to be retained in order for the model to have an equilibrium point is two, which of course leads to the logistic model. Later (in Chapter VIII) Lotka generalized the approach to a system of differential equations. One special case was Lotka’s host-parasite model, now known as the Lotka-Volterra predation model.

More recently, Lev Ginzburg (1986) published an article on first principles of population dynamics, in which he suggested the analogy between the exponential growth law and Newton’s First Law. Usually the exponential law is formulated in terms of first-order derivatives or differences. For example, the realized per capita rate of change can be interpreted as the rate of change (first temporal derivative) of log-transformed N :

$$r = \frac{dN}{N dt} = \frac{d}{dt} (\ln N) \quad (12)$$

Instead, Ginzburg proposed to write down the exponential law in terms of the *second* derivative of $\ln N$:

$$\frac{d^2}{dt^2} \ln N = 0 \quad (13)$$

Furthermore, Ginzburg proposed that instead of using Eq. (3) as the basis of population dynamics models, we use a second-order model such as

$$\frac{d^2}{dt^2} \ln N = f\left(N, \frac{dN}{dt}\right) \quad (14)$$

Ginzburg calls this approach “the inertial view” (Ginzburg 1998). In the 1986 paper, he attributed inertia to intrinsic causes and illustrated its effect on predator-prey interactions. Subsequently, Ginzburg developed models showing that one particular intrinsic factor, the maternal effect, may lead to second-order oscillations (Ginzburg and Taneyhill 1994, Inchausti and Ginzburg 1998). I agree with the premise that underlies much of Ginzburg’s work, that second-order dynamics (that is, dynamics characterized by delayed density dependence) are widespread in nature and deserve to be studied (Turchin 1990, Turchin and Taylor 1992). However, we part ways when it comes to explaining the causes of oscillations in empirical cases: whereas Ginzburg emphasizes intrinsic population

mechanisms, I believe that the majority of cases of oscillatory dynamics in ecology (if not all) are explained by trophic interactions.

Another very interesting recent paper addressing the issue of general laws in ecology is by John Lawton (1999). Lawton (1999: 178) states several deep universal laws that underpin ecological systems: (1) the two laws of thermodynamics, (2) the rules of stoichiometry (particularly, conservation of matter), (3) natural selection, and (4) physical principles governing diffusion, mechanical properties of materials, etc. These principles are not ecological laws (and, more specifically, not laws of population ecology, with which I am concerned in this paper). However, they may underlie some of the postulates I discussed above (for example, the rate at which consumers transform prey biomass into their own should clearly be subject to thermodynamic laws). I am also in agreement with Lawton's discussion of population dynamics (1999: 179–180). Although he does not explicitly formulate a set of laws for population ecology, similarly to what I attempt in this paper, he emphasizes the importance of qualitative classes of population dynamics and of general theoretical models.

Another recent proposal of general laws in ecology is due to Bertram Murray (2000). The first law of population dynamics according to Murray (2000) is: "A population with constant age-specific rates of survival and initial size of cohorts maintains a steady state". Note the difference between this statement and the exponential law. Murray's first law implies a population maintaining a steady state, while exponential law implies exactly the opposite – an unregulated population that is either exploding to infinity or going extinct. The key difference between the two alternative laws is in the assumed mode of reproduction. While the exponential law is derived by assuming that the *per capita* rate of reproduction is constant, Murray's first law assumes that the *total* rate of reproduction is constant. But does it really make sense to make this assumption? Suppose that every time step (e.g., a year) the Murray-type population has 1000 recruits added to the first age class (Murray's "initial size of cohorts"). This number is independent of the total number of reproducing adults in the population. Whether we have a million, just 10, or even zero reproducing adults, the population always gets an infusion of 1000 recruits. Thus, Murray's assumption of constant number of recruits implies spontaneous generation! This can be more clearly seen if we slightly simplify Murray's model by assuming that the death rate in his population is independent of age (this simplification does not affect the main argument). Then, we can write the following differential model that describes the dynamics of the Murray population:

$$\frac{dN}{dt} = S - dN \quad (15)$$

where S is the number of recruits added to the population per unit of time, and d is the per capita death rate of organisms. Note that this is a special case of Model (2), since (15) can be obtained from (2) by setting $b=0$ (that is, assuming that the only new recruits are produced by the process of spontaneous generation, and there is no reproduction from the extant population).

Furthermore, Murray's first law imposes population regulation by force, rather than allowing it to arise naturally as a result of density-dependent feedback. As a result, Murray's first law has the same logical relationship to the exponential law as the Aristotle's first law of motion to the law of inertia. Recollect that Aristotle's law of motion says that a body will come to a state of rest if there are no forces acting on it. Murray's law says the same thing about a population (where a "rest" is the population equilibrium). By contrast, in Newtonian dynamics, a body will come to a rest if there is some force that opposes motion, for example, friction. Similarly, our modern understanding of population dynamics implies that population density would move towards an equilibrium only if some specific ecological mechanisms would cause decreased survival/fecundity when population density gets too high, and increased survival/fecundity when density gets too low.

Murray's first law provides a nice illustration of my claim above that the exponential law is not a trivial statement, because it is possible to come up with an alternative equation on which to base ecological theory. The big question, of course, is which law provides a better basis for the theory. Just as Aristotelian notions of mechanics were abandoned in favor of Newtonian ones, it is a demonstrable fact that ecological theory is overwhelmingly based on the exponential equation. (I do not wish to make this statement too absolute: Eqn (15) may provide a reasonable starting point for modeling certain restricted cases, such as populations in sink habitats whose dynamics are dominated by immigration.)

Finally, in a recent book Alan Berryman (1999) proposed a set of five fundamental principles underlying population dynamics: (1) exponential growth, (2) cooperation, (3) competition, (4) circular causality, and (5) limiting factors. Our approaches are quite similar. In fact, we share the first principle (exponential growth). There are also some analogies between the principles of self-limitation and trophic oscillations that I proposed here and Berryman's third and fourth principles. Additional principles in Berryman's codification arise primarily because he considers a greater variety of "forces" than I did here. For example, his second principle of cooperation is essentially the Allee effect. In sum, our approaches appear to be closely related.

Conclusion

The exponential, logistic, and Lotka-Volterra predation models are covered by all serious ecological textbooks. As I argued in this paper, the reason that these three elementary models are of such importance is because they introduce and illustrate the three foundational concepts of population dynamics: exponential population growth, self-limitation, and trophic oscillations. None of the elementary models can be considered as a realistic model for any real-life population. The exponential model generalizes very nicely when population structure and exogenous effects are added, but no population can really grow exponentially forever. Few real populations show the classical S-shaped pattern of growth predicted by the logistic model, and adding realism to it can result in very different dynamical patterns. I know of no ecological populations, laboratory or field, that could be even approximately described by the Lotka-Volterra predation model. In short, the three elementary models are no more than *metaphors* for the corresponding concepts of population dynamics. Yet, they lay bare some of the fundamental features of population dynamics, and serve as simplest models embodying each principle.

In this paper I argued that these three foundational principles of population dynamics are conceptually very similar to laws in certain fields of physics, such as classical mechanics. The exponential law is a direct analogue of the law of inertia in that it provides the starting point for a mathematical description of dynamics of population systems. The other two principles, self-limitation and trophic oscillations, have a somewhat different logical status. If the exponential law tells us how the system should behave in the absence of any forces acting on it, the other two laws capture the most important essence of two of the most important “forces” that can act on a population: population self-limitation and trophic interactions. Other important forces, such as mutualism or direct (“interference”) interspecific competition can probably be codified with their own laws (see Berryman 1999, for example). Incidentally, exploitative competition is better modeled as an indirect interaction, mediated by a shared resource (MacArthur 1972). Thus, exploitative competition is not a binary interaction (= “elementary force”), but a complex one, being a property of a system of three or more interacting components (minimally, two consumers and one resource).

There is no denying that certain physical systems, such as the solar system, can be predicted by laws of classical mechanics much better than any real ecological population, even in the laboratory. However, note that most of the real-world physical problems are much harder to predict than planetary motions. Consider the proverbial apple. In the real world, there is weather (wind and rain), there are branches (that may move

unpredictably as a result of wind), and there are willful humans who could pluck the apple before it had a chance to fall down of its own accord. Real physical systems are much harder to predict than is portrayed by ecologists suffering from physics-envy. Surely an important aspect of Newton’s genius was in selecting a perfect system – planetary motions – to apply his theory to. By contrast, ecologists insist on asking really tough and messy questions, such as how many species should a community have (note that, as far as I know, physicists have craftily avoided even asking the messy question of how many planets should be rotating around the Sun). What we ecologists should do is first cut our teeth on more manageable problems. The obvious place to start in population ecology is the puzzle of population oscillations. This is a big and exciting problem, of high intellectual and applied interest in its own right. Moreover, once we test the general theories and approaches on population oscillations, we should be able to extend the resulting insights to systems with messier dynamics. My survey of case studies suggests that simple ecological models can predict population oscillations with accuracy of up to 90% (Turchin unpubl.). It may be that the study of population oscillations will do the same for ecology that the study of planetary motions did for physics.

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References

- Aarssen, L. W. 1997. On the progress of ecology. – *Oikos* 80: 177–178.
- Bartlett, M. S. 1966. An introduction to stochastic processes. – Cambridge Univ. Press.
- Berryman, A. A. 1999. Principles of population dynamics and their applications. – Stanley Thornes Publ.
- Brown, J. H. 1997. An ecological perspective on the challenge of complexity. *EcoEssay Series No. 1.* – National Center for Ecological Analysis and Synthesis. Santa Barbara, CA. Available at <http://www.nceas.ucsb.edu/fmt/doc/?nceas-web/resources/ecoessay/brown/>.
- Brown, J. S. 2001. Ngongas and ecology: on having a world-view. – *Oikos* 94: 6–16.
- Cherrett, J. M. 1988. Key concepts: the results of a survey of our members’ opinions. – In: Cherrett, J. M. (ed.), *Ecological concepts*. Blackwell Scientific, pp. 1–16.
- Chesson, P. L. 1982. The stabilizing effect of a random environment. – *J. Math. Biol.* 15: 1–36.
- Fisher, R. A. 1937. The wave of advance of advantageous genes. – *Ann. Eugenics* 7: 355–369.
- Ginzburg, L. R. 1972. The analysis of the “free motion” and “force” concepts in population theory (in Russian). – In: Ratner, V. A. (ed.), *Studies in theoretical genetics*, Novosibirsk, pp. 65–85.
- Ginzburg, L. R. 1986. The theory of population dynamics: I. Back to first principles. – *J. Theor. Biol.* 122: 385–399.
- Ginzburg, L. R. 1998. Inertial growth; population dynamics based on maternal effects. – In: Mousseau, T. A. and Fox, C. W. (eds), *Maternal effects as adaptations*. Oxford Univ. Press, pp. 42–53.

- Ginzburg, L. R. and Taneyhill, D. E. 1994. Population cycles of forest Lepidoptera: a maternal effect hypothesis. – *J. Anim. Ecol.* 63: 79–92.
- Inchausti, P. and Ginzburg, L. R. 1998. Small mammals cycles in northern Europe: patterns and evidence for a maternal effect hypothesis. – *J. Anim. Ecol.* 67: 180–194.
- Kingsland, S. E. 1995. *Modeling Nature: episodes in the history of population ecology*, 2nd ed. – Univ. of Chicago Press.
- Lande, R. 1998. Demographic stochasticity and Allee effect on a scale with isotropic noise. – *Oikos* 83: 353–358.
- Lawton, J. H. 1999. Are there general laws in ecology? – *Oikos* 84: 177–192.
- Lotka, A. J. 1925. *Elements of physical biology*. – Williams and Wilkins.
- MacArthur, R. H. 1972. *Geographical ecology*. Harper and Row.
- Malthus, T. R. 1798. *An essay on the principle of population*. – J. Johnson, London.
- May, R. M. 1973. On relationships among various types of population models. – *Am. Nat.* 107: 46–57.
- May, R. M. 1974. *Stability and complexity in model ecosystems*, 2nd ed. – Princeton Univ. Press.
- Maynard Smith, J. 1974. *Models in ecology*. – Cambridge Univ. Press.
- McIntosh, R. P. 1985. *The background of ecology: concept and theory*. – Cambridge Univ. Press.
- Murray, B. G. 1992. Research methods in physics and biology. – *Oikos* 64: 594–596.
- Murray, B. G. 2000. Universal laws and predictive theory in ecology and evolution. – *Oikos* 89: 403–408.
- Pearl, R. and Reed, L. J. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. – *Proc. Natl. Acad. Sci. USA* 6: 275–288.
- Quenette, P. Y. and Gerard, J. F. 1993. Why biologists do not think like Newtonian physicists. – *Oikos* 68: 361–363.
- Roughgarden, J. 1998. *Primer of ecological theory*. – Prentice-Hall.
- Royama, T. 1981. *Fundamental concepts and methodology for the analysis of animal population dynamics*, with particular reference to univoltine species. – *Ecol. Monogr.* 51: 473–493.
- Royama, T. 1992. *Analytical population dynamics*. – Chapman and Hall.
- Schaffer, W. M. 1985. Order and chaos in ecological systems. – *Ecology* 66: 93–106.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. – *Biometrika* 38: 196–218.
- Turchin, P. 1990. Rarity of density dependence or population regulation with lags? – *Nature* 344: 660–663.
- Turchin, P. 1995. Population regulation: old arguments and a new synthesis. – In: Cappuccino, N. and Price, P. (eds), *Population dynamics*. Academic Press, pp. 19–40.
- Turchin, P. 1999. Population regulation: a synthetic view. – *Oikos* 84: 153–159.
- Turchin, P. and Taylor, A. D. 1992. Complex dynamics in ecological time series. – *Ecology* 73: 289–305.
- Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. – *Nature* 118: 558–600.
- Weiner, J. 1995. On the practice of ecology. – *J. Ecol.* 83: 153–158.