

# Ecology is not rocket science

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**Ecology is the foundation of the methods used in conservation, pest, rangeland, forest and fisheries management. A theme among many ecologists is the need to justify the science as a rigorous discipline. Coupled with this is the notion that physics represents an ideal model of a rigorous science. To that end recent discussions in the literature have placed emphasis on identifying Laws of ecology. In particular, Malthusian growth has been identified as a prime candidate for an ecological law, and much has been written favorably comparing the expression to Newton's laws of motion. Malthusian growth is shown here to be a poor example of a potential ecological law, largely due its numerous *ceteris paribus* conditions and lack of universality. In fact, as a simple linear model, Malthusian growth fails to adequately address the nonlinear complexities that make ecology such a rich and fascinating discipline. Ecological theory would do well to ignore comparisons to other sciences and focus on explaining the complex dynamics within ecology.**

## Introduction

The management of systems exhibiting complexity is not more apparent or important than in natural ecosystems. With the world's fisheries in global decline, rangeland desertification spreading and the IUCN red list growing annually there is no doubt about the importance of understanding management with regards to environmental issues. Issues such as the spread of new diseases (think West Nile Virus, Chronic Wasting Disease, avian influenza, to name a few), invasive species, and multiple resistance bacteria it is clear that there is a substantial ecological component to problems facing the medicine, agriculture, city planning, recreation, public health and a myriad other organizations.

The management of natural systems, either through conservation, restoration, in-

tegrated pest management, fisheries regulations or other means is based scientifically on ecological results. Good management practices require some level of confidence that an action taking will result in a specific outcome. Causality in ecology has proven difficult and generalizations of results are even more challenging for the science. Ecology requires a firm philosophical foundation that will allow a framework of theoretical results to inform empirical studies which can be utilized by managers to implement policy decisions. Ultimately, understanding ecology is critical to organizing our societies for a sustainable future.

The sciences that are most directly associated with the notion of complexity are also those sciences in which the debate about laws governing them still holds sway (Fodor, 1989; McIntyre, 1998; Mikulecky, 2000; Carroll, 2003; Hausman, 2003; Lyman & O'Brien, 2004). Consider the role of laws in ecology. Although much attention has been given to this question recently, the most frequently suggested laws are plagued with problems that raise doubt about their validity. Ecologists frequently compare their science to physics, and particularly Newtonian mechanics which is often taken as an ideal formulation of science. Recently proposed ecological laws have been equated – or at least favorably compared – to Newton's Laws of Motion. Unfortunately, there appears to be much confusion about the nature and structure of Newton's Laws of Motion that casts doubt on the usefulness or validity of such comparisons. Such comparisons, even if invalid, do not obviate the proposed laws from lawhood, but further examination demonstrates that for one of the most common of the proposed ecological laws, there can be little support for it. Even if the suggested laws are not sufficiently law-like, there may be other suitable candidates, so a formulation of ecology in the mold of classical mechanics might be conceivable. However, before such a venture is seriously pursued a more important question remains: what is – or should be – the

theoretical structure of ecology? As we shall see, laws, and in particular physical laws, carry with them a certain concept that the processes they describe are either simply expressions of the laws or additive assemblages of the laws. Ecological processes are strongly resistant to the development of additive functions that adequately describe such processes. Ecological processes are complex and as such aggregative laws are likely unsuitable as a theoretical foundation to underpin the science.

### The role of Law

The notion of a law of science is problematic (Armstrong, 1983; Cartwright, 1983; Van Fraassen, 1989; Carroll, 1990; Lange, 1993; Lewis, 1994; Giere, 1999; Maturana, 2000; Murray, 2000) and with respect to ecological laws several approaches are used. A general working definition for such a law is a factual truth (as opposed to a logical truth) that is spatio-temporally universal, supports counterfactuals and has a high level of necessity (or resilience as per Cooper, 2003). This definition precludes simple patterns unless such patterns demonstrate a high level of necessity. Berryman (2003) argues for principles rather than laws in defining governing equations. Berryman's use of principle derives from general definitions of laws and principles and is quite different from a more scientifically oriented definition (Parker, 1989). Lawton (1999) divides laws into general and universal and argues that the idea of a general law is more appropriate for ecology. Lange (2005) discounts both Berryman and Lawton claiming that both give a definition of a law that is simply a general truth. Murray (2000) argues for the existence of universal ecological laws. In each case some aspect of ecology has been nominated as a law (Table 1). Ecology is a broad science and any likely law will be with respect to a narrow subdiscipline. I will restrict my further consideration of ecological laws to population dynamics. This subdiscipline provides an exemplary case, being one of the most highly quantified and seemingly physics-like aspects of ecology. Population ecology, is of course, importantly tied to organizational structures as it is coupled with economic theory for man-

agement of natural resources and is the foundation of understanding disease dynamics to which public health systems must respond.

The need for laws in a science is something that is not universally agreed upon (van Fraassen, 1989; Giere, 1999; Shrader-Frechette & McCoy, 1993), but a consistent theoretical framework for a science does appear to be necessary. Theoretical ecology is founded on the concept of the "model" which is taken here to be a mathematical, or more broadly, algorithmic construction that reproduces a quantitative (or qualitative) dynamic observed in nature. The model is, by necessity, a restricted image of reality. Models vary in their intended descriptions of nature, with some describing a process that has occurred or is only repeatable in a qualitative sense, while other models attempt to provide a predictive capability for systems that operate on scales too large to experimentally manipulate or for systems where experimental manipulations have the potential for irreversible change (e.g., conservation of endangered species). It could be argued that models that are well supported for specific species or populations would be laws where the universality is defined over the population or species. Most ecologists would argue that universality at such a small scale is not very useful for ecology and would simply be defining away the issue that universality is difficult to observe in ecological theory. Thus many ecological models are ill suited for consideration as laws.

A theoretical framework provides coherence for the collected body of facts, models and relations among them. More broadly, the theory of a discipline is viewed as an overarching interpretation of a body of knowledge and is intimately linked to the principle of falsifiability. Although many argue against the need for a strict Popperian falsifiability in ecology or science in general (Murray, 2000), without a method for determining the validity of a theoretical construct, there appears to be little hope in determining which of two or more competing models is more correct. In the absence of a consistent theoretical framework ecology is a body of numerous models that are used to only describe particular systems

| Law   | Specification   | Source                   |
|---|---|--------------------------|
| First Law of Population Dynamics                      | A population with constant age-specific rates of survival and initial size of cohorts maintains a steady state.   | Murray, 1979             |
| Second Law of Population Dynamics                     | In the absence of changes in age-specific birth and death rates, a population will eventually establish a stable age distribution   | Murray, 1979             |
| First Law of Evolution                                | Genotypes and phenotypes with the greatest Malthusian parameter increase more rapidly than those with smaller Malthusian parameters.  | Murray, 2000             |
| Second Law of Evolution                               | In the absence of changes in selection forces, a population will reach and remain in an evolutionary steady state.  | Murray, 2000             |
| Third Law of Evolution                                | Selection favors those females that lay as few eggs or bear as few young as are consistent with replacement because they have the highest probability of surviving to breed again, their young have the highest probability of surviving to breed, or both. | Murray, 2000             |
| First Law of Population Dynamics – Exponential Growth | A population will grow (or decline) exponentially as long as the environment experienced by all individuals in the population remains constant.   | Turchin, 2001            |
| Second Principle – Self Limitation                    | There has to be some upper bound beyond which population density cannot increase.   | Turchin, 2001            |
| Law of Consumer-Resource Oscillations                 | A pure resource-consumer system will inevitably exhibit unstable oscillations.  | Turchin, 2001            |
| First Principle – Geometric Growth                    | All populations grow at a constant logarithmic rate unless affected by other forces in their environment.   | Berryman, 2003           |
| Second Principle – Cooperation                        | There is a positive relationship between individual fitness and the numbers or density of conspecifics.   | Berryman, 2003           |
| Third Principle – Competition                         | The per-capita growth rate of a population is limited directly by its own density via competition.  | Berryman, 2003           |
| Fourth Principle – Interacting Species                | When populations are involved in a negative feedback with other species or components of the environment, oscillating population dynamics occur.  | Berryman, 2003           |
| Fifth Principle – Limiting Factors                    | Of all the biotic and abiotic factors that influence a population, one must be limiting.  | Berryman, 2003           |
| Kleiber Allometry                                     | Basal metabolism rate is proportional to a $\frac{3}{4}$ power of body weight   | Colyvan & Ginzburg, 2003 |

**Table 1** Proposed laws of ecology

or kinds of systems. And ecologists have realized that as the models increase their generality, their applicability decreases via the loss of accuracy in predictions and increasing number of parameters necessary to extend the models. These models, in and of themselves, provide valuable insights, particularly with respect to our prediction and manipulation of the systems. But if each ecological system requires its own unique model, then theoretical ecology is nothing more than a form of quantitative natural history. While natural history is the backbone of ecology and fundamental to the science, this descriptive methodology does not yield broad theoretical constructs. As Watt (1971) points out, without theoretical underpinnings ecology will “all be washed out to sea in an immense tide of unrelated information.” So, are there then no generalizations to be made about ecological processes? If so, it would seem that ecological theory becomes so much quantitative stamp collecting. Ironically, the notion of quantitative stamp collecting might apply to physics as it is composed of a collection of laws, theories and models that are not intimately or explicitly connected across scales and systems.

Ecology is fundamentally different from much of the physical sciences (Ulanowicz, 1999) in that it is both contingent (historically dominated) and mechanistic. Mikkelsen (2003) describes ecology more broadly as caught in tension between the idiographic and the nomothetic. The interplay between the historical processes and mechanical processes are at the heart of the theory of ecology. The laws proposed for ecology are almost exclusively mechanistic in nature and ignore contingency and mathematical frameworks in which contingency can operate. Any attempt at a formulation of a law in ecology currently may best be restricted to a verbal rather than mathematical structure, owing to the diversity of mathematical formulations that describe the same overall dynamic with entirely different processes.

### Newtonian mechanics and Malthusian growth

**T**he difference between physical and ecological processes becomes clear when considering the strenuous effort to com-

pare Newtonian mechanics to population dynamics. Comparisons are often made between Newton’s First Law of Motion and Malthusian growth with the intention of showing a favorable relationship between the conceptualizations of Malthus and Newton. In fact, there is little in the two conceptualizations to indicate any commonality. To get to the root of these comparisons and their shortcomings we must understand the laws being compared.

Consider Newton’s First Law, which states that, an object’s center of mass remains at rest or moves in a straight line (at a constant velocity,  $\vec{v}$ ), unless acted upon by a net outside force. This can be expressed mathematically using Newton’s Second Law of Motion as,

$$\vec{F} = m \frac{d\vec{v}}{dt}$$

The equation is made with a vector notation. This is important for our discussion of Newton’s First Law because an object remains at rest or moving in a straight line when the net (sum of the vectors) forces are zero. The equation describes the First Law precisely when,

$$d\vec{v}/dt = 0,$$

which implies that an object will remain at constant velocity in the absence of a net force, whether that velocity is 0 or some vector quantity.

While the equation would imply that Newton’s First Law is simply a special case of the Second Law, it is more than that. Newton’s First Law defines the inertial frame of reference for which the other two laws are valid. This also will be an important distinction between Newton’s and Malthus’s expressions.

Newton’s Laws of Motion describe an ideal system completely, acknowledging the provisos that the objects, velocities, and distances are not too big or too small (where too big or too small would require Relativity or Quantum Theory, respectively). The state of an object in this framework is composed of its location, velocity and acceleration. If I kick a soccer ball it will roll according to these rules. The force I apply to the ball is added to the force

of friction as the ball travels across a surface and from these an estimate of the ball's trajectory can be derived. I can create arbitrarily more detailed models of the motion by including more details about the shape of the ball and texture of the surface, but increasing details such as these just means adding or refining vectors of force. Claims regarding the failure of Newton's First Law are based on two concepts; the first is the misperception that the law must operate in isolation and that in and of itself it does not predict the motion of objects. Rather it always functions in an aggregative manner with the other laws, again with the proviso that the object is not too big or too small and the velocities are not too fast. The forces acting on any body are elegantly additive, with the important feature that force is always expressed in the same units (or convertible to the same units). The second is that the law (coupled with the other laws of motion) do not account for all of the interactions between the ball and my foot and the surface it is rolling across. This is true enough but electromagnetic forces and the loss of heat energy really do not affect the general predictive quality of Newton's laws under the majority of instances when it is invoked. Reality is wildly complex, but in this case the laws give an approximation that is more than satisfactory. This, of course, is the distinction between scientific laws and natural laws at the heart of Cartwright's (1983) claim that all scientific laws are false.

Turning to Malthusian growth, the difference between ecology and physics becomes evident. Malthus's basic assumption is that each individual reproduces on average at a constant rate and given that level of reproduction a population will grow or decline exponentially. This implies that the environment remains constant – there is no effect of increasing density (hence space and spatial heterogeneity are absent), change in resources, interactions with other species, or changes in abiotic influences. That said, Malthusian growth can be expressed as,

$$N_t = N_0 e^t$$

Malthusian growth has been compared favorably to Newton's Law of Inertia based on several criteria. However, these criteria are insufficient to support the notion that exponential growth represents an ecological law. Consider the argument that both laws are not directly observable in real-life situations. The only time Malthusian growth might occur in a natural setting is with the introduction of new species to certain environments, but such growth is limited to a very few generations. In a mere 40 generations starting with two univoltine individuals the discrete form of Malthusian growth predicts more than one trillion individuals if the growth rate is 2. Malthusian growth predicts that at about 175 generations there would be more individuals than there are atoms in the earth. It is equally clear that not all introduced or invasive species demonstrate Malthusian growth or even an approximation of such growth. If we consider highly controlled environments, the closest we might come to such a system would be a chemostat, but the density of the organisms increases rapidly with the physical limitations of the chemostat volume placing a hard bound on population growth so that exponential growth occurs only for a very limited number of generations. The universality of Malthus's equation is directly limited by its formulation. The equation predicts all populations with an average growth rate greater than zero will increase unboundedly. A further argument against the use of Malthusian growth is presented by Elgin and Sober (2002) who argue that forward-directed dynamical laws do not provide covering-law causal explanations.

On the other hand, instances of Newton's First Law are observable in numerous forms. Note that all the objects resting on a desk are in fact at rest. This of course, is only one end of the law, but the law with constant non-zero velocity is easily achieved by any object falling to earth and reaching terminal velocity. Terminal velocity is exactly the situation when the net forces acting on the object are zero. The force of gravity is equal in magnitude to air resistance and each have opposite directions. Although there are clearly other forces working on the bodies, the overwhelmingly large effects of the forces of drag and

gravity dominate the system and allow both description of the process and prediction of the process with sufficient accuracy. Here, one can argue that the gravitational force by itself is insufficient to explain the interaction of two or more masses under all conditions, as Cartwright (1980) does. A fundamental question then, is the discrepancy in the predicted movements of the masses unaccounted for or can it be explained by the addition of other laws, such as Coulomb's Law? If the net forces can be described by the additive effects of more than one law, then each law can be seen as valid under a simple proviso.

Often, ecologists' efforts to show that Newton's Law can be favorably compared to ecology are based on incomplete statements of the physical law. Berryman (2003) states that "all inanimate bodies move with uniform motion in a straight line unless affected by external forces" and Turchin contends that inertia describes the motion of a body in the absence of forces exerted on it. Colvan and Ginsberg (2003) state that Newton's Law describes a system where "there are no mechanical forces." None of these statements fully addresses Newton's First Law. Inertia does not only describe motion in the absence of external forces (which is likely an impossibility in our universe), but it describes motion when the net forces are zero within the given inertial frame of reference (which occurs relatively frequently in our universe). As such, these comparisons fail to account for the fundamental interaction between Newton's First Law (which define the frame of reference for the system) and other laws of physics. For example, a person bouncing a ball in the aisle of an airliner will see the ball fall in a straight line and bounce back up. The inertial frame of reference of the observer and the ball are within the aircraft traveling 500 mph. In rare cases, Malthusian growth might appear to provide a similar frame of reference but even then the framework is not aggregative or additive.

Malthusian growth is ontologically dissimilar from Newtonian mechanics, but this in and of itself does not disqualify it as a law. But now consider the conditions stated earlier for lawhood. A law must be factually true. The for-

mulation of the law by its very nature simply precludes this condition. Malthusian growth allows for any population to increase without bounds. Such a statement necessarily contradicts the physical law that no two objects can occupy the same space at the same time. Since any unbounded population of organisms must necessarily be bounded by that region of the earth's biosphere capable of supporting the species, unbounded growth in a finite space is impossible. It has been suggested that Malthusian growth may occur during some initial invasions but no data definitively shows exponential growth for more than a few generations. Likewise many invasive species do not exhibit such growth. Clearly Malthusian growth is not spatially and temporally universal. The failure of many species to recover from overexploitation indicates a failure to support counterfactuals. "In the absence of overharvesting, populations will increase exponentially" is the simple form of a counterfactual that is implied by the Malthusian growth formulation. Unfortunately, many species do not spring back. It might be argued that the population would spring back if given release from predation, disease, etc. and given no space or food restrictions and thus Malthusian growth would support the counterfactual. The problem is that for just about all species, we are unable to construct an experiment meeting the idealized conditions and thus cannot confirm the statement. Here, Malthusian growth might be a law but one so far removed from reality as to be useless. It might also be argued that the rate of growth is now unity for the population thus leveling the total population. Again, no natural population has ever been demonstrated to have a growth rate of 1. While an average value of one would result in a bounded time series, we would have little predictability for the next time step unless we understand the causes of the perturbations.

### Ecological mechanics?

When adding to ecological laws to develop a coherent system it is unclear where to turn next. Unlike Newtonian mechanics, the processes that operate on a population are not vectors, do not function in

the same manner, and are not necessarily additive. Population dynamics operates on a scalar value and we have numerous models that differ from each other by fundamental processes. Any additions to the Malthusian growth replace the constant  $r$  by a function and in most cases a nonlinear function.

Consider the proposed law of self limitation (Turchin, 2001). A host of functions have been suggested to describe the nature of negative density dependence (e.g., the logistic, Allee, Beverton-Holt, and Ricker, among many others). While self limitation appears to be a common process, the form of the process remains undetermined and there is as yet no evidence that a single function governs a substantial proportion of populations. Although each of the recent works proposing population laws refers to the notion of “forces” acting on populations, this appropriation of a Newtonian term lends an air of similarity without substance. Self limitation can take the form of cannibalism, physiological changes, strict competition for resources, or other processes including a host of indirect interactions. The point is that each of these processes functions in a different manner and the notion that each is a force, somehow equivalent at some fundamental level, only confounds the complexity by which populations operate.

In fact, in each of the basic population laws proposed, multiple functions can accomplish the stated process. In the case of the Berryman’s (2003) Limiting Factors, that one biotic or abiotic factor regulates the population, it is unclear that this statement is necessarily complete as stated. For example, Lockwood and Lockwood (1989, 1991) demonstrate that population limitation may be associated with the combination of multiple abiotic factors and that while a single factor is sufficient to limit the population, limitation is achieved with the interplay of multiple factors prior to the limit imposed by any single factor. In fact, self organization can also explain a population dynamic in which no limiting factor can be ascribed and the population’s current value is highly contingent upon its past spatial configuration (Adami, 1995; Lockwood & Lockwood, 1997). Other research on spatially explicit chaotic dynamics

indicates that long term transients can persist in a population resulting in highly unstable dynamics (Hastings, 1997). These transients are not revealed if the population is allowed to equilibrate after many generations.

One problem with assigning mechanistic functions as laws is the inherent duplicative nature of the mechanisms in ecology. Since more than one mechanism may describe a process, both counterfactuals and universality are called into question.

### Contingent and complex

The basic ecological models often appearing in ecology texts (e.g., single species dynamics, consumer-resource dynamics, competition and the like) are mechanistic and do not lend themselves to the notion of history. The consideration of contingency is important in ecology. Metapopulation ecology, invasion ecology and biodiversity are but three ecological disciplines that are greatly influenced by contingent factors. Evolution informs population dynamics as well as community dynamics and at its heart evolution relies on contingencies: genetic drift, mutation and environmental variability in time and space all significantly shape evolution, and in turn ecological dynamics. Much of physics is profoundly ahistorical, with the exceptions of cosmology and some of astronomy. For example, Newton’s laws describe the motion of an object by its instantaneous position and forces, not by its past motions. In fact, physics strongly embraces the uniformity principle that all processes and properties are constant throughout space and time (excepting the short duration following the Big Bang). Ecology is rife with entirely new properties and processes – predators were not the first life forms and photosynthesis evolved millions of years after the origin of life. New species with novel capacities have occurred throughout the history of life, and will no doubt continue to form in the future.

How do we describe ecological processes? More than ever, *complex* is the term used to capture the fullness of ecological dynamics (Milne, 1998). Many now refer to populations and communities as complex adaptive systems (Levin, 1998, Bissonette & Storch, 2002; Sole,

*et al.*, 2002; Grimm, *et al.*, 2005; Levin, 2005). Adaptive implies functional change to contingencies. If a population did not experience a changing environment, as with the idealized Malthusian population, then adaptation would be unnecessary.

Complex systems, particularly ecological systems are considered to have self-organizing dynamics (Pascual & Guichard, 2005). Generally the system is metastable and responses to external changes result in a reordering of the state to a new metastable state with scale invariance describing the overall dynamics. This is similar to the concept of autocatalysis in which the product of a reaction catalyzes the reaction which has also been put forth as an operational property of ecosystems (Ulanowicz, 2002). When combined with the radical contingencies of complex, ecological systems, such an approach would seem to have considerable promise for powerful models without bogging down in the terminology of laws.

Definitions of complexity are, like definitions of scientific laws, problematic (Chu, *et al.*, 2003). But consider the relationship given by Wimsatt (1997) describing system properties as aggregative or emergent. He defines emergent properties as non-aggregative and a property of a system is aggregative if it: 1) allows for the intersubstitution of parts, 2) maintains qualitative similarity with the addition or subtraction of parts, 3) is unchanged when the parts are reaggregated, and 4) exhibits no cooperative or inhibitory relations among the parts.

Wimsatt does not explicitly refer to complexity but the logical coupling of emergence and complexity seems to allow the use of this definition of emergent properties to be, at the least, a surrogate for complexity. Under this definition of complexity, there is no strict separation between the complex and the aggregate but a relative scale of complexity. Properties can be more complex compared to other properties, but no single property can be said to be strictly complex, although a property can be said to be purely aggregative.

Wimsatt points out that the archetypal cases of aggregativity are Newton's laws. And it is evident that population dynamics for a

single, isolated, ideal Malthusian population is an aggregative property. But just as clearly, no actual population or any other proposed law for population ecology when combined with Malthusian dynamics fits the definition of aggregative (the fourth property – the absence of cooperation and inhibition among parts – is applicable only for idealized populations free of intraspecific behavioral responses). In fact, most populations and communities would not be considered to have any of the four conditions, except under rare and limited situations. Thus the complex nature of ecology removes from consideration the notion of physics-like aggregative laws.

### All other things being equal...

Scientific laws are not well or discretely defined, and perhaps a statement's law-likeness is a continuous property of our ability to model a natural phenomenon. A model becomes more law-like the fewer the *ceteris paribus* conditions it contains (*ceteris paribus* is the caveat of "all other things being equal" which is a standard assumption in the development of scientific laws meant to rule out an unspecified set of relevant – but less important – factors in the phenomenon of interest). Malthusian growth has so many *ceteris paribus* conditions that no natural population can ever be considered to obey the law for more than a few generations. While it is argued that all laws require associated *ceteris paribus* conditions, there is a clear distinction in the practical application of Newton's Laws and Malthusian growth or even Hardy-Weinberg equilibrium. The *ceteris paribus* conditions of Newton's Laws over the scale of universality are such that other forces can be considered negligible. For those physical systems where other forces such as electromagnetic forces are too large to be negligible, the laws are additive in effect. Malthusian growth to be applied for an arbitrary time interval (or more precisely, number of generations) requires the population to have unlimited space and resources. The population must not have any interactions with other populations that would result in nonlinearities in the dynamics. These conditions are so extreme ecologically that they can never be met.

The result is that the Malthusian Law has no real instances. Laws regarding complex processes should not be given a pass on the direct applicability of the law to the natural world.

### Complexity in ecology

**M**odels from complexity science are applied to many population ecology problems. Catastrophe theory has been applied to plankton (Kemp, *et al.*, 1984; Greve, 1995), insects (Lockwood & Lockwood, 1989, 1991) forest dynamics (Frelich & Reich, 1999), fisheries (Jones & Walters, 1976) and livestock (Loehle, 1985); self organized criticality to insect outbreaks (Lockwood & Lockwood, 1997), bird populations (Milne, 1997) and rainforest community dynamics (Solé & Manrubia, 1995); and chaos has been applied to a wide range of systems including insects, marine fish, microorganisms and .

The discussion has been restricted to population ecology, but there are proposed laws of ecology that exist outside the level of population. Most notable are allometric relationships (West, *et al.*, 1997; West, *et al.*, 1999; Gillooly, *et al.*, 2001; Brown, *et al.*, 2004). Generally applied at the ecosystem scale, this work, labeled the Metabolic Theory of Ecology, indicates that universal fractal scaling of metabolic processes exists. While this work has spurred important advances in ecology, its broad application is not without criticism (Darveau, *et al.*, 2002; Cottingham & Zens, 2004; Clarke, 2004; Cyr & Walker, 2004; Marquet, *et al.*, 2004; Glazier, 2005; Makarieva, *et al.*, 2005; Nee, *et al.*, 2005; Niven & Scharlemann, 2005; Clarke, 2006) some of which has direct applicability to considering the overall results candidates for lawhood. In particular, the universality and necessity (from a philosophical perspective) are called into question. This is not to say that the results are not without tremendous merit, but rather it highlights the difficulties in finding laws in ecology.

### Conclusions

**I**n the absence of a consistent, reliable definition of a law, the question regarding laws in ecology would appear to yield a relative answer at best. Ecological theory does not inter-

act with empirical ecology in the same manner as is found in physics and it should be clear that ecologists should not attempt to ape the physical sciences in an effort to validate or ground their science.

The scales in ecology are such that empirical studies are all but impossible for many *in situ* populations and communities. For example, to determine the efficacy of marine protected areas as a means of fishery management requires empirical studies to extend to decades as the life spans of many of the species are extremely long, if they are known at all. As such, the theoretical models of marine reserves do not necessarily generate predictive hypotheses that can then be tested, but rather provide insight into the long-term dynamics. As such the models must be robust to a range of parameter variations and confidence is gained if qualitatively similar results are arrived at from different theoretical approaches. This methodology is far removed from the manner in which physics has developed. It also implies that the universality of many ecological models will remain unknown for a considerable period of time.

It is important to note that the only purely aggregative properties in the natural world are the conservation laws (mass, energy, momentum and net charge) in physics (Wimsatt, 1997). Vulgar reductionism (*sensu* Wimsatt, 1997) will never explain ecological processes in terms of these four laws alone. Understanding complex phenomena cannot occur without understanding the parts, the interactions of the parts comprising the system, and the history of the parts and the system. While ecology is complex, there is no reason to consider ecological systems as necessarily devoid of laws. However, the framework of an aggregative set of laws clearly is inappropriate, and a different concept of laws will be required if the desire remains to place ecology within such a framework. And it should be noted that there is yet to be a convincing argument that such a framework is the only or best approach to ecological science. Other approaches such as the one proposed by Ulanowicz (1999, 2002) suggest that substantial progress can be made while avoiding the issues surrounding laws.

The laws presented to date are largely dynamical in nature and take into consideration the processes that operate in the absence of historical context. In fact, much of ecological theory has been constructed around this underlying concept that the dynamics operate in a machine-like fashion and that variation is added on top of the mechanics as an extra error term. Physics is grounded by the ideal of Platonic forms. As examples, all electrons carry equal charge and variation in the speed of light is attributable only to measurement error. Ecology is generally absent such notions, as there is not an ideal population of wolves and no ideal desert in which variation is due to observational error alone, yet the theoretical constructs reduce the rich biological realism down to an atomistic individual approach. Elsasser (1981) addresses the notion of heterogeneous classes of objects in biology and suggests that “mathematical” laws are to be replaced by a more set-theoretical notion of organization. While addressing the metaphysics of biology, this approach does not appear to have generated an explicit solution to the question of laws in ecology. Of course, we are limited in expressing contingency in theory as either: we do not have enough detailed data to model the variation from all the possible sources, or we are faced with the pressing human need to provide a predictive statement for an unpredictable future. Some complexity models account for the historical nature of the process, namely chaos and self-organized criticality. Importantly, both demonstrate that we can place in context the overall dynamics but are not able to offer precise predictions based on the model. Uncertainty is inherent in the system, and such complexity (along with quantum probabilities) may apply to physical systems as well, further undermining the simplistic perception of physics that seems to captivate ecologists. Indeed, modern physics might be said to be maturing towards a more complex and contingent understanding of abiotic properties, forces, and entities as ecology is avidly pursuing an increasingly antiquated version of pre-20<sup>th</sup> century physics.

Some may argue that ecologists are aware of the contingency and non-reductive

nature of ecology when compared to physics, but the direct comparison of proposed ecological laws to physical laws implies that that understanding does not fully translate into the philosophy of ecologists. Accepting the complexity of ecology and the weakness of models such as Malthusian growth and the logistic (see Hall (1988) for a critique of this construct) is belied by the fact that the standard population dynamics and ecology texts all use these equations as first principles for laying the ground work of ecological theory (MacArthur & Connell, 1966; Ehrlich & Roughgarden, 1987; Edelman-Keshet, 1988; Murray, 1989; Gotelli, 1995; Hastings, 1996).

A practical distinction between the laws of physics and those proposed in ecology is the demonstrability of the physical laws. Ignoring the important philosophical considerations regarding the truth or validity of the laws, simply put, Newton’s laws are robust, testable and are of practical necessity for a range of processes that can best be described as operating on a human scale. The proposed laws of ecology have limited empirical support at this point, with limited tests and only a limited practical necessity. As such, the use of these laws to draw conclusions for human systems, such as sustainable development, conservation and agriculture is fraught with risk.

At this point, the proposed laws of population ecology are insufficient to be considered highly law-like due either to their lack of universality or their abstractions (or overwhelming *ceteris paribus* conditions) that take them too far from real ecological systems to provide any useful information. Rather than nominating previously stated models for lawhood, ecological theorists should be attempting to mathematically describe the general empirical patterns that have been identified. In one important comparison to physics, the catholic need for “mechanistic” models in ecology should be tempered by the fact that much of physical law is predictive but not mechanical. The law of gravity describes what happens and predicts what happens – but does nothing to elucidate the mechanics of what is happening.

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