Physics, Philosophy, and . . . Ecology

Serge Luryi

Imitation is the sincerest form of flattery, and physics has been profitably flattered by all walks of science. Those who fail to imitate us do so at their peril. No such peril is in the cards for Lev Ginzburg of Stony Brook University and Mark Colyvan of the University of Queensland in Australia, who together wrote a free-flowing essay on the theoretical foundations of ecology.[1] This is a delightful little book, 182 pages in small format (14×21 cm^2). I recommend it highly as a true pleasure to read.

The central question of theoretical ecology concerns the growth of populations. We may all have heard that populations grow exponentially, $N(t) = N_0 \exp(rt)$, where the rate of growth r is determined by environmental factors affecting the mortality and "power of the loins" in the population. This type of growth is called Malthusian after the English minister-turned-economist Thomas Robert Malthus (1766–1834). The adjective carries a somewhat pejorative connotation in lay circles, invoking Darwinian struggle and survival of the fittest. Ecologists, however, are people who refer to N as abundance and for whom an extinction of said abundance is a routine matter described by a negative r. Ecologists do not mind the word Malthusian in the least.

Every reader of PHYSICS TODAY can write a first-order differential equation that has Malthusian growth as a solution. The main point of Ginzburg and Colyvan's book is that this equation is *not* the fundamental equation for population growth. They advocate that the fundamental equation is a first-order equation for r, which can also be viewed as a second-order equation for the abundance. That new fundamental equation implies a revolution in theoretical ecology, not unlike the revolution in physics produced by our ancestors 300 years ago in their transition from the Aristotelian point of view, where things move only when acted upon by a force, to Newtonian science, where objects will move freely on their own but will accelerate under a force.

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Newton and ecology

Throughout their book, Ginzburg and Colyvan relentlessly pursue the Newtonian analogy. Malthusian growth is akin to uniform linear motion, $dr/dt = 0$. Interesting things happen when the right-hand side is nonvanishing but equals something you might call a "force." The driving force of ecology may itself depend on N, in which case one can get, for example, a periodic motion—that is, an oscillating abundance. The physical nature of such a force is a little murky but becomes clearer when a discrete version (in terms of generations) of the population equation is considered. We learn from the authors, probably with a certain dismay, that males are irrelevant to evolution; only mothers and daughters matter. Grudgingly letting this pass and reading further, we find that the "daughters' reproduction responds not only to the daughters' current conditions but also to the conditions their mothers experienced." That delayed response is the simplest example of what is called the maternal effect and it provides the basic mechanism of inertia.

Oscillations in population abundance have been observed among insects, small mammals, birds, and other groups. Although they are not describable by a first-order differential equation, they can be well described by two coupled first-order equations. Because of that coupling, all earlier attempts at understanding the oscillatory phenomena in population growth revolved around various predator–prey models. Ginzburg and his collaborators were the first to challenge that point of view by proposing maternal effects as the driving force of an inertial ecological pendulum. Their model has at least one notable success, which the book calls the case of "missing periods." The period of population oscillations is empirically at least six generations and the absence of shorter periods is hard to understand in a predator–prey model without ad hoc assumptions. In their maternal-effect single-species model, the missing periods follow naturally from the fact that $2\pi \approx 6$ (generations).

A field ripe for revolution

As described by Ginzburg and Colyvan, theoretical ecology is a field ripe for revolution, and Ginzburg, a mathematician-turned-ecologist, is an eager and capable revolutionary. Colyvan is a professor of philosophy, and the book contains a lot of that as well. The philosophy, however outrageous, should not scare away the prospective reader as it is presented in a very lighthearted way. The main point of the philosophical discourse is to examine what constitutes a law of nature and to stake a claim that ecology has the right to have laws. Despite the most welcome lightheartedness of the discussion, the reader, initially disposed to award this basic right without question, becomes almost prepared to withdraw the grant.

What saves the day for ecology is a series of exquisite empirical scaling laws, referred to as the "allometries." The most spectacular of these is the Kleiber allometry (after the Swiss American scientist Max Kleiber, 1893–1976) that the metabolic rates of different organisms scale with their body weight as $m^{3/4}$ and this scaling relationship persists over 16 orders of magnitude, from unicellular organisms to elephants! No, there is no misprint in the exponent, it is indeed 3/4 rather precisely and not 2/3 as one would expect if the metabolism were proportional to a smooth chemical contact area. I believe drums can be heard at this point, calling upon the physicist to come to the rescue—armed with fractals and higher spatial dimensions. (See the article by Geoffrey B. West and James H. Brown, PHYSICS TODAY, September 2004, page 36.)

You may well be tempted to develop your own revolutionary brand of ecology. Perhaps, after all, populations must be described by distributions that obey a Boltzmann-like kinetic equation!

Reference

1. L. Ginzburg, M. Colyvan, *Ecological Orbits: How Planets Move and Populations Grow*, Oxford U. Press, New York (2004). ■