

A Modest Proposal for Unifying Macroevolution and Ecosystem Ecology

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The first American Naturalist appeared in March 1867. In a countdown to the 150th anniversary, the editors have solicited short commentaries on articles from the past that deserve a second look.

Modern macroevolutionary thought is firmly rooted in the theories, models, and conventions of population biology. The most common mathematical models for describing long-term trait change, either along a phylogeny or paleontological time series, are formally the same as those that describe evolution within populations. And most of the hypotheses that we want to test with these and other models revolve around how species interactions—and competition, in particular—shape patterns of diversity across deep time; think adaptive radiations, coevolution, and diversity-dependent diversification. As such, macroevolution and phylogenetic biology have been rather seamlessly incorporated into community ecology (phylogenetic community ecology, or ecophylogenetics) and the emerging trait-based research program. There is a lot of exciting work happening now at the intersection of these fields; for example, there has been a recent burst of methods for more explicitly modeling character displacement in diversifying clades (e.g., Nuismer and Harmon, 2015, “Predicting Rates of Interspecific Interaction from Phylogenetic Trees,” *Ecology Letters* 18:17–27).

However, the interplay between macroevolution and ecology has been very limited in scope. Macroevolutionary biologists have tended to synonymize ecology with community ecology, leaving the phylogenetics revolution isolated from whole fields of ecology. Chief among these is ecosystem ecology. Recently, researchers have started thinking about how the flow of energy and nutrients through ecological systems is related to the underlying population dynamics (e.g., Michel Loreau, 2010, *From Populations to Ecosystems: Theoretical Foundations for a New Ecological Synthesis*, Princeton Uni-

versity Press, Princeton, NJ), but we have hardly even begun to consider how these system properties have evolved over long time periods.

Remarkably, the possibility of such a project was proposed nearly 40 years ago by Joe Felsenstein, one of the key players in the development of modern statistical macroevolution. In “Macroevolution in a Model Ecosystem,” published in *The American Naturalist* in 1978, Felsenstein invented a series of nested models to explore how ecosystem properties change as lineages evolve and diversify. In the first model, energy flows through a population of identical individuals; then two genotypes with different energetic efficiencies compete in this population according to a simple, two-allele population genetics model; then the distribution of energetic efficiencies across a large number of lineages evolves over time (this is what Felsenstein refers to as macroevolution); then the environment changes such that optimizing energy efficiency comes with a risk; then Felsenstein incorporates trophic structure, such that energy is not lost from the system but is consumed by higher levels; and finally, he adds a mechanistic form of predation (or something resembling it), so that populations at lower levels do not increase without bound. The end result is a toy version of an ecosystem, in which the dynamics of the system are not only changing but evolving due to natural selection. Most remarkable is that his model suggests the possibility that the total energy content of an ecosystem may be generally predicted by adaptive evolution of energetic efficiencies.

While undoubtedly creative, the article has been more or less ignored since its publication; it has been cited only four times as of February 2017 (Web of Knowledge), with three of those coming from outside of biology in journals like *Dialectical Anthropology*. (Felsenstein’s 1985 work “Phylogenies and the Comparative Method” is, in contrast, the second-most-cited paper in this journal’s 150-year history.) However, perhaps this is understandable; the work’s prescience is not at all obvious. Indeed, its central conceit is that this is a rather silly thing to be writing about—something better suited to (very) late-night conversations at the pub than journal clubs. The paper opens with a discourse on exobiology

("Suppose that we suddenly discovered that life existed somewhere else in the universe. . .") and ends with an extensive, numbered section titled "Limitations." We suspect that Felsenstein was slightly embarrassed about being seen as taking this too seriously. And in a way, it is a bit silly: the ecosystems described by the models are barely recognizable as ecosystems, the evolutionary dynamics are like a caricature of beanbag genetics, and the models seem to defy empirical tests.

However, the cartoonish simplicity of the model allows Felsenstein to offer his key insight, which is tacked onto the discussion almost as an afterthought—the evolution of energetic efficiency can be considered a gain of information. Felsenstein borrows from communication and systems theories to compute the information content per individual in his evolving ecosystem and suggests that one could calculate the total adaptive information content, though he concedes that this idea is "informal at best" (p. 189). This argument built on other attempts in ecology to integrate energy and information flow to understand constraints on how ecological systems grow and develop. In this context, information has a long history in ecological systems theory, most notably in the pioneering work of Ramon Margalef (e.g., 1958, "Information Theory in Ecology," *General Systems* 3:36–71). Robert MacArthur, in whose memory Felsenstein's paper was dedicated, also made use of information theory (1955, "Fluctuations of Animal Populations and a Measure of Community Stability," *Ecology* 36:533–536) before abandoning this approach and creating most of community ecology as we now know it. And Van Valen proposed something akin to a law of conservation of fitness (1976, "Energy and Evolution," *Evolutionary Theory* 1:179–229), whereby organisms in a community are participants in a zero-sum game: any information received by one population is taken from another. But Felsenstein pushed this idea further to integrate adaptive processes, showing that, in principle, the information content of an evolving system should be expected to be dynamic and potentially knowable. This idea was revolutionary at the time (it still is!) and anticipated some cutting-edge developments happening today.

Recently, Frank (2012, "Natural Selection. V. How to Read the Fundamental Equations of Evolutionary Change in Terms of Information Theory," *Journal of Evolutionary Biology* 25: 2377–2396) demonstrated that the fundamental equations of evolutionary change, normally expressed in statistical quan-

ties such as variances, can be rewritten in terms of change in information. (He seems to be unaware of Felsenstein's contribution to the topic.) From this, it is apparent that evolution by natural selection is literally a transfer of information from the environment to the genetic code of the organisms adapting to it. Completely independently, ecological systems theorists have revitalized the use of information as a measure of growth and stability of ecological systems characterized by diversity—the very subjects of interest of mainstream ecology and evolutionary thinking (e.g., R. E. Ulanowicz, S. J. Goerner, B. Lietaer, and R. Gomez, 2009, "Quantifying Sustainability: Resilience, Efficiency and the Return of Information Theory," *Ecological Complexity* 6: 27–36). Thus, energy flux through a system can be explicitly related to changes in allele frequencies in its constituent populations, suggesting that these two currently disparate fields could potentially be unified.

Such unification could open up the possibility of answering questions that we could never even ask before. A unified understanding of evolutionary change with the general properties of living systems as understood in terms of mass, energy, and information flows could help sharpen our focus on problems of both basic and applied importance. For example, a major topic in contemporary ecology is the relationship between biodiversity and productivity (i.e., ecosystem function)—How has this relationship changed as clades diversified over macroevolutionary time? And how have interactions between flow of energy and information in systems constrained macroevolution? Felsenstein stated that his contribution was to explore "laws governing rates of change in macroevolution" (p. 177), in contrast to a second type of general property of living systems, the universal constants or constraints, valid throughout the evolutionary process. These two types of general properties might be considered goals of science, and the integration of energy flow, information flow (adaptation and evolution), and the distribution of mass over time in ecosystems might achieve both. We should renew our efforts to identify these general properties.

In *The American Naturalist*

Felsenstein, J. 1978. Macroevolution in a model ecosystem. *American Naturalist* 112:177–195.

———. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.