RESEARCH: ECOLOGY

# Ecological Science and Statistical Paradigms: At the Threshold

Brian A. Maurer

Ecological science aspires to provide usable answers to difficult problems. In doing so, ecologists face severe technological and conceptual challenges in basic and applied arenas (1). As a result, some ecologists voice the concern that the field has entered a critical period where its governing paradigms are being continually questioned (2). These intellectual difficulties are compounded by serious shortages in funding and in social commitment to support the field and its findings. These pressures from within and without are beginning to reshape the nature of ecological research. As this transformation proceeds, it is useful to reflect on changes in the practice of ecology that will improve its positive impact on society. One of these is the evolution of statistical practices and philosophies to establish a rigorous and conceptually sound ecology for the next millennium.

**Before and after.** Long-term climatic changes favoring a different plant community obscured and modified the effects of the removal of rodents from these plots in the Chihuahuan desert. The photograph on the left was taken in 1977, shortly after experiments commenced. The photograph on the right, from nearly the same perspective, was taken in 1995. A decrease in grass cover and an increase in shrub density is apparent.

Ecosystems are among the most complex systems known to science. Interactions among parts are so diffuse in space and time that, with the exception of a few unusual cases, the boundaries of most ecosystems cannot be effectively delineated. This makes it extremely difficult to establish cause and effect relations among the observable components of an ecosystem. Descriptions of the dynamical behavior of an ecosystem often require the use of nonlinear functions, time lags, and other mathematical complexities (3), so that unambiguous quantitative predictions that can be subjected to standard statistical evaluation are impossible (4). Conventional statistics often require assumptions about the nature of the data that are not easily met in ecological research. Even when the statistics are robust to departures from assumptions (as some are), the larger problem of attempting to infer causality from the outcomes of formal tests remains unsolved. Inferences of causality ultimately assume knowledge of an underlying process model, but such models often are difficult to formulate and analyze.

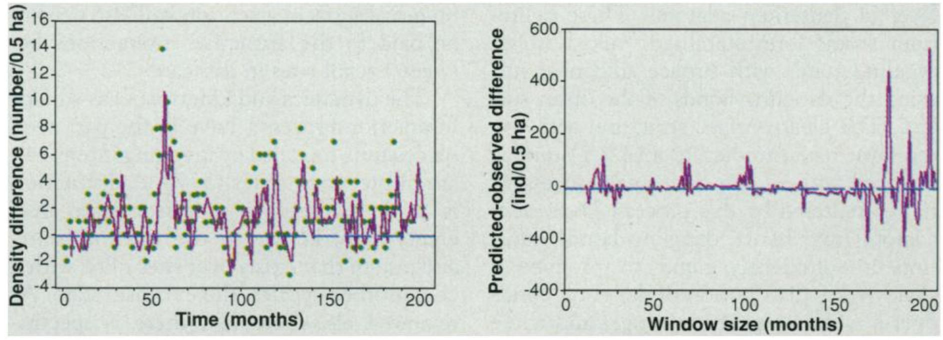
An example illustrates some of these problems. Most ecological theory assumes that ecosystems can be modeled by linear differential equations describing deviations of species population densities about their equilibria (5). A 17-year experiment in the Chihuahuan desert (see the photos above) produced clear evidence that two groups of rodents compete for limited seed resources (6). Monthly censuses from the two replicate control plots containing all competing species were used to estimate the parameters of the community matrix, the solution to the linear differential equations. This solution can be used to predict densities of species when their competitors are removed from the ecosystem (7). With parameter estimates from control plots, densities of smaller rodent species were predicted on experimental plots where their dominant competitors were removed. The results of this exercise were illuminating (see the graphs, next page). Although there were persistent differences between control and experimental plots, prediction errors made by the linearized model increased with time. The community matrix model failed in this ecosystem because of fundamental changes in the organization of the ecosystem as a result of recent climate change (8).

These difficulties are not insurmountable. Their solution, however, requires ecologists to adopt more sophisticated approaches and philosophies for data analysis. Linear thinking about ecosystems—assumptions that they are "balanced" or "stable," for example—is being replaced by the view that ecosystems are constantly changing and that those changes depend to a large extent on conditions experienced by an ecosystem before its measurement. But in accepting this newer perspective of how ecosystems behave, ecologists must differentiate between multiple alternative models that represent different hypotheses about mechanisms, yet are consistent with the same data. Thus, hypothesis tests cannot be conducted as simple probabilistic decisions between two clearly defined alternatives regarding a single parameter. Rather, they must be expressed and analyzed as decisions regarding the likelihood of one of several alternative, multiparameter models providing the best explanation for a particular data set (9).

Statistical analysis of complicated, multiparameter hypotheses will require two new skills of ecologists. First, theoreticians must develop more models that are empirically testable, with parameters for which rigorous empirical estimates can be obtained. Second, field ecologists must be conversant in the relevant theory and be prepared to design sophisticated experiments and observational studies that provide data to analyze the multiparameter models developed by theoreticians.

Both theoreticians and field ecologists must be cognizant of the appropriate statistical issues needed for model analysis. One of the organizing principles in statistics most relevant to the kind of model analysis needed is maximum likelihood (10). Most simple statistical tests are based on this principle, and ecologists would do well to learn their statistics from the likelihood perspec-

The author is in the Department of Zoology, Brigham Young University, Provo, UT 84602, USA. E-mail: brian_maurer@byu.edu




**Rodents compete for seeds.** (**Left**) Difference in densities of species of small rodents between plots with and without large rodents in a Chihuahuan desert ecosystem. **Actual data deviate from the model's prediction.** (**Right**) Comparison of effects of species removal actually observed and the differences predicted by a model that assumed densities could be modeled as small deviations away from average densities. Window size refers to the length of the time series used to estimate model parameters and predict densities. Average densities converge on equilibrium densities for long time series (*7*).

tive so that they will be prepared to expand upon the principle when faced with assessing the likelihood of competing complicated models.

Another critical advance needed in ecology is the adoption of a more sophisticated view of causality. Relevant processes that affect the data collected about an ecosystem often operate on different spatial and temporal scales (*11*). Accounting for the effects of such multiscale causality requires ecologists to simultaneously adopt both holistic and reductionistic perspectives on process-based explanations. In particular, many ecologically relevant process models can be described by macroscopic parameters determined by the statistical properties of many short-term, small-scale processes.

Consider the problem of predicting why the geographic range boundary for a species exists at a particular location. Relevant processes include the physiological functioning of individual organisms at the range boundary, the consequent reproductive rates of the populations that contain them, larger scale dispersal movements of individuals among populations, and geographic-scale trends in the environment. Each of these processes operates on different spatial and temporal scales. Parameters describing ecological processes at one scale are macroscopic parameters describing statistical outcomes of processes at smaller scales. For example, the birthrate of a single population is determined by the success of many individuals at obtaining and processing sufficient energy to exceed their metabolic requirements, and therefore having excess to expend on reproduction. A fruitful avenue for development of empirically relevant theory would be to frame models by using statistical mechanics designed for biological processes. Initial attempts to develop such a field have been overly simplistic, often relying on strict analogy to statistical mechanics developed from equilibrium thermodynamics.

The challenges faced by ecology have pushed the field into a new realm of endeavor, where both theoretical and empirical ecologists need to be trained in more sophisticated statistical techniques. Ecologists should be prepared to develop more complicated explanations for ecological phenomena by incorporating processes that operate at multiple scales. A lot of hard work and a little luck may ensure the emergence of an ecological science in the next millennium that will provide effective, scientifically sound tools for analyzing human impacts on the world's biological resources.

### References


1. J. Lubchenco *et al.*, *Ecology* **72**, 371 (1991).
2. D. B. Botkin, *Discordant Harmonies, a New Ecology for the Twenty-first Century* (Oxford Univ. Press, UK, 1990); R. H. Peters, *A Critique for Ecology* (Cambridge Univ. Press, UK, 1991).
3. G. Sugihara and R. M. May, *Trends Ecol. Evol.* **5**, 79 (1990); T. Mullin, *The Nature of Chaos* (Clarendon, Oxford, UK, 1993); A. Hastings *et al.*, *Annu. Rev. Ecol. Syst.* **24**, 1 (1993).
4. P. Yodzis, *Ecology* **69**, 508 (1988); R. E. Ulanowicz, *Ecology, the Ascendent Perspective* (Columbia Univ. Press, New York, 1997).
5. E. C. Pielou, *Mathematical Ecology* (Wiley, New York, 1977); J. Roughgarden, *Theory of Population Genetics and Evolutionary Ecology* (Macmillan, New York, 1979); P. Yodzis, *Introduction to Theoretical Ecology* (Harper and Row, New York, 1989); M. Bulmer, *Theoretical Evolutionary Ecology* (Sinauer, Sunderland, MA, 1994).
6. J. H. Brown and J. C. Mung er, *Ecology* **66**, 1545 (1985); J. H. Brown and E. J. Heske, *Science* **250**, 1705 (1990); T. J. Valone and J. H. Brown, *ibid.* **267**, 880 (1995).
7. B. A. Maurer, *Untangling Ecological Complexity* (Univ. of Chicago Press, Chicago, IL,1998).
8. J. H. Brown, T. J. Valone, C. G. Curtin, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 9729 (1997).
9. R. Hilborn and M. Mangel, *The Ecological Detective* (Princeton Univ. Press, Princeton, NJ, 1997); S. Lele *et al.*, *Ecology*, in press; Z. Zeng *et al.*, *ibid.*, in press.
10. A. W. F. Edwards, *Likelihood* (John Hopkins Univ. Press, Baltimore, MD, 1992).
11. R. E. Ricklefs, *Science* **235**, 167 (1987); S. L. Pimm, *The Balance of Nature?* (Univ. of Chicago Press, Chicago, IL, 1991); R. E. Ricklefs and D. Shluter, *Species Diversity in Ecological Communities* (Univ. of Chicago Press, Chicago, IL, 1993); M. A. Huston, *Biological Diversity* (Cambridge Univ. Press, Cambridge, MA, 1994); J. H. Brown, *Macroecology* (Univ. of Chicago Press, Chicago, IL, 1995); M. L. Rosenzweig, *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, UK, 1995).


**SURFACE CHEMISTRY**

# Direct Imaging of Adsorbates and Precursors on Surfaces


David A. King


There can be few fields of scientific endeavor that have advanced so dramatically and contributed so much to transforming humankind's modus operandi over the second half of this century as the science of solid surfaces. Surface scientists now have at hand, for example, the remarkable immediacy of direct, real-space images of atoms and molecules at surfaces, made possible by scanning tunneling microscopy (STM). For transformations to our lifestyle we need only think of the ramifications of the transistor and the microchip industry, a technology dependent on surface preparation and processing. The present issue of *Science* contains two demonstrations of the power of STM to reveal details of dynamic processes at surfaces. On page 545, McEllistrem *et al.* (*1*) display successive snapshots of dangling bonds (unsaturated valence states) diffusing about on a silicon {100} surface, and on page 542, Brown *et al.* (*2*) report their imaging of a precursor state to benzene chemisorption on Si{111} and describe the dynamics of the transfer between states—the first direct molecular observations of a so-called (*3*) intrinsic precursor state.


The author is in the Department of Chemistry, University of Cambridge, Cambridge CB2 1EW, UK. E-mail: eld1000@cus.cam.ac.uk