Ecology goes macro

Taking a bird's-eye view reveals the hidden order of ecosystems.

Pattern and Process in Macroecology
by Kevin J. Gaston & Tim M. Blackburn
Blackwell Science: 2000. 377 pp. £39.99, $79.95 (pbk)

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Creatures great and small: the jay (above), willow warbler (left) and green woodpecker occupy different woodland niches.

Ecological systems are paradigmatically complex. They are composed of spatially and temporally intricate interacting networks of different entities, such as species, whose functioning generates the conditions for their own existence.

Ecologists have traditionally tried to understand ecological systems by working with a limited subset of species in a well-defined area, usually a small one, and characterizing their interactions through observation or experiments, usually of short duration. This strategy has revealed myriad mechanisms of direct and indirect interactions between species, but fails to provide an understanding of the dynamics of the whole system.

Unsurprisingly, under this view, ecological systems are pictured as highly idiosyncratic, and explanations of their functioning become contingent on the organisms present, and the particularities of the environment, space and time. Such contingency makes any generalization of experimental results venturesome, at best. However, such a reductionistic or 'microscopic' view can be fruitfully complemented with 'macroscopic' approaches, which sacrifice the detail and contingency of the local scale in the hope of identifying general principles or statistical patterns in ecological systems. In a paper published in 1989, James Brown and Brian Maurer dubbed this approach 'macroecology', which is the subject of Kevin Gaston and Tim Blackburn's book.

The authors aim to show that the macroecological approach is interesting and informative and to "promulgate an understanding of why it is such an important part of the broader programme of research into ecology". They start with a description of what the macroscopic perspective entails and end with a chapter attempting a synthesis of patterns and processes.

The book is organized along four main axes of macroecological enquiry: species richness, range size, abundance and body size. The analysis of patterns, processes and explanation along these four axes is, for the most part, exhaustive and provocative. Although I do not agree with several of their explanations and find their synthesis still rudimentary, their analysis will surely spur much research in macroecology.

To make their analysis accessible to a broad spectrum of ecologists, the authors chose the birds of Britain (an area of 230,000 km^2) as an exemplary large-scale assemblage with which to explore macroecological patterns and process. They aim to illustrate how processes and patterns at this scale provide insights that can be essential for understanding the structure and dynamics of small-scale local assemblages, as exemplified by the birds found at Eastern Wood (0.16 km^2) in the county of Surrey. This is probably the first comprehensive macroecological analysis of a local assemblage.

The choice of birds is not surprising, given the British enthusiasm for them and the enormous amount of data collected about them (the first complete census of Eastern Wood birds was made in 1949 and records run almost uninterrupted until 1979). What is so special about Eastern Wood, besides having well-watched birds? The answer is simple — nothing. That is precisely the point the authors want to make: The macroecological approach is applicable to any ecological system.

Gaston and Blackburn place much emphasis on showing that ecological systems are continuous across scales — that patterns and dynamics at local scales are not independent of processes operating at larger scales.

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However, in making apparent the benefits of this approach, they also highlight its limitations. The first of these is that most of the macroecological patterns discussed in the book are of species richness, abundance, range size or body-size distributions at different spatial scales. This emphasis on spatial embedding relegates

to a secondary position the equally important role of processes occurring across time. These are manifest in historical contingencies that are known to affect macroecological patterns such as body-size distributions (the 'temporal embedding problem'). Second, because macroecology is mostly concerned with, although not limited to, the search for statistical regularities, the analysis of patterns is usually restricted to particular taxa for which large amounts of data are available. To what extent does knowledge generated for a particular taxon extrapolate to communities or assemblages of diverse organisms living in the same habitat?

Although it is wise to start the study of complex ecological systems in a simple way, I think macroecology should go beyond this taxon-based approach to the study of the ecological systems in which particular taxa are embedded. Resolution of this 'biotic embedding problem' requires more emphasis on the empirical analysis of macroecological patterns across taxa within communities and less on compilation studies for particular taxa.

Throughout the book, the authors correctly point out that macroecology rests heavily on the use of the comparative methodology — the description of patterns and the development and testing of hypotheses using information on the distribution and covariation of traits (such as abundance and body size) across species. In this kind of analysis, species are not independent realizations but are linked to each other by shared ancestry, which raises the statistical problem of non-independence of data. The authors acknowledge this, cautioning on the need to remove the potentially confounding effect of shared ancestry by using phylogenetically independent comparisons, which supposedly remove the phylogenetic component from the pattern.

This is a contentious issue, however, as the phylogenetic history of taxa is not independent of their ecology. To some extent, what we call history is the history of the ecological interactions between species and their environments, and that is reflected in extinction and diversification patterns through time. When phylogenetic signals are removed from the data, their ecological correlates are also removed. Further, even if we could assume that ecology and phylogeny are independent, too much emphasis is placed on removing potential phylogenetic effects on patterns and too little on actually quantifying how much variance in the pattern is explained by phylogeny and why it is stronger in some groups or for some traits than others.

Macroecology is in essence a discipline of synthesis, whose main aim is the search for general principles or natural laws underlying the seemingly endless variability of life in its many forms of organization. After reading Gaston and Blackburn's book, however, it is clear there is still a long way to go. Macroecology is becoming stuck in contingent explanations for many of the large-scale patterns it addresses. However manageable this contingency could be, more effort should be directed to get beyond it.

The structure and function of present-day ecological systems can be regarded as the results of the unfolding process that started with the biotic Big Bang that was the emergence of life on Earth. The task of the ecologist is to disclose the hidden order and the rules that govern this process of unfolding. Gaston and Blackburn's book is an important step along this path — an authoritative characterization of the status of this research programme in ecology, a thorough pattern-by-pattern analysis and a provocative statement on what macroecology is and what we should expect from it. ■

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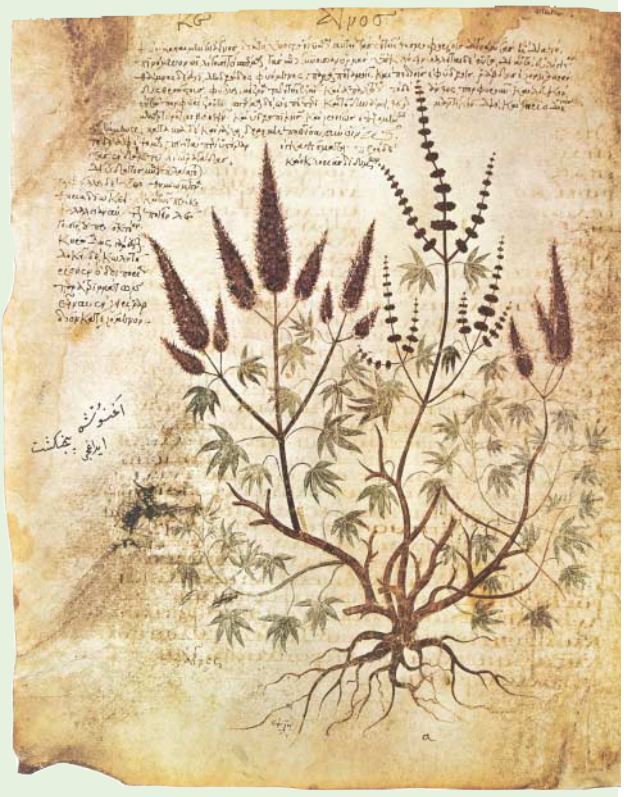
The art of botany



A page from the sixth-century Byzantine *Codex Aniciae Julianae*, the oldest illuminated copy of the writings of Dioscorides, ancient botanist and pharmacognosist.

This is one of around 500 botanical illustrations, covering 15 centuries, in the trilingual book *Ein Garten Eden*, which accompanies an exhibition of some of the Austrian National Library's extensive collection.

The exhibition runs until 31 October 2001 at the Austrian National Library in Vienna.

***Garden Eden: Masterpieces of Botanical Book Illustration* by H. Walter Lack (available in English, German and French; Austrian National Library, US$39.99, £19.99, DM49.95, FF262.50).**

What you see …

Visual Disturbances following Gunshot Wounds of the Cortical Visual Area

by Tatsuji Inouye (translated by M. Glickstein & M. Fahle)
Oxford University Press: 2000 (German original published by Wilhelm Engelmann: 1909). 101 pp. $25

Daniel L. Adams and Jonathan C. Horton

The cerebral cortex is divided into dozens of areas, each devoted to processing some element in the human repertoire, such as vision, hearing, touch or movement. A basic principle of neuroscience is that many areas contain an orderly, topographical representation of the function that they serve.

The first such map was made for the visual cortex by a brilliant young Japanese ophthalmologist, Tatsuji Inouye. On 8 February 1904, shortly after his graduation from Tokyo University, the Russo-Japanese war erupted. Inouye's duty was to assess visual loss in Japanese soldiers following brain injury so that their pensions could be adjusted suitably. Dissatisfied with this mundane task, Inouye set out to discover exactly how the visual world is represented in the brain. The resulting monograph was published in German in 1909. Unfortunately, only a handful of copies were printed, and Inouye left science soon afterwards to pursue medicine. His seminal contribution was lost, until Glickstein and Fahle provided this translation of a photocopy of the original, which they had discovered in the