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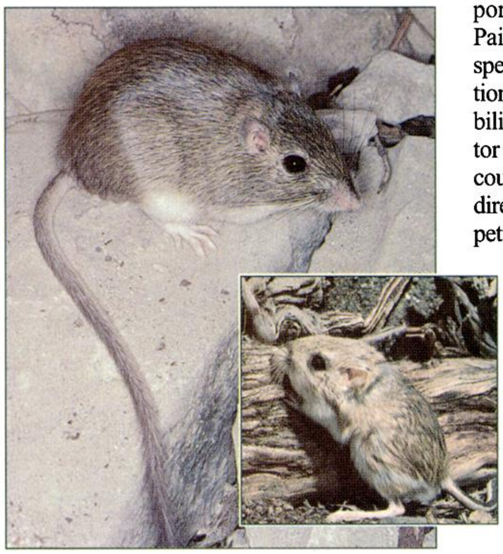
PERSPECTIVES: ECOLOGY

Keystone Species—Hunting the Snark?

William Bond

Ecologists widely acknowledge that physical and chemical resources, such as soil and climate, set the potential limits to the characteristics of an ecosystem, but whether they also set the actual limits is the subject of vigorous debate (*1*). Do plant and animal species, as they interact with one another, shift the ecosystem far from the conditions that one would predict from the resources available? We know that invasive species, introduced accidentally or intentionally, often have major, and sometimes entirely unexpected, repercussions on the invaded environment (*2*). Less is known about whether native species have similarly powerful impacts on their ecosystems. One of the difficulties with assessing the impact of native or invading species is that ecosystems often respond slowly to the addition or removal of species. This slow response is epitomized by the marathon 23-year study of a desert ecosystem reported by Ernest and Brown on page 101 of this issue (*3*).

In 1977, Brown and his colleagues set up experiments in the Chihuahuan desert of southeastern Arizona in the United States that were designed to exclude a guild of seed-eating rodent, the kangaroo rat (*Dipodomys*), from a desert ecosystem. By cutting calibrated holes in the fencing around their study plots, the investigators were able to selectively exclude kangaroo rats, the largest of the seed-eating desert rodents, but not smaller rodent species. Fast forward 10 years, and, as one might predict, smaller seed-eating rodents and seed-eating ants that normally would have had to compete with kangaroo rats for seeds were more abundant in the study plots than in the control plots. The plant community in the study plots had also changed because seed predators were now selecting different seeds. The repercussions extended to birds whose numbers declined because of changes in plant cover and even to a fungal pathogen, which increased because of the denser population of its host plant (*4*).



Pocket monsters. The kangaroo rat (*Dipodomys*) **(inset)** and the pocket mouse (*Chaetodipus baileyi*).

CREDIT: KANGAROO RAT, TOM MCHUGH/PHOTO RESEARCHERS, INC; POCKET MOUSE, JOHN & GLORIA TVETEN/KAC PRODUCTIONS

The experiments continued long after the initial results were reported, and now, in their new work, Ernest and Brown provide an update 20 years on. They report that in 1996 there was a sudden change in the ecosystem of the fenced study plots with the arrival of the seed-eating pocket mouse (*Chaetodipus baileyi*). This species, just small enough to get through the holes in the fencing, quickly colonized the study plots and is now consuming nearly as many seeds as the kangaroo rats once did. So will the ecosystem revert to its original condition now that the pocket mouse can apparently compensate for the loss of the kangaroo rats, or will the compensation be only partial because of the unique properties of the new colonizer?

The Ernest and Brown study indicates that single species, or small guilds of species, can have marked influences on ecosystem properties through a complex chain of direct and indirect effects. Species with a large biomass (mass per unit area) or productivity (rate of biomass production) might be expected to have impressive impacts on large ecosystems. What many ecologists find intriguing is that some species, such as the kangaroo rat, seem to have effects on ecosystems out of all proportion to their relative abundance. Robert Paine first labeled such species "keystone" species (*5*). Challenging the then-current notion that diversity in an ecosystem brings stability, he pointed out that a single rare predator species feeding on a dominant herbivore could effectively control the ecosystem by indirectly opening up living space for less competitive herbivores.

The keystone concept has great popular appeal. Stories of complex chains of events triggered by small beginnings hold wide fascination. Because other kinds of interactions could also have impacts on many species, the keystone concept has expanded to encompass species as diverse as pathogens and pollinators. Keystone species are so influential that one might predict that they would be a major focus of conservation policies. Protected areas without a keystone species, for example, would be subject to cascading losses of species as the effects worked their way through the system. For legislation and policy to take special account of keystone status, we would need to know which species are keystones, how common they are, in which ecosystems they occur, and the magnitude and nature of their effects on ecosystems (*6*, *7*). But is the keystone concept of practical use for flagging species for legal or policy purposes? Critics have given an emphatic "no" and argued for abandoning the seductive metaphor altogether (*7*, *8*).

A principal problem is that evidence for the existence of most purported keystones is anecdotal. Experimental work of the kind conducted by Ernest, Brown, and their colleagues is the exception. Another difficulty relates to the idea that a keystone species is much more important than others relative to its proportional abundance. That begs the question of how important any species is in an ecosystem. In theory, we could experimentally delete species one by one, measure the ecosystem impacts, and generate a frequency distribution of im-

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The author is in the Botany Department, University of Cape Town, Private Bag, Rondebosch, South Africa. E-mail: bond@botzoo.uct.ac.za

portance relative, say, to proportional abundance. Despite the formidable practical obstacles, some ecologists have tried to do just that, but have only deleted a fraction of species in the food web. These experiments in turn have revealed the difficulty in indexing the importance of species and in measuring their impacts on an ecosystem (*9*). The problem is implicit in Ernest and Brown's paper. Although *Chaetodipus* is already consuming almost as many seeds as the kangaroo rats once did, it may not match the kangaroo rat guild regarding other impacts on the desert ecosystem. Such impacts are loosely defined and could mean anything from changes in species richness to changes in nutrient fluxes, depending on the interests of the observer. There is no consensus on what to measure as an indicator of the importance of a species to an ecosystem, nor does such a consensus seem likely.

Another tricky problem is that the importance of a species might change in different places or at different times (*6*). Practical considerations limit the size of ecological experiments and therefore their domain of relevance. For example, studies of intertidal keystone predators are based on just a few meters of shoreline. But the intertidal ecosystem is highly variable, and a species that is a keystone predator in one area may not be in a neighboring area where, say, sandy overwash rather than predation controls species composition. So, a species that may be highly valuable in one place and at one time may or may not be important in another place or at another time.

The most successful exploration of how plants and animals control ecosystems comes from manipulating shallow lakes. Lakes are very convenient for large-scale ecosystem experiments, in part because their boundaries are clearly defined. Lake ecosystems also respond rapidly to manipulation. In a classic study of trophic cascades in a lake, changes in species and ecosystem characteristics triggered by manipulating piscivorous fish occurred in just 7 years (*10*). Contrast that with the long response time of Ernest and Brown's desert ecosystem. The result is that lake ecologists no longer argue about the relative importance of abiotic and biotic elements as regulators of ecosystem properties. Both are clearly important. The understanding gained by experimental manipulations, coupled with theoretical and technological advances, means that ecologists are able to make informed predictions and interventions to improve water and ecosystem quality. They have reached the stage where knowledge of the system, and the parts played by its component species, can be put into practice.

For the rest of the world, especially its terrestrial parts, our understanding is still rudimentary. We know from case studies that some rare species have very large effects on some ecosystem properties. We are a long way from identifying these species, or their potential impacts, with any confidence. The same is true, however, for the widely recognized problem of invading species (*2*). They too are idiosyncratic with respect to which ecosystems they invade, where, and with what effects. They can have enormous impacts on ecosystem properties. But predicting which species may become invasive, which ecosystems are liable to be invaded, and at what cost is still an important problem. Yet despite intensive study, the best general predictor of whether a species will become invasive, and to what effect, remains its history of invasiveness elsewhere (*2*). For native species in native ecosystems, well-documented case studies, such as the kangaroo rat in its desert ecosystem, could fulfill a similar role in warning of the potentially large consequences of losing influential rare species.

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PERSPECTIVES: MOLECULAR BIOLOGY

The Histone Modification Circus

Shelley L. Berger

There's an old circus routine that begins with a little car driven into the arena. One clown climbs out, then another emerges and another and another until the audience laughs and wonders how many more can possibly appear. The sequential discoveries of a series of distinct covalent modifications of histone proteins bring this absurd circus skit to mind. Several recent reports are beginning to bring order to the apparent chaos of the many histone modifications that are required for the regulation of gene expression. One of these reports, by Nakayama *et al.* (*1*) on page 110 of this issue, examines how histone modifications regulate the silencing of genes. The authors propose a chronological order for a dual histone modification step and elucidate how each modification contributes to gene silencing.

Histone proteins associate with DNA to form nucleosomes, permitting copious amounts of DNA to be neatly packaged into the nucleus. Histones are also direct regulators of gene expression because they can alter the accessibility of gene sequences in the DNA to components of the transcription and replication machinery that must bind to DNA to carry out their work. Addition of acetyl groups (acetylation) to amino acids in the amino terminus of histones provides a valuable model for understanding other histone modifications. The acetylation model is useful because acetylation strongly correlates with gene activation, and because many of the acetyltransferase enzymes that acetylate histones are coactivators of transcription, recruited to promoters by DNA-bound activators. From these observations a model emerges that elaborates the importance of acetylation in promoter-specific alterations of repressed chromatin. This model is substantiated by the finding that certain histone deacetylases—enzymes that remove acetyl groups from histones—are transcriptional corepressors that are recruited to chromatin by DNA-bound repressor proteins.

But why are there so many distinct types of histone modifications, and what is the precise mechanism through which they alter gene transcription? Indeed, the list of well-characterized modifications continues to grow, with the recent addition of phosphorylation (*2*, *3*) and ubiquitination (*4*, *5*). With the Nakayama *et al.* paper, another histone modification—methylation (the addition of methyl groups to histones)—now takes center stage (*1*, *6*, *7*). These investigators (*1*) describe the relation between histone methylation and deacetylation during gene silencing in the fission yeast. Their study builds upon the recent identification of the histone methyltransferases (enzymes that add methyl groups to histone amino acids) SuV39h1 in mammals, and its homolog Clr4 in yeast (*8*). Classical genetics had revealed that the genes encoding these enzymes and their relatives in the fly are required for maintaining certain chromosomal regions such as the centromeres in an inert (heterochromatic) state.

Nakayama *et al.* developed a specific antibody that detects methylation of amino acid lysine 9 (Lys-9) in histone H3, which is a substrate of the Clr4 methyltransferase in fission yeast. They used this antibody in chromatin immunoprecipitation assays to monitor specif-

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The author is in the Molecular Genetics Program, The Wistar Institute, Philadelphia, PA 19104, USA. E-mail: berger@wistar.upenn.edu