Diversity

A Conversation on Refining the Concept of Keystone Species

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Since its introduction in 1969, the concept of keystone species has become well-established but increasingly ill-defined. The concept's potential significance to conservation biologists is that it designates species that exert influences on the associated assemblage, often including numerous indirect effects, out of proportion to the keystone's abundance or biomass. As such, keystone species should be of special concern to environmental managers and policy makers. In December 1994, Hal Mooney and Jane Lubchenco convened a workshop as part of the United Nations' Global Biodiversity Assessment. Nine participants contributed to the discussion in an effort to catch the sense of the deliberations, to identify vexing issues, and to pose embarrassing questions and legitimate challenges. Each participant played multiple roles in the dialogue reported below. The "keystone cops" included W. Bond, J. C. Castilla, G. Daily, J. Estes, B. Menge, S. Mills, R. Paine, M. Power, and D. Tilman.

Dr. Knowitall: The concept of keystone species has become fashionable in ecology and conservation biology. Care to explain it?

Empiricist: Paine (1969) described it narrowly for a marine rocky shore in which a starfish, through selective predation on a competitively superior prey, maintained resources for a host of other species.

Skeptic: But hasn't that meaning been distorted by others to the point where it has become useless (Mills et al. 1993)?

Empiricist: Possibly, but consider the value of established, if imprecise, terminology for communicating general concepts. The original metaphor was intended to convey a sense of nature's dynamic fragility and the unsuspected consequences of removing (or adding) species. As George Orwell noted, some pigs are more equal than others, and the same applies to all species. Besides, we now know enough to make the concept more inclusive and precise.

Dr. Knowitall: Okay. What was the original science underlying the concept?

Empiricist: Actually, the idea is of some antiquity. Darwin's comparison of grass species richness in a mowed and unmowed plot might be its first appearance. Tansley (1949) recognized that the existing floral landscape in Britain owed much to the elimination of grazing or browsing mammals by neolithic peoples. One shouldn't forget Brooks and Dodson's (1965) classic description of how a fish organizes both the zoo- and phytoplankton assemblages in a small lake. After Paine, there was a flurry of studies. Perhaps the best-demonstrated cases are those on sea otters in the northeast Pacific (Estes & Palmisano 1974; Estes & Duggins 1995), on fish (Power et al. 1985) in prairie streams, and the trophic cascades in lakes (Carpenter & Kitchell 1993). And even though interactions are slower and the signals more subtle, we now have McLaren and Peterson's (1994) study of wolf effects in Michigan and the sweeping influences of foxes in the Aleutians (Bailey 1993). Of course, we cannot ignore human impacts: Human exclusion experiments along the central Chilean shore (Duran & Castilla 1989) have revealed effects at the multi-trophic level of harvesting, and very complex recovery dynamics.

Skeptic: That's a pretty esoteric list: some charismatic megafauna, a few fish, and even humans. I see little of

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cosmic value here, especially given the top-down bias toward community organization.

Dr. Knowitall: I agree. It is a rather monolithic view of nature. Anyone care to suggest a more general definition that includes other kinds of interactions, other habitats?

Empiricist: Let me try a quick fix, but one I'm nervous about. Expand the definition of keystone species to include diseases such as rinderpest (Sinclair & Norton-Griffiths 1982), chosen biological control agents—for instance, the insect enemies of Klamath weed (Huffaker & Kennett 1959), the subtle mutualists critical in some plant pollination systems (Bond 1994), and perhaps even the nitrogen fixers whose presence governs a whole flora's dynamics (Vitousek 1990).

Skeptic: Isn't this like sweeping intellectual dirt under some ecological rug? An answer serving all masters probably provides few useful solutions. Couldn't one argue that all species play some role, albeit generally unknown, at some time or place? Why single out those few that have been studied? Are dams on free-flowing rivers "keystones" because they disrupt the movement of fishes carrying temporarily parasitic clam larvae? Should one be tempted to call mules keystone species when their urine serves as an essential sodium source for butterflies? Surely the physical environment has some influence on species' well-being, distribution, and abundance.

Empiricist: Another quick fix. Why not identify as critical processes those physical forces such as fire and other kinds of disturbance that modify landscape pattern and reallocate biomass? There's strong rationale for the distinction between biological influences (keystone species) and physical influences (critical processes). The former are clearly susceptible to the losses in biodiversity caused by humanity's increasing domination of the organic world. Further, major legislation in the U.S. related to biodiversity issues takes a species-level approach.

Skeptic: Dramatic, but how realistic? How do you propose to cope with the biological variation so characteristic of differing temporal and spatial scales? Don't all your sweeping conclusions about a species' ecological importance depend on context?

Empiricist: It's my turn for the last word. Context dependence poses a challenge because interaction intensity will obviously vary in space and time and, with it, the importance to the community of individual species. Thus, we increasingly understand why juvenile steelhead trout are strong interactors under some but not all conditions (Power 1995), and it's equally clear that the role of the original keystone species, a starfish, varies substantially along gradients of productivity and wave exposure (Menge et al. 1994).

Dr. Knowitall: I guess it's important to know something about such species, especially when and where they interact strongly within their assemblages. How could one recognize them a priori?

Skeptic: Isn't that the fundamental question? You tell me that inspired natural history is probably an essential ingredient but that dictum is devoid of guidelines. We can't see microbes in nature. How can rote observation help identify a keystone species if the competitive dominant is essentially absent and the controlling agent correspondingly uncommon? You are not allowed to experiment on endangered species or national symbols, and some other species are experimentally intractable, as are certain environments. Given the environmental crisis, sexy yet empty concepts won't provide useful guidelines for either phenomenon recognition or essential management decisions.

Empiricist: You've made two basic errors. The first is a failure to acknowledge that natural assemblages are dynamically interconnected. One view of keystone species is that their importance stems from a dynamic influence exercised at any trophic level, often producing a cascade of effects, many of which are indirect. Obviously, the most robust (but also limited) way to probe community organization is experimentally. That's been done and is being done with increasing frequency as ecologists master new techniques and tricks. Your second mistake is to assume that our knowledge is insufficient to provide guidelines. In fact, surveys including both aquatic and terrestrial systems do produce useful generalizations. As in weather forecasting, ecological prediction is not without uncertainty, but the following hallmarks seem to apply. Keystone consumers tend to be of high trophic status or major modifiers of their environments. Large size alone can be misleading, however, because parasites and disease can be significant. Sometimes the controlled species is competitively superior to others in its guild. In other circumstances, keystones are strong interactors—for instance, critical pollinators in plant-mutualist systems. We don't fully understand the role of productivity, and we have almost no information about either the possible interplay between complexity and species diversity or the relative intensity of interaction between the component species. Have patience; we've made lots of progress on some of the critical topics.

Dr. Knowitall: Surely your hypotheses, tests, and analyses can be refined. Any suggestions for short-cut procedures or a role for theory?

Empiricist: Do I detect a softening of your viewpoint? There's no substitute for hard work, but there are ways to ease the problem. One can glean insight from the knowledge of native peoples or experienced naturalists. Periodic outbreaks, such as in the crown-of-thorns starfish (Birkeland & Lucas 1990), provide momentary probes of the assemblage's fundamental organization, as do disease epidemics. Comparisons before and after invasions, change associated with unintended elimination of certain species, and deliberate eradication of others all provide invaluable clues about relative influence. Applied ecology is a rich source of inspiration, especially when some undesirable species is reduced in importance or eliminated. Furthermore, adaptive management of commercially important species may provide insights. Theory is poised to make contributions by suggesting alternative predictions generated by models assuming different frequency distributions of interaction strengths. Theory could also guide the direct collection of further empirical information on such distributions. New models also aid in distinguishing how the sequence of species assembly, and the ecological character of those species, determines the eventual composition of the community. Within the foreseeable future it should be possible to discuss per capita rates as the interaction currency for species at higher trophic levels and biomass for those at lower levels. Keep the faith; we're making progress.

Dr. Knowitall: What are the caveats and rewards of the keystone species concept for conservation biologists and resource managers?

Empiricist: The attractiveness of the keystone concept is the focus on the entire assemblage and the recognition that one species can have a disproportionate effect on its many associates. It appeals to biologists because it synthesizes substantial natural historical information into relatively simple managerial protocols. For resource managers and conservationists, it may be successfully applied to issues ranging from ecosystem function to community restoration. And caveats? One, of course, is to use common sense. Single-species management blind to relationships of the larger, associated community is unlikely to preserve the suite of species and processes important in maintaining natural ecosystems. Equally inappropriate is haphazard management treating all species within guilds or trophic levels as equals. The concept of keystone species addresses these shortcomings by insisting on an interactive, multi-species perspective.

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