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Management and policy must explicitly consider the complexity of interactions in natural systems

L. Scott Mills, Michael E. Soulé, and Daniel F. Doak

Will the extinction of a single species in a community cause the loss of many others? Can we identify a set of species that are so important in determining the ecological functioning of a community that they warrant special conservation efforts? The answer to these questions hinges on the existence of a limited number of species whose loss would precipitate many further extinctions; these species have often been labeled keystone species.

The term *keystone species* has enjoyed an enduring popularity in the ecological literature since its introduction by Robert T. Paine in 1969: Paine (1969) was cited in more than 92 publications from 1970 to 1989; an earlier paper (Paine 1966), which introduced the phenomenon of keystone species in intertidal systems but did not use the term, was cited more than 850 times during the same period.

As used by Paine and other ecologists, there are two hallmarks of keystone species. First, their presence is crucial in maintaining the organization and diversity of their ecological communities. Second, it is implicit that these species are exceptional, relative to the rest of the community, in their importance.

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The term *keystone species* is poorly defined and broadly applied

Given the assumed importance of keystone species, it is not surprising that biologists have advocated that key or keystone species be special targets in the efforts to maximize biodiversity protection (e.g., Burkey 1989, Frankel and Soulé 1981, Soulé and Simberloff 1986, Terborgh 1986) and as species in need of priority protection (e.g., Cox et al. 1991). Management to protect keystone species has been suggested to resolve general policy and land-use dilemmas. For example, it has been proposed that management for individual keystone species should be a focus for the management of whole communities (Rohlf 1991, Woodruff 1989). Further, Carroll (1992) argues that managed keystone species could be used to support populations of other species in reserves that would otherwise be too small to contain viable populations. Conway (1989) suggested that, for restoration, keystone species are necessary to help reestablish and sustain ecosystem structure and stability.

Such policy recommendations imply that a clear operational definition exists for *keystone species*. In contrast, we argue that the term is broadly applied, poorly defined, and nonspecific in meaning. Furthermore, the type of community structure implied by the keystone-species concept is largely undemonstrated in nature, although it has fundamental implications for conservation and food-web theory. These ambiguities and uncertainties motivate this discussion of the implications of the keystone-species concept for ecology and conservation, as well as the dangers inherent in shaping conservation strategies around keystone species.

The varied meanings of the term *keystone species*

The term *keystone species* was originally applied to a predator in the rocky intertidal zone:

> [T]he species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the keystone of the community's structure, and the integrity of the community and its unaltered persistence through time...are determined by their activities and abundances (Paine 1969).

Subsequently, the term has been applied to many species at many trophic levels. For heuristic purposes, we have collapsed the usages of *keystone species* into five types (Table 1). This categorization is not meant to imply mutually exclusive groups or an exhaustive review of the term's application, but rather to show the diversity of keystone effects referred to in the literature.

Keystone predator. Paine (1966, 1969) noted that experimental removal of some rocky intertidal carnivores (such as the starfish *Pisaster*) led to nearly complete dominance of the substrate by one or two sessile species (mussels), resulting in greatly decreased species diversity. In this and other cases, the importance of the keystone predator derived from two requisites (Paine 1969, Pimm 1980): the predator preferentially ate and controlled the density of a primary consumer, and the consumer was capable of excluding (through competition or predation) other species from the community. Essentially, then, the early connotation was that keystone predators are important because they control the densities of important competitor or predator species.

Predators have also been labeled *keystone* when they control the densities of other types of ecologically significant prey species. For example, sea otters (*Enhydra lutris*) have often been referred to as keystone predators (e.g., Duggins 1980, Estes and Palmisano 1974) because they limit density of sea urchins (*Strongylocentrotus* spp.), which in turn eat kelp and other fleshy macroalgae that form the basis of a different community than is present in their absence (VanBlaricom and Estes 1988). Thus, otter removal has community-level influences, by releasing from predation a primary consumer that eats a plant that harbors other organisms.

Other authors have ignored the original requisites for the keystone-predator label and merely require that the species in question has a major effect on community composition. Risch and Carroll (1982) described fire ants (*Solenopsis geminata*) as keystone predators because their absence increases the number of individuals and species of arthropods potentially harmful to agriculture. The ants are generalist species preying on herbivores, which in turn are not highly competitive; hence, neither of the original requisites for keystone predators apply.

Table 1. Categories of presumed keystones and the effects of their effective removal from a system.

Keystone category	Effect of removal
Predator	Increase in one or several predators/consumers/competitors, which subsequently extirpates several prey/competitor species
Prey	Other species more sensitive to predation may become extinct; predator populations may crash
Plant	Extirpation of dependent animals, potentially including pollinators and seed dispersers
Link	Failure of reproduction and recruitment in certain plants, with potential subsequent losses
Modifier	Loss of structures/materials that affect habitat type and energy flow; disappearance of species dependent on particular successional habitats and resources

Keystone prey. In a theoretical analysis that assumed no competitive interactions between prey species, Holt (1977, 1984) demonstrated that a preferred-prey species that is able to maintain its abundance in the face of predation (via a high reproductive rate) can affect community structure by sustaining the density of a predator, thus reducing the density of other prey. Holt (1977) called such a predator-tolerant prey a *keystone species* "inasmuch as its properties control the density of the predator and restrict the range of parameters open to other prey." As an anecdotal example, Holt describes the contraction of habitat use of arctic hares after the introduction of snowshoe hares on Newfoundland, indicating that the snowshoe hare may have increased lynx populations, which then heavily preyed on the more vulnerable arctic hare. As the term *keystone prey species* was used by Holt, removing the keystone prey species would increase, not decrease, overall species diversity in the community.

However, Noy-Meir (1981) suggested that Holt's model involving a predation-tolerant keystone prey could be modified so that the removal of keystone prey would decrease species diversity. If the predator switches to the keystone prey when numbers of other prey species are low, then sensitive prey that otherwise would have been driven to extinction may coexist in the presence of the predator-tolerant keystone prey. Thus, we again see that the label *keystone* has been applied to species whose removal would either increase or decrease species diversity in their communities.

Keystone mutualists. Some species have been considered to be keystone because they are critical to mutualistic relationships. Gilbert (1980) introduced the term *mobile links* to describe "animals that are significant factors in the persistence of several plant species which, in turn, support otherwise separate food webs." The implication was that mobile links are a kind of keystone species, and mobile links have since been frequently cited as examples of keystone species. In addition to the mobile-link pollinators and seed dispersers described by Gilbert (1980), other examples of this type of keystone species include hummingbird pollinators and mammalian dispersers of mycorrhizal fungi (Wilcox and Murphy 1985).

Keystone hosts. If mobile links, or keystone mutualists, depend critically on ecologically important host plants, then it follows that these hosts also receive the label *keystone*. Included in this group are those plants that support generalist pollinators and those fruit dispersers that are considered critical mobile links (Gilbert 1980). Terborgh (1986) considered palm nuts, figs, and nectar to be keystone resources because they are critical to tropical forest nectar or fruit eaters, including primates, squirrels, rodents, and many birds. Together, these vertebrates account for as much as three-quarters of forest bird and mammal biomass.

Keystone modifiers. The activities of many species greatly affect habitat features without necessarily having direct trophic effects on other species. If the modified habitat affects the survival of many other species, the modifying species has been considered a keystone species. The North American beaver (*Castor canadensis*) was described as a keystone species because its dams alter hydrology, biogeochemistry, and productivity on a wide scale (Naiman et al. 1986). Likewise, the Brazilian termite (*Cornitermes cumulans*) has been called a keystone species because loss of its large, abundant, and uniquely structured mounds would likely precipitate loss of obligate and possibly opportunistic users of the mounds (Redford 1984).

Many species have been called keystone herbivores because their foraging causes drastic habitat modification. Based on the observation that large herbivores (more than 1000 kg) can readily convert closed thicket or forest into open grassy savanna, Owen-Smith (1987) posited a keystone-herbivore hypothesis to explain the late Pleistocene extinction of approximately half of the mammalian genera with body masses of 5–1000 kg. This theory posits that the elimination of large herbivores initiated vegetational changes that were deleterious to the fauna.

A keystone-herbivore hypothesis was also advanced to describe red-naped sapsuckers (*Sphyrapicus nuchalis*), which create sap wells in tree bark, thereby providing resources for other herbivores (Ehrlich and Daily 1988). Sea urchins have been called keystone because their grazing prevents the change from a system dominated by encrusting algae to a system dominated by large, fleshy algae (Fletcher 1987, see also VanBlaricom and Estes 1988). Similarly, pocket gophers (*Thomomys bottae*) were described as keystone because they maintain mountain meadow communities by slowing down aspen invasion of the meadows (Cantor and Whitham 1989). After the removal of what they called a "keystone guild" of kangaroo rats (*Dipodomys* spp.), Brown and Heske (1990) documented drastic changes in vegetation type and accompanying changes in the rodent community. Clearly, the distinction between keystone predation and keystone modification becomes fuzzy for those species that modify habitat through predation on plants.

Useful contributions of the keystone-species concept

We have seen that the label *keystone* has been applied to a plethora of species with very different effects—both qualitative and quantitative—on their communities. Given the diversity of the usages of the term *keystone species* in the ecological literature, what are the contributions and liabilities of this concept for ecological and conservation research?

One fundamentally important contribution is the attention these studies have drawn to differing interaction strengths in community food webs. Robert Macarthur (1972) first advocated close scrutiny of interaction strengths, defining a strong interactor simply as a species whose "removal would produce a dramatic effect." Studies of presumed keystone species have certainly demonstrated the presence of strong interactors in many systems.

To gain some quantitative feel for the extent to which the removal of presumed keystone species may decrease overall species diversity, we reviewed all published studies we could find that refer to a species as a keystone and that predict or describe specific community composition changes occurring on removal of the presumed keystone. Despite the fact that investigators encountered enormous methodological problems and employ different trophic and taxonomic criteria to circumscribe the relevant assemblage, an interesting consistency is revealed (Table 2). Ecologists identify as keystone those species whose removal is expected to result in the disappearance of at least half of the assemblage considered. For reasons we will detail below, however, we hasten to warn against the use of a 50% loss rule as an operational criterion for identifying a species as keystone.

Table 2. Predicted or observed effect of removing presumed keystones, based on articles in which authors called a species *keystone* and predicted a community composition change upon removal.

Author	Presumed keystone (community type)	Effect of removal
Paine (1966, 1969)	Starfish (rocky intertidal)	Observed reduction of system from 15 to 8 species
Fletcher (1980)	Sea urchins (subtidal)	Observed takeover of large fleshy algae, resulting in loss of approximately one-half of grazers
Terborgh (1986)	Palm nuts, figs, and nectar (tropics)	Predicted loss of one-half to three-quarters of total bird and mammal biomass
Owen-Smith (1987)	Herbivores more than 1000 kg (Pleistocene)	Hypothetical mechanism for loss of approximately half of mammalian genera during late Pleistocene

The second important contribution of the keystone paradigm is its implication that only a small minority of species have strong interactions that affect community composition. In other words, reference to a particular species as keystone implies that it is unusual, standing out from the majority of the other species in its effects on community structure or function. If we define the community importance of a given species as the percentage of other species lost from the community after its removal, we can illustrate this assumption by plotting, for a hypothetical community, the relative community importance of each species (Figure 1). The keystone concept assumes that frequencies of community-importance values are strongly skewed, with only a few species having large effects on the composition or structure of the community (Figure 1a).

In contrast to this assumption, food-web theorists have generally assumed either that species-by-species interaction strengths are drawn from symmetrical distributions (e.g., Figure 1b, normal distributions; Cohen and Newman 1988) or else are uniform (Figure 1c, an implicit assumption of static food webs; see Pimm and Kitching 1988). Although species-by-species interaction strengths are unlikely to directly correspond to community-importance values as defined here, there is likely to be considerable correlation between the two. In particular, it is difficult to imagine a species having a large effect on species diversity (community importance) without having strong interactions with other species. Thus, the keystone concept's implicit assumption about interaction strengths appears to be in conflict with the more explicit, but not necessarily more realistic, food-web models (Lawton 1992).

This apparent dichotomy between food-web theory and the keystone-species concept is certainly worth exploring. The two conceptualizations imply different patterns of community structure and hence require different conservation strategies. If many or most species are of similar importance (Figure 1b,c), any efforts to save

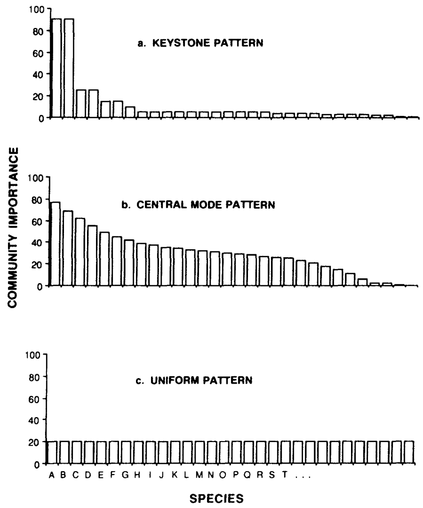

Figure 1. Expected distributions of community importance values (percent of species lost from a community upon removal of a given species) for a hypothetical community based on the keystone-species model (**a**) and based on food-web theory (**b** and **c**). Axes are arbitrarily scaled to demonstrate the general shape of the distributions.

only a few keystones will inevitably fail to protect the rest. Conversely, if only a few species have strong interactions/community effects, then detailed understanding and protection of the few important taxa would be critical to the well-being of the overall community.

What do the data say about this conflict? To date, only one study has addressed the distributions of interaction strengths in part or all of an ecological community. Paine (1992) developed an index of per capita interaction strength and found that only two of seven species of intertidal grazers strongly affect brown algae, which are their major food and also a profound modifier of the local environment. These results indicate "a few strong interactions embedded in a majority of negligible effects" (Paine 1992), supporting an assumption of highly skewed interaction strengths (Figure 1a). Although suggestive, it is premature to generalize this result: Paine looked at only one type of interaction for each species (herbivory of brown algal sporlings) and he looked at only a subset of the grazers within a single community. Indeed, his finding that 29% of the species were strong interactors could be interpreted as indicating that a large fraction of species have strong effects. Clearly, more studies of this type are needed in many more communities.

Keystones and conservation

What role should the keystone-species concept play in conservation efforts? Currently, implementation of the Endangered Species Act often amounts to emergency-room conservation (Scott et al. 1987), whereby the bulk of conservation resources are spent on single species that are on the brink of extinction. In the absence of comprehensive biodiversity legislation and/or increased funding and support for the Endangered Species Act, it has been suggested that "The Act could serve as an extremely useful tool for preserving keystone species, thus indirectly benefiting the many other life forms in some way dependent upon those species" (Rohlf 1991; see also Burkey 1989, Westman 1990).

We see both technical and philosophical liabilities associated with reliance on keystone species in a conservation context. (See Landres et al. 1988 for a parallel critique regarding labeling certain species "indicator species.") The overriding technical difficulty is one of definition. Before keystone species become the centerpiece for biodiversity protection or habitat restoration, we must be able to say what is and is not a keystone species.

Lacking any a priori definition, the best way to identify keystone species would be perturbation experiments whereby the candidate keystone species are removed and the responses of a predefined assemblage of species are monitored. Such tests would require adequate experimental replication and careful attention to defining the relevant assemblage (MacMahon et al. 1978 give a useful organism-centered definition of community), as well as consideration of time scales over which responses should be measured.

Bender et al. (1984) evaluated mathematical approaches for evaluating the consequences of the inevitable omission of certain species in perturbation experiments and the impact of lumping together the interactions of related groups of organisms (e.g., combining data for related ant species to measure the effect of removing a granivorous rodent). Extraordinary difficulties await researchers attempting such experiments (see Bender et al. 1984, Carpenter et al. 1985). The problem of objectively defining which species are keystone makes *it likely* that subjectively chosen subsets of species will be so labeled, whereas other species of similar importance will be ignored.

Even if keystone species *could* readily and reliably be identified for a given location at a given time, several philosophical dangers arise. First, the term is burdened with historical connotations that, as shown earlier, mean different things to different people. The lack of a clear operational definition hinders any political or legal implementation. Second, the term *keystone species* is misleading because it indicates the existence of a species-specific property of an organism, when in actuality the keystone role is particular to a defined environmental setting, the current species associations, and the responses of other species (Gautier-Hion and Michaloud 1989, Jackson and Kaufmann 1987, Levey 1988, Palumbi and Freed 1988). Thus, it is exceptionally difficult to confidently define a priori which local populations (not to mention species) are keystone (Elner and Vadas 1990, Foster and Schiel 1988). Another problem is that removal of combinations of nonkeystone species could have effects as large as removal of a keystone.

Finally, a conservation criterion that favors the maintenance of keystone species—and with them the majority of species in a community—may fail to protect other species of interest to conservationists or the public at large. For example, spotted owls, wolverines, grizzly bears, and California condors may have little role in the maintenance of species richness in their respective habitats, yet the protection of these charismatic species has been advanced because their fates are thought to indicate the integrity or health of their habitats, or because the viability of many such species requires large areas; these areas may ensure, in turn, sufficient habitat heterogeneity and space for large numbers of other species, some of which may have specialized requirements.

In sum, both the complexity of ecological interactions and ignorance of them militates aganst the application of the keystone-species concept for practical management recommendations. Despite its heuristic value, we see more harm then good in the formalization of the term in laws and policy guidelines that have rigid practical implications.

Conclusions

The lack of data addressing both the range of interaction strengths within communities and the generality of trends across communities leads us to suggest that neither the science of ecology nor the protection of biodiversity is advanced by continuing to label certain species as keystone. Instead, we advocate the study of interaction strengths and subsequent application of the results into management plans and policy decisions. Emphasizing strengths of interactions instead of a keystone/nonkeystone dualism is more than a semantic improvement; it recognizes the complexity, as well as the temporal and spatial variability, of interactions.

Although Paine's 1992 study is compelling in its demonstration of the existence of just a few strong interactors for the rocky intertidal zone, no data address whether other systems have similarly distributed interaction strengths. Paine's tantalizing results should inspire theoreticians to explore the implications of assemblages structured with many weakly interacting species and only a few strong interactors. At the same time, further empirical studies could assess, at the level of both short- and long-term effects (Carpenter and Kitchell 1988), the generality of skewed interaction strengths and trophic cascades (e.g., Carpenter et al. 1985, Paine 1980, Power 1990) or mesopredator release in the absence of a larger predator (Soulé et al. 1988).

If they abandon the keystone-species concept and the rigid structure it imposes on species interactions, investigators are less likely to assume that interactions or their strengths and distributions are constant in space and time. The concept has been useful in demonstrating that under certain conditions some species have particularly strong interactions, and we recognize that in recommending the abandonment of a popular and evocative concept there is a danger of making it more difficult for biologists to communicate with policy makers, managers, and the public. We think, however, that the inconvenience caused by the dropping of the label *keystone species* will, in the long run, be compensated by the development of management and policy guidelines that more explicitly accounts for the complexity of interactions in natural systems.

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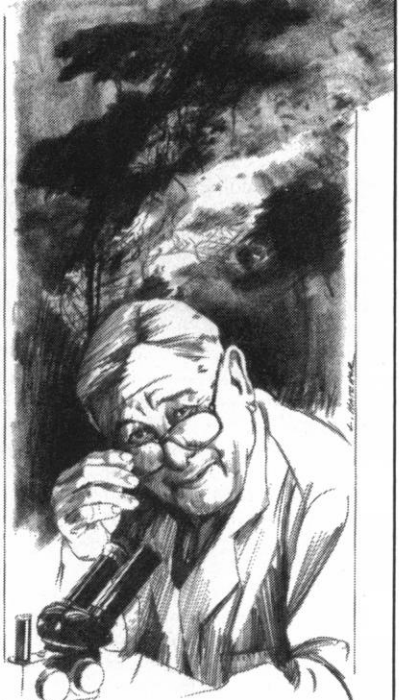

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