Challenges in the Quest for Keystones

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Identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems

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Many ecologists believe that all species were not created equal. For example, it is well known that the most abundant species play a major role in controlling the rates and directions of many community and ecosystem processes. These dominant species are often crucial for the mainte-

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> **A keystone species is one whose effect is large, and disproportionately large relative to its abundance**

nance of their communities, because they typically provide the major energy flow and the three-dimensional structure that supports and shelters other organisms (Ashton 1992, Dayton 1985, Duran and Castilla 1989, Gentry and Dodson 1987, Paine and Suchanek 1983, Strong 1977).

Many experiments, however, have demonstrated that some less abundant species, often called keystone species, also have strong effects on communities and ecosystems (e.g., Paine 1969). Keystone species differ from dominant species in that their effects are much larger than would be predicted from their abundance. Ambiguity in the use of the term *keystone* and the lack of an operational definition have led to criticism of its continued application in research and policy contexts (Mills et al. 1993, Simberloff 1991). In this article we clarify the keystone concept, discuss its relevance to management processes, and suggest additional research that needs to be performed.

Defining keystones

We offer a definition of *keystone* that has been expanded from the original usage of Paine (1969), in which keystone referred to a species that preferentially consumed and held in check another species that would otherwise dominate the system. To better reflect its current use, we define a keystone species as one whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance.

To develop a more operational definition for keystone species, one must define the strength of the effect of a species on a community or ecosystem trait. This measure, which we call community importance (CI), is the change in a community or ecosystem trait per unit change in the abundance of the species. (Our approach is a generalization of the concept of community importance in Mills et al. [1993].) In mathematical terms,

$$CI = [d(trait)/dp] [1/(trait)]$$

where p is the proportional abundance (in most cases, proportional biomass relative to the total biomass of all other species in the community) of the species whose abundance is modified. *Trait* refers to a quantitative trait of a community or ecosystem. Potential community or ecosystem traits include productivity, nutrient cycling, species richness, or the abundance of one or more functional groups of species or of dominant species. Experiments that evalu-
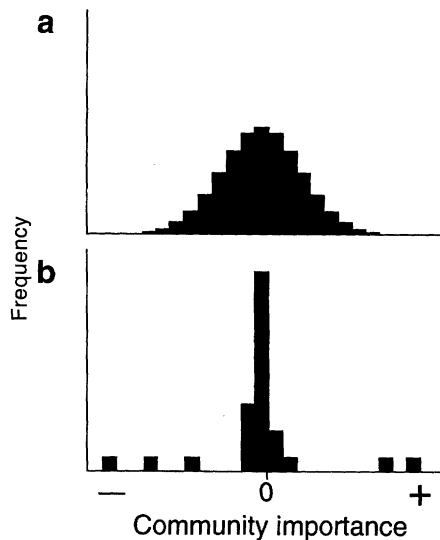
Figure 1. Possible frequency distributions of community importance values for all species in a given community. Positive values occur when a community characteristic decreases after a species is deleted; in the absence of a mutualist, for instance, the target dominant species would also decrease. Negative values occur when a community characteristic increases after removal of a species, as would be the case if the characteristic were the abundance of another species and the first species were a consumer of that species. Community importance (CI) values may be normally distributed around zero (a), in which case most species would have immeasurably small effects, and keystones would be rare. (b) In some communities, the CI distribution may have several modes, with keystone species falling into modes that are sufficiently far from zero.

ate the community importance of a species by changing its abundance should proceed long enough for indirect effects to become evident. The full derivative is used here, rather than a partial derivative, because it includes all the direct and indirect effects of the species.

In practice, it is difficult to measure the effects of small changes in species abundance. More commonly, an attempt is made to study a species' impacts by removing it entirely. If it can be removed, then

$$CI_i = [(t_N - t_D)/t_N] \, (1/p_i)$$

where t_N is a quantitative measure of the trait in the intact community or ecosystem, t_D is the trait when species i has been deleted, and p_i is the

proportional abundance of species i before it was deleted. If a species has an effect in direct proportion to its abundance, CI_i would be 1 (if, after the species deletion, the community or ecosystem characteristic decreased) or –1 (if the characteristic increased). If species i is a keystone, the absolute value of CI_i is much greater than 1.

Although the frequency distributions of community importance values for species in natural communities are unknown, several shapes seem plausible (Figure 1). In some communities, the distribution may be close to normal, with its mean near zero (Figure 1a). Three experimental studies of interaction strength have found, however, that although the majority of species in the guilds or assemblages studied had impacts close to zero, a few species exerted strong effects (Figure 2). Paine (1992) measured the impacts of seven invertebrate grazers on a rocky intertidal kelp sporeling assemblage; Fagan and Hurd (1994) studied impacts of a preying mantid on more than 12 orders or families of arthropod prey in an old field; and Rafaelli and Hall (1992) studied impacts of predatory birds, fish, and invertebrates on marine invertebrates in mudflats and mussel beds. Fagan and Hurd (1994) did not resolve prey to species, and Rafaelli and Hall (1992) could manipulate predators such as shorebirds only as groups of species. By contrast, Paine's (1992) was a pairwise study, but only because he measured the impacts of each consumer on a simplified reference state composed almost entirely of a single, competitively superior prey species. Nevertheless, these studies show the feasibility of using experimental field approaches to estimate interaction strength.

How are interaction strengths and community importance values of species related? Paine's interaction strength (Paine 1992) was computed as $[(t_N - t_D) / t_D] \, (1/n)$, where t_N is the abundance of the prey in the presence of the consumer, t_D is prey abundance in the absence of the consumer, and n is the number of consumer individuals stocked in experimental arenas. This measure differs from our index of community importance, $[(t_N - t_D) / t_N] \, (1/p_i)$, in
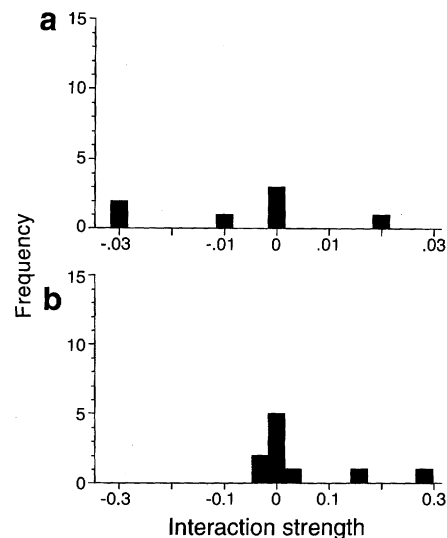
Figure 2. Field measurements of interaction strength from studies of (a) invertebrate grazer impacts on kelp sporelings (Paine 1992) and (b) mantid impacts on arthropod prey (Fagan and Hurd 1994). Interaction strengths (per individual) are calculated as $[(t_N - t_D)/t_D] \, (1/n)$, where t_N is the abundance of kelp sporelings in the presence of intertidal grazers (a), or the density of arthropods in the presence of praying mantids (b); t_D is prey abundance in the absence of these consumers, and n is consumer density in experimental arenas. Interaction strengths were measured eight months or 21 days after experiments were initiated in Paine's and in Fagan's and Hurd's studies, respectively.

three ways. First, we normalize species impacts by dividing by the trait (e.g., prey abundance) in the presence, rather than the absence, of the consumer (t_N versus t_D). Second, whereas Paine's measure is a per capita effect, we suggest normalizing the species' impact by its proportional biomass. Finally, the numerators of these terms may differ if community importance is measured in a largely intact natural community and interaction strength is measured as impact on a simplified reference state representing a key component of the community (e.g., Paine 1992). Interaction strength and community importance are strongly related, however, and should, under most circumstances, be positively correlated. Community importance is in theory more generalizable and realistic than interaction strength if the latter is measured in simplified "ref-

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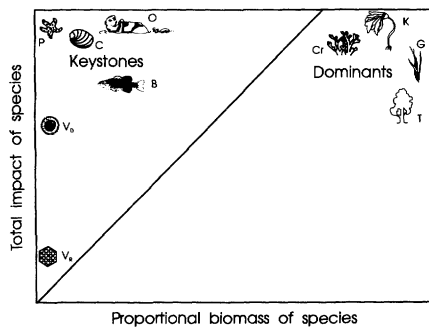
Figure 3. Total (collective) impact of a species (absolute value of community impact x proportional abundance of a species: $|CI_i| \times p_i$) versus its proportional abundance, p_i. Points representing a species whose total impact is proportional to its abundance would fall along the diagonal line X = Y. Keystone species have effects that exceed their proportional abundances by some large factor. They also have total effects that exceed some threshold. Therefore, although a rhinovirus that made wildebeests sneeze (V_R) might have a total effect that far exceeded that expected from its low biomass, it would not be a keystone species if the total effect fell below the threshold. On the other hand, a distemper virus (V_D) that killed lions or wild dogs might have a collective effect of sufficient magnitude for keystone species designation. *Pisaster* (P), sea otters (O), the predatory whelk *Concholepas* (C), and freshwater bass (B) have large, and disproportionately large, impacts on their communities. Trees (T), giant kelp (K), prairie grass (G), and reef-building corals (Cr), which dominate community biomass, would have total impacts that are large, but not disproportionate to their biomass. Positions of letters designating keystone and dominant species on this figure represent educated guesses. Quantitative values that should be prescribed for thresholds of absolute total collective impact (vertical position required for keystone status) and factors by which keystone effects should exceed a species' proportional abundance (distance above the line X = Y required for keystone status) may vary with the community trait (e.g., species richness, biomass of other species or guilds, primary productivity, nutrient or soil retention, albedo) under consideration.

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erence state" communities. Simplification, however, increases the ability of ecologists to measure interaction strength by reducing environmental noise.

If interaction strength and community importance are positively correlated, and if the distributions of interaction strengths documented in these studies prove widespread, community importance should also commonly be distributed as in Figure 1b. Clearly, the variance, skew, and number of modes of any such distributions are of great ecological importance. The greater the variance and skew, the more species have CI values with unusually high absolute values. Such species would be keystones, with a disproportionate effect on the composition and/or functioning of communities and ecosystems. Our intuition and limited experience suggest that only a small proportion of the species in most communities are likely to be keystones.

It is premature to prescribe numeric thresholds for applying the keystone designation, but with more data and development of the theory, one could choose quantitative criteria. Two conditions should be fulfilled. Keystone species would have absolute values of CI that were much greater than 1, and the absolute value of the total (collective) effect of the species on its ecosystem ($|(t_N - t_D)/t_N|$) would also have to be great enough to be detectable in typically noisy natural systems and to profoundly influence the structure and dynamics of these systems. Figure 3 depicts our view of the relationship of keystone and dominance status to the abundance of species and their total effects on their communities or ecosystems.

Case studies

Since the publication of Paine's (1966, 1969) papers establishing the importance of top-down influences by starfish in rocky intertidal communities and the broader notion of keystone species, there have been many published examples in a broad array of ecosystems, taxa, trophic levels, and ecological processes (Table 1). These case studies, which have recently been reviewed by Bond (1993), Mills et al. (1993), and Menge et al. (1994), make several important points. First, keystone species, as we have defined them, have been demonstrated or suggested to occur in all of the world's major ecosystems. Second, keystone species are not always of high trophic status. Third, keystone species can exert effects, not only through the commonly known mechanism of consumption, but also through such interactions and processes as competition, mutualism, dispersal, pollination, disease, and by modifying habitats and abiotic factors (as "keystone modifiers"; Bond 1993, Mills et al. 1993).

Both diversity and trophic-level considerations suggest that keystone species are most likely to occur near the top of the food chain. Top predators typically have high per capita effects and low collective biomass, relative to lower trophic levels. Nevertheless, keystones may occur at other trophic levels. For example, certain plant species may be keystone resources for pollinators or dispersers if they flower or fruit in times of scarcity (e.g., *Didymopanax*; Worthington 1982). Soil cyanobacteria and endolithic lichens may be keystone producers in the Negev Desert. They fix nitrogen and support snails, whose grazing breaks down rock and creates soil (Shachak and Steinberger 1980, Shachak et al. 1987). The community impacts of Negev cyanobacteria and lichens appear large relative to their small biomass.

Species whose primary impact on the community is not primarily trophic can also be keystones. Possible examples include keystone modifiers (Mills et al. 1993), also known as "ecosystem engineers" (Lawton and Jones 1995): beavers, which swamp forests and meadows (Jenkins and Busher 1979, Naiman et al. 1986, Pollock et al. 1995); gophers and leaf cutter ants, whose tunnels pipe water through hillslopes (Elmes 1991, Montgomery and Dietrich 1995); and badgers, whose mounds maintain diversity in prairie floras (Platt 1975). Although such species would not have been considered keystones in Paine's original formulation, they meet our criteria, because their impacts are obviously important and are typically disproportionate to their abundance.

Approaches

Keystone species can be detected through a variety, or better, a combi-

Table 1. Demonstrated or likely keystone species or guilds and their mechanisms of action.

Ecosystem	Citation(s)	Keystone species or guild	Target of direct effect	Mechanism of effect	Evidence
Marine					
Rocky intertidal	Paine 1966, 1974	*Pisaster ochraceus* (predatory starfish)	mussels	consumption	experimental, comparative
	Menge 1976	*Nucella lapillus* (predatory snail)	mussels	consumption	experimental
	Hockey and Branch 1984	*Haematopus* spp. (black oystercatchers)	limpets	consumption	comparative
	Castilla and Duran 1985, Duran and Castilla 1989	*Concholepas concholepas* (predatory snail)	mussels	consumption	experimental
Rocky subtidal	Estes and Palmisano 1974	*Enhydra lutris* (sea otter)	sea urchins	consumption	comparative
Pelagic	May et al. 1979	*Balaenoptera* spp. (baleen whales)	krill	consumption	historical reconstruction
	Springer 1992	*Theragra chalcogramma* (walleye pollock)	zooplankton, smaller fish	consumption	historical reconstruction
Coral reef	Hay 1984	herbivorous fish, sea urchins	seaweeds	consumption	experimental, comparative
	Carpenter 1988, 1990	*Diadema antillarum* (herbivorous sea urchin)	seaweeds	consumption	experimental, comparative
	Hughes et al. 1987	*D. antillarum* (herbivorous sea urchin)	marine plants	consumption	experimental, comparative
	Birkeland and Lucas 1990	*Acanthaster planci* (coral-eating starfish)	corals	consumption	comparative
	Hixon and Brostoff 1996	*Stegastes fasciolatus* (territorial algivorous damselfish)	schooling parrotfish and surgeonfish	protection of seaweeds within territories from heavy grazing	experimental
Soft sediment	Van Blaricom 1982	*Urolophos halleri, Myliobatis californica* (carnivorous rays)	amphipods	consumption, disturbance	experimental
	Oliver and Slattery 1985	*Eschrichtius robusta* (gray whales)	amphipod mats	consumption, disturbance	comparative
	Oliver et al. 1985	*E. lutris* (sea otters)	bivalves	consumption	comparative
	Kvitek et al. 1992	*E. lutris* (sea otters)	bivalves	consumption, disturbance	experimental, comparative
Freshwater					
Lakes and ponds	Brooks and Dodson 1965	*Alosa pseudoharengus* (planktivorous fish)	zooplankton	consumption	comparative historical reconstruction
	Zaret and Paine 1973	*Cichla ocellaris* (piscivorous fish)	prey fish	consumption	comparative
	Power and Gregoire 1978	harbor seals	salmonid fishes	consumption	comparative
	Carpenter et al. 1985, Mittelbach et al. 1996	*Micropterus salmoides* (piscivorous fish)	planktivorous fish	consumption	experimental, comparative
	Morin 1981, 1983	*Notophthalmus viridescens* (salamander)	anuran tadpoles	consumption	experimental
Rivers and streams	Power et al. 1985	*Micropterus salmoides* and *Micropterus punctatus* (piscivorous bass)	algivorous minnows	consumption	experimental, comparative
	Naiman et al. 1986	*Castor canadensis* (beaver)	trees	consumption, habitat modification	comparative
	Cooper 1988	*Oncorhynchus mykiss* (predatory trout)	benthic invertebrates, anuran larvae	consumption	experimental, comparative
	Power 1990	*O. mykiss, Hesperoleucas symmetricus* (predatory steelhead, omnivorous minnow)	invertebrates and fish fry	consumption	experimental
Terrestrial					
Grasslands	Tansley and Adamson 1925	*Oryctolagus cuniculus* (rabbit)	herbs and grasses	consumption	experimental, comparative
	Sinclair 1979	Rinderpest	ungulate grazers	disease epidemic	comparative
	Huntly and Inouye 1988	*Geomys bursarius* (pocket gophers)	underground plant tissue	consumption, burrowing	comparative, experimental
	Cantor and Whitham 1989	*Thomomys bottae* (pocket gopher)	aspen roots	consumption	experimental, comparative
Arctic marsh	Kerbes et al. 1990	*Chen caerulescens* (lesser snow goose)	grasses and sedges	consumption	experimental, comparative
Woodlands	Laws 1970	*Loxodonta africana* (elephants)	trees	consumption	comparative
		Anoplolepis custodiens (seed-dispersing ant)	seeds of proteaceous plants	seed dispersal	comparative
	Terborgh 1986	*Ficus* spp. (fig trees)	vertebrates	resource provision	comparative
	Cox et al. 1991	*Pteropus* spp. (flying foxes)	large-seeded fruits	seed dispersal	comparative
	McLaren and Peterson 1994	*Canis lupus* (wolves)	moose	consumption	comparative, historical reconstruction
Desert	Shachak et al. 1987	*Euchondrus* (snails)	lichens	consumption, rock weathering, soil formation	comparative, experimental
	Brown and Heske 1990	*Dipodymys* spp. (kangaroo rats)	seeds	consumption	experimental
Tundra, taiga, or alpine	Laine and Niemela 1980	predatory ants	birch trees	consumption	comparative, experimental
	Bryant 1981	*Lepus americanus* (snowshoe hares)	trees	consumption	experimental, comparative
	Huntly 1987	*Ochotona princeps* (pika)	subalpine vegetation	consumption	experimental

nation of approaches. These approaches include natural history observation, historical reconstruction, comparative studies, manipulative field experiments, and adaptive management (sensu Walters 1986) that extracts information from ecosystem changes that follow large human impacts. Each approach has distinct advantages and limitations.

The original work on the keystone concept was compelling in that

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it employed two strong approaches—the experimental and the comparative method (Paine 1966). Experimental removal of a species is the most convincing way of determining interaction strength, but it has logistic limitations. An exhaustive experimental analysis based on community manipulation would require $\sum_{r=1}^{n} n!/r!(n - r)!$ treatments in a community containing n different species (Wootton 1994), a prohibitive number in most cases. This problem can be partly overcome by combining experiments with modeling approaches such as path analysis (Schemske and Horvitz 1988, Sokal and Rohlf 1981, Wootton 1994). Path analysis, a sequence of multiple regressions and correlations structured by an a priori hypothesis (Wootton 1994), holds great promise because it requires manipulating only one or two strongly interacting species and then monitoring the responses of a potentially large number of other community members. An added benefit is that it quantifies both direct and indirect interaction strengths. A second logistic limitation of manipulative experiments is that they are typically more restricted in scope than are observational studies. It is usually not apparent how far results obtained from isolated field experiments can be generalized to other spatial, temporal, or biotic contexts. Finally, social, ethical, and technical factors may limit the extent to which some species and communities of interest can be manipulated.

Comparative studies (of habitats in which densities of species of interest vary) overcome many of the limitations of the experimental approach, but they inherently involve a loss of rigor, given that many factors (in addition to the one of interest) may differ among disparate sites and that larger study sites are increasingly difficult to replicate (Carpenter 1989). However, a combination of comparative and experimental approaches can be powerful (e.g., Menge et al. 1994, Paine 1966), with the comparative observations suggesting both the hypotheses to be tested experimentally, and, subsequently, the factors that may determine the generality of experimental results.

Much of the work on putative keystone species has, partly by necessity, been descriptive in character. The importance of natural history observations and intuition in identifying keystone species cannot be overstated. Inferences based solely on descriptions can, however, be misleading. For example, a predator-prey interaction may appear unimportant if the prey is rare in the predator's diet. This rarity could arise, however, if the prey is so vulnerable to the predator that it has already been depleted by the time the system is first observed. Such prey may rebound dramatically when predators are removed (Estes 1995, Huffaker and Kennett 1959, Paine 1966, Power 1990). Understanding and management of potential keystone species has also often followed a descriptive, narrative approach, based on a series of sequentially formulated and revised hunches about how the world works locally. This is a promising approach if combined with experimental (adaptive) management (Walters 1986).

An increasing number of large-scale "natural experiments" are occurring through massive human habitat alteration and associated biodiversity loss. Where such impacts are unavoided or have already occurred, ecologists should capitalize on them to assess the influence and prevalence of apparent keystone species (e.g., Sparks et al. 1990, Terborgh 1986). For example, much of what we know about keystone species has come from studying the results of overhunting or overfishing of sea otters (e.g., Estes et al. 1978), of baleen whales (May et al. 1979), and of walleye pollock (Springer 1992). Unfortunately, poor knowledge of the structure and dynamics of natural ecosystems before massive human impacts often limits our ability to understand changes. This situation has been aggravated by the tragic loss of knowledge of indigenous peoples of their own natural ecosystems as they are displaced by large-scale development schemes.

Challenges

Identifying keystone species is fraught with difficulty. It requires bridging temporal and spatial scales, levels of organization, and diverse taxonomic groups. Ideally, experimental demonstrations of keystone effects would come from manipulations of single species; in practice, these manipulations can be hard to achieve. For instance, exclosures may exclude more than one member of a guild or trophic level. If exclusion produces a dramatic change, it will not be obvious whether the unmanipulated condition is maintained by a single keystone species, or by a group of species with similar effects. In some cases, relative impacts of single species are unknown, yet groups of species are known to have impacts that are disproportionately large relative to their collective biomass (Brown and Heske 1990, Power 1990). Some combination of species-by-species manipulations and natural history detective work (e.g., documenting the dietary preferences, feeding rates, and performances over various environmental conditions of possible keystone consumers) is necessary to distinguish keystone species effects from strong collective impacts of guilds or trophic levels ("diffuse predation" in Menge et al. 1994). Although the clearest application of the keystone concept is to single species, detection of what provisionally may be called "keystone guilds" is often a useful step, both for advancing scientific understanding and for management.

Another challenge is to determine the time required to assess the impacts of changes in species' abundances. The effects of a particular species perturbation may require a long period of time to manifest themselves. The best known and most compelling examples of keystone species come from manipulative experiments (Carpenter et al. 1985, Paine 1974, Power et al. 1985) or from spatial or temporal contrasts of habitats in which the purported keystone species were present or absent (Estes and Palmisano 1974, Owen-Smith 1988). Indirect effects in aquatic communities often manifest themselves more rapidly than in terrestrial systems (Estes 1995), due in some cases to the more rapid turnover times of aquatic autotrophs. In some, perhaps most, terrestrial systems, total responses to keystones may require more time than is avail-

able for scientific observation. The full impact of top predator removal from tropical forest ecosystems takes decades to centuries to become apparent and considerably longer to ripple through different elements of the community (Dirzo and Miranda 1990, Terborgh 1986). Brown and Heske's (1990) demonstration of the critical role of heteromyid rodents as desert granivores (Table 2) took more than ten years of experimental maintenance before the strong effects appeared. Funding for the research had ended, and the now well-known findings were largely a result of the authors' interest and persistence.[1]

Calculating the interaction strength and related community importance of a particular species to evaluate its potential keystone status requires linking the action of individuals through their populations to community- and ecosystem-level effects. It also demands monitoring responses of potentially diverse groups, a task that challenges the breadth of most scientists' taxonomic experience. These challenges are among the greatest in ecology today; but overcoming them does not guarantee a general result, because the impact of a particular species is potentially context dependent.

Identifying keystone species a priori by their traits

Given the difficulties of identifying keystone species and the short time remaining if we are to apply this knowledge to their conservation, it would be useful if such species could be identified a priori (i.e., before experimental removal or extinction). Are there traits that make species likely to play a keystone role? Paine's *Pisaster* is a keystone predator because it preferentially consumes and suppresses mussels, which in the absence of this starfish can be dominant space holders. Estes' otters are active and mobile, and they feed voraciously on sea urchins, potentially destructive grazers (Estes et al. 1978). These traits—high consumption rates relative to prey production and differential impacts on potential dominant species—would seem likely to

characterize keystone consumers in other systems.

Traits that predicted keystone species were not, however, clearly evident in a survey of well-studied marine and freshwater keystone species (Menge et al. 1994). Preferential predation on dominant species appeared both in systems that had or lacked keystone predation (Menge et al. 1994). Eleven other possible traits of predators, prey, or habitats were surveyed, but none consistently distinguished systems with keystone interactions. In general, we are pessimistic about developing what Steve Carpenter has called "A Field Guide to the Strong Interactors,"[2] based on species traits alone. Field guides typically have range maps. For strong interactors, we would need range maps of the variation in their impacts, not only across geographic space but also across gradients of disturbance, productivity, physical factors, and abundances of other species. In short, we need to understand better how context affects species interaction strength if we are to predict the roles particular species may play in a particular context.

Context dependency

An increasing body of evidence suggests that keystone species are context dependent. That is, keystone species are not necessarily dominant controlling agents in all parts of their range or at all times, but instead play keystone roles only under certain conditions. Along the Oregon coast, the original keystone species *Pisaster ochraceus* occupies an unambiguous keystone role on wave-exposed rocky headlands (Menge et al. 1994), the "context" in which Paine (1966, 1974) originally demonstrated the keystone concept. In more wave-sheltered habitats, however, the impact of *Pisaster* predation was weak or nonexistent (Menge et al. 1994). In sheltered areas, prey input rates were low, and at one site, periodic, unpredictable sand burial, not starfish predation, was the overwhelming force eliminating mussels from the lower shore. Thus, in a rocky intertidal habitat, *Pisaster* occupied a keystone

role under one context but a nonkeystone role in other contexts, even though the specific locations were sometimes only tens of meters apart (Menge et al. 1994). Table 2 summarizes various types of evidence documenting other context dependencies that potentially affect the keystone status of species or the impacts of guilds that may include keystone species.

We know little about the causal factors that underlie the variation in impacts of particular species in different settings. Figure 4 illustrates possible context dependencies for annual plants, sea urchins, and freshwater fish, whose respective impacts and status as keystone or dominant species change with time since disturbance (Figure 4a), deletion of predators (Figure 4b), or ecosystem productivity (Figure 4c). For example, riverine fishes play keystone roles as top predators in food chains that control algal biomass in rivers, but only following scouring winter floods (Figure 5; Table 2). More quantitative field studies and development of theory are needed before we can understand, let alone predict, how species interaction strengths will change in various contexts or across ranges of conditions. Nevertheless, testable hypotheses can be formulated from trends that may occur with diversity, trophic position, and time for which species have been associated.

Diversity. In Paine's original (1969) demonstration, keystone species affected community diversity. The converse may sometimes be true—community diversity may affect keystone status. The more species that are trophically similar to a species in the food web (or functionally similar to a species in the interaction web; Menge and Sutherland 1987), the greater the chance that deleting that species would cause compensatory increases in species functionally similar to it (Frost et al. 1995). This argument suggests that loss of species diversity may thrust more of the remaining species into keystone roles (Chapin et al. 1995, Lawton and Brown 1993, Tilman and Downing 1994).

Support for this hypothesis is unfolding on South Pacific islands, where archaeological excavations

Table 2. Context dependency in keystone effects, with demonstrated or suspected causal factors.

Habitat (citation)	Species (type of organism)	Context dependency	Factor underlying context dependence
Marine			
New England rocky intertidal (Menge 1976)	*Nucella lapillus* (carnivorous gastropod)	keystone in low turbulence areas, not in high turbulence areas	wave forces
New England rocky intertidal (Lubchenco 1978)	*Littorina littorea* (herbivorous gastropod)	keystone on permanently submerged substrata, but not on periodically submerged substrata	change in competitive ability of algal food
New Jersey soft bottom (Peterson 1979)	*Callinectes sapidus* (carnivorous crab)	keystone in low turbulence areas, not in high turbulence areas	wave forces
Chilean rocky intertidal (Castilla 1981)	*Concholepas concholepas* (carnivorous gastropod)	keystone in high turbulence areas, not in low turbulence areas or where sea squirt prey dominate	wave forces, vulnerability of prey
Oregon rocky intertidal (Menge et al. 1994)	*Pisaster ochraceus* (carnivorous starfish)	keystone on wave exposed headlands, nonkeystone in wave-sheltered areas	prey mortality from sand burial
California kelp beds (Harrold and Reed 1985)	*Strongylocentrotus franciscanus* (herbivorous sea urchin)	keystone in areas with little drift kelp, nonkeystone in areas with much drift kelp	degree of herbivory on locally growing food, of "donor control"
California salt marsh (Pennings and Callaway in press)	*Cuscuta salina* (parasitic plant)	keystone effect strongest where salicornia host most dominant	variation in host traits and availabilities
Freshwater			
Wisconsin lake (Carpenter 1992, Lathrop and Carpenter 1992)*	*Stizostedion vitreum, Micropterus salmoides, Esox lucius* (piscivorous fish)	keystones when phosphorus inputs are low to moderate, not when phosphorus inputs are high	phytoplankton productivity and species composition
California rivers (Power 1995)	*Onchorynchus mykiss, Hesperoleucas symmetricus* (invertebrate-eating fish)	keystones following scouring winter floods, not during drought years	overwinter mortality of predator-resistant primary consumers
California rivers (Power 1992)	*O. mykiss, H. symmetricus* (invertebrate-eating fish)	keystones over boulder-bedrock substrates, not over gravel	habitat structure
Southeastern US ponds (Fauth and Resetarits 1991)	*Notophthalmus viridescens* (carnivorous salamander)	keystone in presence of *Siren*, not in absence of this predator	prey density
Swedish lakes (Diehl 1992)	*Perca fluviatilis* (carnivorous fish)	keystone in absence of macrophytes, weaker effects with macrophytes	habitat structure
Terrestrial			
South African shrublands (Bond 1984)	*Anoplolepis custodiens* (seed-dispersing ant)	keystone in sclerophyll shrublands, not in other shrublands, grasslands, and savannah	presence of alternative seed dispersers
African savannah (Dublin 1990)	*Loxodonta africana* (elephants)	keystone in fire-disturbed or sparse woodlands, nonkeystone in dense, undisturbed woodlands	prey (tree) size
South Pacific Islands (Cox et al. 1991, Rainey et al. 1995)	*Pteropus* spp. (large frugivorous bats)	keystone on islands where large frugivorous birds have been exterminated, probably not where they remain	presence of alternative seed dispersers
West African villages (Garrett 1994)	Lassa virus (agent of lethal human hemorrhagic fevers)	potential keystone where humans contact the African brown rat (*Mastomys natalensis*)	density and habitat use of animal reservoir of virus
Islands, Gulf of California (Polis et al. in press)	*Metepiera arizonica, Argiope argentata* (spiders)	spiders can suppress herbivores unless parasitized by pompilid wasps	weather, which determines availability of wasp's adult food
Southwestern US meadows (Cantor and Whitham 1989)	*Thomomys bottae* (root-eating pocket gophers)	gophers suppress aspen invasion of meadows except on rocky outcrops	physical refuge for prey from burrowing herbivore
(Brown and Heske 1990)	*Dipodomys* spp. (seed-eating kangaroo rats)	kangaroo rats may prevent transition from shrubland to grassland only near biogeographic zone of transition between two vegetation types	rainfall mediated rates of plant recruitment, growth, survival, and outcomes of competition

*S. R. Carpenter, 1992, personal communication. University of Wisconsin, Madison, WI.

have documented that extinction of frugivorous and nectar-feeding birds followed human settlement (Steadman 1995). On Mangaia, Cook Islands, for example, all of the avian frugivores and nectar-feeders have been extirpated (Steadman and Kirch 1990), leaving one species of flying fox (*Pteropus toganus*) as the last volant vertebrate pollinator and seed disperser capable of carrying large-seeded fruits (Rainey et al. 1995). On Guam, where flying foxes have also been nearly eliminated by human hunting, sampling efforts detected not a single vertebrate-dispersed seed, whereas comparable efforts on Samoa, where bats are still abundant, revealed much more vertebrate seed dispersal (Pierson et al. in press). Because seed disperser (and pollinator) guilds on isolated tropical islands are depauperate to begin with, and further impoverished by human impacts, species in these guilds may play crucial keystone roles in maintaining plant diversity (Cox et al. 1991, Elmqvist et al. 1992).

A counter-argument, however, can be made that as human impacts degrade ecological communities, keystones and the ecological organization they maintained may both be lost, leaving dysfunctional remnant assemblages of those species that happen to be able to survive in the highly altered environments. When species loss following human impacts is not incremental but massive, remnant species seem less likely to take on keystone roles, because the community architecture once maintained by species interactions has also collapsed (Paine 1995).

Trophic position. Above, we have contrasted species that exert strong effects by virtue of their large biomass (dominant species) with keystone species, whose strong effects emanate from their per capita (or per biomass) impact. The distribution of dominant species versus keystone species may vary across trophic levels. Energy flow considerations dating back to Lindeman (1942) suggest that basal species, which have more biomass, might have lower per biomass effects, whereas keystone species may be more prevalent at higher trophic levels. This hypothesis awaits tests in real ecosystems, where pat-

Figure 4. Three scenarios that suggest that interaction strengths, and hence keystone or dominant status, can change for a given species under different circumstances. (a) Successional changes in the dominance and total impact of annual herbs following fire in South African savannah: Immediately after fire, annuals sprout and make up most of the plant biomass (A_{Early}). Over time, woody shrubs and tree seedlings reinvade and make up increasing proportions of the total community biomass. The annuals at this stage (A_{Middle}) strongly determine sites at which the later successional plants can colonize, both positively (if annuals provide safe sites, such as more favorable microclimates for survival of seedlings) and negatively, if annuals compete with woody seedlings. During the third stage, annuals disappear (biomass becomes undetectable; A_{Late}). (b) Changes in the status of consumers with addition or deletion of predators that can control them: Sea urchins, when suppressed by otters (U_{Otter}) have low abundance, and low per capita effects if, for example, their kelp food has begun to escape in size (enlarge in girth so urchins cannot easily sever their fronds). If otters are deleted, urchins may increase in numbers and collective biomass to the point at which they can denude kelp forests and maintain so-called urchin barrens (U_{Kelp}). Whether their impacts are disproportionate to their biomass will depend on their per capita feeding rates and the extent to which they graze drift versus attached kelp. Grazing drift kelp (U_{Drift}) greatly reduces urchins' impacts on local communities even where they are abundant, because local permanent habitat structure is not altered. (c) Possible impacts of visually feeding predatory fish along a productivity gradient. In oligotrophic communities, predatory fish may effectively suppress prey, with cascading impacts on other species or trophic levels (F_{Oligo}). In mesotrophic communities, fish may be less effective per capita in controlling prey, if prey have faster population growth or more refuges, due to proliferating aquatic vegetation (F_{Meso}). In eutrophic communities, fish may be even less effective as predators if algal blooms reduce visibility, and fish biomass may be reduced by periodic kills due to oxygen depletion by vegetation (F_{Eu}).
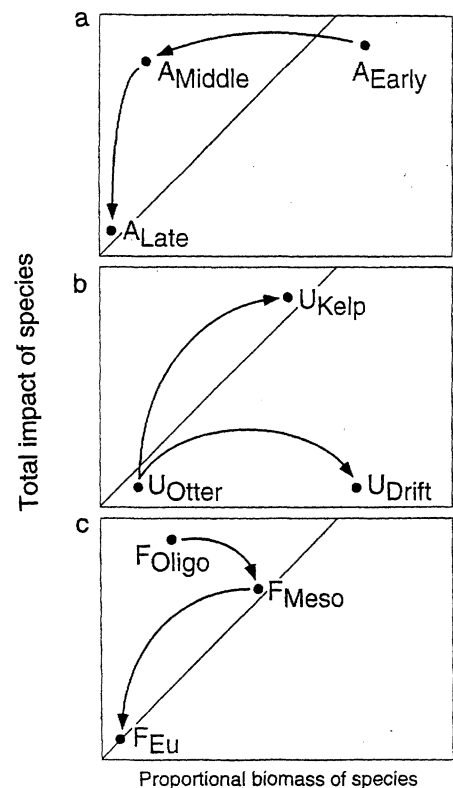
terns may vary, perhaps systematically, among ecosystem types. For example, inverted trophic pyramids (of biomass) are common in aquatic systems. Does this imply that aquatic plant species, or the herbivores that consume them, may more commonly play keystone roles than their counterparts in terrestrial systems?

Time. Species living together in nature may have radically different histories of association with one another. At one extreme, an interaction may be old and include enough of the interacting species' evolutionary histories to encompass the development of those traits that determine the nature of their interactions. At the other extreme are species that

have come together recently. Is there a relation between the length of species associations and the strength of their interactions? For example, are recently added species more likely to play keystone roles in communities and ecosystems than those with long histories of association? There is some evidence, both paleontological and contemporary, for new species being strong interactors. The paleo-ecological literature provides evidence that biotic interchanges often are followed by abnormally high rates of extinction in the recipient biotas (Vermeij 1991, Webb 1985, but see Lindberg 1991). Many well-documented contemporary examples come from the literature on invasions by alien species (e.g., Bailey
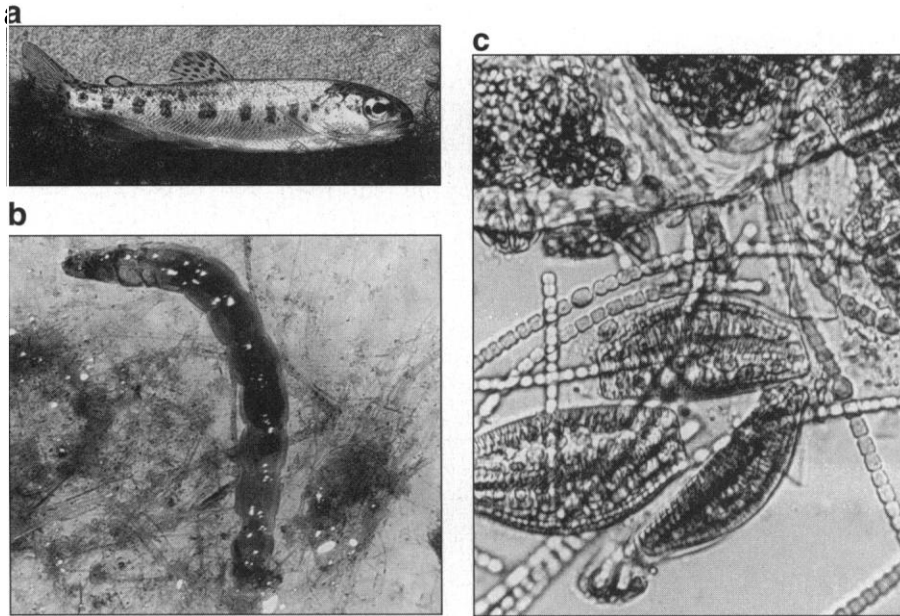
Figure 5. Interactions among (a) juvenile steelhead (*Onchorhynchus mykiss*), (b) chironomid larvae (*Pseudochironomus richardsonii*), and (c) algae (*Cladophora, Nostoc,* and *Epithemia*) can be strong, but vary between drought and flood years.

1993, D'Antonio and Vitousek 1992, Kitchell and Crowder 1986, McDonald et al. 1990, Vitousek 1990, Zaret and Paine 1973), which can have dramatic and widespread consequences for communities.

Application to preserve selection and management

The keystone concept has great relevance for identifying the most suitable areas for biodiversity preserves. To date, areas to preserve have been selected by comparing the species present in alternative areas and choosing those areas that contain the most diversity or the most irreplaceable species (Pressey et al. 1993). Systematists have developed methods for including taxonomic uniqueness when setting priorities for species conservation (Vane-Wright et al. 1991). Although these criteria are valid, they are static. Natural communities are not museum collections. The diversity or particular species that conservation managers seek to preserve may be lost if the dynamic fragility of communities and ecosystems contained within preserves is not taken into account in managing them. Dynamics have been incorporated into management models, but only at the level of single-species populations. Research on the population consequences of habitat frag-

mentation has provided additional guidelines on the minimal areas and spatial network of preserves needed to minimize extinction risk for particular species (e.g., Soulé et al. 1992). These too have been translated into general sets of rules or procedures that are widely used by practitioners in biodiversity assessments (e.g., Mace and Lande 1991).

Far less attention has been paid to the assessment of the critical ecological processes that maintain whole communities or ecosystems (but see Leigh et al. 1993). Some, although not all, of these processes are driven by keystone or critical species. Approaches to identifying critical ecological processes, species that may drive them, and their mode of action are, today, the most glaring omissions in the conservation biologist's toolbox for selection and design of preserves. Methods are needed for detecting species likely to be strong interactors, including potential keystone species, in rapid biodiversity surveys.

If we can identify keystone species in various ecosystems, it will be useful to set aside critical areas and to manage them so as to maintain these keystones, instead of solely focusing on endangered local species or geographical hot spots of biodiversity. If local keystones cannot be identified, the keystone concept points to the need for a cautious management

strategy that takes into account potential surprises from small interventions or changes. In particular, the keystone concept shows how:

- the loss of some species of low abundance may have surprisingly dramatic effects;
- the preservation of a species of concern may depend on the distribution and abundance of other species with which the target has no recognized interaction; and, conversely,
- the loss of a species, such as a top carnivore, may reverberate to affect members of seemingly disparate guilds, such as plants or decomposers.

These insights from the keystone concept suggest three key points related to policy and management. First, land managers should carefully consider the consequences of the loss of species for which no obvious role in the ecosystem has been discovered. The keystone species concept indicates the need for a design with a wide margin of safety for managed lands to guard against the loss of those organisms with disproportionately high community importance values. Second, introduced alien species may, like keystone species, have potential strong effects disproportionate to their biomass. More commonly, however, introduced aliens may become dominant species in new habitats that lack the parasites, pathogens, predators, or competitors that controlled invaders in their native ecosystems. These invaders, at the onset of invasion, can be relatively cryptic, and managers can play keystone roles themselves by eradicating such invaders before they become well established.

Finally, we note the lack of a well-developed protocol for identifying potential keystone species. We urge that when a potential keystone role is suggested for a given species, effort be directed toward obtaining real evidence for this hypothesis. The field is littered with far too many untested anecdotal "keystone species."

Future directions

The keystone concept has been invoked for almost 30 years by ecolo-

gists to interpret and publicize their findings in a variety of ecosystems. Nevertheless, ecologists still lack the empirical basis needed to detect, interpret, and predict general patterns in the occurrence of keystone species or to apply the concept for management. We do not yet have quantitative data with which to position species on Figures 3 and 4. Few if any studies indicate how community importance is distributed among species in communities. Generally, community importance should be correlated with field measurements of interaction strengths, as measured in the studies of keystone consumers by Paine (1992), Fagan and Hurd (1994), and Rafaelli and Hall (1992; Figure 2). Quantitative data on nontrophic keystone species are even more scant than on keystone consumers. Mutualists, such as pollinators or seed dispersers, are most likely to have keystone effects if they interact with many species that depend on the services provided (Gilbert 1980) or if they strongly affect the performance of a species that is quantitatively or qualitatively important in a system. Studies of both kinds of keystone mutualists exist, but none has gone far beyond the anecdotal in documenting community- or ecosystem-level impacts (Bond 1993, 1994). In general, species with nontrophic effects may be most important if they affect the performance and population dynamics of species that are potential dominants, as demonstrated for keystone consumers. Testing this hypothesis deserves more attention.

In the effort to refocus the term *keystone* for ecological research, and to make it more useful for policy makers concerned with preserving biodiversity, we confront a tradeoff between flexibility and rigor. The community importance index offered in this article is quantified in an objective and generally repeatable fashion, within the constraints imposed by noisy natural ecosystems. Yet it also can be tailored to a considerable degree by the investigator. He or she chooses, based on the natural history of the system and the purpose of the study, which community trait (e.g., species richness, albedo, arthropod biomass, nutrient retention) is to be monitored. (These

macroscale community traits are likely to be causally linked, and unraveling their connections is another important avenue of research needed for understanding and preserving natural ecosystems.) Although we tend to favor per biomass measures, the investigator needs to decide whether per capita measures are more useful or more feasible for specific systems and questions. The spatial and particularly the temporal scope of monitoring following the manipulation will strongly affect the estimate of a species' community importance. Therefore, the researcher must use his or her best judgment about the temporal and spatial scales over which most of the important feedbacks occur. The investigator must also decide whether impacts or responses of species, rather than of groups of species, must be isolated. Detailed resolution of pairwise interactions on a species-by-species basis is important for detailed understanding of the mechanisms of community interactions, but it cannot be a first priority when assessing potential keystones under most biodiversity triage scenarios.

Methods for rapid assessment of potential keystones would be an extremely useful addition to the conservation biologist's toolbox. As the database on demonstrated keystone species grows, it should be mined for patterns that may forecast likely keystones by their attributes, or contexts in which species with certain attributes are likely to play strong roles. Both community importance and interaction strength (and therefore the status of species as keystone or dominant species) are context dependent, simply because performances of organisms change with variation in their environments. Although this ecological truism ensures that results from specific field studies will be difficult to generalize, examination of the nature of context dependencies may lead to more fundamental generalizations. Keystone status depends not only on the properties of that species with a disproportionate influence, but also on the species with which it interacts and the physical arena containing and constraining these interactions. Appreciating this aspect of the keystone concept will lead to answers to the

important questions that remain about keystones more quickly than would exclusive focus on the traits of keystone species alone.

Among the important unanswered questions are the following: How are interaction strengths distributed among species in various communities? Are keystone species common? Are communities structured by keystone species common? Are keystone species more prevalent in some types of communities or ecosystems than in others (aquatic versus terrestrial, ancient versus recently assembled, diverse versus depauperate)? Are taxonomically unique species more or less likely to be keystone species than species with close contemporary relatives? Is our present focus on keystone consumers at high trophic levels warranted, or are we overlooking species at lower trophic levels that play other cryptic but critical keystone roles? We hope that natural ecosystems remain intact long enough for such questions to be addressed, but this outcome depends critically on accelerating the feedback between science and management.

Acknowledgments

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