



# FLAGSHIPS, UMBRELLAS, AND KEYSTONES: IS SINGLE-SPECIES MANAGEMENT PASSÉ IN THE LANDSCAPE ERA?

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## Abstract

Because it is so difficult to monitor and manage every aspect of biodiversity, several shortcuts have been proposed whereby we monitor and/or protect single species. The indicator species concept is problematic because there is no consensus on what the indicator is supposed to indicate and because it is difficult to know which is the best indicator species even when we agree on what it should indicate. The umbrella species (a species that needs such large tracts of habitat that saving it will automatically save many other species) seems like a better approach, although whether many other species will really fall under the umbrella is a matter of faith rather than research. Intensive management of an indicator or an umbrella species (for example, by transplant or supplemental feeding) is a contradiction in terms because the rest of the community to be indicated or protected does not receive such treatment. A flagship species, normally charismatic large vertebrate, is one that can be used to launch a conservation campaign because it arouses public interest and sympathy, but a flagship need not be a good indicator or umbrella. And conservation flagship species is often very expensive. Further, management regimes of two flagship species can conflict. Ecosystem management, often on a landscape scale, is a proposed solution to problems of single species management. Keep the ecosystem healthy according to this view, and component species will all thrive. However, conservationists have concerns about ecosystem management. First, it is variously defined and many definitions emphasize the commodities ecosystems provide for humans rather than how humans can protect ecosystems. Second, the term 'ecosystem health' is ill-defined and associated with an unmoderated, superorganismic view of the ecosystem. Third, ecosystem management seems focused on processes and so would appear to permit losses of species so long as they did not greatly affect processes like nutrient-cycling. Fourth, ecosystem management is often implemented by adaptive management. This may make it difficult to study the underlying mechanisms driving an ecosystem and to know when an entirely new management approach is

needed. Thus, some ecosystem management as a Trojan horse that would allow continued environmental destruction in the name of modern resource management.

The recognition that some ecosystems have keystone species whose activities govern the wellbeing of many other species suggests an approach that may unite the best features of single-species and ecosystem management. If we can identify keystone species and the mechanisms that cause them to have such wide-ranging impacts, we would almost certainly derive information on the functioning of the entire ecosystem that would be useful in its management. Some keystone species themselves may be appropriate targets for management, but even when they are not, our understanding of the ecosystem will be greatly increased. Keystone species may not be a panacea, however. We do not yet know how many ecosystems have keystone species, and the experiments that lead to their identification are often very difficult. © 1998 Published by Elsevier Science Ltd. All rights reserved.

**Keywords:** adaptive management, ecosystem health, ecosystem management, endangered species, flagship species, indicator species, keystone species, landscape ecology, umbrella species.

## INTRODUCTION

In an era of burgeoning conservation needs and tightening budgets, an increasingly loud claim is that the scope of conservation management must be expanded to achieve economies of scale and efficiency. According to this view, managing populations of particular species of interest will lead us to fall further and further behind in meeting the challenge of preserving biodiversity, as more and more species fall below a threshold of imperilment and funding in no way keeps pace with their individual needs. The only way to deal with this challenge is then seen to be to manage at least entire ecosystems, if not whole landscapes, by unified methods designed to save all their inhabitants at one time.

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However, the precise objectives of such methods have not often been articulated beyond vague aims to 'preserve the environment' or to 'maintain biodiversity', and it is not always clear exactly how management of such high-level entities as ecosystems will supersede management of their component species. This paper attempts to understand the specific goals of management at the ecosystem level and higher, and also to compare proposed procedures to those of traditional management focused on individual populations and species.

The examples used to elucidate these matters will be primarily North American, largely because of the author's familiarity with conservation on that continent. A large fraction of the discussion relates to management actions aimed at satisfying the Endangered Species Act (1973) of the United States. This legislation has become the major vehicle for protecting biodiversity in the United States (Mann and Plummer, 1995). It is reactive, rather than proactive, and explicitly targets species and populations, in that it specifically provides protection for species (and, in certain instances, some populations rather than entire species) that are already felt to be doomed to extinction if new action is not taken to redress their decline. However, often the Act has been invoked to save entire ecosystems because, under some circumstances, it provides for protection of the habitat of an endangered species, and that habitat includes the biotic as well as the abiotic habitat. Thus, a recent interpretation by the Supreme Court says that the Act can prevent habitat destruction (Baker, 1995) if such destruction 'harms' endangered species or populations. The Endangered Species Act also mandates that, in addition to calling a halt to most activities causing the decline of an endangered species, a management plan must be produced that will rehabilitate the species by bringing its population size above the threshold of endangerment. These management plans have become the testing ground for various ideas on how and at what level to conserve nature in the United States.

#### Indicator, umbrella, and flagship species

Because monitoring and managing all aspects of biodiversity that might interest us (including species richness and composition, physical structure, and processes) are so difficult, a variety of shortcuts have been proposed whereby attention is focused on one or a few species.

The most venerable of these approaches is that of the indicator species. Managers use indicators for two different reasons—first because their presence and fluctuations are believed (or hoped) to reflect those of other species in the community, and second because they are believed to reflect chemical and/or physical changes in the environment (Landres *et al.*, 1988). However, there is no reason why a species particularly sensitive to chemical pollution, for example, need necessarily reflect the status of a large number of other species, so I will restrict my consideration to the first type of indicator species.

Criteria for choosing such indicator species are very controversial (Landres *et al.*, 1988), at least partly because of confusion over what the indicator should indicate. Generally, we want an indicator to indicate the 'health' of the system, but different persons view different things as constituting health. For example, whether species richness alone, independently of species' identities, contributes to the functional health of a community or ecosystem is hotly debated and currently under intensive study (Baskin, 1994; Tilman and Downing, 1994). For some persons, species richness itself ecosystem health—the tacit goal of all conservation should be species richness, and, *ipso facto*, a rich community is a healthy one. For still others, structural diversity and aspects of function (like nutrient cycles) are the *sine qua non* of health, independently of species richness or composition. The *reductio ad absurdum* of this confusion of goals is the proposition (Noss, 1990) that we should monitor *virtually everything* as indicators—a large group of species, dominance-diversity curves, canopy height diversity, percent cover, nutrient cycling and predation rates, etc. The problem is that this full set of indicators leaves nothing to be indicated, as opposed to measured directly. Of course the absence of resources to do all this measurement was the *raison d'être* for indicator species in the first place!

Even if we concede at the outset that all we want the indicator species to indicate is the presence and population trends of a group of other species in a community of interest, it is not so obvious how to choose the best species for this purpose. At the very least, we would need a pilot study measuring co-occurrence patterns and correlations of population fluctuations, plus ease of monitoring, for all species in the group. To my knowledge, such a pilot study has never been attempted. The scale of observation would also be important for an indicator (Mellé and Carroll, 1994; Weaver, 1995). Species like the large vertebrates discussed below might be excellent indicators for other species that require massive, continuous tracts of habitat, but they may not be good indicators of species such as insects that might do very well in a landscape fragmented into small patches, so long as the habitat of the patches was appropriate.

*Faute de mieux*, often vertebrate species are chosen as indicators simply because they are so charismatic that a manager feels obliged to monitor them anyway and nourishes the vague hope that such a 'flagship species' (see below) will fortuitously reflect the health of the entire system. For example, the US Forest Service is mandated to use 'management indicator species' to assess the impacts of any proposed management procedure on the system as a whole and chose the northern spotted owl *Strix occidentalis caurina* to serve this role for the Pacific Northwest region. The specific grounds were that the owl (1) was on the threatened species list for Oregon, (2) is a species of special interest (because it is an attractive bird that typifies a beautiful forest type),

and (3) represents other species that depend on old growth (Lee, 1985). There is no inherent reason why the fact that this bird is threatened and of special interest would mean that its fate reflects those of other species. It is convenient for the Forest Service to assume that it does, because they would monitor it anyway because of its interest and threatened status.

The fact that few data support the indicator function of the owl need not mean its choice is completely misguided. The rationale is that the owl is closely tied to old-growth rain forest, the amount of this habitat has been drastically reduced by logging, and other species requiring this habitat are likely to be threatened also. However, because the other species are not charismatic vertebrates, they have not been studied enough for us to know how threatened they are. Because the owl requires such large amounts of old-growth for survival and reproduction (c. 800 ha per pair in the middle of its range [Simberloff, 1987]), saving enough of this habitat for the owl would almost surely save enough of it for other species. Thus, the spotted owl would serve not only as an indicator but as an 'umbrella species' (Shrader-Frechette and McCoy, 1993), a species with such demanding habitat requirements and large area requirements that saving it will automatically save many other species. Wilcove (1993) has called wide-ranging vertebrate species such as the owl 'coarse filters' and suggested that their preservation would save entire ecosystems.

Perhaps this reasoning is correct, but without many more supporting data, we can question the utility of the spotted owl as an indicator or umbrella species. First, there is even some controversy about the extent to which the spotted owl absolutely requires old-growth forest (e.g. Mickey, 1994), although the great majority of qualified workers believe that it does. Second, although other threatened species are apparently restricted to old-growth forest in the Northwest, it is far from certain that they need the same parts of the forest as the owl does, and, although saving the owl should help save many of them, it will not save them all. For example, the exact status and habitat requirements of three amphibians of special concern are not well known (Welsch, 1990). Two of these require rather specialized aquatic microhabitats that, although often associated with habitat used by spotted owls, are obviously not identical to it. We might also ask about the 6000 insect and other arthropod species typical of the old growth. Certainly some old-growth specialist arthropods would be protected by large reserves for the owl, but the precise habitat requirements of most species are very poorly known (Lattin, 1993). Unless additional coastal habitat were added, enormous proposed reserves for the owl would not provide adequate protection for anadromous fish or the marbled murrelet *Brachyramphus marmoratus*, another threatened bird (Franklin, 1994), both of which depend on old-growth forest but for only part of their life history.

The legal status of the owl as an indicator species under the National Forest Management Act has led to an undue focus on this particular species to the exclusion of all that it is supposed to indicate. For example, logging industry representatives frequently suggest management procedures specifically targeted at owls, like moving or feeding them, artificially enhancing their prey density, or providing added shelter, in order to 'boost their populations so that logging quotas can be raised (e.g. Craig, 1986). The Forest Service proposed moving owls from site to site. Lost in such suggestions is the recognition that single-species management of an indicator species is a self-contradiction (Simberloff, 1987). After all, if the species' status is artificially improved, it no longer indicates the status of all the species it is supposed to represent. Would we also add food or shelter for other birds, mammals, amphibians, and insects of the old-growth forest, and move them around? I will return to this point below.

A similar example is that of the red-cockaded woodpecker *Picoides borealis* of the US Southeast. This bird resides primarily in forests of longleaf pine *Pinus palustris*, which have declined largely because of logging over the last 150 years from about 28 million ha to only 10 million ha of old growth and 4 million ha of second growth (Simberloff, 1994a). Most of the latter differs substantially from the primary forest, notably in the relative youth of the oldest trees and the composition of the ground cover. One of the first listed endangered species in the US, this colonial woodpecker is unique among regional woodpeckers in excavating its cavities in old, diseased trees.

The precipitous decline of this striking bird has finally led the Forest Service to organize its management of 11 national forests totalling 1 361 100 ha around a recovery plan for the red-cockaded woodpecker (US Department of Agriculture, 1995). These 11 forests have 31 other species listed as endangered or threatened (14 half animals and half plants) and 71 proposed for such listing. The reason for the precarious status of almost all these species is either that the habitat has simply been destroyed in one fell swoop or that it is gradually changing because the fires that frequently swept these forests during the growing season are now suppressed. Because the authors of the proposed woodpecker management scheme envision both more mature longleaf pine forest (albeit with a time lag) and more growing-season fires, they see almost no disadvantages and many potential benefits for all these other species. No substantial study supports any of these contentions, and only four pages of the management plan are devoted to this issue, as opposed to hundreds that discuss timber production. For example, another species typical of longleaf forest that has undergone a great decline, Sherman's fox squirrel *Sciurus niger shermani*, will be restricted from using some cavities that will be preserved in optimal condition for the woodpecker by a mechanical device preventing enlargement. For most species of special

concern. much less is known about their biology, so the impact of the management plan cannot be guessed with much assurance.

The Florida panther *Felis concolor coryi* is the quintessential 'flagship species' (Shrader-Frechette and McCoy, 1993)—a species that has become a symbol and leading element of an entire conservation campaign. The panther is identified with Florida (Shrader-Frechette and McCoy, 1993) and has been used as a poster-animal in both public and private campaigns for broader conservation objectives. A disjunct subspecies of the widely ranging cougar, it is slightly distinctive morphologically and is gravely threatened. Some 40 individuals remain, restricted to undeveloped areas of south Florida, among the regions of the US undergoing the most rapid development and habitat destruction. The main problems for the panther are the dramatic decline in its favoured prey animal, the white-tailed deer *Odocoileus virginianus*, owing to habitat destruction (Shrader-Frechette and McCoy, 1993) and the fragmented nature of remaining panther habitat, which causes individuals to cross highways, incurring substantial mortality. It would be no trivial matter to sequester land sufficient for an increased population, as male home ranges average 550 km<sup>2</sup> and female home ranges 300 km<sup>2</sup> (Cox *et al.*, 1994), and land in Florida is very expensive. In fact, although Florida has by far the largest state fund in the US for purchase of conservation lands, the budget could easily be exhausted simply by purchases of potential panther habitat.

However, Florida has numerous other threatened taxa, including 51 other mammal, bird, reptile, and amphibian species and subspecies (Shrader-Frechette and McCoy, 1993). Of course, panther habitat could serve double-duty. Areas proposed specifically for panther conservation have at least 24 of these 51 taxa, plus 29 threatened plant species and subspecies (Cox *et al.*, 1994). Other species may be even better umbrellas. For example, proposed conservation areas for the Florida black bear *Ursus americanus floridanus* include more threatened vertebrates and many threatened plants (Cox *et al.*, 1994). Of course, to evaluate the relative merits of potential umbrella species and to determine how many of them are needed, we would need a full analysis of the costs of the proposed purchases, the likelihoods of survival of each species in the umbrella, etc. At least the latter aspect of the analysis would be extremely difficult. No method incorporating all the potential threats to species survival can currently be used with much confidence.

The panther is so charismatic that thousands of Floridians pay \$66 annually to have an automobile license plate with its picture. These funds go towards conservation, as do others generated in various private appeals featuring the panther. On the other hand, the attempt to preserve the panther at both state and federal levels has been enormously expensive, ca \$1.4 million (J. Cox, pers. comm.) in addition to land-acquisition costs

for the new. 12001) ha Panther National Wildlife Refuge. Costs have included a journal (*Coryi*) devoted solely to this animal, extensive field management projects, and field and laboratory studies. Are the benefits generated by the panther conservation program worth the costs? Could the funds devoted to it have greater conservation benefit if spent otherwise? No significant research treats these questions.

An irony is that the panther may not survive long even with this expenditure, at least not without successful translocation to other regions of Florida (Shrader-Frechette and McCoy, 1993; Cox *et al.*, 1994). In fact, some might argue that the very procedure that has now been adopted to forestall a decline from hypothesized inbreeding depression will eliminate the Florida panther quickly at least eliminate it as *Felis concolor coryi*. After the discovery that one of the two populations already contains genes from escaped captive Central or South American cats (O'Brien *et al.*, 1990), the federal government and state have now embarked on a plan to import and release individuals of another *F. concolor* subspecies from Texas to increase effective population size (Dold, 1995).

But what happens when the flagship sinks or there is no flagship?

That the Florida panther might disappear or evolve into another species leads us to question from yet another direction the wisdom of hinging an overall conservation strategy on a single charismatic threatened flagship species. Suppose the population disappears? Will public emotional investment in this species turn to despair and disenchantment with conservation in general? Would not the money have been better spent on a combination of conservation projects to preserve other species and educational programs to teach the lay public about the importance and inherent attractiveness of the myriad less dramatic species that dominate any ecosystem?

Worse, suppose a region has no threatened species, charismatic or mundane, to begin with? This is precisely the situation in the Alaskan rain forest, such as the huge (6812 000 ha) Tongass National Forest in Alaska. Although parts of this region are revered for spectacular vistas as well as large populations of dramatic animals (such as the grizzly bear, *Ursus arctos*), no one forest-dwelling species qualifies for protection under the Endangered Species Act. The United States has no law that specifically protects communities or ecosystems. Thus, the Endangered Species Act has been pressed into service for this purpose because it protects the 'critical habitat' of listed species, and the habitat can be construed as the biotic habitat, such as old-growth trees for the spotted owl, as well as the physical context. It is widely recognized that this approach will not suffice for all communities and ecosystems, as exemplified by the Tongass case, and that what is needed is some sort of 'Endangered Communities Act' or 'Endangered Ecosystems Act' (e.g. Hunt, 1989; Meffe and Carroll, 1994).

But the political climate in the United States makes prospects for passage of such an act, at least one in which conservation would take precedence over economic considerations, extremely dim in the near future.

It is an irony that the Endangered Species Act itself is endangered, and the main reason is anger by a segment of the public over use of the Act to sequester large tracts of habitat designated as critical habitat for some endangered species (Mann and Plummer, 1995). In fact, a lawsuit recently decided by the US Supreme Court (Babbitt vs Sweet Home) sought to prevent use of the Act to protect habitat (and therefore entire communities) by stating that Congress had never meant the term 'harm' to a species in the Act to mean destruction of habitat, but only direct killing of an animal or plant, say by shooting or burning an individual. The Court rejected the narrow interpretation of 'harm' by a 6-3 vote (Baker, 1995). A prime example of anger at this use of the Act is the spotted owl debate, in which it was abundantly clear to all parties that the stakes were not the spotted owl, which was only a surrogate for the old-growth forest it inhabits. It was the eventual listing of the bird under the Act and the designation of that forest as its critical habitat that greatly reduced logging in the Northwest but also precipitated the crisis surrounding the Act.

#### Species conflicts under species management

Single-species management, of flagships, umbrellas, endangered species, or any others, can lead to the odd circumstance that management of one species conflicts with management of another species (Committee on Scientific Issues in the Endangered Species Act [CSIESA, 1995]).

Ash Meadows, a series of deepwater springs on 20 000 ha of desert uplands near Las Vegas, harbors at least 26 endemic plant and animal species and subspecies, many of which are federally listed as endangered. Their management needs are not identical. For example, the Ash Meadows naucorid *Ambrysus amargosus* is the only aquatic insect protected under the Endangered Species Act, and its population is still declining because of habitat alteration to favor the Devil's Hole pupfish *Cyprinodon diabolis* (Polhemus, 1993). But the pupfish, which numbers 200-500 individuals restricted to a single 3 m x 15 m pool probably for its entire existence, is unlikely ever to be delisted (Middleton and Litschewager, 1994), and management is almost certain always to favor a charismatic fish over an insect.

In the Everglades of Florida, management plans for two extremely charismatic, federally listed birds are in conflict (Graham, 1990). On the one hand, the Everglades snail kite *Rosirhamnus sociabilis plumbeus*, reduced to some 600 individuals by wetland degradation and agricultural and residential development, feeds almost exclusively on freshwater snails of the genus *Pomucea* and is thus an extreme habitat specialist

(Ehrlich *et al.*, 1992). The kite needs high water levels, which increase snail production. On the other hand, the wood stork *Mycteria americana*, reduced to perhaps 10 000 pairs by swamp drainage and cutting of the cypress trees it favors for nesting, would be facilitated by lower water, which concentrates prey populations (Ehrlich *et al.*, 1992). The US Fish and Wildlife Service opposed a proposal by the Everglades National Park to modify water flow to improve stork habitat on the grounds that the change would be detrimental to the kite.

In California, the giant kangaroo rat *Dipodomys ingens* depends primarily for food on non-indigenous plants, and these rodents continually disturb the habitat to the advantage of these exotics and detriment of native plants, including the endangered *Caulanthus californicus* (Schiffman, 1994). Because the native plants used by the kangaroo rat are now rare or even extinct, there is no obvious management solution to this dilemma.

#### Ecosystem management

Ecosystem management is a suggested solution to the problems posed by single-species management focused on indicator, umbrella, and flagship species. This is a fluid concept that has exploded on the resource management scene following a technical session of the American Association for the Advancement of Science Annual Meeting in 1991 (Swank and Van Lear, 1992). There is no consensus definition of 'ecosystem management' (Grumbine, 1994; Soulé, 1994); even the various US federal agencies all have different working definitions (Morrissey *et al.*, 1994). Several agencies (e.g. the Department of Commerce) even forswear an attempt to define 'ecosystem management' explicitly, although these agencies, as do all the others, see ecosystem management as a dramatic new approach that will solve many problems. The excitement seems to be engendered largely by a feeling that ecosystem management will produce economies of scale. Single-species management seems costly and inefficient. Expenses for activities such as building excluders for potential red-cockaded woodpecker holes, moving individuals around, and extensive laboratory and field studies of the physiological ecology of individual species would seem to be limitless as species after species is added to the threatened list. 'If we keep the entire ecosystem healthy (Morrissey *et al.*, 1994), would not populations of all its component species automatically be healthy?'

There are common elements in virtually all definitions of ecosystem management. The key feature is a focus on ecological processes rather than individual species (Meffe and Carroll, 1994). For some workers, ecological processes are seen as keeping an ecosystem healthy (at least in some conceptions of ecosystem health). In other words, the processes are not the valued entities *per se*, but the processes are believed to maintain the species and communities that are valued (Bourgeron and Jensen, 1993; Franklin, 1994). However, at the level of

implementation and management. the processes themselves often seem to have become the valued elements. For example, among US federal agencies, many list maintenance of processes or functions as either the first goal of ecosystem management or the only goal. And an attempted consensus document (Keystone Center, 1993) produced by representatives of many government agencies and private organizations listed maintaining processes as the first aspect of ecosystem management. This focus on processes is seen as a Trojan horse by some conservation biologists, as will be discussed below.

The emphasis on processes automatically leads to a broad spatial scale with a focus on landscapes. One definition of landscape ecology (Golley, 1993) is "the study of how land patterns influence processes". Of course, landscape ecology also answers a growing interest in large-scale phenomena, while it is quite clear that at least some single-species management can be conducted without considering the structure and dynamics of the landscape. Thus, ecosystem management, though not simply the management version of landscape ecology, is very closely related to the latter discipline.

Another feature shared by many definitions of ecosystem management is that it is holistic: a trait seen as clearly distinguishing it from single-species management. This feature might seem trivial after all, holists study systems as systems. However, it is important to realize that holists are committed to the view that it is impossible to understand the components of a system *except* as parts of the system. Thus, they would argue that insightful, effective single-species management is not only expensive and inefficient, but is impossible, because the species exists only as part of the ecosystem.

Yet another aspect of ecosystem management in most definitions is that humans are part of the ecosystem, or at least of most ecosystems. There are two subtle consequences of this view.

First, although this point is rarely articulated in scientific publications, this conception of ecosystem management casts into doubt the very idea of excluding humans from selected areas, as somehow antithetical to the nature of an ecosystem. Of course, this is an extreme view (which is probably why it is rarely written down), but the implication is clear that such restricted areas should play at best a limited role in conservation. The title of a recent exposition of ecosystem management for forests (Shepard, 1994) says it all: "Modern forest management: it's about opening up, not locking up".

Second, humans use resources, and such resource use is conceived as a natural process not inherently dangerous to ecosystem health. Biologists and environmentalists, if they advocate ecosystem management at all, tend to see its key goal as maintaining biodiversity (e.g. Meffe and Carroll, 1994). In short, humans should manage ecosystems to protect other species and communities. However, many people, especially in management agencies, have a very different focus (e.g. Overbay, 1992; Jensen and Everett, 1993), namely the goods and

services that ecosystems provide to humans (Grumbine, 1994). In other words, humans should manage ecosystems primarily in response to human resource needs. The Forest Service and some other US agencies have in the past attempted to resolve this conflict by the philosophy of 'multiple use', at least since the Multiple Use Sustained-Yield Act of 1960 (Kessler *et al.*, 1992). The assumption was that the managed land could serve all purposes, although in practice the human resource needs were greatly emphasized. But this as only an assumption. Now that there is public pressure to pay more attention to protection of other species and communities, the validity of the entire multiple-use framework is in question (Wagner, 1994). It may well be that ecosystem management, at least in some ecosystems or large parts of them, will have to serve one or the other goal almost exclusively. It is important to state explicitly that multiple use may not be possible (Grumbine, 1994).

A final feature common to many conceptions of ecosystem management (e.g. Kessler *et al.*, 1992; Everett *et al.*, 1993) is that adaptive management (Walters, 1986; Walters and Holling, 1990) will be the scientific basis for it. Adaptive management is essentially project-as-experiment, and the key aspect that seems to attract many adherents in ecosystem management circles is that management goals and methods are changed in the course of the project. The aegis for adaptive management is that the effects of a procedure are very uncertain because mechanistic understanding of a system is rather poor (Walters and Holling, 1990). This state of affairs certainly obtains for many components of proposed plans for managing ecosystems. Adaptive management has had some successes, as, for example, in some fisheries in which simply adjusting yearly limits in accord with the catch has prevented overfishing, without any detailed understanding of the mechanisms of the underlying population dynamics (Policansky, 1986).

A contentious aspect of adaptive management is whether the changing procedures and goals really permit improved mechanistic understanding of the system. Walters and Holling (1990) contend that adaptive management leads to scientific understanding, but their defense of the proposition that this understanding is scientific, even if it is not the customary analytical type of scientific knowledge, suggests the contention is controversial. Is an 'experiment' for a short enough time to be considered adaptive (in the ecosystem-management sense of subject to modification in the course of the project) really a scientific experiment? And is there adequate replication and control, especially if the project is at an ecosystem or landscape scale? Many studies in ecology are called 'experimental' that do not really qualify for this status (Underwood, 1990). The importance of this problem for conservation is that the term 'experiment' has a scientific cachet and may suggest a kind of rigor that is, in fact, absent from a management scheme. Wiens (1992) has pointed to a distressing lack

of experiment in landscape ecology. So the combination of an adaptive management approach in a framework that is often at a landscape scale should force us to pay close attention to whether a proposed plan is scientifically grounded.

Another problem with adaptive management is that, with its continual modification of procedures in light of observations, there is no clear stopping point, no moment of truth at which we can say that a particular hypothesis is rejected. Is there any way, then, to decide that an entire management approach should be rejected (Simberloff, 1994h)?

### Is ecosystem management a panacea or a Trojan horse?

Some conservation biologists have argued that ecosystem management is leading to 'species-bashing' (Soulé 1994), that valuable, scientifically tested management procedures are being jettisoned on the grounds that they are outmoded remnants of a discarded paradigm, single-species management.

Also, from the standpoint of species conservation, it is disturbing that many ecosystem processes can be preserved even as the component species normally responsible for them are lost (Tracy and Brussard, 1994). As an example, second-growth forest of low diversity often has greater primary productivity than does the diverse old-growth forest it replaces. Is it therefore an acceptable substitute for the original? Similarly, energy will flow and nutrients will cycle in ecosystems of very few species: does it really suffice to maintain just the processes? It seems likely that many threatened species, including flagship species like the spotted owl, red-cockaded woodpecker, and Florida panther, could disappear entirely from an ecosystem without major or even detectable change in key processes. Many of these charismatic vertebrates are top carnivores, thus of low total biomass and primary productivity. Unless their preferential feeding controls a species that would otherwise be dominant (see Keystone species management, below), their absence would probably not substantially affect the rest of the ecosystem.

The fact that various ecosystem processes are maintained even as species disappear is but one aspect of an important difference between conserving ecosystems and conserving species. Species and even entire guilds can disappear, and they need not be replaced by others that share many of their traits. But if a particular type of ecosystem disappears, some other one will replace it, and the high-level functions such as energy flow and nutrient cycling will still take place, even if details and rates change.

Another concern with ecosystem management as a guiding paradigm for conservation is that, whereas a species is usually easy enough to define, the boundaries of an ecosystem are not so apparent, and which ecosystems are so similar as to be representatives of the same type is often not a trivial question (Tracy and Brussard, 1994). It seems entirely possible that an area of conser-

vation concern could be consigned to oblivion on the grounds that it is not a part of an ecosystem that is being managed, or that the ecosystem is just another representative of a type already well-represented in a refuge system.

The absence of a consensus definition for ecosystem management also worries conservationists, as does the fact that many working definitions appear to emphasize what humans can get out of the ecosystem rather than how they can aid its other component species. The absence of a consensus definition is, in fact, part of a larger problem. The entire concept of 'ecosystem health' is quite fluid, and, as observed above, there is no consensus about what constitutes a healthy ecosystem. There is a spectrum from utilitarian ideas to ecosystem-centered ones (Wagner, 1994). An example of a utilitarian view is that of the USDA Forest Service (1993): "Forest health is a condition where biotic and abiotic influences on the forest ... do not threaten resource management objectives now or in the future. For the Forest Service, a forest ecosystem provides commodities to humans, and management objectives reflect this conception. An ecosystem-centered view of health envisions the sustenance of all the components per se, independently of whether the ecosystem as a whole can provide commodities: "A forest in good health is a fully functional community of plants and animals and their physical environment. A healthy forest is an ecosystem in balance (Monnig and Byler, 1992).

Thus, although 'health' seems at first blush to be such a universal virtue that no one could object to it as a goal, in practice, a goal of ecosystem health could be used to the detriment of conservation of particular species. This paradox could arise, for example, if sustainable production of a commodity like a certain kind of wood could be prevented by maintenance of a bird like the spotted owl or the red-cockaded woodpecker. In the utilitarian conception, such a bird would be inimical to ecosystem health. Of course, the exact meaning of 'sustainable' and how we would assess sustainability is central to this potential problem. But here again we have a concept that has many definitions about which there is no consensus (Meffe and Carroll, 1994). This debate is well enough known and sufficiently complex that I will not summarize it here.

Founding a management paradigm on ecosystem health is bound to lead to disputes and misunderstandings. This is because it is appropriate to the metaphor of the ecosystem as superorganism, a metaphor with ancient roots but one that is imperfect (Simberloff, 1980). Although there are analogies between an individual organism and a community or ecosystem, there are many sorts of integrity that typify organisms but that communities and ecosystems lack (Simberloff, 1980; 1992). Of course, the view that communities or ecosystems are superorganisms was greatly influenced by holism (Simberloff, 1980), and the commitment to holism in many working definitions of ecosystem management.



noted above, can now be seen as associated with a problematic criterion for assessing management success.

Even determining the health status of an individual organism is difficult. Determining, at least to the satisfaction of all parties, whether an ecosystem is healthy is hopeless. We have seen that different people have different definitions of health and different conceptions of ecosystems, and that even the physical boundaries of an ecosystem are often in doubt. Truly, ecosystem health is not a workable goal.

Further, the integral relationship of adaptive management to many conceptions of ecosystem management is worrisome to conservationists. There are two problems. First, the possible absence of a clear criterion for rejection of a hypothesis and the continually changing management practices may make it impossible to proceed by normal scientific means to study the underlying mechanisms of the system and thus to conceive of entirely new ways to manage it or its component species. Second, the focus is on the entire ecosystem rather than on individual species. This fact suggests that ecosystem management would not nurture the sorts of experiments and observations on single species that have often provided great insight into not only their own biology but the structure and function of entire systems (examples given below).

Finally, it is often said that single-species management 'doesn't work' (see, for example, Cushman, 1995; Mann and Plummer, 1995), as witness the fact that several listed species managed under the US Endangered Species Act have nonetheless disappeared. Some of these species, at the time of listing, were almost certainly already extinct (McMillan and Wilcove, 1994). Others that had substantial populations when listed, such as the dusky seaside sparrow *Ammodramus maritimus nigrescens*, were grossly mismanaged, and non-biological factors, such as lax law enforcement, led to their demise (Walters, 1992). It was not the inability of biologists to know enough science to save these species that doomed them. Rather, the knowledge was there or could have been gathered, but economical, political, or social concerns came to dominate the programs.

### Keystone species management

A slightly different orientation to single-species management might be more effective than the alternatives discussed above. The concept of the keystone species () suggests that, at least in many ecosystems, certain species have impacts on many others, often far beyond what might have been expected from a consideration of their biomass or abundance. Paine originally studied a starfish that selectively preyed on a species that would otherwise have been competitively dominant. The starfish thereby prevented that dominance and allowed numerous other species to coexist. The definition of 'keystone' has been expanded (see Bond, 1993; Menge *et al.*, 1994), and species not near the top of foodwebs have also been seen as keystones. For example, Gilbert,

(1980) termed 'keystone mutualists' plant species that support many animal species whose activities may themselves support many other species. And species may serve as keystones by virtue of how they change the physical structure of the environment, as do beavers *Castor canadensis* with their dams (Naiman *et al.*, 1986; Pollock *et al.*, 1995). Many species provide shelter for numerous other species. In the longleaf pine forest, gopher tortoise *Gopherus polyphemus* burrows are home to 332 other species (Jackson and Nilsen, 1989), some of which use this microhabitat obligatorily, while the holes that red-cockaded woodpecker clans laboriously excavate in longleaf trees are the only such holes present and are used by at least 22 other species (Harlow and Lennartz, 1983), including the fox squirrel as noted above.

The expansion of the keystone species concept has led some researchers to criticize it as so fuzzy that it is impossible to say what is and what is not a keystone species; they go so far as to charge that it is dangerous to apply the concept to management (Mills *et al.*, 1993). However, to discard the idea would be to throw the baby out with the bathwater (deMa nader and Hunter, 1994). It seems more reasonable to refine it. A recent such effort (Power *et al.*, 1996) aims to quantify the criteria for designation as a keystone species and attempts to separate the concept from that of the 'ecological dominant', or species whose great biomass and abundance make it crucial for an entire community and allow it often to constitute the physical structure of the community.

Power *et al.* (1996) are pessimistic about the prospects for concocting a list of attributes that would *a priori* identify a keystone species inexpensively and efficiently. I agree. It is telling that much of the literature on keystone species is experimental in either the narrow sense of controlled manipulation (e.g. Paine, 1969) or the broader sense of some 'natural experiment' without strict control and replication, like an introduction of a species (Simberloff, 1991) or a removal of one (e.g. rabbit *Oryzotolagus cuniculus*, Harper, 1969; American chestnut *Castanea dentata*, references in Simberloff 1997; and beaver *Castor canadensis*, references in Naiman *et al.*, 1986; Hackney and Adams, 1992; Pollock *et al.*, 1995). In the latter cases, it is more difficult to draw inferences, but before-and-after comparisons or spatial comparisons between sites where the event occurred and those where it did not can often be quite suggestive.

Understanding the role of keystone species certainly requires inspired natural history (Paine, 1995), and there is no real shortcut for obtaining sufficient insight into the dynamics of an ecosystem. However, because a keystone species approach is focused squarely on an understanding of the mechanisms that underlie the function and structure of an ecosystem, it appears that it might suggest entirely new ways of managing a problem, rather than the successive-approximation approach that dominates adaptive management. For



example, keystone species are sometimes context-dependent (Paine, 1995; Power *et al.*, 1996). The same species in what look like two similar ecosystems may be a keystone in one but not the other. Research to understand these differences has led to quite profound understanding of the functioning of entire systems (Paine, 1995).

Management of keystone species may combine some attractive features of single-species management and ecosystem management. If the keystone affects many other species in its community, it may well be that facilitating its growth and reproduction would support the many species it interacts with as well. To the extent that the keystone is functionally crucial to a suite of other species, its management may maintain them. This proposition is a hypothesis rather than a fact. One would want to know the reasons for the keystone role of a particular species: what causes populations of so many other species to depend on this one?

From a scientific standpoint, the appeal of studying keystone species is apparent: such study is in the tradition of normal, analytic science. If this research is insightful enough, the knowledge it provides about the functioning of the target ecosystem should lead to an ongoing research program and progressively more profound and complete knowledge of the ecosystem. Such knowledge could hardly fail to aid management even if it should turn out that managing this particular keystone will not be a major component in a strategy to maintain the whole system. Further, profound knowledge of the mechanisms whereby the keystone species affects others, whether or not it leads to managing the keystone itself, would certainly provide further insights into how to maintain or replace various functions to make conservation increasingly efficient and assured. And a focus on keystone species and their role in the conservation of other species would force us to consider species directly, rather than processes that might or might not maintain them.

Finally, management based on keystone species would avoid ambiguities. We would not be relying on a battery of terms—ecosystem health, ecosystem management, adaptive management, sustainability—that mean different things to different people. Thus, managers, scientists, and the public would all know the were talking about the same thing.

This proposal is not meant to say that all problems are solved in identifying keystone species and using them as a conservation tool. It could be that study of many keystone species will determine that they usually cannot be managed efficiently as the centerpiece of a conservation strategy. We would still be left, however, with greatly increased understanding of the species and their ecosystems. It may also turn out that not all ecosystems of interest have keystone species. To some extent, the definition is arbitrary—what fraction of the species in a community must be governed by the candidate species in order for the latter to qualify as a key-

stone? Whatever the criterion, it is conceivable that, in some ecosystems, there are no species whose fates are integrally linked to those of many other species. Again, we would be left with a lot of useful knowledge about ecosystem structure and function in this case, even if we were not provided with an immediate conservation tool. Finally, there have not been many detailed studies of keystone species and how to recognize them. Thus, we need much basic research just to get started, and such information has not been gathered for many ecosystems. Nevertheless, it is hard to believe that truly effective management plans will ever be forthcoming without such knowledge.

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