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The role of science in the preservation of forest biodiversity

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Abstract

Forest management must change radically to maintain biodiversity. ‘Biodiversity’ has many components, but only one has been measured unambiguously – species richness – although there is recently much emphasis on structural, process, and functional diversity. So we must determine exactly what aspects of biodiversity to seek, and why. A battery of suggestions about how to achieve this re-focus on biodiversity (e.g., ecosystem management and the ‘new forestry’) are catchwords rather than guides on how to manage forests on the ground. These suggestions stem from an ill-defined concept of ‘forest health,’ which can be seen variously depending on the desired role and state of a forest. Ecosystem management for some versions of forest health may even decrease some forms of biodiversity. A decline in species richness need not lead to a decline in the process diversity or rates. Evidence that species richness contributes to ecosystem maintenance and function is scant. Thus, effective management for biodiversity (generally species richness) entails a frank commitment to maintain biodiversity as an end, not as a means. Some suggestions to maintain forest biodiversity while still allowing timber production, such as uneven-aged stand management and various burning regimes, are focused squarely on species richness per se, but they are hypotheses, not scientifically validated procedures. Existing empirical measurements on such techniques are usually on the amount and sustainability of timber harvest, not on how well they maintain species richness. A wealth of scientific research is needed, involving landscape-level field manipulations and careful natural historical observations on the effects on various species. The idea that forests can always serve multiple uses, including wood production and maintenance of all species, is an untested hypothesis. It may be incorrect; maintaining some species may require extensive pristine tracts. The major requirement for almost all research needed to manage forests for biodiversity is extensive and intensive monitoring. The concepts of umbrella and indicator species as management shortcuts are barely tested. Their utility can be validated only by intensive field study. Valuable umbrellas and/or indicators may exist for some forest systems. However, management procedures should not evolve towards management of indicator species, as the indicator might cease to indicate the status of other species. By contrast, managing an umbrella species is not an inherent contradiction in terms, but different umbrella species may shelter different sets of species, so management for one might be inimical to the other. The concept of keystone species may be useful in forest management. If the fates of particular species determine those of many others, managing for such keystones may effectively maintain species richness. But recognition of a keystone species requires well-designed experiments.

1. Introduction

Most forest management will have to change drastically to preserve biodiversity. A battery of suggestions have arisen recently to effect this change: ‘the new forestry, ecological forestry, ecosystem management, structural retention, new perspectives’, etc. I will try to show that these terms mean different things

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to different people, that most rest on an ill-defined concept of 'ecosystem health' or on a nebulous notion of a balance of nature, and that successful management of biodiversity will likely require much more traditional scientific experimentation, including substantial monitoring. Thus, even though a revolution in forest management is widely heralded nowadays (e.g., Kohm and Franklin, 1997), it is not founded on specific scientific tests, and prescriptions are vague.

Traditionally, forest management was construed as ensuring lucrative short-term wood production. This approach was more akin to engineering than to biological management and has left a legacy of university 'forest engineering' departments. However, this viewpoint led to a failure to see the forest for the trees. Preserving biodiversity requires us to see a forest as a community of species rather than a wood factory. But, given a commitment to preserve the whole forest community, how exactly can this goal be accomplished, and what role will science play?

2. Biodiversity

The average citizen thinks of 'biodiversity' as the number of species in a system (species richness); that is usually what conservation biologists mean by 'biodiversity.' Technically, it is much more. Often it is characterized as 'diversity' at three levels: genetic, species, and ecosystem e.g., OTA (1987). And it is not always clear in the technical literature whether diversity at any of these levels is measured by simply counting entities (genes, species and ecosystems) or by some more complex algorithm (e.g., an information theoretic index). Again, to the lay public, and to conservation biologists, 'diversity' almost always means number of entities. More recently, some scientists refer to structural and process diversity as key components of biodiversity (e.g., Franklin, 1988; Franklin et al., 1989). Of course, how one counts structures and processes is even less evident than how one counts ecosystems.

Given this welter of meanings, we must be very certain what someone is seeking who aims to manage forests for biodiversity. In this paper, unless qualified, 'biodiversity' will mean number of species, as it does to most of the public.

3. Ecosystem health and the balance of nature

Ecosystem health also means different things to different people, and its relationship to biodiversity is not established except for the tautological situation in which number of species is defined as a measure of ecosystem health (e.g., Rapport, 1989). The problem is that ecosystem health is defined according to what is seen as the 'purpose' of the ecosystem (Rapport, 1989; Wagner, 1994; Wicklum and Davies, 1995). One extreme of a spectrum of views is utilitarian, in which the purpose of the forest is to produce timber, and a healthy forest allows one to extract a lot of timber. The U.S.D.A. Forest Service (1993), p. 4, for example, says, "forest health is a condition where biotic and abiotic influences on the forests (that is, pests, silvicultural treatments and harvesting practices) do not threaten resource management objectives now or in the future". The other extreme may be termed ecosystem-centered: "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, p. 16). Generally, utilitarian views conceive of forest health as robust and protecting us, whereas ecosystem views, see it as fragile and requiring our protection.

So even though it seems superficially that no one could object to forest health, a goal of forest health could be inimical to conserving various species if, for example, one had a utilitarian view of forest health. American Senator Murkowski (1996), leading the charge for greater logging in national forests, believes that "the nation faces a forest health emergency" largely because timber harvests are too low. Widespread use in some forestry circles of metaphors like 'decadent' for old-growth forest epitomizes this problem. For example, Craig (1986) argues that 'decadent' old-growth would be 'dysgenic,' characterized by low genetic diversity and high levels of pathogens and pests.

There is a more fundamental flaw with the concept of ecosystem health: it connotes a highly organized ecosystem, with homeostatic mechanisms making it robust against external stress in the same way that individual animals have defenses against biotic and abiotic stresses (Wicklum and Davies, 1995; Simberloff, 1997). This superorganismic metaphor for an ecosystem is venerable (Egerton, 1973; Simberloff,

1984) but imperfect (Calow, 1992; Wicklum and Davies, 1995). Homeostatic mechanisms of animals are naturally selected and genetically based; to the extent that ecosystems achieve equilibria at all, they are determined by physical, chemical, and biological properties of the system (Calow, 1976) and are temporary artifacts of observation, but not intrinsic system-properties (DeAngelis and Waterhouse, 1987; Wicklum and Davies, 1995).

The whole notion of ecosystem health is really a version of the idea of a balance of nature (see the quote from Monnig and Byler given above), which goes back at least to ancient Greece (Egerton, 1973; Simberloff, 1984). The extremes of the spectrum of views of forest health exactly mirror a spectrum of ideas on a balance of nature. Some, such as many of the Greeks, saw the balance of nature as a robust phenomenon, tending to resist stress and to protect nature (and humankind) from perturbations, including our own thoughtless actions. Others, such as many writers of the Middle Ages and present-day conservationists, perceive the balance to be a fragile phenomenon, one that we (or God in the Middle Ages) must protect by inputs and/or careful management. Beginning with Alfred Russel Wallace in the 19th century, as forcefully stated by such 20th century ecologists as Charles Elton, Paul Ehrlich, and Charles Birch, scientists cast doubt on the utility of the balance of nature on the grounds that it is unfalsifiable – almost any observation can be construed as evidence that nature is balanced. Thus, almost all ecologists today have ceased worrying about whether nature is balanced and focused instead on relationships between its various parts. But, probably for psychological reasons, the notion of a balance of nature is embedded in the popular mind, and many conservationists speak of saving the balance of nature or managing for a balanced nature. For the same reasons that forest health is not a workable goal in management for maintenance of biodiversity, neither is a balance of nature.

4. Ecosystem management

In forestry, ecosystem management is trumpeted as a solution to conservation problems (Simberloff, 1997). As with ecosystem health, there is no consensus definition of 'ecosystem management' (Grumbine, 1994, 1997; Soulé, 1994). In the US, various governmental agencies all have different definitions (Morrissey et al., 1994); all agencies have adopted it as a governing paradigm, though some (e.g., the Department of Commerce) do not even attempt a definition. The underlying idea is that, if we keep an entire ecosystem healthy, all its component species should be healthy. The previous discussion of ecosystem health should alert us to the potential problems in the goals and methods of ecosystem management.

A key feature in almost all the myriad definitions of ecosystem management is a focus on ecological processes rather than individual species (Meffe and Carroll, 1994). In some incarnations, ecological processes are perceived as keeping an ecosystem healthy, and the ultimate goal of the management (and conception of ecological health) is to maintain species and communities (e.g., Bourgeron and Jensen, 1993; Franklin, 1994). For others, the processes themselves seem to be what ecosystem management is designed to preserve. For example, many US agencies list maintenance of processes and functions as the first or only goal of ecosystem management. This focus on processes has alarmed many conservation biologists. Soulé (1994) fears that sound procedures developed to maintain threatened species will be discarded as representatives of an old-fashioned paradigm, single-species management. Many ecosystem processes can be preserved even if component species are lost (Tracy and Brussard, 1994). Energy flows and nutrients cycle even in species-poor communities. Some threatened species (such as charismatic vertebrate top carnivores) could doubtlessly disappear from their ecosystems with little effect on key processes (Simberloff, 1997). Some processes typically function at greater rates with fewer species. For example, the primary productivity of second-growth forest of low species richness often exceeds that of diverse old-growth forest.

Another prominent feature of most resource management agency definitions of ecosystem management is that humans are typically part of ecosystems (e.g., Salwasser and Pfister, 1994). There are two crucial consequences of this conception for forestry. First, it tends to lessen the management prominence of areas from which human activity is excluded, as exclusion of humans is antithetical to the very notion of a normal ecosystem. The title of a recent plan to apply ecosystem management to forestry (Shepard, 1994, p. 218) is eloquent: "Modern forest management: It's about opening up, not locking up". Second, the fact that humans use resources is seen as 'natural', but not dangerous to ecosystem-health. Whereas conservation biologists, if they advocate ecosystem management, see its goal as maintaining biodiversity (e.g., Meffe and Carroll, 1994), resource managers often believe that the desired outcome is production of goods and services by the ecosystem for humans (e.g., Jensen and Everett, 1993; Grumbine, 1997). This is another reflection of the dichotomy in conceptions of the balance of nature and ecosystem health – does the balance (health and ecosystem management) protect and serve humans, or is it something humans use to protect the rest of nature?

Many US agencies, including the U.S.D.A. Forest Service, have attempted to finesse this conflict by the philosophy of 'multiple use' (Kessler et al., 1992). Overbay (1992), p. 5, sees no problem: "for the Forest Service, ecosystem management means to produce desired resources, values, uses, products, or services in ways that also sustain the diversity and productivity of ecosystems". Signs marking the entrance to many US national forests say 'land of many uses'. But the assumption that forests could always produce all desired endpoints is now being questioned (Barthod, 1994; Grumbine, 1994; Wagner, 1994). Some ecosystems may not be managed to the satisfaction of all parties. In a landscape dominated for many centuries by human activities, as in much of Europe, some biotic communities may be so well adapted to traditional activities that ecosystem management in favor of these activities will help (and may even be necessary for) conservation of threatened biodiversity. For example, some British insects are so tied to particular, waning cultivation techniques that they are endangered (Thomas and Morris, 1995). But a marriage of the interests of the ecosystem-centered view of forest management and the utilitarian, human-centered view is likely to be globally rare.

5. Biodiversity as an end vs. biodiversity as a means

As noted above, some definitions of ecosystem health include high biodiversity (e.g., Rapport, 1989). For others, function and process are primary determinants of ecosystem health. The desire to justify conservation in utilitarian terms has led to a major thrust to show that normal ecosystem processes provide valuable economic services – for example, flood or fire control, pollination, climate moderation, waste degradation (Ehrlich and Mooney, 1983; Daily, 1997) – and a concomitant thrust to show that biodiversity (=species richness) contributes in maintaining these ecosystem functions. In other words, species richness is desired either for its own sake (as an ethical or aesthetic matter) or because it facilitates valuable processes. A burgeoning literature on the latter claim (e.g., Schulze and Mooney, 1993; Vitousek et al., 1995) provides scant evidence that biodiversity (species richness) per se is important for ecosystem function (Beck, 1997), despite widely publicized claims to the contrary.

There are two traditional hypotheses about the relationship between species richness and ecosystem function and two newer ones (Lawton, 1994). The classic rivet–popper hypothesis (Ehrlich and Ehrlich, 1981) pictures a madman randomly removing airplane rivets. Some rivets may not be crucial to the functioning of the airplane, but, at some point, removal of a rivet will cause the plane to crash. In terms of ecosystem function and the analogy of rivets to species, it is important to note that the rivet–popper hypothesis is agnostic about exactly why the plane crashes. It could be some cumulative effect of just too many missing rivets, or it could be that the last rivet removed had a unique function, and had a different rivet been removed at that point, the plane might still be flying.

The redundancy hypothesis (Walker, 1992), perhaps the most popular current hypothesis relating species richness to ecosystem function, states that many species in a species-rich ecosystem belong to groups of functional equivalents. Loss of any one group member might not cause much decline in its function, but loss of the last member could be catastrophic. Thus, on average, loss of species richness causes ecosystem functional decline, but, if managers knew enough about species' functions, they could allow for many species to be lost without a disaster. Note that one interpretation of the rivet-popper hypothesis is actually the redundancy hypothesis.

Lawton (1994) and Naeem et al. (1995) propose two other hypotheses. One is the null hypothesis that there is no relationship between species richness and ecosystem function, and the other is the idiosyncratic response hypothesis: loss of some species causes decline of some ecosystem functions, but the effects depend on the specific sequence of loss. Again, both the rivet–popper hypothesis and the redundancy hypothesis can accommodate the idiosyncratic response hypothesis.

Much evidence for both a relationship between species richness and ecosystem function and the cause of any such relationship is outlined by Beck (1997). Older studies were correlational and had too much uncontrolled variation to demonstrate the desired relationship convincingly. Occasionally they showed a negative relationship between species richness and ecosystem function, but conservation biologists (e.g., Christensen et al., 1996) ignore these findings and focus on ones showing a positive relationship.

Several recent experiments aim to test the relationship of species richness to ecosystem functions directly. Two experiments find such a relationship and have received enormous publicity. However, both are flawed and can provide limited guidance (Beck, 1997). The Ecotron experiment (Naeem et al., 1994, 1995) constructed small communities of four trophic levels with three species richness levels. In some ecosystem features (e.g., primary productivity), there was a decline with fewer species, in others no change. However, the experiment did not control for abundance (except for plants), which was correlated with species richness. Thus, any relationship between species richness and an ecosystem process could be an artifact of a relationship between abundance and that process. Additionally, these were very small communities (maximum of 31 species) in very small spaces, and the fact that only three species richness treatments were devised also limits the extrapolation that can be drawn from these results.

Tilman et al. (1996) looked at ‘communities’ of one trophic level – common prairie perennial herbs – on 147 3×3 m plots in Minnesota. They sowed various combinations of seeds of 24 species onto bare plots to produce seven different species richness levels, then measured primary productivity and nitrogen retention. They found a positive relationship between species richness and both variables, although the data show such a relationship only for richness of five species or below. In addition to the special kind of community they used, the other serious limitation is that their seeding treatment, used to produce different species richness, is confounded with a continuing weeding treatment that almost certainly affects primary productivity, and perhaps nitrogen retention (Beck, 1997).

Two more recent experiments and an observational study cast doubt on the relationship between species richness and ecosystem function. Tilman et al. (1997) planted and weeded 289 Minnesota plots, each of them 169 m^2, to produce seven species richness levels of up to 32 Prairie perennials. In addition, the species were assigned to functional groups on the basis of physiological and morphological traits. They found that species richness did affect plant productivity and several of the other response variables, but that number of functional groups and especially identity of functional groups were far better predictors of these variables. As in the study by Tilman et al. (1996), the ‘community’ of one trophic level limits extrapolation; the weeding process was not adequately described to determine if it is a confounding factor. Also, the plots of productivity do not actually portray a positive relationship with species richness beyond four species or with functional diversity beyond two functional groups.

Hooper and Vitousek (1997) did not explicitly look at species richness; rather, they constructed serpentine grassland plots with ten different plant composition treatments involving four functional groups of plants (with two species each). They did not find increasing productivity with increasing numbers of functional groups, but they did find that particular functional groups were crucial; in particular, plots with the functional group consisting of the two perennial bunchgrass species had highest productivity. Similarly, a particular functional group, rather than the number of them, caused the greatest reduction in inorganic soil nitrogen. To further understanding of the role of species richness in this system, subsequent experiments would have to vary both numbers and identities of species within the functional groups.

Wardle et al. (1997) studied the relationship between plant species composition and various ecosystem-level properties on 50 islands of different areas in the northern Swedish boreal forest zone. Because fire frequency increases with area, the islands have different species compositions. In general, species composition had a major effect on ecosystem properties, whereas species diversity was largely determined by species composition and furthermore was negatively related to ecosystem process rates. The key finding was that one early successional tree species, *Pinus sylvestris*, has favorable litter quality (thus increasing process rates) but depressed species richness. On the other hand, greater ecological stresses on smaller islands (owing to the higher concentrations of phenolics, lower pH, and reduced availability of nitrogen) prevented competitive dominance, thereby increasing species richness, but favored the presence of species that retard ecosystem processes.

In sum, although the Ecotron and earlier Minnesota grassland experiments are often cited as demonstrating a positive relationship between species richness and ecosystem function, the best that can be said is that they are extremely limited in terms of types of ecosystems and numbers of species, the experimental design needs improvement, and the field of experiments on species richness and ecosystem function is in its infancy. The most recent experiments, plus the observational research by Wardle et al. (1997), suggest a much more important role for species composition, although the experiments are still on very special types of communities and the observational study is on plants only. One might think, as does Grime (1997), that the latest results should lead to less conservation concern about species richness and more about function. Others disagree. P. Kareiva (cited by Yoon, 1997a), for example, argues that species richness functions as a sort of probabilistic insurance policy. The more species present, the more likely that key functions will be maintained. This view is a version of the redundancy hypothesis.

No one would deny the likelihood that formerly species rich ecosystems reduced to a fraction of their original species richness (a dozen or so species, or fewer) will decline in some functions (cf. Grime, 1997). What is not demonstrated yet is if, even on average, an ecosystem with 350 species functions better, or is more likely to be stable, than one of 349 species. The take-home message is that, if our goal is to manage forests to preserve biodiversity, we must be committed to the value of biodiversity in its own right, and not as a means to some other function. Thus, the science that is needed is on how to maintain species, not on how to maintain various forest functions by substituting species for one another.

6. What should scientists do next?

Terms now used to characterize management to maintain biodiversity are catchwords that signal a commitment to this goal rather than scientifically demonstrated methods. They may suggest scientific experiments, but they are currently just ideas, all versions of ecosystem management. The ‘new forestry’ (Franklin, 1989, 1990), for example, is a collection of suggestions (like leaving some slash rather than clearing or burning it) that all sound reasonable, in that they would provide a habitat for species that lack it under previous logging regimes. However, they are largely untested. Few controlled, replicated experiments indicate exactly how each of these proposed modifications would affect species richness, much less biodiversity as a whole. Would the number of species increase? More importantly, which species would constitute the increase? How much slash would have to be left to achieve how much of an increase? In what spatial configuration would it have to be left? Some Fennoscandian research on species in dead wood left in logged areas (e.g., Samuelsson et al., 1994; Kaila et al., 1997) and in old trees, logs, and snags (Berg et al., 1995) shows the sort of data that must be gathered, while there is abundant evidence on the importance of downed trees to some species of stream biota (e.g., references in U.S.D.A. Forest Service and cooperating agencies, 1993). But this research must now be transformed into controlled experiments comparing results in replicated treatments consisting of different logging regimes, and this kind of research must be conducted worldwide. Data are the real need (Franklin et al., 1997). This is a major research agenda, but the new forestry and ecosystem management cannot be evaluated without it.

As a specific example, consider the long leaf pine (*Pinus palustris*) forests of the southeastern United States. These forests once covered 28 million ha; ca. 600 ha of old growth remain, plus perhaps 4 million ha of second growth. This habitat loss menaces species highly adapted to this type of forest, of which one – the red-cockaded woodpecker (*Picoides borealis*, RCW) – is a federally listed endangered species. This fact has forced the national forests and forest industry to devise plans to maintain this species – not to maintain biodiversity in general. The Forest Service has produced a management plan for national forests containing the bird (U.S.D.A. 1995). A variety of timber harvest techniques are proposed. Specific sizes of the logged areas are a maximum of 10 ha in regions in which the RCW is deemed at severe or extreme risk. Evidence exists that all proposed harvest methods except perhaps single tree selection can, in certain circumstances, regenerate long leaf pine trees at an acceptable economic rate (Baker, 1987; Farrar and Boyer, 1991; Boyer, 1993). However, there is little evidence on the impact of most of them on RCW (but see Connor et al., 1991 on irregular shelterwood methods) and almost none on their effects on other inhabitants of long leaf forest (but see Brennan et al., 1995 on vertebrates).

Further, overlaying the several proposed harvest regimes are various procedures designed to maintain RCW populations – for example, constructing artificial cavities to mimic cavities this species either finds or laboriously excavates, and removing birds from larger populations to sites of smaller populations in which nest holes (either natural or constructed) are available. In addition, prescribed burning on a 2–5 year cycle will be used to reduce midstory hardwood vegetation, and in some instances it appears the goal is to mimic the natural fire regime. This is in line with the recent forestry literature advocating various logging regimes that simulate aspects, such as timing and extent, of natural disturbance regimes (e.g., DeLong and Tanner, 1996). Thus, 'as many prescribed burns as possible' (U.S.D.A. 1995, p. 190) will be during the growing season, when most lightning-caused fires occur in long leaf forests. However, burning may be used year-round when conditions permit. Natural firebreaks, such as streams, will be used whenever possible, and all plowlines will be kept at least 61 m from RCW cavity trees. Specific sizes of the burned areas are not specified.

As with the harvest methods, the population consequences of such habitat management techniques for the RCW have barely been studied; the possible consequences for the myriad other species have scarcely been considered. Thirty-six mammal species and 85 bird species in addition to the woodpecker inhabit long leaf forest (Engstrom, 1993), as do 187 rare vascular plant taxa (Walker, 1993), 72 reptile and amphibian species (of which a third specialize in this habitat (Guyer and Bailey, 1993)), and at least 4000 arthropod species, including perhaps 10% that are endemic (Folkerts et al., 1993). An Appendix (Costa, 1995) to the Forest Service plan (U.S.D.A. 1995) addresses the potential consequences of the proposed regime for 15 plants, seven mammals, three birds (in addition to the RCW), four reptiles, and one insect, and it finds them minimal at a regional scale. However, this opinion rests almost wholly on non-experimental evidence, the literature on many of these species is small, and the basis for expert opinion is sometimes murky. In any event, the opinion specifically (p. 3) does not address the effects of the proposed techniques within each component national forest and leaves this matter to be assessed as specific management procedures are adopted by each forest. Except where a species' geographic range is almost wholly on non-national forest land, it is difficult to see how an assessment of no adverse regional effect can be confidently stated in the absence of an assessment of what might happen in each forest.

What is needed, in addition to a rigorous experimental design for each technique, is sufficient monitoring to be able to make credible statements about how various procedures are affecting a substantial fraction of the species. This is a tall order; in fact, it is one of the key challenges facing conservation biology – to establish sufficient monitoring programs to be able to detect trends and effects (Yoon, 1997b). The monitoring outlined for the long-leaf pine forests (U.S.D.A. 1995) is restricted to the RCW and its habitat; after all, the management plan (U.S.D.A. 1995, p. 1) is "for the management of the red-cockaded woodpecker and its habitat". Yet it is already suspected that other species in this type of forests are affected by the pattern of fragmentation, especially through increased predation and herbivory rates (Simberloff, 1993).

One traditional way to circumvent such extensive monitoring is through 'indicator species', whose presence and fluctuations are thought to signal those of other species (Landres et al., 1988). However, the pilot studies to establish that a proposed indicator co-occurs with a set of species, and that its population fluctuations reflect those of the other species, are laborious and expensive, and they have therefore rarely if ever been conducted (Simberloff, 1997). Rather, the species routinely chosen as an indicator is one that is easy to monitor and thought to be typical of the habitat housing the community one wishes to maintain.

Again, such a choice represents a hypothesis, but without the pilot study, it is not a scientifically tested hypothesis. Should an indicator species be found, it is important that management procedures do not evolve towards managing the indicator, a development noted above for the RCW, as the indicator would then cease to indicate the fate of the suite of species it is supposed to indicate.

Management of a keystone species can perhaps aid in maintaining biodiversity (Simberloff, 1997). A keystone species is one with impacts on many other species, far beyond what might have been expected from its numbers or biomass (Paine, 1969). For example, in the long leaf pine forest, the gopher tortoise (*Gopherus polyphemus*) is a keystone species because 332 other species use its burrows (Jackson and Milstrey, 1989), while the RCW is a keystone because the cavities it constructs, often the only such holes present, are used by at least 22 other species (Harlow and Lennartz, 1983). However, one can imagine management procedures for the gopher tortoise that would effectively transform the forest into a pasture, obviously inimical to most species that use RCW cavities. So we may have an instance of dueling keystones! Clearly, if one manages so that a keystone species is maintained, it will help maintain many other species, but it will not necessarily benefit all of them. Such management must not be at the expense of an entire suite of species. Another problem with using keystone species is that it is unclear how many ecosystems have keystones, and the criteria for defining them are still evolving (Power et al., 1996). Certainly the research to establish which species are keystones and why will require laborious field experiments and inspired natural history (Paine, 1995).

An 'umbrella species' (Shrader-Frechette and McCoy, 1993) is another popular idea for circumventing a crushing load of monitoring. An umbrella species is one with such broad habitat requirements and large area needs that saving it will automatically save the community of interest. Thus, almost by definition, if one can identify and maintain an umbrella species, one will have substantially succeeded in maintaining biodiversity. However, as with indicator species, suggested umbrella species have been reasonable guesses, like wide-ranging birds, and the extent to which they fulfill the criterion would have to be tested. This approach has rarely, if ever, gone that far. Unlike with indicator species, managing an umbrella species need not necessarily contradict the conservation rationale of the umbrella. After all, the maintenance of an umbrella species by definition causes the maintenance of an entire suite of species with similar habitat requirements. On the other hand, highly specific, non-habitat-centered procedures, such as genetic manipulation of the umbrella species, would defeat its purpose.

Costa (1995) outlines reasons why the RCW is an umbrella species for the long leaf pine community. James et al. (1997) suggest that fire history is ultimately the key determinant of RCW populations, affecting soil nutrient dynamics and, therefore, ground cover composition, as well as the state of long leaf pines themselves. Further, proper management of the fire regime should aid the persistence of all native inhabitants of old growth long leaf pine forests, as these have evolved adaptations to frequent, lightning-caused fires. In this instance, then, a prescription for maintaining the ecosystem of interest seems straightforward. What remains to be determined is how to meld this prescription with one or more of the various timber harvest regimes cited above, to produce an economically viable forestry industry. Such a method would constitute a real instance of ecosystem management satisfying both economic and conservation goals.

7. Conclusions

A major scientific thrust will be needed to transform ideas on managing forests for biodiversity into practical, effective tools. The key components of this thrust will be careful natural history, controlled and replicated field experiment, and intensive monitoring. There are no ways to circumvent these requirements, though a serious investment in validating such concepts as umbrella, indicator, and keystone species may ultimately lessen the continuing monitoring burden.

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