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CHOOSING THE APPROPRIATE SCALE OF RESERVES FOR CONSERVATION

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■ **Abstract** Over the past ten years the scientific basis for reserve selection and design have rapidly developed. This period has also been characterized by a shift in emphasis toward large spatial and organizational scales of conservation efforts. I discuss the evidence in support of this shift toward larger scale conservation by contrasting the success of fine-filter (genes, populations, species) conservation and coarse-filter (communities, habitats, ecosystems, landscapes) conservation. Conservation at both organizational scales has been successful and merits continued support, although fine-filter conservation is more straightforward. Ecological theory suggests that conservation at large scales is preferred. Despite this preference, both fine- and coarse-filter conservation objectives have been met by small reserves. In many landscapes there are no opportunities for the conservation of native species diversity that encompass a large spatial scale. Thus, reserve selection at any organizational scale may include conservation at a variety of spatial scales. A variety of methods have been suggested that integrate across scales of conservation. Some, such as umbrella, flagship, and indicator species, remain very problematic. Reserve selection algorithms and gap analyses, in contrast, offer promising opportunities to increase the efficiency of conservation at all scales.

INTRODUCTION

Conservation is limited by a small pool of resources directed toward a large and not entirely attainable goal: saving global representation of all unique populations, species, communities, and ecosystems within their natural context. Maximizing efficiency in the protection of biological diversity is critical. Conservation actions are constrained by past losses of biotic resources and prioritized by threats to remaining resources. Exactly how to prioritize threatened natural resources for protection is an area of particular interest to conservation biologists. A large body of recent conservation literature has attempted to center protection strategies on large scales (19, 27, 30, 35, 102, 116). This emphasis on large-scale conservation is exemplified by the recent adoption of ecosystem-based management policies by

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18 US federal agencies (19, 26, 44). The US Fish and Wildlife Service, the agency principally responsible for implementing the Endangered Species Act, has typified this shift in emphasis by adopting an approach of ecosystem-based management (5, 6). My goal is to review issues of organizational (i.e., species, ecosystems) and spatial scale (reserve size) with respect to the protection of biological diversity. In particular, I assess the degree to which the emphasis on large scales is supported by scientific evidence.

Targets of conservation efforts range from genes, populations, and species to communities, habitats, ecosystems, and landscapes (60, 87). I use the term "fine-filter" to refer to conservation efforts directed at genes, populations, or species (sensu The Nature Conservancy; 97, 102). The term "coarse-filter" (sensu The Nature Conservancy) is used to refer to conservation efforts aimed at communities, ecosystems, or landscapes. This terminology is useful because it obviates the often confusing distinction between communities and ecosystems, both of which are often described by their dominant vegetation. For example, Wisconsin (152) and Illinois (58) have focused on describing communities for conservation purposes using dominant vegetation, while Noss et al (104) uses many of the same descriptors to describe endangered ecosystems.

During this review I highlight several points regarding the contrast between fine- and coarse-filter conservation. First, coarse-filter conservation, although scientifically appealing for a variety of reasons, is made difficult by a lack of general and objective measures of success or failure. Resolving this difficulty may be the greatest challenge for conservation biology during the coming decade. Second, conservation planning often inappropriately equates priorities for coarse-filter conservation of ecosystems and those for fine-filter conservation of large vertebrate species. Conservation programs ought to adopt approaches that distinguish, but also incorporate, concerns at both scales. Third, focusing protection on large sites, to exclusion of small sites, entails considerable sacrifices with respect to capturing diversity. A large share of diversity is restricted to sites where large reserves are not an option. If a conservation target is solely embedded within a human-dominated landscape, which they frequently are, then small reserves may be the only protection option. Finally, I argue that conservation actions at any organizational level may appropriately entail small or large reserves.

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FINE-FILTER CONSERVATION

Any conservation target that is protected must have attributes that can be quantified in order to measure the success or failure of management. Although there are multiple rationales for fine-filter conservation, the simplest is this: Populations and species must be saved from extinction in order to preserve biotic diversity. The simple objective of preventing extinction makes evaluation of success straightforward. Fine-filter targets are identifiable: If a species can be documented as rare within a state or country, then it is an appropriate conservation target. Formal

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programs exist for identifying species at risk. International conservation organizations identify species as vulnerable, threatened, or endangered (62, 171). Mace & Lande (78) have incorporated quantitative measures of threat into these categories. Additional work continues to fine-tune these generally accepted threat categories (67, 149). Using these widely accepted criteria, Red Data books provide international lists of vulnerable, threatened, and endangered taxa (24, 62, 171). Within the United States and Canada, state-based Natural Heritage programs classify threat by the number of extant populations and the degree of threat to those populations to track threatened species (83).

This is not to assert that all target identifications are unambiguous. Subspecies, isolated populations, and hybrids, in particular, present problems. For the purposes of federal listing of endangered species (93), the rule for specifying targets of fine-filter conservation is that they be evolutionary significant units (ESUs). An ESU is a lineage that is evolutionarily isolated (93). With recent advances in molecular genetics, techniques exist with which to measure the degree of genetic isolation of proposed targets (93). For example, the Florida panther (*Felis concolor coryi*) has evidence of introgression from South American genotypes (105). Despite this introgression, the Florida panther retains its designation as a distinct ESU because of its isolation from remaining other *Felis concolor*. Molecular taxonomy has confirmed that the red wolf (*Canis rufus*) is a hybrid between the gray wolf (*C. lupus*) and coyote (*C. latrans*). With unclear directives regarding hybrids, it is not clear how this evidence will affect listing for the red wolf (13).

Another advantage of fine-filter conservation is that evaluation is clear: Persistence is success, extinction is failure. Populations can be monitored from year to year to estimate critical demographic parameters. Demographic data can be used to predict population trajectories and estimate population viability (150). Although a thorough viability analysis frequently requires more demographic data than are available (45), the methods are well developed (9, 146, 166). Despite sophisticated techniques for estimating risk, setting the threshold level of acceptable extinction risk (e.g., 90% probability of survival for 100 years) is subjective (93). Although scientists may debate the choice of threshold levels, assigning an acceptable level of extinction risk for recovery remains an agency decision that may negotiated upon by stakeholders.

Finally, fine-filter programs have a history of legislated protection. Within the United States, the Endangered Species Act (ESA), designed to protect species and their critical habitat, has been called the strongest conservation legislation ever enacted (4, 111). Passed in 1973 and later amended, the ESA provides for the protection and recovery of endangered species and their habitats (93). Nonetheless, the ESA is a political tool and subject to variable application. A recent spate of lawsuits has found that the US Fish and Wildlife Service (USFWS) and Department of Interior have acted in an arbitrary and capricious manner in not taking listing action on behalf of certain endangered species (144).

Despite the considerable number of potential advantages that fine-filter conservation programs hold, they have often been cited as fatally flawed (e.g., 127, 165,

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170). One reason is that the problem of conserving biodiversity species by species is simply too large. As of August 1998 a total of 1143 species of vertebrates, plants, and invertebrates appeared on the ESA list (168), yet the IUCN (171) lists over 4500 species of plants alone that are at risk of extinction within the United States. Given that arthropod diversity far outstrips plant diversity, and that plants at risk outnumber all listed species 4 to 1, the ESA can only be considered a partial listing based on extinction risk and policy priorities.

Once a species is listed, funds are often insufficient to implement protection measures. Expenditures of the US Fish and Wildlife Service on behalf of endangered species in 1995 were distributed such that most species received no discernible funding for recovery actions, while the top ten funded species received more than 90% of all funds (S Johnson, USFWS—168a).

Since its inception, the ESA has resulted in the recovery and delisting of five species within the United States (168). Past recoveries are principally a result of two measures: alleviating predation pressure and reducing pollutants that cause reproductive failure. It is much more difficult to recover species where habitat degradation and loss are the primary causes of endangerment. Yet, habitat loss and degradation are the most frequent causes of species endangerment (39, 178).

The lack of recovery, however, only serves to raise the question of whether recovery ought to be the benchmark of success or failure of the ESA (21). There are clear weaknesses in both legislation and implementation of the ESA (21, 47, 63, 93, 127, 128). These include: 1. undue attention to high profile species (47); 2. insufficient protection of critical habitat (21, 127, 128); 3. a lack of critical data with which to construct a recovery plan (127, 132); 4. insufficient funding to implement recovery actions (93); 5. insufficient attention to interagency cooperation (21); 6. inappropriate attention to future uncertainty in population size (21, 47, 93, 127); and 7. delaying of listing actions until populations are at critically low numbers (21). An example of this final problem is *Pritchardia munroi*, a Hawaiian palm listed in 1992. At the time of listing this species was known from a single individual whose entire seed crop is devastated each year by nonnative predators (37, 156). Extinction of this species in the wild seems inevitable.

If species are not listed until they face a palpable likelihood of extinction, then the abeyance of extinction may be a better benchmark of success. Since 1973 only seven listed species within the United States have gone extinct (168; tecopa pupfish *Cyprinidon nevadensis calidae*, longjaw cisco *Coregonus alpenae*, blue pike *Stizostedion vitreum glaucum*, Santa Barbara song sparrow *Melospiza melodia graminae*, Sampson's pearly mussel *Epioblasma sampsoni*, Amistad gambusia *Gambusia amistadensis*, dusky seaside sparrow *Ammodramus maritimus nigrescens*). Given an average population size among listed species of 1075 for vertebrates, 999 for plants, and 120 for invertebrates (177), we might expect that more species would have gone extinct during this time. Without quantitative measures of extinction risk for each endangered species, it is impossible to calculate an exact number of expected extinctions, but consider the following: Mace (77) analyzed quantitative measures of extinction risk to predict that 100% of "critical"

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and 67% of "endangered" species are likely to go extinct within the next 100 years. Although Mace's criteria for "critical" and "endangered" species are not the same as under the ESA, quantification of extinction risk has been shown to increase, not decrease, the number of species in these high risk categories (76, 137). Using this estimate, we can adopt a few simplifying assumptions to predict how many species ought to have gone extinct between the inception of the ESA in 1973 and 1998. I make the conservative assumption that all endangered species fit Mace's endangered category (none are critical). I also assume that extinction is a stochastic process and that the suite of 1143 currently listed endangered species have actually been endangered since 1973. Under these conditions, one expects that during the past 25 years (1143 species $\times$ .67 species $\times$ 25/100 years $=$) 192 listed species should have gone extinct. Despite the simplicity of these assumptions, I assert that the seven observed extinctions represents a significant benchmark of success of the ESA.

The difficulty with fine-filter protection, however, rests in the fact that organisms require habitat. Habitat protection may involve multiple species, stakeholders, and habitats. Habitat Conservation Plans (HCP's) are currently the principal tool for both protection planning and issuing take permits for listed species under the ESA (93). The HCP process grew out of 1982 amendments to the ESA (93) and is an integrated plan intended to provide sufficient habitat for the long-term persistence of endangered species within a region or ecosystem. Early reviews of HCPs are mixed. The National Research Council (93) claims that the San Bruno Mountains (California) HCP has successfully protected resources, while Shilling (141) finds that the Yolo County (California) HCP principally provides a mechanism to avoid protection of critical species. Mann & Plummer (79) assert that HCPs are costly and inefficient and should be avoided. Further reviews of HCPs are needed to assess their success.

COARSE-FILTER CONSERVATION

Coarse-filter conservation has several distinct conceptual advantages over fine-filter conservation. First, coarse-filter conservation seeks to preserve not just targeted species and their immediate habitats, but also potentially important ecosystem linkages and processes (e.g., 116). These processes include attributes that vary over the short-term, such as nutrient flux and primary productivity, as well as longer term processes, such as natural disturbance regimes, soil development, or natural selection and evolution (88). Second, coarse-filter conservation can preemptively protect resources before they become critically endangered (19, 40, 102). In this sense, coarse-filter conservation actions may be more efficient by capturing more diversity for each action. Third, conservation arguably ought to extend beyond the preservation of species diversity and natural processes to include a broader array of environmental concerns, such as sustainable harvest of species and the sustainability of ecosystems within human-altered landscapes (19).

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Despite the appealing logical motivation for coarse-filter conservation, implementation is not a simple task. A variety of attributes of ecosystem value fall under the banner of coarse-filter conservation. The relative conservation value of ecosystems may be assessed by (*a*) endangerment of ecosystems (104); (*b*) hotspots of species diversity within ecoregions (2, 33, 121, 124, 169); (*c*) representation among habitat types (46, 58); or (*d*) critical ecosystem functions (30, 88). It is the multitude of valued attributes of ecosystems that make coarse-filter conservation difficult. There is no a priori basis upon which to prioritize one set of attributes over another. For example, do we value endangered habitats more or less than diverse areas? Is function more or less important than diversity? With unclear priorities, it follows that measures of success for coarse-filter conservation are also unclear.

A healthy, well-maintained ecosystem changes through time (19, 51, 88). For example, Meyer (88) defines natural ecosystems as open, temporally varying, spatially heterogeneous systems with flux and linkages across boundaries. These ecosystems are dependent upon both direct and indirect effects among species and have functions that depend on species diversity (88). A number of studies, recognizing the dynamic nature of ecosystems, attempt to identify critical attributes with respect to ecosystem management. For example, Christensen et al (19) recommend that the focus of ecosystem management goals should be on ecosystem trajectories and behavior. Similarly, Norton (95) suggested five axioms of environmental management for ecosystem health: 1. ecosystems are dynamic objects with fluxes; 2. ecosystem processes are interrelated; 3. ecosystems are hierarchically arranged with respect to time and space; 4. ecosystems are self-organizing and self-maintaining; and 5. some ecosystems are more fragile than others.

I use a "parking lot" analogy for evaluating suggested rules for ecosystem management. Without exception, a parking lot fits the aforementioned descriptions of functioning ecosystems: there is flux, species diversity, hierarchical arrangement, temporal and spatial variation, stability and variable fragility. If one can describe a parking lot as a healthy ecosystem without violating any major premise of ecosystem rules, then I argue that the rules are not very helpful. The obvious difference between parking lots and natural ecosystems is in the magnitude of the attributes. Specifying appropriate magnitude, however, may be difficult. For example, natural processes of allochthonous and autochthonous sedimentation cause lakes to become marshes or peatlands through time. If this process takes thousands of years, we call it succession. If this process takes decades as a result of anthropogenic increases in nutrient and sediment load, we call it environmental degradation. Given that we have quantitatively studied most natural processes for less than a century, we are not equipped to provide exact estimates of natural rates of variability or acceptable rates of change for many ecosystem processes affected by humans. Thus, we use a combination of observations, models, and theory to make predictions of natural rates. Nonetheless, criteria for success or failure are sometimes a matter of uncomfortably broad interpretation.

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Therein lies the principal challenge of all coarse-filter strategies. The magnitude of critical variables depends on the community, habitat, or ecosystem in question. A desert will have different critical attributes than a lake, forest, prairie, or ocean. Further, every particular geographic location carries unique attributes of size, initial condition, and context within its landscape such that no two deserts are likely to have the same expected attribute values. Since ecosystems vary, their evaluation criteria pose a multivariate problem with few objective guidelines (19).

Lacking general objective criteria, evaluation is an issue with ecosystem management. Brunner & Clark (14) evaluated three approaches to improving ecosystem-based management and concluded that neither clarification of general goals nor creating a better scientific foundation were necessary for making better decisions regarding ecosystem management. Instead, they advocate a practice-based approach that stresses societal and practical considerations along with science when making management decisions. Similarly, Grumbine (48) stresses the need to integrate social and scientific needs into management. Buzzwords of ecosystem management include "contextual thinking," "adaptive management," and "ecological integrity" (48). These are all relative concepts that enhance management flexibility and potential but also inhibit accountability of management actions. With no general rules we risk the criticism that every project is claimed a success even if it results in environmental degradation or diversity losses. If all management constitutes successful management, then ecosystem management is destined for a short period of utility. Despite the need for flexibility, specific benchmarks are required to evaluate specific management actions.

One way to alleviate uncertainty in defining appropriate goals is to use reference ecosystems as benchmarks for management (e.g., 107, 175). Most ecosystems provide some sort of background historical descriptions from which to benchmark. Nonetheless, these are likely to be inadequate in most cases. For example, longleaf pine (*Pinus palustris*) ecosystems of the southeast are a conservation priority because they are rich in endangered species and are a critically endangered ecosystem (104). In particular, the federally listed red-cockaded woodpecker (*Picoides borealis*) is dependent upon mature pine trees for nesting sites, and longleaf pine is a preferred species (36, 72). Perhaps as a result of this conservation concern, longleaf pine savannah is a particularly well-studied habitat. Longleaf pine dynamics in response to fire have been described using the old growth Wade Tract in southern Georgia (42, 118). Noel et al (94) compared longleaf pine forest structure across the Gulf Coast with the Wade Tract and found the latter to be structurally different from other stands. Although structural differences can be largely attributed to stand age, we cannot predict what proportion of these differences are driven by location. We know something, albeit considerably less, about arthropod diversity (50) and nutrient dynamics in response to fire (180). Less than 2% of the original 33 million ha of longleaf forest remain, and less than 0.5% of what is left is old growth (86, 104). As a result, longleaf pine conservation and restoration from Virginia to Texas will likely draw upon experiences gained from the Wade Tract. With few

intact old-growth stands, we cannot estimate the variation in vital processes among complete longleaf pine savanna ecosystems, and we know little regarding the appropriateness of this model for longleaf pine conservation.

Despite these many uncertainties, the abstract description of the problem may overstate actual difficulties. General rules have already been enunciated (88, 95). The chief objective for conservation biologists may be to fit attribute values of specific cases into these guidelines. Aplet & Keeton (1) define the "historic range of variability" (HRV) as the bounds of ecosystem structure and functions prior to disturbance by post-Columbian humans. Recognizing the unique nature of ecosystems, Aplet & Keeton suggest establishing ecosystem-specific HRV values as the principal guideline for ecosystem management. Historic range of variability, and similar constructs, encourage parameterization of critical ecosystem values and suggest management guidelines.

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SPATIAL SCALE

Increasing emphasis on larger reserves has been argued from the perspective of both coarse- and fine-filter approaches. With respect to coarse-filter targets, large reserves have the ability to capture a mosaic landscape of different habitats as well as habitats in different stages of maturity or succession (102, 117, 143). Biological reasons to support large reserve size on behalf of fine-filter targets are that large reserves (*a*) have the unique ability to protect species with large habitat requirements (22, 65, 173); (*b*) minimize negative impacts of reserve borders and edge effects (71, 81, 84, 182, 159); and (*c*) typically support large populations with lower extinction probabilities (15, 112). There may also be simple pragmatic reasons to support a preference for large reserves. Large reserves may be preferred over small reserves because they are logistically easier to manage. Alternatively, large reserves may also be easier to acquire when located in regions where real estate values are low compared to urbanizing landscapes (AP Dobson, unpublished data).

Small Reserves Can Be Effective for Some Targets

Diamond (31) proposed six reserve design guidelines based on island biogeographic theory. While not explicitly stated, these guidelines prioritize the objective of minimizing the likelihood of extinction of a fine-filter target. These guidelines, adopted by the International Union for the Conservation of Nature and Natural Resources (61), are commonly cited regarding reserve selection (102, 115) and continue to be elaborated upon (139, 140).

Diamond's (31) first guideline asserts that a large reserve is better than a small one. A principal argument for increasing size is that larger reserves decrease extinction risk. Most empirical data support this contention (15, 112), and, all things being equal, securing large areas is an appropriate planning objective. Noss &

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Cooperrider (102) consider any reserve less than 1000 ha as "tiny," with a clear implication that tiny reserves are a low conservation priority (101). The corollary to the "more is better" paradigm, however, is not "small is bad." Small size, by itself, is not cause to dismiss potential reserves. For example, Cowling & Bond (28) compared species-area relationships on mainland and island patches of Fynbos in South Africa and conclude that isolated reserves of 4–15 ha are sufficient to maintain floristic diversity for long periods of time.

The high degree of habitat loss in many regions leaves no alternative for conservation. Prioritization of large sites discourages consideration of many critically endangered species restricted to small potential reserves. For example, MacDougall et al (75) found that seven of nine habitat types in southeastern New Brunswick have a small total area and that 57% of all rare plants were found in these spatially restricted habitats. Turner & Corlett (167) review the evidence of species losses in small (<100 ha) tropical forest remnants. They conclude that while these remnant patches fail as reserves for most large mammals, they are likely to retain a considerable proportion of their plant diversity for decades. Turner & Corlett (167) summarize their findings by concluding that something is better than nothing in an environment where tropical forest is being lost at an alarming rate. Similarly, the largest numbers of California's rare plants are found in mixed chaparral, valley grassland, and coastal scrub (113). Nearly 80% of the over 1700 rare plant taxa are found in these three habitats. Very little habitat remains of either valley grassland or coastal scrub, and most of what is left is found in small patches (54, 55, 90). Although mixed chaparral is a widely distributed habitat type (49), the largest number of rare chaparral taxa are found on serpentine (113), which is frequently isolated to small patches.

Over 60% of the flora of Mauritius is endemic to the Mascarene Islands (Mauritius, Reunion, and Rodrigues), and approximately 80% of this flora is endangered (157). Less than 5% of the area of Mauritius remains in native vegetation. Median patch size of the 21 largest natural habitats remaining on Mauritius is 280 ha, with only a single site exceeding 1000 ha (129). Four of seven biotic regions, and three of five general vegetation types (e.g., rain forest), are not represented in any patch larger than 500 ha (129). More than 80 plant species of Mauritius have gone extinct; another 20 species are known from fewer than 10 individuals (157). Although there is concern regarding the persistence of diversity in small sites (130), it seems more of an error to fail to try than to try but fail. Further, if preserving diversity is envisioned through restoration of larger habitat patches, the process must begin by protecting representatives of this diversity.

A second reason for not abandoning small sites is that reserve size does not necessarily predict population size nor diversity. Owing to the positive correlation between site size and degradation, habitat quality must be considered in tandem with size. For example, large tallgrass prairie sites are frequently low-quality habitats that have a history of grazing and lack disturbance-sensitive, prairie-dependent plants and butterflies (110). Species-area curves of plant diversity on tallgrass prairies suggest that a 2-ha area of tallgrass prairie is often more diverse

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than much larger sites (126). Similarly, butterfly and leafhopper diversity levels off at sizes of isolated reserves much less than 100 ha (110). Most Midwestern states have lost an excess of 99% of their original tallgrass habitat (126, 131). As a result of this habitat loss, small reserves are the norm. The Nature Conservancy owns more than 100 tallgrass prairie reserves, 97% of which are less than 1000 ha (153). Nearly a third (70 of 236) of the dedicated nature reserves in Illinois are less than 10 ha in size (85), and an estimated 75% of remaining high-quality prairie sites in Illinois are less than 2 ha (126). Nonetheless, the existing suite of small reserves in the Midwest has been effective at capturing prairie diversity. Despite near total habitat loss, and a century of isolation in small fragments, there are few endangered species (10 plants, 2 insects) in the tallgrass prairie ecosystem (126). With a legacy of selecting prairie reserves on the basis of plant diversity, reserves in northern Illinois and southern Wisconsin have also effectively captured prairie-dependent insect diversity (110). In Illinois, restricting protection programs to large grasslands would have resulted in protection of fewer populations of many of the states' sensitive plant and insect species. Klein (69) argues that small prairie conservation has been so successful that restoration of sites such as schoolyards is a valuable exercise not just for education, but for conservation of ecosystem attributes.

A third reason not to abandon small reserves is that many species are naturally restricted to small patches. Diamond's second guideline states that single large reserves are better than several small ones. This guideline triggered a long and often heated debate over the ability of single large or several small (SLOSS) reserves to capture biological diversity (151). The SLOSS debate has been thoroughly reviewed elsewhere (87, 102, 151). Suffice it to say that protection is a prerequisite for maintaining diversity. If diversity is finely distributed over numerous small sites, then protecting small sites is warranted. For example, small isolated granitic outcrops of the southern Appalachians contain a number of endemic species (64). The chief threat to these species is trampling by visitors (64). Rather than focus on creating large reserves, appropriate actions involve increased protection of existing small patches. Similarly, serpentine outcrops of California have an evolutionary history of isolation. Semlistch & Bodie (138) note that 87% of Carolina bay wetlands along the southeast Atlantic coast of the United States are less than 4 ha in size, the US Corps of Engineers cutoff for regulatory protection. They also note that these small and often isolated Carolina bays are vitally important for maintaining breeding populations of amphibians. Conservation of diversity on serpentine, southern Appalachian outcrops, and Carolina bays will rely more on protecting a large number of patches, rather than protecting a few large sites.

The previous examples notwithstanding, not all conservation targets are well protected by small sites. Several studies have focused on assessing isolation and fragmentation effects on a suite of native scrub vegetation of San Diego. These studies generally indicate strong size-related effects and rapid degradation of small patches of this community type (11, 12, 158). Conservation planning needs methods for predicting when small reserves can effectively protect and maintain

diversity. The answer to this question is likely to be habitat specific. Nonetheless, we may gain some clues from certain ecosystems. The degradation of the aforementioned scrub habitats is strongly influenced by nonnative species. Sites surrounded and invaded by aggressive nonnatives are likely to be unsuccessful. Polis et al (119) identify ecosystems that depend on the influx of energy across landscape boundaries through subsidized food webs. It is likely that ecosystems that are heavily augmented by energy flow from adjacent ecosystems are not likely to succeed in maintaining diversity in isolation.

The Case for Holistic Reserves

The importance of large reserves is often argued on the basis of completeness. Large sites can support the full suite of regional natural diversity and the interactions that support this diversity. This concept has been enunciated by a number of authors. Pickett & Thompson (117) define a "minimum dynamic area" as the smallest area that contains patches unaffected by the largest expected disturbances. Large size is required to allow recolonization from undisturbed patches within the reserve. Shugart & West (143) argue that in order to maintain a landscape in dynamic equilibrium, a reserve ought to be 50–100 times larger than a typical large disturbance. Some versions of these arguments, however, appear practically untenable. Recalling that the recent Yellowstone fires were larger in size than the National Park, Grumbine (47) wonders whether the fact that Yellowstone is too small to be in dynamic equilibrium (143) is relevant to its functioning as a reserve. Nonetheless, how big is big enough remains an important question for conservation biologists.

Arguments for large reserves using minimum area concepts assume that only large sites can sustain a disturbance regime supporting the full array of habitats at different stages of succession; that large sites containing many patches support a more complete array of species than a suite of isolated sites that lack interactions among patches; and that disturbance results in local extirpation of species such that recolonization is a necessity. Empirical data do not universally support these assumptions. Most disturbances can dramatically reduce populations, but extirpation is not a general expectation. For example, there is concern that managed fire in small prairie remnants may jeopardize insect populations (108, 160, 161). Panzer (109) studied the potential of managed fire to cause the extirpation of vulnerable, prairie-restricted butterflies and leafhoppers on small (<100 ha) isolated prairie remnants. Panzer found no evidence that managed fires caused insect population extirpations over a six-year study. While populations of most species observed declined as a result of fire, they also tended to rebound quickly. Siemann et al (145) observed a similar response of insects to fire in a Minnesota prairie: a strong negative short-term effect, rapid rebounding, and no evidence of extirpations. These sorts of data suggest that tallgrass prairie reserves in the Midwest protect the historic range of variability despite being distributed in many small and isolated reserves. This example does not argue for a preference toward small

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reserves. Nonetheless, I argue that size and isolation of coarse-filter targets alone is not sufficient to dismiss them as valuable conservation targets.

Large Size Is Required for Some Targets

There is no substitute for large reserves for certain conservation objectives. For example, large size is a defining attribute of wilderness (99, 102). Similarly, a common concern of humanity is to assure that ecosystems continue to provide a supply of clean water (30). It would be ludicrous to assert that conserving a small reserve within a large watershed protects the hydrology of that watershed. On the other hand, this raises an important issue regarding ecosystem conservation: Degraded ecosystems may support many types of vital ecosystem functions. Research on the relationship between diversity and ecosystem function predicts that relatively low diversity ecosystems retain nearly full capacity of ecosystem functions such as nutrient flux and primary productivity (e.g., 134, 164). Thus, large degraded ecosystems provide benefits to humanity independent of their diversity. Whether these benefits are endangered, and hence represent a conservation benefit, remains a matter of interpretation.

Conservation has often focused efforts toward vertebrates with large habitat requirements. This emphasis is justified on the basis that society places more value on larger vertebrate species (174). Despite a bias toward funding conservation of larger species, we still often lack sufficient habitat for viable populations of large vertebrates (22, 65, 173). Problems relating to providing habitats for lions, tigers, and bears are well known, but these problems extend to many species in many regions. The existing suite of Midwestern tallgrass reserves has failed to protect species with large habitat requirements. Grassland birds in Illinois have declined throughout the twentieth century (56, 57). Grassland birds, formerly dependent upon pasture lands, are currently restricted to a few large but low-quality grasslands (56, 57). In this case, however, the fact that they thrive on low-quality sites benefits the birds. The potential exists to increase protection for grassland by focusing on large low-quality sites. There may even be a potential to create bison reserves within this context (154). The result, however, is that the negative correlation between site size and habitat quality in tallgrass prairie has resulted in a tension between balancing the needs of the few species that require large habitats versus the many species that require high-quality habitats (133).

INTEGRATING ACROSS SCALES

Reconciling the need for continued fine-filter conservation while accommodating coarse-filter conservation is a central issue of conservation planning (46, 53, 91, 123, 162, 163). Several approaches are being explored to assess the extent to which fine- and coarse-filter conservation objectives can be simultaneously met. I detail several common approaches below.

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Fine-Filter Targets for Coarse-Filter Objectives: Flagships, Umbrellas

Fine-filter conservation targets have been used to augment coarse-filter conservation under the guise of flagship and umbrella species concepts (142, 147). A flagship is a species that can garner resources in support of conservation as a result of its popularity. It has been shown that vertebrates, the larger the better, make effective flagship species owing to their public appeal (174). Fine-filter efforts on behalf of flagship species provide collateral protection of the habitats upon which they depend. There are, however, problems with using flagship species as a surrogate for coarse-filter conservation (147). First and foremost is the cost of dishonesty. If the flagship species is not located in a particular reserve or potential reserve, then there arises a problem justifying conservation actions on the coarse-filter target (147). If an ecosystem is the target of conservation, then reserve design ought to rely on a coarse-filter approach and not a fine-filter surrogate.

The umbrella species concept provides another expression of collateral value in conservation (102). Umbrellas are species with large area requirements such that other species are protected through conservation actions directed at the umbrella species. As with flagships, the use of umbrella species is logically appealing, but often problematic when considering specific cases (147). In particular, species with large habitat requirements may act as leaky, or partial umbrellas. For example, black rhinos in Namibia have been considered for use as umbrellas for other large herbivores because they have large home ranges. Berger (10) found that rhino behavior during extreme wet and dry cycles differed significantly from that of six other large herbivores: Other herbivores moved between habitats, while rhinos did not. As a result, protection programs aimed specifically at rhinos may fail to protect other species adequately by virtue of partially nonoverlapping habitat requirements (10).

Hierarchical Reserve Design

A variant of the umbrella approach is to use vertebrates to set coarse-filter reserve priorities (102, 176). Noss & Harris (103) proposed a tiered strategy for reserve design. Multiple use module (MUM) strategies include core reserve areas with a high degree of protection surrounded by buffer habitats with less protection. Core areas may then be connected through corridors (102, 115). Hierarchical reserve design plans such as MUMs are recommended in several recent conservation texts (87, 102, 115). Hierarchical reserve designs have been published for Florida (29, 98) and western Oregon (100) and are in development elsewhere (102, 115).

An assumption of hierarchical reserve design is that buffers enhance the ability of the core reserve to protect critical resources. Chief supporting evidence for the utility of buffer areas comes from a large number of studies on detrimental edge effects (71, 81, 84, 182, 159). A keyword search of only two conservation

journals (*Biological Conservation, Conservation Biology*) found in just the past six years 38 studies that addressed edge effects (1993–1998). There can be no doubt that a multitude of deleterious edge effects can diminish the effectiveness of reserves. The problem with mitigating edge effects is that different species have vastly differing effective edge widths. Typically edges are narrow (<100 m) with respect to plants (e.g., 84) and wide (>1 km) with respect to animals (159). Thus, an appropriate buffer for one species may be insufficient for another species and overkill for another. Reserve buffers are defined with respect to particular threats and the species that benefit from this protection.

Another key assumption of hierarchical reserve design is that dispersal corridors decrease extinction likelihoods (103). Several studies have attempted to document the utility of dispersal corridors, but supporting evidence has been found in fewer than half of these empirical studies (8). Studies that document corridor usage by wildlife typically do not take the additional step of addressing whether corridor usage affects demographic rates (8). In contrast, corridors may carry serious disadvantages such as providing avenues for exotic species, disturbance, or disease (59, 148), the same negative effects that make habitat edges poor reserves. Clinchy (23) further questions the utility of corridors by modeling alternative hypotheses for why adjacent reserves may have similar fates independent of corridors or their usage. After reviewing the evidence and recognizing the equivocal support for corridors, Beier & Noss (8) suggest that the burden of proving that connecting reserves lacks utility remains on those who would destroy the connections. To turn this around, I suggest that the burden of proof ought to rest on those who would divert needed conservation resources away from core habitats in favor of establishing dispersal corridors.

Despite these constraints, hierarchical reserve design may be the appropriate strategy for the protection of target species. Inherent in the idea of hierarchically designed core areas, buffers, and corridors is a target species to which these units are scaled. As such, hierarchical reserve design is an elaborate fine-filter program and not a coarse-filter strategy. We must not assume that a hierarchical plan is a coarse-filter program simply by virtue of large area.

Predicting Conservation Value: Indicators, Hotspots

Indicator species are those that predict the presence or diversity of other taxa (142). It is logically appealing to posit that attributes that make a habitat rich in one suite of species may also give rise to high diversity in other groups. The arduous task of identifying high priority conservation sites may be eased by using indicator taxa and not an exhaustive survey of diversity. An obvious first step in using indicator species is specifying the intent of the indicator. Nonetheless, vertebrates have often been used as indicator species without clear objectives as to what they were supposed to indicate (70, 147). Caro & O'Doherty (17) identify three types of indicator species in use those that predict attributes of: (*a*) ecosystem condition, (*b*) biodiversity, or (*c*) population trends in species that are difficult to sample.

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Unfortunately, empirical studies where the objectives are clear have also yielded equivocal results. Supportive results have typically used narrowly constrained indicators. For example, high correlations have been documented between tiger beetle (Cicindelidae) diversity and Lepidoptera in both North America (18) and Amazonia (114). Martikainen et al (82) found that white-backed woodpeckers (*Dendrocopos leucotos*) co-occur with a high number of threatened saproxylic beetles with which they share a common resource: decaying wood. Dufrene & Legendre (34) successfully apply phytosociological methods to discern patterns of covariation among plant species in order to better detect which species are the best indicators of overall diversity.

In contrast, many studies fail to support indicators as shortcuts, perhaps because they use a scale of measure that is too coarse. For example, Prendergast et al (121) and Prendergast & Eversham (120) lump diversity within 10 km^2 grid cells in England and then find low covariation among groups that may be using different habitats within those grid cells. Dobson et al (33) and Flather et al (38) failed to find strong covariation in taxon diversity but used all of North America as a study region. Weaver (172) used coarsely lumped recognizable taxonomic units (RTUs) of arthropods (e.g., mites, thrips, beetles) to assess covariation, but they did not find strong patterns. Caro & O'Doherty (17) suggest selection criteria that may help to identify successful indicators. Given the equivocal support, the current use of indicators is debated (2, 125) and requires empirical data to justify utility in each case.

Identification of biodiversity hotspots (92) in order to prioritize reserve selection is another method whereby fine-filters are used to predict coarse-filter value. Several studies have used biodiversity hotspots to identify conservation priorities (32, 33, 89). As with indicator taxa, there are important issues of scale to consider in the utility of biodiversity hotspots. When faced with reserve selection, however, hotspot information may not be sufficient, as one would also like to know the degree to which hotspots of diversity overlap in constituent species (179).

Selecting Reserves: Minimum Sets, Gap Analysis, and Gap Analogs

A variety of approaches has been developed to prioritize the selection of reserves for the protection of biological diversity. One approach uses algorithms that maximize selection efficiency in order to capture each conservation target in a potential reserve (7, 20, 43, 68, 80). Any attribute, fine- or coarse-filter, may be used as input data for reserve prioritization (122). Nonetheless, minimum set algorithms prioritize the representation of rarity in selection and are most frequently applied to fine-filter targets (e.g., species occurrences). These searching algorithms are complex, and a number of different methods have been proposed (20, 28, 41, 74). The scale of the units, not surprisingly, is important to the efficiency of reserve selection algorithms. Smaller selection units are observed in some cases to be more than an order of magnitude more efficient at identifying required reserves (122). Smaller scales, however, require more specific data. In addition, cells for

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the selection algorithms are abstractions on the physical landscape that may not reflect realistic reserve boundaries. For example, Lombard et al (73) map the density of endemic species and vegetation types in 9 km^2 grid cells, and they prioritize them for reserve selection for a portion of South Africa. Yet, it is not clear from this study whether 9 km^2 grid cells are realistic reserve units.

Gap analysis is a way to plan protection programs by assessing the degree to which existing reserves have already captured existing biotic diversity. Similar to minimum-set algorithm methods, gap analysis seeks to maximize the coverage of the full representation of all biotic resources. Using a geographical information system (GIS), gap analysis builds regional coverages of biotic and abiotic attributes such as vegetation cover, animal distributions, rare species occurrences, and land ownership (136). Overlays of information are used to distinguish resources that are protected in the existing reserve network from those that are not (gaps). Gap analysis is agnostic on whether to prioritize fine- or coarse-filter targets and is typically used to develop a mixed strategy that incorporates both scales. Nonetheless, since the emphasis in gap analysis is on landscape units, the bias is typically toward coarse-filter targets.

Less formal programs aimed at targeting gaps in protection abound. For example, during the 1970s, Illinois developed a program to prioritize reserve acquisition toward unprotected habitats and rare species (58). Similar programs exist in many other states. Haufler et al (53) advocate identifying reserves based on coarse-filter targets, and then overlaying potential reserve areas with rare species occurrences in order to identify gaps. Priorities can then be adjusted in order to capture the full spectrum of biological diversity. Regardless of the specifics, separately identifying fine- and coarse-filter targets and then designing methods to protect both are appealing strategies.

There are two principal limitations to gap analysis and its many less formal analogs. First, location data for species typically lack specificity. As a result, data layers on species distributions often rely on habitat descriptors to predict species occurrences (16, 136). For example, if there is no way to determine which habitat patches a particular species occupies, then all appropriate habitats within the region may be assumed to represent occurrences. Second, habitat descriptors are typically limited to attributes described with satellite imagery (136). Thus, habitat classification may be crude relative to the biotic variability observed on the ground (16). Despite these limitations, gap analysis has gained considerable popularity. Regional analyses are being published (16, 66, 155), and a national gap analysis program (GAP) is currently underway (115).

CONCLUSION

It has been posited that the era of species conservation is over (147) and that ecosystems integrated within landscapes will be the conservation unit of the future (106). Although these statements may be prophetic, we currently operate in an environment where knowledge of species endangerment far exceeds that of threats

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to ecosystem health and stability. Yaffee (181) suggested that the Endangered Species Act is important as a benchmark for societal values. Human society, along with scientists, is wrestling with issues of what it is about the natural world that merits protection and at what cost (95, 96, 124). Species protection legislation represents a line in the sand defining unacceptable negative impacts of humans in the natural environment. It remains a challenge to ecologists to formally delineate the line in the sand within the context of coarse-filter conservation.

The emerging emphasis of conservation on larger organizational and spatial scales has been punctuated by extremes. For example, Barrett & Barrett (3) characterize early conservation efforts as focused on: 1. bounded natural areas often small in size; 2. management for stability and persistence in systems assumed to be at equilibrium; and 3. diversity as objects of natural heritage value. In contrast, the "new" conservation focuses on processes and context in open systems that are generally large and interconnected (3). Within this context, management is active and assumes non-equilibrium dynamics. Although there is some truth to this description, abstract caricatures often fail in specific examples. For example, Midwestern tallgrass prairie conservation has long since adopted the view that non-equilibrium dynamics are the norm and active management is a necessity (25). Fire management of tallgrass prairie has been common practice for at least twenty years (126, 135).

Conservation managers have been both blessed and cursed by the attention of academic biologists. In an effort to find tools to maximize the efficiency of conservation, scientists rapidly suggest and then sometimes test new ideas for conservation. The immediacy of conservation encourages management agencies to adopt these new ideas before empirical knowledge is able to verify their efficacy. This has led to overenthusiasm for ideas that were later found to be only weakly supported (e.g., 52, 150). Academicians are principally rewarded for novelty. Research support is more readily available to work on a novel approach to conservation than it is for increasing our biological understanding of a particular conservation target. Society expects resource management agencies to use the best possible scientific information in decision-making, yet there is ambiguity as to what the best scientific information is. There are many competing protection strategies available. Within this context there is one clear message: Theory is nice, but empirical data are required before abandoning tried methods in favor of novel ideas. Nonetheless, a body of evidence is now building around several strategic conservation planning tools. While shortcuts such as indicators, flagships, and umbrellas are not gaining as much support as we would like, minimum set algorithms and gap analysis seem to hold great promise for conservation planning.

Through this review I have made several general points with respect to the organizational and spatial scale of conservation. First, no matter what we view to be a minimum area for long-term viability of a conservation target, we cannot sustain biological resources until we protect them. If this entails protecting smaller units than we would like, then we ought to prefer the risk of losing diversity in small reserves over the guaranteed loss of diversity by neglect. Second, accepting non-equilibrium dynamics, disturbance ecology, and patch dynamics as paradigms

of ecology does not require a preference for coarse-filter reserves. Embracing coarse-filter conservation is not linked to the abandonment of fine-filter conservation. Fine-filter actions remain some of our most successful programs, and we should expect them to continue to succeed. Similarly, embracing ecosystem-based management does not entail restricting conservation to large reserves. Choosing the appropriate spatial scale for reserves entails careful consideration of the alternatives. If a fine- or coarse-filter target is contained within a small parcel of land, then the appropriate action may entail a small reserve. Even with a hierarchical design, many good conservation projects encompass significantly less than the 1000s hectares required for conserving integrated ecosystems in a complex landscape. In aggregate, these points are in sharp contrast to the trend in conservation to restrict protection actions toward spatially large reserves in order to protect coarse-filter objectives and fine-filter targets with large habitat requirements.

Early conservation efforts may have inordinately focused attention on capturing fine- and coarse-filter targets of diversity as static objects of natural history, much as one would assemble a museum. Conservation actions are now redressing this by appropriately focusing efforts on conserving interactions among species and processes within ecosystems. Ecologists have argued the need to move away from the crisis-driven approach of species conservation (40, 170). While I agree with the sentiment, avoiding conservation crisis by adopting coarse-filter priorities to the exclusion of fine-filter conservation all but guarantees the crisis to be resolved through extinction. The effort to increase emphasis on coarse-filter approaches for large reserves must abandon neither fine-filter conservation nor conservation at small spatial scales. Conservation, in order to be effective, must strive to balance the protection of countable objects of diversity and the protection of natural processes. This balance will entail a broad array of programs and strategies on a variety of spatial and organizational scales.

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