A Regional Landscape Approach to Maintain Diversity

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Land managers have traditionally assumed that achieving maximum local habitat diversity will favor diversity of wildlife. Recent trends in species composition in fragmented landscapes suggest, however, that a more comprehensive view is required for perpetuation of regional diversity. A regional network of preserves, with sensitive habitats insulated from human disturbance, might best perpetuate ecosystem integrity in the long term. *(Accepted for publication 5 May 1983)*

Diversity of habitats and species has been a primary consideration for deciding which sites should be preserved (Goeden 1979, Margules and Usher 1981) as well as in management plans for parks, forests, wildlife areas, and nature preserves (Siderits and Radtke 1977, Thomas et al. 1979). But with recent developments in applied biogeography and landscape ecology, the maximum diversity concept has grown complicated. At what scale should diversity be measured and managed?

It is not often that conservation-oriented ecologists and land managers interact and discuss the issues, choices, and consequences involved in particular management decisions. I attempt with this paper to provide a basis for such communication and to examine the concept that long-term maintenance of diversity requires a management strategy that considers regional biogeography and landscape pattern above local concerns. Managers of parks, wildlife areas, and other public-use lands have traditionally been interested in maintaining maximum habitat diversity within each unit. This maximum local diversity strategy, although based on good intentions, may operate at the expense of the species and communities most in need of protection at a regional level (Faaborg 1980, Noss 1979, 1981, Samson 1980, Samson and Knopf 1982, Verner 1980).

A major goal of preservation is the perpetuation of indigenous ecosystem structure, function, and integrity. Furthermore, in a deteriorating landscape, all parks, preserves, and wildlife areas should have perpetuation of natural ecosystems as a principal goal. But individual ecosystems, the traditional focus of ecology, should not be seen as separate entities (Hansson 1977). Almost all ecosystems are "open" and exchange energy, mineral nutrients, and species. Particularly in highly heterogeneous regions, the landscape mosaic may be a more appropriate unit of study and management than single sites or ecosystems. *Landscape* has been variously defined, usually in somewhat ambiguous terms. I follow the more precise definition of *landscape* by Forman and Godron (1981) as a "kilometers-wide area where a cluster of interacting stands or ecosystems is repeated in similar form." A landscape is therefore an ecological unit with a distinguishable structure. The importance of the landscape concept is in its recognition that the structural components of a landscape interact (Forman 1981, Forman and Godron 1981).

WHY MAINTAIN DIVERSITY?

Conservationists are very much concerned with diversity, striving "to preserve viable populations of as many as possible of the species that inhabited the pristine landscape" (Terborgh 1976). Of course, each species is ultimately doomed to extinction as it fails to keep pace with changes in the environment, many brought on by evolutionary "advances" in other, interacting species (Stenseth 1979, Van Valen 1973, 1977). The goal of conservation is not to stop a natural process, but rather to abate the accelerating pace of species loss associated with human dominance of the biosphere (Ehrlich and Ehrlich 1981). Biologists have learned that individual species harbor unique genetic material and are components of functional ecosystems, systems that provide a vast spectrum of essential "public services" (Ehrlich 1980, Ehrlich and Mooney 1983). It is in this sense that preservation of species diversity assumes incontrovertible importance.

It is helpful to recognize three basic scales of diversity. *Alpha diversity* is the number of species within a single habitat or community (Whittaker 1972). In most cases, a single habitat is assumed to be a small area (a few hectares or less) of uniform vegetation structure. *Beta diversity* reflects the change in species composition along an environmental gradient or series of habitats. I follow Karr (1976) in interpreting alpha and beta diversities as roughly equivalent to the within- and between-habitat diversities of MacArthur (1965). This is counter to a strict definition of beta diversity, but is more useful for land managers. Finally, the total species diversity of a large geographic region (e.g., a landscape or larger) has been called *gamma diversity* (Whittaker 1972). These three basic scales or types of diversity may be affected differently by human land use practices in a given area. The habitat diversity for which land managers often strive is artificial beta diversity, a patchwork of different habitat types. For simplicity, the term *diversity* in this paper

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will at all times denote "simple" diversity, or richness—the number of species (or habitats) within a defined area.

WHY MANAGE FOR EDGE AND BETA DIVERSITY?

The "edge effect" has been a fundamental principle of wildlife management (Allen 1962, Dasmann 1964, Leopold 1933) and is a major factor encouraging a maximum local diversity philosophy. *Edge* is defined as the place where plant communities meet or where successional stages or vegetative conditions within plant communities come together (Thomas et al. 1979). It has long been observed that edges are rich in wildlife, since wildlife "occurs where the types of food and cover which it needs come together" (Leopold 1933). Along an edge, animals from each of the abutting communities or vegetation types may be found, together with animals that make frequent use of more than one vegetation type and those that actually specialize on edge (Johnston 1947). Edge has high cover density (Johnson et al. 1979) and food availability, in accordance with a high primary productivity (Ranney et al. 1981). Game animals are commonly edge-adapted, as are the animals (e.g., birds) of suburban and many urban and agricultural landscapes (Butcher et al. 1981, Whitcomb et al. 1976).

More work has been done relating birds to habitat conditions than for any other faunal group. The vertical distribution of foliage within a habitat is correlated with the number of resident bird species (Karr and Roth 1971, MacArthur 1964, MacArthur et al. 1962, Recher 1969), as is the interspersion of vegetation types. This patchiness or horizontal complexity of vegetation profiles is a major determinant of the variety of breeding species in a particular area (MacArthur and MacArthur 1961, Roth 1976, Temple et al. 1979). This beta diversity principle was anticipated by Lay (1938), who demonstrated an increase in bird species with the establishment of small clearings in a Texas forest.

Managers increase beta diversity primarily by maintaining a variety of patches of different successional age. This also increases edge effect. Meadows are periodically burned or mowed, thickets and row crops are interspersed, plots of hardwoods are cut here and there, and pines and fruiting trees (often nonnative species) are planted. Trails wind everywhere. These management practices are implemented to increase the variety and interdigitation of habitat types and thereby ostensibly favor a wide variety of both game and nongame wildlife (Faaborg 1980). That this maximum habitat diversity philosophy is deeply entrenched in the land management professions is evident from the literature. For example, in a chapter of a widely used wildlife management text (Giles 1971), Yoakum and Dasmann (1971) urge managers to "develop *as much edge as possible*" (italics mine), because "wildlife is a product of the places where two habitats meet." The National Forest Management Act of 1976 requires that a diversity of plant and animal communities be maintained to meet multiple-use objectives (Boyce and Cost 1978). Many have followed the advice of Siderits and Radtke (1977) that "a diverse wildlife population will require a planning approach that ensures a diverse environment." The area of land over which maximum diversity is attained is usually not specified, but the general emphasis on edge development and measurement suggests that it is the individual management unit rather than the regional landscape. Hence maximum beta diversity is the goal and gamma diversity (except in the case of very large units) is ignored. Alpha diversity is also generally ignored, perhaps because species number within a given vegetation stand is less tractable than the variety of stands in an area.

COMPLICATIONS OF THE MAXIMUM LOCAL DIVERSITY APPROACH

Almost all schemes for evaluation of habitat and wildlife potential consider diversity to be of fundamental importance. Emphasis on sheer numbers of species and habitats can, however, be dangerous when applied simplistically and irrespective of regional ecology. Particularly in manipulated areas, beta diversity may include nonnative species and species typical of domesticated environments. Are such species in need of preserves for survival? Many conservationists have questioned whether widespread and opportunistic species should be considered equal to more sensitive species in ecological evaluation and the design and management of preserves. Diamond (1976), for example, contended that "conservation should not treat all species as equal but must focus on species and habitats threatened by human activities." Edge species in particular, which are mostly widespread and "weedy" (Terborgh 1976, Whitcomb et al. 1976), are rarely in danger of extinction in a human-dominated landscape.

The problems associated with a maximum local diversity approach to conservation have been noticed primarily through work in applied biogeography (*sensu* Wilson and Willis 1975), which is an extension (and sometimes over-extension) of island biogeographic theory (MacArthur and Wilson 1963, 1967) to land use planning and the design of nature preserves. Nature preserves and forest fragments have been portrayed as islands because they are patches of natural habitat in a matrix or "sea" of culturally modified land (Diamond 1975, Diamond and May 1976, Forman et al. 1976, Galli et al. 1976, Sullivan and Shaffer, 1975, Terborgh 1974, 1975, 1976, Wilson and Willis 1975). The species-area relationship (Arrhenius 1921, Gleason 1922, Preston 1960, 1962) has been found to apply to habitat islands for many organisms. Interestingly, species-area and island biogeographic considerations do not by themselves argue against a maximum local diversity strategy. Indeed, conservation implications drawn from such studies are perhaps correctly applied only to achieving maximum species richness under conditions approaching equilibrium (Margules et al. 1982, McCoy 1982). The diversity of a whole landscape has not been considered, at least not explicitly. One must go beyond the strict model of equilibrium island biogeography to determine which species and communities in a biogeographic region should be targeted for priority conservation efforts.

As a nature preserve or habitat fragment becomes increasingly isolated from other, similar habitat, fewer species may be found than in sample areas of equal size within extensive habitat blocks (Miller and Harris 1977). But in many cases of habitat insularization, species richness does not seem to change, or may even increase; species composition, however, often shifts towards taxa with low area requirements or high edge affinities. These compositional trends associated with decreases in habitat island size or increases in isolation are often predictable (Faaborg 1979, Lovejoy and Oren 1981, Lynch and Whitcomb 1978, Ranney et al. 1981, Whitcomb et al. 1981). The first species to be extirpated from small fragments are frequently high on the trophic pyramid or are the larger or more specialized members of feeding guilds (Wilson and Willis 1975). Species with variable populations dependent on patchy or unpredictable resources seem particularly sensitive (Karr 1982, Terborgh and Winter 1980). Whitcomb et al. (1981) determined that the birds least tolerant of forest fragmentation in the eastern deciduous forest region (USA) tend to be neotropical migrants, forest interior specialists, open nesters (as opposed to cavity nesters), and/or ground nesters. Neotropical migrants, which typically comprise 80-90% of the breeding avifauna in extensive tracts of eastern deciduous forest, account for less than half the birds of small, isolated tracts (Whitcomb et al. 1976, 1981). Thus life history strategy can be an important component of vulnerability in a human-dominated landscape, as Levenson (1981) and Hoehne (1981) have also concluded for plants. Continual loss of native species from a landscape is certainly contrary to goals of preservation.

The deterioration of regional diversity as individual habitat patches become smaller follows from the minimum area requirements of many populations. Management for maximum diversity within individual units could exclude many species from the regional landscape if patch sizes fall below the threshold required for colonization or persistence of populations of area-dependent species. Relatively unbroken habitat blocks up to thousands of square kilometers in extent may be necessary to sustain populations of many species in the long term (Robbins 1979, Terborgh 1974, Whitcomb 1977). If habitats are fragmented within preserves in addition to outside them, the area-sensitive species may gradually drop out of the regional biota (Faaborg 1980, Noss 1981, Samson 1980, Samson and Knopf 1982).

DETRIMENTAL EFFECTS OF INDUCED EDGE

The rare species of "undisturbed" forests are particularly sensitive to habitat alteration (Noon et al. 1979), and human disturbance of forest interiors can have pronounced effects on species presence and frequency (Hoehne 1981, Whitcomb et al. 1976). Management for edge effect through habitat subdivision is clearly a perturbation of considerable magnitude to forest interior specialists, particularly in forest islands with large perimeter/area ratios. The perimeter of any forest island is edge habitat. Edges commonly extend 10-15 m into the forest on the east, north, and south sides, and up to 30 m on the west side (e.g., in southern Wisconsin forests, Ranney et al. 1981). When forest islands become small, there is an increase in edge area relative to interior. Edge flora, more tolerant of dry conditions, may replace interior species in small forests (Ranney et al. 1981), with the result that forest islands below a certain size are unrepresentative of the presettlement forest ecosystem. A very small forest may be entirely edge habitat.

Induced edge habitat in forests may also affect fauna. Swaths cut through forests for roads, electric transmission lines, sewer lines, and even wide trails not only stress the mesic (moist) habitat of certain species, but can destabilize entire faunal communities (Anderson 1979, Whitcomb et al. 1976). In such cases overall species richness may temporarily increase with the influx of edge-adapted opportunists, but only at the expense of the forest interior species. Birds are useful as ecological indicators in this dilemma. Corridor edges are frequently colonized by avian brood parasites (e.g., cowbirds), nest predators, and nonnative nest-hole competitors (e.g., starlings). These opportunists are usually abundant in the urban-agricultural matrix and easily invade woodlots with introduced edge (Brittingham and Temple 1983, Noss 1981, Robbins 1979, Whitcomb 1977, Whitcomb et al. 1976). Anderson (1979) found that the number of migrant birds decreased significantly, and community diversity was destabilized in a Tennessee deciduous forest after a transmission-line corridor was cut. Road and powerline corridors may also serve as at least partial barriers to the movements of small mammals (Oxley et al. 1974, Schreiber and Graves 1977) and could potentially disrupt normal dispersal patterns and population dynamics.

An illuminating study by Gates and Gysel (1978) documented some insidious effects of artifical edge. They found that a field-forest edge habitat attracted a variety and abundance of open-nesting passerine birds, but functioned as an "ecological trap." The authors determined that, although edge contains the structural cues of the mixed forest in which these birds presumably evolved, pairs nesting near the edge had smaller clutches and were subject to higher rates of predation and cowbird parasitism than those nesting in either adjoining habitat interior. These results supplement the increasing evidence that birds characteristic of forest interior habitats are unable to maintain their populations where edge is abundant (Robbins 1979). Management for high habitat diversity and edge not only degrades faunal communities, but may also accentuate negative effects of fauna on flora. Bratton and White (1980) reported that manipulation of habitat to support a huntable deer herd can result in heavy browsing in adjacent natural areas and further endanger a number of rare plant species.

An uncritical acceptance of the maximum habitat diversity philosophy may be inimical to the preservation of regional diversity if applied routinely in a number of management units across a landscape. Although local (beta) diversity may be increased by management practices that enhance habitat patchiness and edge effect, this local increment is obtained at the expense of those species most in need of protection. The increment generally comprises species that are common in the urban-agricultural matrix. Even the local increase in diversity may be ephemeral if forest interior species gradually drop out of the biota. Clearly, management for maximum diversity can be a "trap" (Verner 1980). Some positive and negative effects of management for each of the three general scales of diversity are summarized in the box (opposite).

A REGIONAL LANDSCAPE APPROACH

Ecologists, land managers, and planners have traditionally ignored interactions among the different elements in a landscape and, with rare exceptions, have looked at landscape elements as separate ecosystems (Forman 1981). A criterion of habitat homogeneity is often applied to field studies to focus attention on a tractable set of variables. But field naturalists have known for a long time that many organisms habitually move among "different" communities. MacArthur et al. (1962) recognized that some bird species may require two or more types of vegetation profiles rather than some mean profile. Karr (1968) suggested that, although it is important to control as many variables as possible in a scientific endeavor, it is also necessary to determine what occurs in areas characterized by an interdigitation of habitat types. These observations open the door to *landscape ecology*, the study of the interactions and fluxes of energy, mineral nutrients, and species among clustered stands or ecosystems (Forman 1981, Forman and Godron 1981). Landscape ecology deals with an ecological mosaic of patches with continuously varying degrees of connectedness and recognizes the importance of matrix and corridors to terrestrial habitat island dynamics.

Managing for Different Scales of Diversity*

SCALE	METHODS	ADVANTAGES	DISADVANTAGES
Alpha (within-habitat)	Achieve optimum levels of limiting resources (e.g., food supply) to ameliorate interspecific competition; increase structural complexity (e.g., vertical strata, substrate) to provide more physical niche space; control unwanted species.	Increased number of species within habitat, and/or increased population levels of particular species; desired community structure maintained.	May be arduous and costly to implement; considerable uncertainty about effects of management actions on particular species (undesirable species could reach pest proportions, and critical species could decline).
Beta (between-habitat, including "edge effect")	Maintain variety of successional stages; intersperse different habitat types; construct roads, trails, and other swaths.	Increased local species richness; increased population levels of edge-adapted species (e.g., many game animals); increased human recreational potential.	Decreased population levels or extirpation of interior specialists; proliferation of "weedy," opportunistic species; community destabilization; possibly decreased regional diversity (may limit options for regional diversity).
Gamma (regional)	Preserve sufficiently large areas of unaltered indigenous ecosystems on a regional scale; interconnect habitat patches; limit human intrusion in sensitive areas.	Adequate population levels and genetic variation of indigenous species maintained; critical ecosystem processes perpetuated; long-term human welfare promoted.	Some loss of local species richness with declines in edge species; more land taken out of "productive" human use; short-term economic losses.

* The three strategies are not necessarily mutually exclusive.

For any landscape, the model natural ecosystem complex is the presettlement vegetation and associated biotic and abiotic elements. Preservation activities would ideally maintain high-quality examples of presettlement-type ecosystems in approximate proportion to their former abundance in the region. This does not mean trying to hold nature static. Rather, *preservation* should imply perpetuating the dynamic processes of presettlement landscapes. Landscapes are constantly changing, gradually or episodically, over geological and evolutionary time with geomorphological processes, climatic change, and the origin and extinction of species. They change more rapidly with local or regional species turnover, meteorological events, and other aspects of disturbance. Within a landscape, however, the suite of disturbances and successions within a cluster of stands is relatively constant (Forman 1981).

A regional landscape approach to preservation demands an integration of ecological evaluation methodologies, coordinating data from individual species occurrences to regional landscape patterns. Rare species are generally the most vulnerable to extinction and must therefore receive priority attention in evaluation and protection programs (Adamus and Clough 1978, Terborgh and Winter 1980); but there is danger in overemphasizing rarity to the exclusion of other criteria. There are several categories of rare species, some of which may not be overly prone to further endangerment. Some rare species, such as key predators that regulate diversity of lower levels in the food chain, may have profound ecological importance; others may be redundant or nonessential to ecosystem function (although they nonetheless constitute unique genetic material and would be worthy of equivalent ethical consideration). There is also a problem of scale: species rare locally may be relatively common regionally or vice versa (Margules and Usher 1981). With regional diversity and ecological integrity as the goal, the rarity criterion is probably most appropriately applied regionally and/or globally.

Debate continues over whether one large preserve or several smaller preserves are optimal for preservation of regional diversity, with theory often yielding conflicting advice (Higgs 1981, Margules et al. 1982, Simberloff and Abele 1982). But in a human-dominated landscape, as Diamond (1976) pointed out, "the question is not which reserve system contains more species, but which contains more species that would be doomed to extinction in the absence of refuges." Much of the preserve size controversy has begged this important question, although Humphreys and Kitchener (1982) showed that vertebrates most in need of conservation (retained only in preserves) are favored by large reserves. Moreover, the focus on numbers of species tends to obscure the fundamental point that saving complete ecosystems is what is at stake, and natural ecosystems do seem to have a minimum critical size (Lovejoy and Oren 1981, Nilsson 1978). In regional landscape planning, preservation of whole ecosystems with the full complement of indigenous genetic diversity is the ideal. This demands a complex of both large and small preserves and as many as possible, taking advantage of auspicious protection opportunities when they arise. This "combined strategy" (Kushlan 1979) is designed to maintain both species and ecological processes in a landscape.

THE IMPORTANCE OF INTERCONNECTIONS

The interconnections among the patches in a landscape may be at least as significant to maintenance of diversity as the size of the patches. It has been suggested that linking devices, such as forested corridors or stepping-stones of small forest tracts, might encourage dispersal of interior species between forest islands (Butcher et al. 1981, Diamond 1975, Willis 1974). Dispersal between patches is crucial to the prevention of genetic stagnation in small inbreeding populations (Miller 1979). Wegner and Merriam (1979) found that birds and small mammals use fencerows between woodlots much more than they travel across open fields, and they suggested that well-vegetated fencerows may relieve the barriers created by open fields. MacClintock et al. (1977) demonstrated the value of biogeographic position in maintaining species composition in fragmented forests. In their study, a small forest tract connected by a corridor to a nearby extensive forest system was characterized by a typical forest interior avifauna, in contrast to the depauperate condition of similar but isolated forest fragments. Margules et al. (1982) have noted, however, that proximity to the extensive forest was not separated from corridor effects in this study. In any case, MacClintock et al. (1977) did confirm the importance of minimal isolation to preservation of diversity. Concern about disease transmission along corridors (Frankel and Soulé 1981) has not been validated empirically.

There are several types of biogeographic corridors (Forman and Godron 1981). A basic distinction is between strip corridors and line corridors. Strip corridors are wide enough to maintain interior conditions in their centers, whereas line corridors (tree lines, fencerows, etc.) are essentially all edge habitat. Since some interior species will not live in or even migrate through extensive lengths of unsuitable habitat (Forman and Godron 1981), strip corridors are usually preferable to lines. Anderson et al. (1977) found that a powerline corridor through forest would have to be somewhat wider than 60 m to function as a strip corridor by providing field interior habitat for birds. On the other hand, wooded corridors through agricultural land may need to be over 100 m wide to retain forest-interior tree species like beech in Wisconsin (Ranney et al. 1981).

A regional landscape approach to preservation should therefore recognize the importance of broad corridors connecting habitat islands. Fencerows and shelterbelts should be widened whenever possible. Regional planners should draw corridors of natural habitat onto their blueprints. Park planners might connect significant patches of habitat within a given park, which would minimize island effects while still permitting development of considerable land area. Stream corridors, which can be effective avenues of dispersal for terrestrial as well as aquatic organisms, particularly if they are wide and contain some upland habitat, should be protected wherever possible.

MANAGEMENT GUIDELINES

Large, essentially unmanaged areas unquestionably offer the best prospects for long-term maintenance of ecosystem processes and integrity. But in a fragmented landscape, such areas often no longer exist. We can attempt only to approximate the pristine, presettlement condition, and this new landscape will not "manage itself" (Diamond 1981). In large tracts of old-growth forest, natural disturbance creates a "shifting-mosaic steady state," a dynamic but regionally persistent ecosystem complex that "would range from openings to all degrees of stratification" (Bormann and Likens 1979). The old-growth complex thus contains, in approximate steady state over some intermediate time span, all community types that might be classified within a bioregion, from prairies and bogs to shrub and climax forests. The high vertical and horizontal complexity of this old growth supports a correspondingly high diversity of flora and fauna (Schoen et al. 1981). To assure a rich landscape, conservationists should protect old growth wherever it occurs. Where possible, acreage should be expanded by allowing artificial successional areas to mature.

The complication in restoring a semblance of the old-growth system in a fragmented landscape is that the natural pattern of disturbance and recovery has been so terribly disrupted that the shifting mosaic has virtually nowhere to shift. In natural landscapes *unmodified by man,* disturbances are patchy in time and space and range from the removal of individual trees to devastation of many square kilometers (Wright 1974). The continual shifting, destruction, and renewal of patches generally assures that many seral stages and community types are maintained simultaneously on a regional scale. Degenerative changes in some portions of the landscape are balanced by regenerative changes in other portions (Bonnicksen and Stone 1982, Bormann and Likens 1979, Pickett and Thompson 1978, Sprugel 1976, Whittaker 1953). But in fragmented systems, both disturbance and lack of disturbance can be threats to regional diversity. A small but intense fire may obliterate a virgin forest remnant; a relict prairie without fire may be invaded by shrubs. This dilemma arises because of the small sizes and artificial boundaries and spacing of most surviving habitat islands. When preserve size is small relative to the scale of disturbance, the full range of compositional changes may be experienced locally (White and Bratton 1980). The smaller the preserve, the more necessary is vigorous protection *and* management to retain or restore the conditions for which the preserve is set aside (Diamond 1981, Pyle 1980).

CONCLUSIONS

Through an integration of concepts, the landscape paradigm identifies patterns that might otherwise go unnoticed. These patterns include regional trends in extinction and colonization, relative abundances of species and habitat types, and spatiotemporal dynamics of the structural components of a landscape.

Species composition and abundances, not simple number of species, assume primary importance in the context of regional preservation. Native species are preferred over those exotic to the landscape and rare or reduced species over the widespread and superabundant. The presettlement landscape (allowing for natural dynamism) is the ideal condition against which contemporary diversity and composition are evaluated. Management of the land to achieve maximum critical habitat area and insulate species with high extinction probabilities is the most prudent approach to long-term conservation.

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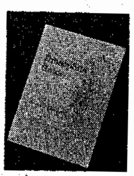

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