
Paleoecology and the Coarse-Filter Approach to Maintaining Biological Diversity

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Abstract: *The difficulties of saving millions of species from extinction often cause conservationists to focus on a higher level of biological organization, the community. They do so for two reasons: (1) communities are considered important biological entities in their own right, and (2) conserving representative samples of communities is seen as an efficient way to maintain high levels of species diversity. This approach will work if the chosen communities contain almost all species. Because it potentially saves most but not all species, community conservation is a "coarse-filter" approach to the maintenance of biological diversity, and contrasts with the "fine-filter" approach of saving individual species. Paleoecological information on the distribution of plant taxa in North America, however, indicates that most modern plant communities are less than 8,000 years old and therefore are not highly organized units reflecting long-term coevolution among species. Rather, they are only transitory assemblages or co-occurrences among plant taxa that have changed in abundance, distribution, and association in response to the large climate changes of the past 20,000 years. During periods when climate changes are large, communities are too ephemeral to be considered important biological entities in their own right. Large climatic changes are also*

Resumen: *Las dificultades en salvar millones de especies de extinción muchas veces lleva a los conservacionistas a enfocarse a un nivel más alto de organización biológica: la comunidad. Ellos lo hacen por dos razones: 1. las comunidades son consideradas entidades biológicas importantes en su derecho, y 2. conservando ejemplos representativos de las comunidades se considera manera eficiente de mantener niveles altos de diversidad de especies. Esta aproximación aprobechada trabaja si las comunidades escogidas contienen casi todas las especies. Al salvar potencialmente la mayoría, pero no todas las especies, la conservación de comunidades es solo una aproximación gruesa para el mantenimiento de la diversidad biológica, y contrasta con la mayor resolución que representa el de salvar especies individuales. Sin embargo, información paleoecológico sobre la distribución de la taxonomía de plantas en Norte América indica que las comunidades más modernas de plantas tienen menos de 8,000 años y por eso no son unidades bien organizadas reflejando coevolución de largo plazo entre las especies. Más bien, son ensamblajes transitorios o concurrentes entre la taxonomía de plantas que han cambiado su abundancia, distribución y asociación en respuesta a cambios grandes climáticos de los últimos 20,000 años. Durante periodos cuando los cambios de clima son grandes, comunidades son muy efímeras para considerarse entidades biológicas importantes. Cambios grandes climáticos también*

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likely to occur during the next century because of increased concentrations of CO₂, and we therefore propose that the coarse-filter approach to selecting nature reserves should be more strongly influenced by the distribution of physical environments than by the distribution of modern communities. Ideally, nature reserves should also encompass a broad enough range of environments to allow organisms to adjust their local distribution in response to long-term environmental change, and should be connected by regional corridors that would allow species to change their geographic distributions.

Introduction

Maintaining biological diversity has become a primary goal of conservationists in recent years (Soulé 1986; O.T.A. 1987; Wilson & Peter 1988), but the undertaking is of such overwhelming complexity that specific strategies are difficult to formulate. How can millions of species be saved from extinction when the majority have not even been described? One solution to this problem is to focus conservation efforts on a higher level of biological organization, the community. In the most general terms, a community is a set of populations that occur in some place (Schoener 1986). The population sets can range from a pair of species to all the organisms in an area; the spatial scale can range from a jar of culture medium to a biome (ca. 1 million sq. km). Often communities are defined as assemblages of all interacting, or potentially interacting, populations — i.e., the entire biological component of an ecosystem. Much ecological theory (e.g., about succession or energy flow) has proceeded from the assumption that communities are internally regulated natural systems within which species have evolved. This view of communities underlies two reasons why conservationists advocate using a community approach to maintain biological diversity. First, many ecologists believe that particular communities are important biological entities in their own right, and thus have intrinsic value as a component of biological diversity (Salwasser, Thomas, & Samson 1984). In other words they are recognizable and somewhat predictable, and have emergent qualities such that the whole community represents more than the sum of the component species. Second, many ecologists believe that communities have a predictable structure; thus, a representative sample of extant communities will harbor the vast majority of species (Norton 1986). If this assumption is correct, maintaining communities is an efficient way to maintain species diversity.

Our paper uses paleoecological data illustrating the distribution of plant species in eastern North America during the last 18,000 years (Davis 1981; Jacobson, Webb, & Grimm 1987; Webb 1987) to question these

son probables durante el próximo siglo por las concentraciones crecientes de CO₂, y nosotros, por esta razón, proponemos que la aproximación gruesa de seleccionar reservas de la naturaleza debe ser más influenciada por la distribución de ambientes físicos que por la distribución de comunidades modernas. Idealmente, las reservas de la naturaleza también deben considerar un rango suficientemente amplio de ambientes diferentes para permitir a los organismos a ajustar su distribución local en respuesta a cambios ambientales de largo plazo. Así mismo las reservas deben, en lo posible, formar corredores regionales que permitan a las especies cambiar su distribución geográficas.

views of communities and to suggest other strategies for conservation. These data, which are derived from pollen stratigraphies in lake sediments, show that the plant communities that dominate eastern North America today developed only within the last 4,000–8,000 years and therefore are not the end products of much longer periods (millions of years) of coevolution. Because increased concentrations of atmospheric CO₂ may be inducing large changes in climate (MacCracken & Luther 1985; Peters & Darling 1985), we have also used inferences drawn from paleoecological studies as a guide in recommending the design of nature reserves that may maintain a high level of biological diversity into the future.

The Paleoecological Perspective

Past Changes in Climate and Plant Communities

Today's distribution of species and communities represents one frame from a movie whose previous frames record continuously changing distributions and associations of taxa. These changes have been caused primarily by the large, quasiperiodic changes in climate of the Quaternary period, which began about 2.5 million years ago. During this time span, global climate has fluctuated substantially and frequently enough to produce more than 20 glacial/interglacial cycles (Broecker & van Donk 1970). These are linked closely to regular periodic fluctuations in solar insolation that result from known astronomical variations involving the tilt of the earth's axis, the precession of the equinoxes, and the obliquity of the orbit around the sun (Imbrie & Imbrie 1979; Berger et al. 1984). Recent studies (Pisias & Shackleton 1984) have shown that natural variations in atmospheric CO₂ have probably also been associated with the glacial/interglacial cycles, although cause and effect relationships have yet to be established.

During the past 700,000 years, each glacial/interglacial cycle has lasted for about 100,000 years (Ruddiman, Raymo, & McIntyre 1986). The first 80,000–90,000 years of each cycle are characterized by

increasingly glacial conditions, until a glacial maximum is reached; this maximum is followed immediately by an abrupt warming, and then by about 10,000 years of mild, interglacial conditions. During the last 2.5 million years, the climate has been substantially different from its current state at least 90% of the time, and the present interglacial, known as the Holocene, began about 10,000 years ago, after a colder, more glacial period lasting about 100,000 years.

Paleoecologists have discovered that these major swings between glacial and interglacial conditions have profoundly influenced regional environments and thus the distribution of biota. Their evidence comes primarily from stratigraphic studies of plant fossils — especially pollen grains — contained in lake sediments and peat deposits (Birks & Birks 1980; Berglund 1986; Delcourt & Delcourt 1987; Huntley & Webb 1988b). These sedimentary deposits are analogous to continuous monitors for permanent plots that have been in place for thousands of years; characteristics of the depositional basin determine the temporal and spatial scale of the “plot” that is sampled (Jacobson 1988; Prentice 1988).

Pollen stratigraphic studies have shown that when the most recent ice age was at its maximum (18,000–20,000 yr B.P.), vegetation in areas south of the ice sheets in eastern North America and Europe differed greatly in composition and configuration from what is present today (Davis 1981, 1986; Webb 1987; Jacobson, Webb, & Grimm 1987). From then until 10,000 yr B.P., many pollen samples record evidence of plant communities that are not analogous to any modern communities (Overpeck, Webb, & Prentice 1985). Specifically, large regional reconstructions have shown that postglacial expansions and contractions of the ranges of various plant taxa were highly individualistic, and that, in most cases, the vegetation patterns and communities of today did not start to appear until the last 6,000 to 8,000 years (Webb 1987; Jacobson, Webb, & Grimm 1987; Ritchie 1987). For example, the extensive boreal forest biome, dominated by spruce (*Picea*), fir (*Abies*), and birch (*Betula*), did not exist in eastern North America as recently as 8,000 yr B.P. (Webb 1987), and the hemlock (*Tsuga*) and beech (*Fagus*) forests of northeastern North America formed only about 6,000 years ago (Fig. 1) (Jacobson, Webb, & Grimm 1987; also see Davis 1969, 1983; Sjörs 1963). The broad-scale changes in species distribution, abundance, and association have also led to variations in communities that cover smaller areas such as wetlands, mountain tops, and river valleys (Janssen 1967).

Many additional examples of long-term community changes appear in data from other taxonomic groups (e.g., mammals — Graham 1986) and from other parts of the world, such as southwestern North America (Van Devender 1986; Thompson 1988), tropical Africa (Livingstone & Van der Hammen 1978; Livingstone 1982),

South America (Colinvaux 1987), and Australia (Walker & Chen 1987). Contrary to popular impression, the diverse tropical forests of today have been at their present location, composition, and extent for only a relatively short time (the last few thousand years), and they apparently differ in major ways from their configuration during full glacial times. For example, Colinvaux (1987) describes how disturbances such as flooding, fire, and erosion may have led to frequent readjustments of vegetation (even locally) during the last 10,000 years in the Amazon basin. Paleoecological evidence is still sparse for tropical regions of the world, and more work will be necessary to determine whether anything like the modern communities existed through time in some restricted habitats; thus far not a single example of this has been documented.

The paleoecological evidence presented above is inconsistent with the notion of persistent communities or associations at any scale. How can the boreal forest be the product of a complex array of coevolutionary processes involving dozens or even hundreds of species, if two of its major organisms, spruce and birch, became codominants in the community only 6,000 years ago, after an interruption in codominance for 20,000 to 100,000 years? Six thousand years may seem long, but it represents relatively few generations for many tree species. Most modern plant communities have therefore probably had little long-term coevolutionary significance, at least for dominant tree taxa (Davis 1981; Botkin 1980), and paleoecological evidence suggests that coevolution between plant species has not led to bonds that hold major plant communities together in the face of large climatic changes. This perspective undermines the idea that plant communities are sufficiently independent to be considered separate components of biological diversity and to have value as such.

Response Surfaces and Plant Environment Relationships

The prospect of CO₂-induced changes in climate requires us to consider modern species in terms of their long-term environmental responses, rather than just in terms of their geographic distribution or community relationships. Such a perspective is useful for conservation planning. Vegetational response surfaces show the distributional responses of a species in relation to environmental variables such as temperature and precipitation (Fig. 2) (Bartlein, Prentice, & Webb 1986; Webb, Bartlein, & Kutzbach 1987). They also show how the modern co-occurrence of two or more species may take place in only a small fraction of the response surfaces of each; therefore, even slight changes in climate can lead to differing responses in these species (Fig. 2). Such individualistic responses can lead to taxa developing new associations, and thus communities, as the climatic environment changes in each locality and across broad regions.

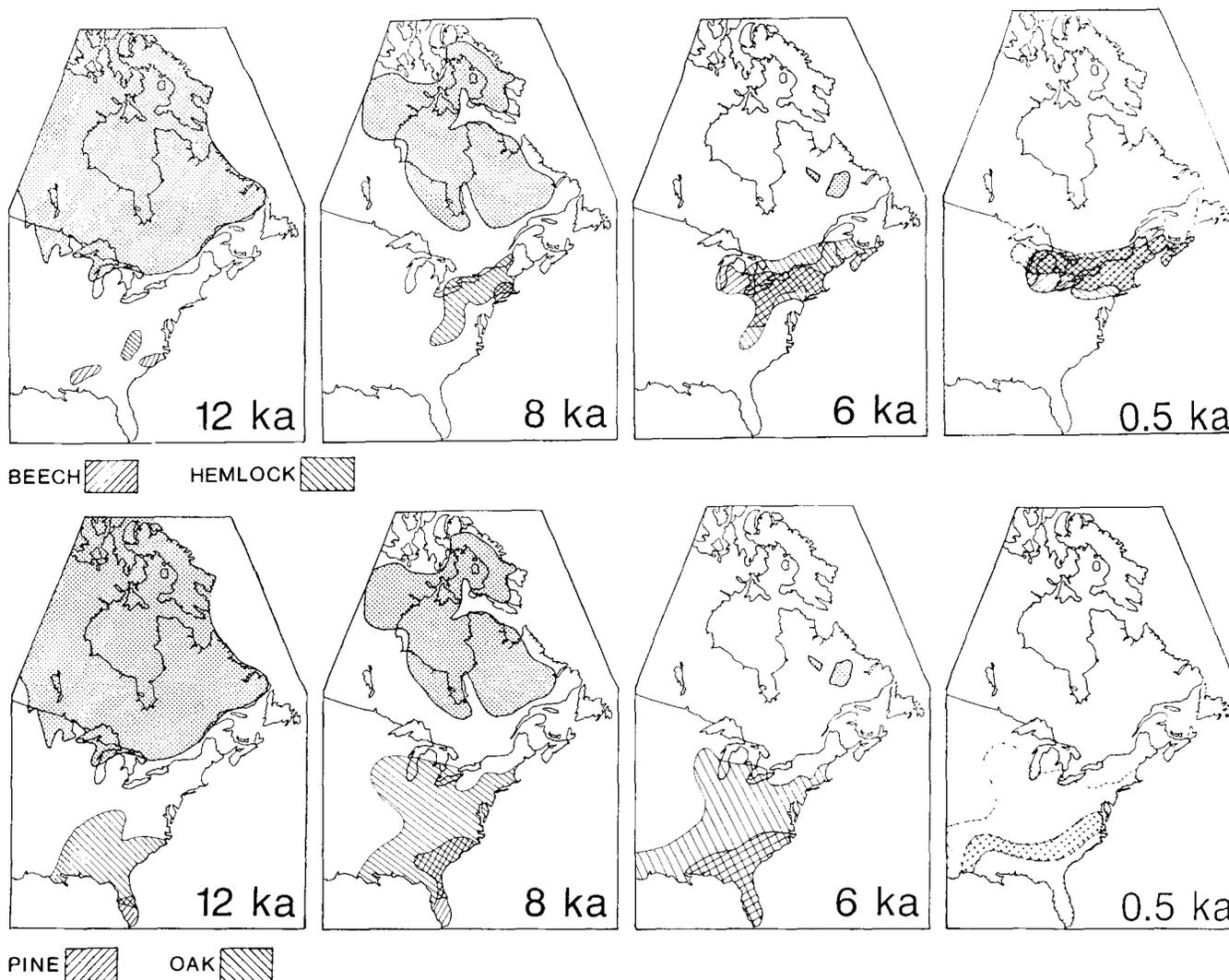


Figure 1. Location of regions with 5% beech (*Fagus*) pollen and 5% hemlock (*Tsuga*) pollen (in the upper row maps) and 20% southern pine (*Pinus*) pollen and 20% oak (*Quercus*) pollen (in the lower row of maps) at 12,000, 8,000, 6,000, and 500 yr B.P. with the stippled area in the north showing the shrinking Laurentide ice sheet from 12,000 to 6,000 yr B.P. Source: Modified from Plates 1 and 2 in Jacobson, Webb, & Grimm 1987.

This potential for individualistic behavior among plant taxa helps us resolve one concern posed by the coarse spatial resolution on our maps (Fig. 1) and data sets. Our data do not rule out that plant assemblages similar to some of those today may have existed continuously, in small, isolated areas. For this to have happened would require (1) the continual existence (somewhere) of the particular climate that will support such a community, and (2) successful simultaneous biogeographic shifts for all of the species involved. The nature of climate change over 5,000 years or longer makes the first condition unlikely, especially for macroclimatic patterns (Ruddiman & Wright 1987; Jacobson, Webb, & Grimm 1987). Modeling of past climates shows that the spatial combinations of temperature and precipitation values and their seasonal variations dif-

fered at 18,000 and 9,000 yr B.P. from those occurring today (Kutzbach & Guetter 1986). Furthermore, the broad-scale reorganizations that are shown by Webb (1987) and Jacobson, Webb, & Grimm (1987) imply that the modern broad-scale communities did not arise from the proliferation and spreading out of isolated local relicts of these communities that had remained intact since the last interglacial.

Vegetation Changes During the Past 1,000 Years

The vegetation changes illustrated in Figure 1 may underestimate the transitory character of the vegetation across eastern North America today. Quantitative analyses of rates of vegetational change during the past 18,000 years have shown that the past 1,000 years have

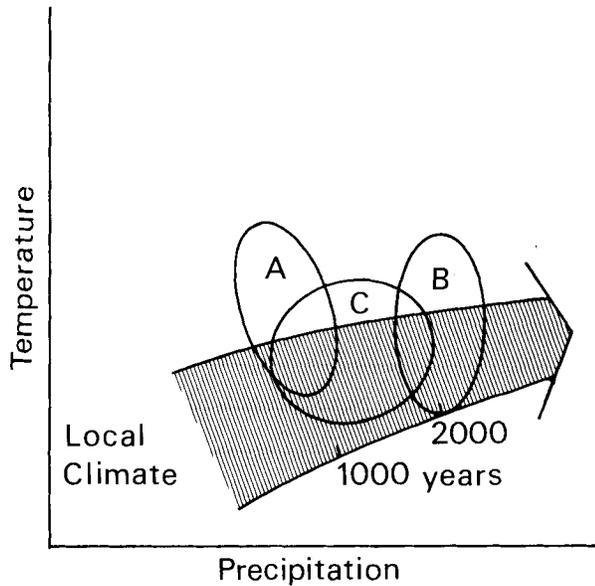


Figure 2. Regions in climate space, i.e., within a coordinate system defined by climate variables, occupied by species A, B, and C. Arrow indicates a hypothetical change in local climate induced by a global climatic trend over 100-year intervals. Note the small region in climate space in which the species distributions overlap. The hypothetical climate change leads to species A and C appearing together, but C species remains after A becomes extinct locally. Later B joins C and then keeps growing after C becomes locally extinct. Some of the independent changes on Figure 1 are of this character.

been a time of unusually rapid and synchronous vegetational change throughout eastern North America (Jacobson, Webb, & Grimm 1987). These recent vegetational changes have been quite different from one region to another, but the synchronicity of the changes across eastern North America implies a climatic cause.

Although this recent period of vegetational change has coincided partially with broad-scale disturbance of landscapes by expanding Euro-American populations, it was underway for at least 500 years before Columbus reached the Americas. Furthermore, it is consistently evident in trends such as the climatically induced southward expansion of boreal taxa (e.g., spruce and fir) in a broad latitudinal band from Minnesota (Webb, Cushing, & Wright 1983) to Quebec (Webb, Richard, & Mott 1983) and Maine (Anderson et al. 1986). Post-Columbian disturbances of the landscapes of eastern North America have been significant, but the changes that began as much as 1,000 years earlier appear to have been even greater, and are probably continuing today (Jacobson, Webb, & Grimm 1987). In fact, classic studies of plant communities have been focused on areas such as Minnesota's "Big Woods" (Daubenmire 1936),

which first developed only a few hundred years ago during the "Little Ice Age" (Grimm 1983).

Conserving Communities to Maintain Species Diversity

The Coarse-filter Approach

The idea that conserving communities may be an efficient way to maintain species diversity is implicit in a metaphor used by The Nature Conservancy (1982): coarse filters and fine filters (Noss 1987a). Saving biological diversity by the coarse-filter approach involves conserving communities; it assumes that a representative array of communities will contain the vast majority of species (Fig 3). (The Nature Conservancy has estimated that 85–90% might be saved this way.) The fine-

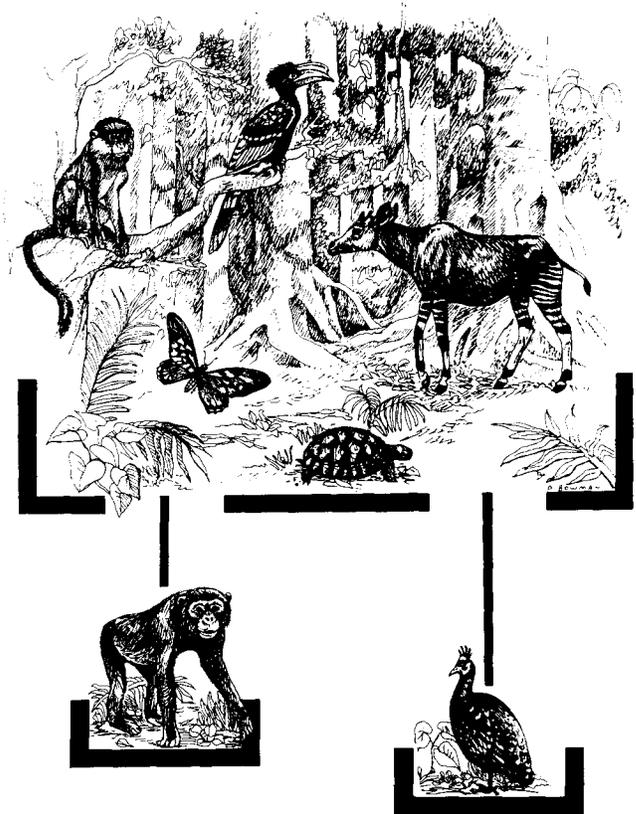


Figure 3. The coarse-filter approach to maintaining biological diversity focuses on protecting a representative array of communities, and is based on the assumption that these communities will encompass the vast majority of species. The fine-filter approach focuses on saving individual species that slip through the coarse-filter. As illustrated here, the coarse filter has been used to save a tract of Zaire's forest, while the fine-filter approach has been employed for the bonobo or pygmy chimpanzee (*Pan paniscus*) and Congo peafowl (*Afropavo congensis*).

filter approach of saving individual species can then be used to save some of the species that "slip through" the coarse filter. The fine-filter approach focuses on learning the needs of species that are at risk and then providing for these needs, often through intensive management. In regions where conservation efforts are curtailed by a severe lack of money (e.g., developing nations) or a dearth of information about individual species (e.g., tropical forests), the fine-filter approach will be limited to a handful of conspicuous species.

To envision how the coarse-filter/fine-filter approach would work, imagine a consortium of agencies collaborating to create a forest reserve system for eastern North America with the goal of maintaining viable populations of most of the region's forest biota — roughly 10^4 to 10^5 species. If the Nature Conservancy's assumption is correct, the consortium could achieve its goal of maintaining 85–90% of the species pool by establishing an array of large, well-distributed forest reserves representing all the regional forest types. It would be a relatively efficient program, because achievement of the same goal through activities focused on individual species would be nearly impossible. However, some species would not be preserved in the reserves because they are too rare to be included by chance alone. To take an extreme example, the *a priori* odds are heavily against Virginia round-leaf birch (*Betula uber* [Ashe] Fern.), a species confined to a single small valley, occurring in any reserve, unless there was a special effort made to include it.

A community classification scheme is impractical for predicting the distribution of very rare, patchily distributed species. Such a scheme would require defining a "Virginia round-leaf birch community type" and scores of others, nearly one each for rare species. Even some moderately common species might have to be dealt with individually if their distributions were unusual or unpredictable. These are the species for which the fine-filter approach was designed, and it would be unwise to try to preserve them via the coarse-filter approach. If communities were internally regulated, long-term entities, only very rare species would pose a problem for the coarse-filter approach. The vast majority of species would be so closely linked to other species — so inextricably part of their community — that their distributions could be predicted from the distribution of a few dominants. The reductionist view of communities (Fingegan 1984) and the paleoecological perspective on communities, however, indicate that species are generally too independent of each other to allow prediction of many distributions (especially through time) from knowledge of a few dominants. Some pairs or small groups of species do have interactions that have led to coincident distributions — tightly evolved symbioses such as parasite/host are extreme examples — but these relationships are exceptions.

The fact that most species react individually to their biological and physical environments, and not as components of a community, does not invalidate the coarse-filter approach. The independent behavior may mean that the estimate that 85–90% of species could be preserved by a coarse-filter approach is overly optimistic, but it does not mean that the distribution of individual species is random. The question becomes, how can conservationists use an understanding of species distributions and their environmental relationships to maintain the high levels of species diversity?

Physical Environments and the Maintenance of Diversity

The distribution of organisms reflects the influence of biological factors such as competition, predation, and symbiosis; physical factors such as climate, soils, and topography; and historical factors such as barriers, land bridges, and changing climates (Ricklefs 1987). Furthermore, the importance of various factors varies for different temporal and spatial scales. Out of this potentially complex array of factors, certain patterns emerge. One such pattern is that species may grow in the same places because they coincidentally share a need for a similar range of physical conditions, rather than because of elaborate interactions between them. In extreme cases, such as with serpentine soils, the biota may even be quite distinctive. Consequently, the coarse-filter approach would function best if it concentrated primarily on the identification and protection of a variety of environments, especially unusual ones, rather than communities. This statement requires elaboration because it may appear too indirect a way to maintain biological diversity; why be concerned about maintaining reserves with a particular configuration of climate, soils, and topography if the goal is to maintain biological, not physical, diversity?

Recall that the goal of the coarse-filter approach is not to maintain communities per se, but rather to preserve communities as a way of maintaining a high level of species diversity. Community conservation is just a means to an end. We believe that a better means to the same end would be conservation plans that take into account the current location and potential changes in physical environments. In other words, we advocate basing the coarse-filter approach on physical environments as "arenas" of biological activity, rather than on communities, the temporary occupants of those arenas. Physical environments can be defined by variables — for example, mean, minimum, and maximum annual temperature, soil moisture, nitrogen availability, etc. — that are critical to a wide range of organisms. In contrast, current communities are just assemblages of organisms and taxa growing at particular locations today, and the current presence and abundance of these taxa is no guarantee of their long-term survival, especially if the

environments are changing. Preservation of contemporary communities may be an efficient way to place most species under some sort of protection, but their long-term survival will depend upon well-designed reserves that allow species to move and survive environmental changes. A focus on environments is therefore the key to species preservation.

An apparent advantage of focusing on physical variables is that they are often easier to inventory and map. Topography is relatively stable and is already well mapped in many areas. Where it is not, it can be easily mapped with remote sensors. Climatic regimes can be interpolated from meteorological data and topography, and soils have been mapped from the ground in many regions. However, it would be unwise to delineate sites arbitrarily by their physical features without reference to biological distributions. By examining species distributions, certain common boundaries are likely to become apparent; if these boundaries can be related to threshold responses to physical factors, then the basis for a meaningful classification of physical environments can be developed. Species that are especially useful for defining particular physical environments can be designated as indicator species. (Foresters first used the term to refer to herbs and shrubs that indicated differences in the physical environment too subtle to be discerned from the trees [cf. Westveld 1953]). In many cases, of course, sharp, local boundaries in the distribution of plants are probably related to factors such as where fires have burned or heavy grazing has occurred and not to the physical environments.

Paleoecological studies have shown that diverse landscapes have supported diverse vegetation types over long periods during which climates have changed. For example, during the past 10,000 years midwestern forests on flat, sandy glacial outwashes have differed consistently from nearby forests on fine-grained glacial till (Brubaker 1975; Jacobson 1979), even though the species composition in both habitats types has changed. In Britain, geologic and edaphic factors, aided perhaps by human disturbance, have apparently allowed sites with chalk grasslands to support distinctive vegetation for much of the past 10,000 years (Bush & Flenley 1987). The sensitivity of species and communities to climate change varies among soil and habitat types (Bernabo 1981), and knowledge of such sensitivity differences can be important in planning.

Problems with a Community Focus

One further problem in focusing on preserving communities is that the distribution of community dominants may not be particularly sensitive to environmental differences that are important to other species. In other words, the coarse-filter approach may be too coarse. This problem can be illustrated by an example from

northeastern North America, where red spruce (*Picea rubens* Sarg.) is a dominant species in many types of forest. The Society of American Foresters (1967) recognized six forest types in which red spruce was a major component; in one of these types, "Red spruce," the red spruce is either pure or dominant. This type occurs in Maine on coastal islands, on thin-soiled sites at high elevations, and on lowland, poorly drained flats. These are quite different physical environments, and an environmental, as opposed to community, classification would distinguish among them. We do not know enough about all the biota of red spruce communities in these three environments to assess how extensive the differences would be, but many exist. For instance, Swainson's thrushes (*Catharus ustulatus* Nuttall), bay-breasted warblers (*Dendroica castanea* Wilson), red maple (*Acer rubrum* L.), and northern white cedar (*Thuja occidentalis* L.) are relatively much more common in lowland stands, whereas gray-cheeked thrushes (*Catharus minimus* Lafresnaye), blackpoll warbler (*Dendroica striata* Forster), mountain ash (*Pyrus americana* [Marsh.] DC), mountain paper birch (*Betula cordifolia* Regel.) and mountain maple (*Acer spicatum* Lam.) are usually only found in high-elevation stands. Coastal forests are more similar to high-elevation forests than to lowland forests, although they lack gray-cheeked thrushes and mountain maples (personal observation; Davis 1966; Noon 1981; Widoff, personal communication).

Another red spruce forest type, "Red spruce-yellow birch" (*Betula alleghaniensis* Britton), provides an example of an additional problem associated with community classifications. Following selective cutting and birch diebacks, many sites that once supported this type (lower slopes and moist well-drained flats) are now largely dominated by balsam fir (*Abies balsamea* [L.] Mill.) and red maple, species that were formerly considered only associates in this type (S.A.F. 1967). In just a few decades this community has been transformed almost beyond recognition. Similarly, in the Great Lakes region, late nineteenth century selective cutting and fires changed mixed pine forests of *Pinus strobus* L. and *P. resinosa* Ait. to communities of sweetfern *Comptonia peregrina* (L.) Coult, aspen *Populus* spp. suckers, and scrubby oaks *Quercus* spp. (Whitney 1987). It is difficult to generalize about how such major changes in the dominants may be reflected by the community as a whole.

The Value of Communities

The significance of modern communities is not greatly diminished because specific communities are short-term or even recent features of the landscape. The production of organic matter by a mangrove swamp or the beauty of an alpine meadow are just as important whether the systems have been in existence for ten

years or ten million years. The fruit produced by a plant species may be as important to the survival of a frugivorous endangered species whether the two species have coexisted for a few decades or hundreds of generations. A rare community (e.g., one dominated by species that usually do not coexist) is of some biological interest even if it is transitory and loosely organized.

Our concern is in identifying the best strategies for maintaining a high level of species diversity. We believe that this goal may often be achieved most efficiently if a coarse-filter approach is used with a primary focus on physical environments rather than on specific extant communities. This approach, however, need not be the only one used by conservationists. Sometimes the inextricable relationship between communities and physical environments will make it preferable to think in terms of ecosystems. Sometimes even the fine-filter approach will be most suitable, especially if there is adequate information and money. For example, the easiest way to identify habitat for a rare butterfly, *Mitoura besseli* Rawson and Zigler, is to search for a stand of Atlantic white cedar *Chamaecyparis thyoides* (L.) BSP, rather than to seek the special combination of climate and soils that would probably provide a suitable environment for the butterfly and the cedar upon which they lay their eggs (Opler & Krizek 1984). In this example, communities are the basis for a fine-filter approach to maintaining species diversity. The conservation of biological diversity is too complex for monolithic approaches; and preservation of populations, species, communities, physical environments, ecosystems, and landscapes must all be considered, when deemed appropriate.

Recommendations for Nature Reserves

Much has been written about the optimal design of nature reserves (e.g., Diamond 1975; McLellan et al. 1986). In light of the potentially large climate changes that may accompany increased concentrations of CO₂, we found our paleoecological perspective helpful in formulating the following three recommendations for designing reserves.

1. *Decisions about where to locate nature reserves should be influenced by the distribution of particular local physical environments.* Imagine a group of conservationists with enough money to purchase and manage a new 100 ha reserve, trying to decide between acquiring their region's only outcrop of serpentine bedrock, or the only forest dominated by white oak in the region. All other things being equal (e.g., neither site had a population of a known rare species), we would advocate acquisition of the serpentine site on the assumption that this site is more "special" and more likely to support unknown or rare species consistently through time.

2. *Nature reserves should contain a range of envi-*

ronments to allow organisms to adjust their local distribution in response to long-term environmental change. For example, if a reserve encompassed a significant gradient of temperature or precipitation, organisms might be able to move within the reserve to adapt to global and regional climate changes. Not all reserves can be extensive enough for this purpose, and this idea is probably applicable mostly in mountainous areas where climatic gradients are significantly compressed by elevational differences. Peters & Darling (1985) expressed a similar idea in pointing out that reserve designs should anticipate predicted changes in regional temperature and moisture conditions resulting from carbon-dioxide-induced climate changes and consequent shifts in latitudinal and altitudinal distributions of organisms.

3. *Nature reserves should be connected as much as possible by large-scale (continental) corridors that would allow species to change their geographic distributions in response to climate changes.* The need for habitat corridors to allow organisms to move among nature reserves, thus maintaining gene flow and minimizing local extinction events, has been extensively discussed (Noss & Harris 1986; Simberloff & Cox 1987; Noss 1987b). However, the need for bands of suitable habitat along which organisms can shift their geographic distribution is obvious only from a long-term perspective. Ideally, there would be wide, almost unbroken, stretches of undisturbed ecosystems running north-south to allow for latitudinal range shifts in response to temperature changes, and east-west to allow for longitudinal shifts in moisture patterns. Such a system would be difficult to establish, but a modest facsimile might be feasible. For example, the 300 m wide corridor of forest being assembled between Georgia and Maine to accommodate Appalachian Trail hikers may also facilitate major range shifts by some species. Maintenance of properly spaced "islands" with suitable habitats could accomplish the same goal for taxa able to disperse or be dispersed over long distances. For example, adequately spaced wetlands are currently essential for the annual migrations of certain waterfowl and other birds. Over longer periods of time, other taxa may be able to shift their range boundaries by such habitat-hopping. Overall, the need for species to change their geographic distributions argues against a narrow focus on reserves and corridors and requires a policy of good stewardship for the entire landscape (Huntley & Webb, 1988a).

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Literature Cited

- Anderson, R. S., R. B. Davis, N. G. Miller, and R. Stuckenrath. 1986. History of late- and post-glacial vegetation and disturbance around Upper South Branch Pond, northern Maine. *Canadian Journal of Botany* 64:1977–1986.
- Bartlein, P. J., I. C. Prentice, and T. Webb III. 1986. Climate response surfaces based on pollen from some eastern North American taxa. *Journal of Biogeography* 13:35–57.
- Berger, A., J. Imbrie, J. Hays, G. Kukla, and B. Saltzman, editors. 1984. *Milankovitch and Climate. Parts I and II.* Reidel, Dordrecht, the Netherlands.
- Berglund, B. E., editor. 1986. *Handbook of Holocene Palaeoecology and Palaeohydrology.* John Wiley & Sons, New York.
- Bernabo, J. C. 1981. Quantitative estimates of temperature changes over the last 2,700 years in Michigan based on pollen data. *Quaternary Research* 15:143–159.
- Birks, H. J. B., and H. H. Birks. 1980. *Quaternary Palaeoecology.* Edward Arnold, London, England.
- Botkin, D. B. 1980. A grandfather clock down the staircase: Stability and disturbance in natural ecosystems. Pages 1–10 in R. H. Warming, editor. *Forests: Fresh Perspectives from Ecosystem Analysis. Proceedings of the 40th Annual Biology Colloquium.* Oregon State University Press, Corvallis, Oregon.
- Broecker, W. S., and J. van Donk. 1970. Insolation changes, ice volumes, and the O-18 record in deep-sea cores. *Reviews of Geophysics and Space Physics* 8:169–197.
- Brubaker, L. B. 1975. Postglacial forest patterns associated with till and outwash in north-central Upper Michigan. *Quaternary Research* 5:499–527.
- Bush, M. B., and J. R. Flenley. 1987. The age of the British chalk grassland. *Nature* 329:434–436.
- Colinvaux, P. 1987. Amazon diversity in light of the paleoecological record. *Quaternary Science Reviews* 6:93–114.
- Daubenmire, R. F. 1936. The "Big Woods" of Minnesota: Its structure and relation to climate, fire, and soils. *Ecological Monographs* 6:233–268.
- Davis, M. B. 1969. Palynology and environmental history during the Quaternary period. *American Scientist* 57:317–332.
- Davis, M. B. 1981. Quaternary history and the stability of forest communities. Pages 132–153 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest succession, concepts and application.* Springer-Verlag, New York.
- Davis, M. B. 1983. Quaternary history of deciduous forests in eastern North America. *Annals of the Missouri Botanical Garden* 70:550–563.
- Davis, M. B. 1986. Climatic instability, time lags, and community disequilibrium. Pages 269–284 in J. Diamond and T. J. Case, editors. *Community Ecology.* Harper & Row, New York.
- Davis, R. B. 1966. Spruce fir forests of the coast of Maine. *Ecological Monographs* 36:79–83.
- Delcourt, P. A., and H. R. Delcourt. 1987. *Long Term Forest Dynamics of the Temperate Zone: A Case Study of Late-Quaternary Forests in Eastern North America.* Springer-Verlag, New York.
- Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural preserves. *Biological Conservation* 7:129–146.
- Finegan, B. 1984. Forest succession. *Nature* 312:109–114.
- Graham, R. W. 1986. Response of mammalian communities to environmental changes during the late Quaternary. Pages 300–313 in J. Diamond and T. J. Case, editors. *Community Ecology.* Harper & Row, New York.
- Grimm, E. C. 1983. Chronology and dynamics of vegetation change in the prairie-woodland region of southern Minnesota. *New Phytologist* 93:311–350.
- Huntley, B., and T. Webb III. 1988a. Discussion in B. Huntley and T. Webb III, editors. *Vegetation History. Volume VII in H. Leith, editor. Handbook of Vegetation Science.* Kluwer Publishers, Dordrecht, the Netherlands. (In press.)
- Huntley, B., and T. Webb III, editors. 1988b. *Vegetation History. Volume VII in H. Leith, editor. Handbook of Vegetation Science.* Kluwer Publishers, Dordrecht, the Netherlands. (In press.)
- Imbrie, J., and K. P. Imbrie. 1979. *Ice Ages: Solving the Mystery.* Harvard University Press, Cambridge, Massachusetts.
- Jacobson, G. L., Jr. 1979. The palaeoecology of white pine (*Pinus strobus* L.) in Minnesota. *Journal of Ecology* 67:697–726.
- Jacobson, G. L., Jr. 1988. Ancient permanent plots: Sampling in paleovegetational studies. In B. Huntley and T. Webb III, editors. *Vegetation History. Volume VII in H. Leith, editor. Handbook of Vegetation Science.* Kluwer Publishers, Dordrecht, the Netherlands.
- Jacobson, G. L., Jr., T. Webb III, and E. C. Grimm. 1987. Patterns and rates of vegetation change during the deglaciation of eastern North America. Pages 277–288 in W. F. Ruddiman and H. E. Wright, Jr., editors. *North America and Adjacent Oceans During the Last Deglaciation. The Geology of North America, Volume K-3.* Geological Society of America, Boulder, Colorado.
- Janssen, C. R. 1967. Stevens Pond: A postglacial diagram from a small *Typha* swamp in northwestern Minnesota, interpreted from pollen indicators and surface samples. *Ecological Monographs* 37:145–172.

- Kutzbach, J. E., and P. Guetter. 1986. The influence of changing orbital parameters and surface boundary conditions on climate simulations for the past 18,000 years. *Journal of Atmospheric Sciences* **43**:1726–1759.
- Livingstone, D. A. 1982. Quaternary geography of Africa and the refuge theory. Pages 523–536 *in* G. T. Prance, editor. *Biological Diversification in the Tropics*. Columbia University Press, New York.
- Livingstone, D. A., and T. Van der Hammen. 1978. Palaeogeography and palaeoclimatology. Pages 61–90 *in* *Tropical Forest Ecosystems*. UNESCO (Paris). *Natural Resources Research* **14**:61–90.
- MacCracken, M. C., and F. M. Luther. 1985. Projecting the Climatic Effects of Increasing Carbon Dioxide. DOE/ER-0237, Carbon Dioxide Research Division, Department of Energy, Washington, D.C. (available from N.T.I.S., Springfield, Virginia 22161).
- McLellan, C. H., A. P. Dobson, D. S. Wilcove, and J. M. Lynch. 1986. Effects of forest fragmentation on New and Old World bird communities: Empirical observations and theoretical implications. Pages 305–313 *in* J. Verner, M. Morrison, and C. J. Ralph, editors. *Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press, Madison, Wisconsin.
- Nature Conservancy. 1982. *Natural Heritage Program Operations Manual*. The Nature Conservancy, Arlington, Virginia.
- Noon, B. R. 1981. The distribution of an avian guild along a temperate elevational gradient: The importance and expression of competition. *Ecological Monographs* **51**:105–124.
- Norton, B. G., editor. 1986. *The Preservation of Species: The Value of Biological Diversity*. Princeton University Press, Princeton, New Jersey.
- Noss, R. F. 1987a. From plant communities to landscapes in conservation inventories: A look at the Nature Conservancy (USA). *Biological Conservation* **41**:11–37.
- Noss, R. F. 1987b. Corridors in real landscapes: A reply to Simberloff and Cox. *Conservation Biology* **1**:159–164.
- Noss, R. F., and L. D. Harris. 1986. Nodes, networks, and MUM's: Preserving diversity at all scales. *Environmental Management* **10**:299–309.
- Office of Technology Assessment. 1987. *Technologies to maintain biological diversity*. OTA-F-330. Congress of the United States, Washington, D.C.
- Opler, P. A., and G. O. Krizek. 1984. *Butterflies east of the Great Plains*. Johns Hopkins University Press, Baltimore, Maryland.
- Overpeck, J. T., T. Webb III, and I. C. Prentice. 1985. Quantitative interpretation of fossil pollen spectra: Dissimilarity coefficients and the method of modern analogs. *Quaternary Research* **23**:87–108.
- Peters, R. L., and J. D. S. Darling. 1985. The greenhouse effect and nature reserves. *Bioscience* **35**:707–717.
- Pisias, N. G., and N. J. Shackleton. 1984. Modelling the global climate response to orbital forcing and atmospheric carbon dioxide changes. *Nature* **310**:757–759.
- Prentice, I. C. 1988. Principles of vegetation sensing by pollen analysis. *In* B. Huntley and T. Webb III, editors. *Vegetation History*. Volume VII *in* H. Leith, editor. *Handbook of Vegetation Science*. Kluwer Publishers, Dordrecht, the Netherlands. (In press.)
- Ricklefs, R. E. 1987. Community diversity: Relative roles of local and regional processes. *Science* **235**:167–171.
- Ritchie, J. C. 1987. *Postglacial Vegetation of Canada*. Cambridge University Press, Cambridge, England.
- Ruddiman, W. F., M. Raymo, and A. McIntyre. 1986. Matuyama 41,000 year cycles: North Atlantic Ocean and northern hemisphere ice sheets. *Earth and Planetary Science Letters* **80**:117–129.
- Ruddiman, W. F., and H. E. Wright, Jr., editors. 1987. *North America and Adjacent Oceans During the Last Deglaciation*. *The Geology of North America*, Volume K-3. Geological Society of America, Boulder, Colorado.
- Salwasser, H., J. W. Thomas, and F. B. Samson. 1984. Applying the diversity concept to National Forest management. Pages 59–69 *in* J. L. Cooley and J. H. Cooley, editors. *Natural Diversity in Forest Ecosystems*. Institute of Ecology, University of Georgia, Athens, Georgia.
- Schoener, T. W. 1986. Overview: Kinds of ecological communities — ecology becomes pluralistic. Pages 467–479 *in* J. Diamond and T. J. Case, editors. *Community Ecology*. Harper & Row, New York.
- Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. *Conservation Biology* **1**:63–71.
- Sjörs, H. 1963. Amphi-Atlantic zonation, Nemoral to Arctic. Pages 109–126 *in* A. Love and D. Love, editors. *North Atlantic Biota and Their History*. Pergamon Press, Oxford, England.
- Society of American Foresters. 1967. *Forest Cover Types of North America*. Society of American Foresters, Washington, D.C.
- Soulé, M. E., editor. 1986. *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Thompson, R. S. 1988. Vegetation dynamics in western United States: Modes of response to climate fluctuations. *In* B. Huntley and T. Webb III, editors. *Vegetation History*. Volume VII *in* H. Leith, editor. *Handbook of Vegetation Science*. Kluwer Publishers, Dordrecht, the Netherlands. (In press.)
- Van Devender, T. R. 1986. Climatic cadences and the composition of Chichuahuan Desert communities: The late Pleistocene packrat midden record. Pages 285–299 *in* J. Diamond and T. J. Case, editors. *Community Ecology*. Harper & Row, New York.
- Walker, D., and Y. Chen. 1987. Palynological light on tropical forest dynamics. *Quaternary Science Reviews* **6**:77–92.

Webb, T., III. 1987. The appearance and disappearance of major vegetational assemblages: Long-term vegetational dynamics in eastern North America. *Vegetatio* 69:177-187.

Webb, T., III, P. J. Bartlein, and J. E. Kutzbach. 1987. Climatic change in eastern North America during the past 18,000 years: comparisons of pollen data with model results. Pages 447-462 in W. F. Ruddiman and H. E. Wright, Jr., editors. *North America and Adjacent Oceans During the Last Deglaciation. The Geology of North America, Volume K-3*. Geological Society of America, Boulder, Colorado.

Webb, T., III, E. J. Cushing, and H. E. Wright, Jr. 1983. Holocene changes in the vegetation of the Midwest. Pages 142-165 in H. E. Wright, Jr., editor. *Late-Quaternary Environments*

of the United States. Volume 2, *The Holocene*. University of Minnesota Press, Minneapolis.

Webb, T., III, P. J. H. Richard, and R. J. Mott. 1983. A mapped history of Holocene vegetation in southern Quebec. *Sylogues* 49:273-336.

Westveld, M. 1953. Ecology and silviculture of the spruce-fir forests of eastern North America. *Journal of Forestry* 51:422-430.

Whitney, G. G. 1987. An ecological history of the Great Lakes forest of Michigan. *Journal of Ecology* 75:667-684.

Wilson, E. O., and F. M. Peter. 1988. *Biodiversity*. National Academy Press, Washington, D.C.

