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Prioritizing for Investments in Biodiversity*

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INTRODUCTION

The single greatest cause of species extinction is human activity (World Conservation Monitoring Centre 1992). Estimates of current extinction rates suggest that we will experience a global loss of diversity at a rate of between 1 percent and 11 percent per decade over the next century (Reid 1992). Related concerns include the loss of genetic diversity within populations as a result of local extinctions, habitat fragmentation, and selective breeding practices in some resource species. Such massive changes in global diversity have occurred only a few times in geological history (Erwin et al. 1987) and could have a profound effect on the ecological order of life on Earth and, as a consequence, on the social, economic and political organization of human society.

The challenge we face is to respond to this threat in a concerted fashion as efficiently and effectively as possible. This is not an easy task and we face a number of key challenges. The first is the lack of consensus on the nature and magnitude of the pending changes to global biodiversity. The second is disagreement pertaining to the species concept and the measurement of diversity itself. The third is the absence of complete global and regional data. The fourth is possible conflicts among regional jurisdictions, each facing a unique set of local priorities. Finally, the resources available for investment in biodiversity preservation are limited.

The purpose of this paper is not to resolve these issues, but to assess briefly some of the scientific challenges we face as we attempt to establish priorities in biodiversity conservation, and to propose a general strategy for prioritizing for investment in biodiversity conservation.

HABITAT

Habitat alteration and destruction are the key factors affecting the diversity of natural communities. The alteration of habitat can take place directly through changes in land use from urbanization, agriculturalization and resource extraction. It can also occur indirectly as a result of pollutant discharge, the introduction of exotic species, or changes in global climate due to increasing atmospheric CO_2.

Habitat is in a constant state of succession. Within any given area with the potential to support a particular habitat, it is possible to identify several successional stages. The area covered by a particular habitat type is a function of the maximum potential area suitable for that habitat and of the rates of habitat loss and renewal. Figure 1 provides a simple representation of how the processes of habitat loss and renewal interact to yield a quasi-equilibrium area for a particular habitat. This model represents the rate of habitat renewal, *R*, as a function of the area of habitat, *H*, the maximum area which is potentially available for establishment of that habitat type, H_{max}, and the specific renewal rate, *r*. This relationship is given in equation 1.

***R = r* ท *H* ท *(*H_{max} *- H)/* H_{max} (1)**

In the case shown in Figure 1, H_{max} is normalized to unity, and *r* is set at 0.05.

This simple formulation is consistent with some basic observations. First, if a habitat type has been completely destroyed, the absence of colonizing species will make renewal impossible. Second, if the total area available for a particular habitat type is already fully developed, further increases cannot occur. Finally, the maximum rate of habitat renewal or regeneration will occur at some intermediate level of habitat where there is both area available for recolonization and adequate existing habitat to provide a source of immigrating populations for recolonization.

The rate of habitat loss is affected by many factors. A simple representation, shown in equation 2, is that of a negative exponential (see Sinclair et al. 1995) where H_o is the initial habitat area, H_t the area at time t, and d is the specific loss rate.

$$H_t = H_o e^{-dt} \quad (2)$$

Although an over-simplification (Sinclair et al. 1995), this formulation shows that, as habitat declines, the absolute rate of loss tends to decrease since the natural causes of loss are directly area-dependent. For losses instigated by human activity, the rate decrease is due to heightened efforts at conservation. Solving (2) for the instantaneous rate of loss over all areas of habitat yields a relationship between the rate of habitat loss, and the habitat area.

$$D = H(1 - e^{-dt}) / t \quad (3)$$

Several habitat-loss functions are illustrated by the positively-sloped lines in Figure 1, where the specific loss rates are set at 0.01, 0.02 and 0.03.

The interaction between the process of habitat renewal and habitat loss yields a given quasi-equilibrium area for a particular habitat type. The equilibrium habitat area, H_{eq}, is obtained at the intersection of the loss and renewal curves. These are stable equilibriums. If H is greater than H_{eq}, the rate of loss will exceed the rate of renewal and habitat area will decline, and vice versa if H is less than H_{eq}, the rate of renewal is greater than the rate of loss and habitat area will increase. In environments where human activity has increased the specific loss rate, (increased d) the loss curve pivots upward, resulting in lower values of H_{eq}. It is the ratio of the specific loss rate to the specific renewal rate that determines the equilibrium area. Figure 2 shows how the equilibrium habitat area is a function of the ratio of the specific loss rate and the specific renewal rate, d/r.

From a management perspective, what we must establish are the lower limits to H_{eq}. Sinclair et al. (1995) termed this value the *habitat constant*, H^*. If our objective is to rationally manage biodiversity, then we need to choose a value of H^* that allows us to optimize its preservation. An informed decision as to the value of H^* requires an understanding of the link between habitat area and biological diversity.

There are two general strategies that can be used to affect H^*. The first is the establishment of preserves and the second is effectively managing off-reserve areas in such a way as to optimize biodiversity by controlling loss and renewal rates (Sinclair et al. 1995).

HABITAT AREA AND DIVERSITY

That there is a positive relationship between habitat area and the total number of species is indisputable. As the area that is being examined increases so does the total number of species within the area. The general formulation for the species-area relationship is given in equation 4,

$$\log S = C + Z \log A \quad (4)$$

where S is the number of species and A is the area. The coefficient Z is dependent upon habitat type and is commonly thought to vary between 0.15 and 0.4 (Connor and McCoy 1979). This implies that a loss of 90 percent of the available habitat will result in a decrease in species richness of between 13 to 36 percent. Figure 3 provides a graphical representation of the change in species richness which might occur as a result of decreases in habitat area according to equation 4. Given the scale of habitat erosion which has occured already in some key areas (see Figure 4)[1], the magnitude of the global biodiversity crisis is clear.

As with most simple models, formulations such as those outlined in Figure 1 to 3 break down when confronted with the complexities of natural systems. For example, the geographic separation of similar habitat types provide for a rescue effect by which species facing local extinction can be "rescued" by immigration from a neighboring "island" of a similar habitat type (Brown and Kodric-Brown 1977). Conversely, as habitat fragmentation and alteration continue, the distance between such habitat "islands" increases and the potential for a rescue effect declines. Recent empirical evidence supports this contention showing that as both habitat "patch" size declines and the distance between patches increases, species diversity is compromised (Klein 1989; Newmark 1991). These simple models also neglect the complexity associated with habitat heterogeneity, species identity and the size of the population in question. This has caused some authors to question the usefulness of these predictive models for managing or planning biodiversity strategies (Boeckeln and Gotelli 1984; Zimmerman and Bierregard 1986).

Although these simple models demonstrate rather effectively the strong relationship between habitat and species diversity, their simplicity predisposes them to failure when confronted with empirical data from specific natural systems. The absence of a unifying model which is rigorous enough to withstand scientific, and possibly more importantly, legal scrutiny, and which is sufficiently versatile to be applied to a wide range of conservation issues presents one of the major challenges facing conservation biologists. Given the profound limitations on the theoretical basis for conservation planning, the competing demands for land use, and the limited financial resources available, how should we prioritize for investments in biodiversity conservation?

APPROACHES TO IDENTIFYING AREAS OF CONCERN

In the absence of a model that is able to withstand rigorous scrutiny, the challenge is to develop empirical methods for selecting areas for conservation priority. The key elements of any empirical system are the development of measures of biodiversity and the ranking of various sites.

Species Diversity

The simplest approach to identifying areas of conservation priority is to locate and preserve areas with the greatest species richness. Mittermeier (1988) and Mittermeier and Werner (1990) have shown that a few, primarily tropical, countries possess a large fraction of the world's species diversity. The use of species inventories within geopolitical regions allows for the identification of areas of particular concern for conservation. Because they are located within a single political unit, their potential for successful conservation action improves. A major deficiency in this approach is that it does not address any aspect of the uniqueness of the organisms being considered. As a result there may be a fair degree of overlap in the species represented on reserves. In short, using species richness as the sole indicator of regions of high conservation priority does not recognize the importance of endemic species, i.e., those that occur in only one area. This approach also ignores many other important aspects of natural communities that affect biodiversity, such as the stability or fragility of certain landscapes and species groups, the rarity of some species, and scale effects. Although serving as a key starting point in conservation, this approach is not a sufficient basis for the development of global and regional strategies for biodiversity preservation.

Diversity Indices

The use of any index as a surrogate for complex phenomena involves considerable oversimplification. The two elements employed in most diversity indices are species richness and some indication of the relative rarity or commonness of the members of the species set. Since quite different communities can have similar diversity index values, and different indices will often have very different values for any specific community, the usefulness of these indices has frequently been challenged, (e.g., Hurlbert 1971). However, many studies do use one index or another, and their usefulness is generally accepted as long as we are aware of the implicit limitations (Huston 1994). Margules (1989) showed that the relative priority of conservation sites can change dramatically depending on which index is used.

Endemic Species Richness

To account for elements of species rarity, Myers (1988, 1990) identified 18 areas that have high concentrations of endemic species. These areas have been termed "hot spots." Together, these hot spots, which cover only 0.5 percent of the earth's surface, contain 20 percent of its plant species. It is clearly impossible to carry out an endemic analyses for all species on the planet. However, if endemism follows similar patterns between taxa, then endemic species conservation strategies focussed on a particular taxon will yield enhanced returns. In some, but not all, cases this appears to be true (Bibby et al. 1992), which suggests that evaluation of endemic species richness may be an important strategy in identifying "hot spots" for conservation priority.

Critical Faunal Analysis

Critical faunal analysis is designed to identify the minimum set of areas that would contain at least one viable population of every species of a given plant or animal group (Atkinson and Vane-Wright 1984; Vane-Wright et al. 1991). A key element in identifying those areas that merit conservation priority is the concept of complementarity. The most efficient use of resources is to preserve those areas that in the first instance maximize the number of species represented. After choosing the first site on this basis, the second preserve should be selected so as to maximize the number of new species not represented in preserve 1, and so on. This approach is biased in favor of areas with high numbers of endemic species. When used on a global level, critical faunal analysis can be used by countries to establish their own national and regional conservation priorities. A step-wise approach like this has been used by Margules and co-workers (Margules et al. 1988) to select networks of reserves to maximize biodiversity.

Taxic Weighting

The measurement of diversity, or species richness, depends upon the taxonomic competence of the field evaluator; and its value will depend on the resolution of current debates on the basis of the species concept. Even if we accept these limitations and constraints, we are also forced to confront the issue of the relative value of species. Are all species equal? From a scientific perspective, is the Siberian tiger equivalent to a species of cyanobacteria. From an aesthetic or emotional perspective, the tiger would most certainly be viewed as more significant; but is there a scientific approach to assessing this relative valuation? Atkinson (1989) stated that "given two threatened taxa, one a species not closely related to other living species and the other a subspecies of an otherwise widespread and common species, it seems reasonable to give priority to the taxonomically distant form." Vane-Wright et al. (1991) have shown that approaches to the relative valuation of species which are based solely on taxonomic rank are also of limited value since they do not account for the number of species in a given taxonomic group, and hence for the number of closely related species.

What is needed is a defensible measure which is sensitive to both taxonomic distinctiveness or rank, and the number of species associated with a particular group. Through further refinement of a cladistic approach, Vane-Wright et al. (1991) developed a system which incorporates both taxonomic rank and the number of species in a particular group. Their approach is based on the information content of the hierarchical cladistic classification.

Figure 5 provides an example of the derivation of an index of taxonomic distinctness, or weight, as outlined by Vane-Wright et al. (1991). The example is based on a fully pectinate classification for five terminal taxa, A-E. Column I indicates the number of groups to which each terminal taxon belongs within the system, these numbers being the basic measure of taxonomic information. For example, species A belongs to 4 groups (AB, ABC, ABCD, ABCDE), while species E belongs to 1 group (ABCDE). Column Q gives the quotient of the total information for the whole group (in this example, total information = 14) divided by the information score for each terminal. Column W gives the standardized weight for each terminal, obtained by dividing the Q-values for each terminal taxon by the lowest Q-value (in this case, Q_{min} = 3 ท 5). Column P gives the percentage contribution of each terminal taxon to the total diversity, in terms of the aggregate values for Q or W. The totals row (T) gives the aggregate scores under I, Q, W and P. (This is modified from Vane-Wright et al. 1991.)

Vane-Wright et al. (1991) extended this approach to indicate how it could be used to determine areas of priority for conservation. The method involves summing the taxic weights of all species in each area of concern and focussing efforts on the conservation of the area with highest total weight. Once the area of highest priority has been identified, the area of second priority is determined by assessing the "complimentary" taxic weight of each remaining area. This is accomplished by not including those species accounted for in the area(s) already set aside for reserves. This approach implies that the area of second priority may not recessarily be the region with the second highest total taxic weight. It will instead be the region with greatest taxic complementarity to the first reserve.

Figure 6 shows such an example, where the weights of 5 taxa (A-E) are from Figure 5, and the matrix indicates the taxa represented in each of three potential reserves, R1, R2 and R3. Once R3 has been selected, R1 is preferred as the second choice, even though its taxic weight score, considered alone, is less than that of R2. In the figure, row T gives the total (aggregate) scores for all five taxa, and for each of the three regions; row P1 gives the percentage diversity scores for each of the three regions at the first step, indicating that R3 is the top-priority region; row P2 gives the percentage diversity scores for the remaining two regions with respect to the taxa complementary to those occurring in R3, and indicates that R1 is the second priority. (This example is based on Vane-Wright et al. 1991).

By including cladistic analysis, this approach accounts for both species richness and taxic uniqueness. Although there is potential to modify this type of assessment to suit local circumstances, the magnitude of the task facing taxonomists in carrying out such analyses for all species and all regions is staggering.

A STRATEGY FOR PRIORITIZING

Much of the literature dealing with strategies for biodiversity conservation focuses on the topics addressed above, especially on how and where to select areas of prime importance. The selection of areas for the establishment of nature reserves is undoubtedly a critical part of any global strategy, but it cannot succeed unless supported by a broader approach. Three arguments underscore the weakness of a strategy which focuses entirely on reserves. First, with realistic projections for the human population reaching ten billion within a few decades, the prospect for the establishment of large parks in fertile regions, especially in the tropics, is extremely low. Second, funding for biodiversity conservation of the 'aesthetic' type will be inadequate, and political support will be minimal. Finally, and most importantly, when land-use management surrounding the reserves is ignored, the reserves will come under severe pressure eroding their integrity (Sinclair et al. 1995).

At this point we would like to return to Figure 1, 2, and 3, and use the simple models these figures represent as a guide to thinking about alternative strategies. A pure 'reserve strategy' would place a small part of the earth in reserves. The amount reserved would depend upon the habitat type, the species area curve for that habitat and a decision as to what proportion of the biodiversity in that habitat type should be preserved. This strategy ignores the vast areas that are outside the reserves, which would suffer major losses in habitat integrity and biodiversity. As pointed out above (and see also Sinclair et al. 1995) this strategy in isolation may have a very small chance of success. The extreme alternative strategy, one without reserves, but with all effort aimed at designing land-use practices to maximize biodiversity in all man-modified habitats, would accept, a priori, a significant loss of biodiversity.

We believe that a mixed strategy, one which embraces reserves where possible, but that also focuses on the design and development of sustainable land-use practices in non-reserve areas, has the highest chance of success. There are several advantages to this approach. First, a strategy based on maintaining a biologically diverse landscape will be much easier to sell to political and commercial interests. Scientific evidence attests to the need for biodiversity in agro-ecosystems if we want to manage these systems with biological rather than chemical control (e.g., Harmsen 1990). Sustainable land use in agriculture, forestry, recreation and urban environments is becoming an acceptable concept mainly because of its long-term economic necessity. Sustainable landscapes are biodiverse. A second advantage to treating the maintenance of biodiversity in non-reserve areas as a priority is its effect on the preservation of habitat integrity in the reserves, which are much more likely to survive when the surrounding and intervening areas are managed for relatively high biodiversity as well.

The most difficult aspect of a mixed reserve/non-reserve strategy is the necessity of accepting *a priori* some irretrievable loss of biodiversity. This is the price of a long-term policy that will guarantee the survival of a global patchwork of both human-modified and natural landscapes. We believe that despite complexities of implementation, this is the preferred strategy. To attempt, at this stage in our history, to preserve all, or even most, of our current biological diversity through the establishment of more and better protected reserves alone is not sufficient.

CONCLUSION

Habitat preservation is the central element in the conservation of biodiversity, and the erosion of habitat integrity in many parts of the world, including some key habitats, presents a global threat to species conservation. A body of pure and applied bioscience is developing which focuses on problems related to the concepts and preservation of biodiversity. This branch of ecology is still in its infancy, and provides neither a generally acceptable theoretical framework nor an adequate database to guide us into the future. We have briefly touched on the scientific problems facing us. What is biodiversity? How do we measure it? How does it relate to spatial and temporal scale effects? How do we deal with such ecological problems as endemism and taxic weighting? The current literature focuses mainly on the questions of where, and how large biodiversity reserves should be.

The main emphasis of this paper, however, is on a simple general model in which the biodiversity of any habitat is a function of an intrinsic, biological renewal process and a partly extrinsic decay or destruction process. We use this model to focus on alternative strategies for biodiversity preservation, and conclude that the best strategy accepts political and economic constraints by advocating the establishment of networks of reserves coupled with measures to conserve biodiversity in all landscapes.

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