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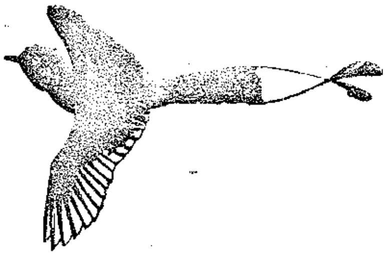

OUTLINE OF LECTURES GIVEN AT THE FIRST NATIONAL WORKSHOP ON CONSERVATION BIOLOGY

Organised by
Centre for Ecological Sciences, Indian Institute of Science
Nov. 10 to 22 1986

By

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December 1986
Technical Report No. 39

I. PATTERNS OF BIOLOGICAL SPECIES DIVERSITY

1. Introduction

It is obvious that before making any attempt to conserve biological diversity we must try to understand how much biological diversity exists on earth, how it is distributed and what factors determine the levels of biological diversity. 10 million is a common estimate for the total number of species of living organisms that may be present on earth. A very large proportion of these are insects and indeed there are more species of beetles than any other kinds of organisms. Why 10 million and why so many beetle species? In order to simplify matters, let us ask a simpler question. What determines the number and composition of species in a particular community? Is it possible to predict these or, the consequences of removing or adding some species? Do the members of a biological community come together mearly by chance or are there underlying biological processes that lead to well defined and structured communities?

It may sound surprising but we are only just beginning to approach these questions and have no more than vague answers. Even the precise definition of a biological community is not easy. A community is usually defined as an assemblage of mutually interatcing species. But biological species usually interact with their neighbours so that it is not clear where one community ends and another begins. The presence of obvious natural boundaries is usually helpful because we can speak of the biological community in a fresh water pond. In the absence of any such natural boundaries, the species area curve is usually one of the methods of delimiting a community.

The definition of diversity is also a matter of some difficulty. The most commonly used index of diversity is usually the number of species. This however does not take into account the relative numbers of individuals of the different species constituting a community. For instance, two communities are rated equally if both have two species each, although in the first community 50% of the individuals may belong to each species while in the second community 99% of the individuals may belong to a single species and only 1% to the other. It is clear therefore that a good index of diversity should consider both the number of species as well as their relative abundances. Two commonly used indices of diversity which satisfy this criterion are the Simpson´s Index (Simpson, 1949):

$$\lambda = \sum_{i=1}^{S} p_i^2$$

and the Shanon-Weiñer index (Pielou, 1966; 1975):

$$H' = -\sum_{i=1}^{S} (p_i)(\ln p_i)$$

where S is the number of species and is the proportion represented by the ith species. Here if each species is equally abundant, the maximum value of diversity index is obtained as:

$$H_{max} = \ln S$$

Thus, $H'/H_{max} = E$, a measure of the the equitability of species in the community.

A large number of indices of diversity have been developed but as their relative merits and demerits are still being evaluated, the number of species is advocated and often used as an index of diversity (Connell, 1978).

2. Distribution of Biological Species Diversity:

Many broad generalisations can be made regarding the distribution of animal and plant species diversity on the earth.

A. A gradient of increasing diversity is usually seen as we move from the poles to the equator. This has been documented for a variety of organisms including mammals, birds, insects, other invertebrates and plants (Fischer, 1960; Simpson, 1964; Price, 1975;).

B. Diversity usually decreases as we move up the slope of a mountain (Whittaker, 1977; Yoda, 1967).

C. Terrestrial communities normally have greater diversity per unit area compared to marine communities.

D. Islands usually have lower diversity per unit area compared to continents (Williamson, 1981).

E. Habitats with extreme environmental rigour such as hot springs or polar deserts usually have very low diversity.

F. In Benthic communities in the oceans, shallow regions have low diversity while deeper regions have higher diversity.

G. One notable exception is that fresh water planktonic communities are more diverse in the temperate regions compared to their tropical counterparts.

H. Other exceptions may arise when we look at specific groups. For instance, Ichneumonid wasps are more diverse in the temperate regions than in the tropics (Owen and Owen, 1974).

3. Factors affecting distribution of species diversity

A number of factors have been invoked to explain the observed patterns in the distribution of biological species diversity. Most of these factors (hypotheses) usually explain only the patterns observed in a particular situation. There does not yet appear to be any satisfactory general theory applicable to a wide variety of situations.

A. The Time-Stability hypothesis:

Life almost certainly originated in the tropics and later spread to the temperate regions. The entire biota in the temperate regions has been repeatedly destroyed because of glaciation and other catastrophic climatic events. There has thus been relatively little time for communities to evolve in the higher latitudes. This may be the reason for their poor diversity. In contrast communities have been evolving in the tropics for a very long time and apparently without serious catastrophic interruptions. This may be the reason for their species richness or diversity (Fischer, 1960; Sanders, 1968). In recent times however there has appeared some evidence that the tropics may also have undergone fairly drastic climatic changes in the past (Livingstone, 1975). A second point made by this hypothesis is that biological communities would also be evolving faster in the tropics because of the uniformly suitable conditions for life through out the year. In contrast, very little can happen during the temperate winters. In recent years again it is being increasingly realised that the transition from the wet to the dry season in many tropical areas may have fairly drastic consequences for the biota even if not as drastic as the change from summer to winter in the temperate regions. Some evidence for the time-stability hypothesis is provided by a study of fossil Foraminifera which shows that a declining trend in species richness from the equator to the poles was present even 70-80 million years ago. Besides, the average age of the species seen in the tropical fossil records was about 15 million years while those of the temperate regions was about 25 million years. Tropical species thus seem to be evolving faster (Stehli et al 1969). Another kind of evidence for this hypothesis comes from a study of the number of insect species associated with different tree species in Britain. All trees found in Britain must have recolonised after the last glaciation, about 10,000 years ago. There appears to be a fairly strong positive correlation between the number of insect species associated with a tree species and the time for which that tree species has been growing in Britain after recolonisation. In other words, insects have had a longer time to evolve on trees that have been growing longer in Britain and the availability of this longer time appears to have produced more species (Birks, 1980).

B. The Predation hypothesis:

Robert Paine (1966) pioneered the hypothesis that removal of a key predator increases species richness or diversity. His studies of inter-tidal communities of Molluscs and Echinoderms off the coast of the state of Washington, are well known. By removing a starfish called Pisaster, the key predator in a community consisting of at least 15 species, he found that a small number of species (8 in this case) are able to dominate and eliminate all others. In the kinds of communities that Paine studied, competition for space among the sedentary filter feeders is very crucial. In the absence of Pisaster, a few species are successful in competing for space and thus dominate the community.

the predator does is to harvest these dominating species and keep their numbers low. This permits even those species which are inferior at competing for space to coexist in the community. Janzen (1970, 1971) has extrapolated this idea to explain tropical tree species diversity. The number of seeds to fall to the ground is expected to decrease as one moves away from the tree. Conversely, the probability of seed survival is expected to increase progressively as one moves away from the parent tree. This is because seed predators are likely to be concentrated near the parent tree as they might use the parent tree itself to search for seeds. The optimum recruitment will thus be at some intermediate point where these two curves intersect. This mechanism might help space out the individuals of a species and also might permit members of other species to grow inbetween, thereby increasing the diversity. It should be emphasised that predation may not be expected to increase diversity under all circumstances. The introduction of a predatory fish namely Cichla ocellaris in the Gatun lake in Panama is known to have resulted in a drastic reduction in diversity (Zaret and Paine, 1973). There must clearly be situations when predators are not coevolved with their prey or predators themselves are fugitive species, so that they would exterminate their prey species leading to a reduction in diversity.

C. Productivity Hypothesis:

It has been suggested that increased productivity would increase species diversity (Connell and Orias, 1964). Combined with the factor of climatic stability and increased habitat heterogeneity, increased productivity might concievably support a greater diversity. For instance, there is a significant correlation of the number of common rodent species with productivity in both the Sonoran and Mojave deserts (Brown, 1975). Productivity by itself however cannot always be expected to work in this fashion. In fact there is a good evidence of a negative correlation between diversity and productivity in some lake ecosystems (Whiteside and Harmsworth, 1967).

D. Latitude-Area Hypothesis:

It is interesting that due to the spherical shape of the earth, there is much more area (both water and land) in the tropical regions than near the temperate regions. This might itself permit greater population sizes and higher diversity in the tropics (Osman and Whitlatch, 1978). This difference is further exaggerated because the distribution of clouds makes it possible for the region around the equator have a uniformly condusive temperature (Terborgh, 1973).

E. Succession Hypothesis:

Studies of deciduous forests in Eastern North America show a clear increase in tree species diversity with succession (Monk, 1967). It is of course possible that succession is associated with changes in other environmental factors such as soil moisture and calcium levels which might inturn affect species diversity.

F. Habitat Heterogeneity Hypothesis:

Although climatic stability and the absence of catastrophic changes such as those caused by glaciation have been suggested as being responsible for the higher levels of diversity in the tropics, an intermediate level of disturbance might actually promote diversity in the tropics. An excellent example of this would be a large tree fall in a tropical forest. An obvious mechanism by which such disturbance might promote diversity is by increasing the heterogeneity in the habitat and thus creating more niches. MacArthur (1965) has argued that there may be more speies in the tropics both because of an increase in the number of species per habitat as well as an increase in the number of habitats per unit area. In support of these ideas MacArthur and MacArthur (1961) and later Martin Cody (1974) have provided evidence for the increase in bird species diversity with increase in environmental heterogenity.

G.The competition hypothesis or the Niche diversification hypothesis:

The niche of an organism is usually broadly defined as the sum total of its exact ecological requirements. It is usually believed that two species having identical niches cannot coexist; one will eliminate the other. An organism´s niche may be defined along many different resource axes. Much theoritical and empirical work has been done in the area of competition and its effect on niche diversification. When species having similar niches coexist, they are expected either to reduce their niche bredths or increase their niche overlap. There are a variety of examples of organisms changing their morphology, physiology and behaviour during coexistance with other species having similar niches. Infact, Hutchinson (1959) showed that for species to coexist, the larger species has to be at least 1.3 times larger in linear dimension or twice as large as the smaller species in weight. This so called 1.3 size ratio has come to be rcognised as something of a rule in ecology. Since Hutchinson's work this rule has been found to hold good in many other communities including those of spiders (Uetz, 1977), tiger beetles (Pearson and Mury, 1979), lizards (Pianka, 1969), salamanders (Krzysik, 1979), squirrels (Emmons, 1980), bats (McNab, 1971), desert rodents (Brown and Lieberman, 1973), and ofcourse many kinds of birds which provide the most spectacular examples (Cody, 1973; Diamond, 1973). It is also true that many exceptions and criticisms of the Hutchinson's rule have appeared in the literature in recent years (See for instance Horn and May, 1977).

Assuming that interspecific competition plays an important role in structuring biological communities, niche theory predicts that when species coexist, their niches should either become narrower or their overlap become greater compared to the allopatric situation. There are many studies which appear to support these predictions. In summary, coexitance is made possible by niche shift (also called character displacement) (Fenchel, 1975; Giller and McNeill, 1981; Nilsson, 1965), reduction in niche width or increase in niche overlap.

The importance of interspecific competition itself is being seriously questioned by many ecologists in recent years (See Shoener, 1983; Connell, 1983 and Strong et al 1984 for contrasting views) especially by those working with insects where competition does appear to be relatively weak and unimportant. For instance, Donald Strong (1982) has shown quite clearly that a number of species of phytophagus beetles coexist on the leaves of a tropical monocot *Heliconia*. The total damage caused to leaves is very marginal and both observation and experiments show quite convincingly that interspecific competition is irrelevent. It appears therefore that like all other factors mentioned before, interspecific competition also explains certain patterns for certain species but cannot be generalised. There has however been some effort to provide a general integrated model for the observed patterns of biological species diversity (Cracraft, 1985; Connell, 1978; Huston, 1979).

II THE THEORY OF ISLAND BIOGEOGRAPHY

Islands provide a relatively simple and consequently attractive situations for studying the distribution of biological diversity. The first and to date the only serious attempt to develop a general theory of island biogeography was that of MacArthur and Wilson (1963; 1967). Their theory states that the number of species on an island is determined by an equilibrium between the rates of immigration of new species and extinction. It follows that islands which are closer to the mainland should have more species than distant ones because immigration to closer islands would be easier. It also follows that larger islands should have more species than smalleer ones, because extinction would be less likely on larger islands where larger populations can be maintained. These three predictions of the theory of island biogeography have been repeatedly verified. The most interesting empirical studies are certainly those of Simberloff and

Wilson (Simberloff and Wilson, 1969; 1970; Wilson and Simberloff, 1960; See also Simberloff, 1974; Williamson, 1981; MacArthur, 1972; Pielou, 1979) who used methyl bromide to defaunate small mangrove islands and later followed their recolonisation. After about 2 years each of the islands recoverd approximately the same number of arthropod species as they had before defaunation although the species composition was quite different. This lends strong support to the idea that the numbers of species present on each island are an equilibrium between the rates of immigration and extinction characteristic of that island. The prediction that the number of species present on an island is a function of its distance from the nearest mainland or source of immigration has also been verified especially in the case fo birds (Diamond, 1972) although it is true that distance usually has a very weak effect and can often be masked by the effects of other variables (Connor and Simberloff, 1978). As might be expected, the effect of distance can be more easily demonstrated in the case of poorly dispersing groups such as mammals (Grant, 1970). Area of the island on the other hand usually has a rather strong effect with increased area leading to an increase in the number of species. This is usually demonstrated using the species versus area log-log Arrhenius plot which is normally linear with a slope ranging from 0.15 to 0.40 both for real islands as well as for artificial islands such as beakers of water kept along transects to study the immigration of plankton and monoculture plantations of cacao or sugarcane which may be considered as islands as far as immigration by insect pests is considered. (MacArthur and Wilson, 1967; Diamond, 1973; Terborgh, 1974; Cox and Moore, 1980; Maguire, 1963; Brown, 1971; Strong, 1974; Strong et al, 1977; Opler, 1974; Lawton and Shroder, 1977).

III PATTERNS OF SPECIES ABUNDANCE

The relative abundance of different species in a community is also of obvious interest and has been the subject of considerable theoretical and empirical work. Three models of species abundance are frequently encountered in the literature. These are the log series model proposed by Fisher et al (1943), the log normal model of Preston (1948) and the broken stick model proposed by MacArthur (1957). In many situations, a very large number of species are represented by a single individual, fewer individuals are represented by two individuals, even fewer by three individuals and so on until very few species are represented by large numbers of individuals. Fisher et al (1943) showed that such data were best fitted by a logarithmic series which is described by two variables namely, the number of species and the number of individuals in the sample, the relaionship between which is given by

$$S = \alpha \ln (1 + N/\alpha)$$

where S = Number of species, N = Number of individuals and α = Index of diversity. In many situations however, the largest number of species corresponds to an intermediate level of abundance. Preston (1948) showed that the log normal distribution fits a very wide variety of data from many communities. The log normal distribution is described by the formula

$$S_R = S_0 e^{-(aR)^2}$$

where S_R = number of species in the Rth class to the left or right of the modal class, S_o = number of species in the modal class, a = a constant describing the extent of spread in the distribution and e = the base of natural logarithms (2.71828). Strictly speaking, continued sampling of a community should move the log normal curve to the right showing up species which lie to the left of the modal class. Further Preston (1962) also showed that in most communities the log normal has a characteritsic spread (corresponding to an a of 0.2) which he called the canonical distribution. This ofcourse means that given the number of species in the modal class, the total number of species in the community can be predicted. May (1975) has given the following formula to accomplish this:

$$S_T = S_o \sqrt{\pi / a}$$

where, S_T = total number of species in the communities, S_o = number of species in the modal class, π = 3.1419 and a = the constant describing the spread of the distribution which, as mentioned earlier, often takes the value of 0.2. The broken stick model of Robert MacArthur (1957) on the other hand is based on the assumption that resources would be distributed among n species in the manner of a stick being broken at n-1 randomly chosen points and population density being proportional to the resource share obtained by each species. Tthis model leads to a characteristic linear curve when the relative abundances of species are plotted against the log of their rank arranged in decreasing order. In a review of the whole question of biological species diversity and abundance, May (1975) has argued that a log series type of abundance is expected in communities with a small number of species and an even smaller number of dominant environmental factors, a situation in which successive species are expected to preempt a certain fraction k of the resources remaining after preemption by the previous dominant species. A log normal type of abundance distribution on the other hand is expected says May (1975), when the total number of species in the community is very large and the factors determining abundance is also very large. MacArthur´s broken-stick however is thought to be characteristic of small communities consisting of phylogenetically similar species in strong competition with each other. There are many examples of the appropriate types of communities which fit each of these models although many critisisms of the models too exist (Cohen, 1968).

The question of abundance and more so the lack of it is of obvious concern for conservation biology. But how does one define rareness of a species? In a particularly imaginative analysis of rarity with reference to the flora of the British Isles, Rabinowitch et al (1986) have delineated seven forms of rarity. It is common practice to call a species rare if it has a narrow geographic distribution, or a restricted habitat specificity or if it maintains only small local populations whereever it is found. A species may legitimately be considered rare if it shows any of the above three properties but it is clearly very usefull to know for which of the three reasons a given species is rare. What we might be able to do about its rarity will very likely depend a great deal on the type of rarity. Of the 160 species of plants that Rabinowitch et al (1986) were able to classify, 137 had wide geographical ranges while 23 had narrow geographical ranges. Similarly of the 160 species, 66 showed broad habitat specificities while 94 showed restricted habitat specificities. As for population sizes, 149 species maintained large populations at least in some part of their range while 11 had small populations throughout their range. Thus 58 species were considered common because they had a wide geographical range, a broad habitat specificity as well as maintained large populations at least in some places. All the remaining seven types were rare by one criterion or another. Interestingly, the most common kind of rarity was the case of having wide geographical distribution and being able to maintain large populations in some parts of their range but showing very restricted habitat specificities; 71 out of 102 "rare" species were rare because of this reason. This fully justifies, if justification is needed, a conservation strategy that aims at conserving habitats rather than individual species.

IV. THE ROLE OF EDGES IN STRUCTURING BIOLOGICAL COMMUNITIES

This brings us back to the questions raised earlier regarding the definition of a biological community and the criteria for delimiting one community from another. Are biological species distributed randomly in space or are there structured communities? These questions have been most sharply contrasted by phytosociologists who have developed the "discrete community hypothesis" which suggests that plants always exist in characteristic floristic assemblages called associations with well defined edges to each such community and the "independent plant hypothesis" that states that each species has its own independent distribution leading if anything to ill defined edges. These early hypothesis really worried more about distribution of plant species in response to physical factors and did not pay sufficient attention to possible interactions between the plant species themselves. When physical factors do indeed play a dominant role the distribution of species follow the gradient of physical factors quite closely (Brown and Curtiss, 1952; Whittaker, 1956; Shimwell, 1971). When biotic interactions become important however, much clearer associations and boundaries emerge (Diamond, 1973).

An Ecotone is the narrow region where species composition changes rapidly due to sharp changes in environmental conditions. Human interference in forests often results in the formation of sharp edges akin to ecotones. Ecological processes at such edges are strikingly different from those occuring in the interiors of forests. Not only do edges have very different levels of wind, light, predation and moisture levels but are also the points of convergence of contrasting habitats. A recent detailed study of the characteristics of forest edges demonstrated clear cut differences between edges and interiors in species composition with edges containing more xeric and shade intolerant species. More interestingly edges support significantly more basal area of trees and are characterised by substatntially higher productivities and this is true of both saplings as well as canopy trees (Ranney et al, 1981). There are relatively fewer studies of edge effects on animal species, an important exception being that of Whitcomb et al (1981) who have identified "edge loving", "interior loving" or "habitat fragmentation sensitive" and "ubiquitous" species in the eastern deciduous forests of North America.

V. THE IMPLICATIONS OF GENETIC ENGINEERING TECHNOLOGY FOR CONSERVATION

It is now a widely appreciated fact that there has been an explosion of genetic engineering technology. The key discovery that really started it all was that bacteria have certain enzymes called restriction endonucleases which break up foreign DNA to protect the cell from invasion. These enzymes cleave DNA at very specific sequences called palindromes so that the the broken ends have complimentary sequences and may thus be called sticky ends. Moloecular biologists have learned to use these restriction endonucleases to cleave DNA molecules and then use the sticky ends to join DNA fragments from widely different sources and hence engineer hybrid DNA molecules of the desired kind. The rather extensive elaboration of this technique has made it possible to introduce DNA molecules from one organism to another and in many cases it has also been possible to have the foreign DNA transcribed and translated. Most commonly DNA from higher organisms is introduced into bacterial cells so that large quantities of desired proteins such as hormones can be synthesisd in the bacteria. In more recent times we are very close to introducing foreign DNA into higher organisms also. There is for instance a tremendous effort underway to introduce bacterial nitrogen fixing genes into the genome of higher plants so that they no longer have to dependend upon symbiotic relationships with bacteria. The possibility of producing improved varieties of plants by incorporating disease resistance and other "good genes" is really around the corner.

What if any are the implications of this technology for conservation efforts? This question is as interesting as it complicated. On the one hand genetic engineering technology can, in principle at least, have very favourablr consequences for conservation efforts. With improved varieties of crops and horticultural plants land use can be much more efficient therby decreasing the pressure on new land to be brought under cultivation. Genetic engineering technology can sufficiently simplify the task of engineering suitable organisms for effective biological control thus reducing the problems due pollution of the environment by pesticides. It is very intersting that it is at present entirely legitimate to argue that genetic engineering will have exactly the opposite consequences. Cheap and efficient production of vanilla, cocaine and opium in other parts of the world will certainly ruin the economies of Mexico, Bolivia and Turkey, very likely leading to conversion of the remaining forest into agricultural land to grow food for their starving inhabitants. What are the chances that "good" species will accidentally be converted into pest species requiring the use of more pesticides than we do today? These possibilities appear to be very real (Regal, 1986).

There is a different and even more intersting kind of implication of genetic engineering technology for conservation efforts. It would be foolish to deny that molecular biologists are learning very rapidly to resurrect whole plants from tissues and single cells and to resurrect viable genes from DNA banks . The day is probably not very far off when knowledge of the sequence of a DNA molecule alone will be sufficient to synthesise it and introduce it into a living cell and make it work. The inevitable consequence of this is that slowly and steadily, our arguments for the preservation of entire habitats and large populations of wild plants for the sake yet to be discovered drugs and "good genes" are becoming impotent. There is a great deal that molecular biologists can do with frozen material in seed banks, tissue banks and DNA banks not to mention mere DNA sequences. A recent triumph of molecular biology has been to clone and sequence portions of a DNA molecule extracted from an Egyptian mummy (Pääbo, 1986). True, such triumphs will sometimes lead to unwise destruction of habitats even when not absolutely essential or when the claims of molecular biologists are not fully substantiated. But I would like to inderscore the other side of the coin. In my opinion, conservationists should accept the fact that not all species need be or, more importantly, can be preserved in their pristine habitats. Conservationists should therefore devote a lot more effort to defining their priorities. It is time we realised that our conservation efforts can be directed at the levels of complex biological communities, large populations of certain species, small and maybe, captive populations of some special organisms as well as at the level of organs, tissues, cells and gene banks (Swaminathan, 1984). Conservation efforts at all these levels are justified and acceptance of tissue banks or gene banks as the mode of conservation of some species should not be construed as betrayal of the cause of conservation. It should be our effort to identify the sufficient and practical levels at which conservation can be achieved for different species.

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