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Two Decades of Homage to Santa Rosalia: Toward a General Theory of Diversity[1]

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SYNOPSIS. In 1959, in his seminal paper "Homage to Santa Rosalia," G. E. Hutchinson asked, Why are there so many kinds of organisms? This paper focused attention on problems of species diversity and community organization that have occupied many theoretical and empirical ecologists for the last two decades. In the present paper I evaluate the attempt to answer Hutchinson's question by considering three topics. First, I reexamine the main themes which Hutchinson developed in "The Homage" and call attention to the central importance of energetic relationships in his view of ecological communities. Second, I examine the development of theoretical community ecology over the last two decades in an attempt to determine why some avenues of investigation, such as competition theory, have proven disappointing, whereas others, such as the theory of island biogeography, have enjoyed at least modest success. Finally, I suggest that future attempts to understand patterns of species diversity might focus on developing two kinds of theoretical constructs: capacity rules, which describe how characteristics of the physical environment determine its capacity to support life, and allocation rules, which describe how limited energetic resources are subdivided among species.

INTRODUCTION

One of the greatest remaining challenges in biology is to explain the diversity of living things. What determines the number and kinds of animals, plants and microbes that live together in one place? What causes variation in diversity from one place to another? What accounts for changes in the abundance and identity of species over time? How do individual species contribute to the diversity and stability of the natural world? These are largely problems of community and ecosystem ecology. Historical evolution and biogeography provide descriptive information about the development of diversity, and the process of natural selection accounts for the adaptations of individual species to their particular environments. But the capacity of the environment to support species is an ecological property. This capacity is determined ultimately by the physical environment: by availability of energy and other physical and chemical requisites for life and by physical heterogeneity in time and space. More proximally, the capacity of the environment to support species depends on how essential resources are apportioned among species: on relationships between organisms and their physical environment, and on interspecific interactions among the organisms themselves. Each individual species plays a unique role in the ecosystem as a whole; it potentially influences every other species through its interspecific interactions and its effects on the physical environment.

The attempt to provide a general, theoretical explanation for the diversity of living things has a long, distinguished history. Darwin and Wallace made the first great advances, and Lotka and Volterra, Grinnell and Gause, Clements and Shelford, Elton, Lack and Lindemann all made important contributions. In 1959 G. E. Hutchinson in his "Homage to Santa Rosalia" asked, Why are there so many kinds of living things? This seminal paper provided a general synthetic overview of the problems posed by organic diversity and suggested where we might look for the answers. The last two decades have witnessed a tremendous burst of activity as numerous scientists, from field naturalists to mathematicians, have grappled with Hutchinson's question.

How successful has been this effort to develop a general theory of organic diversity? Agreeing to participate in the present symposium has forced me to address this

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question. It has been a difficult, but valuable experience. I have concluded that the record of the last two decades has been very mixed. There have been both successes and failures; some approaches have proven disappointing, but others continue to be promising. Perhaps the greatest disappointment has been emotional. Many of the brightest and most ambitious scientists of the last generation committed their careers to theoretical ecology. Their feverish activity led to great expectations, which have not yet been fulfilled. Despite two decades of intensive investigation, Hutchinson's question remains largely unanswered. Perhaps it is a good time to reflect on the record of the past and to assess the prospects for the future.

THE HOMAGE: AN EMPHASIS ON ENERGETICS

"Homage to Santa Rosalia" is well worth reading, or rereading, more than two decades after its publication. If one considers the state of community ecology in 1959, it was an exceptionally original and insightful contribution. If one considers the present state of the discipline, it still has much to say. Although Hutchinson scarcely mentions the word energy, his basic message is that to understand the diversity of life we should investigate how usable energy is acquired by and apportioned among species. In his final introductory paragraph (p. 147) he states, "In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature. There is quite obviously much more to living communities than the raw dictum 'eat or be eaten,' but in order to understand the higher intricacies of any ecological system, it is most easy to start from this crudely simple point of view." In the remainder of the paper Hutchinson applies this dictum to speculate on the causes and limits of organic diversity.

Hutchinson develops five major themes. These are worth reexamining briefly in view of recent work. First, Hutchinson considers the length and number of food chains. He suggests that the length of food chains is limited by the attenuation of energy as it is passed with low efficiency from one trophic level to the next. He points out that body size and life history characteristics limit the trophic roles that certain species can play. He notes that the enormous diversity of terrestrial animals, which is much greater than that of aquatic ones, can probably be attributed not only to the large number of terrestrial plant species, but also to the architectural and functional diversity of individual plants. Both of these characteristics of terrestrial plants encourage the evolution of herbivorous animals, especially insects, specialized to feed on particular plant species and on certain parts of individuals of those species. Hutchinson then proceeds to discuss the weblike interrelations among food chains and to consider the relationship between structural complexity and dynamic stability. He incorrectly states (p. 149) that MacArthur (1955) has provided ". . . a formal proof of the increase in stability of a community as the number of links in its food web increases." But his main point is that many simple communities should be subject to invasion by new species as a result of colonization or speciation processes, so these communities would increase in diversity and complexity until some upper limit to diversity is reached.

Hutchinson's third theme concerns the effects of productivity and habitable area in limiting diversity. In a very perceptive passage (p. 150) he states "If we can have one or two species of a large family adapted to the rigors of Arctic existence, why can we not have more? It is reasonable to suppose that the total biomass may be involved. If the fundamental productivity of an area is limited by a short growing season to such a degree that the total biomass is less than under more favorable conditions, then the rarer species in a community may be so rare that they do not exist." He goes on to note that area itself may exert a similar influence, so that small islands typically contain fewer species with larger niches than nearby larger islands or mainlands. He attributes these patterns in part to the effects of interspecific competition affecting the allocation of limited energy sources among species. This theme is

developed further in the next section, where Hutchinson considers how similar species can be in their requirements and still coexist. He notes that there appears to be a definite limit, which among closely related species is often reflected in particular ratios (which are now called Hutchinson's ratios) of body size or dimensions of trophic appendages.

Hutchinson's final theme concerns what he calls the "mosaic nature of the environment." In a few well chosen sentences he anticipates much of what has later been said about the concept of environmental grain. He points out that within the constraints inherent in any taxonomic group or trophic level, small organisms almost always outnumber large ones, because (p. 155) ". . . small size, by permitting animals to become specialized to the conditions offered by small diversified elements in the environmental mosaic, clearly makes possible a degree of diversity quite unknown among groups of larger organisms."

Hutchinson summarized his arguments by concluding (p. 155) that ". . . the reason why there are so many species of animals is at least partly because a complex trophic organization of a community is more stable than a simple one, but that limits are set by the tendency of food chains to shorten or become blurred, by unfavorable physical factors, by space, by the fineness of possible subdivision of niches, and by those characteristics of the environmental mosaic which permit a greater diversity of small than of large allied species."

SUBSEQUENT COMMUNITY THEORY: ENERGETICS IGNORED

Most of the themes which Hutchinson developed in "The Homage" were not totally new, but the synthesis of these ideas to address the problem of diversity represented a major innovative achievement. Hutchinson used energetics as the basic currency of ecological interaction to provide a unified conceptual foundation for his arguments.

During the last two decades most of the ideas in "The Homage" have been explored by theoretical ecologists, but the central importance of energetics has largely been ignored. The reason for this appears to have much to do with personalities. By the beginning of the 1960s a growing number of bright, highly motivated scientists were trying to understand the structure and function of complex ecological systems containing large numbers of species. These investigators rapidly sorted themselves into two schools, each influenced by a single dominant scientist; these schools divided the enormous task confronting them into two largely nonoverlapping spheres of influence. One of these schools, led by Eugene Odum, followed the intellectual traditions of Clements, Shelford, Lindemann, and Elton, and viewed the ecosystem, if not as a superorganism in a strict Clementsian sense, at least as a complete holistic system with interesting and important emergent properties. This school, the ecosystem ecologists, concentrated on the flow of energy and matter through the community and emphasized interactions between organisms and the physical environment. In focusing on the ecosystem as a whole, they largely ignored the diversity of the component species and the unique role that each plays. The other school followed Hutchinson's student Robert MacArthur and the traditions of Lotka, Volterra, Gause, Grinnell and Lack. This school, the evolutionary ecologists, concentrated on the ecological and evolutionary interactions between species. They were concerned directly with understanding community organization and species diversity, and they tried to expand the competition models of Lotka and Volterra and the newly developed models of predation (Rosenzweig and MacArthur, 1963) to account for the coexistence of species in increasingly complex communities. Their models were based on changes in population size of one species as a function of population density of other species, however, and they virtually ignored energetics as an explicit currency of ecological interaction. For the past 20 years, evolutionary ecologists have tried to answer Hutchinson's question, "Why are there so many species?" without adopting the synthetic viewpoint based on energetics, that Hutchinson had used to

frame the question and to suggest possible answers.

My general assessment is that evolutionary ecologists have learned a great deal about the adaptive strategies of particular species and the basic kinds of interspecific interactions: competition, predation and mutualism. They have been much less successful in determining how these species and their interactions contribute to the structure and function of communities. I believe there are two reasons for this. One is the failure to appreciate the fundamental underlying role of energetics. The other is the inherent difficulty in trying to understand the organization of complex systems by working from the bottom up, attempting to recreate the whole system by assembling the component parts in proper relationship to each other. A brief examination of the history of science suggests that success in understanding complex systems usually comes from dealing with them on their own terms, taking them apart from the top down, inducing the processes underlying their organization from patterns in the relationships of the components to each other. The alternative approach of trying to recreate the entire system by assembling the components rarely works because, if the system is really complex, there is an overwhelming number of possibilities.

The recent history of theoretical ecology provides numerous examples of how these two problems have plagued efforts to develop a general theory of community organization and organic diversity. For example, May (1973) investigated the relationship between species diversity and community stability. He pointed out that there is nothing about complexity or diversity *per se* which tends to promote stability. He set up model communities in which species interacted at random and tested their stability by simulation. He concluded that complex communities containing diverse species tended to be highly unstable and that the obvious stability of natural communities was probably owing to highly structured (nonrandom) patterns of interspecific interaction. Lawlor (1978) subsequently reexamined May's model communities and pointed out that the assumption that species interact at random violates certain biological constraints which operate on natural communities. The most obvious of these constraints come from trophic structure: The flow of energy through the community is virtually unidirectional; plants (except insectivorous ones) do not eat herbivores, and herbivores rarely feed on carnivores. Lawlor pointed out that because of these constraints, in thousands of simulations of species interacting at random, May would have been unlikely to have obtained a single community with realistic trophic structure. The relationship between species diversity, functional organization, and stability of communities remains a challenging problem.

Before going on to assess two kinds of community theory in some detail, it is worth digressing to point out one area where the theory of evolutionary ecology has been quite successful: the development of optimal foraging theory. I suggest there are two reasons for this success. First, from the initial models of MacArthur and Pianka (1966) and Emlen (1966) through later, more sophisticated and realistic treatments (see Pyke *et al.*, 1977 for a review), energy has been used as an implicit, and usually as an explicit currency. The dictum "eat or be eaten" does so dominate the lives of many animals that much of their behavior can be understood in terms of selection to maximize rates of energy intake while minimizing risk of predation (Sih, 1980). Second, there has been little attempt to develop theories of community organization from the foraging behavior of animal species. Instead, ecologists interested in optimal foraging theory have been content to dissect the foraging behavior of animals to learn the selective and mechanistic processes by which animals make "decisions" about where to look for food, how long to stay in an area, how to search, and what foods to pursue and eat. In this they have been very successful.

COMPETITION THEORY: A DISAPPOINTMENT

In "The Homage" Hutchinson developed what he called "the Volterra-Gause

principle" to ask how similar two species can be in their utilization of limiting resources and still avoid interspecific competition sufficiently to coexist in the same community. Of all the ideas which Hutchinson discussed, this one has received by far the most attention from theoretical ecologists. Virtually all of their endeavors are based on the Lotka-Volterra models of interspecific competition. These equations express competition in terms of α_{ij}, the effect on the population growth rate of species i of an individual of species j relative to the effect of a conspecific individual. Attempts to provide a direct answer to Hutchinson's question led to theories of limiting similarity (MacArthur and Levins, 1967; May and MacArthur, 1972; Abrams, 1975). Levins (1968) extended the Lotka-Volterra model to express the pairwise interactions among all species in a community as the entries α_{ij} in the so-called community matrix. MacArthur (1972) created models of species packing in which he investigated the relationship between coexistence and the availability and utilization of limited resources. Theoreticians were not alone in their enthusiasm for these models. Many more empirical ecologists spent much time studying interspecific competition and trying to measure the α_{ij}'s required to test the theories. Among both theoretical and field ecologists there was widespread belief that interspecific competition was the primary factor which limits diversity, and that working out the mechanisms of competitive interaction was the key to understanding the organization of communities.

In the last few years enthusiasm has given way to disappointment as this approach has proven unproductive. It is worth inquiring into the reasons for this failure so that we may avoid making the same mistakes in the future. There are several problems. First, the models and their predictions are highly sensitive to the underlying assumptions. The results of the theories are crucially dependent not only on the assumptions of the community models themselves, but also on the assumptions of the underlying Lotka-Volterra equations and the logistic equation of population growth. Relaxation of these assumptions in biologically realistic ways may lead to totally different results. Abrams (1975) perhaps has shown this most clearly for the theory of limiting similarity, but similar problems plague most of competition theory. Second, the models are not empirically operational. Not only do they not yield unambiguous, testable (which in ecology usually means qualitative) predictions, they also fail to give the field naturalist a clear idea of what variables he should measure. For example, MacArthur and Levins' (1967) model of limiting similarity suggests that two species cannot coexist if $\alpha_{ij} = \alpha_{ji} > 0.54$. How does one falsify this prediction? How do we interpret an empirically estimated α_{ij} of 0.60 or 0.70? What result is close enough to be construed as supporting the theory and what is sufficient to reject it? More importantly, how does the field ecologist measure α_{ij}? It is generally conceded that it is impractical to measure α_{ij} directly by experimentally manipulating the density of species j and recording the effects on the population growth rate of species i. Besides, if this is done in the field in a community of many species, this method has its own conceptual difficulties (see Schaffer, 1981). Many ecologists have suggested ways of estimating α_{ij} indirectly by measuring overlap in the use of limiting resources (*e.g.*, MacArthur and Levins, 1967; Cody, 1974) or spatial or temporal variation in the relative abundance of species (*e.g.*, Levins, 1968; Crowell and Pimm, 1976; Hallett and Pimm, 1979). All of these methods invoke additional assumptions, which are often difficult to verify in the field. These problems undermine the entire value of the theory. There have been numerous attempts to measure α_{ij} for species interacting in nature, but I doubt that there would be general agreement on a single instance in which it has been measured correctly.

Perhaps the most serious problem with using this kind of competition theory to investigate community organization is the inherent difficulty in trying to understand complex systems by putting together the basic components in proper relationship to each other. As stated earlier, this approach

is usually unproductive because there are just too many possibilities. Consider the implications of Holt's (1977; see also Levine, 1976; Lawlor, 1979) conclusion that even a simple community matrix potentially conceals a large number of indirect interactions which may be as important as the direct, pairwise interactions in determining the structure and dynamics of the community. Current theory suggests that it is very difficult to put even a few species together in such a way as to obtain a biologically realistic, complex system that is stable, yet we are surrounded by natural communities that contain far more species and which persist for long periods of time. The implication is that there must be a set of rules above and beyond those that govern the pairwise interactions among species which dictate the assembly of species into communities.

I suspect that at least some of these rules embody the principles of energetics, which Hutchinson stressed in "The Homage," but which have been largely ignored in subsequent models of interspecific competition. Both individual organisms and ecological communities are thermodynamically unlikely. They maintain their organization only through the continual intake and expenditure of energy. Interspecific competition is important because it enables each species in the community to obtain a share of the limited energy and thus to persist. But I suggest that we would learn more about the structure and diversity of communities by focusing on the patterns of energy allocation among the species than by concentrating, as we have for the last two decades, on the effects of interspecific competition on population dynamics.

ISLAND BIOGEOGRAPHY THEORY: A HEURISTIC SUCCESS

One body of recent theory has, in my opinion, contributed substantially to explaining organic diversity. This is MacArthur and Wilson's (1963, 1967) equilibrium theory of island biogeography and the subsequent work which it stimulated. The value of this theory has been largely heuristic. It has been tested repeatedly, often rejected, and not yet to my knowledge proven to be both necessary and sufficient to account for the diversity of a single insular biota (see Brown, 1978; Gilbert, 1980). Nevertheless, the theory provides an exceptionally useful conceptual framework for investigating the patterns of species diversity and the underlying mechanisms which produce these patterns.

The MacArthur-Wilson model has three characteristics which I believe any successful general theory of diversity must possess. First, it is an equilibrium model. It deliberately ignores the effects of unique historical events, and seeks an ecological explanation for diversity. While it recognizes that successional processes may occur (as in the recolonization of Krakatau), it explains the ultimate limit on diversity in terms of an equilibrium between opposing rates of colonization and extinction. This is not to say that history is unimportant. Geological and climatic changes have had major, long lasting effects on the composition and diversity of biotas. But the patterns of diversity at equilibrium which are predicted by the model, but often not observed in nature, have proven extremely valuable for interpreting the influence of historical events on insular communities (*e.g.*, Brown, 1971).

The second important feature of the model is that it confronts the problem of diversity directly. Number of species is the primary currency of the model. Furthermore, the theory attempts to account for diversity in terms of both relationships between biological processes (in this case, colonization and extinction) and characteristics of the physical environment (island size and isolation). The theory not only recognizes that at equilibrium, diversity must be limited by constraints of the inanimate environment, it also attempts to understand the biological mechanisms through which these constraints affect the number and kinds of species which comprise insular communities.

The third desirable characteristic of the model is that it is empirically operational. It makes robust, qualitative predictions which can be tested rigorously with the kinds of data field ecologists and biogeog-

raphers can be expected to obtain. The MacArthur-Wilson model is one of the few models of community ecology that have been repeatedly and unequivocally falsified (*e.g.*, Brown, 1971). Although some might argue that there must be little merit in an idea that has so often been proven wrong (or at least not quite right), to do so would be to underestimate the heuristic value of the theory. The model has changed the way we think about diversity, and in testing and rejecting it we have learned a great deal about the effects of historical events, physical factors, and ecological process on species diversity.

The MacArthur-Wilson model represents an encouraging beginning, but it is clearly not the ultimate answer. In recent years its deficiencies, even as a heuristic tool, have become increasingly apparent. Perhaps the most serious is the failure of the model to consider the biological mechanisms underlying the processes of colonization and extinction. The model implies that the determination of diversity is a very stochastic process. Species continually colonize and go extinct, the biota at equilibrium is constantly changing species composition, and all of these processes occur essentially at random. MacArthur and Wilson knew that this really was not so, but given the state of biogeography and community ecology in the mid-1960s it was a useful simplifying assumption. If we hope to continue to make progress, however, we must delve deeper and seek more deterministic theories of species diversity and community organization.

Some of the themes of "The Homage" suggest promising places to start. Consider the effect of island area on species diversity. It seems likely, as MacArthur and Wilson suggested, that the influence of area is mediated largely through increasing rates of extinction as island size decreases. What is the biological cause of these extinctions? Actually, there are probably two interrelated causes. As island size decreases so do both habitat diversity and total productivity (on a per island, not a per unit area, basis). A consideration of the relationship between energetics and the mosaic nature of the environment would suggest that the pattern of extinction would be far from random. We would predict that carnivores should go extinct before herbivores of comparable size; further, within the same trophic level, species of large body size should disappear before their smaller relatives, and habitat specialists should go extinct before generalists. In at least one case, these deterministic patterns are exactly what are observed (Brown, 1971). Such results lend encouragement to the effort to develop a general theory of diversity.

PROSPECTS FOR THE FUTURE: INGREDIENTS OF A GENERAL THEORY

It would be unrealistic to suggest that we are now in a position to advance such a theory. We still have much to learn about the limits of diversity and the organization of communities. Much of this knowledge can only come from additional empirical studies. Nevertheless, I suspect that the lack of information is less critical than the insight required to select and assemble existing data and ideas in new and productive ways. What is necessary to answer Hutchinson's question: Why are there so many species?

I will assume that the goal is to construct an equilibrium theory for reasons both heuristic and practical. Historical geological and climatic events have had profound influence on the composition and diversity of some biotas, but, as argued earlier, it is easier to understand the effects of historical perturbations from a conceptual framework that assumes eventual equilibration of rates of origination (either colonization or speciation) and extinction. The assumption of equilibrium is not even terribly unrealistic when applied to much of the earth's present biota. Given a long period of geological and climatic stability (say 10 million or even 100 million years), most ecologists would probably expect to find pretty much the same general patterns of diversity as at present. The Arctic tundra, the Andean altiplano, salt marshes, hot springs, desert oases and small oceanic islands would still support many fewer species than the Amazon rain forest or the Great Barrier Reef.

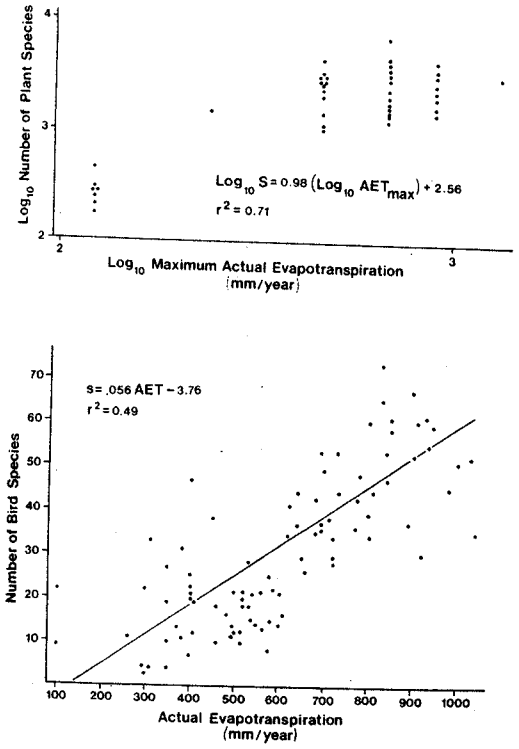

FIG. 1. The relationship between species diversity and productivity for two groups of organisms: above, for terrestrial plants, data compiled from North American local and regional floras by D. H. Wright; below, for birds, data compiled from Christmas counts from non-coastal sites in North America by J. B. Dunning, Jr. and J. Taylor. Productivity was estimated as actual evapotranspiration, which was obtained from a computer-generated map supplied by M. L. Rosenzweig.

Capacity rules

I suggest that a general equilibrium theory of diversity must contain two kinds of constructs, which I shall call capacity rules and allocation rules. The capacity rules define the physical characteristics of environments which determine their capacity to support life. The most important ingredient of the capacity rules is the availability of usable energy. Usable energy can be defined as any essential substance which organisms can potentially (given their constraints) extract from their environment and use to do the useful work of surviving and reproducing. However, for entire ecological communities, availability of usable energy can be measured as the rate of primary production, because the photosynthetic process produces essentially all of the energy used, not only by green plants, but by all other organisms as well. Except in a few environments where physical conditions prevent the oxidation of organic carbon, all of the energy fixed in photosynthesis is utilized by organisms (Hairston *et al.*, 1960). Darwin's "struggle for existence" is largely the struggle of all organisms to obtain usable energy that can be used to produce offspring. The more energy is available in usable form, the more organisms and hence, the more species the environment can support.

That there is a positive, causal relationship between productivity and diversity is not a new idea. Hutchinson, in the passage quoted earlier, suggested it in "The Homage," and it has subsequently been advanced by Connell and Orias (1964) and MacArthur (1972). Our work on communities of seed-eating desert animals has provided empirical support for this concept (Brown, 1973; Brown *et al.*, 1979). Despite these studies, the idea has not been widely accepted.

To show that the correlation between productivity and diversity has some generality, in Figure 1 I present some data analyzed by three of my students. For both terrestrial vascular plants and wintering land birds in North America actual evapotranspiration, a readily obtainable, but crude estimate of primary productivity (see Rosenzweig, 1968; Leith and Whittaker, 1975), accounts for half or more of the variation in number of species. Actual evapotranspiration is a reasonably good predictor of primary productivity because it incorporates the effects of temperature and water availability on photosynthesis, but it neglects other factors, such as soil chemistry, which can have major effects on plant productivity and community organization. Of course for birds, which are primarily carnivores, primary production provides only an indirect, and perhaps a poor estimate of availability of usable energy.

The second component of the capacity rules must be a measure of variation of the physical environment in time and space.

Some highly productive environments, such as salt marshes and hot springs, contain few species. These habitats typically are characterized by extreme physical conditions; ecologists, especially plant ecologists, often refer to them as harsh. But this characterization does not answer Hutchinson's question: if some species can adapt and live there, why cannot others invade? Terborgh (1973) in a very insightful paper proposed an answer. Harshness is indeed relative, but common features of harsh, productive habitats normally include not only unusual physical conditions, but also small size, spatial isolation, and (sometimes) ephemeral existence. Harsh environments contain few species because they have low rates of colonization, a consequence of their spatial isolation and the fact that most species available to colonize from surrounding habitats are unable to tolerate the extreme physical conditions, and high extinction rates, a consequence of small population sizes resulting from inhabiting restricted areas and sometimes from environmental fluctuations. Consequently, it is necessary to distinguish between harsh environments, such as desert oases, hot springs and salt marshes, which are physically distinctive, small and isolated but also productive, and other habitats, such as tundras and deserts, which are abundant and widespread but also contain few species, in this case because they are unproductive.

Although I feel confident that the most important ingredients of the capacity rules are availability of usable energy and the pattern of spatial and temporal variation that determines effective harshness, I am not at all sure how these elements interact with each other and with the organisms to affect diversity. Perhaps the most difficult problem is to develop an accurate measure of harshness, which requires that we assess the effects of spatial and temporal heterogeneity on the capacity of environments to maintain populations in the face of extinction. It will be easier to measure available energy, although for particular guilds of species this must be assessed in terms of usable energy resources. For fruit-eating animals, available energy must be measured as the availability of suitable fruits. In this case, the fact that frugivorous mammals are abundant and diverse only in tropical habitats where fruits are available throughout the year (Fleming, 1973) is certainly consistent with the arguments developed above.

To illustrate a few of the difficulties involved in formulating capacity rules, consider a specific example which Krebs (1978) has used to argue against the generality of the relationship between productivity and diversity. Several studies (*e.g.*, Whiteside and Harmsworth, 1967) show an inverse relationship between the number of zooplankton species and the productivity of temperate lakes. This is true when primary productivity is measured on a per unit area basis, because the highest diversity of zooplankton is found in large, oligotrophic lakes. But what maintains persistent populations of zooplankton, the productivity of a unit of area or the productivity of the entire lake? If, as we might suppose, it is the latter, then the productivity-diversity relationship is supported. My student, D. H. Wright (unpublished reanalysis of the original data), has shown that number of zooplankton species is positively correlated with both area of lake and total productivity (productivity/unit area × area of lake).

Allocation rules

In addition to knowing how the constraints of the physical environment determine the availability of usable energy to organisms, in order to understand diversity we must also learn how available energy is apportioned among species. I call the general patterns and processes of energy subdivision allocation rules, because it is only by obtaining a sufficient share of the total usable energy that a particular species is able to maintain its population and persist as a member of the community. Thus the mechanisms of allocation interact with the capacity rules to determine the number and kinds of species which can be supported at equilibrium. Clearly the ultimate processes underlying the allocation rules are the basic interactions among species populations: competition, predation and

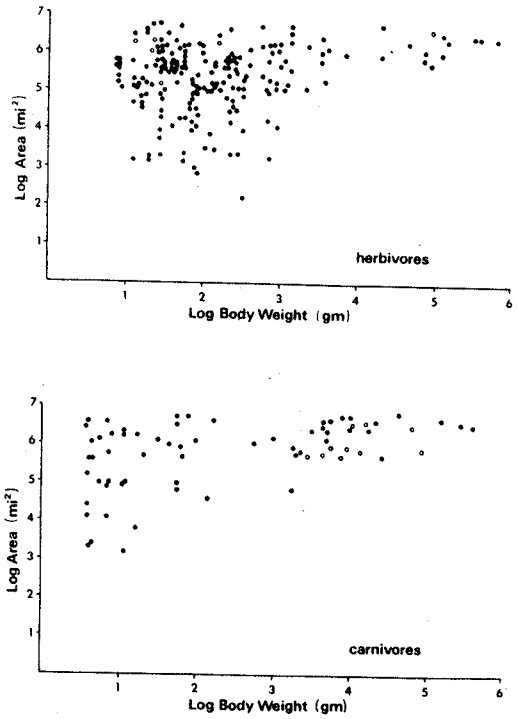

FIG. 2. The relationship between area of the species geographic range and body size for North American land mammals. Areas were measured from the range maps in Hall and Kelson (1959) by planimetry. The taxonomy follows Burt and Grossenheider (1964). Unshaded circles represent species which have larger ranges than the size indicated because their ranges extend beyond the maps into South America. Bats were excluded from the analysis; marsupials, insectivores, and armadillos and carnivores were assumed to be carnivores, and all others were classified as herbivores.

mutualism. But earlier I suggested that it is impractical to attempt to understand community-wide patterns of resource allocation and coexistence in terms of the population dynamics of interacting species. Is there an alternative? I think there is, but the empirical and theoretical bases for the allocation rules are at present even less well developed than those for the capacity rules.

I suggest we start by searching for empirical patterns in characteristics of species which affect their utilization of energy: local abundance, body size, geographic range, and trophic status, and then by developing testable mechanistic hypotheses to account for these patterns. Sufficient work has been done to demonstrate that interesting general patterns are present, but so far these lack a synthetic, mechanistic explanation.

Perhaps the most long recognized patterns are in the distribution of abundance and body size among species within local communities. The common observation that only a few species are common, whereas most are relatively rare has been quantified. MacArthur (1957) fitted the relative abundance of bird species to a broken stick distribution, whereas Preston (1962) noted that the distribution of abundances of many kinds of organisms often is lognormal. Similarly, the fact that within a taxonomic group or trophic level, species of small body size are more numerous than those of large size, was considered by Hutchinson and MacArthur (1959) and later by May (1978), who showed that size distributions also tended to be lognormal.

The community level consequences of these patterns remain to be explored completely. In retrospect, it is perhaps unfortunate that MacArthur ceased to investigate size and abundance distributions, and perhaps discouraged others with his public repudiation of his broken stick models (1966). One recurrent problem, that will face any who pursue this approach, is that of spatial scale. Hairston (1969) showed that the pattern of species abundance distributions varies with the size or spatial area of the community sampled. This is not surprising because species have different spatial distributions depending on their body size, trophic status and other characteristics. Figure 2 depicts the areas of the geographic ranges of North American mammal species. Two patterns are immediately apparent. First, there is a minimum area for the ranges of species which increases with increasing body size. Second, this minimum area is about an order of magnitude larger for carnivores than for herbivores. These patterns suggest that the minimum size of a species geographic range is determined by the probability of extinction. We do not see species with smaller ranges because these species have gone extinct. The probability

of extinction appears to be related to population size which, in turn is affected by body size and trophic position, because these factors determine to a large extent the ability of energy resources to support populations. These patterns of geographic ranges have two other important consequences for community ecologists which should be noted in passing. Most species have much broader ranges than the study areas of community ecologists, and these wide ranges appear to be important in enabling the species to persist over evolutionary time. Also, since the sizes of geographic ranges vary, particular species must coexist with different combinations of other species to form different communities in different parts of their geographic range.

It is not at all clear to me how these patterns of abundance, body size, geographic distribution, trophic position and other characteristics which affect energy utilization should be synthesized and conceptualized to develop useful allocation rules. But the fact that these patterns exist and that they appear to have a common basis in ecological energetics suggests that there may be general mechanisms of energy allocation which limit diversity and determine community organization. The existence of these patterns raises the hope that we can derive general allocation rules to account for species diversity which are not dependent on the details of the population dynamics of particular interacting species.

CONCLUDING REMARKS

Among my colleagues who call themselves community ecologists I detect widespread pessimism and disappointment. Many of them seem to feel that ecological theory has promised far more than it has delivered and that it has not contributed very much that has proven useful for understanding the natural world. Hutchinson's question, Why are there so many species? remains largely unanswered despite a great deal of theoretical and empirical work.

Now, more than two decades after publication of "Homage to Santa Rosalia," I suggest we would still be well advised to pursue the ideas that Hutchinson advanced there. In particular I recommend adopting Hutchinson's emphasis on the fundamental role of energetics in evolutionary and community ecology. The acquisition and utilization of energy in accordance with the laws of thermodynamics remains the best place to start "to understand the higher intricacies of any ecological system . . ." (p. 147).

There are those who will disagree. Some will continue to try to build a theory of community ecology based on population interactions. Others will argue that communities are so complex and unstructured that it is unrealistic to hope to develop a general theory of diversity. I am reluctant to argue strongly against these points of view. Diversity among ecologists, as among other organisms, makes life interesting and leads ecologists to new ideas. The intense activity in both theoretical and empirical ecology has made the last two decades an exciting time, even if the ultimate answers have eluded a generation of bright, dedicated ecologists. Perhaps the lack of immediate success should not be surprising. Ecological communities are perhaps the most complex of biological structures. Who ever thought it would be easy to find out why there are so many species?

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