CHAPTER 3 Ecology and Ecosystems

3.1 G. EVELYN HUTCHINSON

Homage to Santa Rosalia, or Why Are There So Many Kinds of Animals?

The distinguished American ecologist G. Evelyn Hutchinson (1903–1991) was a true renaissance man. His expertise extended beyond the sciences to literature and the arts, and he authored several literary works in addition to his scientific books and articles. Although he made many significant contributions to ecology—especially in the field of limnology, the study of freshwater lakes and ponds—perhaps his greatest achievement was the inspiration he instilled in many of his students at Yale University, who went on to launch their own successful careers in ecology. Hutchinson's broad approach to ecology, which emphasized the importance of mastering the fundamentals of biochemistry, geology, zoology and botany, became known as the "Hutchinson School." He was one of the first prominent scientists to warn that the human race was gaining, through modern technology, the potential to destroy its own environment.

Hutchinson’s literary skills are evident in the following selection from “Homage to Santa Rosalia, or Why Are There So Many Kinds of Animals?” The American Naturalist (May–June 1959). He approaches the fundamental ecological question of why there exists a great diversity of species, with his
characteristically broad, systematic mode of analysis. After considering the requirements of food chains and webs, the role of natural selection, size effects, and other factors that may either limit or promote diversity, he comes to what is still a controversial conclusion among ecologists. Hutchinson contended that there is species diversity partly because ecosystem complexity increases stability.

**Key Concept:** factors affecting species diversity

When you did me the honor of asking me to fill your presidential chair, I accepted perhaps without duly considering the duties of the president of a society, founded largely to further the study of evolution, at the close of the year that marks the centenary of Darwin and Wallace's initial presentation of the theory of natural selection. It seemed to me that most of the significant aspects of modern evolutionary theory have come either from geneticists, or from those heroic museum workers who suffering through years of neglect, were able to establish about 20 years ago what has come to be called the "new systematics." You had, however, chosen an ecologist as your president and one of that school at times supposed to study the environment without any relation to the organism.

A few months later I happened to be in Sicily. An early interest in zoogeography and in aquatic insects led me to attempt to collect near Palermo, certain species of water-bugs, of the genus Corixa, described a century ago by Fieber and supposed to occur in the region, but never fully reinvestigated. It is hard to find suitable localities in so highly cultivated a landscape as the Concha d'Oro. Fortunately, I was driven up Monte Pellegrino, the hill that rises to the west of the city, to admire the view. A little below the summit, a church with a simple baroque facade stands in front of a cave in the limestone of the hill. Here in the 16th century a stalactite encrusted skeleton associated with a cross and twelve beads was discovered. Of this skeleton nothing is certainly known save that it is that of Santa Rosalia, a saint of whom little is reliably reported save that she seems to have lived in the 12th century, that her skeleton was found in this cave, and that she has been the chief patroness of Palermo ever since. Other limestone caverns on Monte Pellegrino had yielded bones of extinct pleistocene Equus, and on the walls of one of the rock shelters at the bottom of the hill there are beautiful Gravettian engravings. Moreover, a small relic of the saint that I saw in the treasury of the Cathedral of Monreale has a venerable and petrified appearance, as might be expected. Nothing in her history being known to the contrary, perhaps for the moment we may take Santa Rosalia as the patroness of evolutionary studies, for just below the sanctuary, fed no doubt by the water that percolates through the limestone cracks of the mountain, and which formed the sacred cave, lies a small artificial pond, and when I could get to the pond a few weeks later, I got from it a hint of what I was looking for.

Vast numbers of Corixidae were living in the water. At first I was rather disappointed because every specimen of the larger of the two species present was a female, and so lacking in most critical diagnostic features, while both sexes of the second species C. affinis,...
After considering the role of natural selection, size effects, and diversity, he comes to the conclusion that Hutchinson considered the complexity of ecological systems.

Our presidential chair, a well-known ecologist and president of a society, then presented the key aspects of his work. In the past, ecologists, often due to neglect, were able to discover new systematics and one of the many areas of interest was the study of food relations and the diversity of species in the terrestrial system. The marine fauna, although it has an area much greater than the terrestrial system, lacks the astonishing diversity found in terrestrial systems (Thorson, 1958). If the insects are excluded, the diversity would be greater. A proper answer to my initial question would be to develop a theory at least predicting an order of magnitude for the number of species of $10^6$ rather than $10^5$ or $10^4$. This is certainly not possible. At most it is merely possible to point out some of the factors which would have to be considered if such a theory was ever to be constructed.

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 easiest to start from this cruelly simple point of view.

**FOOD CHAINS**

Animal ecologists frequently think in terms of food chains, of the form $S_1$ are eaten by $S_2$, of $S_2$ by $S_3$, of $S_3$ by $S_4$, etc. In such a food chain $S_1$ will ordinarily be some holophytic organism or material derived from such organisms. The simplest case is that in which we have a true predator chain in Odum's convenient terminology, in which the lowest link is a green plant, the next a herbivorous animal, the next a primary carnivore, the next a secondary carnivore, etc. A specially important type of predator chain may be designated Eltonian, because in recent years C. S. Elton has emphasized its widespread significance, in which the predator at each level is large and rarer than its prey. This phenomenon was recognized much earlier, notably by A. R. Wallace in his contribution to the 1858 communication to the Linnean Society of London.

In such a system we can make a theoretical guess of the order of magnitude of the diversity that a single food chain can introduce into a community. If we assume that in general 20 per cent of the energy passing through one link can enter the next link in the chain, which is overgenerous (Slobodkin in an
unpublished study finds 13 per cent as a reasonable upper limit) and if we suppose that each predator has twice the mass, (or 1.26 the linear dimensions) of its prey, which is a very low estimate of the size difference between links, the fifth animal link will have a population of one ten thousandth (10-4 of the first, and the fiftieth animal link, if there was one, a population of 10-49 the size of the first. Five animal links are certainly possible, a few fairly clear cut cases having been in fact recorded. If, however, we wanted 50 links, starting with a protozoan or rotifer feeding on algae with a density of \(10^6\) cells per ml, we should need a volume of \(10^{26}\) cubic kilometers to accommodate on an average one specimen of the ultimate predator, and this is vastly greater than the volume of the world ocean. Clearly the Eltonian food-chain of itself cannot give any great diversity, and the same is almost certainly true of the other types of food chain, based on detritus feeding or on parasitism.

**Natural Selection**

Before proceeding to a further consideration of diversity, it is, however, desirable to consider the kinds of selective force that may operate on a food chain, for this may limit the possible diversity.

It is reasonably certain that natural selection will tend to maintain the efficiency of transfer from one level to another at a maximum. Any increase in the predatory efficiency of the \(n^{th}\) link of a simple food chain will however always increase the possibility of the extermination of the \((n-1)^{th}\) link. If this occurs either the species constituting the \(n^{th}\) link must adapt itself to eating the \((n-2)^{th}\) link or itself become extinct. This process will in fact tend to shortening of food chains. A lengthening can presumably occur most simply by the development of a new terminal carnivore link, as its niche is by definition previously empty. In most cases this is not likely to be easy. The evolution of the whale-bone whales, which at least in the case of *Balaenoptera borealis*, can feed largely on copepods and so rank on occasions as primary carnivores, presumably constitutes the most dramatic example of the shortening of a food chain. Mechanical considerations would have prevented the evolution of a larger rarer predator, until man developed essentially non-Eltonian methods of hunting whales.

**Effect of Size**

A second important limitation of the length of a food chain is due to the fact that ordinarily animals change their size during free life. If the terminal member of a chain were a fish that grew from say one cm to 150 cms in the course of an ordinary life, this size change would set a limit by competition to the possible number of otherwise conceivable links in the 1-150 cm range. At least in fishes this type of process (metaphoetesis) may involve the smaller specimens belonging to links below the larger and the chain length is thus lengthened, though under strong limitations, by cannibalism.

We may next enquire into what determines the number of food chains in a community. In part the answer is clear, though if we cease to be zoologists and become biologists, the answer begs the question. Within certain limits, the
The number of kinds of primary producers is certainly involved, because many herbivorous animals are somewhat eclectic in their tastes and many more limited by their size or by such structural adaptations for feeding that they have been able to develop.

Effects of Terrestrial Plants

The extraordinary diversity of the terrestrial fauna, which is much greater than that of the marine fauna, is clearly due largely to the diversity provided by terrestrial plants. This diversity is actually two-fold. Firstly, since terrestrial plants compete for light, they have tended to evolve into structures growing into a gaseous medium of negligible buoyancy. This has led to the formation of specialized supporting, photosynthetic, and reproductive structures which inevitably differ in chemical and physical properties. The ancient Danes and Irish are supposed to have eaten elm-bark, and sometimes sawdust, in periods of stress, has been hydrolyzed to produce edible carbohydrate; but usually man, the most omnivorous of all animals, has avoided almost all parts of trees except fruits as sources of food, though various individual species of animals can deal with practically every tissue of many arboreal species. A major source of terrestrial diversity was thus introduced by the evolution of almost 200,000 species of flowering plants, and the three quarters of a million insects supposedly known today are in part a product of that diversity. But of itself merely providing five or ten kinds of food of different consistencies and compositions does not get us much further than the five or ten links of an Eltonian pyramid.

On the whole the problem still remains, but in the new form: why are there so many kinds of plants? As a zoologist I do not want to attack that question directly. I want to stick with animals, but also to get the answer. Since, however, the plants are part of the general system of communities, any sufficiently abstract properties of such communities are likely to be relevant to plants as well as to herbivores and carnivores. It is, therefore, by being somewhat abstract, though with concrete zoological details as examples, that I intend to proceed.

INTERRELATIONS OF FOOD CHAINS

Biological communities do not consist of independent food chains, but of food webs, of such a kind that an individual at any level (corresponding to a link in a single chain) can use some but not all of the food provided by species in the levels below it. ...
Chapter 3
Ecology and Ecosystems

the old. Secondly, it may occupy an unfilled niche, which may, by providing new partially independent links, increase stability. Thirdly, it may partition a niche with a pre-existing species. Elton in a fascinating work largely devoted to the fate of species accidentally or purposefully introduced by man, concludes that in very diverse communities such introductions are difficult. Early in the history of a community we may suppose many niches will be empty and invasion will proceed easily; as the community becomes more diversified, the process will be progressively more difficult. Sometimes an extremely successful invader may oust a species but add little or nothing to stability, at other times the invader by some specialization will be able to compete successfully for the marginal parts of a niche. In all cases it is probable that invasion is most likely when one or more species happen to be fluctuating and are underrepresented at a given moment. As the communities build up, these opportunities will get progressively rarer. In this way a complex community containing some highly specialized species is constructed asymptotically.

Modern ecological theory therefore appears to answer our initial question at least partially by saying that there is a great diversity of organisms because communities of many diversified organisms are better able to persist than are communities of fewer less diversified organisms. Even though the entry of an invader which takes over part of a niche will lead to the reduction in the average population of the species originally present, it will also lead to an increase in stability reducing the risk of the original population being at times underrepresented to a dangerous degree. In this way loss of some niche space may be compensated by reduction in the amplitude of fluctuations in a way that can be advantageous to both species. The process however appears likely to be asymptotic and we have now to consider what sets the asymptote, or in simpler words why are there not more different kinds of animals?

LIMITATION OF DIVERSITY

It is first obvious that the processes of evolution of communities must be under various sorts of external control, and that in some cases such control limits the possible diversity. Several investigators, notably Odum and MacArthur, have pointed out that the more or less cyclical oscillations observed in arctic and boreal fauna may be due in part to the communities not being sufficiently complex to damp out oscillations. It is certain that the fauna of any such region is qualitatively poorer than that of warm temperate and tropical areas of comparable effective precipitation. It is probably considered to be intuitively obvious that this should be so, but on analysis the obviousness tends to disappear. 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. It is also probable that certain absolute limitations
may, by providing ... it may partition a ... largely devoted to ... by man, concludes ... difficult. Early in the ... will be empty and in ... more diversified, the ... extremely successful ... ability, at other times ... successfully for the ... vision is most likely ... underrepresented ... opportunities will get ... some highly ...

... our initial question ... organisms because ... to persist than are ... through the entry of an ... action in the ... average ... to an increase in ... it times underrepre ... the space may be ... a way that can be ... likely to be asymptotic ... in simpler words ... ... some growth-forms of plants, such as those that make the development of forest ... impossible above a certain latitude, may in so acting, severely limit the number ... of niches ... ...

NICHE REQUIREMENTS

The various evolutionary tendencies, notably metapophesis, which operate on ... single food chains must operate equally on the food-web, but we also have a new, ... if comparable, problem as to how much difference between two species at ... the same level is needed to prevent them from occupying the same niche. Where ... metric characters are involved we can gain some insight into this extremely important problem by the study of what Brown and Wilson have called character displacement or the divergence shown when two partly allopatric species of ... comparable niche requirements become sympatric in part of their range.

... In the case of the aquatic insects with which I began my address, we have over most of Europe three very closely allied species of Corixa, the largest ... punctata, being about 116 per cent longer than the middle sized species macrocephala, and 146 per cent longer than the small species affinis. In northwestern Europe there is a fourth species, C. dentipes, as large as C. punctata and very similar in appearance. A single observation (Brown) suggests that this is what I have elsewhere termed a fugitive species, maintaining itself in the face of competition mainly on account of greater mobility. According to Macan while both affinis and macrocephala may occur with punctata they never are found with each other, so that all three species never occur together. In the eastern part of the range, macrocephala drops out, and punctata appears to have a discontinuous distribution, being recorded as far east as Simla, but not in southern Persia or Kashmir, where affinis occurs. In these eastern localities, where it occurs by itself, affinis is larger and darker than in the west, and superficially looks like macrocephala.

This case is very interesting because it looks as though character displacement is occurring, but that the size differences between the three species are just not great enough to allow them all to co-occur. Other characters than size are ... in fact, clearly involved in the separation, macrocephala preferring deeper water ... than affinis and the latter being more tolerant of brackish conditions. It is also interesting because it calls attention to a marked difference that must occur between hemimetabolous insects with annual life cycles involving relatively long growth periods, and birds or mammals in which the period of growth in length is short and of a very special nature compared with the total life span. In the latter, niche separation may be possible merely through genetic size differences, ... while in a pair of animals like C. punctata and C. affinis we need not only a size difference but a seasonal one in reproduction; this is likely to be a rather complicated matter. For the larger of two species always to be larger, it must never breed later than the smaller one. I do not doubt that this is what was happening in the pond on Monte Pellegrino, but have no idea how the difference is achieved....
A final aspect of the limitation of possible diversity, and one that perhaps is of greatest importance, concerns what may be called the mosaic nature of the environment. Except perhaps in open water when only uniform quasi-horizontal surfaces are considered, every area colonized by organisms has some local diversity. The significance of such local diversity depends very largely on the size of the organisms under consideration. In another paper MacArthur and I (Hutchinson and MacArthur, 1959) have attempted a theoretical formulation of this property of living communities and have pointed out that even if we consider only the herbivorous level or only one of the carnivorous levels, there are likely, above a certain lower limit of size, to be more species of small or medium sized organisms than of large organisms. It is difficult to go much beyond crude qualitative impressions in testing this hypothesis, but we find that for mammal faunas, which contain such diverse organisms that they may well be regarded as models of whole faunas, there is a definite hint of the kind of theoretical distribution that we deduce. In qualitative terms the phenomenon can be exemplified by any of the larger species of ungulates which may require a number of different kinds of terrain within their home ranges, any one of which types of terrain might be the habitat of some small species. Most of the genera or even subfamilies of very large terrestrial animals contain only one or two sympatric species. In this connection I cannot refrain from pointing out the immense scientific importance of obtaining a really full insight into the ecology of the large mammals of Africa while they can still be studied under natural conditions. It is indeed quite possible that the results of studies on these wonderful animals would in long-range though purely practical terms pay for the establishment of greater reservations and National Parks than at present exist.

In the passerine birds the occurrence of five or six closely related sympatric species is a commonplace. In the mammal fauna of western Europe no genus appears to contain more than four strictly sympatric species. In Britain this number if not reached even by Mustela with three species, on the adjacent parts of the continent there may be three sympatric shrews of the genus Crocidura and in parts of Holland three of Microtus. In the same general region there are genera of insects containing hundreds of species, as in Athela in the Coleoptera and Dasyhelea in the Diptera Nematocera. The same phenomenon will be encountered whenever any well-studied fauna is considered. Irrespective of their position in a food chain, small size, by permitting animals to become specialized to the conditions offered by small diversified elements of the environmental mosaic, clearly makes possible a degree of diversity quite unknown among groups of larger organisms.

We may, therefore, conclude 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 characters of the environmental mosaic which permit a greater diversity of small than of large allied species.