The Importance of Paradigms in Scientific Research: the MacArthur Paradigm and Community Ecology

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Ecological systems are complex entities resulting from a multitude of processes operating over long periods of evolutionary time (Loehle 1988). The difficulty involved in attempting to understand these systems has resulted in a fierce debate with regards to our ability to adequately explain patterns and processes in ecology (Loehle 1988). This is especially true in community ecology where the ultimate goal is the formulation of theories to account for the myriad patterns of species associations and their respective causal processes (Wilbur and Travis 1984). The initial reaction of a new adherent to the study of community ecology would no doubt be the rapid development of a close kinship with Sisyphus and his never ending pursuits. Despite this sense of impending futility it is this field in which I have chosen to pursue my thesis research.

The first task of thesis research is the development of a project proposal. For my thesis I will want the proposal to incorporate existing information, suggest some original ideas and make a positive contribution to the study of community ecology, something that may not be easy to accomplish considering the large number of opposing ideas and contending hypotheses already in circulation. The ability to ask the right questions and be confident of their accuracy in targeting the right problems will come only from a clear understanding of the present status of community ecology. I feel that the best way to attain this goal would be to examine the development of the ideas and hypotheses that characterize modern community ecology. To facilitate this task I will try to answer three basic questions. Firstly, how important is it to understand the characteristics of a paradigm and the evolution of its central ideas? In other words, is it necessary to know the history and details of the paradigm in which one is working? Secondly, how important is the MacArthur paradigm? The MacArthur paradigm currently prevails in community ecology and the debate concerning its validity (or at least parts of it) is ongoing. By studying the MacArthur paradigm in detail I can determine how successful it was in influencing the development of community ecology, how ecologists reacted to it when it first appeared and how researchers currently view it. Thus, the pursuit of the second question can aid in the answering of the first. And thirdly, where does my thesis research fit into the MacArthur paradigm? I want to know how my research relates to the current tenets of the MacArthur paradigm. I have related all three questions to the paradigm concept because the development of ecology closely parallels the development of a scientific discipline as perceived by Kuhn (McIntosh 1980). As such, this route should prove to be a beneficial way of examining the characteristics of both.

By examining such factors as the characteristics of paradigms, the recent history of community ecology, the main components of the MacArthur paradigm, and the current status and future direction of this paradigm, I will be able to answer the three basic questions and determine if my thesis proposal does indeed satisfy the requirements I ask of it.

Paradigms

Before discussing any paradigm it is necessary to have a clear understanding of the structure and function of paradigms. In his analysis of the evolution of science and that patterns that exist in its development Kuhn (1970) described how paradigms are the functional units through which scientific progress is achieved. A paradigm can be viewed as a set of theories or models that gain acceptance within the scientific community because they are more successful in incorporating existing knowledge and solving current problems than competing theories or models. For example, several older theories may be discarded because another one proves to be more comprehensive, simpler and accurate (Hull 1974). A paradigm is also capable of funneling further research activities into well focused directions, so its success at the start is in large part due to its promise of success in future research. The use of paradigms is, thus, a fruitful and economical method of increasing our understanding of a scientific field.

The majority of work done within the confines of a paradigm is termed normal science. It consists of the continued articulation of the tenets of the paradigm through examination of those problems that the paradigm deems worthwhile of further study. Three main types of problems, which occupy the vast majority of both empirical and theoretical research, are recognized: determining which facts are significant, matching these facts with the prevailing theories and constructing a more refined and precise theory or set of theories. The result of this practice of normal science is not simply the accumulation of new information, which is beneficial in itself, but the production of a more precise paradigm. This evolving paradigm, in turn, allows researchers to undertake problems that would not have otherwise been considered without the conceptual framework provided by the paradigm. The presence of a Kuhnian paradigm is thus essential to the continued progress of any scientific field.

Recent History of Community Ecology

To understand the impact of MacArthur's work on the study of ecology we must examine the state of community ecology as it existed just prior to the start of MacArthur's publishing career and also, look at some of the reasons why his work was so highly regarded.

By 1950 two views regarding community structuring were at the forefront of ecology in North America (Wiens 1983). The first was developed by Clements who, in the early

1900's, applied the analogy of organisms to communities (McIntosh 1985) such that successional seres in plant communities were regarded as developmental stages and the climax seen as adulthood (Colwell 1985). Clements `supraorganismic theory' of communities, which may well have occupied the role of a Kuhnian paradigm (McIntosh 1975), was widely accepted by most ecologists until about the 1950's (McIntosh 1985). However, by this time Clementsian theory was being reassessed and parts of it discarded in favour of the `individualistic hypothesis' of Gleason (McIntosh 1975). Gleason's particulate view of communities suggested that `communities were assemblages of largely noninteracting species and they exhibited rather little repeatability in structure or organization from place to place' (Wiens 1983). The second view was the opposite of that propounded by Gleason. In 1934 Gause used birds to study the theoretical aspects of interspecific competition developed by Lotka and Volterra (Perrins 1983). From this work and subsequent work came the competitive exclusion principle (or Gause's Law) (McIntosh 1985), which greatly affected the way ecologists viewed problems of community ecology (Perrins 1983). Perhaps as important was Gause's emphasis on the study of the entire community, i.e. holistic ecology (McIntosh 1985). The work of Gause was continued by MacArthur who, in the late 1950's, was the primary force behind the proposal that `communities were tightly integrated entities containing suites of interacting species and exhibiting clearly defined and repeatable structure under similar environmental conditions' (Wiens 1983). This is the point at which a split occurred in ecology. According to Wiens (1983), MacArthurs approach to community studies rapidly became the one which `assumed a position as the guiding focus of the discipline' and as such developed the characteristics of a Kuhnian paradigm. Several reasons why MacArthurs view gained prominence so quickly are provided by Wiens (1983): it proposed new ideas and posed new questions about community structuring, its mathematical theories seemed quite elegant, it neatly explained what was happening in the natural world, and perhaps, after decades of no significant advances regarding the views of Clements versus Gause, ecology in the 1950's was stagnant and ready for some new ideas. By the 1960's ecologists had divided themselves into two schools (Brown 1981). Organismic ecology, founded by Clements, was continued by the ecosystem ecologists led by Odum (Brown 1981) and `transmogrified' into systems ecology (MacIntosh 1980; Simberloff 1980). The evolutionary ecologists, led by MacArthur, continued working on ecological interactions between species and developing the competition models of Lotka and Volterra (Brown 1981). These were the conditions under which, according to Kolata (1974), the `predictive science of theoretical ecology', led by Robert MacArthur, began.

The MacArthur Paradigm

The MacArthur paradigm is composed of a number of different characteristics which established the appropriate ways of studying questions in community ecology (Wiens 1983). Although each characteristic was profoundly influenced by the work of MacArthur and those who followed his lead (Wiens 1983) there are two contributions he made to ecology that are considered to be of prime importance (McIntosh 1980). Firstly,

he influenced the methodology of ecological studies by furthering the use of the hypothetico-deductive method (Fretwell 1975). And secondly, he was instrumental in altering the very nature of ecological research. According to Cody and Diamond (1975: vii),

Within two decades new paradigms had transformed large areas of ecology into a structured predictive science that combined powerful quantitative theories with the recognition of widespread patterns in nature. This revolution in ecology had been due largely to the work of Robert MacArthur.

That one person could exert so strong an influence on an entire scientific field becomes evident from an examination of his publications. Fretwell (1975) found that MacArthurs work did not concentrate solely on one aspect of ecology but permeated virtually all dogma of the field with significant or even seminal writings. According to Fretwell (1975) his most important works dealt with community diversity (MacArthur 1965) and evolutionary ecology (distinction between r vs. k selection) (MacArthur 1961). In the area of population regulation he defined the idea of scramble competition (MacArthur and Levins 1964) and advanced predator-prey theory (Rosenzweig and MacArthur 1963), and in ecosystem theory showed that intrinsic stability was directly related to species diversity (MacArthur 1955). MacArthur evidently had a profound effect on ecology because he is credited with raising the study of communities and ecosystems to the level of an `intellectually challenging branch of ecology' (Krebs 1976) and with `revolutionizing' biogeography (Simberloff 1974). The collective effect of his numerous works is viewed by some to constitute a true paradigm (Wiens 1983) in that they define the questions that require answers and guide subsequent research in a well-focused direction.

At this point it may be timely to present a brief discussion on scientific terminology. What exactly is the MacArthur paradigm: a theory, law or concept? A theory, according to McIntosh (1980), is simply an abstract relationship between different phenomena and their explanatory laws. Loehle (1988) feels that when first proposed theories are immature and it is around these immature theories which many inconclusive debates revolve. Perhaps this is why Hull (1974) refers to much of MacArthurs work as `theories'. Roughgarden (1983) referred to ecological theory as `no more than a collection of tools' to be easily discarded while Peters (1976) felt that competitive exclusion lacked the scientific qualities to qualify as a theory. Scientific laws, according to McIntosh (1980), should be universal generalizations. Process laws are not possible in ecology because they require closed systems, however, causal laws require only that natural phenomena be classified into interconnected groups (Hull 1974). Much of the MacArthur paradigm might classify as causal laws. Regier and Rapport (1978) felt that the lack of ecological laws was delaying the search for a comprehensive theory in ecology while others felt there certainly were no ecological laws (Peters 1980) nor felt there ever could be (Roughgarden 1983). A lack of precision on the part of anything that resembled an ecological law led many people to call things such as the

`competitive exclusion principle' generalizations (Loehle 1988). With this controversy over the exact meaning of laws or theories in ecology it is difficult to classify any part of the MacArthur paradigm as being either. Parts of it have, however, been referred to as a concept. This term has long been used by ecologists to refer to new ideas, finding its ambiguous nature quite useful (McIntosh 1980). Accordingly, I shall herein continue to refer to its various aspects as concepts bearing in mind that other terms, such as theory or law, as well as hypothesis, principle or model, may be applicable, either now or at a future time.

Aspects of the MacArthur Paradigm

Now that we have reviewed the historical circumstances preceding the reception of MacArthurs work and have established that the significance of his research does indeed equal that of a paradigm, the next step is to scrutinize the various parts of the paradigm itself. MacArthurs most influential publications appeared during the period of 1955 to 1972 (Fretwell 1975) and during that time, and in the years since, the ecological literature has witnessed a tremendous proliferation of publications dealing with, or inspired by, his work. Thus, all of his writings have been subjected to a fairly long and rigorous process of critical peer review. Through careful examination of the constituent parts of this paradigm and consideration of the criticisms of his contemporaries we can determine not only the conceptual structure of the paradigm, and thereby achieve a greater understanding of it, but we can also determine the current status of the paradigm as a guiding force in ecological research. Wiens (1983) analyzed MacArthurs writings and those of his colleagues and was able to discern ten aspects that characterized the paradigm and I will use these ten as the basis for the discussion which follows. A complete treatise of each aspect is beyond the scope of this text, therefore I will limit the discussion to a basic description of each, as well as mentioning what are now considered some of their advantages and disadvantages.

1. Detection and explanation of patterns

A major goal of community ecology involves the ability to detect and explain recurrent patterns in nature (Wiens and Rottenberry 1980; Wiens 1983). This emphasis arose from MacArthurs now classic paper (MacArthur 1955) where he demonstrated how repeatable patterns of habitat division by warblers were an indication of the ability of competing species to coexist (Wiens 1983). There have been many studies since then that have examined partitioning of habitat and other resource types in this same context (Morrison 1984; Schoener 1974). The ability to describe these patterns of community organization are certainly valuable tools in the study of ecology, however, a number of papers in recent years have urged ecologists to avoid using the detection of patterns as a goal in itself. Roughgarden (1983) was critical of the view of Strong et al. (1979) that patterns must be discerned before causal processes could be investigated. He argued that the study of causal processes was the more important component. Wiens (1983) found examples where the presence of patterns was used as sole proof for the

existence of certain causal processes. And Wilbur and Travis (1984) described several sources of problems with placing too much faith in the study of patterns: any historical effects that would have influenced pattern formation cannot be evaluated, the number of different variables and their interrelations that can be adequately studied in complex ecosystems is limited, and, arising from this last point, most studies of this kind focus only on a small number of variables.

2. Generality

The more general a pattern and its causal explanation the more useful it was considered to be (Wiens 1983). This view was echoed by Cody (1974) who said that describing general patterns was of prime importance. Intuitively it is desirable to have broad generalizations that can account for patterns involving many different habitats and species. According to Karr (1983) this desire is one of the weaknesses of the MacArthur paradigm. He feels that the search for generalizations has encouraged researchers to search for repeatable patterns and ignore all natural situations where definite patterns were not found.

3. Competition

Interspecific competition is `the primary process producing the patterns of communities... Such interactions lead to the exclusion of marginally adapted species from communities, producing a community structure that is well ordered and highly integrated' (Wiens 1983). This definition illustrates the great appeal of the concept of competition: it is a causal process responsible for the existence of community patterns and it can be applied in all types of ecosystems (i.e. broad generalizations). Thus, it is not surprising that, during what is viewed as the `classical' period of theoretical ecology (the 1960's and 1970's) (Colwell 1985), competition became a deeply entrenched part of the study of communities, and few researchers doubted its importance in shaping those communities (Ricklefs 1975; Diamond 1979). Interspecific competition was described as the `cornerstone of niche theory' (Diamond 1978) and of population ecology (McIntosh 1985), the `driving force of Darwinian reproductive competition' (Colwell 1985), and the primary factor which limits diversity' (Brown 1981). It was also believed that determining the `mechanisms of competitive interactions was the key to understanding the organization of communities' (Brown 1981). Many ecologists still believe that competition is the most important process structuring communities (eg. Brown 1981; Roughgarden 1983; Schoener 1982). However, in recent years there has been an increase in the number of researchers who would like to temper the enthusiasm for competition as the major, if not only, process operating to determine community patterns. They believe that the unrestrained promotion of competition is not justified since its level of importance has not been conclusively proven. Among their concerns are: instances where competition was inferred and alternative null hypotheses given no consideration (Connor and Simberloff 1979), the use of hypotheses that depend on the historical occurrence of competition and thus, cannot be falsified (Wiens

1983), finding evidence for competition in data that can be interpreted in favour of other conclusions (May 1984) and the fact that competition may be favoured because it fits in nicely with the popular mathematical theories of Lotka, Volterra and Gause (Jackson 1981). Various forms of competition have also been used to account for differences between predictions of theory and actual observations. For example, the presence of diffuse competition over entire communities (Wiens 1983) or the effects of `ghosts of competition past' (Connell 1980). The end result, according to Strong et al. (1979) was an uncritical acceptance, in the form of a `paradigm' unto itself, of competition as the primary force structuring communities. This aspect of the MacArthur paradigm is the most studied and certainly the most controversial. The hypothesis that competition between species for limited resources does occur and that it may ultimately influence community structuring is accepted by virtually all ecologists (Ricklefs 1975). However, the extent to which competition is capable of influencing community structure and the degree to which it is affected by the habitat type, species, resource levels and even seasonal changes in the environment, has yet to be determined.

4. Equilibrium

Equilibrium is the state in which a habitat with a given number of resource-based niches is `saturated' with species and where fluctuations in environmental conditions are mirrored by fluctuations in community diversity such that an optimal community structuring is continuously maintained (Cody 1981; Wiens 1983, 1984). During the 1960's and 1970's the assumption of equilibrium was the central dogma of theoretical ecology (Colwell 1985; Karr 1983). However, there have been increasing doubts about the equilibrium status of communities (Wise 1984). For one, it has been shown that some communities do undergo substantial fluctuations over time. Some long term avian studies have shown considerable, and inconsistent, annual changes in diversity (Jarvinen 1978; Winternitz 1976). Seasonally abundant resources in some areas can lead to unsaturated and therefore, nonequilibrial communities (Wiens 1983). Also on a seasonal basis, factors such as local climatic conditions and the status of migratory populations on their wintering grounds can vary considerably and affect community equilibrium (Wiens 1983). And some researchers feel it is impossible to conclusively prove that a community is in equilibrium unless it is studied for a very long time, i.e. decades (Jarvinen 1980). According to Wiens (1983) such studies are not within the tradition of the MacArthur paradigm.

5. Theory

In this aspect of the paradigm ecologists are guided by the theoretical predictions of models of natural systems which determine the type of data that are desired (Wiens 1983). The main benefit arising from this approach was an increase in the respectability of the hypothetico-deductive approach to ecological problems (Fretwell 1975).

6. Comparisons

The existence of patterns and predictions of theory are tested using `natural experiments', i.e. broad comparisons of natural variations in the environment (Wiens 1983). This was thought to be the quickest and most economical method of progressing from hypothesis and predictions of theory to accepted fact (Cody 1974).

7. Selected Examples

The characteristics of form and process in patterns arise from comparing selected case studies and the data predicted from theory (Wiens 1983). The difficulty inherent in this method concerns the tendency of researchers to `force very complex systems to comply with simplistic models' (Karr 1983). The situation is exacerbated because this approach is generally more qualitative than quantitative due to a lack of rigorous statistical analysis of the relationships between theory and reality.

8. Habitat Features

Because of the assumptions of equilibrium and community saturation researchers tended to measure only a few habitat or resource features when studying communities (Wiens 1983). Usually the features considered were those for which competition was thought to be occurring (Cody 1974). This situation was initiated in MacArthurs paper on habitat subdivision in warblers (mentioned previously) and emphasized in a subsequent project (MacArthur and MacArthur 1961) where he correlated bird species diversity (BSD) with a habitat index, foliage height diversity (FHD). MacArthur argued that the close correlation between BSD and FHD he found in several different habitats was proof of the importance of the physical structure of the habitat in determining habitat selection by birds (Wiens 1983). Consequently, vertical vegetation structure became the prime habitat variable in ecological studies of birds (Karr 1983). However, researchers have found that in some cases FHD was more an artifact resulting from data manipulation to ease interpretation than a true variable of interest to the birds (Wiens 1983). It is now clear that other habitat variables are also important (Karr 1983) and that quantifying habitat with a single index is a difficult and misdirected effort (Rotenberry and Wiens 1980a).

9. Field Experiments

Field experiments, where variables such as population densities, vegetation structure and resource densities are experimentally adjusted (Karr 1983), were not considered capable of contributing information useful in solving questions in community ecology (Wiens 1983). Studies in the past decade have changed this view and proven their usefulness. Field experiments have illustrated the absence of interspecific competition in cases where circumstantial evidence had indicated otherwise (Tinkle 1982; Wise 1981b). They have also demonstrated their capability of confirming prevailing hypotheses (Dayton and Oliver 1980; Roughgarden 1983). And if carefully designed,

they can provide valuable insights into the factors responsible for the patterns observed in species assemblages (Simberloff 1976a; Underwood and Denley 1984).

10. Methodology

Research design and field methods have suffered as a result of many of the problems associated with the preceding aspects of this paradigm. The search for generalizations, the faith in competition as the primary structural process in communities, the assumption of equilibrium, the predictions derived from theory and the search for single indexes to describe complex ecosystems have all played a part in ensuring that the design of research projects and the field methods used were, for the most part, at least slightly flawed. For example, data were gathered in opportunistic and nonsystematic fashion (Wiens 1983) and many of the classical procedures lacked sufficient accuracy to detect those types of data needed to understand ecological patterns (Karr 1983). The confidence placed in a few parameters as being the only truly important ones worth measuring has retarded the growth of new methods for studying communities. The literature survey that provided the information given on each aspect of this paradigm indicated that this problem is now an important concern and is currently being addressed, as is evidenced from the preceding discussion on field experiments.

Current Status of the MacArthur Paradigm

The field of community ecology has reaped enormous benefits as a result of the prominence of the MacArthur paradigm. In the three decades since the writings of MacArthur first began to influence ecologists, a great deal of information has been collected on a large variety of different ecosystems and their constituent species. This, in turn, has led to an increase in the understanding of adaptive strategies of many species and the various interspecific interactions that work in conjunction with these strategies; not only competition but also predation and mutualism (Brown 1981). The attempt to achieve some of the goals set by the paradigm resulted in a change of priorities with regards to those aspects of community ecology deemed worthwhile of study. One such change was achieved by substituting the search for broad generalizations with the detailed examination of the complex nature of ecosystems (Karr 1983). Another beneficial change was the realization of the potential of field experiments for providing information valuable to the study of ecological questions. Overall, the MacArthur paradigm was of great benefit to ecologists in that it helped the science of ecology move forward as a fairly unified force and thereby achieved much more than would otherwise have been possible had it maintained its `stagnant' state of the early 1950's.

In addition to describing these numerous benefits that have accrued over the years we also need to examine the shortcomings of the paradigm; those problems that, while still a part of the paradigm, are currently perceived as constraints to further understanding and growth in community ecology. Only through consideration of both the detrimental

as well as the beneficial aspects can we understand fully the current status of the MacArthur paradigm. The most important of these constraints are as follows. The quest for generalizations, which could be applied over large areas and in many diverse environmental conditions, influenced many researchers; repeatable patterns in communities were considered desirable while, unfortunately, any anomalies were ignored (Karr 1983). The assumption of equilibrium, still a crucial part of current theory in community ecology (Schoener 1982), is falling into disfavour (Colwell 1985), and without equilibrium, the concept of competition as the prime force in structuring communities is also undermined (Karr 1983). Observations that agree with hypotheses formed within the assertions of the paradigm are accepted as proof of the validity of the paradigm while alternate hypotheses are not given due consideration (Wiens 1983). As well, many of the current hypotheses of community ecology are unfalsifiable, and the best type of hypotheses, null hypotheses (Strong 1980), are not a traditional part of the MacArthur paradigm (Wiens 1983). The models developed for the study of competitive interactions are not `empirically operational' (Brown 1981). They fail to provide testable predictions and they do not guide field naturalists as to which variables to measure (Brown 1981). And finally, the main problem in the study of community ecology has been `a dependence on a simplistic body of theory that is incapable of accounting for pattern in an exceedingly complex world' (Karr 1983).

The number and scope of these constraints would seem to indicate a number of problems regarding the current status of both the paradigm and community ecology. Brown (1981) made a valid point when he described two very fundamental aspects of community ecology that remain unanswered despite three decades of theoretical and empirical work. First, he feels that despite a large information base regarding the basic types of species interactions, ecologists still have not determined how interspecific interactions determine the structural and functional characteristics of communities. And secondly, no one has yet been able to answer the question posed by Hutchinson (1959), "Why are there so many species?". Brown (1981) also expressed concern over what he felt is `widespread pessimism and disappointment' among ecologists because `ecological theory has promised far more than it has delivered'.

According to Kuhn (1970) when the tenets of the paradigm can no longer match anomalous observations to the conceptual theories or these theories fail to act as an adequate guide for continued research then a scientific revolution must occur such that the existing paradigm is replaced by a new one. Although the past decade has witnessed an increase in the level of disillusionment with the MacArthur paradigm (Wiens 1983) such a revolution is not occurring. Rather, what is no doubt happening is that the paradigm is undergoing a continual process of articulation and refinement wherein selected parts of the paradigm are being replaced `a little at a time'. The period of normal science (discussed previously) in which community ecology currently finds itself has passed through the stages of determining the significant facts and matching these facts with theories. It is now refining these theories while at the same time trying new and different approaches with the first two stages. With so many possible

hypotheses now being explored it is little wonder that the current paradigm in community ecology, in its present state, seems to be in poor shape.

Future Direction of the MacArthur Paradigm

Just as there are innumerable critics of the present state of community ecology so too are there many researchers who would have us believe that theirs is the correct vision for the future direction of research in this field. To discuss all the possible avenues for future research would require an entire essay in itself so I will restrict the discussion to a brief summary of what are likely the most important ones and the salient features of each.

Several points emerge with regards to the design of ecological studies. Firstly, there should be a clear separation between the efforts to describe patterns and the attempts to explain their causal processes (Wiens 1983). Secondly, rigorous methodological procedures must be developed and widely adopted (Wiens 1983). And lastly, more informative experimental protocols must be produced (Roughgarden 1983), for example, carefully designed manipulative field experiments (Wiens 1983). The scope of the projects are also subject to the changing views of researchers. There seems to be a move away from the search for broad generalizations in favour of the intensive study of sets of species in local settings. There is some feeling that these types of studies should not be restricted to groups bounded by taxonomy but should include all species exhibiting similar patterns of resource utilization (Wiens 1983). Ecological studies should also focus on the diversity of factors that would influence each species. Although few researchers doubt the existence of interspecific competition, its importance in influencing community structure and function will remain uncertain until its spatial and temporal persistence is more carefully measured (Karr 1983) and the level of resources in communities is determined (Diamond 1978). Another factor requiring study is the pattern of energy allocation through the community (Brown 1981). Equilibrium theory should not be applied to communities until it is determined whether or not a particular community is stable (Connell and Sousa 1983). And all of these factors should be incorporated into long-term studies. Roth (1976) stated that short-term studies provide only glimpses of what is occurring in communities while Jarvinen (1980) feels that the equilibrium status of communities cannot be determined unless it is studied for decades. And finally, the models that result from these studies need to be improved. Single population or two-species models do not accurately reflect biological reality (McIntosh 1985) whereas better ones may result from moving beyond small-scale empirical studies (Underwood and Denley 1984).

A prevalent theme running through much of this discussion centres on the development of a more theoretical approach to the study of community ecology. The need for a strong theoretical base was emphasized as far back as twenty years ago (Gates 1968, Watt 1971). However, this natural desire for a general theory may be thwarted by the incredible diversity of species and relationships in nature (Whittaker and Levin 1977).

Thesis Proposal

Now that we know what the MacArthur paradigm is, how ecologists currently view it and where future research may be headed, it is possible to review my proposed thesis project and determine its relative position within the conceptual framework of the paradigm. To accomplish this, I will describe the project and how it relates to each aspect of the paradigm and how, in turn, the direction of future research within the paradigm has influenced the design of this project.

The main hypothesis for the study states that due to the seasonally abundant resources and low species diversity that are characteristic of most northern ecosystems subarctic avian communities should exhibit less structure than temperate avian communities. Two points are apparent from this hypothesis. The project has the characteristics of a classical community ecology study in the true MacArthur tradition in that it seeks to determine the patterns of community structure. However, it will also try to relate these observed structural patterns to levels of available resources. According to Holmes and Recher (1986) the vegetation structure, the availability of food resources and the distribution of foraging substrates determine the composition and guild structure of avian communities in forest habitats. Thus, variation in resource availability in the habitat influences the types of species that can forage successfully which in turn, strongly influences guild, and consequently, avian community structure. One objective of this study, then, will be to identify those characteristics of habitat use that are important in determining the structure of avian foraging guilds.

The ability to compare avian community structure in contrasting habitats will help elucidate the importance of such factors as vegetation structure and food resource availability in determining structure (Holmes and Recher 1986). The characteristic habitat of my study area consists of a decadent black spruce forest in which, according to a survey of the Zoological Record (1960-1988), no detailed studies of the avian community have been done. Thus, my study will not only provide new information for a poorly studied ecosystem type but it will also provide useful information that will be comparable with other similar studies. Based on the habitats they studied and the types of methods that were used, I have adopted the field and analytical methods advocated by Holmes et al. (1979) and Holmes and Recher (1986). These two studies examined avian guild structure in north and south temperate broad-leaved forests and found that the foraging opportunities afforded by the habitat were considered `primary determinants of guild structure'. The ability to compare data between temperate broad-leaved forests and subarctic coniferous forests will enable me to determine if similar habitat variables have an equally intensive influence on community structuring in the subarctic.

What I have described thus far is that part of the study concerned solely with the

ecology of the bird species. Miles and Ricklefs (1984) stated that community organization could not be adequately studied unless the relationship between the ecology of each species and their morphology was determined. They found that there was a strong relationship between the ecological space occupied by each foraging guild in Holmes et al.'s (1979) study and the morphological attributes of the species within each guild. The need for further studies to examine the importance of this relationship in determining guild structure is certainly an endeavour worth pursuing.

The final part of the project involves the use of a field experiment. I want to determine how a subtle alteration of the physiognomic structure of the habitat affects avian community structure. By altering the vegetation structure of the subarctic forest the foraging substrate and food resources (i.e. invertebrates) available to the birds is changed. The response of the avian community will provide an indication as to how it is structured, i.e. changes in degree of niche overlap or species diversity in the experimentally disturbed areas.

Because the subject matter of my project lies within the sphere of the MacArthur paradigm it must embody each aspect of that paradigm in some way. It is important to know how my project is affected by each aspect and thus, how its design has responded not only to the overall influence of the paradigm but also to the workings of normal science that are continually seeking to refine the paradigm.

Pattern

The project will certainly look for community-wide patterns but this will not constitute a goal in itself. It will also attempt to determine which variables are important in creating those patterns. I will be aware of the possibility that the patterns may not conform to any preconceived notions. A subarctic environment ensures that the number of habitat and species variables are kept to the minimum possible for a forested environment.

Generality

By comparing the results from this study to other similar ones done in different habitats I can look for differences and/or similarities that might provide insights into those variables important to community structuring. This will be done without searching for broad generalizations which characterize many such studies. In this way the project will emphasize the use of intensive studies on local species assemblages rather than general, extensive studies.

Competition

I cannot ignore the presence of competitive interactions since they are to some extent, responsible for any observed patterns of habitat use. However, I will not try to infer its presence or absence based solely on the presence or absence of community patterns.

Comparisons

Part of this project will involve the comparison of different communities in their natural states.

Habitat Features

The project will not restrict its measurements of the habitat to a few, select variables but will try to incorporate all the biotic and abiotic variables possible.

Field Experiments

As mentioned earlier I will capitalize on the growing respect of field experiments as useful tools in ecological research by using one to examine the effects of habitat disturbance on the avian community.

Methodology

The project will use methods designed to examine many variables related to habitat partitioning, not just a few selected ones. These methods will also ensure that the data collected will be amenable to robust statistical analysis so that all variables and relationships can be analyzed quantitatively.

There are a few problems with the design of this study that are, unfortunately, unavoidable. Firstly, it will be a short-term study, spanning the duration of only one breeding season. The second problem is a result of the first: since it is of short duration it cannot determine the equilibrium status of the community. And lastly, the scope of the subject under study (terrestrial, non-raptorial birds) is bound by taxonomic limits. Despite these drawbacks I feel that the design of this project has adequately considered the theoretical and methodological criticisms of each aspect of the paradigm and has achieved a good compromise between what is ultimately desired in ecological research and what is currently feasible.

Conclusion

Although this essay has been, of necessity, quite long it has provided a wealth of information. And I have found that this amount of information is the minimum required to adequately answer the three basic questions related to thesis proposal development posed at the outset of this essay. It is these three questions to which I now address myself.

Firstly, how important is it to understand the characteristics of a paradigm and the

evolution of its central ideas? Simply put, very important. By learning the basic tenets of a paradigm a person is laying the foundation upon which rests the results of all research conducted within the premises of that paradigm. This understanding is also required if one is to undertake research that is in any way beneficial to their field. A tree must have a solid trunk from which branches can grow.

Secondly, how important is the MacArthur paradigm? When the MacArthur paradigm first started to influence ecological research it was enthusiastically received by virtually all ecologists and subsequently, had a tremendous influence on the development of community ecology. Although many of the tenets of this paradigm are currently being heartily criticized and hotly debated it is still influencing the research direction of this field. As such, its importance is still paramount.

And thirdly, where does my thesis research fit into the MacArthur paradigm? As I have tried to illustrate in the latter part of this essay, right near the front of research activities in some aspects of the paradigm. The proposal does take into account existing information regarding each aspect and, by extending some of the newer research traditions of the paradigm into a poorly studied but widespread ecosystem, the subarctic, it has suggested some original ideas. As such I believe my project will make a positive contribution to the study of community ecology and thus, does satisfy the requirements I ask of it. Perhaps it is possible that ecologists, like Sisyphus, may one day succeed in attaining their ultimate goals, although the burden is still heavy and the summit is still distant.

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