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An Inquiry Into The Nature Of Biogeography

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AN INQUIRY INTO THE NATURE OF BIOGEOGRAPHY

by

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ABSTRACT

The thesis defines Biogeography as the study of the interactions between all organisms and their surrounding environment with particular focus on the spatial organization that they thereby generate. It includes plant and animal species. The inquiry is divided into four components: a critical review of the literature, a set of research examples, an elaboration of significant concepts, and research strategies.

The current textbooks and research in Biogeography stress the concept of the ecosystem. It is argued that the concept is not appropriate to the problem of Biogeography, and furthermore only serves to confuse the distinction between Biogeography and Ecology. The concept is inappropriate because it does not include an explicit spatial component and also it produces a misplaced concreteness. In place of the 'ecosystem' approach, this thesis supports the 'distribution' approach.

A review of the literature does not provide insight into the nature of the problems of biogeographical research. This limitation is rectified by six illustrations of the author's research, which are consistent with the 'distribution' approach. They are itemized below:

(1) Nearest Neighbour Analysis of Tree Species
(2) Spatial Organization of Vegetation Types
(3) The Role of Seed Dispersal in the Formation of Spatial Patterns

(4) Movement Patterns of the Common Murre (Uria aalge)

(5) The Application of Biotelemetry to Biogeography

(6) The Cricket Match as an Analogy

These examples indicate a variety of methodological and conceptual problems from the plant and animal kingdoms. As a set, they support the division of the 'distribution' approach into two paradoxical strategies. First, the 'organism-centred' strategy which focuses on the intrinsic properties of organisms and secondly, the 'space-centred' strategy which emphasizes the characteristics of the environmental space.

This division is the context for the investigation of four significant concepts. These concepts, namely Natural Order, Pattern, Spatial Diversity and Organism Interaction, are closely linked with the conceptual structure of the biological sciences. Indeed, a major premise of the thesis is the existence of conceptual problems, similar in form to the problems of Biogeography, at other levels in the hierarchy of living matter. The philosophical and methodological statements in Theoretical Biology are deemed significant.

The final component of the inquiry translates this alternative definition of Biogeography into four research strategies, consistent with the philosophy and problems articulated in the earlier parts of the thesis. First, it is recommended that there should be an emphasis on Theoretical Biogeography. The discipline must integrate the current developments in Theoretical Biology and Theoretical Geography. The second strategy is the establishment of an Applied Biogeography based on a philosophy of life for all species. This research includes the impact of the human species on other species and the role of Biogeography in changing the consciousness of the human species towards harmonious interaction with other species. Thirdly, field research in Biogeography must recognize the conceptual problems and the instrumentation problems in the discipline. Recent developments in biotelemetry are considered to possess future significance. Finally, the inquiry cannot be divorced from its teaching context; specific examples illustrate this relationship.

Biogeography is concerned with the nature of living matter and the nature of space. The discipline has a significant role in the future of Geography; it must reconcile and integrate the contemporary issues of the biological sciences and the paradox of Geography.

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My parents will be glad that it is finished; certainly, it would never have been completed without their encouragement. The work is dedicated to my sister.

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CHAPTER I

INTRODUCTION

Biogeography has always been a minority interest within the discipline of Geography. There are a number of historical reasons for this situation. In the eighteenth and nineteenth centuries Biogeography could be equated with the activities of the explorer-naturalists, for example, von Humboldt, Darwin, Wallace and Bates.[1] Subsequently, the natural sciences moved into the laboratories and at the same time the linkage between Natural History and Geography disappeared. During the present century, geographers like Sauer have recognized the loss of the linkage and also the need for its rediscovery in Biogeography.

> The field of Biogeography requires more knowledge of Biology than can be demanded of most of us. It is, however, so important to us and so inadequately cultivated from almost any side that we should encourage the crossing of Geography with Natural History wherever the student is competent. In

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[1] The following are illustrative of this period: Alexander von Humboldt, Personal narrative of travels to the equinoctial regions of America during the years 1799-1804 (London: G. Bell and Sons, 1900); Charles R. Darwin, Journal of researches into the Natural History and Geology of the countries visited during the voyage of the HMS Beagle around the world (Glasgow: Grand Colosseum Warehouse Co., 1845); Alfred R. Wallace, Travels on the Amazon and Rio Negro, with an account of the native tribes, and observations on the climate, geology and natural history of the Amazon Valley (London: Ward, Lock and Co., 1889); Henry W. Bates, The Naturalist on the River Amazon, Everyman's Library (London: J. M. Dent and Son, 1910).

> particular, we need to know much more of the impact of human cultures on plant cover, of man's disturbance of soil and surface, of his relation to the spread or shrinkage of individual species, of human agency in the dispersal and modification of plants.[2]

Within the biological sciences, the development of Ecology has counterbalanced the over-emphasis on the indoors and "hard-science" laboratory techniques. Recently, Ecology has been acclaimed the 'critical science'[3] or the 'subversive science'[4] and, in general, the discipline has produced an increase in the public awareness of the "ecological crisis" and the global environment. Biogeography has similarly been influenced by the developments in Ecology. The primary influence has been the adoption of the ecosystem concept, a trend which extends into other fields of Geography.

The writer recognizes a danger in the identification of Biogeography with the ecosystem concept of Ecology. The essential argument is that there is a body of information on living organisms concerning their geography which is distinctive and cannot be subsumed within the ecosystem framework. Bunge makes a supportive assertion from a different set of premises. "It is not ecology but geography that the world needs, since ecology is the 'physical environment minus

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[2] Carl O. Sauer, Land and Life: A selection of the writings of Carl Ortwin Sauer, ed. J. Leighly (Los Angeles: University of California Press, 1969), p. 399.

[3] Murray Bookchin elaborates on this definition in his essay, "Ecology and Revolutionary Thought," Post-scarcity Anarchism (Berkeley California: Ramparts Press, 1971), pp. 57-82.

[4] This definition is well illustrated in Paul Shepard and D. McKinley, eds., The Subversive Science: Essays towards an Ecology of Man (Boston: Houghton-Mifflin Co., 1969).

mankind'. It is geography that puts man in nature."[5]

It is not acceptable to define Ecology as the physical environment minus mankind. Recent developments illustrate that the discipline has expanded to embrace humanity. Secondly, Geography cannot be truly described as the discipline which "puts man in nature," if the sub-discipline of Biogeography has a minority status. This thesis is concerned with the dualism between man and nature and their reconciliation in Biogeography.

The dualism is prevalent in society, science and Geography. There are numerous popular examples: the notion that nature exists for exploitation by man; the idea that technology can solve the present global ecological predicament, or that Geography can ignore other living organisms. Each of these examples requires the existence of the dualism. Schaumacher is one of the many scientists who have clearly articulated the problem.

> Modern man does not experience himself as part of Nature but as an outside force destined to dominate and conquer it. He even talks of a battle with Nature, forgetting that, if he won the battle he would be on the losing side.[6]

In this thesis, Biogeography is broadly defined as the Geography of Living Organisms and then more specifically as the study of the spatial organization of organisms on the earth's surface. While these short definitions are not wholly satisfactory, they are based on certain

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[5] William W. Bunge, "Ethics and Logic in Geography," in Directions in Geography, ed. Richard J. Chorley (London: Methuen & Co., 1973), p. 327.

[6] E. F. Schaumacher, Small is Beautiful: a Study of Economics as if People Mattered, Abacus Edition (London: Sphere Books Ltd., 1974), p. 11.

important assumptions. First, Biogeography is the study of all organisms, only one of which is the human species. (This is not to deny that the human organism has a set of peculiar attributes, but rather that it is necessary to stress the importance of all of the other organisms, precisely because the nature of man will tend towards their neglect and his dominance.) Second, Biogeography, in its study of the interaction and relative location of organisms, necessitates the appreciation of both the specific characteristics of the organism and the dynamic character of environmental space.

Biogeography is concerned with life at the level of the organism, the species and the planet. It is distinct from Ecology. In this thesis, the writer rejects the human abstraction of the ecosystem as a conceptual framework of Biogeography and instead accepts the peculiar paradox of Geography. The paradox is that Biogeography, within Geography, must study the properties of the organism and the properties of the space, and yet it is impossible for the one to exist without the other.

Structurally, the thesis can be divided into four sections, all of which interact and which address the question: what is the nature of Biogeography? Initially, the question is posed against the current literature in the discipline. This approach illustrated the variations which exist in Biogeography and at the same time gives a context for the second section. In the second section the writer provides six research examples of a biogeographical nature which illustrates the practice of Biogeography. These illustrations, in turn, raise a variety of methodological and conceptual problems. The third section develops a number of these concepts, while the last section emphasizes four research strategies for Biogeography. These strategies include an emphasis on the theoretical roots of Biogeography in Theoretical Biology, the need for historical research into the distribution of species, and field work into the biological and physical rhythms of the environment. The final strategy presents suggestions regarding education and curriculum design in the teaching of Biogeography.

It must be emphasized that the thesis is an inquiry. There are innumerable problems and conceptual blockages which have to remain outside of the scope of the thesis. Two final quotations illustrate the nature of these problems. In the first quotation, the concern is the relationship between experience and abstraction, which has a geographical flavour.

> View implies sight, directly or analogously. The concept is of a piece with many other spatially grounded metaphors we commonly avail ourselves of in treating perception and understanding: 'areas' of study, 'fields' of investigation, 'levels' of abstraction, 'fronts' of knowledge, 'waves' of interest, 'movements' of ideas, 'trains' of thought, 'grounds' for analysis, and so on indefinitely. We are used to these conceptualizations by now and have found them productive, so we often forget how thoroughly metaphorical they are and how remote from actual cognitive experience.[7]

Secondly, there is Bertrand de Jouvenel's comment on western man:

> He tends to count nothing as an expenditure, other than human effort; he does not seem to mind how much mineral matter he wastes and, far worse, how much living matter he destroys. He does not seem to realize at all that human life is a dependent part of an ecosystem of many different forms of life. As the world is ruled from towns where men

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[7] Walter J. Ong, S. J. "World as View and World as Event," in Environ/Mental: Essays on the Planet as a Home, eds. Paul Shepard and D. McKinley (Boston: Houghton-Mifflin Co., 1971), p. 64.

> are cut off from any form of life other than human, the feeling of belonging to an ecosystem is not revived. This results in a harsh and improvident treatment of things upon which we ultimately depend, such as water and trees.[8]

Within Geography, this commentary could form the basis for a criticism of the current over-emphasis on urban and economic geography. The problems of urban geography stem from the domination of nature by man; in the city there is both the psychological and geographical separation of man and nature. Within this context, Biogeography must form part of the reintegration, using the criterion of life for all species.

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[8] Bertrand de Jouvenel is cited without footnote in E. F. Schaumacher, "Buddhist Economics," in Sources: An Anthology of Contemporary Materials Useful for Preserving Personal Sanity while Braving the Great Technological Wilderness, ed. Theodore Roszak (New York: Harper and Row, 1972), p. 268.

CHAPTER II

A CONTEMPORARY REVIEW OF THE LITERATURE

Since 1970 there have been a number of new texts on Biogeography; four of them are critically reviewed in this chapter. Each book is analyzed according to its factual content and its overall design. The objective is to establish the difference between the viewpoint of the authors of the texts and this writer. This approach provides a convenient contemporary context for the biogeographical research examples in the subsequent chapters.

The analysis of textbooks is complemented by a study of current research. This study includes the results of a survey of the status of Biogeography in Canadian universities. A criticism of current research papers in the first issue of the Journal of Biogeography and a brief comment on the earlier work of Dansereau complete the overview of the writer's position in relation to others within the discipline.

(1) The Definition of Biogeography: Post-1970 Textbooks

This section reviews four texts, namely:

(a) David Watts, Principles of Biogeography: an introduction to the functional mechanisms of ecosystems (London: McGraw-Hill, 1971).

(b) Joy Tivy, Biogeography: a study of plants in the ecosphere (Edinburgh: Oliver & Boyd, 1971).

(c) Brian Seddon, Introduction to Biogeography (London: Duckworth, 1971).

(d) C. Barry Cox, I. N. Healey and P. D. Moore, Biogeography: an ecological and evolutionary approach (Oxford: Blackwell Scientific Publications, 1973).

(a) Principles of Biogeography

Watts subtitles his text 'an introduction to the functional mechanisms of ecosystems'. It is evident then that Watts regards the ecosystem as the unit of biogeographical study and his recommended approach is the consideration of the mechanisms or processes which permit the ecosystem to function. This subtitle raises certain questions. First, there is the need to define an ecosystem; second, and more significantly, is the ecosystem the appropriate unit of study for the biogeographer?

Odum, in his classic work on the fundamentals of ecology, defines the ecosystem:

> Any area of nature that included living organisms and non-living substances interacting to produce an exchange of materials between the living and the non-living parts is an ecological system or ecosystem.[1]

Although Odum gives a very open definition, this writer disputes the current emphasis on the ecosystem concept in Biogeography. If the ecosystem is defined as the unit of study in Biogeography, then, immediately there is a confusion between Ecology and Biogeography. While the writer does not wish to enter into a discussion of semantic differences, it is necessary to distinguish between what biogeographers

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[1] Eugene P. Odum, Fundamentals of Ecology, 2d. ed. (Philadelphia: W. B. Saunders & Co., 1959).

do and what ecologists do. In other words, is there any real difference in their conceptual frameworks and research methods? It is the objective of this thesis to establish through examples that there is a distinction and thereby to encourage biogeographers to address the fundamental problems of their discipline.

The main limitation of the ecosystem is that it does not explicitly contain a spatial component. This has been recognized by Rowe, who proposes an alternative concept--the "landscape ecosystem".

> Above the level of the organism is the enveloping geographic space, which, on land, is an earth-organism-air 'box' or landscape ecosystem. At this level the biotic and abiotic are coupled into a landscape unit; at this level the ecologist and geographer come together as biogeographers.[2]

Rowe expressed the need for this linkage between Biology and Geography in his earlier writing.[3] A second line of criticism of the ecosystem as the unit of study for the biogeographer has been suggested in personal communication with van Newkirk.[4] Van Newkirk makes the idealistic point that since the ecosystem is a human abstraction then its implementation must result in a control and domination of nature by the human species. Whilst this criticism is implicit in any attempt by man to characterize or classify nature, certain approaches

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[2] J. S. Rowe, "Plant Community as a Landscape Feature," in Essays in Plant Geography and Ecology, ed. K. [illegible]. H. Greenidge (Halifax: Nova Scotia Museum Press, 1969), p. 70.

[3] J. S. Rowe, "Phytogeographic Zonation: an ecological appreciation," in The Evolution of Canada's Flora, ed. R. L. Taylor and R. A. Ludwig (Toronto: University of Toronto Press, 1966), pp. 12-27.

[4] Allen van Newkirk is a freelance biogeographer and poet. He directs Bioregions: a bioregional research and design project, Box 47, Heatherton, Nova Scotia.

may produce a lower degree of domination. For example, the ecosystem is a complex concept which has to be defined and bounded as an area on the earth's surface. The writer considers that the definition of the boundary of an ecosystem is a complex process. Instead of imposing the ecosystem concept and attempting to classify the earth's surface, an alternative strategy would be to map the distribution of species. In this case, the objective would be to seek an understanding of the boundaries and the overlap of distributions. The writer would argue that mapping of species has a lower degree of domination as compared with the identification of ecosystems on the earth's surface.

Returning to the text by Watts, it is obvious from the chapter headings that he is tied to the ecosystem structure, i.e.

1. Introduction
2. Energy Controls in Ecosystems
3. Biogeochemical Cycles within Ecosystems
4. Environmental Limitations in Ecosystem Development
5. Population Limitations within Ecosystems
6. The Time Factor
7. Dynamic Aspects of Ecosystems
8. Man in Ecosystems

Yet, when Watts defines Biogeography, he makes no mention of the concept of ecosystem. "Biogeography seeks to establish patterns of order from the apparent chaos of the multiplicity of life forms present upon the surface of the earth, and in its soil, atmosphere and water bodies."[5]

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[5] David Watts, Principles of Biogeography: an introduction to the functional mechanisms of ecosystems (London: McGraw-Hill, 1971), p. 1.

In the text, Watts does not discuss "patterns of order" (see Chapter V of this thesis). Watts applies the functional approach. He contends that the biogeographer must be "concerned with the mechanisms whereby both plants and animals originate, evolve and organize themselves into assemblages which show particular distribution and affinities."[6] This contention raises further questions in the mind of this writer. Is Watts implying that the functional approach must be "organism-centred"? That is, is it necessary to understand the life history of the organism and to understand the interaction of the organism with its environment, in terms of perception and communication? Is Watts interested in a functional classification of organisms based on the way in which they occupy and utilize space? In fact, it can be seen from the chapter headings above that the functionalism of Watts is centred in the interactions within the ecosystem and not of the individual organism.

Furthermore, Watts claims that Biogeography "evaluates the challenge of the environment and the response to it by organisms of very different genetic structures."[7] This suggests that the biogeographer is concerned with environmental variability over space-time and the organism's response to these changes. Once again, this writer disagrees with Watts on the appropriateness of the ecosystem framework to resolve these problems.

There are a number of practical problems, which Watts clearly identifies, which face Biogeography. First, the factual information

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[6] Ibid.

[7] Ibid.

is imperfect and incomplete; a full account of species and varieties of organism has not been made in many parts of the world. Secondly, the measurement of environmental variables remains imprecise and consequently it is difficult to study the interaction between an organism and its environment. Recognition of these two points must not be permitted to obscure the fundamental problem which is seen by the writer to be the lack of an appropriate conceptual framework for Biogeography. Already it is probably apparent to the reader that the writer reserves for later elaboration this disagreement with respect to the ecosystem concept.

Two final quotations reinforce the different viewpoints. Watts distinguishes between Biogeography and Plant and Animal Ecology: "Biogeography does not confine its attention strictly to environmental-organism relationships <u>per se</u> but places as much emphasis on the explanation of distributional inequalities among organisms."[8]

It is questionable whether this statement is true of current research. If Biogeography is the study of distributional inequalities, then it would seem necessary to use such concepts as 'fields', 'spaces of variables', 'density variations'. This is contrary to a strategy based on a classification of ecosystem components. Finally, Watts describes current research: "A large proportion of current biogeographical research is oriented towards the analysis of smaller component organic-environmental assemblages--termed ecosystems."[9]

There appears to be a basic paradox. All of the definitions

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[8] Ibid., p. 2.

[9] Ibid., p. 5.

of Watts stress the spatial component and yet the actual approach is non-spatial. The writer suggests that a better strategy is to propose non-spatial definitions and to adopt a spatial approach. By way of example, consider the concept of a bioregion. Practically, the bioregion could be approached by mapping the distributions of a number of species. A bioregion is defined according to the coincidence and overlap of the boundaries of the species distributions. Further articulation of the bioregion is given in Chapter VI.

(b) Biogeography: A Study of Plants in the Ecosphere

Tivy limits Biogeography to the study of plants. This writer believes that this is an unnecessary limitation and furthermore he is philosophically unsympathetic to Tivy's justification. She argues that the restriction to plants is ecologically acceptable since plant species compose the bulk of the total world biomass and because they form the base of the food chain. While the argument is factually correct, it must not obscure the pragmatic consideration that biogeographic research has concentrated on plant species because their static nature make them convenient for study. In Chapter IV, the writer illustrates the data collection and conceptual problems of biogeographic research of mobile organisms in space-time.

By default, Tivy does not consider the more complex, mobile organism; the writer believes that this is a dangerous restriction. It is a generally accepted ecological maxim that in unstable environments it is the complex organisms at the top of the food chain which become extinct. Therefore, although it is agreed that plant species can be studied more expediently, this strategy may reduce our awareness of the possibility of the extinction of the human species, a complex, mobile organism at the top of the food chain.

Tivy defines Biogeography in relation to Geography as a whole. For her, the value of Biogeography lies in its application of the ecosystem as an integrated, holistic approach to environmental studies. The writer has already expressed his doubts about the ecosystem in the previous criticism of the Watts' text. Tivy further emphasizes the role of Biogeography as a vital link between Physical and Human Geography and its potential to unify Geography. The writer believes that the idea of linkage is often too simplistic. It suggests the following model:

Physical Geography ——	Biogeography ——	Human Geography
inanimate	animate, non-human	animate, human

Unity can only exist in the way geographers think and in the way in which they define their problem. A better strategy would be to consider Geography (Biogeography) as the discipline which tries to understand the distribution of all species on the earth's surface. This would recognize inherently that the human species cannot be separated from all other species. It would emphasize that the theoretical problem concerns the study of distributions, both continuous and discontinuous, animate and inanimate, and their interactions.

Tivy states that Biogeography is a minority discipline because of the range of phenomena and the difficulty of systematization compared to the other branches of Physical Geography. The writer agrees that there are difficulties. It is very disconcerting to undertake field research in Biogeography (for example, the writer's research in an alpine meadow[10]) and to recognize the complexity of the species distribution and the inadequacy of the current field techniques and analytical methods. These problems have been compounded by an inappropriate conceptual framework. Tivy, like Watts, sees a close similarity between Biogeography and Ecology; she draws the distinction on the basis of scale and emphasis, rather than content or method. The author disagrees once again. Although it is true that current research in Biogeography uses the ecosystem concept and the methods of quantitative ecology, this is because the discipline has not discovered its own conceptual framework and appropriate techniques. These techniques will evolve from Geography and will be based on the fundamental properties of space. If the appropriate techniques do not exist, then the discipline must concentrate on description and the techniques of mapping distributions.

The essence of the viewpoint of Tivy can be diagnosed from the chapter headings of her text.

1. Scope and Development of Biogeography
2. The Organic World
3. Atmospheric Factors
4. Edaphic Factors
5. Biotic and Anthropogenic Factors
6. Plant Evolution and Distribution
7. Effects of Man on Plant Evolution and Distribution
8. Vegetation
9. Vegetation Change and Stability
10. The Marine Ecosystem
11. Trees and Forest Ecosystem
12. Forest Environment and Resources
13. Grasses and Grassland Ecosystem
14. Biological Deserts
15. Exploitation of Organic Resources
16. Conservation of Organic Resources

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[10] Robert V. Maher, "Complexity Analysis of Vegetation Patterns in an alpine meadow" (unpublished M.Sc. thesis, Department of Geography, University of Western Ontario, 1971).

It can be seen that Tivy divides her text into three main components--environmental factors, vegetation types and their description, and their use by man. The first chapter is most interesting in its description of the historical tradition of Biogeography. Tivy emphasizes the role of the explorer-naturalist up to the twentieth century; in the present century, it appears that many of the major contributors in England have been women. Newbigin, for example, considered Biogeography to be synonymous with Synecology, that is the study of plant communities in relation to their environment, whereas Margaret Anderson proposed a more controversial definition of the discipline: "the biological relation between man, <u>considered as an animal</u>, and the whole of his animate and inanimate environment is the essence of Biogeography."[11]

This definition is very interesting, partly because of its similarity with recent statements by modern American poets. One example is the first lines of "Wolf Net" by McClure: "when a man does not admit he is an animal, he is less than an animal. Not more but less."[12]

In general, Tivy has taken a traditional descriptive approach to Biogeography, using a wide range of secondary source material. There are certain similarities with the design of Watts, but she does not provide the detailed bibliographic coverage of the ecological literature which is a distinctive feature of his text.

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[11] Joy Tivy, <u>Biogeography: a study of plants in the ecosphere</u> (Edinburgh: Oliver & Boyd, 1971), p. 2.

[12] Michael McClure, "Wolf Net," <u>Io</u>, No. 18 (1974), p. 143.

(e) Introduction to Biogeography

Both of the Watts and Tivy texts can be described as the result of geographers looking towards the biological sciences and to ecology in particular, whereas the last two texts represent the biological scientists looking towards Geography. (Although Seddon is a geographer by training). This statement may require clarification. For historical reasons, Geography exists as a field of inquiry in both Biology and Geography. Within Biology, the discipline has been divided into Phytogeography and Zoogeography. Phytogeography is exemplified by the research of Good,[13] on the distribution of flowering plants, while Zoogeography is well represented by the nineteenth century work of Wallace[14] on the geographic distribution of animals. In both of these subdivisions of Biogeography within Biology, the primary interest has been in the explanation of geographic distributions of species as the result of environment changes throughout the evolutionary time-scale and over the earth's surface. There is a clear distinction between the ecological approach taken by the geographer and the evolutionary approach of the biologists. In rejecting the narrow ecosystem attitude of the geographers; the writer finds himself more in agreement with Seddon, particularly where Seddon includes a positive geographic element in his design.

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[13] Ronald Good, The Geography of Flowering Plants; 3d. ed. (London: Longman & Co., 1964).

[14] Alfred R. Wallace, The Geographical Distribution of Animals (New York: Hafner Publishing Co., 1962).

In his preface, Seddon states the need for Biogeography:

> For many kinds of plants and animals the threat of extinction grows as human demands increase on the limited resources of this planet.
>
> Man himself cannot survive unless he ensures the continued existence of plant life and animal populations in all their variety.
>
> Geographical uniqueness, as well as being important in its own right, is the key to understanding what role each plant and animal may be capable of fulfilling in peaceful co-existence with man.[15]

The author is in complete agreement philosophically with Seddon in that Biogeography has the potential to change the consciousness of the human species towards all other species. For example, the visual impact of a map showing the shrinking distributions of other species as the human species expands may aid in this change of consciousness.

Once again, the viewpoint of Seddon can be discerned from the chapter headings of his text.

1. Mapping Distributions
2. Distribution as a Geographic Quantity
3. The Influence of Local Factors on Distribution
4. Climatic Control of Plant Distribution
5. Vegetation: Methods of description
6. Vegetation: the Question of Adaptation
7. Vegetation: Classification and Correlation
8. Migration and Dispersal
9. Relicts and Refugia
10. Changes in Distribution with Time
11. Intercontinental Migration

Seddon regards "distribution" as a key word; this can be contrasted to the usage of "ecosystem" by Watts. The text is essentially geographic with numerous maps illustrating the distribution of species at a number of different scales. With regard to this thesis, the

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[15] Brian Seddon, Introduction to Biogeography (London: Gerald Duckworth and Co., 1971), p. v.

first two chapters, describing the problems of scale and mapping of this type of data, are essential reading for the formulation of a true Biogeography which would be an alternative to the present 'ecosystem' Biogeography. In design, Seddon has adopted an organism-centred approach which remains primarily descriptive and inductive. In this sense, the book is limited in its scope and does not address some of the fundamental issues of interest to this author. For example, there is no inquiry into the conceptual problems associated with the study of spatial distribution, nor is there any recognition of the problem of the organism-environment dualism. Accepting these limitations, the writer considers that the organism-centred approach suggests a viable alternative, particularly when balanced by its opposite space-centred approach.

(d) Biogeography: An Ecological and Evolutionary Approach by Barry Cox, Ian Healey and Peter Moore

Cox et al. answer the question: What is Biogeography?, as follows:

> The study of patterns of distribution of organisms in space and time is called Biogeography. Biologists are nowadays rarely satisfied with the mere description of these patterns, and the biogeographer usually wants to discover which environmental factors are the ones which determine or limit the distribution of the species he studies.[16]

The writer agrees that Biogeography is the study of patterns of distribution of organisms in space and time. Later in the thesis,

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[16] C. B. Cox, I. N. Healey and P. D. Moore, Biogeography: an ecological and evolutionary approach (Oxford: Blackwell Scientific Publications, 1973), p. 1.

the writer demonstrates the need for clarification of the concepts of pattern and distribution (Chapter V) and recognition of the methodological problems inherent in their study. Similarly, within Geography, the research worker is not satisfied by mere description and seeks explanation. Without embarking on a discussion of explanation, the writer believes that a valuable piece of biogeographic research would be a comparative study of explanation in Biology and Geography. Two recent publications could act as a starting point.[17] By way of example, the writer does not consider that it is sufficient to seek correlations between a set of species locations and a particular environmental variable. Explanation is another ongoing theme within this thesis and will be developed more fully in a later chapter.

The chapter headings of this text are not as illuminating as the previous examples, primarily because of the popularistic style. However, they are given below for completeness:

1. Patterns of Life
2. The Physical Limitations of Life
3. Making a Living
4. The Source of Novelty
5. Life on Islands
6. The Distant Past
7. The Shaping of Today
8. The Mark of Man: His Early Days
9. The Mark of Man: Modern Problems

In general, the text is evolutionary in the tradition of Biogeography, in Biology, with an extension towards Ecology. There is not the same degree of geographic emphasis which was a predominant feature of Seddon's text.

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[17] See papers by B. Glass, M. Scriven and K. F. Schaffner in Journal of the History of Biology, Vol 2, No. 1 (1969), Special Issue "Explanation in Biology" and the book by David Harvey, Explanation in Geography (London: Edward Arnold, 1969).

An additional insight into the definition of Biogeography is presented by a review of the Cox _et al_. text in the first issue of the _Journal of Biogeography_. The reviewer, Pethick, is at the Department of Geography, Hull University, England, with Watts. Pethick makes a general observation: "Although biogeographical books (and journals) are currently fashionable, the problem of the definition of the scope of that subject remains as intractable as ever."[18] This author believes that the intractability is a function of the discipline and its attempt to study all forms of life over the earth's surface and through evolutionary time. Besides the vast range of the material, there is the underlying problem that there has not been any real breakthrough in the methods for the study and understanding of patterns in space-time. A major premise of this present work is that the primary need of the discipline of Biogeography is to derive a satisfactory conceptual framework based on the development of a theoretical Biogeography.

Pethick further comments on certain omissions:

> The role of biogeochemical cycles in affecting distribution of plants is obvious enough; and it is also a subject central to biogeography, linking the environmental and biotic components. Yet there is no mention of nutrient cycles in the text, nor even of plant mineral nutrition, whose spatial variations play a major role in the distribution of organisms."[19]

The quotation is included because it illustrates very well the different perceptions of Cox _et al_., and Pethick and Watts,

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[18] J. S. Pethick, _Journal of Biogeography_, Vol. 1, No. 1 (1974), p. 71.

[19] _Ibid_.

towards the content of Biogeography. Although Pethick may be factually correct, it is notable that neither Watts nor Cox et al. offer any insight into the methodological problem of how to study these spatial variations.

The first part of this chapter reviewed the contents and inherent viewpoints behind four texts, all written by British academics. This was done on the assumption that a developing discipline like Biogeography should be definable from its texts. In concluding this first part, it is clear that there are two main views of the discipline: the 'ecosystem' view best exemplified by Watts, and the 'distribution' view represented by Seddon. The author is most sympathetic to the 'distribution' view. A second point is the true interdisciplinary position of Biogeography; it has a dual identity in Biology and Geography. This thesis is an inquiry of the nature of Biogeography within Geography; and yet it fully recognizes the existence and overlap of the identical twin in Biology.

(2) The Definition of Biogeography: Current Research Themes

The first part of the chapter only reviewed text books and therefore valid criticism would be that texts do not represent the research of a discipline. In this second part, the author discusses a recent survey of biogeographical research in Canada and also criticizes the papers in the first and only (March 1975) issue of the Journal of Biogeography. A second aspect of this part is that the context is broadened from the earlier focus on British texts to include research in Canada. This Canadianization has been strengthened by a short commentary on the writing of Dansereau, the eminent Canadian biogeographer.

(a) A Survey of Biogeographical Research in Canada. (Spring 1974)

In the Spring of 1974, the author completed a survey of current research in Biogeography in Canada; the purpose of the survey was to discover the variety of viewpoints and associated research interests. The author was interested in knowing whether other biogeographers were concerned with the type of problems which form the body of this thesis. The response indicates that most biogeographers are not questioning the inherent nature of the discipline and generally they adopt the 'ecosystem' view of Watts.

The author does not believe that it is worthwhile to give a detailed analysis of the responses; Appendix A gives a copy of the original letter and also a summary of the responses for the interested reader. It is, however, pertinent to make a number of general observations which relate to the earlier part of this chapter and to the objective of this thesis also.

(1) Biogeography is a developing discipline in departments of Geography in Canada. The evidence indicates that there is a surplus of new positions and correspondingly a shortage of qualified graduates. This situation makes it even more important that Biogeography should possess a well-defined identity, otherwise, the positions will be filled by 'refugee' ecologists. That is not an indictment of Ecology but rather a statement of fact.

(2) Many established Canadian universities do not employ a biogeographer. This historical fact is a commentary on the condition of Geography.

(3) Most respondents equate Biogeography with Plant Geography; very rarely is there any mention of animal species. The general approach is to study the environmental factors. Field work is combined with the use of pedology and palynology laboratories.

(4) Biogeography is often linked with applied research to provide the vegetative component. The common linkages are with the fields of Conservation, Recreation and Land Use studies.

(5) The author recalls two specific points which reflect the distinction between the attitude of the author and the prevalent attitude: (a) It was noted that one undergraduate course was defined as the "Geography of Ecosystems," indicating explicit support for the 'ecosystem' view; and (b) Rounds[20] makes a comment which the author supports strongly: "I have long felt that much work deemed biogeographical has indeed forgotten all about the spatial aspects."

Even though the survey did not cover the total population of biogeographers in Canada and even though some time has passed, the author concludes that there is no substantive research into the fundamental problems of spatial organization of organisms within departments of Geography. Furthermore, there is no attempt to articulate the conceptual problems of the discipline, to inquire into the establishment of a theoretical Biogeography. From the survey, the author

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[20] Richard C. Rounds, Professor, Department of Geography, Brandon University, personal communication.

concluded that this present thesis is an anomaly in biogeographical research in Canada.

(b) Papers in the Journal of Biogeography (March 1974)

The Journal of Biogeography was first published in March 1974, reflecting the development of the discipline. To date (March 1975), only one issue has been received by the writer, this may signify publication problems or problems in the definition of the discipline. The creation of this journal is a significant event for Biogeography which will permit better dialogue within the discipline. Watts, the editor, in the prologue, describes the new journal as a forum in which multi-disciplinary dialogue might take place between research scientists who have a common aim of understanding organic distributions and their relationship to present and past environments. The writer is concerned that the explicit emphasis on multi-disciplinary dialogue may detract biogeographers from any real attempt to define their problem. The first issue contains four papers:

(1) "The pleistocene changes of vegetation and climate in tropical South America," T. van der Hamman.

(2) "An assessment of the usefulness of phytosociological and numerical classificatory methods for the community biogeographer," R. E. Frenkel, C. M. Harrison.

(3) "The distribution of salt pans on tidal salt marshes," J. S. Pethick.

(4) "Influence of waterfowl on the distribution of Beckmannia syzigachne in the Mackenzie River Delta, Northwest Territories," Don Gill.

In the first two papers, the emphasis is on the application of established scientific techniques. Van der Hamman interprets the palynological evidence in tropical South America, while Frenkel and Harrison discuss the utility of a number of methods in Quantitative Ecology for Biogeography. The paper by Frenkel and Harrison illustrates another general trend in the development of Biogeography, namely the arrival, belatedly, of the "quantitative revolution" via Ecology. The writer believes that this trend obscures the real problem of Biogeography, its true definition.

The papers by Pethick and Gill, both geographers, are interesting because they represent the "distribution" view. Pethick applies the method of multiple regression to an investigation of the relationship between salt pan density, marsh height and distance from the sea. This paper was disappointing to the writer of this thesis for two reasons. There was no attempt to study the spatial pattern of the pans over the area. Spatial pattern is used here in the sense of variations in the size, shape and relative locations of these pans, although density does depend upon all these attributes. Another point is that the article does not seek to understand patterns, in the sense defined, by means of comparison with the "fields" of other physical variables.

Gill, in his paper, hypothesizes that heavy concentration of waterfowl have influenced the abundance and distribution of delta flora, notably Beckmannia syzigachne. Gill discovers a coincident presence of a plant spacies and waterfowl and describes the relationship. The explanation of the coincidence of grass species and waterfowl is the location of the flyway of the waterfowl.

In both of these cases, the writer is concerned about the definitions of 'distribution' and 'explanation' and their underlying assumptions. Since this thesis is primarily concerned with the problems of description and explanation of spatial patterns of organisms, a brief example may clarify the point. The writer considers that spatial pattern implies some relationship between individual locations. Consequently, given a set of locations, the problem is to characterize the spatial properties of that set and furthermore to relate these properties to the spatial properties of other sets of information for the same space. There are some strategies which give no information on the 'distribution' of the locations, their distance apart, etc. For example, it is possible to record the values of two variables at a set of locations and then to calculate the correlation coefficient. The locational information is destroyed, often an assumption of this type of strategy is that the points are independent. This is the problem of spatial autocorrelation.

Concluding this cursory review of the first issue of the Journal of Biogeography, the writer believes that the adoption of a "distribution" viewpoint requires an in-depth questioning of the methodologies which presently exist for the solution of the problem of spatial patterns. This, in turn, requires an investigation of scientific method, the concept of explanation and other fundamental philosophical issues.

(c) A Note on the Position of Dansereau in Canadian Biogeography

The final note in this chapter represents a return to the general level of a discussion of Biogeography. Dansereau has been writing on Biogeography for over twenty years; the author recognizes that it is important to relate the inquiry of this thesis to Dansereau's major contribution. As early as 1951 Dansereau had clearly defined the discipline and also had proposed a conceptual framework. Dansereau outlined the breadth of Biogeography: "Biogeography extends across the fields of plant and animal ecology and geography, with many overlaps into genetics, human geography, anthropology and social science,"[21] and he described its subject matter succinctly: "Biogeography studies the origin, distribution, adaptation and association of plants and animals."[22] The writer agrees with the first point and the specific definition is satisfactory in its simplicity. Indeed, as was argued in the criticism of Watts' text, it is not the definitions which are so important but the inherent conceptual framework of the text. Of primary significance in the discussion of Dansereau's viewpoint is his table of levels (see Table 1).

Dansereau has identified five levels: historical, bioclimatological, synecological, autecological and industrial. It is noted that this table is a reduction from the eight levels defined in 1951.[23] The author disagrees with the division of the discipline into levels. In the first place, there is no inherent logic in the division. Indeed, Dansereau himself is content to reduce the number of levels

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[21] Pierre Dansereau, Biogeography: an ecological perspective (New York: Ronald Press Co., 1957), p. v.

[22] Ibid., p. 3.

[23] Pierre Dansereau, "The scope of Biogeography and its integrative levels," Rev. Canadien Biol., Vol. 10, No. 1 (1951), pp. 172-229.

TABLE 1

A Comparison of the Criteria and Units Involved at Each Integrative Level in the Study of Environmental Processes and Relationships

Level	Sciences Directly Involved	Affinities with Other Sciences	Material Studied	Object of Research	Nature of the Limitations	Methods of Study	Conclusions	Units
I. Historical	Historical Plant and Animal Geography Areography	Geology Evolution Phylogeny Paleoclimatology Taxonomy Geography Paleontology	Phyla to Species	Origin, expansion, and decadence Movement in relation to climatic change Distribution Areal affinities	Geological events Paleoclimatological fluctuations	Excavation of fossils Analysis of strata Location of relic areas Plotting of areas Comparison of areas	Evolutionary trends and sequences Occupancy of areas over period of time Extension Disjunction and former continuity	Fossil floras Fossil faunas Isoflors Floras Faunas Types of area
II Bioclimatological	Bioclimatology	Climatology Meteorology Vegetation science	Species to races Plant formation	Behavior in relation to climate area	Climate or climatic factors	Mapping of coincidences of area Study of varvs, pollen profiles, tree rings	Responsibility of individual meteorological factors; cycles	Vegetation zones and formations Life zones Climatic types Isophenes Isobiochores
III. Synecological	Synecology	Autecology Physical geography Pedology Vegetation science	Vegetation Animal populations Communities	Composition, structure, and dynamics of communities	Nature of ecosystem, from habitat to biotope	Physiognomic observation Quadratting	Type of association Nature and orientation Static, dynamic, and area description of units	Ecosystems or communities ordained and classified
IV. Autecological	Autecology	Physiology Genetics Anatomy	Species to races	Reaction to habitat factors considered singly or holocenotically	Chemical, physical and biological factors	Direct measurement of responses Experiment	Nature and gravity of immediate limitations Extension and depth of possible reaction to individual factors	Ecotypes
V. Industrial	Human Ecology	Anthropology Agriculture Forestry Human geography Sociology History	Landscape	Influence of man	Human intervention	Historical recording	Nature, gravity, and duration of disturbance	Land use and resource utilization types.

SOURCE. Pierre Dansereau, Biogeography: an ecological perspective (New York: Ronald Press Co., 1957), p. 5.

without any explanation of the underlying rationale. Secondly, within this framework, there is overlap; for example, climatic factors are significant at the autecological and synecological levels, whilst historical factors are important at the bioclimatological level. Lastly, the author disagrees with the separation of the exploitation by man as a separate level.

These detailed criticisms, aside, Dansereau is a major figure in the articulation of a biogeographic view. His 1972 Massey lectures, entitled "Inscape and Landscape,"[24] indicate the relationship between the human species and all other species. Biogeography, as the study of the Geography of living organisms, is a consistent part of the general "ecological consciousness". This "ecological consciousness" is an ethic of life and diversity of biological organisms rather than adherence to the human abstraction of the "ecosystem". Dansereau's Massey lectures were important in that it was the first occasion that the philosophical position represented by Biogeography had been used to try and change the consciousness of the culture. This subversive aspect of the discipline is elaborated under practical strategies in Chapter VI.

This chapter addressed the general question: What is Biogeography?, in two parts. The first part reviewed four textbooks while this last part considered current research publications. Unavoidably, the choice of material and their review reflects the bias of the author.

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[24] Pierre Dansereau, Inscape and Landscape, Massey Lectures Twelfth Series (Toronto: CBC Learning Systems, 1973).

However, it is maintained that the material represents the current status of Biogeography. This chapter provides a context for the substantive contents of this study. In the next two chapters, the author describes six examples of his own biogeographic research. These examples demonstrate the differences between the viewpoints of the literature given in this chapter and the author's viewpoint. At the same time, the examples provide a basis for a full discussion of the methodological and conceptual problem of the discipline.

CHAPTER III

RESEARCH ILLUSTRATIONS (PLANTS)

Chapter II described the discipline from the contemporary literature. This gives a factual framework to Biogeography but it does not provide any insight into the nature of the methodological and conceptual problems. The aim of Chapters III and IV is to rectify this imbalance using six examples from the author's own research. These illustrations should give the reader an operational definition of Biogeography. They are consistent with the author's perception of the discipline, i.e., Biogeography is the study of the interactions between all organisms and their surrounding environment with particular focus on the spatial organization that they thereby generate. Biogeography includes plant and animal species. This broad definition has been reflected in the selection of the six examples. This chapter contains three examples from the plant kingdom and Chapter IV has examples which are essentially from the animal kingdom.

The first illustration is an application of the nearest neighbour distance methodology to point patterns. The data set contains the location of over one thousand trees belonging to nine species in a hardwood forest. This research represents a methodological development from the writer's M.Sc. thesis.[1] In the M.Sc. thesis the information was collected by quadrat sampling for later analysis. The writer considered that this procedure was locationally imprecise and subsequently investigated the application of distance methods to point patterns.

The second example is a comparison of two approaches to the distribution and form of vegetation cover types. In this example, attention shifts to the interpretation of mosaics of vegetation types. The resource material is a set of maps and aerial photography of a section of the coastal plain of Western Newfoundland. This illustration indicates the problems of explanation and method in the study of spatial organization.

The third example presents a biogeographical illustration of the problematic relationship between process and pattern. The factors which affect seed dispersal and the significance of this process in the establishment of a particular spatial pattern of a species are reviewed. Seed dispersal is intrinsically determined by the number and character of the seeds and their interaction with the micro-variations, both spatially and temporally, of the earth's surface.

These illustrations represent three distinct themes in the author's research. Yet there are certain similarities. The overall concern is the study of spatial organization and, generally, the approach is 'organism-centred'. The author uses the convenient

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[1] Robert V. Maher, "Complexity analysis of vegetation patterns in an alpine meadow" (unpublished M.Sc. thesis, Department of Geography, University of Western Ontario, 1971).

distinction between 'organism-centred' and 'space-centred' approaches in later chapters.[2]

ILLUSTRATION ONE

An application of the nearest neighbour distance method to the analysis of the point pattern of nine forest species in a Northern Hardwood Forest.[3]

The illustration is divided into five sections:

(1) Objectives
(2) Mathematics
(3) Data
(4) Results
(5) Conclusion

(1) Objectives

The research has three main objectives:

(a) to investigate the degree of clusteredness or non-randomness of the point locations of the trees for each of the nine species in a forest;

(b) to investigate the relationship between the average number of individuals in a cluster and the sensitivity of the nearest neighbour statistic for higher orders (a higher order, for example the sixth, refers to the distance to the sixth nearest tree of that species); and

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[2] An 'organism-centred' approach focuses on the organism and its inherent characteristics, whereas a 'space-centred' approach emphasizes the properties of the environmental space, e.g. climatic gradients.

[3] The map (Figure 1) is taken from J. T. Curtis and Grant Cottam, Plant Ecology Workbook (Minneapolis: Burgess Publishing Co., 1969).

(c) to study the relationship between the clustering of one species and a second species. An affinity measure is defined, based on the ratio of the average nearest neighbour distance for one species and the average nearest neighbour distance between that species and a second species.

(2) Mathematics

The method of nearest neighbour distances was developed by Clark and Evans.[4] They define:

$\bar{r}_O$ = observed mean nearest neighbour distance between a set of points

$\bar{r}_E$ = expected mean nearest neighbour distance between a set of points

The expected value is calculated on the assumption of a set of points which are randomly distributed, in accordance with a Poisson probability function with density λ. In this case,

$$\bar{r}_E = \frac{1}{2\sqrt{\lambda}}$$

A ratio $R = \frac{\bar{r}_O}{\bar{r}_E}$ is a descriptive measure of the departure of the observations from a random distribution.

If $R < 1$, it indicates that the observed set of points tends to be clustered;

$R \approx 1$, the observed set of points has a similar distribution to a set of points obeying a Poisson probability function; and

$R > 1$, the observed set of points tends to be evenly spaced.

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[4] P. J. Clark and F. C. Evans, "Distance to nearest neighbour as a measure of spatial relationships in populations," Ecology, Vol. 35 (1954), pp. 445-453.

An index of affinity was devised to study whether the individuals of two different species maintain the same degree of proximity within and between the species. For every individual of one species, distances are calculated to the nearest neighbour of the individual's own species and also the distance to the nearest neighbour of the second species. The average distances are substituted in a formula for I_{ij}, the index of affinity between species i and species j.

$$I_{ij} = \frac{\text{average distance of the nearest neighbour of the } j^{th} \text{ species from the } i^{th} \text{ species}}{\text{average distance of the nearest neighbour of the } i^{th} \text{ species from the } i^{th} \text{ species}}$$

The denominator is the equivalent to $\bar{r}_o$ for the i^{th} species and the numerator is the average of the nearest individual of the species j from each individual of the i^{th} species.

If $I_{ij} > 1$, the average distance between nearest neighbours of species i and species j is greater than the average distance within species i.

And conversely,

if $I_{ij} < 1$, the average distance between nearest neighbours of species i and species j is less than the average distance within species i.

(3) Data

Figure 1 illustrates the location of eleven hundred trees belonging to nine species in a section of Northern Hardwood Forest. Each location was digitized, thereby producing a data set of X, Y coordinates and a species identifier on each card. The data were

The Locations of Nine Tree Species in a Northern Hardwood Forest

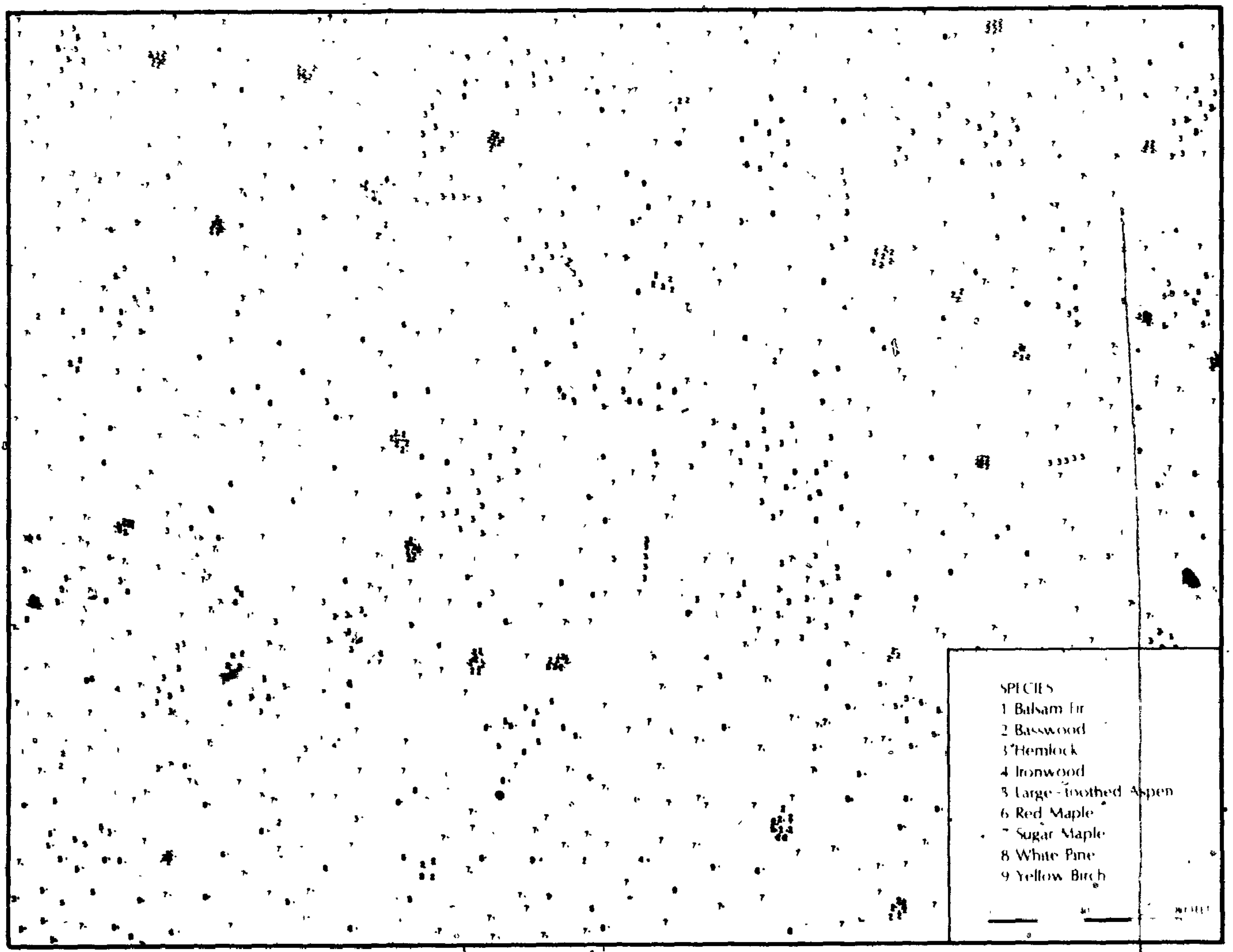

Figure 1

SOURCE: J. T. Curtis and Grant Cottam, Plant Ecology Workbook, 1962.

analyzed using 'Hyperspace', a programming package developed by Goodchild.[5] For each species, a distance matrix is calculated between all individuals. The distance values within the individual vectors are ordered, and hence the first and higher order nearest neighbour distances are easily arranged. The package computes $\bar{r}_O$, $\bar{r}_E$, R, and I_{ij} between specified species.

(4) Results

Three main experiments have been completed on the data; the results are given in Tables 2 to 4. Each experiment has been subdivided into table of results and interpretation. These experiments correspond to the three objectives identified at the outset of this illustration.

Experiment 1: To measure the degree of clusteredness of the nine species.

TABLE 2

Observed and Expected Mean Nearest Neighbour Distances and R-statistic for the Nine Forest Species

Species Identified	No. of Individuals[6]	$\bar{r}_O$	$\bar{r}_E$	R
1	26	165.0	142.4	1.159
2	165	14.6	66.6	0.219
3	192	35.9	62.0	0.579
4	6	214.2	210.0	1.020
5	107	34.8	81.8	0.425
6	39	127.7	121.3	1.053
7	391	46.0	41.3	1.114
8	48	74.4	108.3	0.690
9	25	64.0	153.1	0.418

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[5] The package 'Hyperspace' is available from Dr. M. F. Goodchild, Department of Geography, University of Western Ontario.

[6] A point is excluded if it is possible that there may be a nearest neighbour outside of the study area. Operationally, if the

The table indicates that Species 2 is the most clustered, followed in order by Species 9, 5, 3, and 8. Conversely, the other four species have R values close to unity which indicate similarity with a Poisson distribution based on the same density. These descriptive statistics provide a relative assessment of the degree of clusteredness. However, any measure of significance requires consideration of the different sample sizes.

Experiment 2: To test the sensitivity of the R-statistic to cluster size.

Species 2 represents the most clustered pattern and it is used to test the sensitivity of the R-statistic. The experiment extends only to the fifth order.

TABLE 3

R-statistics up to the Fifth Order of Nearest Neighbour for Species 2

Order	Number of Individuals	$\bar{r}_O$	$\bar{r}_E$	R
1	165	14.60	66.62	0.219
2	161	20.61	99.93	0.206
3	156	32.49	124.90	0.260
4	142	40.93	145.70	0.281
5	133	66.43	163.90	0.405

Table 3 indicates that the higher order results in an increase in the R-statistic towards unity. This observation can be conceptualized as follows: if each cluster had exactly four trees and the

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boundary of the study area is closer to a point than its nearest neighbour, then the point is excluded from the analysis. The number of individuals includes only the points which satisfy this boundary condition.

clusters were a relatively large distance apart, in comparison to the intra-cluster distances, there would be a marked jump in the value of the R-statistic between the third and the fourth order. This would be because the fourth order calculation would include the large inter-cluster distance and therefore increase the value of $\bar{r}_o$. The table indicates a relative break between the fourth and the fifth order for Species 2, but to establish any significance it would be necessary to continue the experiment to higher orders. This type of interpretation must be mediated by other characteristics of R. The R-statistic is based on the average value of $\bar{r}_o$ and therefore if the size of cluster varies within the study area the statistic will not have the same degree of sensitivity. Alternatively, the R-statistic as an indicator of cluster size is dependent upon the density variations in the study area.

Experiment 3: To investigate the affinity between two species.

The index of affinity is calculated between three pairs of species. The experiment is limited because it proved very expensive, in terms of computer time, to manipulate the large distance matrices and to calculate the index for all pair combinations of the nine species.

TABLE 4

Affinity Values Between Species 1 and Species 2, 3 and 4

Species j	1	2	3	4
Species i				
1	1.0	0.72	0.68	0.86

The index permits the general observation that the individuals of Species 3 are more attracted to the individuals of Species 1 than either the individuals of Species 2 or the individuals of Species 4. A second observation is the importance of the relative densities of Species 2, 3 and 4 in relation to the fixed density of Species 1. The density of Species 1 is constant and the denominator in the calculations. The relative densities of Species 2, 3 and 4 in relation to Species 1 is significant in terms of the likelihood of selection of an individual of that species as the nearest neighbour to an individual of Species 1.

(5) Conclusion

This illustration raises a number of points about the methodology and its application to problems of spatial organization. The writer finds the method unsatisfactory for six reasons:

(1) The method is limited to a comparison between a set of locations and an expected set of points derived from a Poisson probability function. Indeed, the method compares the property of average nearest neighbour distance of the observations and a theoretical distribution. It indicates whether the observations can be regarded as a Poisson distribution. If the set of locations are non-Poisson, then further analysis would be necessary to establish the nature of the clustering or the type of uniform distribution.

(2) The method is only concerned with locational information. Since the characteristics of the environmental space and the organism do not form part of the analysis, the explanation must be restricted to the geometry of the set of points.

(3) Dacey[7] has recognized several attributes of spatial pattern. The dependence of the R-statistic upon the average distances means that the method does not permit the extraction or testing of any one attribute.

(4) The method is density dependent. The value of the R-statistic is significantly influenced by the size of the clusters.

(5) A general criticism of this approach is that there may be a number of pattern-generating processes which can produce spatial patterns which cannot be distinguished by this analytical procedure. This point may be linked to the final criticism.

(6) A better appreciation of the sensitivities of the method may be achieved by calibrating the R-statistic and affinity index against sets of points with known characteristics.

ILLUSTRATION TWO

Two approaches to the explanation of the spatial organization of vegetation types in a section of the coastal plain in the proximity of Shallow Bay, St. Barbe South, Newfoundland.

A section of the coastal plain near Shallow Bay was selected to demonstrate alternative approaches to the study of spatial organization of vegetation types. The study area is illustrated in Figures 2 to 4. Figure 2 is part of a map of vegetation cover types produced by Bouchard and Hay.[8] Figure 3 is an aerial photograph of

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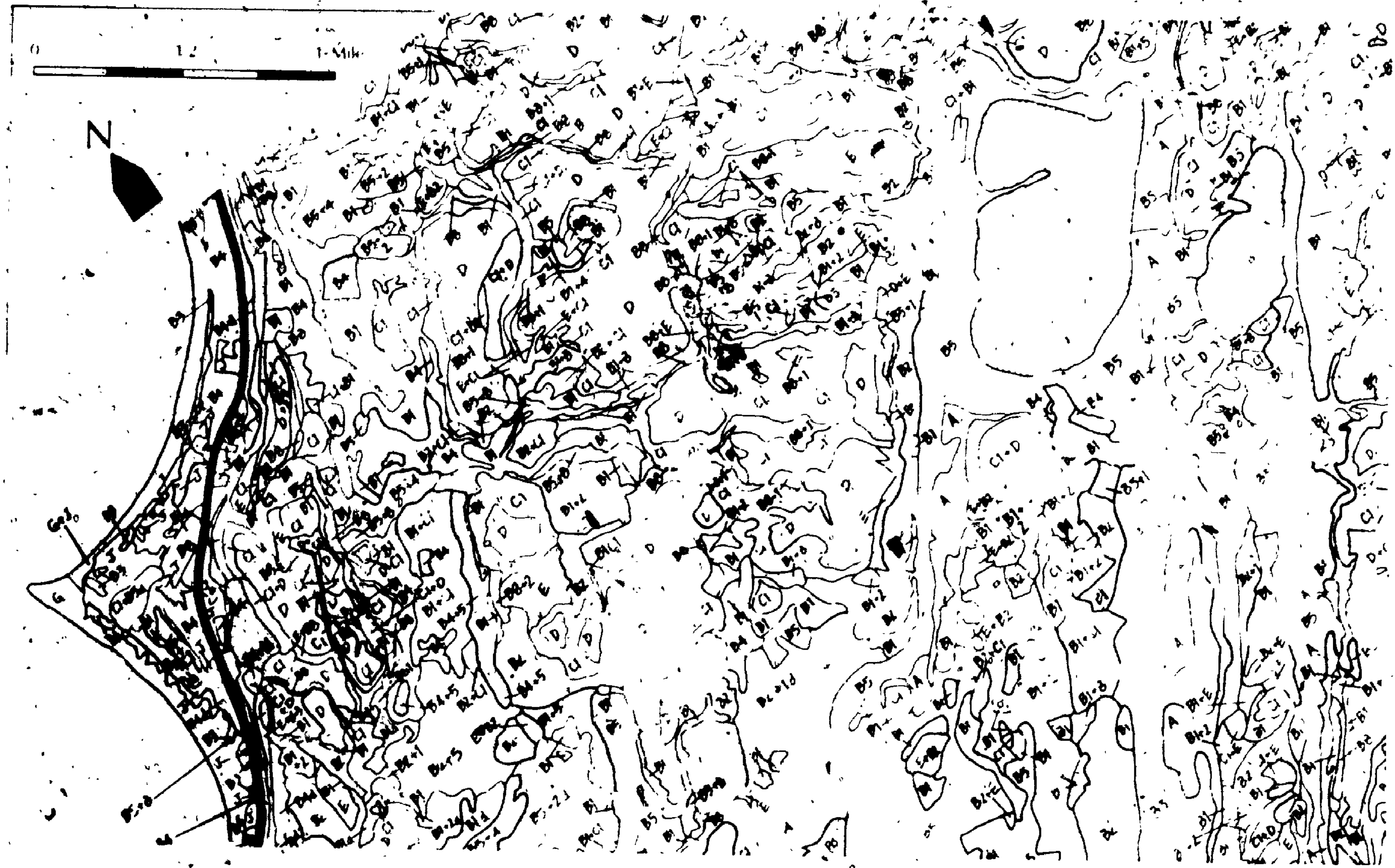
[7] Michael F. Dacey, "Some questions about spatial distributions," in Directions in Geography, ed. Richard J. Chorley (London: Methuen & Co., 1973), pp. 127-151.

[8] The map forms an appendix to the report by Andre Bouchard, The Coastal Plain Vegetation of Gros Morne National Park, Contract 71-186 (Ottawa: Department of Indian Affairs and Northern Development, 1974).



Vegetation Cover Types of the Coastal Plain, Shallow Bay, Newfoundland
Figure 2

SOURCE: Andre Bouchard, The Coastal Plain Vegetation of the Gros Morne National Park, 1974.

TABLE 5

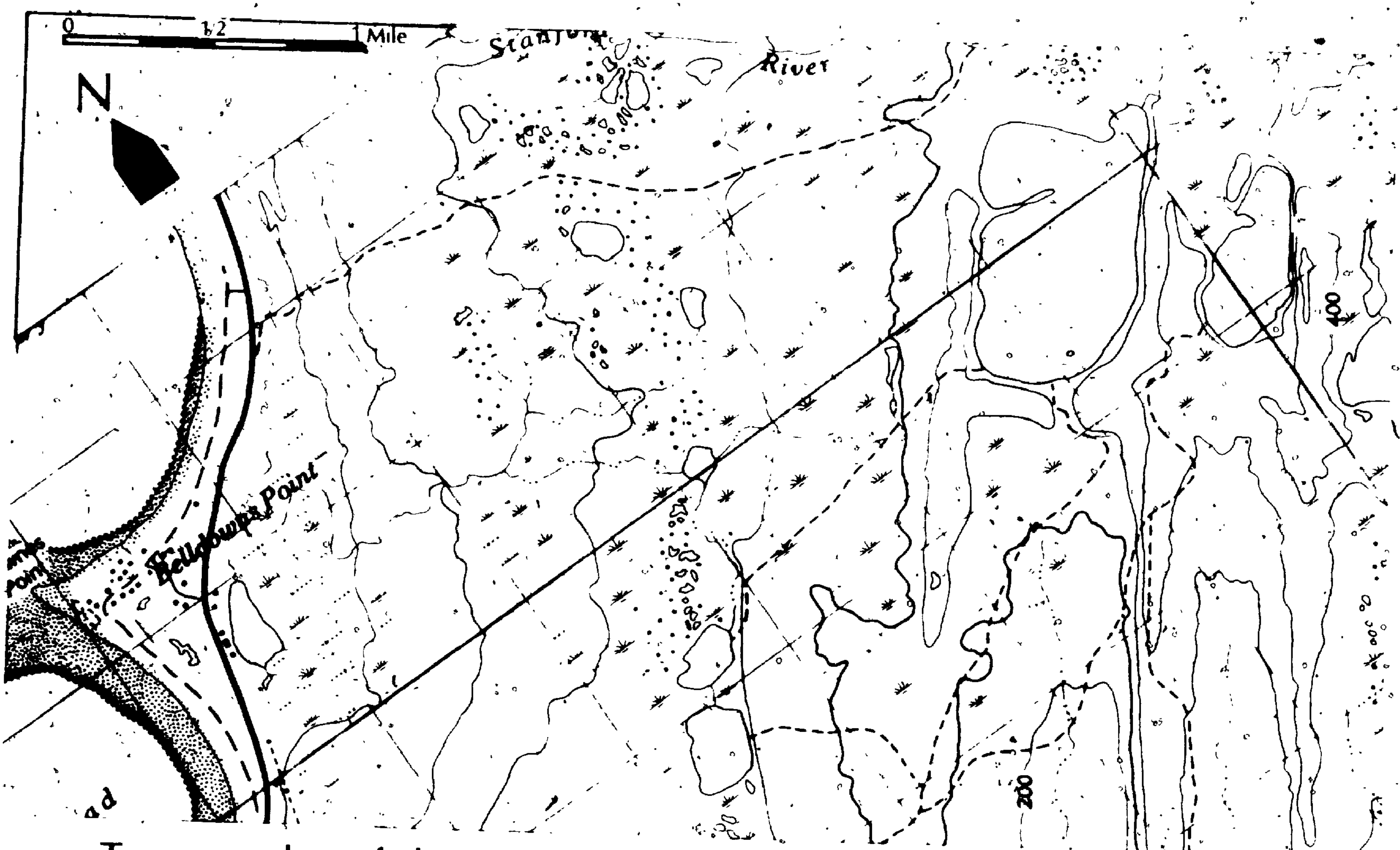
Legend of Vegetation Cover Types Illustrated on Figure 2

A	Secondary growth forest of balsam fir (Abies balsamea)
B1	Black spruce (Picea mariana) scrub
B2	American larch (Larix laricinia) scrub
B3	Wind shaped balsam fir and white spruce (Picea glauca) scrub
B4	Homogenous second growth scrub of balsam fir
B5	Heterogeneous second growth scrub of balsam fir and deciduous shrubs
B6	White spruce scrub
B7	White birch (Betula papyrifera) scrub
B8	Tall meadow rue (Thalictrum polygamum), sweet gale (Myrica gale), meadow sweet (Spiraea latifolia) and speckled alder (Alnus rugosa) scrub
C1	Black spruce and dwarf laurel (Kalmia angustifolia) dwarf scrub
C2	Ericaceous dwarf scrub
D	Peat moss (Sphagnum) and reindeer moss (Cladina) bog
E	Sedge meadow
F	Mosaic of herbaceous plant communities
G	Dunes and sandy seashore community
H	Rocky cliffs community
I	Tidal flat communities
J	Cleared areas

SOURCE: Andre Bouchard, The Coastal Plain Vegetation of Gros Morne National Park, 1974.

Aerial Photograph of the Coastal Plain, Shallow Bay, Newfoundland

Figure 3



Topography of the Coastal Plain, Shallow Bay, Newfoundland

Figure 4

SOURCE: 1:50,000, St. Pauls Inlet, map sheet 12H/13, Edition 2 MCE, Series A 781.

the same area, while Figure 4 provides the equivalent topographic information. These three figures, in combination, permit the interpretation of the spatial organization. This interpretation has been divided into two approaches, identified as the standard and the alternative approach.

Standard Approach

Figure 2 has three distinctive visual features:

(1) The vegetation types possess linearity and their alignment tends to be northeasterly.

(2) There is a band of vegetation type D to the seaward side of the main cover of B5.[9]

(3) Vegetation types D and C1 occur close together, usually C1 is peripheral to D.

One approach to the explanation of these biogeographical features is to seek correlations with the underlying landscape. If available, the geology and soil maps could be used to complement the topographic information (Figure 4). Despite this practical limitation, certain hypotheses can be proposed about the relationship between the vegetation types and the underlying surface. The linearity and allignment is probably the result of a series of low bedrock ridges which run parallel to the major trend of the Long Range escarpment in Western Newfoundland. The topographic map (Figure 4) indicates that the cover type B5 occurs mainly on the well drained land above two hundred feet. It can be postulated that the third feature, the

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[9] Table 5 provides the identification of vegetation types in Figure 2.

relationship between D and C1, is dependent upon the soil moisture gradient at the edge of bogs. To test each of these hypotheses, the research design would require sampling of the vegetation types and the associated 'explanatory' variables for a number of sites. This simple design follows the normal scientific method.

Alternative Approach

This approach poses an alternative set of questions and is also based on a different concept of explanation. Six new questions are put forward:

(1) What determines the shape and size of the individual stands of each vegetation type?

(2) Does the areal extent of a stand depend upon any horizontal environmental gradients?

(3) Does the size of a stand represent a stage in the development of the vegetation type?

(4) Figure 3 shows that certain vegetation types have a characteristic form e.g., a string bog. What type of interaction exists between the organism and its environment to produce a particular shape?

(5) What measures of shape and size are available to permit comparison with other regions?

(6) What variations in size and shape could be expected between regions?

All of these questions are concerned with form rather than the identity of the vegetation type. This concern distinguishes the two approaches. Simpson, in discussing the character of biological explanation, indicates the relationship between this set of questions and the general framework of explanation in Biology; he remarks that:

> ...to understand organisms one must explain their organization. It is elementary that we must know what is organized and how it is organized, but that does not explain the fact or the nature of organization itself. Such explanation requires knowledge of how the organism came to be organized and what function the organization serves.[10]

This quotation expands the illustration into a discussion of natural order and pattern. These concepts are more fully elaborated in Chapter V. In the context of this illustration, the main point is to demonstrate the nature of the two approaches to the same set of information, namely, Figures 2 to 4.

In general, the writer is interested in biological organization on the earth's surface. Figure 3 represents a visual image of this organization; it raises the question of the way in which these lines, shapes and areas indicate the existence of life processes. Furthermore, the writer is interested in the relationship of this image of biological organization and its relationship to the internal organization of the organism or the cell. If biological organization has similar properties at these different scales, then it is expected that the research into the spatial organization within a cell is relevant to the study of spatial organization between organisms. This argument has been developed in Chapter VI, where one of the research strategies investigates the relationship between Theoretical Biology and the development of a Theoretical Biogeography.

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[10] G. G. Simpson quoted in D. Shapere, "Biology and the Unity of Science," Journal of the History of Biology, Vol. 2, No. 1 (1969), p. 4.

At the scale of the earth's surface, the problem of explanation can be exemplified by a consideration of the shape and size of a string bog. The string bog, represented in Figure 3, is a common morphological feature in Newfoundland and Labrador. It is usually an elongated bog with a series of lateral 'strings' of vegetation. In this example, the best approach is the 'space-centred' where it is assumed that there are a number of "fields" of physical variables operating over the space. Several questions can be postulated to seek explanation:

(1) What gradients exist within the string bog, for example in the moisture or the bottom relief?

(2) What controls the size and number of strings? Is there feedback between the water body and the vegetation?

(3) What are the limiting conditions of string formation?

(4) Is the size, shape and internal structure of a string bog a function of the relative rates of change of a number of different processes?

All of these unanswered questions are essentially biogeographical, particularly in the context of a discipline defined as the study of spatial organization of organisms.

These examples make a clear distinction between the two approaches. The standard approach is to identify a number of different grey tones from the aerial photography. Vegetation types are thus classified and characterized in conjunction with field-collected species lists. Explanation is primarily concerned with the relationship between the physical environment of the type and the species composition. There are numerous examples in the ecological literature of the description and classification of vegetation types but there are very few which are concerned with the shape and size of these types. The writer argues that it is the form of the vegetation types which produces the composite spatial organization.

In conclusion, the aim of this brief and essentially visual example is that there are at least two different approaches to the biogeography of part of the earth's surface. Each approach implies a different concept of explanation. Finally, it should be noted that this example concentrates on the vegetation type and not the interaction of the individual species. For human convenience, the information is an aggregation of species but this should not detract from the significant methodological points.

ILLUSTRATION THREE

The role of seed dispersal in the formation of spatial patterns of plants.

The first two illustrations, at the individual organism and the vegetation type levels, emphasized the static pattern. This final example in the plant kingdom illustrates that plant patterns should not be regarded as static phenomena. Over a long time, the dynamics of seed dispersal are significant. This example is 'organism-centred', based on a functional classification of the species. The specific function is seed dispersal.

Seed dispersal can be discussed on the evolutionary time scale and the global spatial scale or it can be considered on a local scale. On the local scale, the focus is on the interactions between the environmental factors at a place and the organism. In this example, the main interest is at the local scale but the evolutionary context offers a useful general framework. Ridley[11] produced a classic text on plant dispersal, which clearly defines the concepts and the mechanisms. Within the evolutionary context, he distinguishes between dispersal and dispersion. Dispersal refers to "the methods by which the plant is diffused or transported from place to place,"[12] whereas dispersion signifies "the results of the dispersal agents, namely the actual localization of the plants in the world in the present epoch or, so far as we know it, in past epochs."[13]

The problem of Ridley, as applied to the dispersion of a plant species, is the question: How did the plant arrive and establish itself in a particular location? This question has two parts. The first part concerns the agent of dispersal, and the second part depends upon the environmental conditions at the site. From the headings in Ridley's text, it is clear that there are numerous alternatives:

(1) Wind
(2) Water
(3) Animals
(4) Birds
(5) Reptiles, Batrachians, Insects, Fish
(6) Simple adhesion
(7) Adhesion through special modification
(8) Adhesion due to viscid exudation
(9) Human agency
(10) Mechanical dispersal

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[11] Henry N. Ridley, The Dispersal of Plants throughout the World (Ashford, Kent: L. Reeve and Co., n.d.).

[12] *Ibid.*, p. x.

[13] *Ibid.*

This list includes a set of external factors which form the physical and biological environment and a set of internal characteristics of the organism. It is the interrelationship between the external factors and the internal character of the organism which forms the framework in this illustration. The relationship is regarded at a short time scale and for a smaller area.

Seddon[14] illustrates the dispersal process at this scale for a forest edge of Engelmann spruce (Picea engelmannii). Figure 5 shows a transect away from the forest edge, demonstrating the relationship between seedfall and distance. This diagram can be developed into a model in two dimensions, which introduces greater complexity. Idealistically, the amount of seedfall may vary over a two-dimensional space. The variation may depend upon the relative wind frequencies from different directions at the time of seedfall. An interrelated factor is the effect of the forest edge on the efficiency of the wind as a dispersal agent. A further complexity is the setting of the seed on all sides of the trees and the relationship between this set and micro-climatic variations.

Seedfall is only part of the process. Once the seeds are on the ground, there may be secondary movements which will modify the distribution. The second major element of dispersal and dispersion is germination. It is the ground conditions which control germination. Within a forest, the probability of germination and successful seedling development depends upon the influence of the existing forest

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[14] Brian Seddon, Introduction to Biogeography (London: Gerald Duckworth & Co., 1971), p. 141.

Seed Dispersal in Engelmann Spruce

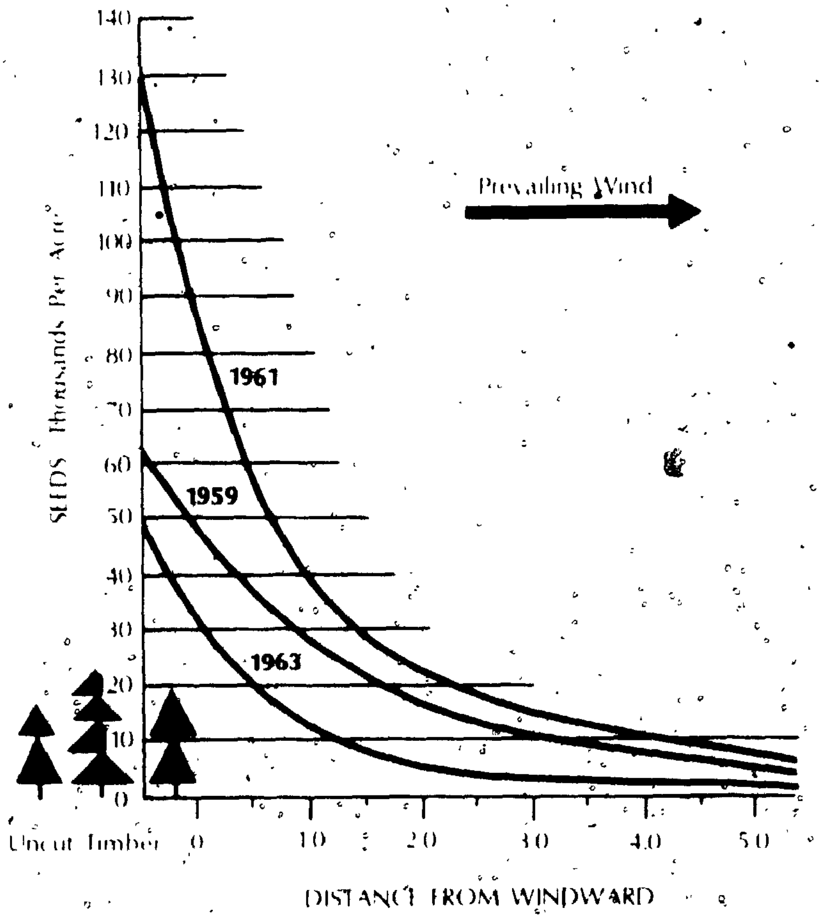

Figure 5

SOURCE: Brian Seddon, Introduction to Biogeography, 1971, p. 141.

cover on the local micro-environment. Without developing this descriptive model any further, it is obvious that the process is complex.

Statistical ecologists and geographers[15] have studied the relationship between dispersal and dispersion but usually in terms of abstract formulations. There exists a need to link the complexity of process more fully with the statistical abstraction. Neymann achieved this type of linkage in his research into contagious distributions. Greig-Smith has described the research:

> Neymann, concerned with recently hatched insect larvae crawling away from egg clusters, assumed random distribution of the larval clusters with the number per cluster also random, but with a limit to the distance to which larvae might crawl, i.e. an arbitrary limit to cluster size.[16]

Neymann combined empirical research with the development of statistical theory. In general, the abstract formulation assumes a uniform environment and therefore the control mechanism resides only within the points. Neither of these assumptions can be accepted. Nature, or environmental space, is a complex mosaic and furthermore, the control of the spatial distribution is dependent on the interaction between the environment and the intrinsic properties of the organism.

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[15] See particularly: B. Matern, "Doubly stochastic poisson processes in a plane," pp. 195-214 and M. F. Dacey, "Regularities in Spatial Distributions: a stochastic model of the imperfect central place plane," pp. 287-310, both in Statistical Ecology, Volume 1, Spatial Patterns and Statistical Distributions, eds. G. P. Patil, E. C. Pielou, W. E. Waters (Pennsylvania: Pennsylvania State University Press, 1971).

[16] P. Greig-Smith, Quantitative Plant Ecology, 2d ed. (London: Butterworth & Co., 1964), p. 80.

A review by Harper et al.[17] on the shape and sizes of seeds provides some insight into the variation of these intrinsic properties of plants. Harper et al. regard the seed as the stage of arrested development of a young plant.

> The special advantage of dormancy is that it enables members of a population to remain insulated from recurrent or sporadic environmental hazards and so ensures the continuation of the population through seasons unfavourable for growth or environmental catastrophies to which the growing plant is not adapted.[18]

The model of the Engelmann spruce is made more complex if the character of the seed and its sensitivity to the environment is included as a factor in the relationship between dispersal and dispersion. In their article, Harper et al. discuss the importance of dispersal to plant succession. Succession is defined as the replacement of one set of plant species by another set over time for a particular area. They state:

> If a species is dependent for survival solely on the replacement in situ of every individual that dies, it is necessary only for the seeds to fall to the ground. But in nature, replacement in situ scarcely ever occurs. Seed dispersal and vegetative spread provide the mechanism for a constant spatial shuffle.[19]

At this time scale, plant distributions are dynamic. It is partly because of the slow rate of change and partly because of the time constraints of most research designs, that the distribution of plant species are regarded as static phenomena. Most studies of plant

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[17] J. L. Harper, P. H. Lovell and K. G. Moore, "The Shape and Sizes of Seeds," Annual Review of Ecology and Systematics, Vol. 1 (1970), pp. 327-356.

[18] Ibid., p. 327.

[19] Ibid., p. 343.

succession are concerned with the structural changes in species composition and not the mechanics of the process.

A further comment by Harper et al. relates seed size and dispersal:

> The more frequently a species experiences the cycle of invasion-colonization-suppression-extinction, the greater is the importance both of dispersal, as a mechanism of escape, and of a high intrinsic rate of natural increase. Fortunately, large seed number, small seed size and high dispersability go readily hand in hand.[20]

This relationship between seed numbers, size and dispersability has evolutionary significance. Lack[21] has recognized the same type of relationship in the clutch size in bird species. It means that a seed plant can be regarded as a pod containing a fixed amount of matter (energy) which can be divided into various combinations. A pod may contain many seeds of small size or range upwards to a few large seeds. This raises the question: how did this spectrum arise, and what factors of the evolutionary environment interacted with that particular characteristic of plant species? Although these evolutionary questions are outside the scope of this work, they do serve to indicate the importance of seed size in the process of dispersal.

This illustration emphasizes the interrelationship between the intrinsic properties of the organism and the agents of dispersal. This relationship determines the changes in the distribution of plant species over time. Although the dynamic nature of the dispersal process may not be apparent during a period of biogeographic research, it is important to explicitly recognize its importance in the study of plant distributions.

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[20] Ibid.

[21] David Lack, The Natural Regulation of Animal Numbers (Oxford: Clarendon Press, 1954).

CHAPTER IV

RESEARCH ILLUSTRATIONS (BIRDS AND ANIMALS)

The three illustrations in this chapter are selected from the animal kingdom. The primary distinction between the two kingdoms is the property of mobility which creates a more complex type of biogeographical problem. Indeed, when the mobile organism is the object of research, there is a dimensional loss; the dynamic nature of the organism cannot be satisfactorily represented by the static image of a map.

The first example is based on the banding recoveries of the sea-bird species--the Common murre (<u>Uria aalge</u>). As a result of the extensive field research by the Canadian Wildlife Service over several decades, it is possible to map the recoveries and interpret the movement pattern of the species throughout the year. This illustration raised several questions about the efficiency of banding as a field procedure for obtaining information on the movements of organisms. The writer became interested in the potential of biotelemetry for this type of problem. Another example discusses the potential of this technique by secondary review of a number of articles. Even though biotelemetry gives accurate information on the movement of an individual in space-time, it does not obviate the interpretational problem or the problem of analysis of the movement trace of the organism.

The final example is an analogy. The idea behind this strategy is to use the movements of participants in a cricket match as an illustration of the fundamental methodological problem. By using the structure of a familiar sport, it is possible to focus on the constraints of different analytical methods. The chapter concludes with a general discussion of the six illustrations, in Chapters III and IV, and their meaning in the context of the discipline of Biogeography.

ILLUSTRATION ONE

Interpretation of the movement patterns of the Common murre (*Uria aalge*) from the recoveries of birds banded at Green Island, Newfoundland.

One of the main recording functions of the Canadian Wildlife Service is the program of bird banding and the collection of band recoveries. This type of activity has operated from the St. John's, Newfoundland office for many years under Dr. L. M. Tuck. Fairly recently, the writer completed a contract[1] to convert this material to punch cards and undertake a preliminary analysis of all the recoveries of Common murre (*Uria aalge*) and Thick-billed murre (*Uria lomvia*) for the North West Atlantic. Complete mapping of these data was undertaken by K. Cooper for an honours thesis.[2] For this illustration a sub-set of the total data has been selected, namely the recoveries of birds banded at Green Island, Newfoundland.

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[1] Contract WE-73-74-95, "Analysis and computerization of banding recoveries of Murres in the North West Atlantic," *Canadian Wildlife Service*, St. John's, Newfoundland, 1973.

[2] Karyn Cooper, "An empirical biogeographical study of Murre recoveries in the North Atlantic" (B.Sc. (Honours) thesis, Department of Geography, Memorial University of Newfoundland, 1974).

Data

Over the last twenty years, Common murres have been banded at various sites in Newfoundland, Labrador and the Arctic. Table 6 indicates the number of birds banded and the recoveries for the selected site, Green Island (see Figure 7).

TABLE 6

Banding Totals and Recoveries Classified According to Year of Banding and Age Class

	Banding		Recovery	
Date	Adult	Immature	Adult	Immature
1951	155	174	3	11
1952	159		3	
1953	139	1000		36
1954		810		43
1955		1169		29
1956		100		1
1957		1100		24
1966		1000		24
1967		1300		47
1969		3087		92
TOTALS	453	9740	6	307

Banding Total 10,193

Recovery Total 313

The age class categories are adult and immature. Immature signifies that the bird was born in that banding year (banding takes place at the colonial nesting site); adult means that the bird was at least one year old at the time of banding. From Table 6, the number of recoveries is 2.98 percent of the total number of banded birds.

Interpretation

The problem is to explain the movement patterns of the Common murre with reference to various environmental factors. Figure 6(a)-(d) illustrates all the recoveries and the season of recovery. The seasons are defined in relation to the breeding season.

(a) April - September	Breeding Season
(b) October - November	Post-Breeding Migration
(c) December - January	
(d) February - March	

Figure 6(a) indicates a concentration of recoveries in the vicinity of Green Island with secondary pockets at the other nesting sites of Cape St. Marys and Baccalieu Island.[3] Generally, the distribution extends along the southeast coast of Newfoundland from the Burin Peninsula to Cape Freels. A detailed study of the individual recoveries for Green Island shows that there has been a marked increase in the region in recent years. This is the result of the introduction of gill-netting by the local fishermen; the birds become entrapped in the fishermens' nets.

Figure 6(b) shows a northward movement of the birds along the coast; the majority of the recoveries are between Cape Freels and the northern tip of the Island, Cape Bauld. By December there has been a reversal and a relative concentration occurs off the south coast (Figure 6(c)). Finally, in the period February and March (Figure 6(d)), recoveries are closer to the nesting colonies, particularly

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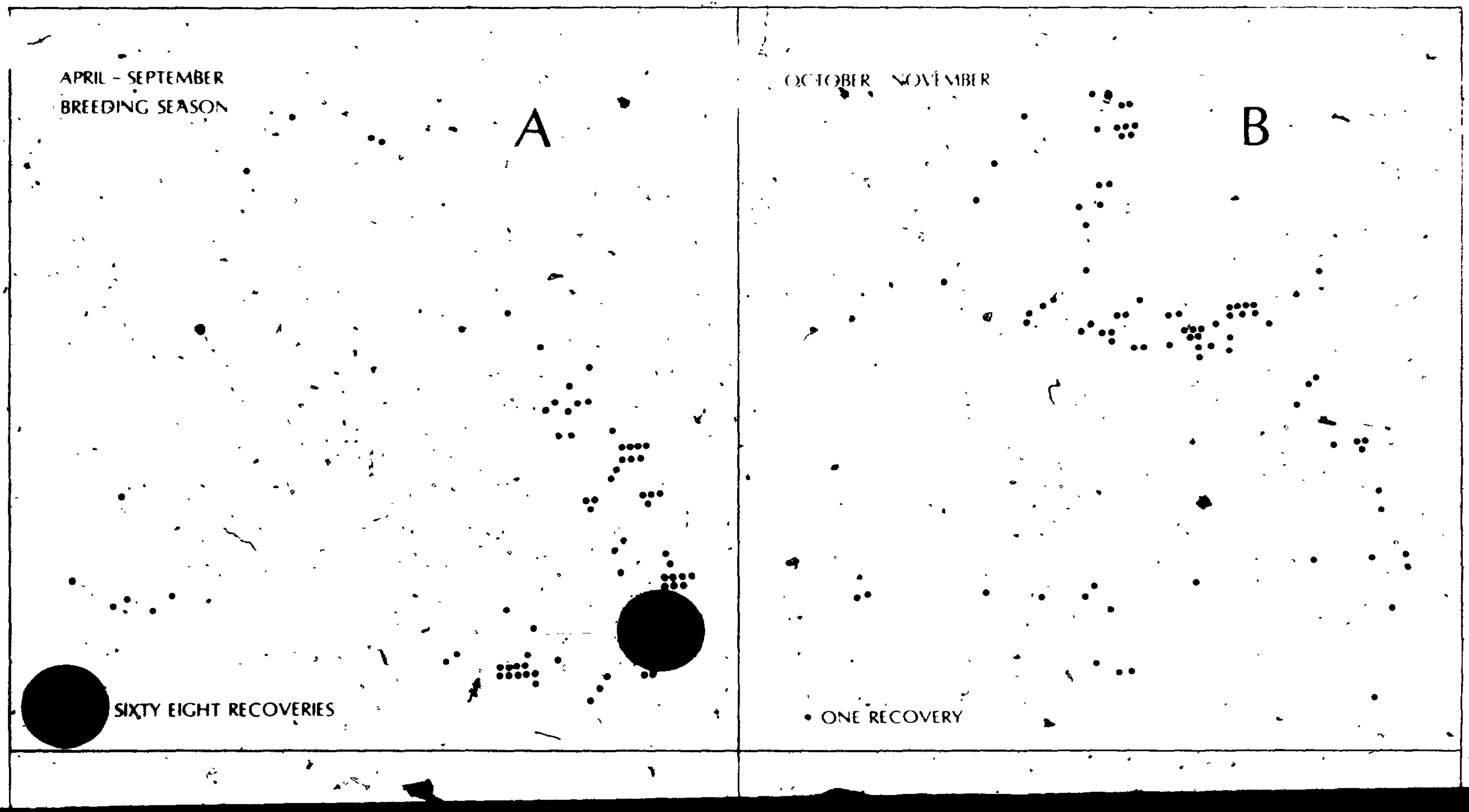
[3] All referenced place-names are illustrated in Figures 7 and 8.

Seasonal Distribution of the Common Murre (Uria aalge) banded at Green Island, Newfoundland 1951 – 1973



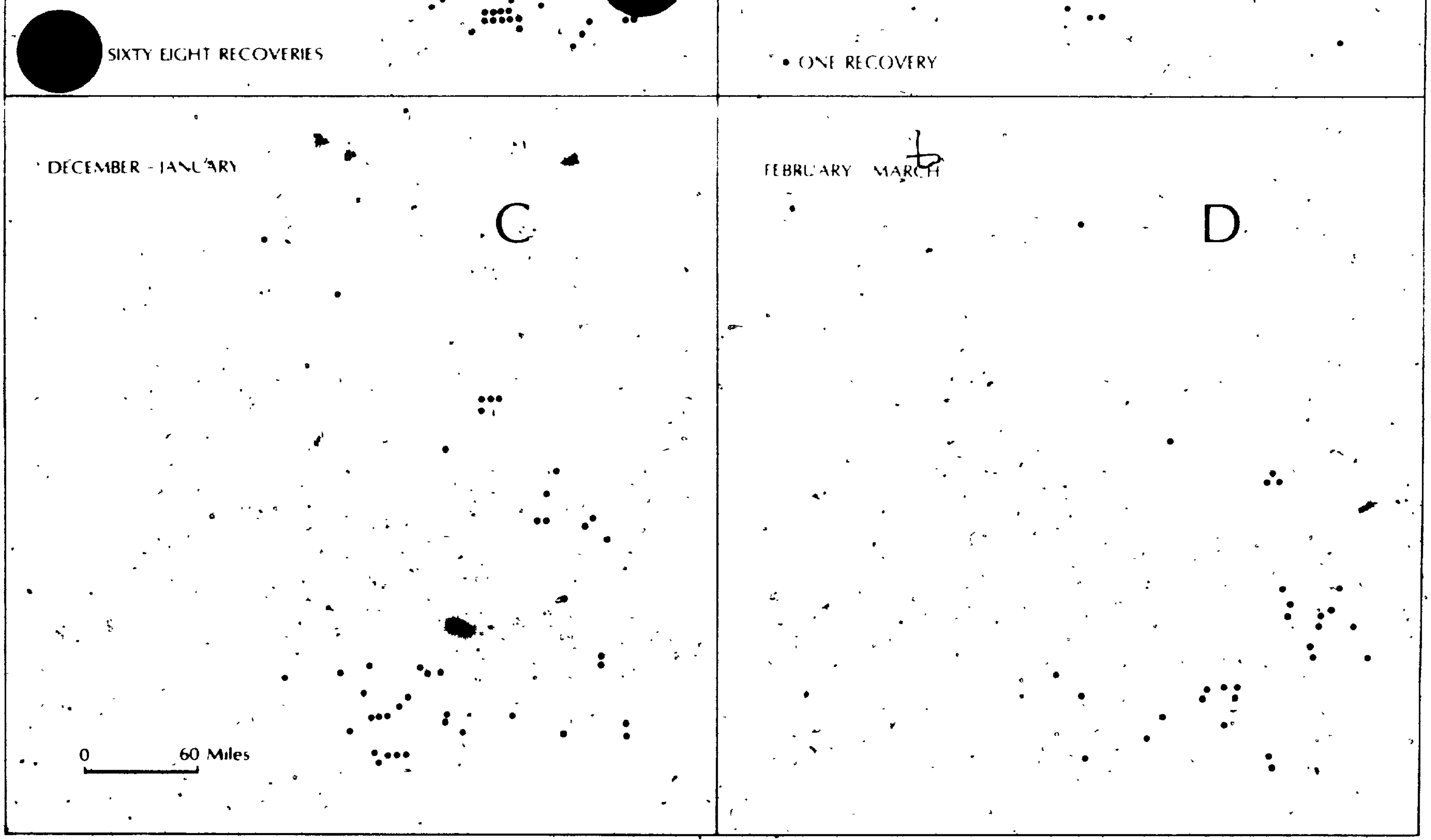

SIXTY EIGHT RECOVERIES
• ONE RECOVERY
DECEMBER - JANUARY
C
FEBRUARY MARCH
D
0
60 Miles

Figure 6

2+2

in the bays of Placentia, Trinity and Conception.

This pattern (Figure 6(a) - (d)) confirms the general observation of Tuck: "it appears that after their initial movement northward, Green Island Common murres, both adult and young, tend to return to winter in the general region of their nesting colony."[4]

A second question is whether there is a change in the distribution of recoveries from one year to the next, contingent on the winter weather. Recoveries are mapped for two years--October 1957 to September 1958 and October 1969 to September 1970 (see Figures 7 and 8). These years were selected because they correspond to the termination of the major periods of intensive banding. It should be noted that the number of recoveries is very different for the years: 1957-8 = 18; 1969-70 = 48; and also that the selected years are twelve years apart. There is, therefore, the possibility of the influence of long time-scale factors.

Both Figures 7 and 8 indicate again high recoveries close to the nesting site in the breeding season. The main concentration is near Green Island, with minor groupings at Cape St. Mary's and Baccalieu Island. At present, it is still not known what degree of inter-colony exchange exists.

Figure 8 shows an extension of breeding season recoveries along the northeast coast. Tuck explains that the breeding season (defined April to September) includes 'early' and 'late' breeding birds. The extension is evidence that the 'early' breeding birds will

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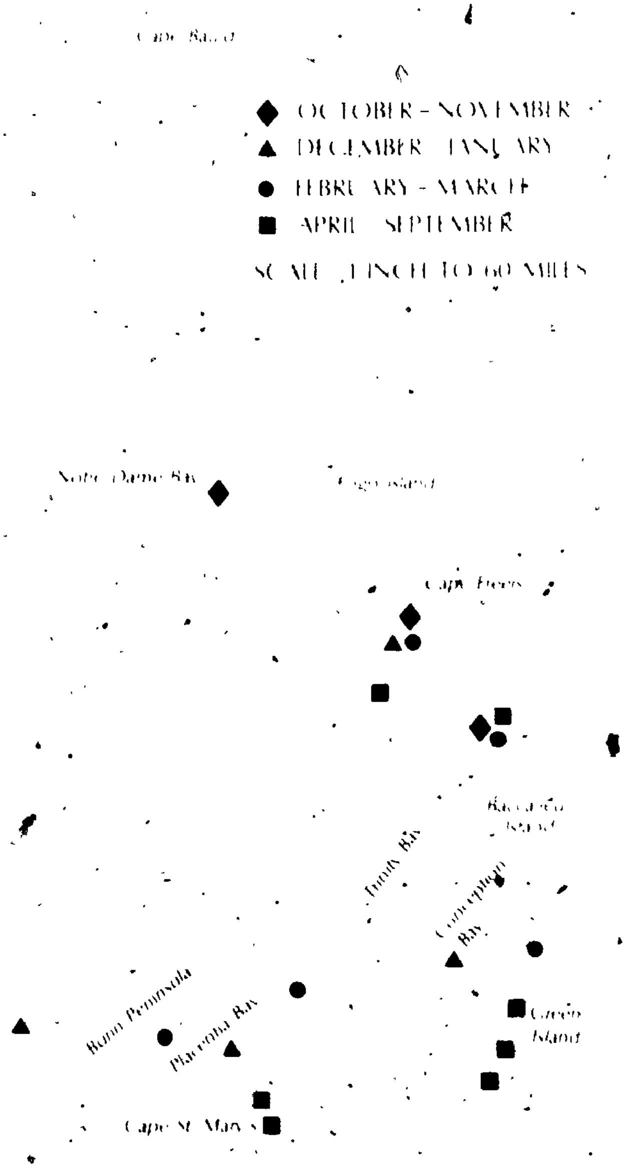
[4] Leslie M. Tuck, The Murres (Ottawa: Queen's Printer, 1960), p. 91.

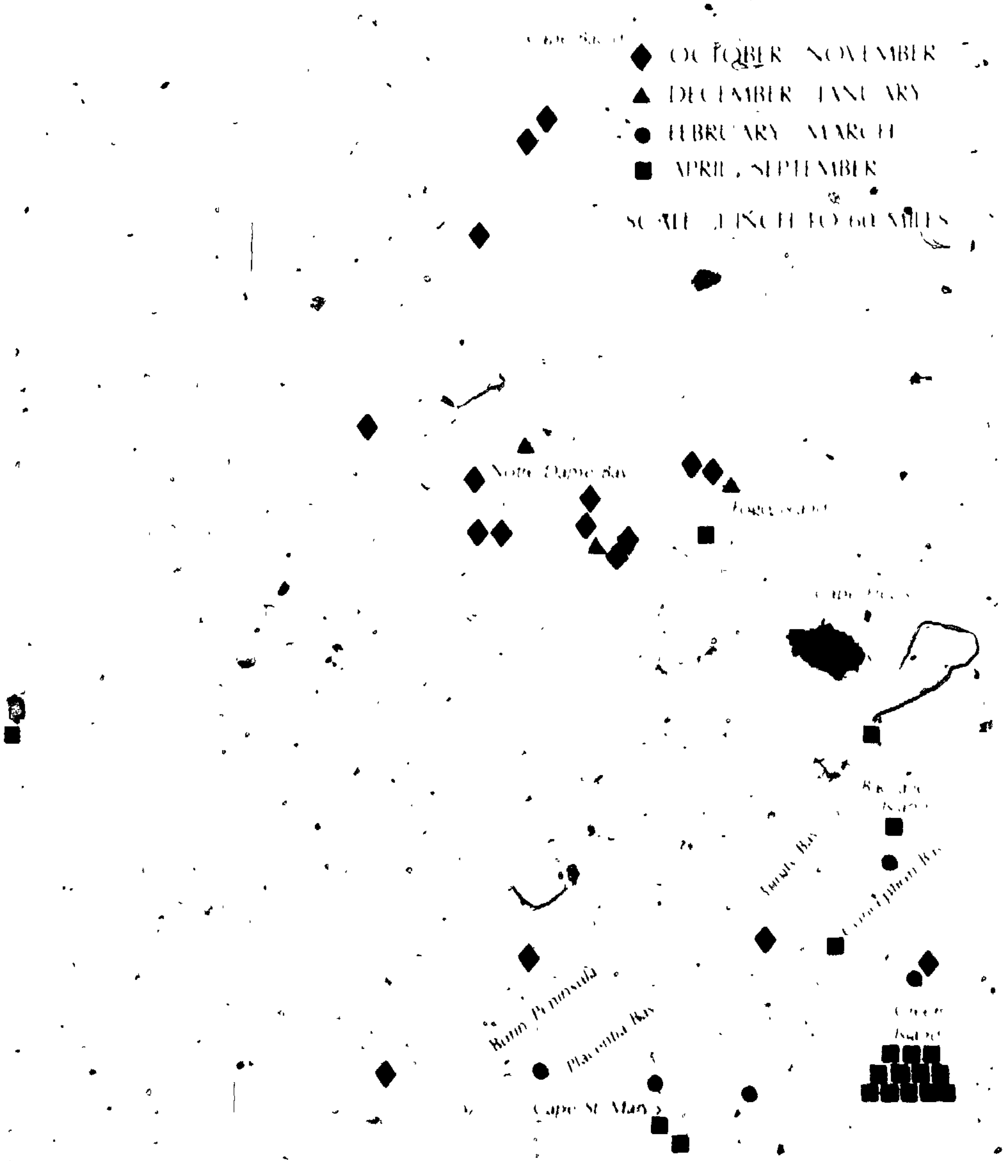
Recoveries of the Common Murre (Uria aalge) banded at Green Island, Newfoundland October 1957 – September 1958



EACH SYMBOL REPRESENTS ONE RECOVERY

Figure 7

Recoveries of the Common Murre (Uria aalge) banded at Green Island, Newfoundland October 1969 – September 1970



*EACH SYMBOL REPRESENTS ONE RECOVERY

Figure 8

have started to move north before September. During October-November, almost all of the recoveries are north of the breeding site. Figure 8 illustrates the point: indeed a line drawn through Fogo Island would clearly separate the Fall recoveries to the north and west from the breeding season recoveries to the south. This pattern is not so evident in Figure 7.

There are very few recoveries in the December-January period; Figure 7 indicates three recoveries in the southern bays, whereas Figure 8 has recoveries in Notre Dame Bay. There are few recoveries for February-March also.

A comparison of the two maps suggests that the winter 1957-58 was more severe than that of 1969-70. There is a lack of Fall recoveries in the North East in 1957, and most of the winter recoveries were off the south coast. If the winter is severe, then the arctic sea ice comes further south restricting the food availability for the seabirds and forcing the murres southwards. This explanation is only tentative because the samples are so small and ice charts are not available for that time period. These maps permit inductive speculation on the relationship between external environmental controls and the movement of the species.

Another aspect of the biogeography of the species is the effect of internal controls. For example, the temporal and spatial variations in the recovery patterns may depend upon the age of the individual. Table 7 is a matrix of recoveries for all the birds banded in the summer of 1969, according to the month of their recovery. The primary feature of the table is the decline in the number of recoveries after the first year. Secondly, there is a tendency for recovery concentration at certain periods of the year. The significant months are June and July and again October-November. The summer concentration can be explained by the practise of gill-netting in recent years, while the Fall concentration is a function of hunting pressure on the North East coast. The murre is used to supplement the local diet in this region.

TABLE 7

Matrix of Recoveries of Common Murres Banded in the 1969 Breeding Season According to the Month and Year of Recovery

Month / Year	7	8	9	10	11	12	1	2	3	4	5	6	Total
1	12	0	0	6	10	4	0	3	1	1	1	8	46
2	4	1	2	3	0	0	1	2	0	0	4	15	32
3	5	0	0	0	0	1	0	2	0	0	0	3	11
Total	21	1	2	9	10	5	1	7	1	1	5	26	89

This table demonstrates the temporal variations in recoveries; it could be supplemented by a map of the spatial variations for birds of different ages.

There are a number of interesting peculiarities and problems which are inherent in bird banding data. A recovery depends upon a number of factors. In this study, there were eight classes of recovery which included oil, gill-net, shot, etc. The main method has been traditionally through hunting for food. Consequently, the probability of a recovery through hunting depends upon the hunting pressure. The hunting pressure, in turn, depends upon the availability of murres, their density and distribution. For example, under certain conditions, there may be a limited stretch of water between the shoreline and the offshore ice; this results in an aggregation of the murres. If this phenomena occurs near a village, then the probability of recovery will increase. An additional factor is the nature of the hunter and the likelihood of a hunter returning the band to St. John's for recording. This likelihood may vary geographically from the Labrador coast to the east coast of Newfoundland.

A further factor is the sampling problem. The number of birds banded is only a sample and therefore the recoveries represent a biased sub-sample of this banded set. For these reasons, it is very difficult to achieve more than a descriptive statement from this type of data. It is, however, possible to articulate in abstract terms the type of explanation required by the biogeographer. For example, each recovery is a point in space-time and its existence at a particular location and time depends upon the properties of a number of interacting surfaces. Food supply may be recognized as a factor which would influence movement patterns of the species. This factor would depend upon certain physical characteristics of Newfoundland waters. The Labrador current, the Gulf Stream and the Grand Banks are all positive features of the sub-marine landscape which affect food supply, whereas the seasonal movement of sea ice would be regarded as a negative influence. These physical characteristics of the marine environment present a dynamic spatial system. The problem remains to relate the sample points to this dynamic spatial system. One approach would be to postulate a probability surface of recovery. This probability surface would change seasonally and annually, depending upon the prevalent weather systems.

This discussion reflects the difficulty of biogeographical research on a sea bird species. The size of the organism and the inaccessibility of the marine environment add practical limitations. There is, however, an advantage of the murre; since it is a colonial species and since the colonies are few in number and relatively accessible, the species can be banded relatively easy. Biotelemetry offers a more reliable technique of obtaining information on the movements of organisms, although bird banding will remain the primary data source for long-term studies into the population levels of species.

ILLUSTRATION TWO

The application of biotelemetry to Biogeography: a review.

Marshall[5] used biotelemetry to map the movements of an individual ruffed grouse. Figure 9 indicates the telemetered positions and the presumed inter-observation straight line movements. The result is a complex spatial pattern. Biotelemetry is a technique for obtaining information on remote and inaccessible living systems which has important implications for Biogeography. In this illustration, the object is to review a number of papers which appeared in

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[5] William H. Marshall, "Ruffed Grouse Behaviour," Bioscience, Vol. 15, No. 2 (1965), pp. 92-94.

Movements of an immature Ruffed Grouse from late Winter through the Breeding Season

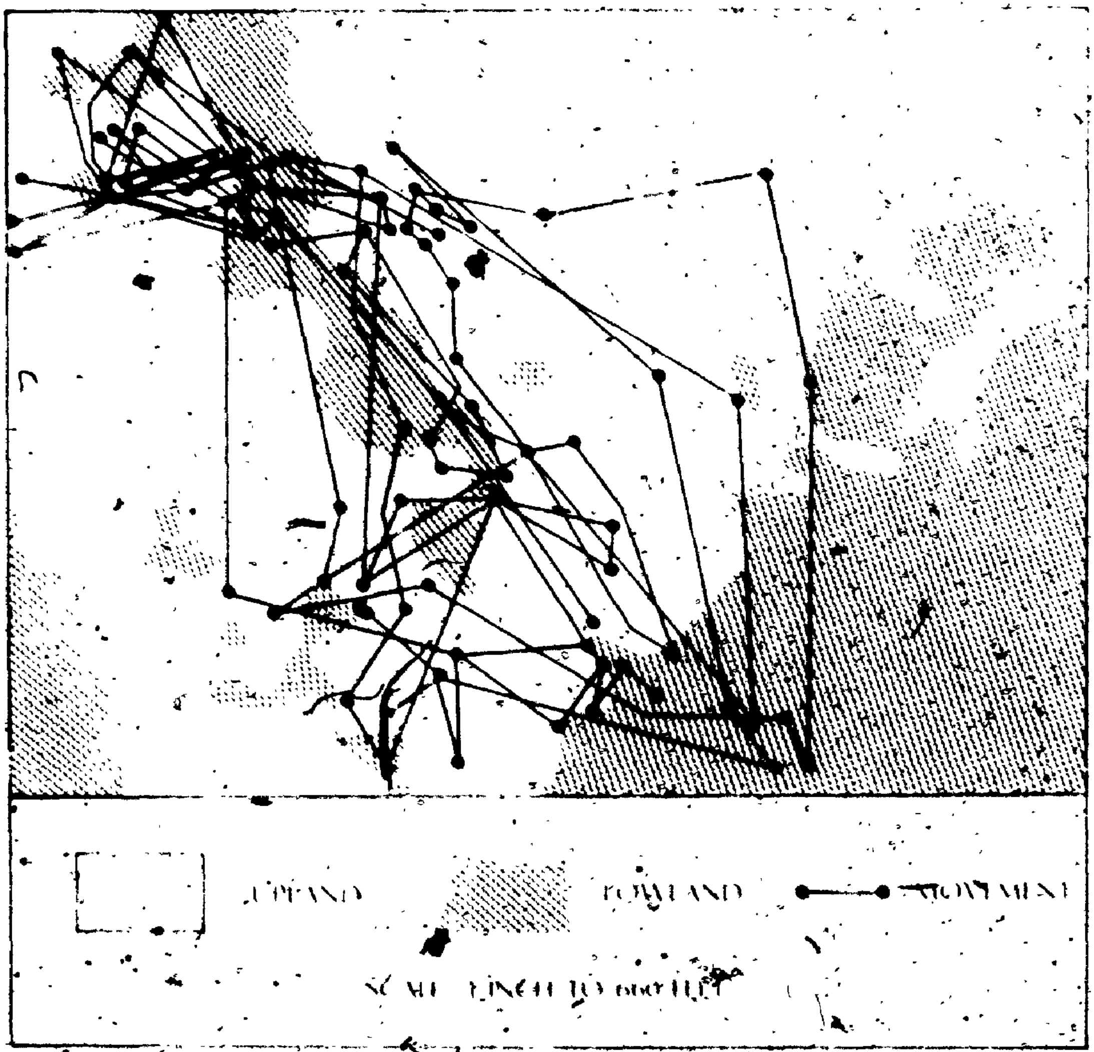

Figure 9

SOURCE: William H. Marshall, "Ruffed Grouse Behaviour," Bioscience, 15 (1965), p. 93.

Bioscience February 1965.[6] Even though the source is dated, it provides sufficiently detailed application description to indicate the pertinence of the technique to Biogeography.

Biotelemetry involves the attachment of a transmitter to the animal and the positioning of a set of receivers which accurately locate the animal in its natural environment. Past research has included species of birds, bears and dolphins. The monitored positions can be recorded directly on to magnetic tape or film and hence it is possible to reproduce the movement pattern of the organism over the research period. This remote sensing of location can be supplemented with behavioural and environmental data by using field receivers to home-in on the individual. Biotelemetry provides more precise information and also information which was not previously accessible to the human observer.

Adams[7] compares the traditional live-trap methods and biotelemetry to obtain data on the home range of an individual. The primary difference is the radical change in the observer-animal relationship. The live-trap method requires bait which introduces the spurious human interference factor; in biotelemetry the equivalent factor is the unknown influence of the transmitter on the animal. A further disadvantage of the live-trap method is that the animal is captured and hence its position remains fixed until released by the observer. Adams

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[6] See particularly, the papers by Lowell Adams, Frank C. Craighead Jr. and John J. Craighead, William Southern and William H. Marshall in the bibliography.

[7] Lowell Adams, "Progress in Ecological Biotelemetry," <u>Bioscience</u>, Vol. 15, No. 2 (1965), pp. 83-86.

describes the merits of biotelemetry for obtaining precise information on home range:

> With the few scattered points obtained by live-trapping, investigators are hard-pressed to define even the boundaries of the range. By combining all points for all individuals in an averaging process, average home ranges can be described, geometric centres located, and frequencies of captives estimated in zones about the centre. With telemetry there are enough locations to depict an individual's home range in detail. Here the internal anatomy of the home range reveals attributes previously masked in the averaging process.[8]

The geometric centre, for example, becomes insignificant in comparison with the various ecological centres of activity which the animal itself displays in frequenting these centres. The animal's location is a behavioural response (feeding, resting) to its environment. This detailed information provides ecologically significant facts on the boundary of the home range, centres of intensive use and areas of disuse. Consequently, home range can be redefined: "home range are those points in time and space occupied by the individual during a specified study period."[9]

Biotelemetry can aid research into such questions as: How does an organism perceive its environment? and How does it know where it is? Craighead and Craighead[10] illustrate this point and also some further advantages. They studied Grizzly Bears (Ursus arctos horribilis) in Yellowstone National Park and make four points:

(a) The presence of the observer does not influence the actions or behaviour of the subject. (They use field radio receivers

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[8] Ibid., p. 86. [9] Ibid.

[10] Frank C. Craighead, Jr. and John J. Craighead, "Tracking Grizzly Bears," Bioscience, Vol. 15, No. 2 (1965), pp. 88-92.

to situate the observer.)

(b) The instrumented animal can be monitored continuously day or night.

(c) It is possible to obtain information on periods of activity, speed of travel.

(d) Physiological parameters can be monitored for free roaming animals.

It is interesting to recognize the constraints imposed on the model by the field design. The twenty-four hour continuous monitoring system permits a new set of insights into the behaviour of an organism. Information on the rate of movement improves the partial, static image (for example, Figure 9). If it is possible to monitor the internal physiological environment and the external environment, then the organism can be studied in terms of the balance it maintains between these two environments. Its movements may reflect this balance. This approach suggests the need for independent environmental studies, since it is difficult to understand the perception and reaction of an organism unless the properties of the areas not frequented by the organism are known too.

Marshall[11] studied this form of organism-environment relationship in the ruffed grouse. The aim was to investigate whether changes in habitat caused by forestry practices affected the grouse movements. The study area was well-instrumented for environmental factors and therefore it was possible to record the bird's reaction to climatic

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[11] William H. Marshall, "Ruffed Grouse Behaviour," Bioscience, Vol. 15, No. 2 (1965), pp. 92-94.

changes. Indeed, Marshall discovered that the ruffed grouse behaviour in cold periods involved a quest for habitats that minimize energy loss and also for foods of high calorigenic value. The organism perceives the variations in the micro-environment and hence optimizes its location according to the above criteria.

There are also examples of the application of biotelemetry in a marine environment, primarily the study of dolphins. The nature of the problem remains the same, except that the movement is in three dimensions. It is possible that marine mammals might be utilized to monitor their aquatic micro-environment. One of the major problems in the development of marine biogeography is the visibility and disturbance created by the human observer in this environment. Yet, it is questionable whether another species should be used for this purpose.

From this cursory review, a new research emphasis for Biogeography can be envisaged, based on the technique of biotelemetry. There are several problems: the technique provides a wealth of information and therefore methods will have to be devised to screen the data. At the same time, it is a new type of information, the movement patterns include time as an integral component and hence different methods of analysis will be required. Biotelemetry is focussed on the individual organism. If the information on the organism's movement can be supplemented by environmental information; then it may be possible to appreciate the organism's perception of environmental gradients and also its locational rules. In any of these endeavours, it will be necessary to develop the appropriate mathematics to permit the interpretation of the movement patterns in comparison to the dynamic environment.

ILLUSTRATION THREE

The game of cricket as an analogy to the methodological problem of studying the spatial pattern of mobile organisms.

This final illustration uses a cricket match to try and express more lucidly some aspects of the methodological problem. The selection of a cricket match reflects the writer's cultural background, but the ideas are obviously transferable regardless of the sport. A cricket match has certain constraints which should be mentioned:

(1) It occurs in a finite space.
(2) There are structural components in terms of time.
(3) The individuals have specific functions.

These constraints and their significance are discussed more fully later.

Consider a set of photographs which have been taken by an invisible movie camera of a cricket match. These photographs, taken by a vertical overhead camera, would illustrate the movement patterns of the individuals (cricketers) over time. Depending upon the resolution of the lens, it might be possible to record the movement of the ball. Let us focus initially on the individuals. The response of a person viewing these photographs would depend upon whether or not they had any knowledge of the game of cricket. There would be a spectrum of responses from the observer who had never heard of the game to the expert who knows the rules and has general experience of cricket. If we adopt a mental outlook that focuses purely on the abstract movement pattern, it is likely that the following observations would be made:

(1) At a short time scale it would be noticed that regularly

there was a complete reshuffling of the individuals. Indeed, there would be two alternating patterns which would correspond to an "Over". Within this alternating sequence, there would be random movements. For example, one or two persons may be moving rapidly for a short distance (the "Bowler" or the "Batsmen" scoring runs or a "Fielder" retrieving a ball).

(2) At a long time scale it would be noticed that everyone moved off the area for a period (lunch or tea interval at the end of "Innings").

These two structural components would be expected at any cricket match, although it is quite possible that other characteristics could be observed at a specific game. For example, the rate of movement might vary over the time period, perhaps prior to an interval.

Let us now consider the activity patterns as a problem to be analyzed. One approach would be to identify each individual player and to record his personal pattern. It is likely that this would show particular regularities on a ball to ball level. With a knowledge of the game, it is apparent that the individual movement pattern would vary with the function being performed (e.g., "Bowler", "Batsman", "Slip-fielder", "Out-fielder").

It is important to notice that we have moved from an overall perception of the "cricket match" characteristic to the peculiar patterns of the individual. This is the standard reductionist approach,[12]

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[12] Arthur Koestler and J. R. Smythies, eds., Beyond Reductionism. New Perspectives in the Life Sciences (London: Hutchinson & Co., 1969).

here "organism-centred". To continue, having recorded the pattern for each individual, a further stage in the analysis would be to compare individual patterns and attempt a classification. The criterion could be total distance of movement or it may include a directional component. It is probable that the focus of activity is around the "Wicket", discernible as a lighter strip of ground.

A subsequent logical step would be to seek similar occurrences of this phenomena and to see whether the structural components of one game exist at the second location. Again, with a knowledge of the game, it would be expected that there would be considerable variations in the individual activity patterns, although the components (1) and (2) identified above would remain the same.

Another approach to this analogy would be to record the incursions or number of individuals present in a particular region at any one time. This would be a "space-centred" approach. The questions which would arise are: (a) How do these numbers change through time? and (b) Is there any pattern within or between regions? If the resolution was sufficient then it would be apparent that the movement patterns were in some way related to the movement of the ball. Similarly, it would be possible to analyze the movement of the ball during the time period and also subsequently relate the individual movements.

The aim of this elaborate description of a cricket match from an odd viewpoint is to demonstrate the analytical problem in the study of movement patterns. It should be recalled that the example is constrained, namely: (1) It occurs in a finite space, (b) There are structural components in terms of time, and (c) The individuals have specific functions.

Several points conclude this analogy:

(1) It is only because of the unreal ideal situation of an invisible camera (invisible so as not to affect the participants in the game) that it was possible to see the major structural components in time (that is, to obtain a perfect record).

(2) It is very convenient to study a bounded space, and also one in which there is very little interference from objects of a similar form or visual 'noise'.

(3) One approach adopted for analysis was to record the movement pattern of an individual over time. With the film record, it was then possible to compare and consider interaction with other individuals. This would be extremely difficult in a less controlled situation.

(4) The second approach was to monitor the space, demonstrating a traditional method of analysis and illustrating some of the shortcomings in terms of trying to understand the system. It implies a structure which does not exist in reality. This permits convenient research at the observational stage and yet creates many new problems at the interpretational stage.

(5) At a larger or global scale, if a particular pattern was discovered in one location then it would be necessary to seek replicate examples in other parts of the world. Having identified similar open spaces, it is possible that they may be empty. There are a number of possible reasons that can be put forward:

(a) not a cricket ground. This would mean that spaces with the same form and photographic texture have multiple functions.

(b) wrong time of the year. The nature of the space depends upon the time of observation.

(c) inclement weather. The space functions only under certain environmental conditions.

These reasons can only be proposed because of the writer's knowledge of the necessary environmental conditions. There are many further questions which can be proposed about the characteristics which distinguish a cricket ground from other spaces.

This analogy presents the most abstract statement of the problem of Biogeography. An underlying theme of the analogy is the current conceptualization of scientific method based on analytical procedures. The illustration once again distinguishes between "organism-centred" and "space-centred" approaches. Furthermore, the notion of an 'invisible camera' has certain parallels in biotelemetry so that the analogy also poses the problem of analysis and understanding of movement patterns in space-time.

Discussion of Research Illustrations

Two different views on the nature of Biogeography have been presented in this thesis. The author has used the labels of 'ecosystem' approach and 'distribution' approach to distinguish the views. From these illustrations it is clear that the thesis is in support of the 'distribution' view. The author has subdivided that particular view into 'organism-centred' and 'space-centred' strategies. These opposing strategies form a paradox which has a greater flexibility and avoids the misplaced concreteness of the 'ecosystem' approach. A second point is that the 'distribution' view, based on the paradox, retains explicitly the spatial component. This is well illustrated by the six examples. In this discussion, each example has been reviewed in detail. These details show the differences between the two views. They also imply several conceptual problems which are developed more fully in Chapter V.

In the first example, a distance methodology was applied to the locations of trees in a forest. This example was essentially spatial since there was no information on the environment or the organisms. Attention was confined to the geometry of the points. The method proved inadequate as an indicator of spatial organization. It was limited to the description of types of patterns into the three categories of clustered, random and uniform. Spatial organization is a concept which implies underlying processes and the explanation of pattern in terms of these interactions. The inadequacy of the method lies partially in the relationship between these different concepts of distribution, pattern and organization. This problem is considered in Chapter V. In addition to these conceptual difficulties, the example raised a more fundamental problem, one which concerns the relationship between an analytical technique and the explanation of organization. There has been a great deal of discussion in the biological sciences[13] on this type of epistemological issue; within

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[13] For example, the epistemological and philosophical contributions in C. H. Waddington, ed., Towards a Theoretical Biology, Vols. 1-4 (Edinburgh: Edinburgh University Press, 1969). These four volumes have been published over a four year period.

this thesis these points are referenced in the sections on Natural Order and Pattern in the next chapter.

The second example presented two alternative ways of studying vegetation types. It emphasized the intrinsic biological character of Biogeography. Secondly, it illustrated that Biogeography tends to ignore the spatial relationships and instead concentrates on the cause and effect linkages at a point. This example suggested that there is a similarity between the spatial organization of species on the earth's surface and the organization which exists within the organism and the cell. Since all three different levels represent living systems, it is assumed that scientists in other biological sciences are also faced with the problem of spatial organization of living matter (see Chapters V and VI).

The third illustration described the relationship between the process of seed dispersal and spatial pattern. It illustrated that process and pattern are inseparable and also that the organism and its environment interact to produce a spatial pattern. The main characteristic of this example was the focus on the properties of the organism. This focus demonstrated the complexity of the interactions between a seed plant and its environment at all stages in the plant's development. A further point was the stress on the dynamic nature of plant patterns over longer time periods.

This chapter attempts to answer the earlier criticism of the literature, that Biogeography is the study of plant species. All these illustrations emphasized the mobility component. Even seed dispersal in the previous chapter showed that the distinction between plants and animals is a matter of degree of independent mobility, time scale of research and tractability. The first illustration described and interpreted the recoveries of the Common murre in the North West Atlantic. Figures 6 to 8 provide maps of recovery points which present a similar interpretational problem to the location of forest tree species. In this case, the writer did not attempt to characterize the set of points, but instead, concentrated on the quality of the data and a general description of the movements of the species. The bird recoveries indicate both location and date, whereas in the case of tree species, the only indicator of time is the age of the individual. This example of bird banding recoveries showed the type of inaccuracies and restrictions of these data for mobile organisms. The author responded to this problem with a review of biotelemetry.

Biotelemetry has the advantage of providing precise location and time information on an individual organism; an obvious constraint is on the number of organisms that can be monitored at any one time. In the cursory review of the technique in this chapter, Marshall's map of the movement of a ruffed grouse (Figure 9) indicated the quality of the information. This level of precision again raises a problem of analysis. There remains a need to interpret a set of movement lines and to compare this pattern with other patterns. This methodological problem has roots in the cricket match analogy. In this analogy the writer has tried to indicate the pitfalls of different strategies. The analogy overcomes the problem of lack of information in studying species other than the human. With a familiar context, it is possible to focus on the underlying structure of the problem.* The conclusion from the analogy is that the problems are not methodological, in the sense of the need for a modified technique, but rather conceptual, concerning modes of thought. The nature of the conceptual framework to the problem of Biogeography is more fully developed in chapter V.

From this summary of the research illustrations, it is now possible to define the nature of the conceptual problem. If we consider a part of the earth's surface, within that space there will exist a number of organisms. These organisms have been classified into species according to their morphology. If we observe the space over a period of time, then we will notice the mobility of certain species at that scale, and also certain changes in the physical environment. All the organisms of the different species will interact with each other and also with their environment. The problem of Biogeography is to develop a conceptual structure to understand the dynamic spatial organization of a segment of nature.

In seeking to develop a conceptual structure, the author has investigated a wide range of disciplines. The primary resource has been the biological sciences, especially Theoretical Biology. The argument, presented in the following chapter, is that there is a certain transferability of concepts up and down the hierarchy of biological matter--cell-organism-globe. A second aspect of the inquiry is the relationship between organism and environment with its parallel of man and nature. Chapter V proposes four alternative concepts. Three of the concepts--Natural Order, Pattern and Spatial Diversity--are considered to be "space-centred", whilst the fourth

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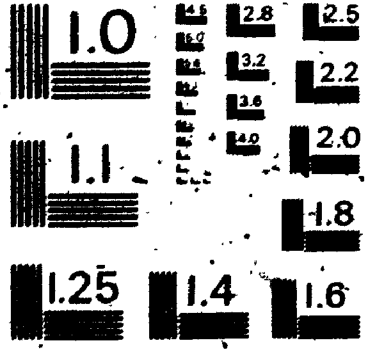

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and last topic--organism interactions--is obviously "organism-centred". These concepts are not mutually exclusive, nor can they be regarded as independent of the six research illustrations in this chapter.

The true nature of the biogeographical problem is well illustrated by a description of gnat behaviour used by Coleman to indicate the complexity of social systems:

> Once when I was sitting on the edge of a cliff, a bundle of gnats hovered in front of me, and offered a strange sight. Each gnat was flying at high speed, yet the bundle was motionless. Each gnat sped in an ellipse, spanning the diameter of the bundle, and by his frenetic flight, maintaining the bundle motionless. Suddenly the bundle itself darted and then hovered again. It expanded and its boundaries became diffuse; then it contracted into a tight, hard knot and darted again--all the while composed of nothing other than gnats flying their endless ellipses. It finally moved off and disappeared. Perhaps also it dissipated and ceased to exist, each gnat going his own way. Such a phenomenon offers enormous intellectual problems: how is each gnat's flight guided, when its direction bears no relation to the direction of the bundle? How does he maintain the path of an endless ellipse? And how does he come to change it, when the bundle moves? What is the structure of control, and what are the signals by which control is transmitted? But the problems are not only substantive; they are also problems of what conceptual framework is best used to describe systematically what goes on--when are the gnats and their actions the best units for describing behaviour, when is the bundle the best unit, and when is still a third more ingenious conceptual scheme necessary?[14]

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[14] James S. Coleman, "Social Systems," in Hierarchically Organized Systems in Theory and Practice, ed. P. A. Weiss (New York: Hafner Publishing Co., 1971), p. 69.

CHAPTER V

SIGNIFICANT CONCEPTS IN BIOGEOGRAPHY

A significant concept is one that is fundamental to the definition of the discipline. At an earlier point in this thesis, Biogeography was defined as the study of spatial organization of organisms. Four concepts are presented in this chapter which, collectively, provide an alternative to the ecosystem concept. It is believed that these concepts offer a better framework to the discipline for several reasons. The collection of concepts are based on the fundamental properties of the organism and the space. The ecosystem is a higher order abstraction derived from these same properties. If Biogeography is to establish itself as a distinct discipline, then it must be defined on the basis of fundamentals and not by transference of a well-established concept from another discipline. The current use of the ecosystem concept only creates unnecessary confusion between the disciplines. Secondly, a collection of concepts provides open-endedness and flexibility. The four concepts are not put forward as a rigid, exclusive set; they are selected because of their relationship with the generalized concept of spatial organization. Another criterion for the selection of these concepts is their ability to provide insight into the biological context of the discipline. The four concepts are: natural order, pattern, spatial diversity, and organism interactions.

Natural order is defined as an underlying quality, often aesthetic, found in natural objects and nature. Science has often been described as the search for order or natural laws. At several contextual levels, if Biogeography is to be regarded as a science, then the understanding of the concept of natural order is fundamental. The second concept of pattern is interrelated to natural order and similarly it is poorly defined in the literature. Pattern has been used as a synonym for spatial organization which has created further confusion. In general, the distinction is that pattern implies description whereas spatial organization implies explanation. Many scientists, including geographers and ecologists, have tried unsuccessfully to study the attributes of pattern. This lack of success is epistemological; current analytical procedures and language are inefficient in the study of complex, multi-dimensional entities and their forms.

The third concept is spatial diversity. It is almost contradictory to envisage diversity within space without a consideration of the things in the space. Spatial diversity is essentially species diversity. In this context, spatial diversity is a scale-dependent concept. The diversity is a function of the size of the space and the size of the organism. Yet, if the space is increased, it is not necessarily true that there will be a corresponding increase in diversity. This concept is often used synonymously with complexity.

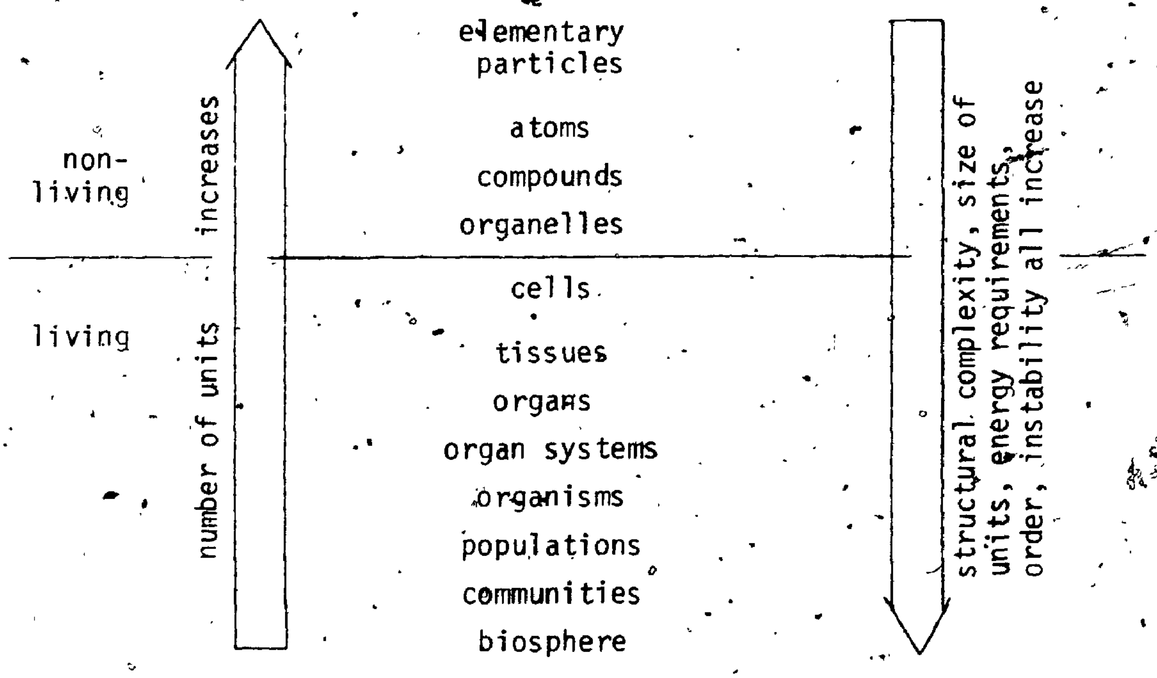
Organism interaction is the fourth concept. The emphasis is on the physical properties of organisms and the factors which influence the organisms' use of space. This concept is basic to an 'organism-centred' approach to Biogeography, whereas the first three concepts are important in the 'space-centred' approach. The above points on spatial diversity reaffirm the two sides of a recognized paradox.

(1) Natural Order

The concept of natural order has always fascinated the scientific mind. It can be found at all levels of the hierarchy of living matter. Weisz[1] illustrated this hierarchy of levels (Figure 10).

FIGURE 10

Hierarchy of Levels in the Organization of Matter



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[1] Paul B. Weisz, The Science of Biology, 4th ed. (New York: McGraw-Hill Co., 1971), p. 19.

Each level represents a dynamic system which contains the sub-system of the next level. At the level of molecular biology, natural order is indicated by the double helix; at the scale of the individual organism, it is the "biologicalness" of the form. This thesis is concerned with the possibility of a similar natural order at the supra-organism level. Supra-organism is defined at the scale of the earth's surface and includes individuals from a number of different species. It is implicit that the subject is spatial organization; yet, of course, it is impossible for any entity to have form without spatial organization.

In many ways, it is a truism that Biogeography is the search for order in nature, since this is fundamental to all of science. MacArthur makes a similar point in his description of goegraphical ecology: "To do science is to search for repeated patterns, not simply to accumulate facts, and to do the science of geographical ecology is to search for patterns of plant and animal life that can be put on a map."[2]

There are similarities between geographical ecology and Biogeography which extend beyond simply equating geography with the map. The recognition by theoretical ecologists of a field of geographical ecology is significant; it implies that ecology and its concepts do not satisfy the problem of space.

A second general statement on natural order and science, from a different perspective, is given by Alan Watts. Watts is interested

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[2] Robert H. MacArthur, Geographical Ecology (New York: Harper & Row, 1972), p. 1.

in the historical premises of Western science:

> The first premise is that there is a law of nature, an order of living things and events awaiting our discovery, and that this order can be formulated in thought, that is, in words or in some type of notation. The second premise is that the law of nature is universal.[3]

The writer accepts these premises with a number of comments and reservations: The acceptance of the premise does not mean that the author is searching for a well-defined deterministic set of relationships. The research is towards a better understanding of the order which is perceived in nature. In this context, Watts raises the critical point about whether this order can be formulated in thought. An alternative view is that the order is imposed by the brain. McCulloch gives this interesting example.

> I happen to have spent two years in measuring man's ability to set an adjustable oblong to a preferred shape, because I did not believe that he did prefer the golden section or that he could recognize it. He does and he can! The same man who can only detect a difference of a twentieth in length, area or volume sets it at 1:1.618 not at 1:1.617 or 1:1.619. So the aesthetic judgement bespeaks a premise knowledge of certain--shall I say privileged?--relations directly, not compounded of the simpler perceptibles.[4]

It appears that the resolution of the relationship between the internal order of the human organism and the external natural order will require a conceptual revolution in the Kuhnian sense. McCulloch's fascinating example indicates a conceptual problem of Biogeography,

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[3] Alan W. Watts, Nature, Man and Woman, Vintage Books Edition (New York: Random House Inc., 1970), p. 58.

[4] Warren S. McCulloch, "What's in the brain that ink may character?" in his collected papers, Embodiment of Mind (Cambridge, Mass.: M.I.T. Press, 1965), p. 395.

namely the inseparability of the order in the mind of the observer and his research into Natural Order.

The most familiar context of the concept of natural order is the form of the organism. Two books are deemed significant here. First, D'Arcy Thompson's classic research described in On Growth and Form.[5] Secondly, the recent reissue of the photography of Strache[6] give a visual reinforcement of order in the individual organism.

D'Arcy Thompson maintains that pattern and process are inseparable. Growth and form of the organism is the result of the interaction of the organism and its environment. In the light of McCulloch's example, it is interesting to read Thompson's comments on conceptual revolution.

> Since this book was written, some five and twenty years ago, certain great physico-mathematical concepts have greatly changed. Newtonian mechanics and Newtonian concepts of space and time are found unsuitable, even untenable or invalid, for the all but infinitely great and the all but infinitely small. The very idea of physical causation is said to be illusory, and the physics of the atom and the electron, and of the Quantum theory, are to be elucidated by the laws of probability rather than the concept of causation and its effects. But the orders of magnitude of space or time, within which these new concepts become useful, or hold true, lies far away. We distinguish and can never help distinguishing, between the things which are of our own scale and order, to which our minds are accustomed and our senses attuned, and those remote phenomena, which ordinary standards fail to measure, in regions where

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[5] D'Arcy Wentworth Thompson, On Growth and Form, 2d ed. (Cambridge: Cambridge University Press, 1963).

[6] Wolf Strache, Forms and Patterns in Nature (New York: Pantheon Books, 1973). Another notable visual document is Hans Jenny, Cymatics (Basel: Basilius Press, 1967).

> (as Robert Louis Stevenson said) there is no habitable city for the mind of man.[7]

Thompson describes the relationship between the concepts of his day and his study of the organism. The same comment is relevant to the current concepts and the study of the supra-organism in Biogeography.

Weiss writes on the scientific and aesthetic aspects of organic form; his remarks aptly capture one conceptual structure employed by this thesis:

> The argument will go about as follows: the universe is built and operates as a hierarchy of dynamic systems and subsystems, each with a defined degree of stability, individuality, autonomy and durability on the level or in the order of magnitude in which it exists--from stellar bodies through populations, organisms, organs, cells, genes, molecules, down to subatomic particles.[8]

The research of Weiss on the dynamics of cell development suggests similarities at the supra-organism level.

For the cell, Weiss states:

> The elements are no longer to be conceived as fluid and independent agents but recognized as forcibly restrained in their potential randomness by the higher collectives in which they belong. And it is the orderliness of these constraints which impose upon the group the over-all regularity of pattern which marks the system as more than a pile of items assembled at random. This rule of order distinguishes organization from chaos.[9]

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[7] D'Arcy Wentworth Thompson, On Growth and Form, 2d ed. (Cambridge: Cambridge University Press, 1963), p. 20. A modern evaluation of D'Arcy Thompson's work is given in P. B. Medawar, The Art of the Soluble (Harmondsworth: Penguin Books, 1969), pp. 25-41.

[8] Paul A. Weiss, "Organic Form: scientific and aesthetic aspects," in The Visual Arts Today, ed. G. Keyes (Middletown, Conn.: Wesleyan University Press, 1960).

[9] Ibid., p. 179.

The objective is clearly established as the search for the rule of order:

> A cell remains basically the same despite the continuous reshuffling and exchange of its molecular populations; an organism remains essentially the same despite the incessant shifting, loss and renewal of its member cells just as a community can retain its character and structure despite the turnover in population from birth, death and migration. These being natural systems of supra-elemental order, the establishment of the various rules of order controlling elemental behaviour in such systems is as imperative a scientific test as is the description of the elements themselves.[10]

It is interesting to apply the conceptual framework at the cellular level to the supra-organism, recognizing the practical implications. Weiss uses 'community' as the unit of study at the earth's surface scale. There is, however, a major distinction between the units of the cell and the organism, and the community. The cell and organism are real bounded entities, whereas the community is a human abstraction which is difficult to define in space. A second point is the effect of scale change on the human observer. The size of the cell and the organism allow the study of the temporal and spatial structure of the unit, and consequently it is possible to move from the description of the elements towards the rules of order. In the case of the community, the human observer cannot perceive the context of the unit in reality; indeed, the observer is usually within the study unit. The scale change also means that many of the processes occur so slowly within the community in relation to the observation process of the human that it is not possible to appreciate the dynamic nature of the unit.

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[10] Ibid.

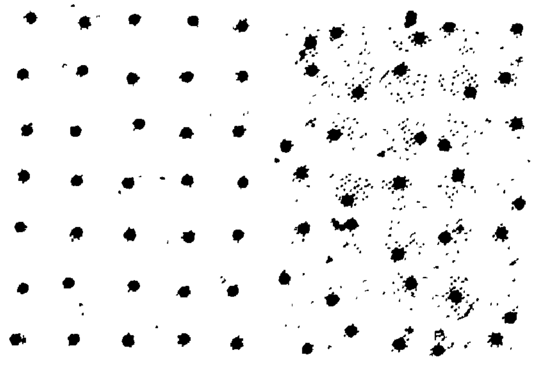
It is significant that biotelemetry has permitted the human observer to appreciate the spatio-temporal structure of another organism for the first time. There is a certain parallel between the use of a cathode ray tube display of an organism's movement in biotelemetry and the laboratory microscope which is used to observe micro-organisms or the interactions within a cell. Presently, biotelemetry is restricted to the observation of a few organisms in the community. Secondly, the cathode ray tube display does not depict environmental information.

The conceptual framework of Weiss emphasizes the dynamic nature of the entities. In Biogeography, the inherent scale problem between the human observer and nature makes direct transfer of method operationally difficult. Biotelemetry has only started to provide information on the movement of organism at the scale of the earth's surface. Even if the information exists, there remains the problem of interpretation and analysis of organization at all levels of the hierarchy. This subject is elaborated later in the thesis.

A second aspect of the research of Weiss into the concept of order is illustrated in Figure 11.

FIGURE 11

Two Systems of Order: Identical Lattices with Different Tolerance Limits



Weiss gives the following commentary:

> There is a message therefore in the beauty of living things, a message I [Weiss] should like to summarise in a last diagram [Figure 11]. It represents two systems of order as two identical lattices of equidistant points defined by the centres of the stippled circles. The circles symbolize the range within which a black dot inside is free to roam--a range that is much wider in the right than in the left half. The black dots mark the station of individual items or events within the system--for instance, that of atoms in a crystal, cells in a tissue or organisms in a group. I have let them assume random positions. Now note that in spite of this factor of uncertainty or, if one wishes, of individual self-expression, the pattern as a whole is well-preserved and stands out clearly in the left half; whereas in the right it is completely lost.[11]

The illustration of order by Weiss is actually concerned with spatial pattern. The left-hand side of the diagram maintains the regular lattice for both the stippled areas and the black dots. In the right-hand side, the regularity exists for the stippled areas but the black dots present an irregular visual image. The underlying rules are known; the wide tolerance or greater number of alternative locations for the dots on the right-hand side results in an irregular pattern. Procedurally, there is no less order in the two areas; the dot is free to locate itself at random anywhere within a certain radius from the centre of a stippled area. The stippled areas maintain a lattice pattern and therefore it is the case with the minimum radius which will produce the closest correspondence between the pattern of black dots and the pattern of stippled areas.

If this model is transferred to a biogeographical context, the black dot may represent an organism and the stippled areas represent areas of the earth's surface which satisfy the tolerance criteria of

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[11] *Ibid.*, p. 190.

the organims. A species with a narrow tolerance range will be forced to be coincident with the location of the controlling factor on the earth's surface. On the other hand, a species with a wide tolerance range will have a greater number of alternative locations.

The main limitation of Weiss' model is that the lattice constraint applied to the stippled area superimposes order. If this constraint is removed, then it is conceivable that the dots in the right-hand side may establish an order which is visually recognizable, whereas the left-hand side may be disordered. It should be noted that there remains a need to define 'order' in this context. This issue is partially addressed in the section on pattern.

Weiss appears to establish a rule about the relationship of one black dot to one stippled area. He creates a lattice pattern of the stippled area which is a rule about the relative positions of one half of the first relationship. He argues that the greater freedom given to the dot then the less likely that the lattice pattern will be reflected by the dots. This does not mean that objects with narrow tolerance limits are more likely to demonstrate order. A second problem of this model concerns visual perception. If the stippled areas were more widely spaced on the right-hand side, then the black dots would appear to resemble a lattice pattern more closely. Scale and context are important properties of the model. They concern the relationship between the dot and stippled area and also between the radius of the stippled area and the distance between the centres of adjacent stippled areas. The effect would be different if the stippled area on the right-hand side were located at a distance of six radii between centres as they are on the left-hand side. The writer will not elaborate this model any further but the example shows the type of problems which exist within the concepts of order and pattern.

Another use of the concept of natural order is provided by Kunz in a lengthy essay on the metric of living order. Kunz proposes a unity in the space of nature, which has obvious biogeographical implications.

> It is beginning to appear that the ultimate meaning of many things and processes, whose diversity sometimes confuses us, are to be sought in the continua in which they occur. Form, function, relationship--all of these can be understood in a total sense only through reference to the full matrix in accord with which the variety of nature expresses itself. The space of nature is one such continuum. Ultimately, it is doubtlessly more fundamental than any other.[12]

Kunz emphasizes the properties of space rather than the properties of the things in space. The writer considers that the two sets of properties are interdependent. Also, Kunz recognizes the demise of materialism and believes that concepts are the only means of making facts meaningful:

> Study of the space of nature, we believe, will in time show that man too is rooted in the non-material reality. As a cognitive, conceptualizing, intuitive being, he is capable of formulating within himself concepts or constructs which turn out to be isomorphic with demonstrated principles operating in the physical universe.[13]

If Biogeography is the study of the space of nature, then the

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[12] F. L. Kunz, "The metric of living orders," in <u>Integrated Principles of Modern Thought</u>, ed. H. Margenau (New York: Cor[illegible]n & Breach, 1972), p. 291.

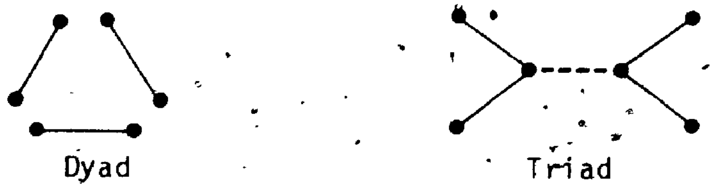
[13] <u>Ibid</u>., p. 293.

philosophical points raised by Kunz are significant to the discipline. This quotation reflects an underlying theme in the research of Bateson and McCulloch.[14]

At a more fundamental level, Kunz questions the primacy of the integer three:

> We live in a three-dimensional world, and the fact that we accept it unquestioningly does not detract from its overriding power over our lives. Three dimensional orthogonality often seems to us to be something which exists only in our minds. But, in fact, such geometry presents to us one of the great universal characteristics of the physical cosmos.[15]

This quotation can be linked with the earlier statement of McCulloch on the order in our mind. While it may seem self-evident, it has significance in relation to McCulloch's research into a logic of relations:

> The exciting things that turn up when you look at the logic of relations is that the triadic relations are the crucial ones. Let me make it clear; the moment you give me triads, all I have got to do is stick two of them together and I've got four arms hanging out. I've got a tetrad. You cannot build with dyads; you can make rings and strings like oxygen but there it ends.
>
> 
>
>
> If you want to build in three dimensions you want something like carbon. Now I know of no relation yet that

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[14] See particularly, Gregory Bateson, Steps to an Ecology of Mind (London: Intertext Books, 1972); and Warren S. McCulloch, Embodiments of Mind (Cambridge, Mass.: M.I.T. Press, 1965).

[15] F. L. Kunz, "The metric of living orders," in Integrated Principles of Modern Thought, ed. H. Margenau (New York: Gordon & Breach, 1972), p. 294.

> cannot be broken down into triads, but there are lots of triads that can't be broken any further. The notion 'between' is such a one--b is between a and c. So is 'a means b to c'. So are all the typical problems of communication inherently triadic.[16]

These two quotations from Kunz and McCulloch indicate the relationship between the question of natural order and the abstract property of number.

Kunz in a later section of his essay makes pertinent comments on the space of nature and space-time. First, he emphasizes the holistic approach:

> what we are trying to indicate is that the whole of life is one process, whose continuity and unity cannot readily be perceived in the examination of individual discrete members, or even species, but only in terms of an appropriate nexus of integrated ideas--perhaps a field or fields.[17]

For the individual organism, time implies process and hence a dynamic approach, again Kunz makes the point:

> It seems a matter of evident fact that no living organism can be properly understood <u>in toto</u> if the dynamic of its life is not taken into account. It is our thesis that living creatures embody a specific and characteristic motion in space-time which is represented in the cycle of birth, growth, maturity, senescence and death--a passage through time which each creature progressively represents, and of which it is the continuing statement and summation.[18]

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[16] This casual style is the result of the design criterion elected by Mary C. Bateson in her book <u>Our Own Metaphor</u> (New York: Alfred A. Knopf, 1972). The book is a personal account of the Wenner-Gren conference on 'The Effects of Conscious Purpose on Human Adaptation' held in 1968. The quotation is taken from page 66. A more formal account of McCulloch's idea can be found in his book, <u>Embodiments of Mind</u> (Cambridge, Mass.: M.I.T. Press, 1965).

[17] F.L. Kunz, "The metric of living orders," in <u>Integrated Principles of Modern Thought</u>, ed, H. Margenau (New York: Gordon & Breach, 1972), p. 338.

[18] <u>Ibid</u>., p. 348.

These quotations are important within the context of this thesis because they offer alternative conceptual frameworks. In the first quotation, Kunz emphasizes the 'field' concept. Biogeography can be regarded as the study of the space of nature in which there are a number of 'fields' of physical variables. The second quotation focuses on the concept of life-cycle. A strategy for biogeographical research is to study the life histories of organisms and the resultant demands on the space of nature. This strategy is mentioned in Chapter VI.

Order can also be discussed in the context of physics and the second law of thermodynamics. The following brief commentary is from an essay by Needham. Needham is concerned about whether the concept of organization has the same meaning for physicists and biologists.

> For the astronomer and the physicists the world is, in popular words, continually 'running down' to a state of dead inertness when heat has been uniformly distributed through it. For the biologists and sociologists, a part of the world, at any rate (and for us a very important part) is undergoing a progressive development in which an upward trend is seen, lower states of organization being succeeded by higher states.[19]

This second part of the world represents the concept of evolution.

Needham presents both sides of the argument and attempts to reconcile the alternative viewpoints. The alternative is that either the concept of organization is the same in both cases or there is a real difference, and order and organization are distinct, where organization is the term preferred by the biologists. Needham

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[19] Joseph Needham, "Evolution and Thermodynamics," in Time: the refreshing river (London: George Allen & Unwin Ltd., 1943), p. 207.

concluded that thermodynamic order and biological organization are two quite distinct concepts. More recently, Medawar has reviewed the debate:

> In my opinion the audacious attempt to reveal the formal equivalence of the ideas of biological organization and of thermodynamic order, non-randomness and information must be judged to have failed. We still seek a theory of order in its most interesting and important form, that which is represented by the complex functional and structural integration of living organisms.[20]

Recent papers by Bohm[21] at the Serbelloni symposia on theoretical biology indicate that the search for a theory of order continues today.

This inquiry into the concept of natural order has resulted in a number of interactive themes. Each theme offers an alternative context for Biogeography. The observation of MacArthur was significant since it indicated that there is a real distinction between ecology and Biogeography. MacArthur used the concept of natural order as the equivalence of scientific method in the biological sciences. Both Watts and McCulloch question whether natural order exists in nature or in the mind, or perhaps both. This interesting problem leads to a consideration of the inseparability of the observer and nature. Weiss presents nature as an ordered set of dynamic systems which has important implications for the transferability of concepts in the

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[20] P. B. Medawar, "Herbert Spencer and the law of General Evolution," in The Art of the Soluble (Harmondsworth: Penguin Books, 1967), p. 66.

[21] David Bohm, "Some remarks on the notion of order," in Towards a Theoretical Biology, Vol. 2: Sketches, ed. C. H. Waddington (Edinburgh: Edinburgh University Press, 1969), pp. 18-60.

hierarchy of living matter. The illustration of spatial order (Figure 11) proved to have greater relevance to the concept of pattern.

Several quotations were included from a significant paper by Kunz but the nature of the abstraction extends beyond the present thesis. Lastly, a brief review of the relationship between natural order and thermodynamics was included. Once again, the subject extends beyond this thesis. All of these alternative concepts and contexts are critical to the discipline of Biogeography. The specific concept of natural order, as a collective of all the interpretations presented in this section, is probably the most fundamental of the four concepts. Yet, each of the subsequent concepts can be linked to natural order.

(2) Pattern

Pattern is a much abused word; often it is used synonymously with arrangement, or distribution, or order. The diagram of Weiss (Figure 11) indicated his confusion between pattern and order. It appears that the concept has different meanings within different fields of research. Since the concept is discussed here in its biogeographical context, the main reference field is the geographical and biological literature. Recently, Dacey has reviewed the status of pattern analysis in Geography. He comments:

> it is ironic that the literature of Geography, which is frequently defined as the study of 'areal differentiation' or 'areal distributions' does not provide a single well-developed conceptual and methodological framework

> that organizes and structures the description, classification and analysis of spatial distributions.[22]

Patterns is restricted in this quotation to spatial distributions, which are defined as sets of points in space. The lack of success within Geography to discover a suitable conceptual and methodological framework has for some time signified to the writer that there are fundamental difficulties with the concept. It is a peculiar fact that the observer can perceive different patterns and make quick visual comparisons but he cannot develop a suitable framework. Part of the problem has been mentioned in relation to the research of Kunz and McCulloch,[23] while the earlier quotation of Ong[24] demonstrates the type of linguistic difficulty.

A second point made by Dacey stressed the methodological aspect:

> One consequence of the lack of an appropriate methodology is that it is not clear what properties and relations need to be emphasized in a compilation of location rules and stochastic spatial distributions that is intended to promote and facilitate the geographic study of map distributions.[25]

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[22] Michael F. Dacey, "Some questions about spatial distributions," in Directions in Geography, ed. R. J. Chorley (London: Methuen & Co., 1973), p. 131.

[23] Kunz and McCulloch stress the inseparability of order in nature and order in the human mind (Chapter V.1). Secondly, they indicate the problem of multi-dimensional space-time.

[24] Ong, as quoted in Chapter I, illustrates the prevalence of spatial metaphors. The writer believes that these metaphors relate to the problem of a suitable language for pattern description.

[25] Michael F. Dacey, "Some questions about spatial distributions," in Directions in Geography, ed. R. J. Chorley (London: Methuen & Co., 1973), p. 131.

This argument is rather circular since it implies that if the attributes of spatial distributions could be defined, then there would be a methodology, and vice-versa.

Dacey illustrates three types of spatial distribution (Figure 12) and also indicates the interaction between the three attributes of spatial distribution using the diagrams of Thomas[26] (Figure 13). The three types of distribution are: clustered, random and regular, while the attributes are: pattern, density and dispersion. It is noted that Dacey has defined pattern as an attribute of spatial distribution. He defines the three attributes as follows:

(1) The pattern of a spatial distribution is the areal or geometric arrangement of the geographic facts within a study area without regard to the size of the study area.

(2) The density of a spatial distribution is the overall frequency of occurrence of a phenomena within a study area relative to the size of the study area.

(3) The dispersion of a spatial distribution is the extent of the spread of the geographic facts within a study area relative to the size of the area.

Figure 13 illustrates the six combinations which have been described by Dacey as follows:

(a) Pattern and dispersion attributes are the same as (d), but different density.

(b) Density and dispersion attributes are the same as (e), but different pattern.

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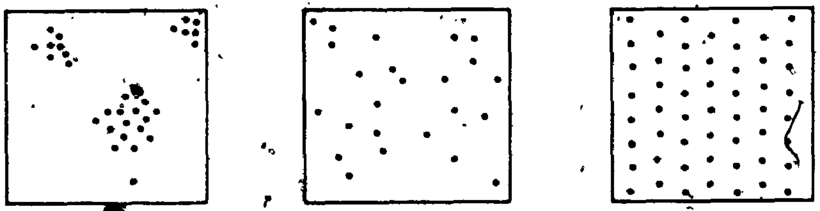
[26] E. Thomas, A Structure of geography: a proto-unit for secondary schools, High School Geography Project, Association of American Geographers (Boulder: University of Colorado Press, 1965).

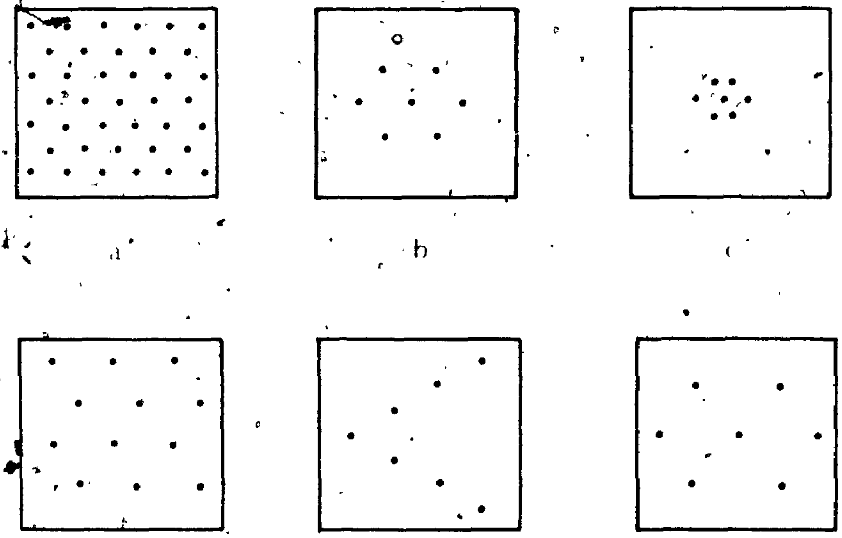
Types of Spatial Distributions



CLU[illegible]ED RANDOM REGULAR

Figure 12

Attributes of Spatial Distributions



a b c

d e f

Figure 13

SOURCE: Michael F. Dacey, Directions in Geography, 1973, pp. 132 and 136.

(c) Density and pattern attributes are the same as (f), but different dispersion.

(d) Pattern and dispersion attributes are the same as (a), but different density.

(e) Density and dispersion attributes are the same as (b), but different pattern.

(f) Density and pattern attributes are the same as (c), but different dispersion.

The writer finds this illustration unsatisfactory for several reasons. First, it is not clear that the attributes are independent. Dispersion and density are both dependent upon the size of the study area, whereas pattern is independent. Secondly, the definition of dispersion appears weak; for example, it is difficult to understand why the dispersion is the same in diagrams (a) and (d). Thirdly, it seems that the pattern is the same in five of the diagrams, excluding (e). It is always equidistant points in a triangular grid. Surely, there are other templates of pattern.

Dacey goes on to say: "it is not possible to use one measure to reflect these attributes of spatial distribution, if, as presumed, they are independent."[27]

This problem occurred in the illustration of tree species locations (see Chapter IV). It means that two distributions may have different attributes and still give the same value for a measure. The reverse argument is also true. If the attributes are not independent, then this does not necessarily mean that the spatial distribution

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[27] Michael F. Dacey, "Some questions about spatial distributions," in Directions in Geography, ed. R. J. Chorley (London: Methuen & Co., 1973), p. 135.

can be characterized by a single measure.

Figure 12 illustrates the traditional classification of spatial distributions. The writer agrees with Dacey on the limitations of this classification, i.e.: "It is difficult to concur with the hypothesis that the positions of spatial distributions on a linear continuum either generates a useful classification scheme or confirms intuitive notions of degree of similarity."[28] The diagram and Dacey's commentary indicate that the study of spatial distributions has a number of recognized limitations and unresolved problems. In relation to Biogeography, it is clear that the examples are limited to the characterization of a set of points in space. This problem is a subset of the general question of pattern in nature. In addition to points, there are also mosaics of areas; secondly, the points or areas may possess qualities, for example, they may represent different species.

The second part of this inquiry into pattern describes the alternative approaches which have been tried in the Biological sciences. These approaches are more akin to Biogeography insofar as they recognize the organic character of the elements. The subject matter has been divided into plant patterns and animal patterns to correspond with the division of the earlier research illustrations.

A. Plant Patterns

Ecology has traditionally regarded the concept of pattern as central to its discipline. Writing in the 1960's, Greig-Smith

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[28] _Ibid._, p. 134.

defined Ecology and Plant Geography as follows:

> They [Ecology and Plant Geography] are largely concerned with the causes of patterns of distributions, patterns of all scales from those of individuals within a small area to those of vegetation types and taxa over the surface of the world.[29]

As a result of increasing specialization in Ecology and because of the conceptual difficulties, the centrality of the concept of pattern has diminished in the biological sciences. Greig-Smith produced a lengthy statement of the 'pattern problem' which is reproduced here because of its relevance to this thesis.

> In any given area, of whatever size, some factors will be constant at any one time, while others will vary from point to point in an area. The smaller the area the greater in general will be the number of constant factors. The magnitudes of the ranges of difference in the varying factors may be considered in terms of their effects on the plant. If the effects of all factors on all species present are relatively small, it will be a matter of chance which species succeeds at any point, and the resulting distribution of individuals (or parts of individuals where such parts are largely independent) will be random. Such conditions of equality of effects of different factors will only hold when the range of values found is well within the limits of tolerance of all species present. This follows from the much greater effect of small differences in an influencing factor when its value is near the limits of tolerance of a species. Now if one or few factors have a disproportionately great effect on performance or survival of a species, then the distribution of that species will tend to be determined by that particular factor or factors. If the values of the factors are themselves randomly distributed, then the distribution of the species will also be random. Field experience shows that most environmental factors do not have a random distribution of different values (consider, for example, such factors as soil moisture and texture). We may thus put forward the hypothesis that departure from randomness of distribution of a species indicates that one or few factors are determining the performance or survival

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[29] P. Greig-Smith, Quantitative Plant Ecology, 2d ed. (London: Butterworths, 1964), p. 54.

> of the species. The converse does not necessarily apply. One factor may be overriding even if a species is randomly distributed. It is unlikely, however, in any community of more than a few species, that the factor will have a predominant influence on one species alone. If more than one species is concerned, whether the effect of the predominating factor is the same for different species or not, correlation between the occurrence or performance may be expected. This correlation gives an indication of predominance of one or few factors even if individuals are randomly distributed.[30]

Greig-Smith is primarily interested in the relationship between plant species occurrence and environmental factors. Other than the equivalence of patterns with non-randomness, he is not concerned with the attributes of spatial distributions and the correspondence of these attributes with spatial variations in environmental factors. This statement of Greig-Smith interests the author in that it suggests a strategy for Biogeography. If it is possible to map the spatial variations of plant species and the spatial variations of various environmental parameters, then the requirement is a methodology which permits comparison between the variations of plant species and one or more of the environmental parameters over the space. This idealization would also create a field research design problem; the nature of these problems are discussed in Chapter VI.

Recent research by Pielou,[31] a mathematical ecologist, has been directed towards the problems described by Dacey. She investigates point patterns of single and multi-species population, with some discussion of mosaics.

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[30] Ibid., p. 55.

[31] E. C. Pielou, An Introduction to Mathematical Ecology (New York: John Wiley & Sons, 1969).

Pielou equates pattern to dispersion and hence creates further terminological confusion. She distinguishes three cases which depend upon the nature of the space and the organism. Her categories are:

(1) Cases in which the organisms are confined to discrete habitable sites or 'units'; for example, caterpillers of a pest species that attack the shoots of a tree. Each shoot constitutes a habitable site and is a natural sampling unit.

(2) Cases in which the organisms have a continuum of space that they can occupy; for example, trees in a forest. If we wish to count individuals per unit, the unit has to be arbitrarily defined.

(3) Cases in which, in addition to the absence of natural sampling units, there are no clearly delimited individuals that can be counted. Not merely do plants occupy a continuum that cannot be subdivided naturally but also, owing to vegetative reproduction, a great many plant species do not occur as distinct individuals amenable to counting.[32]

The point pattern work of Dacey falls into Pielou's category (2), while the majority of biogeographical research can be placed into the two categories (2) and (3). Pielou has been mainly concerned with the mathematics of different theoretical distributions. At present, the methodology is still focussed on a comparison of an observed set of points and a theoretical random distribution, often using some form of index.

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[32] Ibid., p. 80.

Although this review cannot claim to be comprehensive, two generalizations are believed to be valid. The initial emphasis of plant ecology on pattern, represented by the lengthy Greig-Smith quotation, has declined in recent years. It has been replaced by a trend towards energetics and ecosystem studies. Secondly, mathematical ecologists are studying the properties of theoretical distributions, but so far there has been little attempt to combine these theoretical studies with environmental research. Furthermore, the mathematical ecologist has not resolved the types of problems mentioned by Dacey.

B. Animal Patterns

It has already been noted that animal patterns are more complex because of the mobility factor. The illustration of the movements of a ruffed grouse (Figure 9) and Coleman's description of the gnats (Chapter II) showed the nature of the problem. A comprehensive survey of the literature by Brown and Orians[33] is the main resource for this review. These authors make a general point that the study of spacing patterns is an interdisciplinary field between Ecology and Ethology; this writer would argue that this field is Biogeography. They define the central problem of this field in terms of dispersion:

> The dispersion of animals in time and space results, in a proximate sense, from the direct response of individuals to features of the environment and to the presence or absence of other individuals of the species.[34]

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[33] Jerram L. Brown and Gordon H. Orians, "Spacing patterns in mobile animals," Annual Review of Ecology and Systematics, Vol. 1 (1970), pp. 239-262.

[34] Ibid., p. 239.

The problem is concerned with the perception of the organism of its environment, both physical and biological, and its subsequent behaviour. Once again, it is extremely complex, since both the organism and the environment are changing in space-time.

Two main approaches can be recognized in the study of animal patterns. First, there has been considerable research into mapping the location of mobile organisms at a macro-scale. Secondly, there has been a substantive body of research into the concept of territoriality and its significance to spacing and therefore implicitly population density. Wynne-Edwards[35] and Lack[36] have historically maintained opposing views on territoriality. Wynne-Edwards regards territorial behaviour as one of a number of behavioural traits, evolved by interpopulation selection, for preventing population from over-exploiting resources. On the other hand, Lack regards territorial behaviour as evolving as an aid to attracting and keeping a mate, not as a means of competing for other requisites. The result of this debate is that both Wynne-Edwards and Lack provide many examples of the dispersion of birds and animals. There is a wealth of observational material at a geographic or supra-organism scale which would be suitable for biogeographical interpretation.

In concluding this review, Brown and Orians speculate on the direction of this research:

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[35] V. C. Wynne-Edwards, Animal Dispersion in Relation to Social Behaviour (New York: Hafner & Co., 1962).

[36] David Lack, The Natural Regulation of Animal Numbers (Oxford: Clarendon Press, 1954).

> the preliminary success of models which have predicted spacing patterns and territory size on the basis of time and energy budget considerations indicates the power of this approach. The great value of these models is that coloniality and territoriality can be seen primarily as responses to the same factors--i.e., temporal and spatial distribution of exploitable resources.[37]

Within Geography, Haynes[38] studied the relationship between territorial size and the energy budget of the organism. His methodology was primarily dimensional analysis. The above quotation emphasizes the need to study simultaneously the spatial and temporal variations of all the resources within the space. The mobility of the organism requires greater appreciation of the perception and behaviour of the organism to its space-time. This writer continues to mention that biotelemetry offers the possibility of better observational material.

At the outset, the writer mentioned the variety of definitions of pattern. Dacey presented the status of the concept in Geography, with emphasis on the spatial distributions of points. Furthermore, pattern was discussed in relation to plants and animals. Together, they provide a definition of Biogeography. An interesting general observation is that there has been very little success in combining the conceptual and theoretical investigations with the study of the relationship between organism and environment. They remain distinct. This is similar to the trend in Ecology where pattern studies were

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[37] Jerram L. Brown and Gordon H. Orians, "Spacing patterns in mobile animals," Annual Review of Ecology and Systematics, Vol. 1 (1970), p. 253.

[38] Robin Haynes, "Dimensions of Spatial Relationships" (unpublished Ph.D. dissertation, Department of Geography, Pennsylvania State University, 1971).

superceded by process studies and thus far there has been little re-integration.

In addition to the above, the writer has been monitoring current research in engineering on pattern recognition.[39] The objective in this field is to develop languages which will permit recognition of patterns by a computer. As the procedure requires the articulation of pattern to a computer, it may contribute to the study of pattern in nature in the future.

(3) Spatial Diversity

Spatial diversity is a key concept within Geography; it is related to those definitions of the discipline which centre on areal differentiation. Within Biogeography, the concept is linked to the idea of species diversity. The concept of spatial diversity can be understood either as the variation in the density of individuals of a species or as a set of species (e.g. plankton) in space, or the 'mixed-up-ness' of species in a space. In the first case, the approach might be to recognize that a set of individuals for each species has a particular distribution and that there are several sets within the same space. Thus, if each spatial distribution is separated, then the problem is amenable to the analytical strategies of Dacey.[40] Alternatively, if the focus is the degree of order or

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[39] For example, Satosi Watanabe, ed., Frontiers of Pattern Recognition (New York: Academic Press, 1972) and Richard O. Duda and Peter E. Hart, Pattern Classification and Scene Analysis (New York: John Wiley & Son, 1973.

[40] Michael F. Dacey, "Some questions about spatial distributions," in Directions in Geography, ed. R. J. Chorley (London: Methuen & Co., 1973), pp. 127-151.

'mixed-up-ness' between the sub-areas of the space, then one approach is to apply the concepts of order and entropy. In this approach, the common methodologies are based on theoretic measures of complexity.[41]

Three facets of spatial diversity are discussed in this section. First, the concept of diversity is placed in the broad context of ecological concern for an 'ethic of biotic diversity'. The second aspect is a review of the ecological literature on species diversity. Any discussion of species diversity implies that there is a spatial unit and therefore spatial diversity. Species diversity and spatial diversity are paradoxical concepts. Thirdly, the writer elaborates on the nature of spatial diversity and its application to Biogeography.

The significance of an ethic of biotic diversity was strongly expressed at a recent conference on biotic impoverishment.[42] The theme was "the need to develop an ethic of biotic diversity, in which such diversity is perceived as a value in itself and is tied in with the survival and fitness of the human race."[43] This theme reflects the observation of Commoner and Klopfer.[44] Commoner noted the generally

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[41] E. C. Shannon and W. Weaver, The mathematical theory of communication (Urbana: University of Illinois Press, 1948).

[42] A jointly sponsored conference by the Smithonian Institute and the World Wildlife Fund on Biotic Impoverishment reviewed in the article "Scientists talk of the need for Conservation and an Ethic of Biotic Diversity to slow species extinction," Science, Vol. 184 (May 1974). p. 646.

[43] Ibid.

[44] See the contributions of Barry Commoner and Peter Klopfer in Mary C. Bateson, Our own Metaphor. A personal account of a conference on the effects of conscious purpose on human adaptation (New York: Alfred A. Knopf, 1972).

accepted maxim: "whenever a system becomes reduced in complexity, it loses its options and therefore becomes less and less stable."[45]

A classic example given to support this is the application of Western agricultural practices in tropical parts of the world. Western agricultural practices replace the traditional mixture of food crops in a field with a monoculture; the result has been instability in the natural environment. Complexity, in the above quotation, refers to the number and variety of the elements or linkages in the system and is considered synonymous with diversity.

Meanwhile, Klopfer applies the same concept to human society:

> We ought to be concerned with the reduction of diversity within the human population, reduction of the potential for generating new views, which may come about through increased uniformity in our environment...when all of North America is one big urban sprawl, I think that there will be very few people still functioning who share my disposition, which is one that is congenitally incapable of coping with the stress of city life.[46]

While this writer is not arguing for a set of individuals with this congenital disposition, it is agreed that there must be diversity of human habitat. As an aside, it is for this reason that the writer disagrees with the assumptions behind the urban geographic research of Bunge and Eliot Hurst.[47] They assume that the human

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[45] Ibid., p. 269.

[46] Ibid., p. 271.

[47] Explicit statements of their philosophies can be found in William W. Bunge, "Ethics & Logic in Geography," in Directions in Geography, ed. R. J. Chorley (London: Methuen & Co., 1973), pp. 317-331; and Michael E. Eliot Hurst, "Towards a socialist geography: Or how to survive and remain human," Paper presented at the American Association of Geographers, Plenary Session, April 1973.

species is dominant and that the urban sprawl of North America is inevitable. This writer wishes to support the alternative. Finally, the concept of diversity has been used by Bateson[48] in the context of a need for mental flexibility; in this case diversity lies within the individual. At all these levels and within the various contexts, it is argued that there is a value in diversity.

The second aspect of diversity, namely the relationship between diversity and stability, has formed a general debate in Ecology during the 1960's. The recent contribution of May[49] has clarified the relationship and also challenged the idea that complex ecological systems are more stable than simple ones. Prior to the mathematical contribution of May, the ecological research had been characterized by empirical studies of species diversity. Within the discussion of spatial diversity, this writer has focussed on these earlier papers which stress the variations in species diversity over parts of the earth's surface and also the measurement of species diversity.

One of the commonest measures of diversity is the information statistic.[50] Descriptively, if a set of objects are all the same, then there is no diversity. In a probabilistic sense, if we assume a

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[48] Gregory Bateson, <u>Steps to an Ecology of Mind</u> (London: Intertext Books, 1972).

[49] Robert M. May, <u>Stability and Complexity in model ecosystems</u> (Princeton: Princeton University Press, 1973).

[50] See, for example, the following texts: E. C. Shannon and W. Weaver, <u>The mathematic theory of communication</u> (Urbana: University of Illinois Press, 1948); Abraham Moles, <u>Information Theory and Aesthetic Perception</u> (Urbana: University of Illinois Press, 1966); H. Quastler, ed., <u>Information Theory in Biology</u> (Urbana: University of Illinois Press, 1953).

set of black balls, then the probability of selecting a black ball is unity; the diversity is zero and the information content is low. If the balls are all different colours, then the set possesses a high diversity; the probability of selecting a ball of a particular colour would be 1/N, where N = number of balls or colours, and the set would have a high information content.

The main difference between this simple model and natural reality lies in the problem of defining a set. If we wish to describe the diversity of tree species within a forest, it is necessary to define either an area within the forest or consider the whole forest up to its natural boundary. Therefore, any value of species diversity must have an associated spatial parameter. If the problem is to study spatial diversity, then it is essential to define the sample area which in turn defines the scale of the research. Maher[51] has investigated this problem; his thesis gives details of the application of information theory to vegetation patterns. Recently, Hill[52] has published an excellent statement on the methodological problem inherent in the information theoretic approach.

The classic descriptive statement on species diversity was the address by Hutchinson to the American Society of Naturalists in

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[51] Robert V. Maher, "Complexity analysis of vegetation patterns in an alpine meadow" (unpublished M.Sc. thesis, Department of Geography, University of Western Ontario, 1971).

[52] M. O. Hill, "Diversity and evenness: a unifying notion and its consequences," Ecology, Vol. 54, No. 2 (1973), pp. 427-432; also, M. O. Hill, "The intensity of spatial pattern in plant communities," Journal of Ecology, Vol. 61, No. 1 (1973), pp. 225-236.

1959;[53] he posed the question: why are there so many kinds of animals? His address discussed evolutionary ecology, speciation and the requirements of a species from its environment. These topics expand the subject beyond the scope of this thesis. Their importance is that they provide the general context for the significant contribution of MacArthur[54] into species diversity. In an early paper, MacArthur[55] and his brother showed that there is a relationship between bird species diversity and the diversity of foliage height of the tree habitat. They found that more species of bird are found in areas where the trees have a wide range of foliage levels. Diversity of foliage levels was more significant than the diversity of tree species. MacArthur predicted the presence or absence of particular avian species on the basis of the foliage density profiles.

As Klopfer observed later: "every good bird watcher accomplishes much the same, though the process of recognizing the appropriate habitat or microhabitat is largely intuitive and not susceptible to analysis."[56]

Subsequently, MacArthur[57] completed comparative studies in the

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[53] G. E. Hutchinson, "Homage to Santa Rosalia or why are there so many kinds of animals," The American Naturalist, Vol. 93 (1959), pp. 145-159.

[54] Robert H. MacArthur, Geographical Ecology (New York: Harper & Row, 1972).

[55] R. H. MacArthur and J. W. MacArthur, "On bird species diversity," Ecology, Vol. 42 (1961), pp. 594-98.

[56] Peter H. Klopfer, Behavioural Aspects of Ecology, 2d ed. (Englewood Cliffs, New Jersey: Prentice-Hall, 1973), p. 50.

[57] Robert H. MacArthur, "Patterns of communities in the Tropics," Biol. J. Linn. Soc., Vol. 1 (1969), pp. 19-30.

United States, Puerto Rico and Panama. These studies indicate that the relationship between species diversity and foliage diversity varies over the earth's surface; this means that species diversity depends upon several environmental variables. Pianka[58] applied a similar design to the diversity of lizard species in Australian and American deserts. He concluded that the higher diversity in Australian lizard species is a function of the greater environmental heterogeneity and the fact that species have divided the space more finely. The author considers that this explanation is a tautology. If a species evolves in response to a peculiar environment, then it is self-evident that a more diverse environment will contain more species. The most interesting idea which arises from the Pianka explanation is the concept of environmental heterogeneity. There are several questions in the writer's mind: how is environmental heterogeneity to be measured?; what variables and attributes of variables are considered significant to a particular species? This topic will be discussed later in this section.

Elsewhere, Pianka considers species diversity at a global scale and seeks to explain why there are more species in the tropics than at higher latitudes. Pianka identifies six hypotheses in the literature. Of primary interest to this thesis is the second hypothesis, which Pianka terms "the theory of spatial heterogeneity."

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[58] E. R. Pianka, "On lizard species diversity: North American flatland deserts," Ecology, Vol. 48 (1967), pp. 333-51; and E. R. Pianka, "Habitat specificity, speciation and species diversity in Australian desert lizards," Ecology, Vol. 50 (1969), pp. 498-502.

The "theory" has two parts:

(1) there is a general increase in environmental complexity as one proceeds towards the tropics.

(2) the more heterogeneous and complex the physical environment becomes, the more complex the plant and animal communities supported and the higher the species diversity.[59]

Krebs[60] discusses the hypothesis at two scales which can be described as macrospatial and microspatial. At the macrospatial level, Krebs quotes the finding of Simpson[61] that there is a higher diversity of mammals in the mountains than on the lower plains of the United States. The argument is that the greater topographic relief permits a greater range of habitats within an area and hence a higher species diversity. In terms of the polar-tropical gradient, it is difficult for the writer to see where this continental example offers any explanation. There is not a topographic gradient from the arctic to the tropics. A desert mountain range will have a low species diversity regardless of its latitude.

There are a number of complicating factors. First, there is the basic argument, made elsewhere, about the inseparability of organism and environment. In terms of species diversity, the species

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[59] E. R. Pianka, "Latitudinal gradients in species diversity: a review of concepts," The American Naturalist, Vol. 100 (1966), pp. 33-46.

[60] Charles J. Krebs, Ecology: the experimental analysis of distribution and abundance (New York: Harper and Row, 1972).

[61] Simpson cited in Charles J. Krebs, Ecology: the experimental analysis of distribution and abundance (New York: Harper and Row, 1972), p. 516.

themselves create habitats for the development of further species. The environment is modified by the existence of living organisms. Secondly, the definition of a species is dependent on significant morphological differences which are considered adaptive to a specific environment.

If we hypothesize a relationship between species diversity and macrospatial heterogeneity, then both concepts have to be clearly defined. Species diversity has already been defined in this section. Macrospatial heterogeneity implies variations in the topography of the earth's surface and also in the physical properties of the atmosphere above the surface. The important characteristic would be the rate of change of these variables in space-time. The major problem would be to develop a method of studying macrospatial heterogeneity. Since the physical variables are continuous, it would be necessary to impose a sampling procedure at a particular scale. This creates a further problem since the value of a variable like topographic relief is scale dependent. Topographic relief can be defined in a number of different ways: for example, it could be the absolute relief, that is the highest point in the area or it could be a measure of the ruggedness or "broken-up-ness" in the area.

At the microspatial level, Krebs is interested in the variations of rocks and vegetation as they relate to the individual organism. The same criticisms exist at this scale.

From this selected review of the 'theory of spatial heterogeneity', it is evident the ecologists have not been very successful in defining spatial diversity. Their approach has been to propose hypotheses which are based on an "organism-centred' viewpoint rather than a space-continuum viewpoint. These conceptual difficulties are often compounded by lack of information. In some parts of the earth's surface species lists are not available; perhaps it is over-optimistic to expect explanation of these complex relationships between the physical environment and the distribution of species. It is partly because of lack of information that the last work by MacArthur must remain a contribution to theoretical geographical ecology.[62]

The concept of spatial diversity can be discussed, using the opposing sides of the organism-space paradox. From the "organism-centred" viewpoint, the main emphasis is on the habitat, where habitat is the space that the individual occupies for the purpose of food supply and reproduction. A static plant species has direct requirements from its immediate physical environment which remains locationally constant through time, whereas mobile organisms may move in relation to a changing physical environment. Besides these external influences, there are intrinsic factors like territoriality and competition which affect the degree of separation and overlap of individuals and species and therefore affect the spatial diversity.

From a 'space-centred' viewpoint, one area may provide the requirements for a number of mobile organisms at different times. At a basic level, the primary characteristic of an area is the form of the surface. Superimposed and penetrating into the land surface is

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[62] Robert H. MacArthur, Geographical Ecology (New York: Harper & Row, 1972).

the earth's atmosphere. We can conceive of pockets of atmosphere bounded by hill slopes. Each element of space on the land surface experiences a time trace of a large number of variables. Depending upon the nature of the specific hypervolume formed by the variable hyperspace and time, each element of the land surface will prove more or less acceptable to biological organisms. The occupancy of an element by a biological organism is susceptible to change through time which may be directly controlled by rhythms or cycles in the physical or biological environment.

In order to divide the total space, it would be necessary to establish boundary criteria. The boundaries would coincide with the major zones of change for the maximum number or the most important variables arranged over time. This strategy can be complemented by the concept of tolerance limits of an organism. It would be possible to match the set of variable-time traces for an element of space with the organism identity of the element. This type of model would be probabilistic.

It is clear that spatial diversity cannot be divorced either from the properties of the biological organism or from the total environment. In seeking an explanation of observed diversity, it is necessary to understand the processes and gradients that exist in the space. The fundamental problem, therefore, is to characterize these continuous variables in time and space and to relate them to the discrete biological organisms. The writer believes that the paradox between the 'organism-centred' and 'space-centred' approach must be recognized. It is paralleled in the distinction between species diversity and spatial diversity. To reiterate two previous points, the concept of species diversity must include a spatial parameter and, secondly, the concept of spatial diversity must recognize both, the complexities of the physical environment and its interaction with the species, and the nature of space.

(4) Organism Interactions

The dualism between 'space-centred' and 'organism-centred' approaches to the discipline has been established. In this chapter there has been discussion of natural order, pattern and spatial diversity which are primarily 'space-centred' and this last section concerns the effect of the size and communication ability of an organism on its use of space. These two properties are not the only significant properties in this complex relationship but they do provide valuable examples of the approach. The material is confined to the animal kingdom, although the comments are structurally applicable to plants.

The morphology of an organism has evolved in relation to its environment through time. At the simplest level there are obvious differences in form between organisms which inhabit the three physical media of the biosphere--land, sea and air. Each medium has a set of physical characteristics which are determined primarily by density. For example, the marine environment is less variable in terms of temperature and salinity because of the density and continuous nature of the water body. Every organism can be viewed as a dynamic entity with the function and structure of its organs adapted to its normal environment. Mobility is a significant factor here, since it permits an organism to move out of an unsuitable environment. This factor is the primary criterion for distinguishing between plants and animals.

Figure 14 illustrates the interaction between an organism and its environment; in this case, a shark in a marine environment. Vernberg and Vernberg[63] use the diagram to stress the dynamic equilibrium between organism and environment. Fish and other marine species are functionally and morphologically adapted to the medium. The organism responds to the temperature, salinity and depth of the water; these factors, in turn, affect the light availability and density. The density of the medium will control the settling rate of micro-organisms which influence the food supply. These are all interdependent external factors, while the complex process of metabolism controls the internal environment of the organism.

Vernberg and Vernberg make an interesting point on the evolution of organisms in the animal kingdom:

> one of the major evolutionary trends in the animal kingdom has been the development of mechanisms enabling an animal to maintain a relatively constant internal environment independent of the fluctuations in the external environment.[64]

However, organisms still retain different tolerance limits for external, physical factors. Mobility is important in this respect; movement patterns or spatial organization are a regular feature of the daily or seasonal behaviour of an organism, for example bird migration or the diurnal vertical movement of plankton. The organism

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[63] F. John Vernberg and Winona B. Vernberg, The Animal and the Environment (New York: Holt, Rinehart and Winston Inc., 1970), p. 2.

[64] *Ibid.*, p. 4.

Interactions of a Shark and its Environment

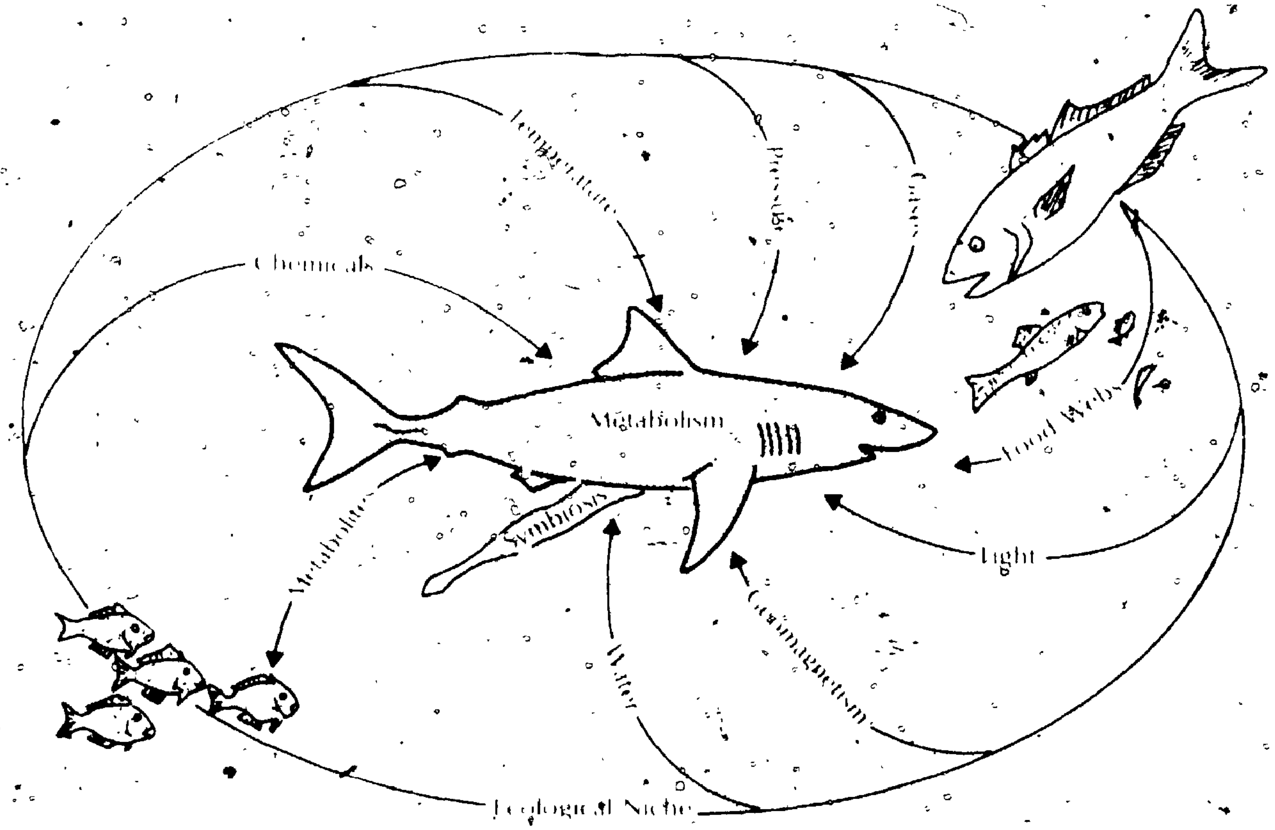

Figure 14

SOURCE: F. J. Vernberg and W. B. Vernberg, The Animal and the Environment, 1970, p. 2.

can be considered to position itself in a three-dimensional space-time of environmental variables.

A fundamental property of an organism is size. D'Arcy Thompson has given numerous examples of size and the associated principle of similitude. The light-hearted description below makes the point.

> Gilbert White of Selborne, finding that a certain little long-legged bird, the stilt, weighed 4¼ oz. and had legs 8" long, thought that a flamingo, weighing 4 lbs. should have legs 10 feet long to be in the same proportion as the stilt's. But it is obvious to us that, as the weights of the two birds are as 1:15, so the legs (or other linear dimensions) should be as the cube roots of these numbers, or nearly 1:2½. And on this scale the flamingo's legs should be, as they actually are, about 20" long.[65]

Size affects the nature of the relationship between an organism and its environment. Hutchinson,[66] developing an idea of Bidder,[67] illustrates the relationship for aquatic micro-organisms. There are three aquatic realms which are characterized by micro-organisms of a set size range. Each realm is identified by a particular physical process.

Realm	Size of Organism	Significant Physical Property
Brownian	$< 1\,\mu$ diameter	molecular movement
Stokesian	$1\,\mu$ - $500\,\mu$	viscosity
Archimedean	$> 500\,\mu$	inertia

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[65] D'Arcy Wentworth Thompson, On Growth and Form (Cambridge: Cambridge University Press, 1963), p. 23.

[66] G. E. Hutchinson, "Scale effects in Ecology," in Statistical Ecology, Volume 1, Spatial Patterns and Statistical Distributions, ed. G. P. Patil, E. C. Pielou, W. E. Waters (Pennsylvania: Pennsylvania State University Press, 1971), pp. xvii-xxvi.

[67] G. P. Bidder, "The Biological importance of Brownian motion (with notes on sponges and Protista)," Proceedings of the Linnaen Society of London, 143 (n.d.), pp. 82-96.

The concept that different processes are significant at different scales of organism has implications for Biogeography. A classification of organisms according to size is important especially if size is related to the sensitivity of the organism to different processes in space-time. For the archimedean realm, Hutchinson notes these organisms have developed the ability to swim using muscular organs and that they have more discriminatory sense organs. The size of the organism is fundamental to mobility and perception, which are both significant to spatial organization.

Hutchinson makes a further observation on the behaviour of organisms and evolution. There is:

> The well-known difference between small animals whose behaviour is based on a stereotyped inherent response mechanism, presumably dependent on genetically determined neural patterns, and large animals, in which the learning has to a greater or lesser degree supplemented such instructive mechanisms.[68]

and furthermore:

> The sequential experiences of large long-lived learning animals take the place of trials by a vast population of small short-lived animals with only inherent responses, trials which will be unsuccessful unless the genetic constitution of the organism is correct.[69]

The relationship between learning and behaviour is outside the scope of this thesis; however, both size and longevity of an organism influence behaviour, which, in turn, affects the use of space. Indeed, there is also a relationship between size and longevity. This has considerable importance when it is recognized that

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[68] Hutchinson, op. cit., p. xxiii.

[69] *Ibid.*, p. xxiv.

certain processes operate at different scales in both time and space. While the full significance of these fundamental relationships has not been investigated by the writer, it can be reaffirmed that the size of an organism results in different classes of interaction with the environment.

The second property of an organism, considered in this thesis, is communication ability. Adams describes the basic relationship between the sense organs and behaviour.

> It would seem self-evident that an animal can respond only to the environment that its sense organs, its motor equipment and its central nervous organization, both innate and acquired make accessible to it; and hence that any inquiry designated to describe, understand or explain its behaviour would necessarily use the environment as one of the variables that condition the behaviour.[70]

Adams was writing in the foreword to a text on behavioural ecology and hence he was emphasizing 'environment'. In this thesis, the interest is already based on 'environment' and concern is primarily with 'behaviour' as it relates to spatial organization. Communication is the process that acts across the organism-environment interface, via the sense organs. For the sense organs, there are corresponding types of perception: vision, audition, chemo-reception, also the perception of gravity, pressure and temperature. Different types of perception are more or less significant to different classes of organisms. Vision is important in mammal species, while chemoreception has primary significance to bees and social ants. Furthermore,

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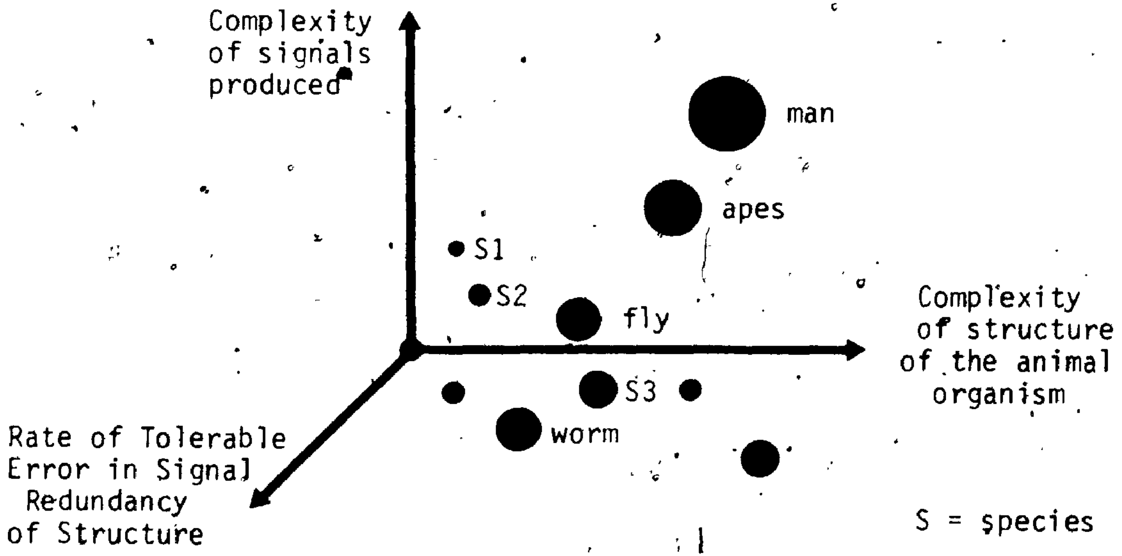
[70] D. K. Adams, in the foreword to Peter H. Klopfer, Behavioural Aspects of Ecology, 2d ed. (Englewood Cliffs, New Jersey: Prentice-Hall, 1973), p. xvi.

the medium affects the message; for example, sound travels at different speeds in air and water. Communication models often represent the process as a simple three component system of transmitter, channel and receiver; however, it is usually a more complex process. Communication often has a number of dependent modalities; for example, in the human species, there is a context (spacing) and although the message may be auditory, there are also visual cues (e.g. facial expression).

Several classifications of organisms have been proposed in the field of animal communication which have applicability to Biogeography. Moles[71] classified organisms according to their communication patterns. Figure 15 illustrates the criteria as applied to a few species. This diagram represents the schema of a communication theorist and requires further explanation by Moles.

FIGURE 15

A Statistical Classification of Communication Patterns



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[71] Abraham A. Moles, "Perspectives for Communication Theory," in Animal Communication, ed. Thomas A. Sebeok (Bloomington: Indiana University Press, 1968), pp. 627-44.

> A statistical classification of communication patterns can be made according to the complexity of signals in relation to the complexity of the structure of the organism which gives rise to them. In fact, this would here be the complexity of the nervous system, a first approximation to it being the logarithm of the number of cells in the nervous system or in a definite part of it. Communication between individuals has another feature which is well known: the number of acceptable errors. Given a large enough set of communication procedures, it is well known that the number is connected to the redundancy of structure of the organism, the tolerable error being determined by the concept of safety. Such a diagram is another of the requisites that the communication theorist would put to the zoologist as a basis for a taxonomy of communication.[72]

Biogeography would also benefit from a classification of this type. There is obviously a relationship between communication processes and spatial interaction between organisms. The general structuralist approach of Moles has appeal to Biogeography because it offers a means of studying the infinite variety of organisms. As Moles says elsewhere: "structuralism is perfectly suitable at the first stage of study."[73]

A second classification of animal communication by Wenner[74] is based on behaviour. Wenner recognizes three categories: intra-individual, inter-individual and animate-environment; only the last two categories are deemed pertinent to Biogeography. The inter-individual class could be represented in spatial organization terms by flocks of birds, schools of fish, and the concept of territoriality.

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[72] _Ibid._, p. 631.

[73] _Ibid._, p. 642.

[74] Adrian M. Wenner, "The study of animal communication: an overview," in _Approaches to Animal Communication_, ed. T. A. Sebeok and A. Ramsay (The Hague: Mouton & Co., 1969), pp. 232-43.

The animate-environment class concerns the perception of the organism of its environment, characterized by the concepts of habitat and home range. The diagram of Vernberg and Vernberg (Figure 14) clearly fits into this category.

A third approach, from the field of animal communication, is the paper by Ramsay[75] on the relationship between social organization and spatial organization. She emphasizes the importance of space to studies of animal communication, which is the reverse of this writer's endeavour to establish the opposite linkage. Ramsay quotes McBride:

> It is apparent...that to consider aggregated or non-aggregated species, we are automatically discussing two-dimensional spatial relationships between animals. It seems probable that these spatial relationships between animals are also basic in animal organization, since most social (or non-social) behaviour can be expressed in terms of distances between animals and their arrangement in space. Close social organization must also mean small physical distances between individuals.[76]

While this last quotation does not offer any insight into the methodological problems of pattern, it does indicate the following type of linkage: spatial-organization ⟶ social organization ⟶ behaviour ⟶ communication ⟶ sense organs.

There is no suggestion here of simple linear relationships, but only that this set of linkages can be followed through this section of the thesis. Indeed, sense organs could be linked to size.

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[75] Alexandra Ramsay, "Time, Space and Hierarchy in Zoosemiotics," in Approaches to Animal Communication, ed. T. A. Sebeok and A. Ramsay (The Hague: Mouton & Co., 1969), pp. 179-199.

[76] Ibid., p. 192. Original source G. McBride, "A General Theory of Social Organization and Behaviour," University of Queensland Papers, Faculty of Veterinary Science, 1(2), pp. 75-110.

In conclusion, it should be stressed again that only two properties have been considered here. They are thought to be of primary significance to spatial organization, although there may be other properties of equal importance. The major conclusion for Biogeography is that organisms should be classified with regard to those properties which influence the processes of perception and mobility of the organism in its three-dimensional space-time continuum. It is important to recognize that the interaction of processes acting at different time scales will impose a structure on living things.

CHAPTER VI

STRATEGIES FOR RESEARCH IN BIOGEOGRAPHY

Prior to a discussion of research strategies, it may be useful to retrace the main points of the thesis. The inquiry commenced with a review of the contemporary literature of the discipline which distinguished between the 'ecosystem' and the 'distribution' approaches. The next chapters contained six examples which illustrated the author's support of the 'distribution' view. These examples raised a number of methodological and conceptual problems. Secondly, they showed a distinction between 'organism-centred' and 'space-centred' studies. In Chapter V, four concepts elaborated the paradoxical nature of this distinction. Also, these concepts indicated various linkages between Biogeography and the biological sciences.

This chapter returns to the pragmatic concern of research approaches in Biogeography. Four strategies are discussed:

(1) Research in Theoretical Biogeography
~~(2) Applied Research~~ in Biogeography
(3) Field Research
(4) The Teaching of Biogeography

These strategies represent projections based on the writer's perception of the discipline and his current research.

Strategy 1 illustrates the potential for a theoretical

Biogeography. The recommended start is the interdisciplinary position between Theoretical Biology and Theoretical Geography. The emphasis is on the current questions in Theoretical Biology and their translation into a biogeographical context.

Strategy 2 rectifies any tendency towards over-emphasis on the conceptual framework of the discipline. The examples are consistent with the 'distribution' view and also with a philosophy of life for all species. Specific topics are the development of a Radical Biogeography, Historical Biogeography, and Bioregions. It includes a concern for the extinction of species.

Strategy 3 emphasizes 'organism-centred' field research, while Strategy 4 illustrates the relationship between the contents of this thesis and the teaching of the discipline. The examples indicate the close interaction between teaching and research activities.

Strategy 1: Research in Theoretical Biogeography

Biogeography is distinctive within Physical Geography in that the object of study is living matter. A basic definitional question is the nature of living matter. While not wishing to take up Schrodinger's question, What is life?,[1] there are certain basic definitions which are relevant to Biogeography. For example, Waddington defines living matter as follows:

> living things do not merely synthesize specific structures out of simple molecules; it is an equally important fact that they reproduce themselves, and indeed it might be

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[1] Erwin Schrodinger, What is Life? (Cambridge: Cambridge University Press, 1967).

> claimed that the most important fact about them is that they take part in the long term process of evolution.[2]

The concept of evolution has major significance for Biogeography at various conceptual levels. First, it suggests the dynamic organism-environment relationship. Although the concept is not primary to spatial organization (in the pattern sense), it does imply the idea of processes, acting internally and externally, and across the boundary between an organism and its environment. Secondly, the writer regards Darwin and Wallace as proto-biogeographers and hence it is important to understand the history of the concept and its relationship to Biogeography. The contextual framework of the theory of evolution and also the recent modifications of the theory are recognized by the writer to be important research topics in Biogeography.[3]

Elsewhere, Waddington defines living matter in the terminology of communication theory: "A system is living if it encodes hereditarily transmissible information, if this information sometimes suffers alterations, and if the altered information is then transmitted."[4] This translation is an example of the systems approach in

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[2] C. H. Waddington, in the introduction to Towards a Theoretical Biology, Vol. 1: Prolegomena, ed C. H. Waddington (Chicago: Aldine Publishing Co., 1968), p. 3.

[3] Resource examples are: Robert Young, "The Historiographic and Ideological Contexts of the nineteenth-century debate on Man's place in Nature," in Changing perspectives in the History of Science, Essays in honour of Joseph Needham, eds. M. Teich and R. Young (London: Heinemann, 1973), pp. 344-438; and the papers of Paul A. Weiss and C. H. Waddington, in Beyond Reductionism. New Perspectives in the Life Sciences, eds. A. Koestler and J. R. Smythies (London: Hutchinson, 1969).

[4] C. H. Waddington, in the introduction to Towards a Theoretical

Theoretical Biology. (Communication Theory is a subset of General Systems Theory.[5]) Biologists have applied this approach to all the levels in the hierarchy of matter. The writer has expressed his reservations about this approach at the level of the earth's surface. While the cell and the organism appear to have well-defined boundaries, the same is not true for the ecosystem. Some general points on the concept of a system are discussed later in this strategy.

The general argument of this strategy is that the establishment of a Theoretical Biogeography must recognize the developments in Theoretical Biology. Recent symposia provide the primary resource.[6] This argument accords with the observation of Longuet-Higgins:

> the most fruitful way of thinking about biological problems is in terms of design, construction, and function, which are the concrete problems of the engineer and the abstract logical problems of the automata theorist and the computer scientist.[7]

The author believes that the characteristics of design, construction and function of a problem in Cell Biology can provide insight into a problem in Biogeography. This exchange is not

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Biology, Vol. 1: Prolegomena, ed. C. H. Waddington (Chicago: Aldine Publishing Co., 1968), p. 3.

[5] The standard resource is Ludwig von Bertalanffy's text, General Systems Theory: Foundations, Developments, Applications (New York: George Braziller, 1968).

[6] The papers of the symposia are contained in Towards a Theoretical Biology, Vols. 1-4, ed. C. H. Waddington (Chicago: Aldine Publishing Co., 1968; Edinburgh: Edinburgh University Press, 1969, 1970 and 1972).

[7] Christopher Longuet-Higgins, "What Biology is about," in Towards a Theoretical Biology, Vol. 2: Sketches, ed. C. H. Waddington (Edinburgh: Edinburgh University Press, 1969), p. 229.

necessarily one way; some biological problems can be directly conceived in a biogeographic framework. Mayr used the example of bird migration to illustrate the problem of causality, but it is also a biogeographical phenomenon. Mayr[8] posed two questions:

(a) What is the cause of bird migration?

(b) Why did the warbler in my Summer place in New Hampshire start his southward migration on the night of the 25th August?

He proposed four causes or explanations:

(1) <u>Ecological</u> - The warbler, being an insect eater, must migrate, because it would starve to death if it should try to winter in New Hampshire.

(2) <u>Genetic</u> - The warbler has acquired a genetic constitution in the course of evolutionary history of its species which induces it to respond appropriately to the proper stimulus from the environment.

(3) <u>Intrinsic Physiological</u> - The warbler flew south because its migration is tied in with photoperiodicity. It responds to the decrease in day length, and is ready to migrate as soon as the number of hours of daylight have dropped below a certain level.

(4) <u>Extrinsic Physiological</u> - The warbler migrated on the 25th August because of a cold air mass with northerly winds, passed over our area on that day. The sudden drop in temperature and associated weather conditions affected the bird, already in a

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[8] Ernest Mayr, "Cause and Effect in Biology," in <u>Towards a Theoretical Biology, Vol. 1: Prolegomena</u>, ed. C. H. Waddington (Chicago: Aldine Publishing Co., 1968), p. 45.

general physiological readiness for migration, so that it took off on that particular day.

This set of information can be viewed as a biogeographical problem, using the organism and space dichotomy. The facts can be ordered as follows:

Organism - insect-eating bird
- migratory bird
- presumed to possess intrinsic trigger mechanism

Space - distribution of insect species over space-time
- change in photoperiodicity over space-time
- air mass movements over North America and their associated temperature and wind characteristics.

Each of the three spatial elements can be elaborated and evaluated.

(a) Distribution of Insect Species

First, it would be necessary to clarify the diet of the warbler, specifically the number of insect species. Subsequently, the critical climatic influences which affect the insect population would have to be established. If migration is a function of food supply, then it is necessary to test the relationship between insect availability over space-time and the changes in climatic conditions over space-time. The critical climatic variable may be the first frost or the general trend in air temperatures.

(b) Photoperiodicity

Photoperiodicity is well-defined by latitudinal parameters and hence the theoretical values may be mapped. If photoperiodicity is significant, then there would be a relationship between migration dates and light availability. A critical test would be the variability of the migration dates over a period of years.

(c) Synoptic Climatology.

The nature of the air masses over North America varies during the year and also between years. If the sequences of air masses with their attributes of temperature, wind speed and direction were mapped, then it should be possible to test the relationship between these variables and migration.

It is apparent that these three factors are interrelated. Photoperiodicity will influence potential heat availability at the earth's surface, which in turn influences air temperatures. Insect population levels may depend upon incoming energy and air temperature, while particular air masses will accentuate positively or negatively the general photoperiodic influence. Mayr argued that photoperiodicity sets the trigger and the bird migrates at the next opportunity when the conditions are favourable.

A detailed research design could investigate the following class of questions. If the bird always departs at the same time (day) from a particular location, then photoperiodicity or some other "fixed" factor is important. This can be tested by consideration of a range of locations, with different photoperiodicity, providing the species is sufficiently wide-ranging. If food supply is critical, then the geographic fluctuations of insect populations can be monitored over a number of years. If synoptic climatology is important, then it should be possible to study the passage of air masses over the region and investigate the relationship of this passage with time of migration. Implicit in all these questions is the notion of variability of the migration in space-time. It is presumed that if migration was studied at a set of locations for a number of years and all the above factors were monitored, then the relative significance of the factors could be evaluated.

Such investigations raise further questions. This type of study has an inherent problem of scale; it is not possible to be in a number of places at the same time and hence requires a co-ordinated research group. Secondly, the best insights into the factors influencing bird migration are more likely to be achieved by the naturalist who observes and experiences the phenomena over a number of years. Unfortunately, the human organism, in general, has become desensitized to this type of natural process. One final observation is that this example is limited to the timing and direction of migration and does not consider the route of migration or the characteristics of the destination. A reverse triggering may be effective on arrival at the destination.

This lengthy elaboration of the example of Mayr illustrates the importance of variation in the physical variables in space-time. It represents a valid biogeographical approach and, at the same time, demonstrates the utility of resources from Theoretical Biology. In this last regard, the concept of Goodwin[9] on the relationship between

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[9] Brian Goodwin, "The division of cells and the fusion of ideas," in Towards a Theoretical Biology, Vol. 1: Prolegomena, ed. C. H. Waddington (Chicago: Aldine Publishing Co., 1968), pp. 134-39.

the division of cells and the fusion of ideas is pertinent. Goodwin uses the terminology of computer hardware to make his point. "Analogue" and "digital" are considered representative of two approaches to the analysis of biological systems. The "analogue" approach emphasizes the dynamic, largely continuous aspects of biological process, e.g. physiological activity, ecological balance; whereas "digital" corresponds to quasi-static, discontinuous and logical aspects of biological phenomena, e.g. speciation in genetics, decision-making in psychology. The author would suggest that the "analogue" corresponds to "space" and "digital" to "organism" in the two approaches in Biogeography. It is interesting that Goodwin stresses the need for a "hybrid" of these two approaches. He suggests that it requires the combination of automata theory and control theory. This same combination may prove fruitful to a Theoretical Biogeography.

Waddington, in his concluding remarks to the first symposium on Theoretical Biology, lists three characteristics of Biology (and therefore, Biogeography):

1. It essentially involves time at three scales: turnover, development of phenotype, evolution; there can be no instantaneous life, nor life that merely undergoes cyclic or reiterative development.
2. It is essentially multi-dimensional; there can be no unit, however complex its internal structure, which can be considered 'living' without reference to the situation not included in the unit.
3. It is essentially organized, in the sense that it exhibits homeorhesis (not homostasis); there can be no living thing which can vary equally easily in all conceivable directions.[10]

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[10] C. H. Waddington, "Concluding Remarks," in Towards a Theoretical Biology, Vol. 1: Prolegomena, ed. C. H. Waddington (Chicago: Aldine Publishing Co., 1968), p. 218.

The concept of multiple time scales, whether three or more, has significance in terms of a temporal framework for Biogeography. From an 'organism-centred' viewpoint, the diurnal, annual and life history time scales would be important, particularly as they relate to rhythms in the physical environment. It has been suggested that the interaction of processes acting at different time scales will impose a structure onto living things. Goodwin has explored this subject at the cellular level in his book, <u>Temporal Organization in Cells</u>.[11] Multi-dimensionality is an essential characteristic of any biogeographical problem in space-time, while context is explicit in the organism-space paradox.

Organization, the third characteristic, has been primary to the discussion of Theoretical Biology. Kornacker states, for example, "organization, which for the moment might be thought of as some set of structure-function relationships, is a dominant feature of all biological systems and appears at all levels from the molecular to the social."[12] Organization, in that sense, corresponds most closely to the concept of natural order described in Chapter V.

The final example of the potential exchange between Theoretical Biology and Biogeography is the research of Levins[13] into complex systems.

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[11] Brian Goodwin, <u>Temporal Organization of Cells</u> (London: Academic Press, 1963).

[12] Karl Kornacker, "Towards a physical theory of self-organization," in <u>Towards a Theoretical Biology, Vol. 1: Prolegomena</u>, ed. C. H. Waddington (Chicago: Aldine Publishing Co., 1968), p. 94.

[13] Richard Levins, "Complex Systems," in <u>Towards a Theoretical Biology, Vol. 3: Drafts</u>, ed. C. H. Waddington (Edinburgh: Edinburgh University Press, 1970), pp. 73-88.

His concepts and definitional statements are perhaps the most useful part to Biogeography. Levins offers pertinent and clear definitions of model, theory and system. Levins defines a model:

> A model is a theoretical construction, a collection of objects and relations, some, but not all, of which correspond to components of the real system. In one sense, it is a simplification of nature. We ignore components which we believe to have small effects, or large effects but only rarely.[14]

Within the limits of this definition, Levins recognizes three distinct characteristics of a model: generality, realism and precision; and yet no model can optimize all three of these characteristics. He proceeds to relate model and theory, in that: "Since there are no universally optimal models, a theory must be a cluster of models which fit together in different ways,"[15] and furthermore, "It is often necessary to treat the same problem with different models. A theorem is then called robust if it is a consequence of different models, and fragile if it depends on the details of the model itself."[16]

It is interesting to the writer that Levins describes the research of MacArthur as possessing generality and some reality but lacking in precision. The text, Geographical Ecology,[17] is presently the best example of a theoretical Biogeography. A critical appraisal of the text represents another research objective.

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[14] *Ibid.*, p. 75.

[15] *Ibid.*

[16] *Ibid.*, p. 76.

[17] Robert MacArthur, Geographical Ecology (New York: Harper & Row, 1972).

A second aspect of Levins' research is his classification of systems into three types--aggregate, composed and evolved.[18]

(a) An aggregate system is one in which the properties of the whole are statistics of the properties of the individual parts; in which the individual parts affect the properties of the whole only by virtue of being part of the mean or the variance.

(b) A composed system is similar to an engineering circuit; the different components may be different kinds of units--condensers, transistors, switches, etc. The properties of the system are no longer derivable from simple statistics of the components. It is a composed system because the properties of each component can be completely specified by study in isolation. They do not affect the mode of response of each other, but only the way in which a signal is processed that passes through all of them.

(c) An evolved system has component sub-systems which have evolved together, and are not even obviously separable, in which it may be conceptually difficult to decide what are the really relevant component sub-systems.

The writer has not advocated a systems approach to Biogeography. However, this threefold classification can be applied to current research in the discipline. The aggregate system implies that the units do not possess other qualities, besides presence and absence. This same implication is inherent in the application of

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[18] Richard Levins, "Complex Systems," in Towards a Theoretical Biology, Vol. 3: Drafts, ed. C. H. Waddington (Edinburgh: Edinburgh University Press, 1970), p. 78.

the information theoretic measures to species diversity. The ecosystem would appear to be a good example of the composed system, while the writer believes that Coleman's description of the gnats illustrates an evolved system (Chapter IV).

This strategy is very open-ended. This writer believes that there are many examples where the concepts and problems of Theoretical Biology may aid in the development of a conceptual framework for Biogeography. This exchange is not necessarily one-way, nor should it be thought to exclude linkages with Theoretical Geography. The main argument is that Biogeography must be based on sound biological criteria, and this requires the recognition of the methodological and philosophical structure of current research in Theoretical Biology. Biogeography is the study of spatial organization of organisms at the earth's surface. Current research into the internal organization of the cell and the organism is pertinent to Biogeography, particularly if the concepts are transferable throughout the hierarchy of living matter.

Strategy 2: Applied Research in Biogeography

'Applied' research is used by the author to signify a wider social context to the discipline. It contrasts with the first strategy which may be regarded to be 'pure' research. This distinction is only for pragmatic convenience. The aim is not to enter into the general debate on relevancy in the social sciences but to define applied research by example. The strategy is divided into three themes: (a) Radical Biogeography, (b) Historical Biogeography, and (c) Bioregions. These themes present complementary research to the predominantly conceptual material in this thesis. Individually, they form separate fields within Biogeography.

(a) Radical Biogeography

Radical Biogeography has been limited to the writer's inquiry into alternative views of the discipline. As a result of this inquiry, the writer offered to edit a special issue of Antipode on Alternative Biogeography. Below is given the writer's initial statement (October 1974) on the question: What is Radical Biogeography?; he prefers the connotation of alternatives in Biogeography rather than 'radical' Biogeography.

> Alternatives in Biogeography
>
> Biogeography has developed rapidly since 1970. This is well-documented, with the evidence of the textbook market [Watts, Cox et al., Tivy and Seddon][19] and the recent publication of the Journal of Biogeography (March 1974). These facts may be interpreted as showing an increased 'ecological awareness' in Geography and may reflect the broader context of the 'ecological crisis'.
>
> The title of the issue [of Antipode] is deliberately ambiguous. It can be read as either the existence of a set of alternative views on the discipline of Biogeography or the existence of a set of alternative views within Biogeography which are pertinent to the discipline of Geography. Primary concern lies with the first statement and yet the context is the second.
>
> The reasoning behind the issue of 'Alternatives in Biogeography' is that the editor and others feel that the present published material does not fully represent the diversity of viewpoint which exists in universities and elsewhere. A personal selection of themes are given below; they indicate a number of alternatives. Papers and ideas

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[19] David Watts, Principles of Biogeography (London: McGraw-Hill, 1971); C. Barry Cox, I. N. Healey and P. D. Moore, Biogeography: an ecological and evolutionary approach (Oxford: Blackwell Scientific Publications, 1973); Joy Tivy, Biogeography: a study of plants in the ecosphere (Edinburgh: Oliver and Boyd, 1971); Brian Seddon, Introduction to Biogeography (London: Gerald Duckworth & Co., 1971).

on these themes and any others will be most welcome.

Themes

A. The biogeographer has close links with the research of ecologists and biologists. This interdisciplinary position results in an awareness of the methodological and philosophical issues in the biological sciences. Some of these issues have implications for Geography; examples include the reductionism debate,[20] developments in theoretical biology,[21] and 'ecological thinking'.[22]

B. Chorley in his examination of one aspect of the ecological approach to geographical methodology promotes the idea that 'man's relation to nature is increasingly one of dominance and control'.[23] This viewpoint can be contrasted to the outlook of the ecologist, Commoner: 'The whole notion that nature is here for us to work on, has, I think, been largely to blame for the kind of mess that we've been talking about'[24] (namely, the 'ecological crisis'). If the biogeographer sympathizes with Commoner, then likewise he may require a 'theory of action'.[25] One suggestion is research into the extinction of species as the result of human dominance.

C. Certain geographers have discussed the survival of the human species. Their ideas are pertinent to Biogeography.

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[20] Arthur Koestler and J. R. Smythies, eds., Beyond Reductionism: New Perspectives in the Life Sciences (London: Hutchinson & Co., 1969).

[21] C. H. Waddington, ed. Towards a Theoretical Biology, Vols. 1-4 (Edinburgh: Edinburgh University Press, 1969).

[22] Gregory Bateson, Steps to an Ecology of Mind (London: Intertext Books, 1972).

[23] Richard J. Chorley, "Geography as Human Ecology," in Directions in Geography, ed. R. J. Chorley (London: Methuen & Co. Ltd., 1973), p. 157.

[24] Barry Commoner, in Our own metaphor, ed. M. C. Bateson (New York: Alfred A. Knopf Co., 1972), p. 251.

[25] Barry Commoner, "Some data for a theory of action" (unpublished paper prepared for the Wenner-Gren Foundation on Anthropological Research, Symposium at Burg Wartenstein on: The Moral and Esthetic Structure of Human Adaptation, 1969).

Eliot Hurst expressed the view in his paper 'Towards a socialist geography: or how to survive and remain human' that: 'We begin with a commitment to humanity; a non-separation of person as geographer. A commitment to further that 'joy in the art of living', to existence, to survival in the most humane terms.'[26]

Secondly, consider the prod of Bunge: 'Geographers must find a definition of the natural state of mankind that is operational, that has some concrete meaning in life, in reality'.

and,

'As a first step it must be seen that man and nature are one'.[27]

From these quotations it is useful to reflect on two points, as a biogeographer: (a) the meaning of survival to different geographers; (b) the non-separation of person and biogeographer.

Eliot Hurst and Bunge support geographic expeditions in our urban centres. It could be argued that the urban centre is not a space where man and nature are one. Secondly, research on urban centres represents survival of the human species at the expense of other species. Biogeography defines survival in terms of survival for all species; this is consistent with the philosophy of Commoner and others. If there is to be a non-separation of person and biogeographer then there is a need for the non-urban alternative to the geographic expedition. The best example known to the editor is The New Alchemy Institute.[28] Their objectives are 'to restore the lands, protect the seas and inform the Earth's stewards'. The task is to shape a world in which man works in harmony with nature.

Biogeography must concern itself with the applied alternative. 'Applied' means the integration of person and geographer; way of life and academic interest.

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[26] Michael E. Eliot Hurst, "Towards a socialist geography or How to survive and remain human", Paper presented at A.A.G. Plenary Session (April 1973), p. 7.

[27] William W. Bunge, "The Geography of Survival," A.A.A.G., Vol. 63, No. 3 (September 1973), p. 290.

[28] The address is: The New Alchemy Institute East, P.O. Box 432, Woods Hole, Mass. 02543.

> D. Part of the applied alternative may be found in bioregional exploration. An excerpt of Allen van Newkirk's 'Bioregional Research Notes #1' indicates the thrust: 'The concept *bioregion* has been introduced to explore the possibility of developing a relatively non-arbitrary method of planning for the wild biological realities of landscape. It may be said that many of the existing methods suffer from an arbitrary mono-species or anthropocentric bias. Where these methods bring varying degrees of ecological criterion to bear it is much to their credit. Nevertheless, as Jean Dorst suggests in his *Before Nature Dies*,[29] 'We must forget the idea that the only way to derive a profit from the earth's surface is by transforming habitats and replacing wild fauna by a few domestic plants and animals that have scarcely changed since man discovered them in Neolithic times. Each region should be studied as a whole to ascertain its potential. It should be determined on the basis of climate, nature of the soil and biological needs'.'[30]
>
> Correspondence, ideas, papers on these themes and any others will be most welcome. It is hoped to produce an issue with inherent biological diversity.

Within this thesis the four themes of that preliminary editorial statement can be elaborated into strategies. Theme A recognizes the need for an ongoing inquiry into the problem of methodology and philosophy which exist in the biological sciences. In part, this theme is the essence of this thesis. Theme B presents the author's concern with the prevalent attitude of man's domination of nature. It is proposed that Biogeography is a discipline which recognizes the paradox that all species are equal, and yet different organisms possess different attributes. The general research strategy would be to study the impact of the human species on other species. A

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[29] Jean Dorst, *Before Nature Dies* (Baltimore: Penguin Book Co., 1970).

[30] Allen van Newkirk, "Bioregional Exploration: methods and aims," September, 1974 (unpublished research notes available by writing to the author at Box 47, Heatherton, Nova Scotia, Canada).

basic resource could be the International Union for the Conservation of Nature (IUCN) Red Book[31] which describes the distribution and number of those endangered species on the earth's surface. Biogeography, in its commitment to the mapping of the distribution of these species, as well as others, could change the awareness of the human species. Some specific suggestions are given in the next section, Historical Biogeography.

The third theme is the integration of person and biogeographer. One possibility is the establishment of biogeographic research centres which study the Biogeography of the region. The objective would be to study and understand the relationship between the human organism and other species. A second objective would be to rediscover a sensitivity of the human species towards other living organisms and the mutual environment. This proposal is contrary to the study of the problem of inequality within the human species. It is not put forward as a substitute for the geographic expedition in the urban centres, rather it is suggested as another viable alternative. The idea is not to repeat Thoreau's experiment but to build on that example, perhaps by integrating certain technological advances in the study of the environment. Initially, the model could be based on a venture like the New Alchemy Institute.

The last theme described in the statement is bioregional exploration, as proposed by van Newkirk. This topic will be fully

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[31] International Union for the Conservation of Nature, The Red Book (Morges, Switzerland: IUCN, n.d.). The book is a loose-leaved volume which is periodically updated.

discussed later. There is, however, a contextual point which is pertinent. Van Newkirk has evolved his concern for Biogeography through literature and politics which contrasts strongly with the route of the author via the computer industry and academia. For the author, it raises various questions about the potential role of the disciplines of Geography and Biogeography in the reintegration of culture.[32]

(b) Historical Biogeography

The general concept is to study the changes in the distribution and densities of species in relation to the changes in the distribution and density of the human species. By way of example, Figure 16 illustrates the changes in the distribution of the American Buffalo in North America. The map is one of sixty-eight maps of species contained in Seton's Life Histories of Northern Animals;[33] Seton has drawn on earlier nineteenth century sources. Even though the buffalo is the classic example of species extinction in North America, it is indicative of the problem and also a biogeographical research strategy. For the North American continent, it illustrates the change in the distribution of native species in response to colonization by the human species from other parts of the earth's surface. Biogeography can make a significant contribution by changing

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[32] Recent publications of Io, Earth Geography Series illustrate the growing awareness of Geography outside of the discipline.

[33] E. T. Seton, Life Histories of Northern Animals, Volume 1: Grass eaters and Volume 2: Flesh eaters (New York: Arno Press, 1974; reprint of 1909 edition).

Range of the American Buffalo

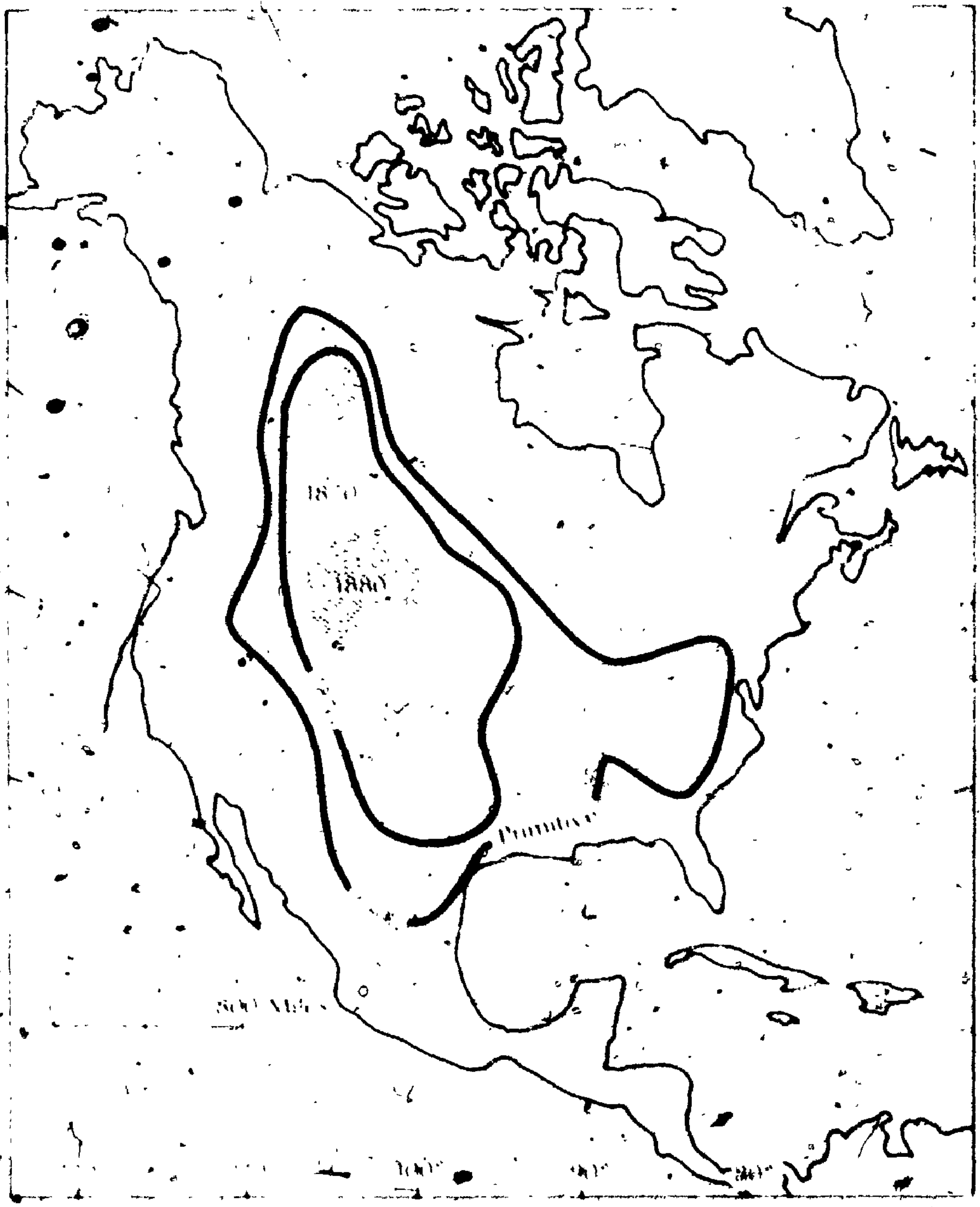

Figure 16

SOURCE: E. T. Seton, Life Histories of Northern Animals, 1909, p. 255.

the awareness of the human species through maps of the changes in the distribution and densities of other species over time. This research need not be confined to the period after European colonization, since archaeological and anthropological evidence is often available.

Philosophically, the objective behind this strategy is to encourage a greater awareness of other species and secondly, to recognize that the monopoly over space and natural "resources" of one species (human species) reduces the total set of "resources" for all species. The present trend is a spiral. If there were a change in human consciousness towards other species, then this would create a greater appreciation of the "humanness" of the human species. This could act as a counter-balance to the present relationship with technology which appears to emphasize the "non-humanness" of the human species.

A further point is that Seton in 1909 adopted a "life-histories" approach to his research on Northern animals. In 1951, Dansereau referenced a similar argument for this strategy:

> Lawrence (1948) has recently made a plea for 'ecological life-histories'. A strong feeling for the necessity of this kind of work has arisen in many quarters and materials are being accumulated towards that end.[34]

The author reiterates this plea and suggests that a major contribution of Biogeography would be to extend the work of Seton and to support

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[34] Pierre Dansereau, "The Scope of Biogeography and its integrative levels," Revue Canadien de Biologie, 10 (1951), p. 27. References, D. B. Lawrence, "Report of the Committee on Ecological Life Histories," Bull. Ecol. Soc. Amer., 29(1), (1948), pp. 19-20.

the developments arising from the plea of Lawrence. In this research, the primary objective would be to provide a picture of the change in the biogeography of a region as the result of human activities.

(c) Bioregions

Allen van Newkirk[35] has proposed the idea of the bioregion and bioregional exploration. It concerns the division of the earth's surface into bioregions based on biological criteria (in contrast to the present political divisions) and to explore and understand the changes in the distribution and ecology of all species in the region over time. The broad aim is to change the consciousness of the human species, away from the present attitudes of human dominance and exploitation. These ideas are elaborated by van Newkirk in his latest research notes. They are included in full here because of their significance to Biogeography:

BIOREGIONS
A Bioregional Research & Design Project

Exploration of the Planet

> Bioregional research is initiated with the conviction that the introduction of a <u>biological configuration of geographical space</u> is called for to equal the energy and imagination of self-inquiring individuals everywhere who actively explore the critical issues of their species and their planet.

A Geography for Life

> Biogeography--the geography of life--is study of the distributions of plants and animals over the surface of the earth. The biogeographer is interested in discovering patterns of areal biological diversity in non-recurrent time and space and may consider the evolution, speciation, migration and ecology of plants and animals. Biogeography is studied that

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[35] Unpublished research notes available from Allen van Newkirk, Box 47, Heatherton, Nova Scotia.

there might be orderly knowledge of the diversity of the planet.

Mapping the Biotic Provinces

It is now recognized that patterns of plant and animal distributions over the surface of our planet are characterized by series of varied gradations and that consideration of this phenomenon is enlarging our knowledge of actual and potential biological diversity. It can also be said that some obvious and extremely subtle differentiations between distributions of various species and species complexes can be usefully compared, described and mapped. Thus at one major synthetic level biogeographers may attempt to map the biologically significant areas of the earth's surface on a systematic basis.[36] Three methods, among others, are often employed. These are (1) floral or faunal provinces which are based on the distributions of taxonomically related groups of plants or animals, (2) biomes which are based on the typical adaptations of plants and animals to climatically-ordered environments, and (3) biotic provinces which are based on the distributions of distinct faunal-floral areas.

Bioregional Planning

The concept bioregion is introduced and defined as a biologically significant area of the earth's surface which can be mapped and discussed as a distinct pattern of plant, animal and habitat distributions and related to range patterns and complex niche habits including deformations attributed to one or more successive occupying populations of the culture-bearing mammal. Bioregions may be delineated as arealographic superimpositions on biotic provinces and are applied for purposes involving the planning, restoration and management of culturally deformed biotic provinces.

A Bioregional Strategy for the Human Mammal

A goal of bioregional research is to encourage development of multiple participatory strategies of cultural adaptation toward restoration of the integrity of wild plant and animal diversity in each of the discoverable bioregions.

To advance recovery of the purposes and values of the human organism the concerns of the Bioregional Research & Design Project include -

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[36] Raymond F. Dasmann, "A System for defining and classifying Natural Regions for purposes of Conservation," IUCN Occasional Paper No. 7 (Morges, Switzerland: International Union for the Conservation of Nature, 1973).

*Mapping of the biologically significant areas of the earth's surface with discussion of their natural and sensate history and of their meeting with cultural history.

*Analysis of the varieties, dynamics and ranges of domesticated areas in comparison with each other, with like analysis of wild areas, and with the continuity of biological evolution.

*Historical reconstructions of wild areas with criterion and suggestions for extension or restoration of the ranges and populations of wild species and species complexes.

*Perceptual problems encountered by the human mammal in apprehension of habitat as an element in the biological configuration of space.

*Cultural adaptations to the significant regions and locales of biological space.

*Bioeconomic and biotechnic instrumentation at the level of bioregions and their locales with concerns for the functional autonomy of natural energy flow--biotic diversity.

*Language, poetry, and mythos as tools of bioregional cognition in the Indo-European, Amerindian and other traditions.

*The reconstructive bioregional arts.

*Human biogeography including (1) late Pleistocene and early Holocene cultural adaptations and dispersals, (2) invasions of the human mammal into wild areas resulting in adaptations or maladaptations, and (3) existing pressures of the human mammal on the ranges and populations of wild species and their habitats.

*Commentary, review and speculation lending itself to themes of bioregional history, consciousness and culture.[37]

Van Newkirk identifies ten strategies, many of which are significant to Biogeography as an academic discipline. The writer discusses four of these aspects below.

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[37] Allen van Newkirk, "Bioregions" (unpublished research notes available from the author, October 1974).

(1) The Mapping of Biotic Provinces

The establishment of suitable criteria for the definition of the boundaries of the biotic provinces is an interesting subject. Ideally, if the distribution of all species was known, then the objective would be to identify significant species. It is probable that evolutionary criterion would be used to delimit distinctive regions of the earth's surface. This approach presumes that the species distributions are continuous and ignores the problem of fragmentation within the biotic province and its relationship to landscape.

The writer considers that it will be necessary to reconcile the landscape ecosystem concept of Rowe[38] and the bioregion. This juxtaposition of concepts can be viewed in terms of the space/organism dichotomy. Biotic provinces can be defined in terms of the species (organism) or they can recognize the character of the landscape (space). In the second case, the geographic features of coast line, mountain range and desert may provide suitable criteria. Again, it is apparent that these criteria are not independent since different life forms and species correspond to different landscapes.

The significant point, behind dividing the earth's surface into biotic provinces, is that biotic distributions override political boundaries. The value of this map is that it establishes an awareness of the earth based on biological criteria.

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[38] J. S. Rowe, "Plant Community as Landscape Feature," in Essays in Plant Geography and Ecology, ed. K. N. H. Greenidge (Halifax: Nova Scotia Museum, 1969), pp. 63-81.

(2) An Analysis of Domesticated and Wild Areas

Van Newkirk wishes to identify and delimit domesticated and wild areas on the earth's surface. This strategy coincides with the concerns of Sauer,[39] regarding the impact of human culture on plant cover. There are several academic points which relate to this strategy. First, there is a continuum between domesticated and wild areas. Furthermore, the earth's surface is a mosaic of domesticated landscapes with wild enclaves and conversely wild landscapes with the occasional human settlement. Secondly, in terms of species, wild species may move and cohabit the same area as a domesticated species. These details aside, it would be a valuable piece of biogeographic research to map some measure of the intensity of human impact over the earth's surface.

(3) The Historical Reconstruction of Wild Areas

In this strategy, it is assumed that there exists historic information on the area prior to domestication. Also, it suggests that the reintroduction of a species into an area will result in the reversion to the historic condition. The author believes that these are rather demanding assumptions. A second criticism is that the reconstructed area will be set within a region where the human species now exists with a much higher density of population. The general observation is that areas of the earth's surface are becoming increasingly inter-dependent and influenced by the impact of the human species.

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[39] Carl O. Sauer, "The Education of a Geographer," in Land and Life: A selection of the writings of Carl Ortwin Sauer, ed. J. Leighly (Berkeley: University of California Press, 1969), pp. 389-404.

(4) Perceptual Problems

Increasingly, the human species is separated from all other species, resulting in mono-specific enclaves. The individual in this environment suffers a loss in his/her perception of nature. A major contribution of Biogeography, and other field-oriented natural sciences, is to re-educate and maintain the awareness of the human species towards all other species.

Since these comments on van Newkirk's strategies are within an academic piece of work, there is a paradox. It is the paradox of the 'literary split', where an individual writes about change and activities rather than doing it. The writer can find partial justification in that active inclusion of these applied examples of biogeographical research does communicate the diverse nature of the discipline and may improve the probability of future implementation.

Strategy 3: Field Research

This short discussion emphasizes the interdependence of field work, methods of analysis and a conceptual framework. In part, this essentially conceptual thesis has developed out of the field problems of the author's previous M.Sc. thesis.[40] The earlier research used quadrat sampling to study the complexity of vegetation patterns in an alpine meadow. Several general criticisms can be restated here before discussing the inherent problems of field work in Biogeography. The first criticism is the loss of all locational

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[40] R. V. Maher, "Complexity analysis of vegetation patterns in an alpine meadow" (unpublished M.Sc. thesis, Department of Geography, University of Western Ontario, 1971).

information in the analysis. For example, over the study area the vegetation was sampled in quadrats, recording presence-absence data for the plant species. The result is a species-quadrat matrix which is the input into an analytical procedure. In reducing the data to a matrix format, the relative position of the quadrats in real space is lost. A second criticism of the quantification procedure is that the species are defined by their row location in the matrix: the qualities of the individual species, for example identity, morphological and functional characteristics are also lost. Thirdly, the earlier research did not resolve the problem of suitable field methods for the study of pattern. While these three criticisms are bound by the context of the M.Sc. thesis, they do reveal more fundamental issues. There is little value in collecting detailed field information if the concepts and current analytical methods do not permit resolution of the problem.

If field work and analysis are separated, for convenience, then there are a number of general points which can be made regarding field research design and Biogeography as redefined in this thesis. In this context, analysis is redefined as description or general interpretation. There are two main field designs, either the 'space-centred' or the 'organism-centred' approach. For example, in the author's study of an alpine meadow, the design was 'space-centred'. The objec~~tive was~~ to understand the variation in the species mix over the area in relation to the variations in environmental variables. In general terms, the scientist is faced with the problem of sampling an infinitely diverse carpet of plant species and at the same time the collection of suitable data, at a comparable scale, on significant environmental factors.

The problem necessitates a clear idea of a "significant factor"; this requires an understanding of the organism-environment interactions of different species. Since microclimatology has only recently designed the equipment to measure with precision, the exchanges for the individual organism, it is optimistic to expect to map the field of an environmental variable over an extensive area.

'Space-centred' research designs require systematic sampling over an area. In the 'organism-centred' design, the identity of the species is given and therefore the problem is to discover its distribution over the earth's surface. It is only recently that the author has reverted to organism-centred research. An example of this type is the research proposal for a biogeographical study of Funk Island, Newfoundland (Appendix B). The proposal concentrates on sea-bird species, their spatial organization and the position of Funk Island in their space-time. Funk Island was selected because of its historical significance in the biogeography of the Great Auk and also other sea-bird species. A second advantage is its finite, insular character.

A second example of 'organism-centred' research is the biogeography of the desert locust (there exists a research programme at the Centre for Overseas Pest Research, London, England). The objective is to understand the relationship between locust movements and microclimatology. This requires an appreciation of the changing nature of the organism and also the variability of the physical environment over the region. Indeed, the problem combines the organism and space-centred approaches.

Field research in Biogeography must include an appreciation of the intrinsic properties of the species and also the spatial variations of the pertinent environmental factor. The biogeographer must have a background in the taxonomy and biology of the species set under investigation and also understand the environmental sciences of Pedology and Microclimatology. The author believes that individual field research in Biogeography should concentrate either on a small, well-defined area, e.g. an island, or on a single species. This strategy has a greater probability of advancing the discipline. In addition to individual research, the nature of Biogeography requires a network of inter-disciplinary research teams over the earth's surface.

Strategy 4: The Teaching of Biogeography

The writer has been teaching courses in Terrestrial and Marine Biogeography over the past three years. It may prove useful to illustrate the relationship between this thesis inquiry and its translation into the teaching context. The strategy is, once again, to illustrate by example, using three factual resources. The first example is a schema for an undergraduate academic course in Marine Biogeography. Secondly, the writer presents a Terrestrial Biogeography workshop which illustrates the application of the 'space-centred' and 'organism-centred' approaches in a teaching context.

Finally, some examination questions in Terrestrial Biogeography show the emphasis of that course. The writer believes that these materials clearly show the distinction between his definition of Biogeography and the definition provided by the textbooks in Chapter II.

(1) Course Outline: Marine Biogeography 3141 Undergraduate

The course has two components:

(a) a set of lectures on the concepts of Biogeography, and

(b) a set of workshops applying some of these concepts to the Marine Biogeography of Newfoundland waters.

The general aim of the course is to increase the awareness of the student on the Biogeography of Newfoundland's marine environment and at the same time suggest a number of alternative research strategies.

A. Lecture Topics

1. General physical properties of the marine environment.
2. The response/adaptation of organisms to this environment.
3. Identification and classification of marine organisms.
4. Classification of marine environment.
5. Properties of selected marine organisms.
    - life cycles
    - intra-specific activity, e.g. breeding
    - inter-specific activity, e.g. food supply
6. Spatial organization
    - between individuals
    - within groups
    - sub-populations

7. Historical viewpoint
   - influence of the changes in the population of the human species
   - pollution, overfishing
   - information sources on population changes in marine organisms
8. Biological rhythms and environmental rhythms
   - (a) Physical environment
     - daily, e.g. light availability
     - seasonal, e.g. ice cover, mixing of ocean currents
     - long-time period, e.g. global trends
   - (b) Organism
     - daily requirements/movements
     - seasonal events, e.g. migration
     - life history
9. Problems of scale

   e.g. relationship between inshore/offshore fishing
10. Special topics
    - (a) Animal migration, e.g. sea-birds, marine mammals
    - (b) Animal communication, e.g. marine mammals

B. <u>Workshops</u>

Workshops are scheduled every two or three weeks. They require the student to investigate information sources on Newfoundland or apply a particular conceptual framework.

(1) The characteristics of Newfoundland waters: a synthesis of current research papers by Fisheries Research Board, St. Johns; Bedford Institute, Halifax and the utilization of available cartographic sources.

(2) The Biogeography of one fish species.

(3) An analysis of fishing catch data as an indicator of the

Biogeography of fish species in Newfoundland waters.

(4) A research design for the study of a coral reef (an alien morphological feature in Newfoundland waters).

(5) The use of a simple computer simulation model of an ecosystem.

This outline is not rigid. In previous course offerings, the content was modified as the result of visiting speakers or the development of a particular line of inquiry either by the students or the research of the author. Secondly, this course follows the one semester course in Terrestrial Biogeography and therefore presumes a knowledge of the ecological concepts developed in that course. From the outline, it is apparent that the author combines a structuralist approach to organisms and their environment with an attempt to increase the awareness of the student of the other species in the bioregion.

(2) Workshop 4: Terrestrial Biogeography

This workshop is the product of the inquiry developed in this thesis. It presents the paradox of the 'space-centred' and 'organism-centred' approach to the student.

Workshop 4 - A conceptual approach to a land mammal
in Newfoundland

Each student should select one species of mammal found in Newfoundland and Labrador. The Conceptual Approach: An elaboration.

Arising from the previous workshop, it is apparent that there is a need to encourage the conceptualization of research problems in Biogeography. This workshop is towards that end.

(a) Consider the organism that you have selected:

What are its intrinsic properties? For example, what is its size, its mobility? How does it use its sense organs to perceive the environment? In its life time, what are the main events and what is its requirement from the total environment to fulfill its needs. Do these requirements change with age? Does the organism, demonstrate daily, seasonal cycles? To satisfy its changing needs through time, is it necessary for the organism to move to different habitats?

(b) Now reverse the process, consider a space. Initially let this space be equal to the home range of an organism. What diversity of life exists in the space. How does the organism respond to the diversity. How does the organism respond to the changes of the physical environment in the space, e.g. microclimate. Identify the other species which may occur in the same space; how will they interact with the organism in this space?

By this time, you should have a mental image of an area, within which there are a number of mobile organisms changing their locations during a day. Each individual will have different requirements related to each other, and the static vegetation cover and the dynamic physical environment.

(c) Now expand the time-scale - this permits the different plant species to change their characteristics, e.g. flower, fruit, leaf, etc. Similarly, mobile organisms have different seasonal needs.

Now expand the spatial scale - this permits a greater diversity of organisms. Initially, the space was restricted to the home range of an individual. Expansion of the scale permits interaction between individuals of the same species.

Finally, do not forget that these scale changes affect the physical environment, e.g. seasonal snow cover, topographic variations.

Requirement

You must set your own questions for this workshop. The above description of the conceptual approach can be applied to your selected species. You must include the following characteristics in the final report.

(1) Wherever possible represent the biogeography of the species by maps and diagrams.

(2) Consider the complete spectra of scales: (a) standing space of an individual - province of Newfoundland and Labrador; (b) 24 hours - centuries.

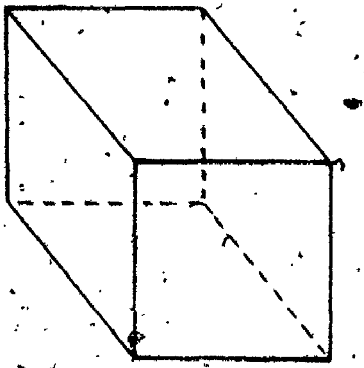
(3) Include the human influence, i.e. the effect of the behaviour, distribution and population growth of man on your selected species.

(4) Pose your own questions; wherever possible indicate the necessary research to provide answers.

(5) Give an introductory structure to your report, i.e. state your questions and your report design.

The main approach must be graphic.

Essentially you have a cube. It represents the province and the atmosphere above it. Subdivide it into smaller cubes. Add the fourth dimension--TIME.



Resources: A partial bibliography and a set of useful references will be available in J4-28.

(3) Examination Questions

It is perhaps unorthodox to include examination questions in a thesis. They are listed here to illustrate the practicality of this alternative Biogeography in the teaching context; their content demonstrates very clearly the distinctiveness of this alternative.

(a) "In the past few years a suspicion has been growing in the minds of our most thoughtful students of animal and human behaviour that territory and social rank are aspects of a single innate force, the drive to dominate. Dominance over a piece of space (territory) lies at one end of a long continuum grading into dominance over one's fellow beings."
Robert Ardrey, 1970, The Social Contract, p. 240.

Discuss. Use examples of territoriality and social rank from either The Bird Kingdom or The Animal Kingdom.

The author considers that the concept of territoriality has a biogeographical context.

(b) Moss[41] defines Biogeography as that subject "which is concerned not with certain forms of relationship as Ecology but with all forms of relationship affecting the distribution, location and space organization of living things as they appear on the surface of the earth."

Discuss this definition in relation to either "Problems of Red Squirrels on Camel Island" or "The Caribou-Lynx Relationship" or "Sea-birds in Newfoundland".

(c) R. J. Chorley in the paper titled 'Geography as Human Ecology' contained in his recently edited book, Directions in Geography, 1973, says:

> the ecological model may fail as a supposed key to the general understanding of the relations between modern society and nature, and therefore as a basis for contemporary geographical studies, because it casts social man in too subordinate and ineffectual a role....Man's relationship to nature is increasingly one of dominance and control; however, lovers of nature may deplore it.

Comment on this statement in relation to Biogeography and secondly, its applicability to policy and reality regarding National Parks in Newfoundland.

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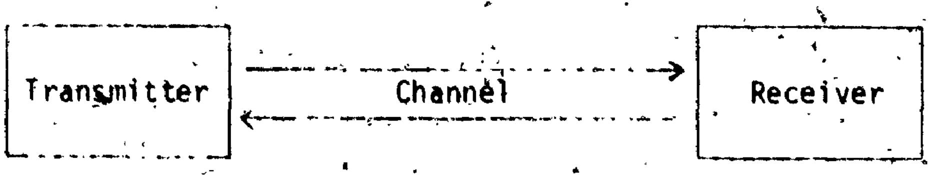
[41] Dr. R. P. Moss is Reader in Biogeography at the University of Birmingham, England.

(d) Communication Theory uses the simple model shown below:



Demonstrate the utility of this model in the study of animal communication. What is the significance of the study of animal communication to Biogeography? Give examples.

It is self-evident that these four questions are consistent with the definition of Biogeography portrayed by the contents of the thesis inquiry.

The writer believes that Biogeography exists as a unique discipline. This has been affirmed from a variety of sources which illustrate the four strategies in this chapter. Biogeography is not dependent upon Ecology for its subject matter or its methods of analysis. While Ecology has provided supportive material in the past, the future conceptual development of the discipline of Biogeography must be within the context of current research in Theoretical Biology. The writer believes that the main inter-disciplinary linkages will remain within the Physical Geography sector, namely, Climatology, Oceanography, Pedology and Geomorphology, but will also include taxonomic and other species-oriented studies in Biology.

CHAPTER VII

CONCLUSION

This chapter re-emphasizes some of the major arguments of the thesis. The most important result of the inquiry is the formulation and exemplification of an alternative definition of Biogeography. Contemporary literature focuses on the ecosystem: this thesis replaces that concept with the paradoxical study of the organism and its characteristics and the properties of environmental space. It is recognized that this distinction between organism and space is purely a pragmatic vehicle for biogeographic research. The retention of a paradox maintains both sides of the object/space problem overtly. The author defines the object/space problem: a dot defines a space, while a space defines a dot; neither can exist without the other.

An advantage of the paradox is that it reduces the likelihood of reification into a rigid dualism. The man and nature dualism is an excellent example, pertinent to this thesis. Two contrary attitudes are presented by Anderson and McClure on one hand and Chorley on the other. Anderson:

> The biological relations between man, considered as an animal, and the whole of his animate and inanimate environment is the essence of Biogeography.[1]

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[1] Margaret Anderson's definition cited by Joy Tivy, Biogeography: a study of plants in the ecosphere (Edinburgh: Oliver and Boyd, 1971), p. 2.

McClure:

> When a man does not admit he is an animal, he is less than an animal. Not more but less.[2]

Chorley:

> the ecological model may fail as a supposed key to the general understanding of the relation between modern society and nature, and therefore as a basis for contemporary geographical studies, because it casts social man in too subordinate and ineffectual a role....Man's relationship to Nature is increasingly one of dominance and control; however lovers of Nature may deplore it.[3]

The author strongly supports the view of McClure and Anderson, recognizing that Biogeography is the study of all species. It treats the human species as yet another species, but appreciates that the human organism has a peculiar set of characteristics. Chorley assumes that man has domination and control over nature with the implication that man has attributes which are outside of natural regulation. The author disagrees with the viewpoint of Chorley, furthermore he believes that it typifies the attitude which forms part of the current predicament in our culture and also within the discipline of Geography. A paradoxical outlook on the man and nature dualism is to accept firstly that man is an animal and then secondly to recognize that peculiarity of man which enables the species to imagine that human relationships, inter-species relationships, and the complete global system are all controllable by the

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[2] Michael McClure, "Wolf Net," in the Special Issue: Biopoesis, *Io*, 18 (1974), p. 143.

[3] Richard J. Chorley, "Geography as Human Ecology," in *Directions in Geography*, ed. R. J. Chorley (London: Methuen & Co., 1973), p. 157.

human species. The author is not arguing against scientific inquiry or technology but for a greater awareness of other species and the animal in man. The present rapid increase in the population of the human species remains a natural phenomena which is taking place at the expense of other species.

In 1967 Crowley made eleven recommendations for the development of Biogeography. His first point was that "Biogeography is a part of Geography, not of Ecology and accordingly should maintain a geographical point of view."[4] Eight years later, it is still necessary to stress this recommendation. At a fundamental level it is irrelevant whether Biogeography is labelled part of Geography or Ecology but the current academic system requires distinctive disciplines and a clear demarcation of disciplinary boundaries. Given this academic context, it is important that Biogeography be recognized as a viable discipline and is not to be confused with Ecology. If Biogeography persists with its current emphasis on the ecosystem, then it is rational that ecologists will perceive an overlap with their field. If, instead, Biogeography is the geography of living things or the study of the spatial organization of organisms, then it is a vital part of Geography.

Chorley has argued that Geography is not Human Ecology,[5] the author would agree and contrarily would argue that Geography is

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[4] John M. Crowley, "Biogeography," Canadian Geographer, II (1967), p. 323.

[5] Richard J. Chorley, "Geography as Human Ecology," in Directions in Geography, ed. R. J. Chorley (London: Methuen & Co., 1973), pp. 155-169.

Human Biogeography. Logically, the current discipline of Geography becomes a subset of Biogeography. An interesting aside on this semantic "merry-go-round" is that Anthropology has recently defined the field of Human Biogeography as the inter-disciplinary region between Anthropology and Geographical Ecology.[6]

To reiterate an earlier argument, what is important is the nature of the problem and the way in which we think about it. The problem identified by this thesis is that there are many ideas, concepts and facts, which exist in both the academic community and the wider culture, which can be demonstrated to represent Biogeography. Presently, these materials are precluded full recognition because of the current definition of the discipline in the literature. This thesis presents an alternative definition, which rectifies the current limitation, indicates the nature of the problem of Biogeography, and proposes a set of positive strategies. These strategies are not speculations. In many cases, they are based on the teaching and research context which forms part of the thesis.

In presenting a diversity of views and materials, the writer is consistent with his belief in the concept of biological diversity. This belief is linked here with a further recommendation of Crowley: "Biogeographers, in addition to publishing their conceptual views, should put the concepts in which they believe into practice in their substantive research."[7]

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[6] John Terrell, "Comparative study of human and lower animal Biogeography in the Solomon Islands," Solomon Island Studies in Human Biogeography No. 3 (Chicago: Field Museum of Natural History, 1974).

[7] John M. Crowley, "Biogeography," Canadian Geographer, 11 (1967), p. 323.

The writer would enlarge the context of Crowley's recommendation to include philosophy and way of life. As Skellam has remarked, "a science considered in isolation from philosophy is like an organism studied in isolation from its environment."[8] In this wider scientific context, the author agrees with the philosophy presented by Goodwin in his thought-provoking essay on "Biology and Meaning".[9] He criticizes the dominant contemporary science:

> Scientists today do not expect to be morally transformed by their activities. They do not, in fact, participate in a relationship with the world that acknowledges the autonomy and the ultimate inviolability of natural processes, the condition for a dialogue with Nature, which has now become something to be penetrated, known and controlled. Participation in a process of mutual transformation is, in fact, expressly ruled out by the contemporary ideal of objective observation, preferably by a machine which cannot change its state except in response to the particular events which it is designed to record.[10]

Biogeography is part of the alternative science which focuses on man's dialogue with his fellow man and with nature. The biogeographer, in attempting to understand himself and his world, recognizes the potential for mutual transformation.

Biogeography embodies a philosophy, described in two final quotations by Bateson and Goodwin. Bateson recognized that:

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[8] J. G. Skellam, "Some philosophical aspects of mathematical modelling in empirical science with special reference to ecology," in <u>Mathematical Models in Ecology</u>, ed. J. N. R. Jeffers (Oxford: Blackwell Scientific Publications, 1972), p. 13.

[9] Brian C. Goodwin, "Biology and Meaning," in <u>Towards a Theoretical Biology</u>, Volume 4, ed. C. H. Waddington (Chicago: Aldine Publishing Co., 1972), pp. 259-275.

[10] <u>Ibid.</u>, p. 263.

> we must begin not only to include ourselves within an understanding of Nature but include our understanding of Nature within our understanding of ourselves, consciously fostering natural behaviour because we have a vision of the whole rather than simply moving within it.[11]

Similarly, Goodwin believes:

> The world is both intelligible and meaningful because we reflect its basic structures and participate in its processes, much as the shape of a fish both reflects the hydrodynamic properties of the water in which it lives and allows it to participate in water movements.[12]

This inquiry forms part of an ongoing dialogue; below the author has summarized the main points. The fundamental question was the nature of Biogeography, which has been answered in four ways. First, a review of contemporary literature and research indicated the distinction between the predominant 'ecosystem' approach and the 'distribution' approach. Secondly, six research examples support the division of the distribution approach into the paradoxical 'organism-centred' and 'space-centred' strategies. These examples raised several methodological and conceptual problems. The third section of the thesis investigated four significant concepts--Natural Order, Pattern, Spatial Diversity and Organism Interaction. Each of these concepts illustrated the relationship between Biogeography and other sciences. Finally, the author presented a number of positive strategies for the development of Biogeography within a broad educational context. Biogeography is

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[11] Mary C. Bateson, Our own metaphor (New York: Alfred A. Knopf, 1972), p. 255.

[12] Brian C. Goodwin, "Biology and Meaning," in Towards a Theoretical Biology, Volume 4, ed. C. H. Waddington (Chicago: Aldine Publishing Co., 1972), p. 275.

concerned with the nature of living matter and the nature of space. The discipline has a significant role in the future of Geography; it must reconcile and integrate the contemporary issues of the biological sciences and the paradox of Geography.

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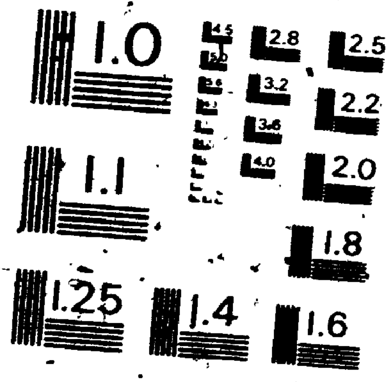

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APPENDIX A

A Survey of Biogeography in Canada, March 1974

This appendix contains a copy of the original letter to all Departments of Geography in Canada and a synthesis of the results.

January 18, 1974

Biogeography

Sir,

I am sending this letter to all Heads of Department of Geography across Canada and I hope that you will have time to direct it to the faculty member who is teaching Biogeography. If there are no Biogeography courses offered by your department, then perhaps this is the end of my letter.

I am teaching courses in Biogeography at both the undergraduate and graduate level here at Memorial University of Newfoundland and interested in discovering what is its current status in Canada. There are three reasons which have motivated this letter:

1. From this September onwards there will be undergraduates completing their programs here having written an Honours thesis in Biogeography. I wish to be able to advise them about the possibilities for graduate study in Biogeography in Canada, in addition to this Department.

2. Conversely, I wish to know what undergraduate programs exist elsewhere so that I am aware of the courses and backgrounds of potential entrants to graduate school here.

3. I am presently free from formal teaching duties so that I can complete my Ph.D. in Biogeography (University of Western Ontario). The thesis concerns various methodological and philosophic

APPENDIX A (Cont'd)

problems associated with the analysis of the spatial pattern of biological organisms. In order to place this thesis into its biogeographical context, I am interested to know what types of study are being undertaken elsewhere.

As this is a general letter, I shall not elaborate more fully on my teaching or research activities; however, I would welcome receiving information about other departments, exchanging ideas, etc.

I am aware of the existence of such communication forums as:

(1) The Journal of Biogeography to be published later this Spring, edited by Dr. D. Watts.

(2) The Biogeographical Research Group as part of I.B.G., co-ordinated by Dr. R. P. Moss.

(3) Efforts of Antipode to produce an issue on Ecology (Dan Amaral, Clark University).

Also, I recollect Crowley's paper in the Centennial edition of the Canadian Geographer which reviewed the status of Biogeography in Canada and provided some basic statistics.

At this stage, I have no preconceived notion about how to proceed from here but for the above reasons, I would welcome a reply to this letter.

Robert V. Maher

APPENDIX A (Cont'd)

Feedback on Biogeography March 8, 1974

This document contains a synthesis of the replies to my open letter on Biogeography, dated January 18th, 1974; copies have been sent to all respondents. (Note: 42 copies of original letter sent to institutions in Directory of Canadian Geography.)

University	Respondent		Status of Biogeography
Manitoba	Dr. W. J. Brown, Head		1
Brandon	Dr. R. C. Round, Chairman	B	2
Windsor	Dr. F. C. Innes, Chairman		1
Sir George Williams	Dr. D. A. Fraser	B	2
Laurentian	J. R. Pitblado	B	2
Alberta	Dr. D. Gill	B	3
Sherbrooke	F. Bonn		2
Montreal	Dr. S. Lavoie		3
Trent	Dr. W. P. Adams, Chairman		1
Queen	Dr. M. Yeates, Head		3
McGill	Dr. P. G. Holland	B	3
Winnipeg	Dr. G. Scott	B	2
McMaster	Dr. B. T. Bunting		0 *
U.B.C.	M. E. North	B	3
Brock	Dr. M. R. Moss	B	2
Memorial	R. V. Maher	B	3
Althouse College, Western Ontario	R. C. Langman, Head		0

0 - No undergraduate courses in Biogeography
1 - Part of Introductory course in Geography
2 - Undergraduate courses in Biogeography
3 - Undergraduate and graduate courses in Biogeography
B - Biogeographer
* - close relationship between microclimatologists - Davies, Rouse and ecologists - Kershaw, Harris.

From the above list, nine faculty are employed as Biogeographers and have either completed higher degrees or are currently undertaking research in this field. In the interests of information exchange, I have taken the liberty of describing the research interests of these nine from the material provided in your replies.

Dr. D. A. Fraser - Sir George Williams

Previously Head, Tree Physiology Section, Petawawa Forest Experiment Station, Chalk River, Ontario.

APPENDIX A (Cont'd)

Paper "Tree responses to seasonal changes in height and temperature" presented to Biogeography Section, I.G.U. Montreal, 1972.

Dr. D. Gill - University of Alberta

Director, Boreal Institute for Northern Studies

M.A., 1965, "Coyote and urban man: a geographic analysis of the relationship between coyote and man in Los Angeles," UCLA.

Ph.D., 1971, "Vegetation patterns and sedimentation in Mackenzie Delta, NWT," UBC.

Don Gill sent curriculum vitae including list of publications. Also, see list of graduate theses.

Dr. P. G. Holland - McGill University

McGill has graduated six M.Sc. students in Biogeography. See attached description of Biogeography graduate programme.

R. V. Maher - Memorial University of Newfoundland

M.Sc., 1971, "Complexity analysis of vegetation patterns in an alpine meadow," University of Western Ontario.

Ph.D. (A.B.D.), "An inquiry into the nature of Biogeography," University of Western Ontario.

Dr. M. R. Moss - Brock University

Ph.D. thesis on "Effects of sulphur in all ecosystem components around the Welland area."

M. E. North - University of British Columbia

M.A., Kansas University - soil; Recent research: vegetation map of Alberta, Pollen Analysis of post-glacial vegetation succession in South East Alberta.

J. R. Pitblado - Laurentian University

Ph.D. (A.B.D.), "Applied Soil Problem in Tanzania," University of Toronto.

Dr. R. C. Rounds - Brandon University

M.Sc., Illinois, "History of population and distribution of deer."

APPENDIX A (Cont'd)

Ph.D., Colorado, "Sociological and legal aspects of wildlife resources."

Current research - project concerning the distribution, movements and population of ungulates (elk and moose) in Riding Mountain, N.P.

Dr. G. Scott - University of Winnipeg

M.A., "Vegetation and soil erosion in Hawaii."

Ph.D., "Savanna and nutrient cycling in East Peru."

Graduate Student Research

(1) University of Alberta

P. Bonnett, "Wildlife in the Urban Environment," M.A., 1971.

A. Landals, "Surface runoff variations in the Yellowknife, N.W.T. area," M.Sc., 1970.

J. Peters, "The ecological implications of trail use in the Cypress Hills, Alberta," M.Sc., 1973.

J. McQuaid, "Trail conditions and management in the Rocky Mountains, Alberta," M.Sc., 1973.

R. Jacobson, "Vegetation and environment in Cultus Valley, Yukon Territory," (M.Sc. in progress).

M. Landals, "The sand dune ecology in northeast Alberta," (M.Sc. in progress).

J. Lore, "Tundra disturbance study, Burwash Uplands, Yukon Territory" (M.Sc. in progress).

D. Outhet, "Erosion processes in the Mackenzie River Delta" (M.Sc. in progress).

L. Seemuth, "Ecology of the Aspen Parklands in Southern Yukon" (M.Sc. in progress).

R. Spencer, "Urban wildlife and wildlife habitat in Edmonton, Alberta" (M.Sc. in progress).

K. Taylor, "Plant succession on an abandoned mine site: Discovery Mines, N.W.T." (M.Sc. in progress).

APPENDIX A (Cont'd)

(2) McGill University - Biogeography Programme

- Recent work by Departmental staff and graduate students includes studies of:

Spatial variation in tree-age distributions in a deciduous forest.
Biomass productivity in different habitats of the Canadian Arctic.
Seasonal change in plant patterns of a deciduous forest.
Plants as indicators of runoff regimes in a desert area of Arizona.
Pedogenesis in the Canadian Boreal and Tundra regions.
The influence of plants on stream-channel morphology.
Distribution of selected metals in some Scottish soils.
The geography of oaks and regional forest types in New England.
Geographical variation in species density of stone walls in Ireland.
Effects of crude oil on terrestrial vegetation.
Vegetation of asbestos mine wastes.
Morphology and seasonal dynamics of mallee vegetation in Australia.
Propagation and behaviour following transplant of a herbaceous ephemeral of southern Canada

Three faculty members:

P. G. Holland (Ph.D. A.N.U.) Plant Ecology, Biogeography
T. R. Moore (Ph.D., Aberdeen) Soil Science
R. C. Zimmerman (Ph.D., John Hopkins) Forest and Range Ecology

(3) Memorial University of Newfoundland

P. Dearden, Plant associations on serpentine bedrock Table Mountain, Newfoundland (M.Sc. in progress).

(4) University of British Columbia

J. Teversham, Vegetation patterns and the relation to sedimentation, Fraser River, British Columbia.

(5) Queen's University

Three M.Sc. theses in Biogeography supervised by Dr. G.K. Rutherford.

S. McAlpine. Some ecological aspects of the spatial distribution of selected species of the genus Panicum with respect to two types of soil in the Kingston area, M.Sc., 1971.

S. Taylor. Forest productivity in the Simcoe uplands region: a study of the effect of soil moisture availability and fertility status on the growth of plantation red pine, M.Sc., 1971.

APPENDIX A (Cont'd)

G. H. Neilsen. Soil moisture and runoff relationships on a forest and pasture site, Gould Lake, Ontario, M.Sc., 1972.

(6) <u>University of Western Ontario</u>

S. Thompson, Analysis of cliff-top communities, Lower Head, Newfoundland (M.Sc. in progress) (Link with Maher via Goodchild)

I may have under-represented research activities or individual interests; however, I felt that it would be useful to circulate this document, however incomplete, <u>now</u>. There may be other faculty who did not respond.

I do not propose any further action; this document completes the circle.

Robert V. Maher

APPENDIX B

Research Proposal for a Biogeographical Study of Funk Island

Funk Island occupies a special place in the natural history of Newfoundland and its surrounding waters. It has historic importance in the story of the demise of the Great Auk and today it is the site of a number of breeding colonies of Common Murres with an estimated total population of over five hundred thousand pairs in 1959. This population represents a high percentage (over 80%) of the breeding population of Common Murres in eastern North America. Both of these facts suggest that the island possesses certain unique attributes in terms of its geographic situation and physical environment. The proposed research is designed to elicit the basic facts regarding the environment and, secondly, to consider the dynamics of the spatial organization of the bird colonies. The island nature of this "flat-topped oblong granite rock, half a mile by a quarter of a mile" implies it may be feasible to understand many of the interactions in this finite space -- finite in terms of fixed boundaries, although open-ended in terms of movement patterns, energy transfer and changes through time.

There are a number of questions to be posed:

(1) At an historic and evolutionary level, why was the Great Auk found on Funk Island? Is it likely that this remote location provided a last refuge from human predation? Did the bird evolve its flightless characteristic in this location? This species was found in other localities; however, such questions of the pleistocene

history of the general area, migratory movement patterns of the Great Auk, offer an interesting problem for interpretation. Certainly, present-day research will not answer in a direct way any of these questions; however, understanding the elements of the biogeography may suggest indirectly certain hypotheses.

(2) Today, there are a number of breeding colonies on the Island, especially the Common Murres which Tuck notes exist in three separate units on the Island. Therefore, the first question is the distinction between these three colonies in terms of physical characteristics. Is each colony stable? Does each colony have an optimum size? How are new colonies formed? Is there differential breeding success between colonies? Is there a ranking of colonies according to prime habitat? How much interaction takes place between birds from different colonies?

(3) At a smaller scale, there are a number of questions regarding individual behaviour and group behaviour. Tuck described the sea-going of the adults and chicks as 'a slow procession', implying organization at the group level. During the breeding season, each individual adult maintains a personal daily pattern; is there interaction of daily patterns between individuals in adjacent nesting localities? This study of an apparent degree of randomness at the individual level and the colony acting as a self-organizing system raises many intriguing questions which can only be understood as the result of intensive research.

The above three sections outlined some of the questions; below

APPENDIX B (Cont'd)

is given the overall design. There are two levels: (A) the whole island and (B) within one colony.

(A) WHOLE ISLAND

(1) Topographic Survey

Set up a number of transects across the island from a main base-line using level and stadia rod. Some of the small cliff features may prove difficult; however, detailed maps with slope and aspect would be produced. This survey would be undertaken before land-coming to establish a base line for detailed quadrat analysis.

(2) Vegetation Survey

It is expected that large areas are bare rock; however, the particular species and their local distributions raise additional interesting questions. The survival of these plant species is dependent upon nutrients supplied from the excreta and detritus of the bird population.

(3) Climatological Data

The maintenance of a station recording variables such as temperature, humidity, precipitation, wind speed and direction would permit interpretation of questions relating to infant mortality and the effect of the climate on daily behaviour patterns.

(4) Bird Survey

Map the nesting sites of different bird species and identify the boundaries of the major colonies. These boundaries will not be rigid but rather permeable zones.

APPENDIX B (Cont'd)

(B) COLONY LEVEL

The overall design to study inter-colony variation will be based on a random quadrat sampling design. The study will involve the selection of sampling regions and then recording density, nesting success for a number of random quadrats within the region. The selection of these regions will require expert advice. Besides the study of inter-colonial variation, the intra-colonial variation as a function of topographic gradient will be studied.

Finally, there will be a number of other short-time scale projects. This category will include studies of the daily movement pattern of individuals within a small area. This intensive work would be undertaken a number of times throughout the season to identify if there is a change in pattern with a change in role and function. A second project would be the banding of all individuals in certain plots (if possible), and ideally locate the precise nesting spot. Therefore, in the subsequent year, it would be possible to collect data on questions such as:

(a) whether individuals return to the same nesting sites,

(b) what is the survival rate between years? and

(c) initiate understanding of the dynamics of site selection over time, as the result of adult mortality and the nesting of the chicks in later years. The selection of the study site would have to be extremely judicious.

The major part of the research at the colony level will be the composition and dynamics of the sample quadrats during the Summer. It is anticipated that film techniques may be utilized.

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Time-Scale

Phase 1 - Basic reconnaissance can best be made prior to 'land-coming', particularly the survey and grid set-up. Organization and installation of research camp will be completed.

Phase 2 - 'Land-coming'. One method of study will be to record the event on film; a film of the complete season is a major objective of the research. In order to monitor the colonization of the study plots, it will be necessary to set up hides in proximity to the three study regions. This period will be extremely busy recording the dynamics of the temporal-spatial structure of colonies.

Phase 3 - Regular monitoring of the study regions requiring a daily routine; however, permitting time for studies on the vegetation and also time to undertake the short-term projects.

Phase 4 - 'Egg-laying' period will require incorporation of survival rate, egg counts into the daily routine. Banding of young chicks and adults will take place in this period.

Phase 5 - Departure of the murres.

Logistics and Equipment

Probably the main problem is the maintenance of a temporary hut with food and water supplies for the total period (April to September). Specialized equipment would include cine-camera and film, tape-recorders, plant press, climatological station, banding and netting equipment, level and stadia, radio transmitter, binoculars. General strategy: land two persons and equipment by helicopter in April. Depending on ice conditions and birds, arrange monthly support visits by air or boat.